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Range extension of *Thomasomys princeps* (Thomas, 1895) (Rodentia, Sigmodontinae) and first record in Venezuela

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Abstract

Thomasomys princeps (Thomas, 1895) is a large, sigmodontine rat and a member of the "*aureus*" group of the highly diverse genus *Thomasomys*. This species is only known from the Cordillera Oriental, Colombia; however, based on a recent examination of specimens of *Thomasomys* from Venezuela, I report the first record of *T. princeps* from Venezuela, in the Páramo del Tamá near the Colombian border. This record extends the distributional range of the species by 360 km northeast, representing the northernmost record of the species and of the "*aureus*" group.

Keywords

"*Thomasomys aureus* group", Colombia, Cordillera Oriental, Ecuador, Páramo del Tamá, Principal Oldfield Mouse, Táchira

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Introduction

Thomasomys Coues, 1884 is a sigmodontine rodent and a member of the tribe Thomasomyini (Pacheco et al. 2015). The genus is endemic to South America in tropical and subtropical habitats along the Andes, where it is distributed from the Cordillera Santa Marta in Colombia and northern Venezuela to central Bolivia, and where it lives from about 1200 m to above 4500 m (Pacheco 2015). Currently, 45 species are recognized in the genus (Pacheco 2015; Brito et al. 2019), and based on phylogenetic analysis of morphological characters, they are contained in seven intrageneric groups (Pacheco 2003, 2015): "*aureus*", "*baeops*", "*cinereus*", "*gracilis*", "*incanus*", "*macrotis*" , and "*notatus*". The Principal Oldfield Mouse, *Thomasomys princeps* (Thomas 1895), is a large species (total length of head and body 173–198 mm) with a long tail (113–131% of total length of head and body) and relatively long hindfeet (36–39 mm). It is a member of the "*aureus*" group, along with *Thomasomys apeco* Leo L. & Gardner, 1993, *Thomasomys auricularis* Anthony, 1923, *Thomasomys pyrrhonotus* Thomas, 1886, *Thomasomys praetor* (Thomas, 1900), *Thomasomys nicefori* Thomas, 1921, *Thomasomys aureus* (Tomes, 1860), *Thomasomys popayanus* J. A. Allen, 1912, and *Thomasomys rosalinda* Thomas & St. Leger, 1926 (sensu Pacheco 2015). *Thomasomys princeps* was described based on a specimen collected from the Bogotá Region, Cundinamarca Department, Colombia, and it is currently known from a few localities along the Cordillera Oriental of Colombia, from 2650 to 3182 m in montane forests (Pacheco 2015; Calderón-Capote et al. 2016). Outside Colombia, *T.*

princeps has been reported from Sangay National Park in Morona Santiago Province, Ecuador (Lee et al. 2015); however, an adequate description of external characteristics and morphological details of the skull and teeth were not provided.

Following the description of *T. princeps* by Thomas (1895), Thomas (1900) and Ellerman (1941) recognized it as a valid species, but Cabrera (1961) relegated it to a subspecies of *T. aureus* without justification, an opinion that was followed by Musser and Carleton (2005) and Voss (2003). More recently, Pacheco (2003, 2015) differentiated *T. princeps* from *T. aureus* and other congeneric species using a unique combination of external and craniodental attributes. Calderón-Capote et al. (2016) found that *T. princeps* exhibited a distinct bacular morphology and also supported its status as a valid species.

Pacheco (2015) reported that four species of *Thomasomys*, *T. aureus* (Tomes, 1860), *T. emeritus* Thomas, 1916, *T. hylophilus* Osgood, 1912, and *T. vestitus* (Thomas, 1898) occur in Venezuela. While Pacheco's (2015) study indicated that the Venezuelan specimen of *T. aureus* from the Táchira Andes could be distinguished in external and cranial characteristics from other populations of *T. aureus*, this specimen was not compared to *T. princeps*. Here, based on a direct examination of the specimen of *T. aureus* from Táchira, and side-by-side comparisons with topotypes of *T. princeps*, I have re-identified the specimen and present the first record of *T. princeps* for Venezuela, which extends the known distribution of this species northeast of Colombia.

Methods

As part of a revision of the genus *Thomasomys*, I visited the mammal collections of the American Museum of Natural History, New York (AMNH); the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); the Field Museum of Natural History, Chicago (FMNH); the Natural History Museum (NHM), London (formerly the British Museum of Natural History, London; BMNH); and the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN). I took external measurements and weight from specimen tags. The head and body length (HBL) was estimated by subtracting the tail length (TL) from the total length. External measurements are reported to the nearest millimeter (mm), and weights to the nearest gram (g). Cranial and mandibular variables were measured to the nearest 0.1 mm using dial calipers mainly following Luna and Pacheco (2002): greatest length of skull (GSL), condyloincisive length (CIL), condylomolar length (CML), length of orbital fossa (LOF), length of nasals (LN), diastema length (LD), length of incisive foramina (LIF), length of maxillary toothrow (LM), breadth of incisive foramina (BIF), breadth of rostrum (BR), breadth of palatal bridge (BPB), breadth of first upper molar (BM1), breadth of nasals (BN), least interorbital breadth (LIB), zygomatic breadth (ZB), braincase breadth (BB), breadth of zygomatic plate (BZP), depth of incisor (DI), and height of braincase (HBC). A total of 15 specimens of *T. princeps* were identified and measured. Age classification followed Carleton and Musser (1989) who presented four age classes: juvenile, young adult, adult, and old adult. Taxonomic identification followed Pacheco (2015).

Results

After a taxonomic revision of *Thomasomys* specimens from the northern Andes, I found one record of *T. princeps* for Venezuela which was previously identified as *T. aureus* (Pacheco 2015). This record constitutes the first of this species from Venezuela (Fig. 1).

New record. VENEZUELA • Department of Táchira, Buena Vista, 41 km SW San Cristobal, near Páramo del Tamá; 07°30′N, 072°24′W; 2400 m a.s.l.; 8 March 1968; SVP leg. 21873; 1 juvenile ♀, USNM 442321.

The vegetation type at the site where the Táchira specimen was collected corresponds to Bosques Ombrófilos montanos siempreverdes, bosques nublados andinos of the Subregión D2 (Cordillera de los Andes), Región D (Montañas) (sensu Huber and Alarcón 1988) or bosques andinos (sensu Huber and Oliveira-Miranda 2010).

Other material examined. COLOMBIA • Cundinamarca, Choachí; 04°31′52″N, 073°55′33″W; USNM 251958 • Cundinamarca, Bogotá region; BM 95.8.1.37-holotype, USNM 251957 • Cundinamarca, Laguna Vergon; 04°32′N, 074°04′W; USNM 251976 • Cundinamarca, Bogotá, Páramo del Verjon; 04°34′N, 074°05′W; AMNH 62769–62770 • Cundinamarca, Bogotá, San Cristobal; 04°34′N, 074°05′W; FMNH 71306–71307 • Cundinamarca, Bogotá, San Francisco; 04°43′44″N, 073° 50′36″W; FMNH 71305 • Cundinamarca, Guasca, Río Balcones; 04°40′N, 073°33′W; FMNH 71300–71304 • Cundinamarca, Municipio Junín, Reserva Biológica Carpanta; 04°34′N, 073°41′W; ICN 11075.

Identification. *Thomasomys princeps* is a large species (HBL 173–198 mm) with a long tail (113–131% of HBL) and relatively long hindfeet (36–39 mm), characterized by a unique combination of external and craniodental characters: dorsal pelage long, thick, and not very fluffy, rich orange-rufous, with a faint, dark band along the midline, richer along the sides; ventral pelage clear orange-buff, not counter-shaded; hairs long, about 15 mm in length, mystacial vibrissae long, extending posteriorly to pinnae when bent; genal 1 vibrissae present. The hindfeet are moderately broad with a dark-brown patch on the metatarsals, silvery whitish on the sides and digits. The tail is long, monocolored, dark brown, covered with short hairs (13 rings per cm), and without a terminal pencil. The hallux is long, extending to the interphalangeal joint of digit II; digit V of pes is very long, claw extending to the base of the claw of digit IV; thenar and hypothenar swollen and overlap; digits whitish and ungual tufts long and silvery; protuberance anus is prominent. The skull is large

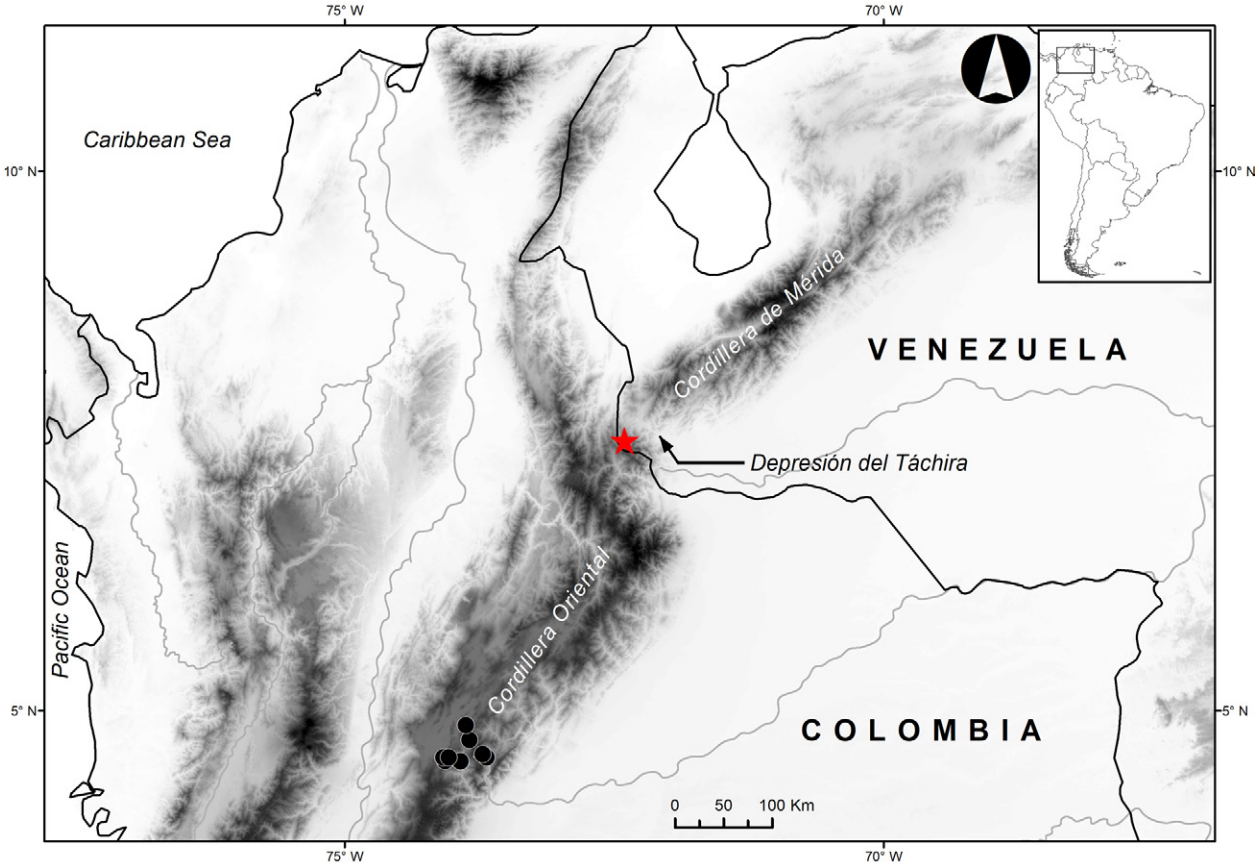

Figure 1. Distribution range of *Thomasomys princeps* following Pacheco (2015). Previous records of *T. princeps* from the Bogotá region are represented by black circles and the new record (USNM 442321) from Venezuela, Páramo de Tamá, by a red star.

Figure 2. Dorsal and ventral views of the skin of the specimen *Thomasomys princeps* (USNM 442321) from Venezuela. Scale bar = 50 mm.

and robust (CIL 36.7–39.4 mm) and rostrum relatively short and broad; braincase oblong, moderately broad, and not inflated; zygomatic plate is broad and vertical; the anterior border of the premaxillae do not project much beyond the upper incisors; premaxillomaxillary-frontal intersection anterior to zygomatic notches; nasals long with a narrow posterior tip that extends beyond premaxillae and usually beyond the lacrimals; incisive foramina large and broad penetrating slightly between M1 anterocones; maxillary septum approaching half the length of incisive foramen; interorbital region narrow and slightly convergent anteriorly, with square margins (not beaded); postorbital ridge distinct; anterior margin of M1 placed anterior to the posterior border of the zygomatic plate; M1 anteromedian flexus shallow, anteroflexus indistinct; the mesopterygoid fossa is broad and

somewhat parallel-sided, without distinct process; posterior opening of the alisphenoid canal large. Capsular process not developed but strongly swollen producing a distinct shelf. Protoflexus M2 indistinct; and ectolophid m1 present (see Pacheco 2015: 672–673 for a detailed description).

The specimen (USNM 442321) agrees with the description of *T. princeps* and has the main diagnostic characteristics of the species (Figs. 2, 3), including the dorsal and ventral pelage coloration, dark metatarsals, the long posterior extension of the nasal, the premaxillo-maxillary-frontal intersection anterior to zygomatic notches; the broad and large incisive foramina that extend between M1s, the anterior position of M1 in relation to the posterior margin of the zygomatic plate, the mesopterygoid fossa broad without distinct process; the short anterior margin of the premaxillae, the capsular process swollen, and the ectolophid on m1 present. This juvenile specimen has measurements that fall within the known range of variation of other examined specimens of *T. princeps* of similar age (Table 1). Compared to *T. aureus*, *T. princeps* has a larger HBL, smaller ratio HFL/HBL, longer nasals, and broader zygomatic plates (Table 1).

Although *T. princeps* is similar to *T. aureus* s.s. (Ecua-

Table 1. External and skull measurements (in mm) of *Thomasomys princeps* (USNM 442321, juvenile) from Venezuela compared to Colombian specimens of *T. princeps* (juvenile) and Ecuadorian specimens of *T. aureus* (juvenile). Adult specimens of *T. princeps* from Colombia and *T. aureus* from Ecuador are also included for comparisons. Information regarding the vouchers is in the Appendix.

	T. princeps **Venezuela**	***T. princeps*** **Colombia**	***T. aureus*** **Ecuador**	***T. aureus*** **Ecuador**	***T. princeps*** **Colombia**
Age class	Juvenile	Juvenile	Juvenile	Adult	Adult
TotalL	382	374.5 ± 14.8 (2) 364–385	344.5 ± 7.8 (2) 339–350	391.5 ± 22 (4) 360–408	412.3 ± 23.3 (6) 369–433
TailL	220	206.5 ± 0.7 (2) 206–207	204 ± 12.7 (2) 195–213	220 ± 14.1 (4) 200–233	227.7 ± 16.4 (6) 196–242
HBL	162	168 ± 14.1 (2) 158–178	140.5 ± 4.9 (2) 137–144	171.5 ± 8.5 (4) 160–180	184.7 ± 8.4 (6) 173–198
TailL/HBL	1.4	1.25 (2) 1.2–1.3	1.5 (2) 1.4–1.6	1.3 (4) 1.3–1.3	1.2 (6) 1.1–1.3
HFL	38	38 ± 1.4 (2) 37–39	37.9 ± 1.3 (7) 35.5–40	37.9 ± 1.8 (15) 35–41	37.8 ± 1.1 (6) 36.2–39
HFL/HBL	23.5	22.7 (2) 21.9–23.4	27.4 (2) 25.7–29.2	21.9 (4) 20–25	20.5 (6) 18.9–22
EAR	25	24	23.5 ± 0.7 (2) 23–24	—	24.2 ± 1.1 (5) 23–26
GSL	38.7	—	37.3 ± 0.6 (2) 36.9–37.7	40.1 ± 1 (11) 38.1–41.7	41.4 ± 0.8 (5) 40.6–42.5
CIL	35.1	33.7	33.8 ± 0.9 (2) 33.1–34.4	36.9 ± 1.1 (12) 35.4–39.5	38.1 ± 0.9 (6) 36.7–39.4
CML	22.7	22.7 ± 0.3 (2) 22.5–22.8	22.6 ± 0.3 (2) 22.4–22.7	24.1 ± 0.8 (13) 22.6–25.9	24.7 ± 0.8 (6) 23.5–25.7
LOF	12.3	12.6 ± 0.2 (3) 12.3–12.8	12.1 ± 0.3 (3) 11.7–12.3	13.0 ± 0.5 (18) 12.3–14.1	13.9 ± 0.2 (7) 13.6–14.3
LN	15	14.7	14.4 ± 0.4 (3) 14.1–14.8	14.9 ± 0.6 (14) 13.9–15.9	16.1 ± 0.8 (7) 15.5–17.7
LD	10.2	9.9 ± 0.6 (2) 9.4–10.3	9.6 ± 0.7 (3) 8.9–10.2	10.7 ± 0.4 (15) 10.2–11.4	11.1 ± 0.4 (8) 10.7–12
LIF	8	7.7 ± 0.6 (3) 7.1–8.2	7.8 ± 0.3 (3) 7.6–8.2	8.6 ± 0.3 (15) 8–9.1	8.6 ± 0.2 (8) 8.5–9.1
LM	6.9	7.2 ± 0.2 (3) 7–7.4	7.2 ± 0.3 (7) 6.8–7.6	7.3 ± 0.2 (18) 6.8–7.8	7.4 ± 0.2 (8) 7.2–7.7
BIF	3	2.7 ± 0.2 (3) 2.5–2.9	3 ± 0.2 (3) 2.8–3.3	3.1 ± 0.2 (16) 2.9–3.5	3.0 ± 0.3 (8) 2.6–3.4
BR	6.3	6 ± 0.3 (3) 5.7–6.2	5.9 ± 0.4 (3) 5.6–6.4	6.6 ± 0.2 (17) 6–7	6.6 ± 0.3 (8) 6.2–7
BPB	3.1	3.1 ± 0.3 (3) 2.7–3.4	2.9 ± 0.1 (3) 2.8–3	3.5 ± 0.2 (18) 3.2–3.9	3.6 ± 0.4 (8) 3.1–4.4
BM1	1.9	2.1 ± 0 (3) 2.1–2.1	2.1 ± 0.1 (6) 2–2.2	2.2 ± 0.1 (18) 2.1–2.3	2.2 ± 0.1 (8) 2.1–2.4
BN	3.7	4.3	3.9 ± 0.3 (3) 3.6–4.2	4.4 ± 0.2 (14) 4–4.7	4.5 ± 0.3 (8) 3.9–4.9
LIB	5.2	5.3 ± 0.1 (3) 5.2–5.4	5 ± 0.1 (3) 5–5.1	5.2 ± 0.2 (17) 4.9–5.6	5.3 ± 0.2 (8) 5–5.6
ZB	19	19.2 ± 0.3 (2) 19–19.4	19 ± 0.5 (3) 18.4–19.3	20.7 ± 0.4 (13) 20–21.2	21.1 ± 0.3 (7) 20.7–21.5
BB	16.3	16.7 ± 0.6 (2) 16.3–17.1	16 ± 0.7 (3) 15.3–16.7	16.6 ± 0.6 (14) 15.9–17.8	17.4 ± 0.9 (8) 16.2–18.8
BZP	3.7	3.6 ± 0.1 (3) 3.5–3.6	3.2 ± 0.2 (7) 3–3.5	3.3 ± 0.1 (18) 3.2–3.6	3.7 ± 0.3 (8) 3.4–4.4
DI	1.9	1.9 ± 0.2 (2) 1.7–2	1.7 ± 0.2 (7) 1.6–2	2.1 ± 0.1 (15) 1.9–2.2	2.2 ± 0.1 (8) 2.1–2.3
HBC	11.4	11.5 ± 0 (2) 11.5–11.5	10.8 ± 0.2 (3) 10.6–11.1	11.2 ± 0.4 (10) 10.7–11.9	12 ± 0.6 (6) 11.1–12.6

Figure 3. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of *Thomasomys princeps* (USNM 442321, juvenile) from Venezuela. Scale bar = 10 mm.

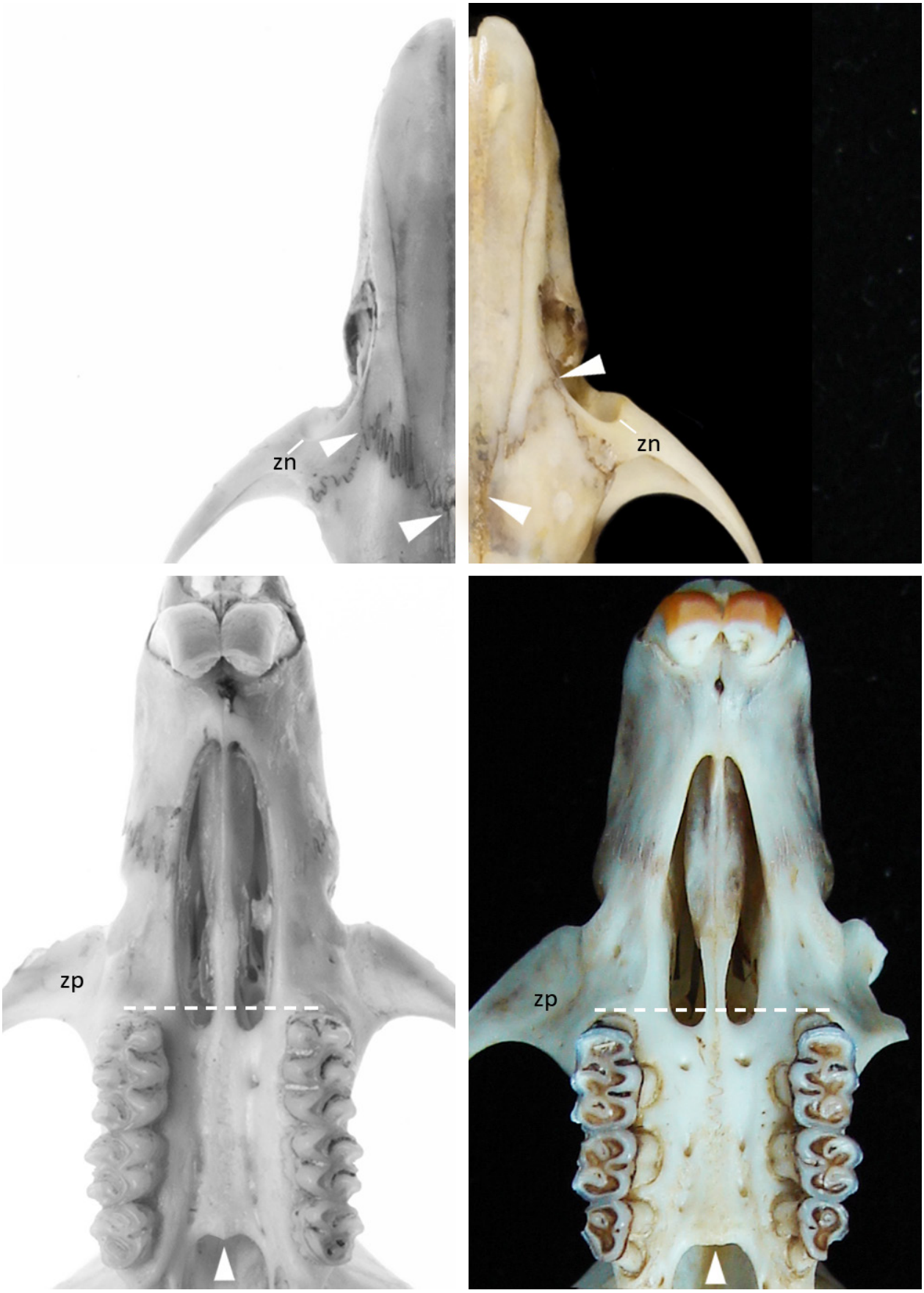

Figure 4. Comparative views of selected characteristics of *Thomasomys princeps* on the right side (USNM 251957, up; ICN 11075, below) and *T. aureus* on the left side (AMNH 46590). Abbreviations: **zn** = zygomatic notch, **zp** = zygomatic plate.

dorean populations), it can be differentiated by the following characters (Fig. 4): the short anterior border of the premaxillae of *T. princeps* does not project much beyond upper incisors; the premaxillary-maxillary-frontal intersection lies distinctly anterior of the zygomatic notch rather than level to it; nasals are longer and usually extend posteriorly beyond the lacrimals; the incisive foramina are broad and oval-shaped rather than narrow, the posterior opening of the alisphenoid canal is comparatively larger; M1 is placed anterior to the posterior border of zygomatic plate rather than level or posterior to them; palatal bone without a posterior process; capsular process are strongly swollen producing a distinct shelf versus absent; M1 anteromedian flexus is shallow and anteroflexus is indistinct versus distinct; protoflexus of M2 is indistinct; and an ectolophid on m1 is present versus absent (see Voss 2003 and Pacheco 2015 for the description of *T. aureus*). In the Cordillera Oriental of Colombia and nearby Venezuela, there are no other species of the "*aureus*" group that could be confused with *T. princeps*.

Discussion

This study represents the first report of *Thomasomys princeps* in Venezuela and extends the current distribution range of the species about 360 km to the northeast from Guasca, Río Balcones (Cundinamarca, Colombia). This specimen was previously misidentified as *T. aureus* because of the scarce material for comparisons (Pacheco 2015); therefore, the northernmost range for *T. aureus* is now restricted to Colombian specimens, near to Risaralda and Caldas (Pacheco 2015; Calderón-Capote et al. 2016). Nonetheless, a full revision of *T. aureus* including representatives of the type locality, presumably Pallatanga in Ecuador (Pacheco 2015), is needed to test if Colombian and Ecuadorian specimens of *T. aureus* are conspecific.

The Táchira specimen was collected at 2400 m, 267 m lower than previously known for *T. princeps*, and near Páramo del Tamá in montane forests. Regarding the Páramo del Tamá, Woodman (2002) commented that Osgood (1912) had already noted that the term "páramo" was used to designate the entire highland area (rather than the open, high-elevation vegetational formation with which it is more currently associated). López-Arévalo et al. (1993) reported this species, based on a specimen misidentified as *T. aureus*, from Biological Reserve Carpanta, Municipio Junín, Cundinamarca, Colombia, and provide a detailed characterization of climate and habitat. Their sampling area was between 3000 and 3100 m and contained montane forests (42%), páramo and an ecotone (58%); however, they did not specify in which habitat *T. princeps* was collected. Calderón-Capote et al. (2016) analyzed the bacular morphology of two specimens of *T. princeps* captured in Encenillo forests, Parque Nacional Natural Chingaza. Mountain forests of "Encenillo" are dominated by *Weinmannia* sp. (Mendoza-C 2007).

The Táchira specimen also confirms *T. princeps* is restricted to the Cordillera Oriental, in a distribution pattern similar to that of *T. laniger* (Thomas, 1895), *T. hylophilus* Osgood, 1912, and *T. niveipes* (Thomas, 1896), as described by Pacheco (2015). Therefore, it is likely the northern range of *T. princeps* is limited by the Táchira depression, a potential biogeographic barrier (e.g., Vuilleumier and Ewert 1978; Cracraft 1985; Quiroga-Carmona and Molinari 2012); but additional sampling in the Cordillera de Mérida is needed to test this hypothesis. Likewise, *T. vestitus* (Thomas, 1898), *T. emeritus* Thomas, 1916, and the thomasomyine *Aepeomys* Thomas, 1898 are restricted to the Cordillera de Mérida (Pacheco 2015) and are currently unknown in the Cordillera Oriental. More recently, Gutiérrez et al. (2015) challenged the role of the Táchira depression as a dispersal barrier for Little Red Brocket, *Mazama rufina*, suggesting that gene flow between populations of *M. rufina* in the Cordillera Oriental and Cordillera de Mérida may have occurred until at least the beginning of the current interglacial period and may continue today. The data available for *T. princeps* and other thomasomyines suggest that the biogeographic pattern is different for these rodents, likely due to their small size and limited mobility, and that the Táchira Depression appears to play a significant role in the distribution of these mountain rodents.

Thomasomys princeps was reported in Ecuador, from Morona Santiago, Sangay National Park (Lee et al. 2015). Recently, Brito et al. (2019) found that the sequence of one of those specimens (QCAZ 11939; KR818905.1 in GeneBank) identified as *T. princeps* formed a strong clade with other sequences of *T. aureus* (MECN 5662, 5666) from Chimborazo, Chambo, Parque Nacional Sangay, Atillo. Brito et al. (2019)'s clade of *aureus-princeps* could indeed represent *T. aureus* s.s., *T. princeps*, or a new taxon, but they made no taxonomic comment. Pending a thorough revision, these specimens (and sequences) from Ecuador are tentatively not recognized here as *princeps* because the identification was not properly sustained by comparisons with the holotype of *T. princeps* or topotypes from Cundinamarca.

The Principal Oldfield Mouse is still a poorly known rodent, currently classified as Data Deficient by the IUCN (Pacheco and Barriga 2019). Sequence data, karyotype, and many morphological attributes (e.g., skeleton, internal organs) are not yet available, limiting the understanding of its phylogenetic position. This contribution considerably extends the northern range of the species and highlights the need to test its presence in the range between Bogotá region and the Colombian border with Venezuela.

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Appendix

Table A1. List of specimens of *Thomasomys aureus* measured for comparisons with *T. princeps* in Table 1. Age classes follow Carleton and Musser (1989).

Catalog no.	Locality	Age class
AMNH 46653	Ecuador: Pichincha, Mt. Mojanda (south) San Jose	Adult
AMNH 64698	Ecuador: Pichincha, Mt. Pichincha, San Ignacio	Adult
AMNH 36280	Ecuador: Pichincha, Pichincha	Adult
AMNH 46577	Ecuador: Pichincha, Guapulo	Adult
AMNH 46583	Ecuador: Pichincha, Pichincha, above Quito	Adult
AMNH 46585	Ecuador: Pichincha, Mt. Mojanda (south slope), Peruchu	Adult
AMNH 46590	Ecuador: Pichincha, outside Quito, La Carolina	Adult
AMNH 46595	Ecuador: Pichincha, outside Quito	Adult
AMNH 46596	Ecuador: Pichincha, outside Quito, La Carolina	Adult
AMNH 46602	Ecuador: Pichincha, Guapulo	Adult
AMNH 46603	Ecuador: Pichincha, Zambiza, NE Quito	Adult
AMNH 46608	Ecuador: Pichincha, Machangara River	Adult
AMNH 46654	Ecuador: Pichincha, Mt. Mojanda (south slope)	Adult
AMNH 46657	Ecuador: Pichincha, Mt. Mojanda (south slope), Piganta	Adult
AMNH 46660	Ecuador: Pichincha, outside Quito, Charipuraz	Adult
AMNH 46665	Ecuador: Pichincha, Machangara River	Adult
AMNH 64701	Ecuador: Pichincha, Guapulo	Adult
MSB 70707	Ecuador: Bolivar, Rio Tatahuazo	Adult
AMNH 46592	Ecuador: Pichincha, Quito, Chaupicruz	Juvenile
AMNH 46593	Ecuador: Pichincha, outside Quito	Juvenile
AMNH 46594	Ecuador: Pichincha, Quito, Chaupicruz	Juvenile
AMNH 46598	Ecuador: Pichincha, outside Quito	Juvenile
AMNH 46601	Ecuador: Pichincha, Machangara River	Juvenile
UMMZ 127115	Ecuador: Pichincha, Mt. Pichincha	Juvenile
USNM 513588	Ecuador: Pichincha, Rio Condor Huachana, 3.45 km NE Lloa	Juvenile