Zootaxa 3669 (3): 223–242
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3669.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:3437B625-05D4-42F5-B18C-8C270E7D9C72

An introduction to the systematics of *Akodon orophilus* Osgood, 1913 (Rodentia: Cricetidae) with the description of a new species

CARLOS F. JIMÉNEZ[1,3], VÍCTOR PACHECO[1,2] & DAN VIVAS[1]

[1]*Departamento de Mastozoología, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Lima 14, Lima, Perú. Teléfono: 0511-4710117*
[2]*Instituto de Ciencias Biológicas "Antonio Raimondi", Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos*
[3]*Corresponding author. E-mail: cfja_80@yahoo.com*

Abstract

The genus *Akodon* is one of the most species-rich rodent lineages in South America. In Peru, this genus contains 14 species subdivided in two groups: *aerosus* and *boliviensis*. *Akodon orophilus* Osgood, 1913 (Rodentia: Cricetidae) is a member of the *Akodon aerosus* group that inhabits the northern Peruvian montane forest, but is poorly characterized and its distribution is vaguely known. We review the status of the species based on morphology, morphometric and karyology, and compared with all members of the *Akodon aerosus* clade from Peruvian montane forests. As a result, we provide a complete redescription of *A. orophilus*, present new information on its natural history, restrict its distribution to the east of Río Marañón, and describe a new species of *Akodon* from Huánuco Department, central Peru, a population previously assigned to *A. orophilus*.

Key words: *Akodon*, Huánuco, montane forest, Peru, Río Marañón, taxonomy

Introduction

The genus *Akodon* Meyen (Rodentia: Cricetidae), with about 41 species, is the most diverse group in the subfamily Sigmodontinae (D'Elía 2003; Musser & Carleton 2005; Smith & Patton 2007; Jayat *et al*. 2010) but its taxonomy is still complex and confusing. Within *Akodon*, five main species groups have been recovered by phenetic and phylogenetic analyses: *aerosus*, *boliviensis*, *cursor*, *dolores*, and *varius* (Smith & Patton 2007; Jayat *et al*. 2010).

Pacheco *et al*. (2009) summarized that 14 species of *Akodon* were known from Peru, belonging to the *aerosus* and *boliviensis* groups. Myers *et al*. (1990) revised the *boliviensis* group based mainly on Peruvian and Bolivian specimens, and provided detailed descriptions for each of the nine species and subspecies. Posteriorly, Jayat *et al*. (2010) expanded the revision of this group including Argentinean specimens. On the other hand, the *A. aerosus* group includes eight species: *A. aerosus*, *A.* cf. *budini*, *A. affinis*, *A. mollis*, *A. orophilus*, *A. siberiae*, *A. surdus* and *A. torques*. They are usually ubiquitous along their ranges, but are not well delimited, and lack a complete and updated morphological characterization. All are present in Peru except *A.* cf. *budini*, *A. affinis*, and *A. siberiae*.

Among the species of the *Akodon aerosus* species clade, *A. orophilus* is one of the least studied species. It was described by Osgood (1913) as *A. mollis orophilus* along with *A. mollis orientalis*, both distinguished mainly on the basis of braincase width and coloration. Thomas (1921) implied that *A. m orophilus* and *A. m. orientalis* belong, together with *A. torques*, to the genus *Microxus* Thomas. However, Osgood (1943) argued that *Microxus* was not different from *Akodon* and elevated *Akodon orophilus* to full species with 3 subspecies: *A. o. orophilus*, *A. o. orientalis*, and *A. o. torques*. This arrangement was later followed by Cabrera (1961). Besides, Patton & Smith (1992) considered *A. orophilus* and *A. mollis* as full separated taxa, supporting Osgood (1943)'s argument, but suggested that an in-depth review of both species was needed because of their great morphological variability among geographic populations. Musser & Carleton (1993; 2005) also accepted *Akodon orophilus* as full species with *orientalis* as a synonym. Patton & Smith (1992) and Smith & Patton (1993; 2007) reinforced the status of *Akodon orophilus* as a valid species based on sequences of cytochrome *b* (*cyt b*), suggesting this species might represent more than one species based on high values of sequence divergence among populations. Recently, Pacheco *et al.* (2012) differentiated *A. orophilus* from Huánuco Department from other congeners based on karyotype morphology.

The aim of this work is to present an introduction to the systematics of *Akodon orophilus*, including a detailed description and diagnosis of this taxon, and to propose the recognition of a new species from Huánuco Department based on a combination of morphological and morphometric analyses plus karyological data.

Material and methods

One hundred and fifty three (153) specimens assigned to *Akodon orophilus* from four localities from Amazonas, three from San Martín, and four from Huánuco Departments were included in the morphological and morphometric analyses (Fig. 1). Specimens examined are housed in the Departamento de Mastozoología del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM) and the Field Museum of Natural History, Chicago (FMNH).

For morphological comparisons, we examined one hundred and eighty three (183) specimens of *Akodon aerosus*, *A. mollis*, *A. surdus*, and *A. torques*, which belong to the *aerosus* clade (Smith & Patton 2007) and are distributed in the Peruvian Andes (Patton & Smith 1992). A list of all the specimens examined and their geographic localities is presented in Appendix 1.

We followed Myers *et al*. (1990) and Pacheco (2003) for the description of external and cranial characters. Patterns of carotid arterial circulation follow Voss (1988) and dental terminology follows Reig (1977). Description of dental characters were based on individuals of ages 1 and 2. The classification of 5 age classes for *Akodon* was based on Myers (1989) where age classes 1 and 2 include juvenile specimens and age classes from 3 to 5 include adults. Smithe (1975) was employed as reference for the description of pelage color.

The external measurements total length (TL), length of tail (LT), length of ear (EAR), and length of hind foot (HF) were taken from skin labels and collector's data. 19 craniodental measurements were taken, adapted from Luna & Pacheco (2002): greatest length of skull (GSL), measured from the tip of the nasals to the posterior margin of occiput; condyloincisive length (CIL), distance from the greater curvature of an upper incisor to the articular surface of the occipital condyle on the same side; condylomolar length (CML), distance from the anterior edge of the first upper molar to the articular surface of the occipital condyle on the same side; length of orbital fossa (LOF), greatest distance of the orbital fossa inside the maxillary and squamosal roots of the zygomatic arch; length of nasals (LN), the greatest length of either nasal bone; diastema length (DL), measured from the posterior alveolar margins of the upper incisor to the crown of the first upper molar on the same side; length of incisive foramina (LIF), distance from the anterior to the posterior edge of incisive foramen; length of maxillary toothrow (LM), occlusal length of the upper molar row; breadth of incisive foramina (BIF), the greatest distance across the incisive foramina; breadth of rostrum (BR), the least breadth between the anteroventral edge of the zygomatic plate; breadth of palatal bridge (BPB), measured between the protocones of first maxillary molars; breadth of first upper molar (BM1), measured across the protocone-paracone cusp pair of the first upper molar; breadth of nasals (BN), the greatest distance across both nasal bones; least interorbital breadth (LIB), the least distance across the frontal bones between the orbital fossa; zygomatic breadth (ZB), the greatest distance across the zygomatic arches; braincase breadth (BB), measured immediately posterodorsal to the squamosal roots of the zygomatic arches; breadth of zygomatic plate (BZP), the distance between the anterior and posterior edges of the zygomatic plate; depth of incisor (DI), distance between greater and lesser curvature of the upper incisor; and height of braincase (HBC), distance from the top of the braincase to the ventral surface of the basisphenoid and basioccipital bones.

All measurements were taken using dial calipers to the nearest 0.01 mm. Data were transformed to natural logarithm to achieve normality. Multivariate statistical analyses of morphometric data were performed using SPPS 13.0 for Windows. Multivariate analysis of variance (MANOVA) was employed to detect differences between both ages four and five and sex for each group. Principal component analysis (PCA) was performed to detect the variation in size and shape and degree of homogeneity among and within populations, using all cranio-dental measurements. In addition, discriminant analysis was employed to pool individuals based on two or more characters and to identify discriminatory variables between groups formed by previous morphological analysis. Individuals and measurements were the same as in the PCA.

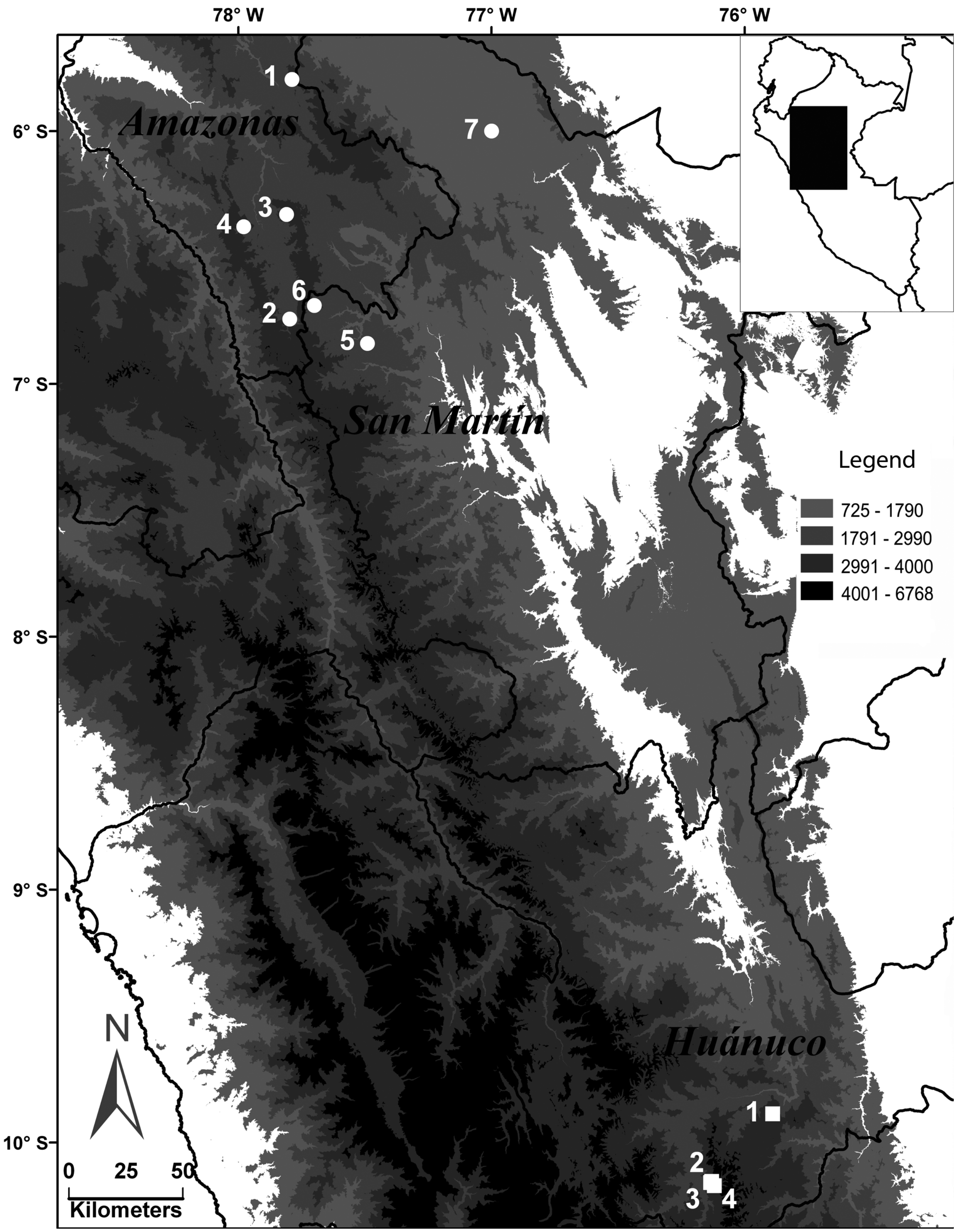

FIGURE 1. Map showing the collection localities of *Akodon orophilus* (●) 1: Hierba Buena, 2: Leymebamba, 3: San Antonio, 4: Huiquilla, 5: Añazco pueblo, 6: Estación biológica Laurel, 7 Puca Tambo; and *Akodon josemariarguedasi* **sp. nov.** (■) 1: Palmapampa, 2: Galloganán, 3: Hatuncucho, 4: Ichocán. Inset: Outline map of Peru, indicating the boundaries of the area shown.

We also compared the four external and 19 craniodental variables with *t*-test to assess statistical differences between *Akodon orophilus* and the new species. Results were considered significant at $P \leq 0.05$. Because MANOVA found no significant differences between both sexes and age classes 4 and 5, these were pooled in following multivariate analyses.

Four males (MUSM 36967, 36970, 36972 and 36983) and three females (MUSM 36971, 36978 and 36984) of *Akodon orophilus* from three localities (Huiquilla, Leymebamba, and Hierba Buena) of Amazonas Department were karyotyped. The chromosome preparation was obtained from bone marrow following a modified method of Ford & Hamerton (1956) for rodents. Metaphases were stained by the standard Giemsa method and chromosome types were classified following nomenclature criteria used by Levan *et al*. (1964).

Results

Our analyses allow us to characterize below *Akodon orophilus* and to recognize a new species, which is compared morphologically and morphometrically with other Peruvian members of the *aerosus* group.

Akodon orophilus Osgood, 1913

Holotype. FMNH 19724, adult male, skin and skull, collected on 26 May 1912 by W. H. Osgood and M. P. Anderson, original number 4795.

Type locality. "...six miles west of Leimabamba, Peru (in mountains near headwaters of Utcubamba River)...," Osgood, 1913 10:98, 2203 m, approximately 6ºS, 78ºW, Leymebamba, Chachapoyas, Amazonas, Peru (Fig. 1, locality 2).

Emended diagnosis. *Akodon orophilus* is distinguishable from other members of the *A. aerosus* species group by the following combination of characters: general coloration uniform olive green, dorsal and ventral pelage not strongly contrasting; contours of posterior edge of nasal smooth, tapering and V-shaped; lacrimals small; zygomatic plate slanted, with the anterior edge sigmoid or slightly convex; antorbital bridge moderately wide; zygomatic notch wide and intermediate in depth; incisive foramina penetrate between first upper molars but comparatively short; diastema intermediate in length; and jaw moderately robust, with delicate capsular projection.

Distribution. The distribution of *Akodon orophilus* encompasses montane forests of Amazonas Department and northern of San Martín Department east side of Río Marañón (Fig. 1). Elevation range is from 1900 to 2860 m.

Morphological description (Fig. 2)**.** Medium size for the genus, overall color dorsal Olive to Brownish Olive. Fur hairs are gray based with a subterminal light brown pheomelanin bands about 1 mm in length, and reddish brown tips; length of pheomelanin bands vary as their coloration. Each hair averages about 9 mm long. Guard hairs are gray at their bases and black at their tips; and extend 3 or more mm beyond fur hairs. The venter is Olive Gray and slightly paler than the dorsum. Fur hairs are Olive Gray at their bases and buffy on the tips, these tips vary in coloration and in length. Chins have some hairs that are totally white. Eyerings are inconspicuous. Hindfeet are dark and covered with bicolored hairs with black at the base and white tips. Forefeet are slightly paler, covered with bicolored hairs with black or brown bases. Ears are covered by delicate and short hairs. Mystacial vibrissae reach anterior margin of ears, some are white and others are black; the submental and interramal vibrissae (1–4) are white, the first are shorter than the second. One to three dark superciliary vibrissae are present; one of them is the longest. One dark genal-1 (sensu Pacheco 2003) is also present. The ungual tufts on manus and pes are white. Tail is slightly contrasting and relatively long, its length is about 83% of the head-body length. The scales on both sides of the tail are black while the hairs on the dorsal surface are black and on ventral side are white. Dorsal hairs are over 2 or 2.5 scales in length at most.

The cranium has a rounded braincase and is slightly elongated. Profile is flat or slightly domed. Rostrum is arched, long, and narrow. Gnathic process is conspicuous. Nasals are somewhat long, extending anteriorly and posteriorly beyond the premaxillae. The nasals present a slightly pointed to rounded anterior edge, and tapering posterior margin, that extend to level of lacrimals and adopt a V-shaped with uniform margin. The nasals project little beyond the premaxilla. The interorbital region is intermediate in width, hourglass-shaped, and without ridges. The diastema is intermediate in length. Fronto-parietal suture is rounded. Zygomatic notches are moderately wide

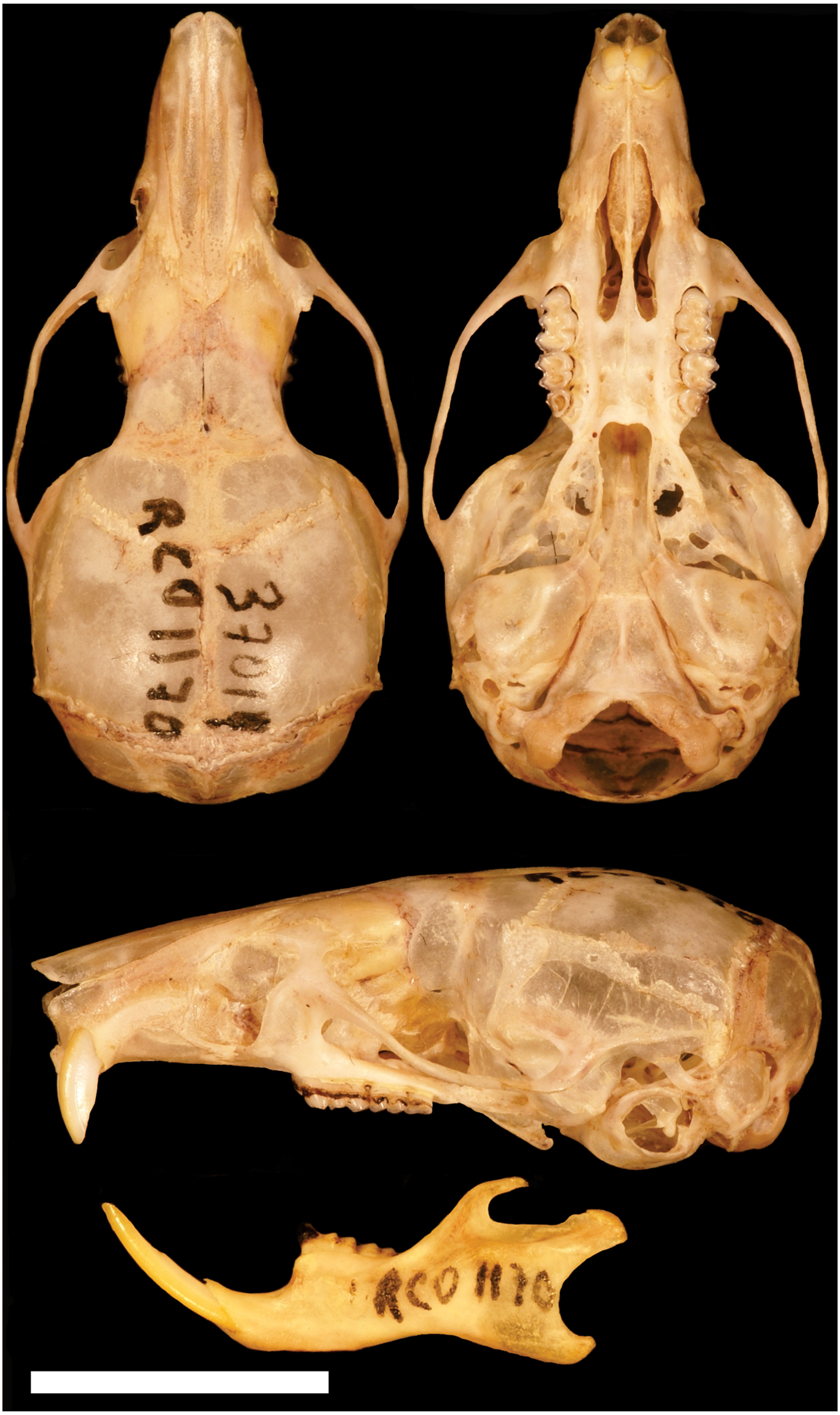

FIGURE 2. Dorsal, ventral and lateral views of cranium and mandible of *Akodon orophilus* s.s. (MUSM 37019). Bar = 10 mm.

and somewhat deep with rounded borders, or sometimes slightly squared. Zygomatic arches are slightly robust and convergent anteriorly with thick malar processes. Lacrimals are small. Lambdoid ridges are well developed especially in old animals, and run in dorsoventral direction. The interparietal is reduced.

The incisive foramina are comparatively short with anterior and posterior borders rounded; the latter is slightly divergent and extends to the protocone of M1. The maxillary septum occupies half or slightly more than half of the incisive foramen length. The anteror-palatal pits are very conspicuous and located at the level of the protocone of M2, while the postero-palatal pits are reduced and located slightly behind the anterior margin of the mesopterygoid fossa or reduced in some specimens. The mesopterygoid fossa is broad and has parallel margins; extends anteriorly to the level of the posterior border of M3 or slightly behind; the anterior margin is rounded, without a noticeable median process; and the breadth is subequal to or narrower than the parapterygoid fossa. Sphenopalatine vacuities are present. Parapterygoid fossa is fenestrated, triangular, and divergent with external margins slightly convex. The auditory bullae are flask-shaped and intermediate in size, with short and broad Eustachian tubes, and with a slight thickening in the dorsal margin in some specimens.

Laterally, the zygomatic plate is somewhat narrow in size and its ventral root is slightly anterior to its dorsal root, therefore inclined backwards from its base; the anterior margin is slightly convex or sigmoid. Antorbital bridge is moderately wide. The posterior ascending process of alisphenoid varies in form and extension but it is always located below the squamoso-alisphenoid groove. The tegmen tympani are in contact or slightly overlapping the posterior processes of the squamosals. The dorsal aperture of the ectotympanic ring is opened or closed. Nasolacrimal foramen is present, its diameter is less than or equals to the size of M2. Oval foramen and the foramen ovale accessorius are approximately the same diameter or less than the length of M3. The optic foramen is equal to or greater than M3 length. Ethmoid foramen is placed dorsal to M3. The carotid circulation is primitive; the sphenofrontal foramen, stapedial foramen, and squamoso-alisphenoid groove are present. Postglenoid foramen is larger than the subsquamosal fenestra and both are rounded; the hamular process of squamosal is thick. Masticatory–buccinator foramen is present and can be divided or not. The sphenopalatine foramen is sometimes hidden by ethmoturbinals and it is smaller than M2 length. The hypoglossal, jugular and stylomastoid foramina are present. Incisors are short, intermediate in length, ungrooved and orthodont, with yellow-orange enamel bands.

The lower jaw is similar to other *Akodon* species. The rami are somewhat delicate. Coronoid process of mandible is delicate and falciform. Lunar notches are deep and wide. Angular process is slightly robust. The condylar process is moderately long and placed posterior to angular process. Lower incisor alveolus without distinct capsular process. Mandibular and mental foramina are present but reduced.

Teeth morphology resembles other members of *Akodon*. Upper molars are crested and main cusps are diagonally arranged. The anterolabial and anterolingual conules of M1 are about equal in size and are divided by a well-developed anteromedian flexus. On the labial side, the anteroflexus and paraflexus are present as well as a posteroloph and an anteroloph. Posteroflexus is very shallow. In lingual side, the hypoflexus is present and the protoslyle is absent. Mesoloph and mesostyle are present but conspicuous only in young animals. M2 has a conspicuous cingulum. Protocone, paracone, hypocone, and metacone are present. M2 has also a mesoloph, mesostyle, and a poorly defined posteroloph. M3 has a protocone, paracone, and hypocone; the protocone being the most developed; the posteroflexus and the paraflexus are present, and the hypoflexus is well developed.

In the lower toothrow, the conids are arranged diagonally with metaconid and entoconid anterior to protoconid and hypoconid, respectively. The m1 has a deep anteromedian flexid. Anterolingual conulid is smaller than anterolabial conulid. Protostylid is well developed but the metastylid is absent. Ectostylid and mesostylid are minute, and a posterolophid with a well-defined posteroflexid is present. The main cusps of second lower molar: protoflexid, mesoflexid, hypoflexid, and posteroflexid are present and arranged diagonally. A tiny mesolophid is present while ectostylid and mesostylid are absent. The third lower molar is “8” shaped.

Karyotype. The chromosome number (2n) and fundamental number (FN) of specimens from Amazonas Department are 26 and 40, respectively. The autosomes are composed by three pairs of large to medium metacentrics, four pairs of large to medium-sized submetacentrics, four pairs of small acrocentrics, and another pair of small metacentrics. The sexual pair consists of a large submetacentric X-chromosome and a small medium-sized acrocentric Y-chromosome (Fig. 3). We also report a XY female from Huiquilla (MUSM 36971). The sex of this specimen was confirmed by examination of its reproductive tract.

Variation. We report some morphological variation within populations of *Akodon orophilus* from Amazonas Department. The specimens from Huiquilla have molars with slightly higher crown compared to other Amazonas populations. This character could be related to diet. The populations from Hierba Buena and Puca Tambo are darker than other populations from Amazonas Department. This coloration is usually associated to environmental wetter conditions (Gogler's rule). The darker coloration of individuals from Puca Tambo was used by Osgood (1913) to distinguish *A. o. orientalis* from *A. o. orophilus*; however, such coloration might also be associated to the moisture level. We failed to find additional discrete morphological differences between the presumed populations of *A. o. orientalis* and *A. orophilus* proper. Then, we supported the placement of *orientalis* as a synonym of *orophilus* by Musser and Carleton (1993, 2005).

FIGURE 3. Standard Giemsa-stained karyotype of *Akodon orophilus* (2n = 26 FN = 40) from Huiquilla, Luya, Amazonas Department. Bar = 10 µm.

Comparisons (Fig. 4, Table 1)**.** Although no other species of *Akodon* is currently known to be sympatric with *Akodon orophilus s.s.*, we compare it with four other species from the *aerosus* group (sensu Smith & Patton 2007) that are distributed in Peruvian montane forests: *A. aerosus*, *A. mollis*, *A. surdus*, and *A. torques*.

Akodon orophilus is distinguishable from *A. mollis* by its darker dorsal pelage coloration; longer tail; larger nasal and premaxillary bones, producing a more noticeable rostral tube; shallower zygomatic notch; a more tapered posterior border of the nasal, thinner incisors, almost inconspicuous capsular projection, small lacrimals, and convex anterior borders of the zygomatic plates. In addition, the karyotype of *A. orophilus* (2n = 26, FN = 40) differs from the diploid number of *A. mollis*: 2n = 22 from Ancash, or 2n = 36-38 from Piura (Patton & Smith 1992).

Akodon orophilus may be distinguishable from *A. aerosus* by its paler coloration, smaller body size and skull dimensions. *A. orophilus* has narrower, longer rostrum, and narrower zygomatic plate with its convex anterior border and deeper zygomatic notch, tapered posterior border of nasal. Thinner zygomatic arch, thinner hamular process of squamosal, smaller oval foramen, smaller lacrimal, smaller median lacerate foramen, shorter parapterygoid plate, less rounded fronto-parietal suture, narrower interorbital region, and narrower braincase. Also, the antorbital bridge and malar process are narrower than in *A. aerosus*. Also, the toothrow is shorter and the jaw is delicate with inconspicuous capsular projection. *A. aerosus* also differs from *A. orophilus* in karyotype, based on the three known diploid numbers of *A. aerosus*: 2n = 22 from Cusco, and 2n = 40 from Ayacucho Department (Gardner & Patton 1976). The population of *A. aerosus baliolus* from Puno with 2n = 38 (Patton *et al*. 1990) was recently elevated to full species by Pacheco *et al.* (2011).

Akodon orophilus can be distinguished from *A. surdus* by a paler coloration, more dense fur, shorter claws, longer tails, and paler and narrower feet. Cranially, *A. orophilus* has narrower and shorter nasals with less tapering posterior borders, narrower braincase, shallower zygomatic notch narrower and less expanded antorbital bridge, longer rostrum, smaller lacrimal, less inflated nasolacrimal capsule. Zygomatic plate slope more slanted backward

TABLE 1. Morphological comparison among six Peruvian montane species of *Akodon*, members of the *aerosus* group (*sensu* Smith & Patton 2007).

Characters	*A. orophilus*	*A. josemariarguedasi*	*A. torques*	*A. aerosus*	*A. mollis*	*A. surdus*
Size	Medium	Large	Medium	Very large	Small	Large
Dorsal pelage	Olive-Brownish Olive	Brownish Olive	Dark Olive Brown	Reddish Cinnamon Brown	Olive	Dark Cinnamon Brown
Ventral pelage	Olive gray	Smoke gray-Whitish	Brownish olive	Olive brown	Olive gray	Olive brown
Tail	Intermediate	Long	Long	Long	Short	Short
Nasal	Long	Long	Long	Long	Short	Very long
Posterior margin	Tapering	Blunt	Tapering	Blunt	Blunt	Tapering
Zygomatic notch (depth)	Intermediate	Intermediate	Intermediate	Shallow	Deep	Deep
Fronto parietal suture	Rounded	Rounded or V-shaped	V-shaped	Rounded	Rounded	Rounded
Lacrimals	Small	Large	Large	Large	Large	Large
Interorbital region (breadth)	Intermediate	Intermediate	Intermediate	Broad	Narrow	Broad
Zygomatic plate (width)	Intermediate	Intermediate	Narrow	Broad	Intermediate	Broad
Zygomatic arch	Robust	Robust	Delicate	Very robust	Robust	Very robust
Malar process	Thick	Thick	Thin and delicate	Very thick	Thick	Very thick
Hamular process	Thick	Thick	Very thin	Very thick	Thick	Very thick
Incisive foramen (length)	Intermediate	Long	Long	Long	Short	Very long
molar toothrow (length)	Intermediate	Short	Short	Long	Intermediate	Long
Oval Foramen	Intermediate	Intermediate	Small	Large	Intermediate	Intermediate
Upper incisors	Short and intermediate	Short and broad	long and intermediate	Short and broad	Short and broad	Short and very broad
Jaw	Intermediate	Delicate	Delicate	Very robust	Intermediate	Very robust
Capsular projection	Indistinct	Indistinct	Indistinct	Well developed	Well developed	Developed

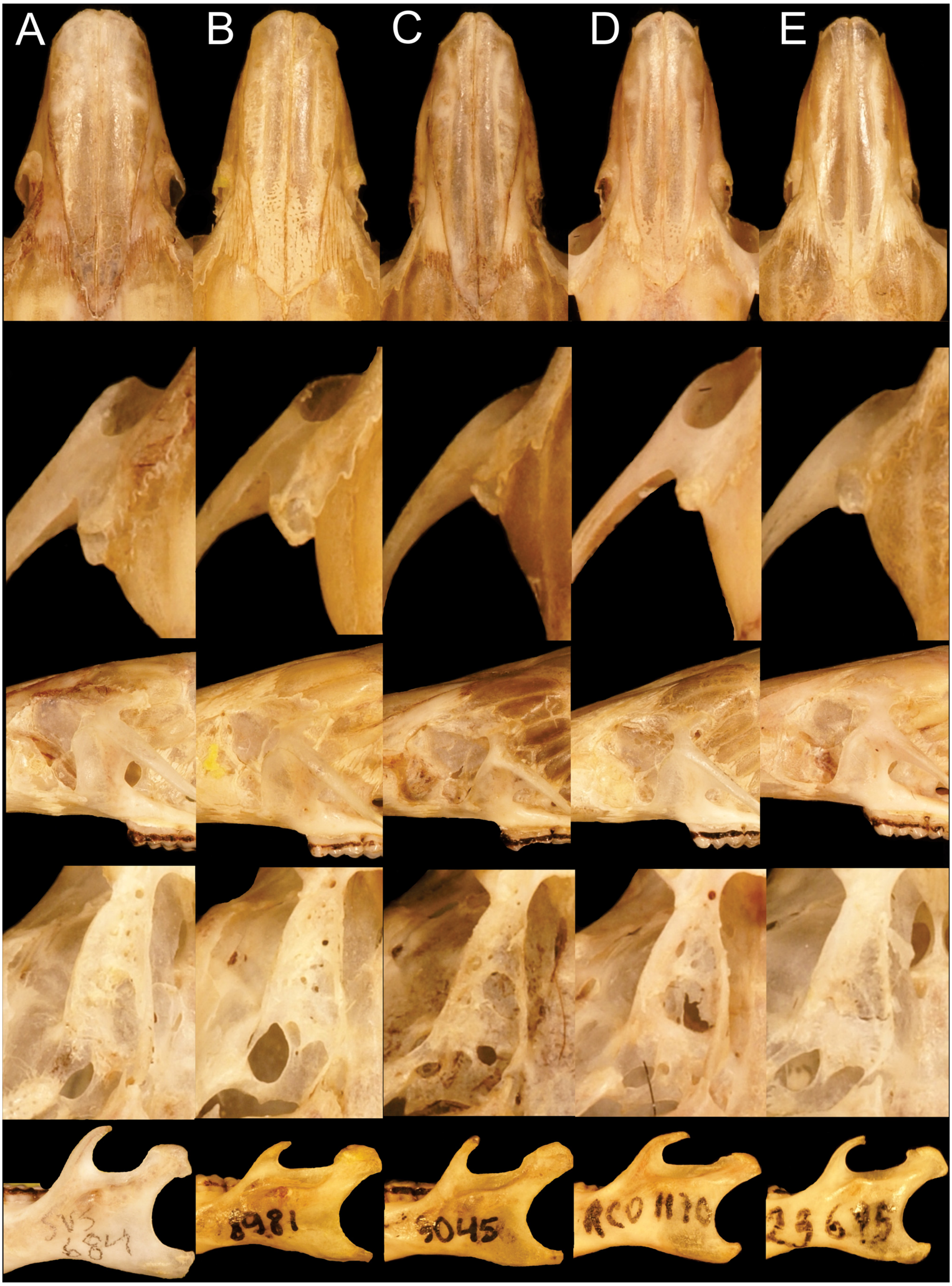

FIGURE 4. Selected morphological traits of the Peruvian *Akodon aerosus* group members. (A: *A. surdus*, MUSM 36600; B: *A. aerosus*, MUSM 8981; C: *A. torques*, MUSM 9045; D: *A. orophilus*, MUSM 37019; E: *A. mollis*, MUSM 23645). First row: rostrum in dorsal view (note the posterior borders of nasals and the configuration of premaxilar and nasal sutures); second row: dorsal view of the antorbital bridge region (note the size of the lacrimals); third row: zygomatic plate in ventrolateral view (note the anterior border and the thickness of the malar process of maxillary); fourth row: mesopterygoid region (note the size of foramen oval and the shape of parapterygoid fossa); fifth row: ascending ramus of the mandible in labial view (note size of the capsular projection).

from the base, narrower zygomatic plate, thinner zygomatic arch, hamular process of squamosal, and malar process. The incisive foramen and mesopterygoid fossa are narrower, the parapterygoid fossa and the molar toothrow are shorter and the jaw is delicate. The karyotype of *A. surdus* is unknown.

Finally, *Akodon orophilus*, compared to *A. torques*, has paler coloration, shorter tail, shorter rostrum; nasal less tapering to the posterior tip; smaller lacrimals; broader zygomatic plate; inconspicuous masseteric tubercle, and larger oval foramen. The nasals project little beyond premaxillae. More robust zygomatic arch, thicker hamular process of squamosal, and broader malar process, fronto-parietal suture is more rounded. *A. torques* has three known karyotypic variants: 2n = 22 and 2n = 24, each from a different, but adjacent geographic area from Cusco department (Patton *et al*. 1990), and the variant 2n = 26 from Ayacucho department (Hsu & Benirshcke 1976).

Natural history. *Akodon orophilus* has been found in simpatry with six species of rodents from montane forests of Amazonas Department: with *Thomasomys notatus*, *T. ischyrus*, and *Nephelomys albigularis* in Leymebamba; with *Microryzomys minutus*, *T. ischyrus*, and *N. albigularis* in Huiquilla; and with *Microryzomys altissimus* and *Hylaeamys yunganus* in Hierba Buena. These mice have also been taken in highland grasslands known locally as "jalca" with *M. minutus*.

Compared with other rodents, this mouse is very common especially in areas with corn and potatoes crops. It represented ca. 46 % of the captured animals during a twelve-night trapping survey in Amazonas department in July and August 2007. Three out of six females collected in the dry season were pregnant. Additional data about the ecology of these rodents are unknown.

Populations from Amazonas might be associated with the Chachapoyan physiographic province established by Young (1992).

Remarks. *Akodon orophilus* includes specimens from Amazonas Department identified as *Akodon mollis* by Myers *et al*. (1990).

***Akodon josemariarguedasi*, sp. nov.**

Holotype. MUSM 22754, adult male, body in alcohol and skull removed, collected on 23 September 2005 by María Peralta, original number 237.

Type locality. Galloganán, Ambo, Huánuco, Peru, 3420 m. 10º 09' S, 76º 08' W (Fig. 1, locality 2).

Diagnosis. *Akodon josemariarguedasi* can be distinguished from congeners by the following combination of characters: dorsal pelage coloration uniformly Brownish Olive, strongly contrasting with Smoke Gray to whitish abdominal region; fur hairs with paler gray-based; tail dark and moderately countershaded; posterior end of nasal blunt with serrated contour; lacrimals large; zygomatic plate with the anterior margin less slanting and convex in its anteromedial area or straight; antorbital bridge moderately wide; zygomatic notch somewhat deep; palate narrow; maxillary toothrow somewhat short; mandible delicate with thin and large condylar process; and deeper lunar notch. The nasal projects distinctly behind of the premaxilla. An internal fossetus between paracone and protocone of M1 is present.

Paratypes. Three specimens collected at the type locality in September 2005: males MUSM 22749 and MUSM 22753 and female MUSM 22759; all consisting of skull and skins.

Etymology. The specific name *josemariarguedasi* is given in honor of the Peruvian writer José María Arguedas (1911–1969) for dedicating his life to understanding the Andean people, their culture and folklore.

Distribution. This rodent is found in four localities of Huánuco Department, south of Río Huallaga (Fig. 1).

Habitat. *Akodon josemariarguedasi* is known from mountain cloud forest of Huánuco Department between 2900 to 3800 m.

Morphological description (Fig. 5)**.** Overall color with marked distinction between dorsum and venter; dorsal surface is Brownish Olive in contrast with venter that varies from Smoke Gray to whitish. Fur hairs project up to approximately 11 mm long. The pheomelanin bands are 1–1.5 mm long. Guard hairs extend by approximately 3–4 mm beyond the fur hairs. Tail is moderately countershaded; with dorsal black hairs extend to 2 or 2.5 ring-scales and ventral hairs almost totally white and extend the distance of 3 ring-scales, it averages about 86% of the length of the head plus body. Eyerings are inconspicuous. Hindfeet and forefeet are covered by almost black hairs. Digits of manus and pes are covered by white hairs.

Braincase is slightly globular, dorsal profile of the cranium is relatively flat. Rostrum is long, slightly arched and narrow; gnathic process is relatively conspicuous surpassing the anterior face of incisors. Nasals are relatively narrow and long, extending well beyond the premaxilla-frontal sutures. Posterior tips of nasal are blunt with irregular outline while anterior margins are rounded. Supraorbital edges are smooth and rounded. The nasals project distinctly behind to the premaxillae. Fronto-parietal suture is slightly U or V-shaped. Zygomatic notches are somewhat narrow, moderately deep, with rounded edges. Lacrimals are large. Zygomatic arches are relatively thick, anteriorly convergent and slightly expanded laterally with thick malar processes and the hamular process of squamosal is thick. Antorbital bridge is moderately wide. Lambdoid crest is well developed and interparietal is reduced. Ventrally, the incisive foramina are relatively long and narrow, extending between protocones of M1 with rounded anterior and posterior edges. Palate is narrow and short or slightly long with shallow palatal groove. Maxillary septum occupies more than half of incisive foramen. Antero-palate pits are very conspicuous placed at level of protocones of M2 while postero-palate pits are inconspicuous and situated at the same level of the anterior margin of mesopterygoid fossa or slightly backward. Mesopterygoid fossa has rounded anterior margin and subequal in breadth to parapterygoid fossa or narrower. Parapterygoid fossa is triangular in shape, the outward edges are convex with small perforations and slightly excavated. The bullae are medium-size with short and broad Eustachian tubes.

In lateral view, the zygomatic plates are relatively narrow, slightly inclined and its anterior edges more convex in the anteromedial parts or straight. The posterior ascending process of alisphenoid is always located under the squamoso-alisphenoid groove. Tympanic ring can be opened or closed. The oval foramen is medium-sized. The accessory foramen ovale diameter is greater than or equal to M3 length, optic foramen is larger or subequal to M3 length. Ethmoid foramen is placed dorsal to M3. Carotid circulation is primitive (pattern 1). Postglenoid foramina are larger than the subsquamosal foramina, both with rounded margins. The masticatory-buccinator foramen is not divided. Sphenopalatine foramen length is lesser than M2 length and almost completely hidden by ethmoturbinal.

Incisors are slightly broad and usually orthodont or proodont. The lower jaw is typical for the genus with slender and delicate rami. Capsular projection is inconspicuous, placed behind of sigmoid notch. The condyloid process is long and extends beyond the posterior margin of angular process. Lunar notch is narrow and relatively deep.

In general dental morphology is similar to other *Akodon* taxa, except for an internal fossetus present between paracone and protocone of M1 and a deeper metaflexus.

Karyotype. 2n = 22, FN = 40, from Huánuco Department, Peru. Both sexual chromosomes are acrocentric (Pacheco *et al*. 2012). In that report, the authors assigned this karyotype to *Akodon orophilus*.

Comparisons (Table 1)**.** *Akodon josemariarguedasi* is compared with five members of the *Akodon aerosus* group that inhabit the Peruvian montane forest where this new species is found: *A. aerosus*, *A. orophilus*, *A. mollis*, *A. surdus*, and *A. torques*.

Akodon josemariarguedasi can be distinguished from *A. mollis* by a more contrasting overall tinge and paler ventral pelage, longer tails, longer nasals. The zygomatic notches are shallower, interorbital region is broader and the incisive foramen is longer. The nasal projects distinctly behind of the premaxilla. The jaw is delicate with inconspicuous capsular projection.

Akodon josemariarguedasi is distinguishable from *A. aerosus* by its paler ventral color, smaller and less robust skull. The nasal is narrower, projecting distinctly behind of the premaxilla. The zygomatic plates are clearly narrower and less vertical with convex anterior border, deeper zygomatic notch, and narrower interorbital region. The foramen oval is smaller and upper molar toothrow is shorter. In addition, the antorbital bridge and the malar process are thinner. The jaw is delicate and the capsular projection is indistinct.

Akodon josemariarguedasi can be distinguished from *A. surdus* by a paler and more countershaded coloration, shorter claws and longer tails. Cranially, the braincase is narrower in *A. josemariarguedasi*. Its nasals are narrower with less tapering posterior border, the zygomatic notches are shallower and the zygomatic plates are narrower and less convex. The interorbital region, the incisive foramen and the mesopterygoid fossa are narrower. The hamular process of squamosal is thinner. The mandible is delicate with inconspicuous capsular projection.

Akodon josemariarguedasi is distinguished from *A. torques* by paler ventral coloration. Body pelage pattern distinctly countershaded. Cranially, the posterior margin of the nasal of *A. josemariarguedasi* is blunt, serrated and less tapering. The zygomatic plate is less sloped and broader. Zygomatic arches are more robust. The malar process and the hamular process of squamosal are ticker and the fronto-parietal suture is more rounded. Upper incisors are shorter than *A. torques*.

Akodon josemariarguedasi differs from *A. orophilus* by its contrasting coloration pattern with paler abdominal region. The posterior margin of the nasal is blunt and serrated, the maxillary septum is thin. Lacrimals are large, and the nasal projects distinctly behind the premaxillae. The palate is narrower. The jaw is delicate, the condylar process is longer and thinner (Fig. 6).

Natural history. *Akodon josemariarguedasi* co-occurs with the sigmodontines *Thomasomys kalinowskii*, *T. incanus*, *Microryzomys minutus*, *M. altissimus*, and *Oligoryzomys* sp. Noblecilla & Pacheco (2012) analyzed the diet composition of 37 individuals of *Akodon josemariarguedasi* (reported as *A. orophilus*) characterizing as insectivorous. They consume mainly adult beetles (90%) and other items such as plant materials (seeds and other plant structures) and fruits.

Remarks. *Akodon josemariarguedasi* apparently includes specimens from Palca (Junín) that were first allocated to *Akodon mollis* by Patton *et al*. (1989), Myers *et al*. (1990), and Smith & Patton (1991). Later, Patton & Smith (1992) reidentified the specimens as *A. torques*; but finally Smith & Patton (1993; 1999; 2007) corrected them to *A. orophilus*. We observed by photos of one specimen from Palca (MVZ 173057) shares some skull features with the new taxon; however a depth and comprehensive examination is necessary.

Morphologic analyses. A principal component analysis of 19 characters found that the first four principal components explained 63.6% of the variance. Although, this value is relatively low; the projections of specimens between the 1st principal component (PC 1) and 2nd principal component (PC 2), and between PC 1 and 3rd principal component (PC 3) clearly showed no or minimal overlap between *A. orophilus* and *A. josemariarguedasi* (Fig. 7), supporting the existence of two species. Variables with the heaviest load on PC 1 were condylomolar length (CML), zygomatic breadth (ZB) and breadth of rostrum (BR). On PC 2 space, individuals are separated primarily by diastema length (DL) and length of incisive foramina (LIF). PC 3 separated individuals by the breath of zygomatic plate (BZP) whereas PC 4 separated by the breadth of first upper molar (BM1) (Table 2).

TABLE 2. Factor loadings on the first four axes of a principal components analysis based on 19 log-transformed cranial variables for adult specimens of *Akodon orophilus* (n = 22) and *A. josemariarguedasi* **sp. nov.** (n = 23).

Variable	PC 1	PC 2	PC 3	PC 4
CML	0.84	0.12	-0.21	-0.03
ZB	0.82	-0.08	0.19	0.02
BR	0.80	-0.19	0.07	-0.05
BPB	0.70	0.03	0.25	-0.14
GSL	0.69	0.38	-0.25	0.13
BB	0.69	-0.48	0.04	-0.03
LM	0.68	-0.11	-0.31	0.13
CIL	0.63	0.59	-0.11	-0.09
LIB	0.61	-0.29	0.35	-0.15
BIF	0.61	-0.04	0.49	0.22
DL	0.20	0.67	-0.05	-0.08
LIF	-0.16	0.64	0.44	0.27
BZP	0.38	0.33	-0.62	0.09
BM1	0.17	-0.48	-0.02	0.72
LN	0.33	0.45	-0.04	0.58
BN	0.39	0.31	0.06	-0.56
DI	-0.41	0.34	0.47	0.10
LOF	0.30	0.30	0.51	0.01
HBC	0.51	-0.45	0.11	-0.07
Eigenvalues	6.13	2.78	1.77	1.41
% of Variance	32.27	14.63	9.31	7.40

FIGURE 5. Dorsal, ventral and lateral views of cranium and mandible of *Akodon josemariarguedasi* **sp. nov.** (MUSM 22754). Bar = 10 mm.

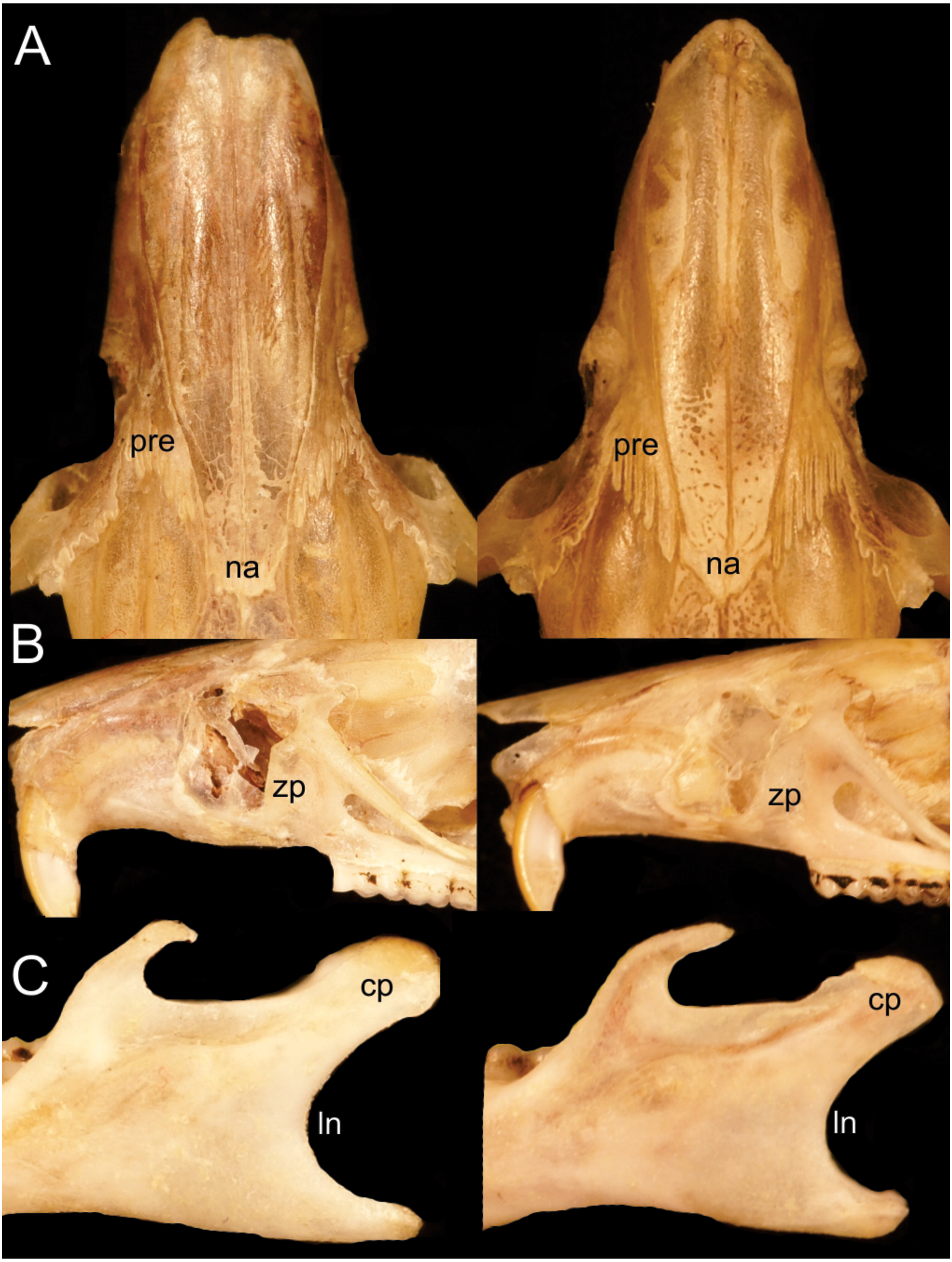

FIGURE 6. Some anatomical differences between *Akodon josemariarguedasi* **sp. nov.** (MUSM 22754; left) and *A. orophilus* (MUSM 37021; right): A: Posterior border of nasals [na] is blunt, its contour is serrated and the nasal [na] projects distinctly behind the premaxilla [pre] in *Akodon josemariarguedasi*. B: Zygomatic plate [zp] with anterior margin less slanting in *Akodon josemariarguedasi*. C: Condylar process [cp] is large and the lunar notch [ln] is deep in *Akodon josemariarguedasi*.

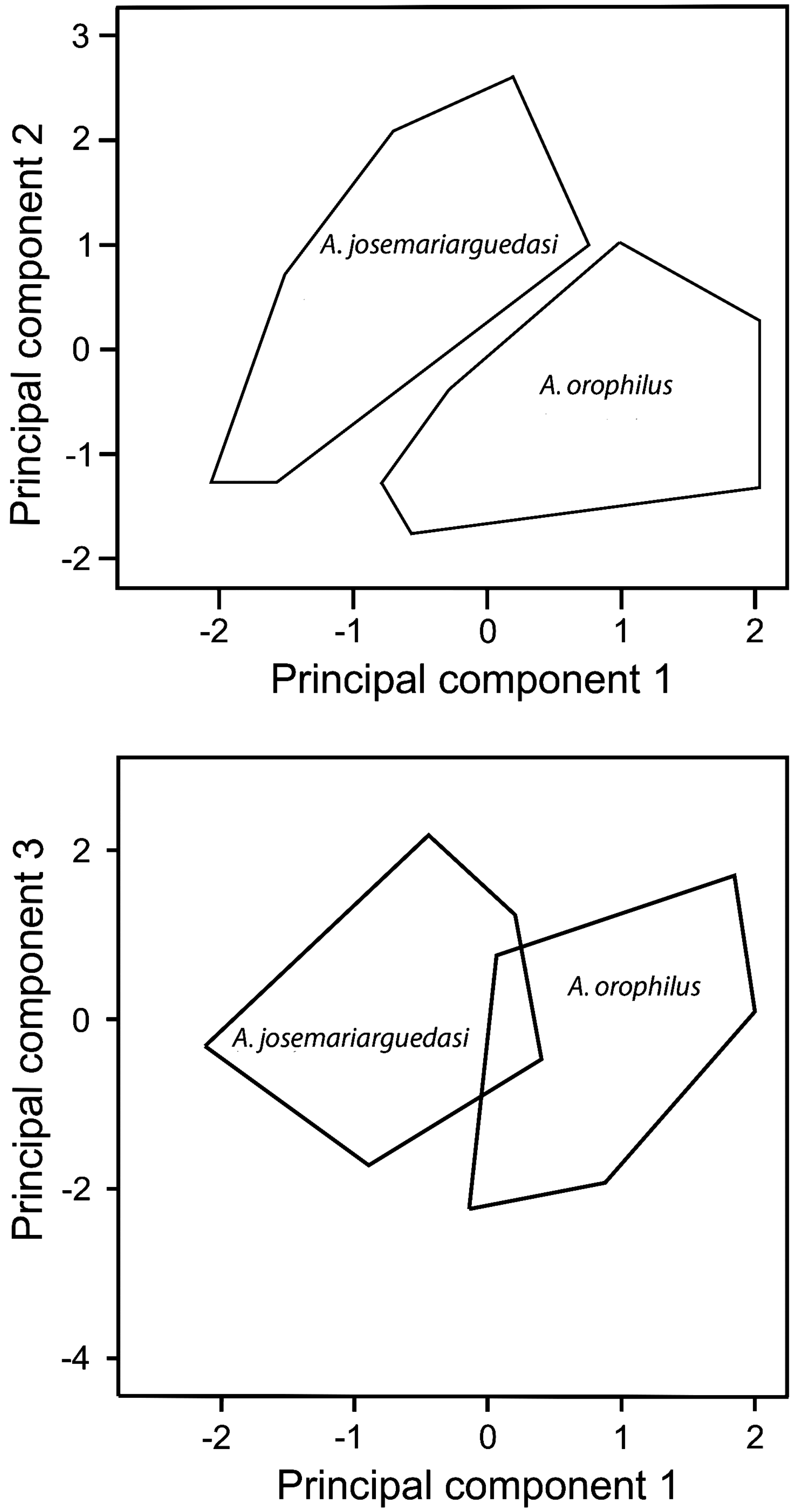

FIGURE 7. Projection of specimen scores for factors 1 and 2 (top) and 1 and 3 (bottom) extracted from principal component analyses, comparing samples of *Akodon orophilus* and *A. josemariarguedasi* **sp. nov.** See Table 2 for variable correlations and explanation of percent variance.

The discriminant analysis showed high percentages of correct classifications, 100% for *A. orophilus* and 100% for *A. josemariarguedasi* with values of Wilk's Lambda near zero (0.09) and high value of the canonical correlation (0.95), indicating a large difference between both species. Moreover, univariate analyses of each character between *A. orophilus* and *A. josemariarguedasi* found significant differences in 14 of the external and cranial dimensions (Table 3).

Karyological analysis. *Akodon josemariarguedasi* (reported as *A. orophilus* by Pacheco *et al*. 2012) differs from *A. orophilus* in the number of chromosomes and the morphology of the pair sexual. *A. josemariarguedasi* has 22 chromosomes whereas *A. orophilus* has 26. The X and Y are acrocentric in *A. josemariarguedasi* while the X is submetacentric in *A. orophilus*. In addition, the Y chromosomes are different in their length. The Y chromosome of *A. josemariarguedasi* has a two third the length of the X chromosome, whereas the Y chromosome is half the length of the X chromosome in *A. orophilus*. We highlighted that the karyotype of *Akodon orophilus* strongly resembles the karyotype of *A. torques* from Yuraccyacu (Hsu & Benirschke 1973), except for the Y chromosome which is acrocentric in *A. orophilus* and submetacentric in *A. torques*.

Discussion

The systematics of Peruvian *Akodon* is still little studied and confusing, especially the species of the *A. aerosus* group, since a detailed revision, including large series of specimens and integrating analyses of morphological and morphometric data is still missing. Besides, considerable variation has been found in sequences of *cyt b* within populations of some members of the *A. aerosus* group (e.g. Patton *et al*. 1990; Patton & Smith 1992; Smith & Patton 2007), and in karyotype formulae of *A. mollis, A. torques,* and *A. aerosus* (Patton & Smith 1992; Smith & Patton 2007). These data suggest that each population of these species could correspond to a different species.

The taxonomy of *Akodon orophilus* has not been yet treated properly. Previous studies recognized *A. orophilus,* as a full species but no study of intraspecific morphological or morphometric variation is still available, in spite that molecular evidence suggests variation among its populations (e.g. Patton & Smith 1992; Smith & Patton; 1993; Smith & Patton 2007). For instance, Patton & Smith (1992) found approximately 5% of *cyt b* divergence between specimens from Huánuco (Unchog) and San Martín (Puerta del Monte) Departments. Posteriorly, Smith & Patton (1993) also added sequences of individuals from Amazonas (Leymebamba) and Junín (Palca) Departments, finding sequence divergence values of 5 to 10% among samples. These values are higher than divergence values reported between *dolores* and *toba* (2.6%, Braun *et al*. 2008) and between *fumeus* and *kofordi* (2.8%, Smith & Patton 2007) suggesting that some *A. orophilus* populations might also represent different species.

Our karyological comparative analysis of *Akodon josemariarguedasi* (2n = 22) and *A. orophilus* (2n = 26), both with FN = 40, supports our hypothesis that the new taxon deserves a valid species status. In addition, both karyotypes are similar to other members of the *aerosus* group, sharing similar chromosomal and fundamental numbers. Although our report of a XY female of *Akodon orophilus* is the first for this species, it is not rare in the genus. This condition has been reported for *A. torques* (Hoekstra & Edwards 2000), *A. mollis* (Lobato *et al*. 1982), and *A. azarae* (Bianchi & Contreras 1967).

Our results, based on morphological grounds, morphometric multivariate space, chromosomal data, and the assessment of qualitative characters support that the specimens from Huánuco Department, previously assigned to *Akodon orophilus*, represent indeed a new species, named here *A. josemariarguedasi*. Our data also support the initial hypothesis that *A. orophilus* may represent a complex of species along its distribution.

Patton & Smith (1992) mentioned that the distribution of *Akodon orophilus* could span as far south as Huánuco Department, however the recognition of *A. josemariarguedasi* from Huánuco Department (south of Río Huallaga) suggests that the range of *A. orophilus* is restricted to montane forest of Amazonas and San Martín Departments. Thus, specimens identified as *A. orophilus* from Huánuco Department or further south should be revised as is the case of individuals from Palca (Junín). Patton & Smith (1992) also displayed the distribution of *Akodon orophilus*, at both margins of the Río Marañón, a hypothetical biogeographical barrier (Pacheco 2002); however, our data demonstrate that *A. orophilus s.s.* is only distributed on the eastern bank of Río Marañón, whereas *A. mollis* is present on the western bank, supporting the role of the Río Marañón as a barrier for montane fauna.

Barnett (1999) and Moreno & Albuja (2005) reported *Akodon orophilus* from Ecuador, apparently contradicting our hypothesis; however, we sustain that such samples from Ecuador correspond to *A. mollis* instead of *A. orophilus*, based on our qualitative evaluation of figures and measurements presented by Moreno & Albuja (2005).

TABLE 3. External and cranial measurements (mm) of adult *Akodon josemariarguedasi* sp. nov. and *Akodon orophilus* compared to other species of the *aerosus* group . Sample size (n), mean (X), standard deviation (SD), and minimum and maximum values are given for each character. Significant differences (t-test; P ≤ 0.05) between *A. orophilus* and *A. josemariarguedasi* are indicated as *.

Character	*Akodon orophilus*			*Akodon josemariarguedasi*			*Akodon torques*			*Akodon aerosus*			*Akodon mollis*			*Akodon surdus*	
	n	X ± SD	Range	n	X ± SD	Range	n	X ± SD	Range	n	X ± SD	Range	n	X ± SD	Range	n	X
TL	21	187.33 ± 8.88	171–201	19	192.32 ± 11.91	176–221	23	188.95 ± 9.29	161-201	26	199.23 ± 19.64	181-270	30	173.97 ± 7.88	161-190	1	183
LT	21	85.19 ± 7.14	74–100	19	89.08 ± 7.94	75–106	23	89.40 ± 6.82	68–100	26	87.37 ± 504	81–100	30	76.66 ± 6.08	67–91	1	70
EAR*	21	16.55 ± 1.24	14–19	19	15.61 ± 1.36	12–17	23	22.62 ± 0.97	21–24	26	24.23 ± 1.39	22–27	30	21.07 ± 1.01	19–23	1	23
HF	21	22.76 ± 1.22	21–25	19	22.84 ± 1.65	21–27	23	15.90 ± 0.99	14–18	26	17.00 ± 1.22	15–20	30	15.20 ± 1.44	13–17	1	17
GSL*	22	27.04 ± 0.30	26.23–27.45	23	26.81 ± 0.38	26.06–27.49	23	26.79 ± 0.41	25.80 – 27.48	26	27.93 ± 0.50	26.70–29.16	30	25.67 ± 0.91	24.23–27.28	1	28.93
CIL	22	24.55 ± 0.37	23.77–25.25	23	24.47 ± 0.44	23.54–25.25	23	24.26 ± 0.43	23.35 – 24.99	26	25.50 ± 0.49	24.39–26.65	30	23.55 ± 0.76	22.44–25.05	1	26.73
CML*	22	16.59 ± 0.31	16.05–17.15	23	16.23 ± 0.24	15.72–16.68	23	15.99 ± 0.28	15.33 – 16.42	26	16.79 ± 1.31	10.63–17.76	30	15.65 ± 0.49	14.98–16.58	1	17.67
LOF	22	8.34 ± 0.18	8.06–8.67	23	8.31 ± 0.17	7.97–8.67	23	8.20 ± 0.19	7.73 – 8.56	26	8.66 ± 0.32	7.71–9.14	30	8.24 ± 0.27	7.72–8.94	1	9.45
LN	22	10.43 ± 0.36	9.79–11.22	23	10.47 ± 0.27	9.90–10.85	23	10.65 ± 0.31	10.08 – 11.28	26	10.82 ± 1.24	9.90–16.50	30	9.90 ± 0.31	9.46–10.51	1	11.43
DL	22	6.83 ± 0.21	6.50–7.27	23	6.87 ± 0.22	6.51–7.16	23	6.85 ± 0.56	4.39 – 7.36	26	7.24 ± 0.22	6.80–7.80	30	6.72 ± 0.38	6.14–7.43	1	7.82
LM*	22	4.39 ± 0.17	3.97–4.82	23	4.22 ± 0.11	3.93–4.43	23	4.25 ± 0.12	4.00 – 4.49	26	4.62 ± 0.14	4.32–4.80	30	4.31 ± 0.65	3.71–5.83	1	4.7
LIF*	22	5.82 ± 0.28	5.28–6.35	23	6.09 ± 0.25	5.61–6.55	23	6.07 ± 0.20	5.72 – 6.45	26	6.14 ± 0.26	5.60–6.70	30	5.55 ± 0.49	4.45–6.26	1	6.42
BIF*	22	2.14 ± 0.12	1.98–2.40	23	1.99 ± 0.11	1.72–2.25	23	2.13 ± 0.09	2.01 – 2.35	26	2.26 ± 0.11	2.08–2.53	30	1.95 ± 0.13	1.69–2.21	1	2.46
BPB*	22	2.98 ± 0.14	2.78–3.20	23	2.71 ± 0.21	2.38–3.15	23	2.89 ± 0.14	2.66 – 3.32	26	3.18 ± 0.21	2.89–3.60	30	2.75 ± 0.20	2.32–3.15	1	3.03
BM1*	22	1.26 ± 0.06	1.17–1.40	23	1.22 ± 0.06	1.12–1.34	23	1.29 ± 0.06	1.20 – 1.43	26	1.42 ± 0.67	1.20–4.72	30	1.22 ± 0.07	1.1–1.37	1	1.35
BR*	22	4.76 ± 0.21	4.25–5.09	23	4.39 ± 0.16	4.07–4.67	23	4.42 ± 0.22	3.98 – 4.87	26	5.14 ± 0.19	4.80–5.55	30	4.48 ± 0.25	3.85–5.14	1	5.93
BN	22	3.09 ± 0.14	2.89–3.32	23	3.10 ± 0.11	2.82–3.30	23	3.07 ± 0.18	2.79 – 3.36	26	3.45 ± 0.17	3.10–3.80	30	2.93 ± 0.17	2.61–3.28	1	3.6
LIB*	22	5.27 ± 0.16	5.05–5.63	23	5.15 ± 0.18	4.87–5.48	23	5.25 ± 0.14	5.01 – 5.50	26	5.66 ± 0.11	5.46–5.90	30	4.99 ± 0.37	4.57–5.75	1	5.52
ZB*	22	13.37 ± 0.34	12.78–14.07	23	12.92 ± 0.31	12.24–13.40	23	13.35 ± 0.29	12.72 – 13.85	26	14.27 ± 0.41	13.58–14.84	30	12.71 ± 0.68	11.57–13.97	1	14.6
BB*	22	12.28 ± 0.31	11.95–13.02	23	11.90 ± 0.29	11.28–12.51	23	12.00 ± 0.24	11.57 – 12.50	26	12.87 ± 0.29	12.10–13.40	30	11.54 ± 0.52	10.88–12.51	1	12.96
BZP	22	2.08 ± 0.14	1.83–2.31	23	2.03 ± 0.10	1.78–2.19	23	1.85 ± 0.16	1.58 – 2.18	26	2.22 ± 0.10	2.00–2.40	30	2.05 ± 0.11	1.83–2.29	1	2.31
DI*	22	1.25 ± 0.05	1.14–1.33	23	1.33 ± 0.05	1.27–1.43	23	1.26 ± 0.07	1.14 – 1.42	26	1.33 ± 0.06	1.25–1.50	30	1.31 ± 0.07	1.17–1.44	1	1.39
HBC*	22	8.45 ± 0.27	7.80–8.85	23	8.21 ± 0.12	8.04–8.54	23	8.35 ± 0.17	8.05 – 8.63	26	8.93 ± 0.25	8.57–9.55	30	8.19 ± 0.27	7.76–8.73	1	8.71

Their individuals have blunt posterior border of nasal, straight anterior margin of zygomatic plate and conspicuous capsular projection as well as, shorter nasals; features that are characteristic of *A. mollis* (see Table 1). Also, our specimens of *A. orophilus* have longer nasal, shorter molar toothrow, narrower rostrum and longer diastema than the Ecuadorian individuals (see Table 2). Alvarado (2005) included *A. orophilus* in his morphometric analysis of Ecuadorian *Akodon* but his study was not designed to test the validity of *A. orophilus*. The principal component analysis did not show a strong separation between both rodents. Therefore, we conclude that there is no confirmed evidence that *A. orophilus* is present north of the Río Marañón.

In conclusion, we argue that *A. orophilus* is restricted to mountain forests of northern Peru, with a distribution bounded by Río Marañón and Río Huallaga. Finally, the recognition of *Akodon josemariarguedasi* as a new species reflects the taxonomic complexity and the need of further research to assess species delimitations within the *aerosus* group. We hope that this work will be the beginning of a progressive revision of *A. orophilus* that shall clarify the status of other populations from the Peruvian eastern montane forest, especially from northern and central Peru.

Acknowledgments

We are grateful to the members of Departmento de Mastozoología del Museo de Historia Natural, Universidad Mayor de San Marcos, especially María Peralta, for their continuing support. We thank James Patton (University of California), Lucía Luna (University of Michigan), Paul Velazco (American Museum of Natural History), and Sergio Solari (Universidad de Antioquia) for their comments and suggestions during various stages of this research. Our gratitude also goes to Bruce Patterson (Field Museum of Natural History, Chicago) for his kindness in providing specimens and to Darrin Lunde and Marissa Altmann (Smithsonian Institution, Washington) for sending photographs of *Akodon surdus*. We are also grateful to two anonymous reviewers for suggestions that improved the manuscript. Financial support was given to V. Pacheco by the Consejo Superior de Investigación, Universidad Nacional Mayor de San Marcos and for the project “Biodiversidad, conservación, impacto ambiental y macrozonificación de los bosques montanos del departamento de Huánuco”.

References

Alvarado−Serrano, D. (2005) Revisión taxonómica y distribución del género *Akodon* (Muridae: Sigmodontinae) en Ecuador. Licenciate thesis. Pontificia Universidad Católica del Ecuador, Quito, Ecuador, 207pp.

Barnett, A. (1999) Small mammals of the Cajas Plateu, Southern Ecuador: Ecology and Natural History. *Bulletin of the Florida Museum of Natural History*, 42 (4), 161−217.

Bianchi, N.O. & Contreras, J.R. (1967) The chromosomes of the field mouse *Akodon azarae* (Rodentia: Cricetidae), with special reference to sex chromosome anomalies. *Cytogenetics*, 6 (5), 306–313.
http://dx.doi.org/10.1159/000129952

Braun, J.K., Coyner, B.S., Mares, M.A. & Van Den Bussche, R.A. (2008) Phylogenetic relationships of South American grass mice of the *Akodon varius* group (Rodentia, Cricetidae, Sigmodontinae) in South America. *Journal of Mammalogy*, 89 (3), 768–777.
http://dx.doi.org/10.1644/07-MAMM-A-269R1.1

Cabrera, A.L. (1961) Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales “Bernandino Rivadavia” e Instituto Nacional de Investigación de las Ciencias Naturales (Ciencias Zoológicas)*, 4, 309–732.

D’Elía, G. (2003) Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. *Cladistics*, 19 (4), 307–323.
http://dx.doi.org/10.1016/S0748-3007(03)00071-9

Ford, C.E. & Hamerton, J.L. (1956) A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. *Stain Technology*, 31 (6), 247–251.
http://dx.doi.org/10.3109/10520295609113814

Hoekstra, H.E. & Edwards, S.V. (2000) Multiple origins of XY mice (genus *Akodon*): phylogenetic and chromosomal evidence. *Proceedings of the Royal Society B: Biological Sciences*, 267 (1455), 1825–1831.
http://dx.doi.org/10.1098/rspb.2000.1217

Hsu, T.C. & Benirschke, K. (1973) *An Atlas of Mammalian Chromosomes*. Springer-Verlag, New York . 7, folio 314.

Jayat, J.P., Ortíz, P.E., Salazar-Bravo, J., Pardiñas, U.F.J. & D'Elía, G. (2010) The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity. *Zootaxa*, 2409, 1–61.

Levan, A., Fredga, K. & Fandberg, A.A. (1964) Nomenclature for centromeric position on chromosomes. *Hereditas*, 52 (2), 201–220.
http://dx.doi.org/10.1111/j.1601-5223.1964.tb01953.x

Lobato, L., Canto, G., Araujo, B., Bianchi, N.O. & Merani, S. (1982) Cytogenetics of South American akodont rodents (Cricetidae). VIII. *Akodon mollis*: a species with XY females and B-chromosomes. *Genética*, 57 (3), 199–205.
http://dx.doi.org/10.1007/BF00056483

Luna, L. & Pacheco, V. (2002) A new species of *Thomasomys* (Muridae: Sigmodontinae) from the Andes of Southeastern Peru. *Journal of Mammalogy*, 83 (3), 834–842.
http://dx.doi.org/10.1644/1545-1542(2002)083<0834:ANSOTM>2.0.CO;2

Moreno, P. & Albuja, L. (2005) Nuevos registros de *Akodon orophilus* (Rodentia, Muridae) en el Ecuador. *Revista Politécnica*, 21 (6), 28–44.

Musser, G.M. & Carleton, M.D. (1993) Familia Muridae. *In*: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammals species of the world: a taxonomic and geographic reference*. Smithsonian Institution Press, Washington, pp. 501–756.

Musser, G.M. & Carleton, M.D. (2005) Superfamily Muroidea. *In*: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal species of the world: A taxonomic and geographic reference*. *Third ed*. The John Hopkins University Press, Baltimore, pp. 894–1531.

Myers, P. (1989) A preliminary revision of the varius group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba* and *varius*). *In*: Redford, K.H. & Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. Sandhill Crane Press, Inc., Gainesville, Florida, pp. 5–54.

Myers, P., Patton, J.L. & Smith, M.F. (1990) A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Peru and Bolivia. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 177, 1–89.

Noblecilla, M. & Pacheco, V. (2012) Dieta de roedores sigmodontinos (Cricetidae) en los bosques montanos tropicales de Huánuco, Perú. *Revista Peruana de Biología*, 19 (3), 313–318.

Osgood, W.H. (1913) New Peruvian mammals. *Field Museum of natural History, Zoological series*, 10 (9), 93–100.

Osgood, W.H. (1943) The Mammals of Chile. *Field Museum of natural History, Zoological series*, 30, 1–268.

Pacheco, V. (2002) Mamíferos del Perú. *In*: Ceballos, G. & Simonetti, J. (Eds.), *Diversidad y Conservación de los Mamíferos Neotropicales*. CONABIO–UNAM. México, D.F., pp. 503–549.

Pacheco, V. (2003) *Phylogenetic analyses of the Thomasomyini (Muroidea: Sigmodontinae) based on morphological data.* Ph.D. dissertation, The City University of New York, New York, EEUU.

Pacheco, V., Cadenillas, R., Salas, E., Tello, C. & Zeballos, H. (2009) Diversidad y endemismo de los mamíferos del Perú. *Revista Peruana de Biología*, 16 (1), 5–32.

Pacheco, V., Márquez, G., Salas, E. & Centty, O. (2011) Diversidad de mamíferos en la cuenca media del río Tambopata, Puno, Perú. *Revista Peruana de Biología*, 18 (2), 231–244.

Pacheco, V., Cordova, J. & Velásquez, M. (2012) First karyotypes of *Akodon orophilus* Osgood 1913 and *Thomasomys* sp. (Rodentia: Sigmodontinae) from Huánuco, Perú. *Revista Peruana de Biología*, 19 (1), 107–110.

Patton, J.L. (1986) Patrones de distribución y especiación de la fauna de mamíferos de los bosques nublados andinos del Perú. *Anales del Museo de Historia Natural de Valparaiso*, 17, 87–94.

Patton, J.L., Myers, P. & Smith, M.F. (1989) Electromorphic variation in selected South American Akodontine rodents (Muridae: Sigmodontinae), with comments on systematic implications. *Zeitschrift für Säugetierkunde (Mammalian Biology)*, 54 (6), 347–359.

Patton, J.L., Myers, P. & Smith, M.F. (1990) Vicariant versus gradient models of diversification: the small mammal fauna of eastern Andean slopes of Peru. *In*: Peters, G. & Hunter, R. (Eds.), *Vertebrates in the Tropics*. Museum Alexanders Koenig, Bonn, pp. 355–371.

Patton, J.L. & Smith, M.F. (1992) Evolution and systematics of akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus *Akodon*. *Memorias del Museo de Historia Natural, U.N.M.S.M*, 21, 83–103.

Reig, O.A. (1977) A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *Journal of Zoology, London*, 181 (2), 227–241.
http://dx.doi.org/10.1111/j.1469-7998.1977.tb03238.x

Smith, M.F. & Patton, J.L. (1991) Variation in mitochondrial cytochrome b sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). *Molecular Biology and Evolution*, 8 (1), 85–103.

Smith, M.F. & Patton, J.L. (1993) The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of the Linnean Society*, 50 (3), 149–177.
http://dx.doi.org/10.1111/j.1095-8312.1993.tb00924.x

Smith, M.F. & Patton, J.L. (1999) Phylogenetic relationships and the radiation of sigmodontine rodents in South America: Evidence from cytochrome *b*. *Journal of Mammalian Evolution*, 6 (2), 89–128.

Smith, M.F. & Patton, J.L. (2007) Molecular phylogenetics and diversification of South American grass mice, genus *Akodon*. *In*: Kelt, D., Lessa, E. & Salazar-Bravo, J. (Eds.), *Studies in Contemporary Mammalian Biology. Papers Honoring the Remarkable Career of Oliver P. Pearson, 1915-2003*. University of California Publications in Zoology, California, pp. 827–858.

Smithe, F.B. (1975) *Naturalist's color guide Parts I and II*. American Museum of Natural History, New York, Part I: 8 pp. + 18 colour swatches, Part II: xiii + 229 pp.

SPSS inc. (2004) SPSS for Windows. Release 13.0 SPSS Inc., Chicago, Illinois.

Thomas, O. (1921) Report on the mammals collected by Mr. Edmund Heller during the Peruvian expedition of 1915 under the auspices of Yale University and the National Geographic Society. *Proceedings of the United States National Museum*, 58 (2333), 217–249.
http://dx.doi.org/10.5479/si.00963801.58-2333.217

Tirira, D. (2007) *Guía de campo de los Mamíferos del Ecuador*. Ediciones Murciélago Blanco. Publicación Especial sobre los Mamíferos del Ecuador 6, Quito, 576 pp.

Voss, R.S. (1988) Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History*, 188 (2), 259–493.

Young, K.R. (1992) Biogeography of the montane forest zone of the eastern slopes of Peru. *Memorias del Museo de Historia Natural U.N.M.S.M.*, 21, 119–140.

APPENDIX 1

Specimen examined.—Voucher specimens are deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM) and the Field Museum of Natural History (FMNH).

Akodon aerosus.—(n = 57) CUSCO: La Convención: Llactahuaman (12°51'54"S, 73°30'46.8"W; MUSM 14632, 14634—36, 14639—40). Paucartambo: Carretera Paucartambo-Pillcopata, km 150 (13°13'38.3"S, 71°37'10.6"W; MUSM 8960—8997). Carretera Shintuya (13°06'02"S, 71°34'08"W; MUSM 16831, 16862, 16870, 16874, 16877, 16894, 16896, 16900, 16902). Paucartambo, km 152 (13°3'16.8"S, 71°32'46.4"W; MUSM 1732, 1741, 1743). Suecia, km 138.5 Quispicanchi: Marcapata, Hacienda Cadena (13°24'0"S, 70°43'1.2"W; MUSM 1745).

Akodon josemariarguedasi **sp. nov.**—(n = 70) HUÁNUCO: Ambo: Galloganán (10º09'32"S, 76º08'10"W; MUSM 22747—22763). Hatuncucho (10º09'16"S, 76º07'45"; MUSM 22764—22779). Ichocán (10°10'15"S, 76°07'12"W; MUSM 36747—36765). Palmapampa (09°53'12"S, 75°53'22"W; MUSM 17763, 17764, 17769, 17773, 17774, 17776—17782, 17784, 17785, 17787, 17792, 17793, 17798).

Akodon mollis.—(n = 77). HUÁNUCO: Punchao: Chinchuragra (09°27'56"S, 76°49'58"W; MUSM 22833—22870). PIURA: Huancabamba: Cerro Chinguela (05°7'36"S, 79°23'24.5"W; MUSM 23663—23681). Nueva York (04º54'26"S, 79º22'31"W; MUSM 23500—23519).

Akodon orophilus.—(n = 83). AMAZONAS: Bongará: Hierba Buena (05°47'45"S, 77° 47'17"W; MUSM 36901—36909, 36965—36969). Chachapoyas: Leymebamba (06°44'37"S, 77°47'51"W; FMNH 19725, 19727, 19729, MUSM 36983, 36984). San Antonio (06°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 (06º50'24"S, 77º29'24"W; MUSM 24387—24389). Estación biológica Laurel (06°41'24"S, 77º42'0"W; MUSM 24390—24392). Moyabamba: Puca Tambo (06º0'0"S, 77º0'0"W, FMNH 19856).

Akodon surdus.—(n = 5) CUSCO: La Convención: Huadquina (13º08'03"S, 72º36'25"W; USNM 194663, 194694). Idma (12º52'60"S, 72º49'0"W; USNM 194657). Monte Carmelo-Koshipiari (12º25'41"S, 72º02'36"W MUSM 36600). Paltaybamba (13º01'09"S,72º43'29"W; USNM 194642).

Akodon torques.—(n = 32) CUSCO: Paucartambo: Pillahuata (13°09'43"S, 71°36'10"W; MUSM 11925—27). P.V. Acjanaco (13°11'47"S, 71°37'11"W; MUSM 6695, 6708—09, 6730, 9041—9048, 9080, 9099, 9112—9114, 9135, 9158, 9163, 9167—9185, 16920, 16931).