

A new species of the Puna mouse, genus *Punomys* Osgood, 1943 (Muridae, Sigmodontinae) from the Southeastern Andes of Perú

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Abstract

The puna mouse, *Punomys* Osgood, 1943, is a poorly known and rather enigmatic taxon in regard to its phyletic relationships within the Sigmodontinae. Since the discovery of the type species *P. lemminus* Osgood, 1943, the genus was considered monotypic and known from few specimens. We describe a second species here based on collections made by CARL B. KOFORD in Puno Department, Peru, in 1951 and 1970. The discovery of this new species supports the hypothesis of a generalized biogeographical subdivision in the southern Andes along both sides of the Lake Titicaca Basin. We also summarize available data on natural history, habitat, reproduction, and systematic position.

Introduction

The puna mouse, genus *Punomys*, is a rather enigmatic Andean taxon whose phylogenetic position within the Sigmodontinae is debatable (reviewed in STEPPAN 1993). Since the description of the type species, *P. lemminus*, by Osgood (1943), the genus has been considered monotypic in the literature. We have been studying the few available specimens of this taxon in search of information regarding its remarkable morphology, phyletic relationships, and natural history. During the course of these investigations, we realized that a series of specimens from Abra Aricoma and the head of the Limbani Valley in the Cordillera Carabaya of northern Puno Department, Perú, shared constant characteristics in external and cranio-dental morphology that, although subtle, distinguish them from members of the species from the Cordillera Occidental in southwestern Perú. We believe that these differences are sufficient to identify a new taxon, and we name this new species below.

Material and methods

Nearly all available museum specimens (preserved skin with skull) of the puna mouse, *Punomys*, were examined in the course of this study. Standard cranial measurements were taken with digital calipers; external measurements were those taken by the preparator as recorded on the specimen tag. The 22 known specimens of this genus come from but seven localities; 11 specimens each of *lemminus* (four localities) and the new species described below (three localities; Fig. 1). Locality records and museum repositories are as follows (MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; MCZ, Museum of Comparative Zoology, Harvard University; AMNH, American Museum of Natural History, New York; and FMNH, Field Museum of Natural History, Chicago):

Punomys lemminus. (1) Arequipa: Huaylarco, 55 mi ENE Arequipa, 15,300 ft (N = 1, MVZ). Puno: (2) San Antonio de Esquilache, 16,000 ft (N = 1, FMNH; holotype); (3) Caccachara (about 5 mi SW crest of the western Cordillera, approximately 50 mi SW Ilave, 16,000 ft (N = 8, MCZ). (4) Tacna: 20 km NE Tarata, 14,600 ft (N = 1, MVZ).

Punomys new species. Puno: (5) Lago Aricoma, 13 mi ENE Crucero, 15,000 ft (N = 1, MVZ); (6) Abra Aricoma, 15 mi ENE Crucero, 15,500 ft (N = 1, MVZ); (7) 8 mi SSW Limbani, 15,000 ft (N = 7, MVZ; N = 2, AMNH).

Results and discussion

We consider that the specimens of *Punomys* from the vicinity of Lago Aricoma and the head of the Limbani Valley in the Cordillera Carabaya of northern Puno Department, Perú, are sufficiently distinct from the type species, *P. lemminus* Osgood, to warrant recognition as the second species of this poorly known genus. We name this new species with pleasure as:

Punomys kofordi, new species

Holotype

Adult female, Museum of Vertebrate Zoology (MVZ) 139588, from 13 mi (20.8 km) ENE Crucero, Lago Aricoma, Department of Puno, Perú, 15,000 ft (4,550 m), approximately 14°17'S, 69°47'W (Fig. 1). Collected by CARL B. KOFORD on 15 July 1970, original number 4418. The holotype is a well-made skin with skull and mandibles in excellent condition.

Paratypes

MVZ 114757 male (skin with skull), MVZ 114758 female (skin with skull), MVZ 116190 female (skin only), MVZ 116191 male (skin only), MVZ 116192 male (skin with skull), MVZ 116193 female (skin with skull), MVZ 116194 female (skin with skull), AMNH 256780 female (originally MVZ 114759; skin with skull), and AMNH 256781 male (originally MVZ 116195; skin with skull) from 8 mi (12.8 km) SSW Limbani, Department of Puno, 15,000 ft (4,550 m); and MVZ 139589 male (skin with skull) from 15 mi (24 km) ENE Crucero, Abra Aricoma, Department of Puno, 15,500 ft (4,700 m).

Distribution

Known only from the high elevations of Abra Aricoma and the adjacent Limbani Valley above 4,500 m in the Cordillera Carabaya of northern Puno Department, southern Perú (Fig. 1).

Etymology

This taxon is named in honor of the late CARL B. KOFORD, who collected the only known specimens while engaged in his studies of vicuña population biology in the upper Limbani Valley (KOFORD 1957).

Diagnosis

Large vole-like mouse with long and lax fur, dark brown above with underparts buffy-gray and not sharply contrasting with dorsal coloration. Tail short, averaging 34% of the total length; hind foot absolutely shorter than *lemminus*. Cranial conformation (Figs. 2 and 3) similar to *lemminus* but distinguished by parallel as opposed to more anteriorly convergent zygomatic arches; anterior root of zygoma squared; zygomatic plate narrow

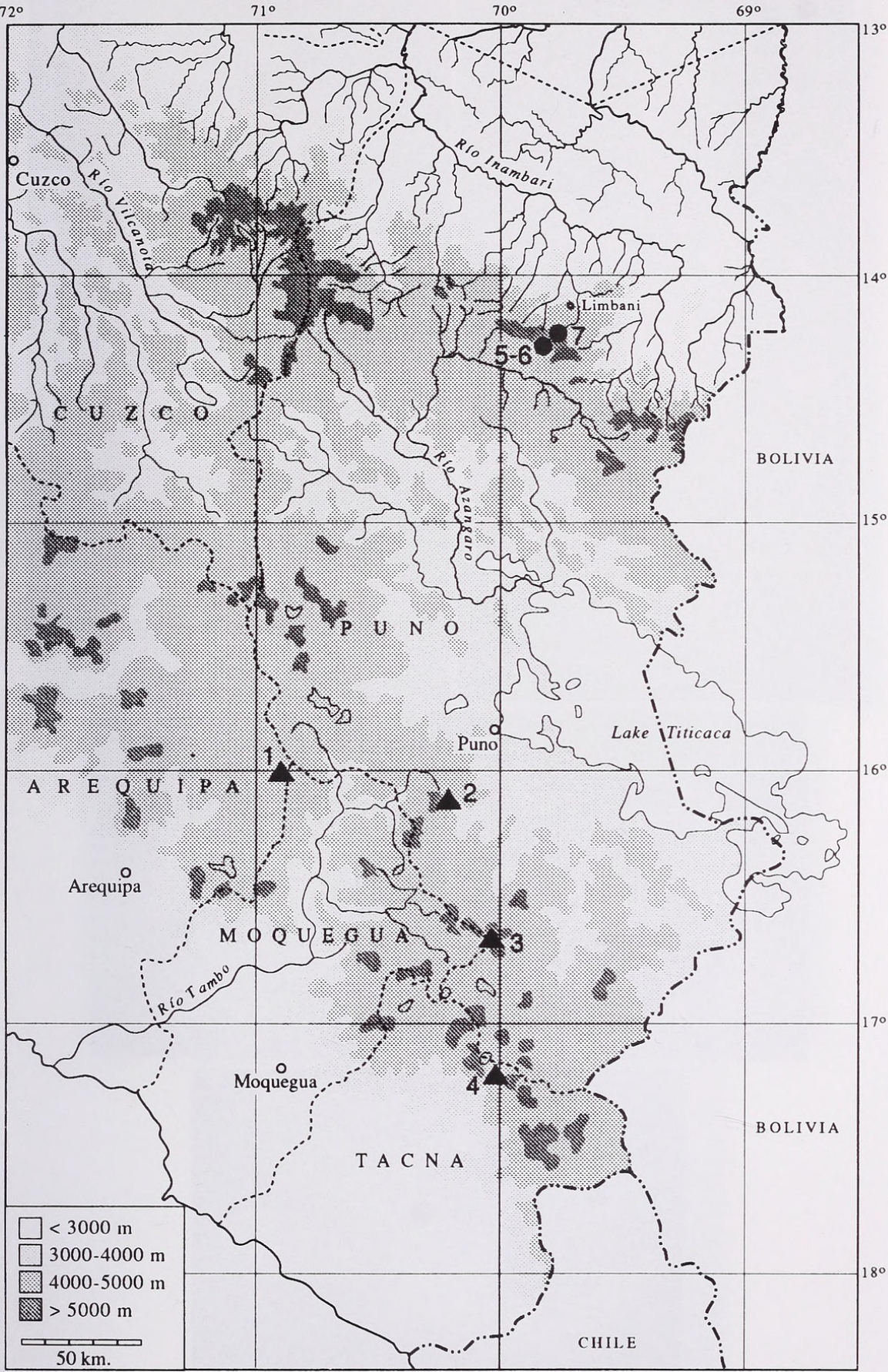


Fig. 1. Map of distribution of the puna mouse, *Punomys*, in southern Perú. Localities are numbered as in the Method and materials; localities 1–4 are of *P. lemminus*, 5–7 are of *kofordi*, new species.

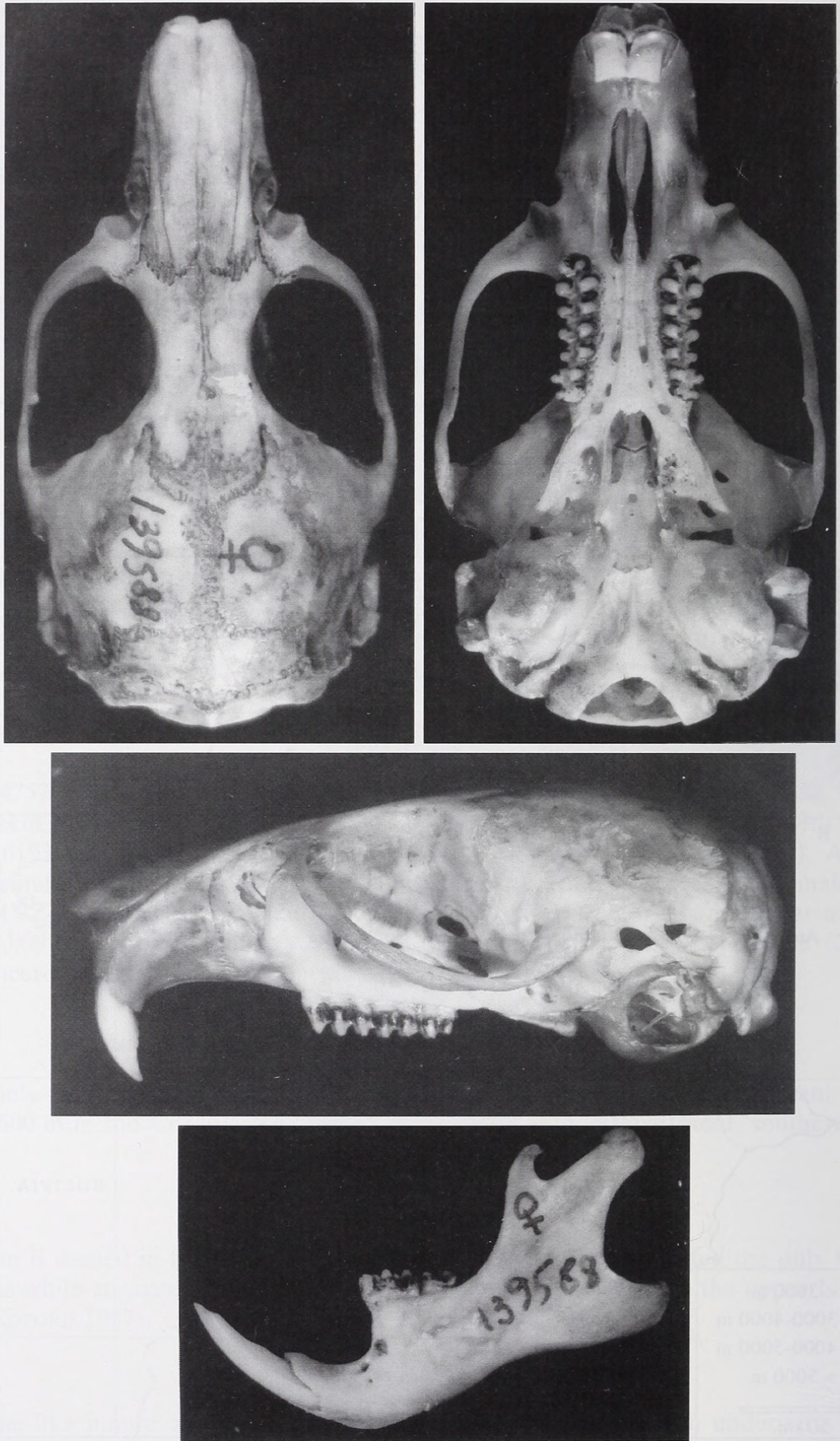


Fig. 2. Dorsal, ventral, and lateral views of the cranium of the holotype of *Punomys kofordi*, new species, MVZ 139588.

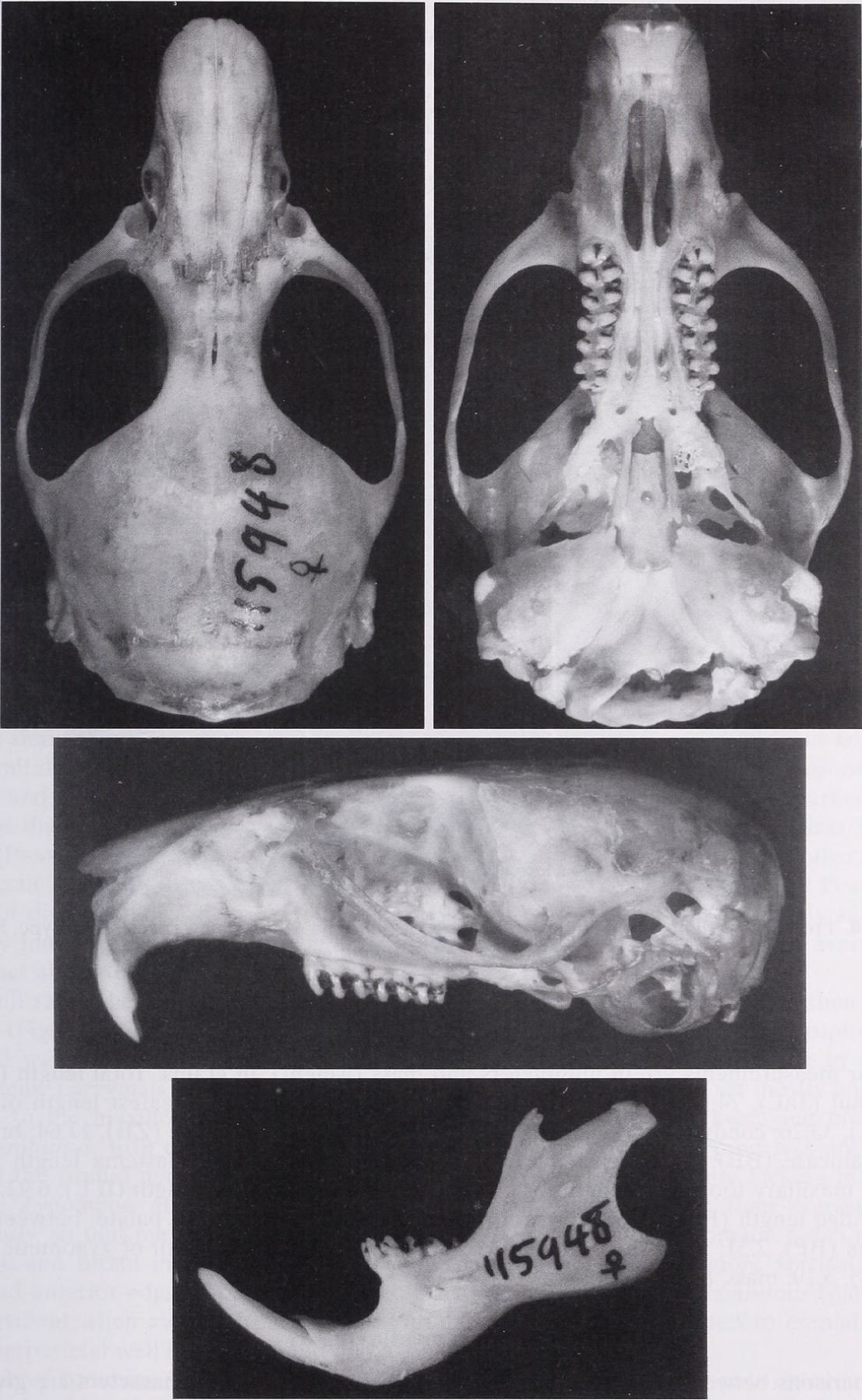


Fig. 3. Dorsal, ventral, and lateral views of the cranium of *Punomys lemminus* Osgood from 20 km NE Tarata, Tacna, 14,600 ft (MVZ 115948).

with frontal edge straight, as opposed to a broad and more posteriorly slanting edge; spine of zygomatic notch angled laterally rather than directed anteriorly, particularly in ventral view; zygomatic notch broad but shallow in comparison to *lemminus*. Nasals not abruptly expanded anteriorly, with posterior v-shaped notch. Palatal bridge short; anterior opening of alisphenoid canal small; and procingular conules of first upper molar subequal in size (Fig. 4).

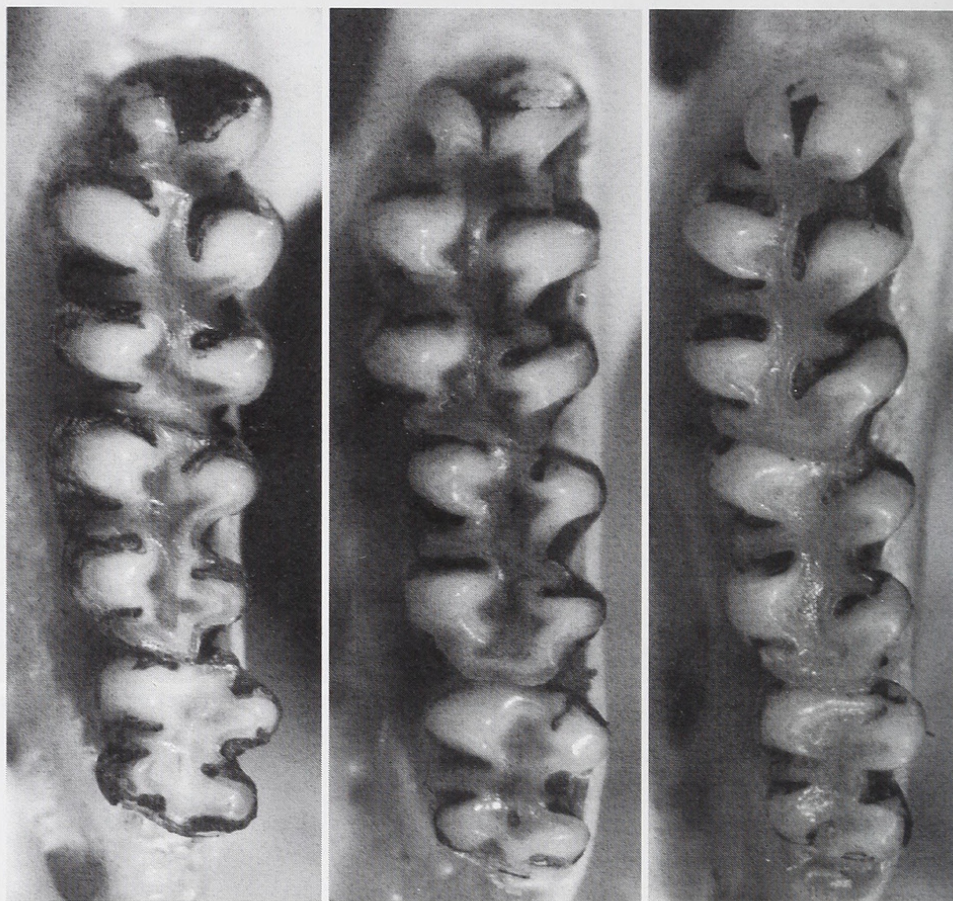


Fig. 4. From left to right, left maxillary tooth rows of *Punomys kofordi*, new species, holotype, MVZ 139588; paratype, MVZ 114758; and of *Punomys lemmius* MVZ 115948.

Measurements of the holotype

Linear measurements are in millimeters and mass (weight), in grams: Total length (ToL), 215; tail (TaL), 74; hind foot (HF), 26; ear, from notch (E), 23; greatest length of skull (GSL), 33.26; condyloincisive length (CIL), 31.50; zygomatic breadth (ZB), 17.64; breadth of braincase (BB), 14.75; least interorbital breadth (IOC), 4.44; diastema length (DL), 8.42; maxillary tooth row length (MTRL), 6.72; incisive foramen length (IFL), 6.92; palatal bridge length (PBL), 6.58; rostral breadth (RB), 7.01; breadth of palate, between first molars (BP), 2.51; breadth of first upper molar (M1B), 2.09; breadth of zygomatic plate (ZPB), 3.19; mass, 82.

Additional measurements

Comparisons between *lemmius* and *kofordi* in selected mensural characters are given in table 1. With available samples, *kofordi* averages larger in four external and craniodental dimensions (HF, IOC, IFL, and PB, all significantly so [$p < 0.05$]), *lemmius* in 13 measurements (ToL, TaL, E, GSL, CIL, ZB, BB, DL, MTRL, PBL, RB, M1B, and ZPB, five significantly so).

Table 1. Measurements of adult *Punomys lemminus* (combined from localities 1, 2, and 4) and of *P. kofordi*, new species (localities 5 through 7). Values are in millimeters and are the mean followed by the range (in parentheses). A * identifies those measurements that are significantly different ($p < 0.05$).

Measurement	<i>P. lemminus</i> (N = 3)	<i>P. kofordi</i> (N = 6)
Total length	194.7 (185–203)	203.3 (191–215)
Tail length*	53.0 (46–61)	69.2 (65–77)
Hind Foot length*	28.7 (28–29)	27.2 (26–28)
Ear height*	24.0 (23–25)	24.7 (23–27)
Greatest length of skull	33.3 (32.5–34.1)	32.9 (31.4–33.9)
Condylolincisive length	31.8 (31.0–32.2)	30.9 (28.8–31.9)
Zygomatic breadth*	18.9 (18.6–19.3)	17.6 (16.2–18.8)
Braincase breadth	15.2 (14.7–15.5)	14.7 (14.5–15.2)
Interorbital breadth*	4.2 (4.0–4.3)	4.4 (4.3–4.5)
Diastema length	8.3 (8.0–8.7)	8.0 (7.4–8.4)
Maxillary tooth row length	7.0 (6.5–7.5)	6.9 (6.7–7.2)
Incisive foramen length*	6.8 (6.7–6.9)	7.0 (6.9–7.2)
Palatal bridge length*	7.4 (6.5–8.0)	6.6 (6.4–6.8)
Rostral breadth	7.2 (7.0–7.6)	6.9 (6.4–7.3)
Palatal bridge width	2.2 (2.1–2.3)	2.3 (1.8–2.9)
First upper molar breadth	2.1 (2.0–2.2)	2.1 (2.0–2.2)
Zygomatic plate breadth*	3.6 (3.5–3.6)	3.2 (2.8–3.4)

Description and comparison

Pelage similar to *lemminus* (as described by OSGOOD 1943 and PEARSON 1951), but *kofordi* is overall darker and underparts do not contrast as in *lemminus*. Specimens of *kofordi* are grayer and darker on the back, the feet and hands are duskier above, the ears darker, the tail less distinctly bicolored, and the belly considerably darker gray with a distinct buffy wash (PEARSON 1957). The generally more dark coloration is typical of many other taxa that occur in the more humid eastern and northern Altiplano (for example, see PEARSON 1958 for discussion of *Phyllotis* and SANBORN 1947 for *Chroeomys*). Tail absolutely and relatively longer in *kofordi* than *lemminus* (34% of total length versus 27% on average); hind feet absolutely shorter (Tab. 1).

Skull rather heavy, shorter and less broad across the braincase and zygoma than *lemminus* (Figs. 2, 3; Tab. 1). Nasals long, well developed but anterior end not abruptly expanded as in *lemminus*, tapering slightly posteriorly to end as a deep notch in most specimens. Lacrymals reduced in size, but larger than in *lemminus* and set mostly antero-lateral to the maxillo-frontal suture. Interorbital region narrow, but averaging broader than *lemminus*, with edges rounded, not beaded; incipient postorbital processes are present at the frontal margin of the fronto-parietal suture in *kofordi* but are lacking in *lemminus*. Zygomatic arch rather robust, sides almost parallel rather than convergent anteriorly, so that maxillary root is more squared than *lemminus*. Zygomatic notch more shallow and broad in *kofordi*, with the spine more obvious due to more vertical, less rounded anterior edge of plate, and projecting more laterally than in *lemminus* (particularly evident when viewed from below). Parietals reduced and restricted to cranial cap, but interparietal well developed and pentagonal in shape.

Incisive foramina long and narrow, with slightly rounded posterior ends extending to the procingulum of first upper molar. Palate complex, dissected by two long and deep sulci that run divergently from incisive foramina to the postero-palatal pit region, usually deeply perforated or excavated at level of the second upper molar. Mesopterygoid fossa relatively deep, nearly extending to posterior margin of third molar in *kofordi* but not in

lemminus; wider and more parallel sided, not narrow and divergent posteriorly as in *lemminus*. Sphenopalatine vacuities moderately large. Parapterygoid plates deeper and shorter than in *lemminus*, somewhat flared and smoothly divergent at their posterior end. The posterior opening of the alisphenoid canal is larger in *lemminus* than *kofordi*. The tympanic bullae are large and inflated. Carotid circulation of Pattern 1 (following Voss 1988), with both inferior and superior branches of the stapedia and the internal carotid arteries present, as evidenced by the enlarged carotid canal and stapedia foramen and presence of a squamosal-alisphenoid groove, sphenofrontal foramen, and groove on the posterolateral margin of the parapterygoid plates (Voss 1988; CARLETON and MUSSEY 1989).

Upper incisors strong and orthodont, with nasals extending slightly in front of the level of upper incisors. Zygomatic plate narrower in *kofordi*, front edge straight to slightly slanting posteriorly rather than strongly curved posteriorly as in *lemminus*. The sphenofrontal foramen is partially coalesced with the orbital fissure and the alisphenoid strut is absent. The trough for the masticatory-buccinator nerve is more well developed in *kofordi*, and the perforation in the squamosal resulting from the squamosal-alisphenoid groove is larger. Subsquamosal fenestra fairly open; hamular process of squamosal moderately developed although usually slender with posterior end expanded and curved upward. The tegmen tympani is well developed and overlaps the squamosal. The mastoid is large; the mastoid fenestra is present but small and round in *kofordi*, larger and more irregular in shape in *lemminus*.

Molars combine coronal hypsodonty and high, sharp-angled individual cusps in the unworn dentition (Fig. 4). The molar toothrows exhibit a strong tendency to divergence posteriorly, less so in *kofordi* than in *lemminus*. The first molar appears strongly curved, with the procingulum divergent anteriorly. Anterolabial and anterolingual conules in first upper molar of more nearly equal size in *kofordi*; in *lemminus*, the anterolabial conule is more developed, so that the first upper molar is more strongly divergent. Main cusps in first molar are well developed, the lingual cusps more anteriorly placed than labial ones. Occlusal surface of molars complex due to presence of both labial and lingual styles, with the lingual styles more developed. Parastyle and mesostyle on the labial side and proto-style and enterostyle on the lingual side well developed. Posteroloph and a "lingual posterostyle" (the metaconule of OSGOOD 1943) distinct although not well developed. Anteroloph and posteroloph of second upper molar usually distinct but not well developed; enterostyle and mesostyle well developed. Third upper molar with the four main cusps still distinct; anteroloph and enterostyle present; mesostyle is minute or absent; posteroloph appears more distinct in *lemminus* than in *kofordi*. Occlusal view of the lower molars show same complexity of structure as the upper molars, with the labial styles more developed than those on the lingual side.

Habitat range

The genus *Punomys* has the highest elevational range (above 14,600 feet [4,400 m] in the Cordillera Occidental and above 15,000 ft [4,500 m] in the Cordillera Oriental) than any other species of mammal. *Punomys kofordi* is known from only three closely adjacent localities in the Cordillera Oriental north of the Lake Titicaca Basin, and *P. lemmius* has been recorded from four, widely spaced localities in the Cordillera Occidental to the southwest of this Basin (Fig. 1 and PEARSON 1951, 1957). The two general areas of distribution share a common high elevation and are apparently closely related floristically (MOLINA and LITTLE 1981), but are quite different in available moisture. A single wet season occurs sometime between October and April, and supplies an annual average precipitation above 400 mm in the Cordillera Oriental, but only between 100 to 400 mm in the Cordillera Occidental (CABRERA 1968). This difference is the basis for the recognition of the Wet Puna versus Dry Puna ecosystems, respectively, by TOSI (1960) and TROLL (1968).

PEARSON (1951, 1957) summarized the habitat range of the 11 known specimens of *P. lemminus* (including the holotype) in the Cordillera Occidental. Here, *P. lemminus* was always encountered among rocks in barren, broken areas near yareta (*Azorella compacta*) and clumps of its favorite food plants, the tola shrub *Senecio adenophylloides* and the ground rosette herb *Werneria digitata*, and not far from water. It was commonly seen during the day, "... feeding or scurrying from the shelter of one rock to another" (PEARSON 1951, p. 150). At Caccachara (a high valley about 5 miles southwest of the crest of the western Cordillera [16°41'S, 70°04'W], approximately 50 miles southwest of Ilave, Puno Department; PEARSON 1951), the eight specimens taken were collected with other typically high elevation rodents, including "*Akodon*" *andinus* (see PATTON and SMITH 1992), *Chroeomys jelskii*, *Calomys lepidus*, *Phyllotis xanthopygus* (listed as *P. darwini* by PEARSON 1951), *Auliscomys* (= *Maresomys* following BRAUN 1993) *boliviensis*, *A. sublimis*, *Chinchillula sahamae*, *Neotomys ebriosus*, *Lagidium peruanum*, and *Abrocoma cinerea*.

In the region of Abra Aricoma in the Cordillera Carabaya (of the Cordillera Oriental) in northern Puno Department, CARL KOFORD records the habitat and habits of *P. kofordi* as follows (fieldnotes in MVZ archives; see also PEARSON 1957): individuals were found in holes under mossy rocks, under rocky piles, or at the base of steep slopes and cliffs, usually close to *Senecio* bushes. Individuals were seen both during the day and at night, and several animals were observed to use a common burrow opening. Suitable microhabitats were recognized by the presence of cuttings or flowers of *Senecio* layering the floor of holes. At or near the type locality of *kofordi*, other mice collected included *Chroeomys jelskii*, *Phyllotis xanthopygus*, *Auliscomys pictus*, *Neotomys ebriosus*, and *Chinchillula sahamae*; *Lagidium peruanum* was seen but not collected. This is generally the same assemblage of species that occurs with *P. lemminus* in the Cordillera Occidental, with the exception that *Auliscomys pictus* is replaced by *A. sublimis* and that "*Akodon*" *andinus*, *Auliscomys boliviensis*, and *Calomys lepidus* were not recorded.

PEARSON (1982) distinguished a Southern Altiplano Group of rodents, restricted to the areas south of the Río Acarí in the southern Altiplano region of Peru (see Fig. 2 in PEARSON 1982, p. 282). This group is comprised of various species or subspecies of *Phyllotis*, *Auliscomys*, *Chinchillula*, *Punomys*, *Chroeomys*, *Akodon*, *Bolomys*, and *Galea*, and the area includes the northern distributional limit of tuco-tucos, *Ctenomys*. However, a previously unrecognized biogeographical subdivision of the southern Andes on both sides of the Lake Titicaca Basin is also apparent at either the species or subspecies level. In the dry, mountainous zones to the south of Lake Titicaca are *Phyllotis osilae osilae*, *Auliscomys sublimis*, *Auliscomys boliviensis*, *Punomys lemminus*, "*Akodon*" *andinus*, *Akodon berlepschii*, *Akodon boliviensis*, *Akkodon subfuscus arequipae*, *Bolomys amoenus*, *Chroeomys jelskii pulcherrimus*, and *Galea musteloides*. In contrast, the wetter puna of the Cordillera Oriental contains a rodent assemblage consisting of *Phyllotis osilae phaeus*, *Punomys kofordi*, and *Chroeomys jelskii cruceri* and *inambarii*, as well as other species with wider distributions that do not occur in the Cordillera Occidental, such as *Auliscomys pictus*, *Oxymycterus paramensis*, *Akodon puer*, *Akodon subfuscus subfuscus*, and *Oligoryzomys* sp. B (sensu CARLETON and MUSSEY 1989). The Dry Puna of the Cordillera Occidental appears to contain a larger assemblage of rodents than does the Wet Puna, but sample efforts in both areas have been rather minimal. The relative distinctness of the rodent faunas of these two regions is especially noteworthy, given the likelihood that the cordilleras on both sides of the Lake Titicaca Basin would have been capped by glacial ice repeatedly throughout most of the Pleistocene (CLAPPERTON 1983; MERCER 1984).

Reproduction

NOWAK (1991) states that *Punomys lemminus* breeds during the wet season, which is from November to April in the Altiplano of southern Perú. This is presumably based on the re-

cord of a pregnant female with two embryos taken at Caccachara, Puno, on 7 November, while three individuals taken in earlier months (September and October) contained no embryos (PEARSON 1951) and no juveniles were collected during these months. A second female specimen of *lemminus* taken by PEARSON (MVZ 115948) at 20 km NE Tarata, Tacna, on 28 January 1952, also contained two embryos. However, within the series of *kofordi* from the Cordillera Carabaya, four females taken from June to September carried embryos or were post-lactating, with a litter size ranging from 2 to 3, and juvenile specimens were also obtained. While data are sparse, it appears that the two species may breed at different times of the year, *lemminus* in the wet season, *kofordi* in the dry. Females of both species have four pair of nipples in pectoral, axillary, abdominal, and inguinal positions.

Remarks

Punomys is a poorly known and rather enigmatic taxon of incompletely understood biogeographic affinities. As currently understood, the two species now recognized come from widely separated regions in southern Perú, although potentially suitable high elevation habitat connects the Cordillera Oriental and Cordillera Occidental along the border of Puno and Cusco departments (Fig. 1). Although this area has been very poorly sampled biologically, the two species would have been geographically separated for much of the Pleistocene by the expanded glacier of the Quelccaya Ice Cap in the Cordillera Vilcanota (KESSLER 1984).

The phylogenetic relationships of the puna mouse are equally obscure. VORONTZOV (1959) placed the genus in the tribe Phyllotini, an action to which OLDS and ANDERSON (1989) and BRAUN (1993) agreed, based on morphological criteria. However, HERSHKOVITZ (1962) and REIG (1980, 1984) did not affiliate *Punomys* with the phyllotines; rather they suggested the genus be maintained as incertae sedis to emphasize its unique combination of morphological attributes. STEPPAN's (1993) cladistic analysis of 96 craniodental, skeletal, external, and soft anatomical characters supports the position of HERSHKOVITZ (1962) and REIG (1980, 1984). His analysis indicates that *Punomys* lies outside the phyllotines, near the base of the phyllotine-akodontine-scapteromyine radiation. STEPPAN (1993, p. 190) also argues that "... putative synapomorphies supporting the definition of Phyllotini are the moderate to large ears (>0.16 head and body length), the parapterygoid fossa being broader than the mesopterygoid fossa (narrower in *Punomys*), the very open sphenopalatine vacuities (partially constricted in *Punomys*) and the complete loss of a mesoloph (present in *Punomys*).". However, *Punomys* does have ears of moderate size (>0.16 head and body length), the ratio of parapterygoid fossa to mesopterygoid fossa width (sensu OLDS and ANDERSON 1989, p. 60) is greater than 1, and the sphenopalatine vacuities, while partially constricted in *lemminus*, are more open in *kofordi* (see also OLDS and ANDERSON 1989). These statements may indicate a closer relationship between *Punomys* with (or included within) the Phyllotini than previously suggested. REIG (1986) proposed that *Punomys* may represent an early descendent of a protophyllotine stock.

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Zusammenfassung

Eine neue Art der Punamaus, Gattung Punomys Osgood, 1943 (Muridae, Sigmodontinae) aus den südöstlichen Anden von Peru.

Die Punamaus, Gattung *Punomys* Osgood, 1943, ist ein wenig bekanntes und in bezug auf ihre verwandtschaftliche Stellung innerhalb der Sigmodontinae recht rätselhaftes Taxon. Seit der Entdeckung der Typusart *P. lemminus* Osgood, 1943, von der nur wenige Exemplare bekannt sind, wurde die Gattung als monotypisch angesehen. Die Autoren beschreiben hier eine zweite Art auf der Grundlage von Aufsammlungen, die CARL B. KOFORD 1951 und 1970 im Puno District in Peru gemacht hat. Die Entdeckung dieser neuen Art stützt die Hypothese einer grundsätzlichen biogeographischen Unterteilung der südlichen Anden auf beiden Seiten des Titicaca-Sees. Verfügbare Daten zu Naturgeschichte, Lebensraum, Fortpflanzung und systematischer Stellung werden mitgeteilt.

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