A NEW SPECIES OF *THOMASOMYS* (CRICETIDAE: SIGMODONTINAE) FROM CENTRAL BOLIVIA

UNA NUEVA ESPECIE DE *THOMASOMYS* (CRICETIDAE: SIGMODONTINAE) DE BOLIVIA CENTRAL

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ABSTRACT

We describe a new species of *Thomasomys* from the eastern slopes of the central Bolivian Andes. This is a medium-size long-tailed rodent phenetically similar in external and cranial features to *Thomasomys notatus*, although genetically it appears most closely related to species in the *Thomasomys oreas* complex. Phylogenetic analyses of morphological and molecular data indicate that the new species presents a unique combination of characters. The new taxon inhabits the upper montane rain forest, and appears to be arboreal; it is known only from the type locality.

Key words: Yungas, Cochabamba, upper montane rain forest, Thomasomyini

RESUMEN

El género *Thomasomys* es uno de los complejos taxonómicos más interesantes de los Bosques Andinos sudamericanos. En este trabajo y utilizando evidencia morfológica y molecular describimos una especie de la región de Corani, en el bosque yungueño Cochabambino. Esta especie se parece a *Thomasomys notatus* en la coloración de la piel y algunos rasgos del cráneo pero parece estar más emparentada filogenéticamente con las especies del complejo *Thomasomys oreas*. La especie en cuestión se conoce solamente de dos especimenes que provienen de una sola localidad (la localidad típica) y parece ser arbórea.

Palabras claves: Yungas, Cochabamba, bosque pluvial montano, Thomasomyini

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INTRODUCTION

Between 1984 and 1993 a collaborative project between the American Museum of Natural History (AMNH, New York), the Colección Boliviana de Fauna (CBF, La Paz, Bolivia), the Museum "Noel Kempff Mercado" (MNKM, Santa Cruz de la Sierra, Bolivia), and the Museum of Southwestern Biology (MSB, New Mexico) conducted surveys of mammals and their ectoparasites in Bolivia (e.g., Anderson, 1997; Gardner, 1991; Dunnum et al., 2001; Salazar-Bravo et al., 2002a, 2002b; Cook and Salazar-Bravo, 2005). One new genus (*Tapecomys*), 2 new species (*Tapecomys primus* and *Carollia manu*) and 1 subspecies (*Andalgalomys pearsoni dorbignyi*) have been fully or partially based on the material collected as part of this project (e.g., Olds et al., 1987; Anderson and Yates, 2000; Pacheco et al., 2004).

In 1993 our team surveyed mammals across the eastern slopes of the Andes in central Bolivia between the cities of Cochabamba and Santa Cruz de la Sierra. There have been many biological inventories along this road, including those of Alcide d'Orbigny who between 1830 and 1832 collected the first known mammals for the country (Hershkovitz 1987). However, due to the inhospitable terrain, few expeditions have sampled the intermediate elevations between 2000 and 3500 m. The unstable slopes along the Bosques de Yungas render trapping difficult and areas in this elevation range often are undersampled or bypassed completely. It is no surprising then that most of the new records (e.g., *Rhagomys*, Villalpando et al. *in press*) or new species (*Marmosops creightoni*, Voss et al. 2004a) of mammals for the country come from these regions. Among the 23 species of cricetid rodents we found in the 8 localities visited along this transect we trapped 3 species of *Thomasomys* occurring sympatrically at a locality ca. 60 km east of the city of Cochabamba. Two of them (*Thomasomys australis* and *Thomasomys oreas*) had been trapped elsewhere, but the third species was sufficiently different to require further comparisons. Morphological and molecular analyses showed that the third species is distinct from other known members of the genus; below we describe and name it as a new species.

MATERIALS AND METHODS

To place the new taxon in the context of the genus *Thomasomys* our approach is 2-fold; first, we use over 100 discrete morphological characters to address its phylogenetic relationships to all known taxa in *Thomasomys* and its close allies. Second, molecular data (sequences of the mtDNA cytochrome *b* gene) are used to a) test the hypothesis that *Thomasomys* is a monophyletic clade, and b) address the phylogenetic relationships of the new taxon with other species in *Thomasomys* for which homologous data exist.

Morphologic Data Analyses

Terminology of external, cranial, and dental anatomy follows Carleton and Musser (1989), Voss (1993), Steppan (1995), Musser et al. (1998), Luna and Pacheco (2002), and Pacheco (2003). Capitalized color nomenclature follows Ridgway (1912). Standard measurements, including total length (TL), tail length (LT), hind foot length (HF) and ear length (Ear), were obtained from specimen labels. Head + body length (HBL) is TL minus LT. Cranial measurements used here are defined and illustrated by Voss (2003)

and include: CIL, condylo-incisive length; LD, length of diastema; LM, occlusal length of the maxillary molar row; BM1, breadth of the first maxillary molar; LIF, length of left incisive foramen; BIF, breadth across both incisive foramina; BPB, breadth of the palatal bridge; BZP, breadth of the zygomatic plate; LIB, least interorbital breadth; ZB, zygomatic breadth; DI, depth of upper incisor; BIT, breadth across both upper incisor tips.

Phylogenetic Analyses of Discrete Morphological Characters

The 2 individuals known of the new taxon were scored for phylogenetic analysis of discrete morphological characters according to character descriptions and character-state coding in Pacheco (2003). Only 111 of his 145 characters were scored for the new taxon; the remaining 34 characters were scored as missing in the resulting data matrix because we lacked digestive and reproductive tracts, and because we could not score the lower molar row and some jaw characters. Pacheco's matrix includes 64 ingroup and 16 outgroup terminals (80 taxa total) and thus with the inclusion of the new taxon the final matrix contained 81 taxa. We restricted our analyses to the 111 characters that were available for the new taxon. This matrix was submitted to a Maximum Parsimony phylogenetic analysis in PAUP* 4.0b10 (Swofford 2002) with a heuristic search with 250 random addition replicates and TBR branch swapping. All characters were weighted equally and multistate transformations were ordered following the criteria presented by Pacheco (2003). Measures of clade support were assessed using parsimony jackknife (500 replicates, 10 random additions, 30% characters deleted per replication) and bootstrap (500 replicates, 10 random additions). Morphological synapomorphies were documented by examining PAUP* outputs and visualized using MacClade 4 (Maddison and Maddison, 2002). In the diagnosis and description of the new taxon we used only those character changes which were unambiguously optimized irrespective of the type of character transformation used.

Molecular Data Analyses

DNA was isolated with the use of DNAeasy kits (Qiagen) from either frozen or ethanol-preserved tissues. Mitochondrial cytochrome *b* gene (cyt *b*) sequences were obtained using a combination of primers and protocols slightly modified from the literature (e.g., Smith and Patton, 1999; Salazar-Bravo et al., 2001). In all cases, both heavy and light DNA strands were sequenced and compared. Alignment, visualization and translation of obtained sequences were performed with modules in Lasergene for Windows (DNASTAR, 2003).

The entire cytochrome *b* gene sequence of the 2 specimens of the new taxon were obtained and added to a database of cyt *b* sequences of species of *Thomasomys* and various outgroups. Because the cytochrome *b* gene sequences of sigmodontine taxa vary in length (Smith and Patton, 1999; D'Elia, 2003), we restricted our analyses to the first 1134 base pairs of the sequence, following the criteria presented by D'Elia et al. (2003). We attempted to obtain molecular data for all known Bolivian species of *Thomasomys*; additionally, we included as many homologous sequences as possible from Peruvian (mostly from GenBank) and Ecuadorian taxa (generated by us). Our complete matrix included 15 taxa in *Thomasomys* plus multiple representatives of various tribes and "unique lineages" in the Sigmodontinae and in essence is the same one used by D'Elia

et al. (2003), except that in our case we did not include representatives of any of the other cricetid (sensu Steppan et al. 2004) subfamilies (namely Arvicolinae, Cricetinae, Neotominae, or Tylomyinae). All analyses were rooted with homologous sequences of 4 species of *Sigmodon*.

This dataset was submitted to a phylogenetic analysis using the criteria of Maximum Parsimony in PAUP* with heuristic searches (250 random sequence additions) and TRB branch swapping. As measures of clade support we used parsimony jackknife (500 replicates, 10 random additions, 30% characters deleted per replication) and bootstrap (500 replicates, 10 random additions). Uncorrected sequence divergences among haplotypes and groups of haplotypes (i.e., average haplotype distances) were calculated with PAUP*. Sequences obtained for this work have been deposited in GenBank under Accession Nos. DQ914643 to DQ914654 .

Karyotypes

Chromosomal preparations for the 2 individuals of the new taxon were obtained following Anderson et al. (1987). Metaphase cells were photographed and scored to determine the diploid and fundamental numbers; at least 10 metaphase plates from each individual were scored to verify the chromosomal counts. Nomenclature for chromosome morphology and fundamental number (FN) follows Patton (1967).

RESULTS

Phylogenetic Analysis of Morphological Characters

With all characters weighted equally and multistate transformations ordered in 40 characters, a total of 99 equally most parsimonious trees were resolved, each 1050 steps long (CI=0.1667 and RI=0.6280). Our consensus tree (Fig. 1) agrees with Pacheco's (2003) analysis of the Andean Thomasomyines in one fundamental way: based on the phylogenetic analysis of discrete morphological characters, *Thomasomys* is polyphyletic. Our results, however, suggest several clades incongruous with Pacheco (2003). Among these: a) *Abrawayaomys ruschii* forms a sister taxa relationship with *Chilomys*, b) *Rhipidomys* does not form a monophyletic group, c) *Thomasomys notatus* is not the sister taxon to a clade formed by *Thomasomys oreas -- Thomasomys gracilis*, and d) there is at least weak evidence for a clade of Atlantic Rainforest taxa (i.e., *Juliomys*, *Wiedomys*, *Wilfredomys*, *Delomys*, and *Phaeonomys*).

Only 5 clades in the consensus tree received support values (either jackknife or bootstrap) above the cutoff level of 50%. Most of these were terminal clades that represented closely related species within a genus, for example *Rhagomys*, *Chilomys*, and *Delomys*. The only group in *Thomasomys* that received any level of support above the 50% cutoff value was the *Thomasomys oreas* complex, which included the nominal species plus 2 unnamed species (*Thomasomys* sp8 and *Thomasomys* sp9), and *T. gracilis* with a bootstrap value of 69%, but no jackknife support above 50%. The only basal node with >50% jackknife support was that defining the Atlantic Rainforest taxa as sister to the remaining ingroup taxa at 58% bootstrap support.

In the strict consensus tree, the new taxon appears in an unresolved polytomy with respect to the remaining *Thomasomys* species, as are *Thomasomys baeops*, *Thomasomys*

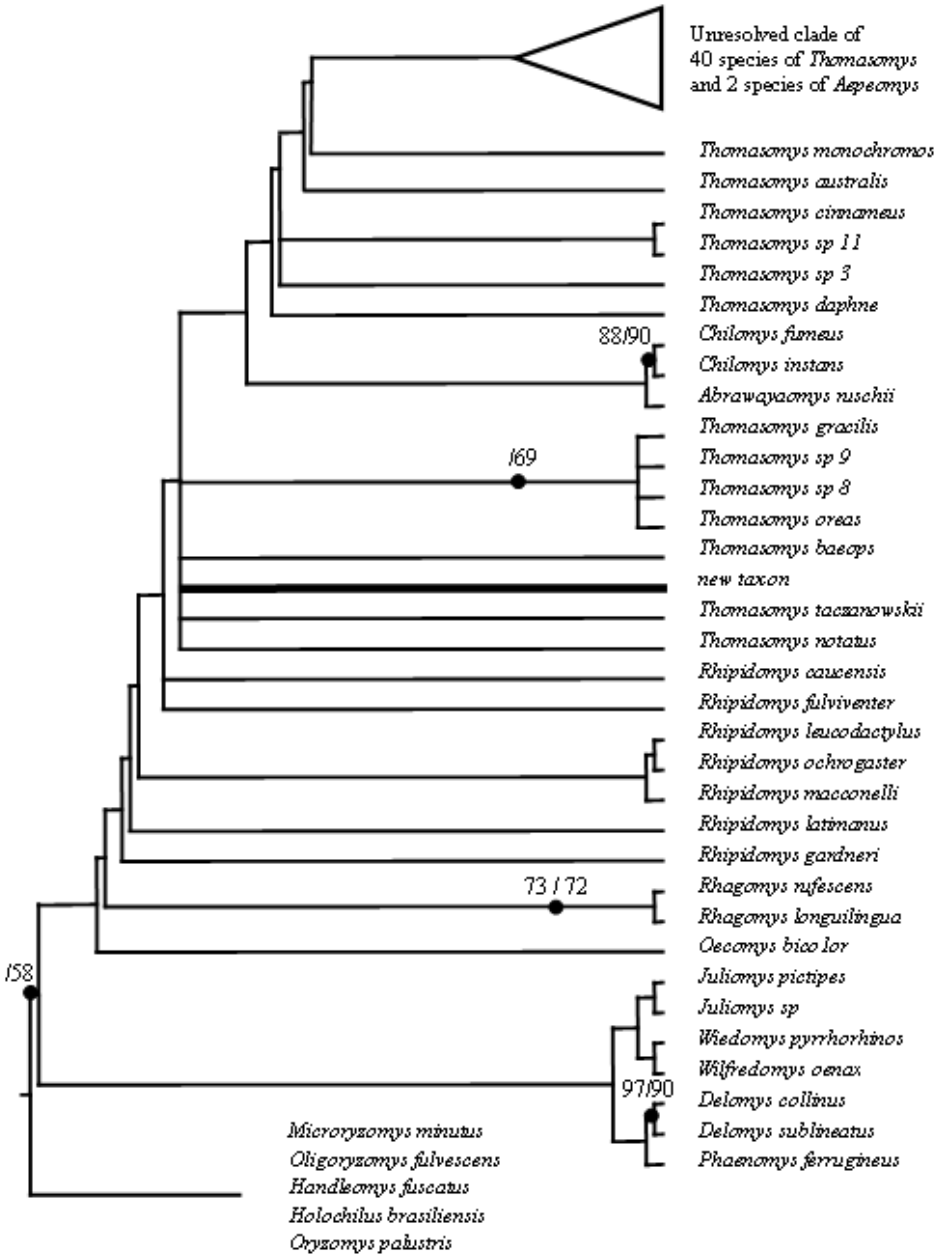

Figure 1. Strict consensus tree of the 91 shortest trees (length 1050, CI = 0.1667, RI = 0.6280) obtained on a heuristic search of phylogenetic analysis using Maximum Parsimony of 81 taxa and 111 discrete morphological characters from members of the genus *Thomasomys*, its close allies and several outgroup taxa. Numbers above branches indicate parsimony jackknife (left of the diagonal) and bootstrap (right of the diagonal) values for each basal node. Only values above 50% are reported. Notice the unresolved position of the new taxon (branch and name in bold) with respect to other species in *Thomasomys*.

notatus, and *Thomasomys taczanowski*.

Phylogenetic Analysis of Molecular Characters

We obtained from 403 to 1140 base pairs (bp) of the cytochrome *b* gene for species of *Thomasomys* sequenced for this work, including the entire sequence for both the holotype and the paratype. The dataset analyzed phylogenetically had 669 variable characters of which 553 were parsimony informative. Two shortest trees were found, each 7664 steps long. Despite the high level of homoplasy in the dataset (CI=0.1567 and RI=0.401) the strict consensus tree shows a good level of resolution with only 2 polytomies, both in groups outside *Thomasomys*. In this region of the tree the topology of the consensus tree is similar to that presented in D'Elia et al. (2003). The consensus tree (Fig. 2) shows strong jackknife support (91%) for the monophyly of this group but only moderate bootstrap support (75%). Like D'Elia et al. (2003) we found that *Chilomys* is the sister taxon to *Thomasomys*, although with low levels of support (jackknife support of 57%). In the tree, the new taxon is more closely related to species of the *Thomasomys oreas* complex with moderately high levels of support (jackknife, 90%; bootstrap, 70%). With the exception of the sister taxa relationships of the following pairs of species (*T. baeops* – *T. taczanowskii* and *T. australis* – *T. daphne*), all other phylogenetic hypothesis were only weakly supported.

Sequence Divergence

As quantified by uncorrected sequence divergence (p-distances, Table 1), the new taxon is markedly different from other species of *Thomasomys*, and is phenetically most similar to *T. oreas* (mean p-distance of 12.7%), and most dissimilar from Peruvian *T. notatus* (mean p-distance of 17%). In this arrangement of taxa, intraspecific comparisons varied from 0.1% divergence between individuals of *T. ladewi* from the same locality, to 2.9% divergence between individuals of *T. daphne* from localities separated by approximately 286 km in Bolivia and Peru. The average sequence divergence among species in *Thomasomys* is 12.9%; the lowest level was 6.4% divergence between *T. taczanowskii* and *T. baeops*.

In summary, phylogenetic analyses of morphological and molecular characters failed to provide robust hypotheses of relationships among the species of *Thomasomys* included. What is clear, however, is that both genetic distance and phylogenetic placement indicate equal uniqueness of the specimens of the new taxon in comparison to other taxa currently recognized as species, and thus we name it as follows:

Thomasomys andersoni, new species
(Figures 3-9)

Holotype. AMNH 268734, young adult female (Fig. 3), collected 30 July 1993 by Jorge Salazar–Bravo (original number JSB 659) in an elfin forest near the headquarters of the Corani hydroelectric plant (17° 12′ 43″ S, 65° 52′ 09″ W, GPS coordinates, map datum WGS 84) at 2,630 m, Department of Cochabamba, Bolivia (Fig. 4). The holotype is a standard skin with cranium (mandible missing, probably lost during cleaning of skull) and partial skeleton, in good condition; chromosome slides and cell suspensions housed at the Museum of Southwestern Biology (NK 30587); heart, liver and kidney tissue, originally preserved in liquid nitrogen, maintained at –76°C in the frozen collection of

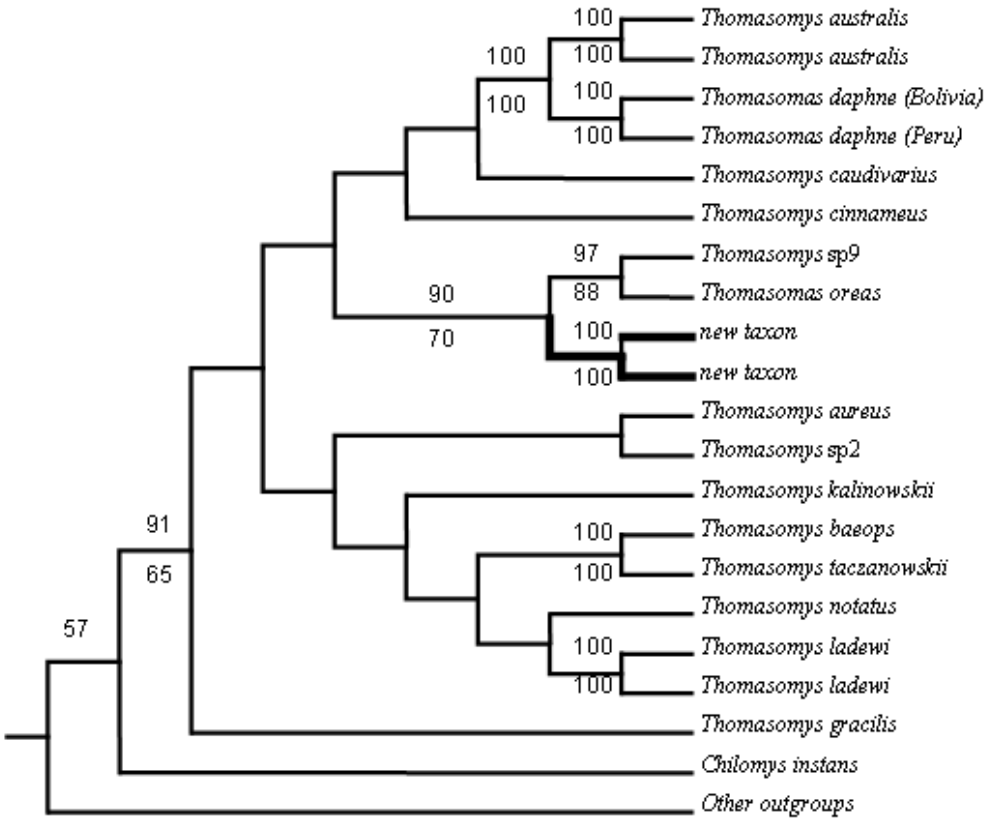

Figure 2. Strict consensus tree of the 2 shortest trees (length 7664, CI=0.1567, RI=0.401) obtained on a heuristic search (250 replicates of randomly added taxa) of phylogenetic analysis using Maximum Parsimony of variable length sequences, from 403 to 1134 base pairs, from the mitochondrial cytochrome *b* gene sequence data for 88 taxa. The tree is rooted with 1 sequence each of 4 species in the genus *Sigmodon*. Parsimony jackknife and bootstrap values are respectively indicated above or below the branches. Notice the position of the new taxon (name and branch in bold) as the sister group to a clade of species of the *Thomasomys oreas* complex.

the Division of Genomic Resources of the Museum of Southwestern Biology.

Paratype. Only 1 other specimen (standard skin with cranium, jaw and partial skeleton, plus associated frozen tissues, cell suspension, and cell spreads bearing number NK 30588) is known and is hereby designated as paratype (Fig. 5). This old adult female was trapped 30 July 1993 by Jorge Salazar-Bravo (original field number JSB 660), and is cataloged in the Museum of Southwestern Biology (MSB 146437).

Etymology. Named for Dr. Sydney Anderson, Curator Emeritus of the American Museum of Natural History and author of the first "Mammals of Bolivia" (Anderson 1997); his interest in Bolivian mammals spanned 4 decades culminating in several field trips from the mid 1980s to early 1990s; the species herein described was collected on

Table 1. Uncorrected percent sequence divergence (x100) within and among cytochrome *b* haplotypes from 15 species of *Thomasomys* and outgroups.

		new taxon	2	3	4	5	6	7	8
1.	new taxon	0.2							
2.	*T. aureus*	16.3	-						
3.	*T. australis*	14.7	12.2	0.5					
4.	*T. baeops*	15.9	11.9	10.7	-				
5.	*T. caudivarius*	15.4	14.3	12.0	13.1	-			
6.	*T. cinnameus*	14.4	13.3	12.0	11.7	10.8	-		
7.	*T. daphne*	14.0	14.9	7.9	12.4	12.5	12.6	2.9	
8.	*T. gracilis*	16.3	16.3	12.9	13.1	11.8	12.3	13.7	-
9.	*T. kalinowskii*	15.3	12.3	11.6	10.8	11.7	10.2	13.2	12.2
10.	*T. ladewi*	13.4	11.5	11.4	11.6	12.2	10.4	13.0	12.1
11.	*T. notatus*	17.0	14.1	13.9	11.9	13.6	13.3	14.7	14.1
12.	*T. oreas*	12.7	13.2	12.5	12.2	13.6	12.7	14.2	12.5
13.	*T. taczanowskii*	16.7	12.6	11.9	6.4	13.5	12.9	13.6	13.9
14.	*T.* sp2	15.2	12.3	12.3	12.5	13.0	13.0	13.5	14.4
15.	*T.* sp9	15.3	14.5	14.8	12.7	13.4	12.7	15.6	13.4
	outgroups	19.2	18.6	18.6	17.3	18.0	16.9	18.3	18.2

		9	10	11	12	13	14	15	16
1.	new taxon								
2.	*T. aureus*								
3.	*T. australis*								
4.	*T. baeops*								
5.	*T. caudivarius*								
6.	*T. cinnameus*								
7.	*T. daphne*								
8.	*T. gracilis*								
9.	*T. kalinowskii*	-							
10.	*T. ladewi*	9.9	0.1						
11.	*T. notatus*	13.2	11.3	-					
12.	*T. oreas*	12.4	10.5	12.9	-				
13.	*T. taczanowskii*	12.0	11.6	13.9	12.2	-			
14.	*T.* sp2	11.7	11.1	12.7	14.1	12.1	-		
15.	*T.* sp9	15.3	12.2	15.9	7.5	14.9	13.8	-	
	outgroups	18.0	17.7	18.7	17.8	18.3	18.1	19.2	18.8

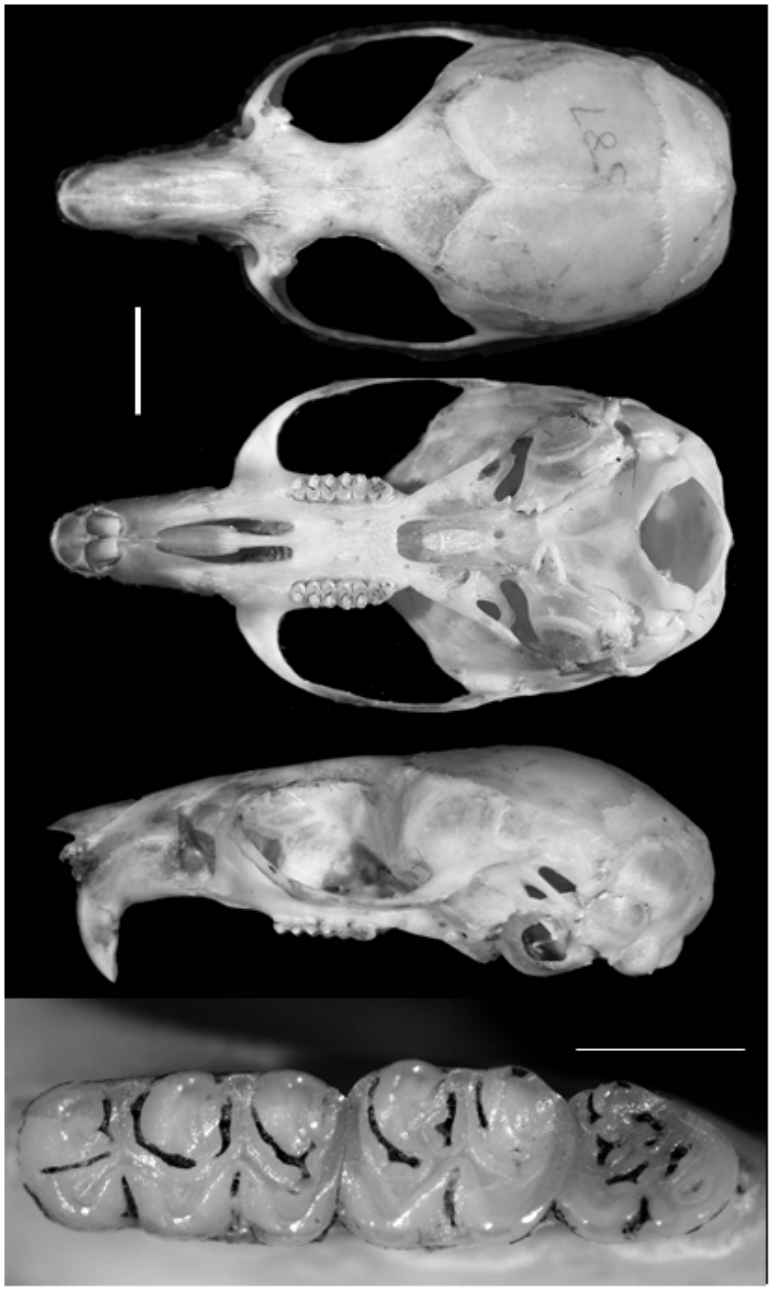

Figure 3. Cranium and occlusal view of the upper molar row of the holotype of *Thomasomys andersoni* (female, AMNH 268734). Scale bar equals 5 mm for the cranium and 1.25 mm for the molar row.

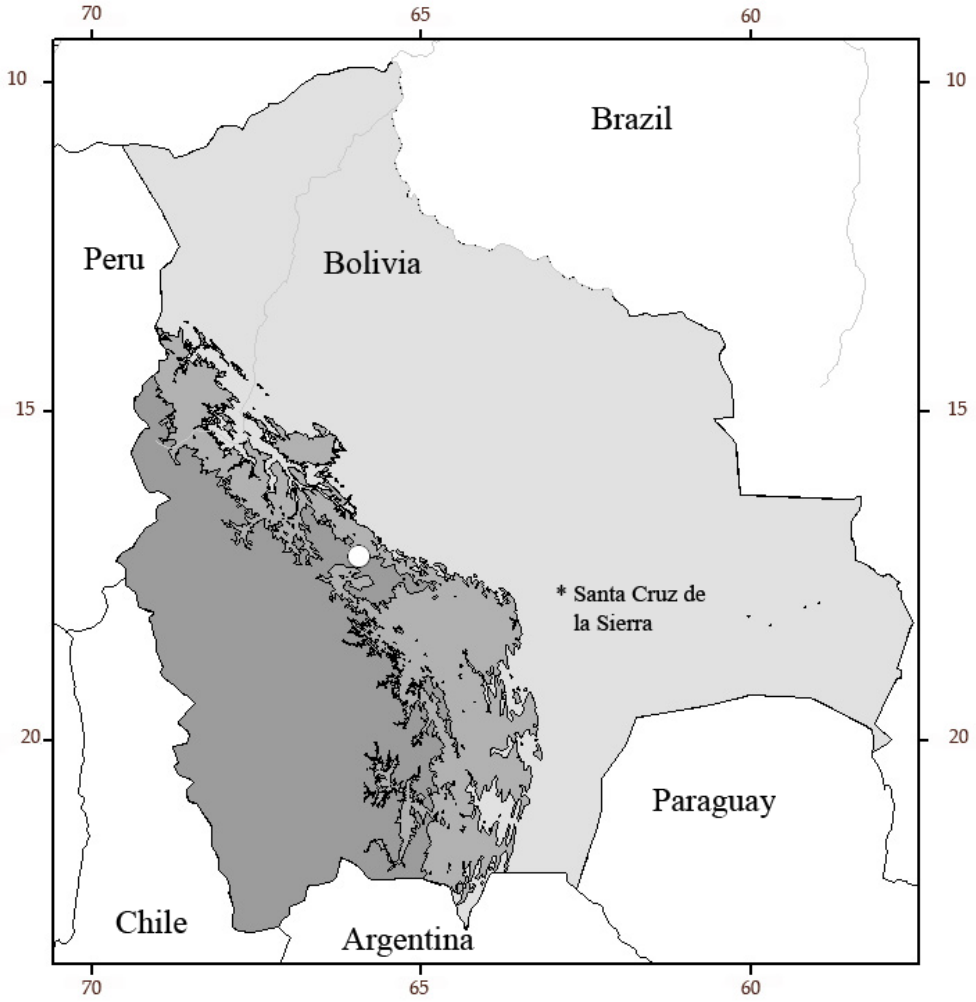

Figure 4. Map of Bolivia. Areas in light gray are above 1000 m, those in dark gray are above 3000 m. The open circle denotes the type locality (2,630 m) of *Thomasomys andersoni*, new species.

Figure 5. Cranium of the paratype of *Thomasomys andersoni* (female, MSB 146437). Scale bar equals 5 mm.

one of these trips. An undeterred champion of Bolivian collections of natural history, he has been instrumental in the academic formation of Bolivian personnel, including that of the senior author.

Diagnosis. A species of the subfamily Sigmodontinae (sensu Reig, 1980), diagnosable by the following combination of characters: medium-size (HBL=109 mm, CIL=27.21), dorsal coloration dull Brownish Olive, ventral coloration Olive Buff with a yellowish tinge and a distinct Strotian Yellow pectoral marking; moderately long mystacial vibrissae; tail slightly longer than head and body; interorbital region with rounded supraorbital margins, without ridges; straight fronto-nasal profile; broad and vertically oriented zygomatic plate; zygomatic arches convergent anteriorly; orbicular apophysis of malleus small, not basally constricted; parietal-supraoccipital suture narrow; bunodont and brachydont molars with weak labial cingula; accessory labial root of M1 present; orthodont yellowish upper incisors; short hallux (first phalange not extending beyond metatarsal of digit II) and long digit V of pes (claw of digit V extending about half the length of phalange 2 of digit IV). Analyses of the cytochrome *b* gene sequence data suggest several potential molecular synapomorphies which we do not list because molecular data are available for only a few species in *Thomasomys*.

Description

External Morphology: *Thomasomys andersoni* is a medium-sized mouse with soft, dense, and long dorsal fur (average length = 11 mm). Body pelage with a conspicuous demarcation between the dorsal and ventral pelage. Dorsal pelage dull Brownish Olive turning to Ochraceous Tawny on the sides; guard hairs uniformly dark. Ventral pelage Olive Buff, with hairs grayish at base, dull whitish mixed in with Buffy Yellow at tips; thoracic region with a distinct Strotian Yellow pectoral marking. Genal, mystacial, superciliary, and carpal vibrissae present; mystacial vibrissae long, extending posteriorly to just behind the pinnae. Pinnae proximally covered with short blackish hairs, about the same color as of the hairs covering the head. Metacarpals and digits of manus whitish; metatarsals chocolate brown, but digits of pes white; claws on manus ventrally closed at base. Digits in both manus and pes with ungual tufts of silvery hairs, more conspicuous in pes. Hind feet relatively short and broad; progression of size in digits IV, III, II, V, I, with IV, III, and II progressively smaller. Claw of digit V nearly reaching the base of claw of digit IV. Plantar pads large and fleshy; no gap between the thenar and hypothenar pads (in pes); soles of feet naked. Tail about as long as head and body (46–53% of total length), uniformly brown, without any trace of white, and covered with short thick hairs, scales large; distinctly penicillate (last 8-10 mm).

Cranium and Mandible: Rostrum of moderate proportions, not long but narrow and with shallow zygomatic notches. Interorbital region narrow (LIB ca. 28% of ZB; see Voss (2003)) with smooth sides and hourglass-shaped (not beaded, ridged or squared). Zygomatic arches convergent anteriorly and widest at the roots. Lateral view of the skull flattened from mid-frontals to tips of nasal bones; zygomatic plate broad (BZP ca. 8.2% of CIL; see Voss (2003)) with anterior margin sloping slightly backwards from base. Incisive foramina long (averaging 79% of diastema length), extending posteriorly to but not between molar alveoli, widest just behind the premaxillary/maxillary suture. Palate broad and short (as defined by Hershkovitz (1962)) and smooth, with

2 to 3 pairs of conspicuous posteropalatal foramina, but posterolateral palatal pits small, simple, and generally inconspicuous. Mesopterygoid fossa long and broadly U-shaped, with anterior margin smooth; not perforated dorsally by sphenopalatine vacuities (at least in the only 2 specimens known). Parapterygoid fossa (=lateral pterygoid plates) narrow, concave but shallow and perforated (in the older specimen) by pits between the pterygoid and sphenoid part of the plate as well as by the posterior end of the alisphenoid canal. Posterior opening of alisphenoid canal large and oval-shaped. Alisphenoid strut present; carotid circulation characterized by the presence of conspicuous sphenofrontal and stapedial foramina and squamosal-alisphenoid groove (pattern 1 of Voss (1988)). Postglenoid foramen and subsquamosal fenestra of about the same size, the latter slightly larger in the holotype, separated by a narrow hamular process (= post-tympanic hook) of the squamosal which sits on the periotic and reaches the mastoid. Tegmen tympanic overlapping the posterior suspensory process of squamosal across the middle lacerate foramen. Stapedial spine of bulla free (not appressed against bulla), ovoid in cross-section and almost reaching alisphenoid. As in other species of *Thomasomys* the carotid canal is small and bounded by the basioccipital and the ectotympanic portions of the auditory bullae. Auditory bullae uninflated and nearly flask-shaped, with bony eustachian tube differentiated from the capsular region of the bulla, extending and reaching the pterygoid lobes. Orbicular apophysis of malleus enlarged and wide at base (not constricted).

Upper incisors large, orthodont, and colored light-yellow; molar rows in parallel series composed of small, pentalophodont and brachydont teeth. As in other species of the genus, interpenetration of labial and lingual folds is only to toothrow axis with paraflexus and metaflexus bending posteriorly around the paracone and metacone, respectively. Antercone of M1 divided by an anteromedian flexus which defines subequal anterolabial and anterolingual conules. Anterolophs and mesolophs well developed in M1 and M2 fusing lingually with the mesostyle. Enterostyle present as a low stylar cusp.

In the paratype, the coronoid process is well developed and falciform, subequal in height to the mandibular condyle and defining a deep sigmoid notch. Angular notch noticeably excavated and angular process located almost even yet anterior to the condyloid process. Lower incisor capsule small relative to the size of the dentary and not projecting far upward. Lower incisors thin and with light yellow (almost white) pigmented faces.

Post-cranial Skeleton: The 2 known individuals of this species have 13 ribs, 19 thoracicolumbar vertebrae, 4 sacral vertebrae, 33 caudal vertebrae and an enlarged neural spine on their second thoracic vertebrae. The sternum of the paratype contains 5 sternebrae and a long xiphoid process (at least twice as long as sternebra I).

Karyotype: The 2 individuals of *Thomasomys andersoni* have a diploid complement of 44 all acrocentric chromosomes (2n=44, FNa=42); the X chromosomes appear to be acrocentric as well although they could not be identified unequivocally due to the lack of males in the sample.

Morphological Comparisons. Based on the phylogenetic analyses of discrete morphological characters presented in Fig. 1, we cannot unequivocally associate *Thomasomys andersoni* to any taxon currently recognized in the genus. *Thomasomys baeops* and *T. taczanowskii*

share a number of morphological and molecular synapomorphies and appear as sister taxa in the phylogenetic analysis of molecular data with high levels of support (100% jackknife and bootstrap values). These species are currently restricted to the northern Peruvian (*T. taczanowskii*) and the Ecuadorian Andes (*T. baeops*).

Two species of *Thomasomys* are sympatric with *T. andersoni* at its type locality: *T. oreas* and *T. australis*. The latter is easily distinguishable from *T. andersoni* by its smaller body size, shorter ears, longer tail, short, narrow and chisel-like upper incisors and the lack of pelage countershading. *Thomasomys andersoni* merits further comparisons with *T. oreas* and *T. notatus*, the latter an allopatric taxon, currently known only from eastern Peru; as with various other species of small mammals however, it is possible that *T. notatus* will also be found in similar environments in western Bolivia.

Thomasomys andersoni and *Thomasomys oreas* have distinct countershading in body pelage, approximate similar tail length, and dark patches on top of the hind feet which contrast with paler toes and sides. They can be distinguished from each other because the dorsal pelage in *T. andersoni* is dull olive brown as opposed to rich yellowish brown (Prout's brown) in *Thomasomys oreas*; patterns of face coloration also serve to tell these species apart: the eye ring in *Thomasomys oreas* is darker that in *Thomasomys andersoni*, while the cheeks in the former are brighter (and more like the gular area) than in the latter. The ventral pelage in *Thomasomys andersoni* has a greenish/yellowish hue which becomes a yellowish pectoral shield whereas in *Thomasomys oreas* the ventral coloration is warm pinkish buff over plumbeous black. The skull of *Thomasomys andersoni* is larger than that of *T. oreas* for animals of about the same age. The rostrum in *T. oreas* is narrow, pointed, and tapers forward (Fig. 6); by contrast, the rostrum in *T. andersoni* is comparatively wider, longer, and presents a distinct straight fronto-nasal profile (Fig. 7). The auditory bullae in *T. oreas* are large and conspicuously inflated, to the point that the Eustachian tubes are indistinct, giving the bullae a globe-like shape. By contrast, the tympanic bullae in *T. andersoni* are uninflated and flask-shaped (Fig. 8)

Thomasomys andersoni and *Thomasomys notatus* overlap in all external and craniodental measurements (with the exception of Least Interorbital Breadth, Table 2) and require more detailed comparisons. They share many qualitative traits in common: both have genal vibrissae and moderately long mystacial hairs, body pelage distinctly countershaded; pencil-tipped tails; similarly proportioned hind feet with dark metatarsal patches, broad palates; broad and vertically oriented zygomatic plates, alisphenoid strut; and complete carotid arterial circulation.

However, *Thomasomys andersoni* and *T. notatus* differ in other points of comparison in external or cranial characters. Pelage in *T. andersoni* is similar to that of *T. notatus*, but darker, more ochraceous and longer dorsally (mean = 11 vs. 6 to 7 mm in *notatus*). By contrast *T. notatus* is more grayish and has a well-defined blackish streak down the middle of the back, from withers to rump, not present in *T. andersoni*. Ventrally, the pelage in *T. andersoni* is grayish tinged with buffy tips and presents a pectoral shield, whereas the undersurface in *T. notatus* is soiled whitish and has no pectoral markings. Ears are on average longer in *T. andersoni* (mean = 20.5 mm) than in *T. notatus* (mean = 19), but may overlap in some individuals. Insofar as the sample size permits, the only discriminant morphometric variable between *T. andersoni* and *T. notatus* is that of the Least Interorbital Breadth (LIB, Table 2), in which *T. andersoni* is comparatively and absolutely larger ($\geq$ 4.44 mm), although that of *T. notatus* ranges up to 4.38 mm.

In a dorsal cranial view, *T. andersoni* is distinguishable by having a narrower, slightly longer rostrum and a broader, rounder, and smoother interorbital region

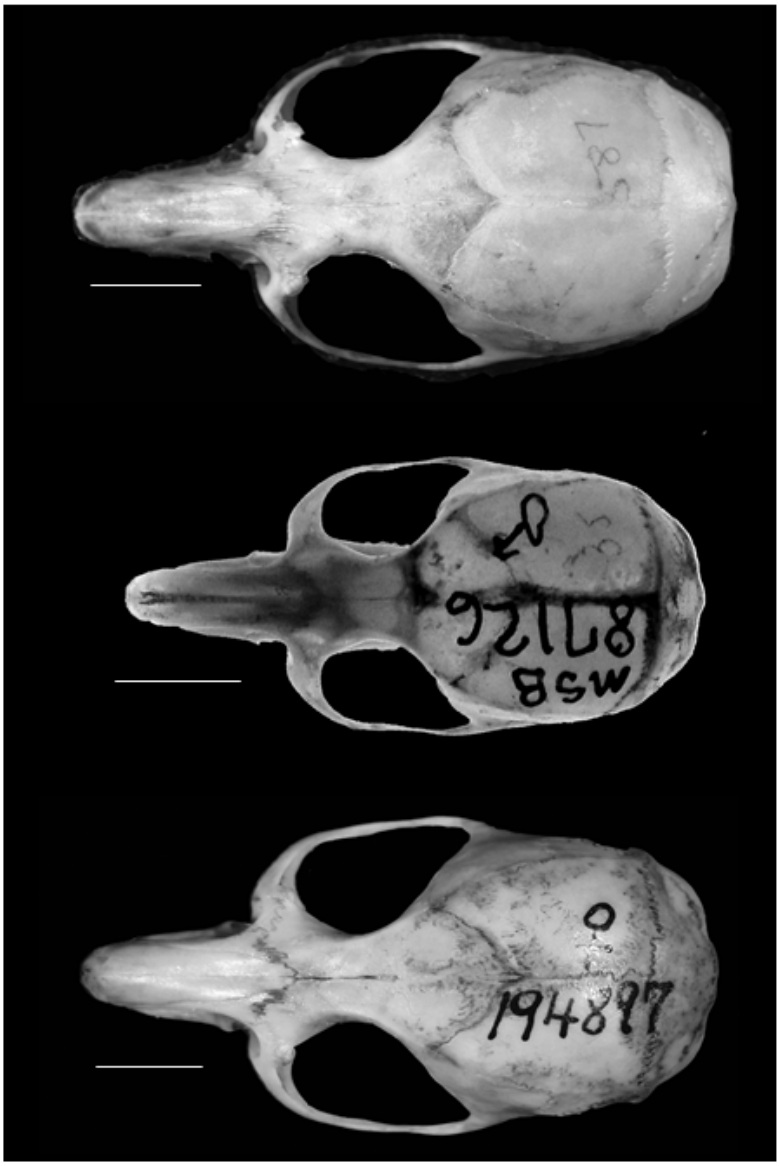

Figure 6. Dorsal view of crania of 3 species of *Thomasomys*, from top to bottom: *T. andersoni* (holotype), *T. oreas* (male, MSB 87126), and *T. notatus* (female, USNM 194897). Scale bar equals 5 mm.

Figure 7. Lateral view of crania, same specimens as in Fig. 6. Scale bar equals 5 mm.

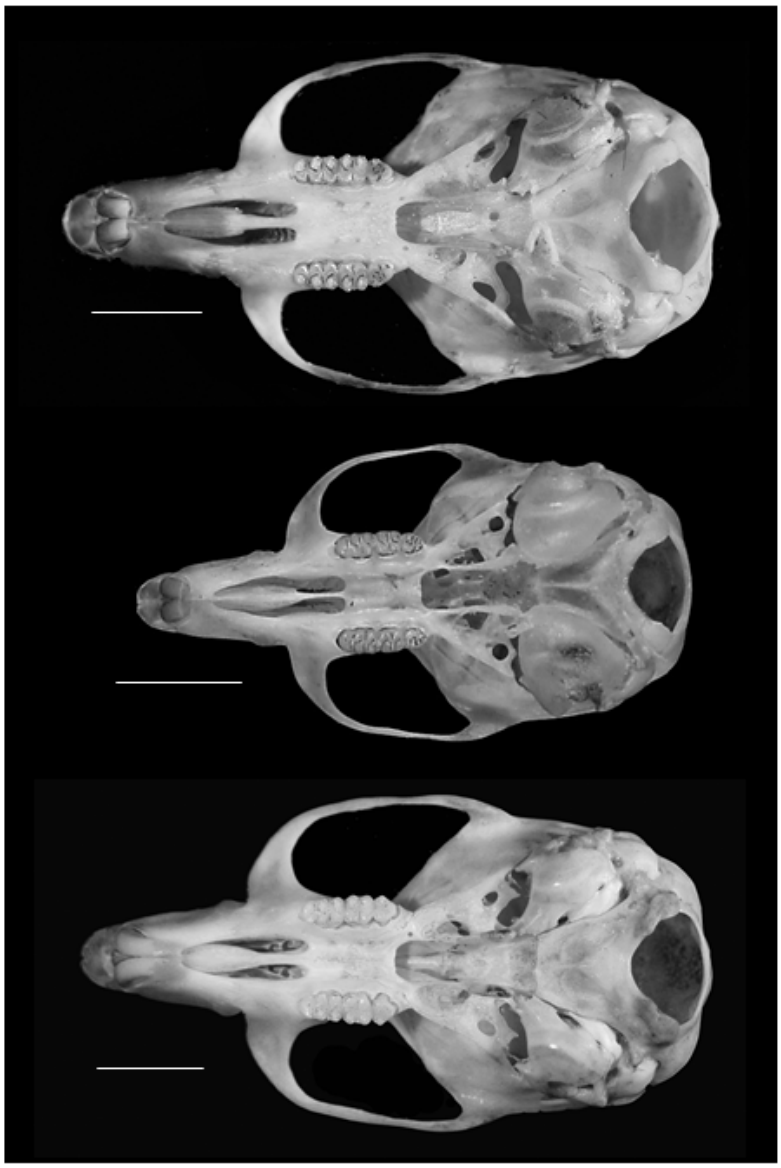

Figure 8. Ventral view of crania; same specimens as in Fig. 6. Scale bar equals 5 mm.

Table 2. Some measurements for *Thomasomys andersoni* and *Thomasomys notatus* from Perú. Measurements in mm and weight in grams. Weight in *Thomasomys notatus* is a mean of 7 individuals.

	Thomasomys andersoni		*Thomasomys notatus*		
	AMNH 268734	MSB 146437	Type (USNM 194548)	Mean (N = 9)	Range
TL	230	238	283	236.55	215-257
LT	122	128	155	126.56	100-144
HBL	108	110	128	110	92-130
HF	22	26	27	25.78	24-28
Ear	20	21	18.5	18.83	17.5-20
GLS	30.14	31.13	33	29.09	27.07-31.85
CIL	26.48	27.93	30	26.14	24.18-28.57
LD	7.53	8.17	na	7.40	6.86-8.25
LM	4.62	4.6	4.6	4.34	4.13-4.51
BM1	1.26	1.32	na	1.26	1.22-1.29
LIF	5.95	6.29	7.1	5.84	5.18-6.46
BIF	2.05	2.02	na	1.95	1.73-2.14
BPB	3.34	3.11	na	2.98	2.62-3.35
BZP	2.21	2.24	na	2.23	1.78-2.56
LIB	4.55	4.44	4.2	4.23	3.94-4.38
ZB	15.41	15.9	17.4	14.98	13.99-15.67
DI	1.53	1.47	na	1.56	1.28-1.78
BIT	1.79	1.79	na	1.68	1.28-2.82
Weight	35	38	na	36.14	23-52

(Fig. 6). By contrast, the rostrum of *T. notatus* is proportionally wider and shorter, and possesses a narrower interorbital region with slightly raised edges forming low supraorbital ridges. The upper incisors of *T. andersoni* are narrow, weakly pigmented, and orthodont, while those of *T. notatus* are comparatively wider and opisthodont (Fig. 7).

The premaxilla in *T. andersoni* is long, extending posterior to the nasals, whereas in *T. notatus* the premaxillae is only moderately long and terminates at the same level as nasals. Although difficult to quantify, the tympanic bullae in *Thomasomys andersoni* is slightly larger and less flask-shaped than that of *Thomasomys notatus*. These species also differ in the shape of the orbicular apophysis of the malleus; in *T. andersoni* this presents a bony structure with the proximal portions wider than the distal portion, whereas in *T. notatus* the body is proximally constricted rendering it bulb-shaped (Fig. 9)

Thomasomys andersoni and *T. notatus* have similar upper molars, both species

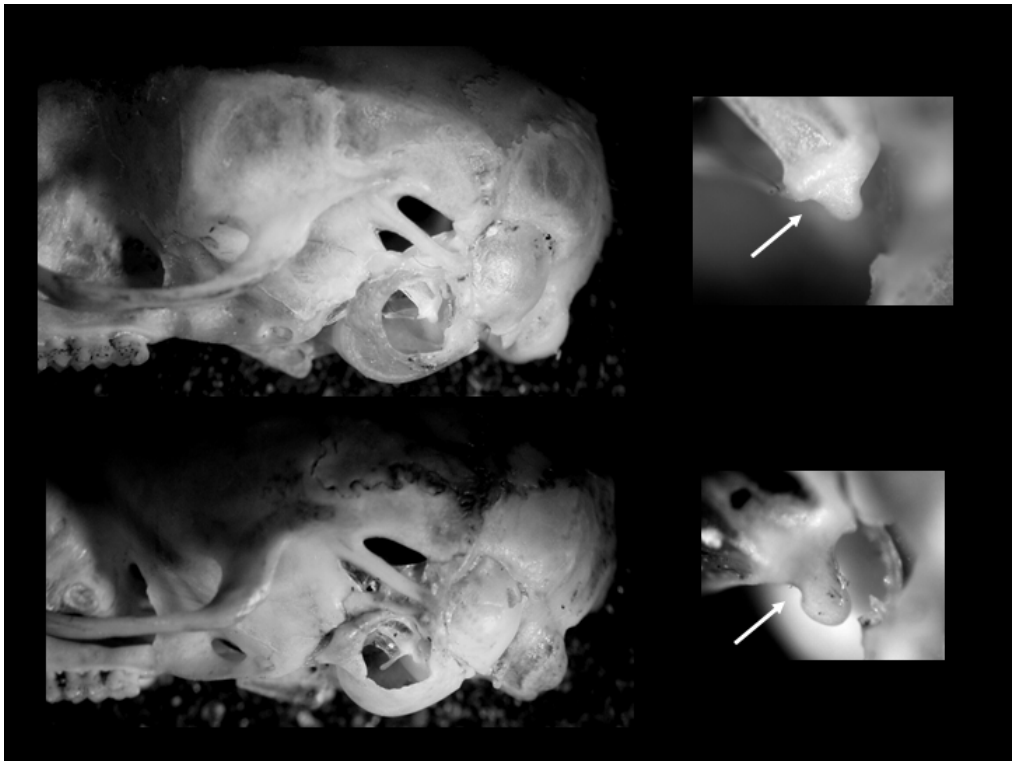

Figure 9. Crania of *Thomasomys andersoni* (holotype; above) and *Thomasomys notatus* (USNM 194547; below). Notice the ventral development of the tympanic bullae (slightly larger in *T. andersoni* than in *T. notatus*) and the structure of the orbicular apophysis of the malleus in the same 2 specimens (right panes). This structure is not basally constricted in *T. andersoni* (top right, arrow), while it is knob shaped in *T. notatus* due to a basal constriction (bottom right, arrow).

presenting distinct M1–M2 paralophules; however, the labial cingulum at the end of the anteroloph and mesoloph is more conspicuous in *Thomasomys notatus*. M2 presents a distinct protoflexus in *Thomasomys notatus* that is not present in andersoni and M3 in *Thomasomys andersoni* is somewhat larger and more rounded in general shape, whereas it is more triangular-shaped in *T. notatus*. These comparisons apply to only 1 individual *T. andersoni* (the holotype) because the paratype is so old that the occlusal surfaces are heavily worn. Moreover, these comparisons may be further enhanced when new material of the species herein described is obtained.

Natural History: The 2 specimens of *Thomasomys andersoni* were collected the same day at the type locality; attempts to secure more individuals of this species were unfruitful, although the site was populated with traps for several consecutive nights, and again 3 weeks later. The climate of the region is very humid, with daily fog and mist and low temperatures; biogeographically, the type locality is in the Province of the Bolivian-Peruvian Yungas, one of 5 in the Andean Biogeographic Region of Navarro

and Maldonado (2002). According to these authors, the type locality of *Thomasomys andersoni* has a flora dominated by the species *Ocotea jelskii* (Lauracea), and *Podocarpus oleifolius* (Podocarpaceae). Data on the structure, ecology, and floristic composition of a forest near the type locality can be found in Zarate et al. (1999).

The 2 specimens of the new species were trapped at the base of the crown (at ca. 2 m above ground) in a short tree at the bottom of a small ravine. This tree (max height <6 m) had a short trunk and a wide crown. The base of the crown was fairly wide (ca. 20 cm), and covered with litter (depth of ca. 5 cm). We also collected 7 other species of rodents at the general site, including *Thomasomys australis*, *Thomasomys oreas*, *Rhipidomys austrinus*, *Akodon fumeus*, *Akodon mimus*, *Oryzomys levipes*, and an undescribed species of *Oligoryzomys* ("spB" of the *flavescens* group of Carleton and Musser 1989); however, only the 2 known specimens of *T. andersoni* were trapped on the tree, all the other species came from traps set on the ground. Because of this, we suggest that *Thomasomys andersoni* is at least partially arboreal, a fact also supported by the structure of the hind feet, which are short and broad.

DISCUSSION

A better understanding of the genus *Thomasomys* and its phylogenetic relationships is beginning to emerge, although there is still much room for improvement. Whereas the morphological data compiled by Pacheco (2003) -- a portion of which was used herein in the context of *T. andersoni* -- indicates that *Thomasomys* may be polyphyletic, molecular data appear to contradict the validity of more than 1 genus for this assemblage of species. However, sequence data is available for only a few taxa, and thus a compelling case to support either contention cannot be made. The apparent contradiction between a well-supported hypothesis on morphological grounds and the lack of support of such hypothesis based on the analysis of gene sequences has been already reported in the literature for South American sigmodonts (e.g., Smith and Patton, 1999; D'Elia, 2003). The sister taxa relationship found between *Thomasomys* and *Chilomys* is proposed on the basis of phylogenetic analysis of mitochondrial gene sequences alone. *Chilomys* has yet to be included in any phylogenetic analysis of nuclear sequences conducted in the context of the phylogeny of the Sigmodontinae (e.g., D'Elia, 2003; Weksler, 2003) and thus, until further studies are conducted, this hypothesis cannot be tested independently.

With respect to *Thomasomys*, the tree in Fig. 2 lacks strong support for most clades based on the phylogenetic analysis of cytochrome *b* gene sequences. We suggest this is due to poor taxonomic coverage, as our analyses included only 15 species (named and unnamed) of *Thomasomys*, while Pacheco (2003) recognized over 50. A lack of support in phylogenetic analyses may be the result of long branches, themselves artifacts of extinction or sparse taxon sampling (Horovitz 1999). An elegant example of increased congruence in phylogenetic analysis by the inclusion of "missing links" is presented in Voss et al. (2004b). We predict therefore, that increased taxonomic and geographic sampling will augment resolution in the phylogenetic hypothesis of *Thomasomys*, although it is unclear whether the lack of congruence between Pacheco's (2003) morphology-based hypothesis and 1 based on molecular data will be reconciled.

Our results strongly support the sister taxa relationship between *Thomasomys baeops* and *T. taczanowskii*, based on the phylogenetic analyses of molecular characters.

To our knowledge this relationship has been reported only by Pacheco (2003), who suggested the erection of a new genus (his "New Genus B") to include these 2 species. Based on the analyses of molecular data, *T. cinnameus* from the Paramos of El Cajas National Park in Ecuador is only distantly related to *T. gracilis*, a taxon with which it was historically synonymized (see for example, Musser and Carleton, 1993). In this respect, we concur with Voss (2003) that these species (*T. cinnameus* and *T. gracilis*) are separate taxonomic entities deserving specific status.

Data compiled in Table 1 indicate that species of *Thomasomys* included in these analyses range in sequence divergence from 6.17% to 16.87%, with an average of 12.7%. As expected, the same hierarchical pattern of phenetic divergence has been found, with the same gene, for other taxa of South American sigmodonts (e.g., Smith and Patton 1993; D'Elia 2003).

The karyotype of *Thomasomys andersoni* (2n = 44, FN = 42) is similar both in number and in structure (mostly acrocentric elements) to the karyotypes of several species of *Thomasomys* from Colombia, Peru, and Ecuador (Table 3), but it is most phenetically similar to that of *Thomasomys aureus* in that both species have fully acrocentric complements. Interestingly, only 1 species of *Thomasomys* (*Th. niveipes*) differs from the generalized pattern of 2n = 40-44 which appears to be the norm for the genus; in this species the karyotype (2n=24, FN=42) is composed of mostly biarmed elements which resemble the condition in *Aepeomys lugens*. To what extent these phenetic similarities reflect evolutionary history must wait for the availability of molecular data for the latter, as cladistic analysis of morphological data were inconclusive (Fig. 1, and Pacheco, 2003).

With *Thomasomys andersoni* the number of native mammals known to occur in Bolivia is 358, suggesting a rate of increase since 1980 of about 7.4 species per year (Salazar-Bravo et al., 2003). This rate is close to the average of 8 species per year calculated for the Neotropics by Patterson (2000). Elsewhere, we predicted that new species and records for Bolivia will come from areas poorly represented in faunistic

Table 3: Known diploid (2N) and fundamental (FNa) numbers of species of *Thomasomys*.

Species name*	2N	FN	Reference
T. niveipes	24	42	Gómez-Laverde et al. 1997
T. laniger	40, 42	40	Aguilera et al. 2000, Gómez-Laverde et al. 1997
T. monochromos	42	42	Gardner and Patton 1976
T. aureus	42	42	Gardner and Patton 1976
T. sp.	44	42	Gardner and Patton 1976
T. vestitus	44	42	Aguilera et al. 2000
T. andersoni	44	42	this contribution
T. kalinowskii	44	44	Gardner and Patton 1976
T. notatus	44	44	Gardner and Patton 1976
T. taczanowskii	44	44	Gardner and Patton 1976

*Identification of species valid at the time of publication.

inventories (Salazar-Bravo et al., 2003); notably, this new species comes from a geographic area that is readily accessible along a major road, and only 60 km from a major city (Cochabamba). It does come from a vegetation belt, however, which is usually bypassed or undersampled by faunistic inventories. As mentioned, this is quite likely the result of logistics, unstable terrain, and difficult field conditions; it clearly shows how much yet remains to be learned about the mammalian diversity and endemism in the eastern slopes of the Andes of Bolivia.

ACKNOWLEDGMENTS

This contribution is respectfully presented to honor O. P. Pearson. As serendipity would have it the type locality of *Thomasomys andersoni* is within 15 miles of places that Pearson visited in 1955 (e.g., 15 mi ENE Tiraque) while working on his revision of *Phyllotis* (Pearson 1958). We thank the following curators for allowing the use of specimens in their care: B. D. Patterson (FMNH); J. L. Patton and Chris Conroy (MVZ); M. D. Carleton and H. Kafka (USNM); Joe Cook, Bill Gannon, and Cindy Ramotnik (MSB); Eric Yensen (Orma Smith Museum of Natural History); Julieta Vargas M. (CBF). Several of the specimens reported herein were collected as part of a collaborative research grant to TLY and Sydney Anderson (BSR 9015454, and BSR 89200617). Special thanks are due to Dr. Victor Pacheco, for confirming our suspicion on the specific status of the species described herein, and for revising a group who many considered too complicated to work on. Our colleagues Jon Dunnum, Marcela Gómez-Laverde, Lucia Luna, Sergio Solari, and an anonymous reviewer read earlier versions of the manuscript providing several valuable comments.

APPENDIX 1: SPECIMENS EXAMINED

Acronyms for institutions are as follows: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Museum of Vertebrate Zoology (MVZ); United States National Museum (USNM), Colección Boliviana de Fauna (CBF), Division of Genomic Resources (DGR), Museum of Southwestern Biology (MSB). All NK numbers denote specimens stored in the Division of Genomic Resources of the MSB. Asterisks (*) indicate specimens measured and Pilcrow signs (¶) denotes specimens used in molecular analyses. For samples with fewer than the 1134 bp (see material and methods section), the number of unambiguous bases scored is given in brackets. Accession numbers for sequences obtained from GenBank in brackets.

Thomasomys aureus (1). Peru: Cuzco, 72 km NE (by road) Paucartambo, km 152 (MVZ 170076¶ [U03540])

Thomasomys andersoni (2). Bolivia: Cochabamba, Corani Hydroelectrical Plant (AMNH 268734 *¶, MSB 146437*¶)

Thomasomys australis (2). Bolivia: Cochabamba, Corani Hydroelectrical Plant (MSB 70447¶ [769bp], AMNH 268736¶ [1107bp])

Thomasomys baeops (2). Ecuador: Bolivar, Rio Tatahuazo (MSB 70704¶ [772bp], MSB 70705)

Thomasomys caudivarius (2). Ecuador: Bolivar, Rio Tatahuazo, 4 km E Cruz de Lizo (MSB 70712, MSB 70714¶ [749bp])

Thomasomys cinnameus (2). Ecuador: Azuay, Cajas (NK30922, NK30932¶ [783bp])

Thomasomys daphne (2). Bolivia: La Paz, Sayani (AMNH 268737¶[771bp]); Peru: Puno, 9 km N Limbani (MVZ 171502¶ [AF108673])

Thomasomys gracilis (6). Peru: Cuzco, Machu Picchu (USNM 194798, USNM 194800, USNM 194802), Ocobamba Valley (USNM 194807, USNM 194808), 90 km SE (by road) Quillabamba (MVZ 166668 [AF108674])

Thomasomys kalinowskii (1). Peru: Junin, 16 km NNE (by rd) Palca (MVZ 172598¶ [AF108678]; this species was identified as *Thomasomys* sp. by Smith and Patton 1999, but it was re-identified as *T. kalinowskii* by V. Pacheco [pers. com, June 2003])

Thomasomys ladewi (5). Bolivia: La Paz, Rio Aceromarca (AMNH 264779, AMNH 264980, MSB 68483 ¶ [734bp], MSB 68484¶ [761bp], MSB 68485)

Thomasomys notatus (11). Peru: Cuzco, Amambaya (MVZ 173968*, MVZ173969*, MVZ 173970*, MVZ 173971*), Paucartambo (MVZ 166706*¶ [AF108676] , MVZ 171503*, FMNH 172380*, FMNH 170696*), Torontoy (USNM 194897*, USNM 194547), Machu Picchu (USNM 194898*)

Thomasomys oreas (2). Bolivia: La Paz, Pelechuco (CBF 4041*), unknown locality (CBF 4954*); Bolivia: Cochabamaba, Corani Hydroelectrical Plant (MSB 87126¶ [403bp])

Thomasomys taczanowskii (5). Peru: Cajamarca, 35 km WNW Cajamarca (MVZ 137928, MVZ 137930, MVZ 137931), Rio Zaña (MVZ 182003; MVZ 181999¶ [AF108675]; the latter was identified as *Thomasomys ischyurus* by Smith and Patton, 1999, but it was re-identified as *T. taczanowskii* by V. Pacheco T. [pers. com., June 2003])

Thomasomys sp2 (1). Bolivia: Cochabamba, 28 km by road of Comarapa (AMNH 260422¶ [771bp])

Thomasomys sp9 (1). Peru: Cuzco, 32 km N Paucartambo (MVZ 166703¶; this species was identified as *Thomasomys oreas* by Smith and Patton, 1999, but it was re-identified as *Thomasomys* sp9 by V. Pacheco T. [pers. com., June 2003])

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