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Description of a new species of arboreal rat of the *Rhipidomys fulviventer* group, from Venezuela (Rodentia: Cricetidae)

Descripción de una nueva especie de rata arborícola del grupo *Rhipidomys fulviventer*, de Venezuela (Rodentia: Cricetidae)

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ABSTRACT

Arboreal rats of the genus *Rhipidomys*, belong to a taxonomic group of Neotropical distribution, included in the tribe Thomasomyini. In Venezuela, the *Rhipidomys fulviventer* group contains four taxa (*R. fulviventer*, *R. tenuicauda*, *R. venustus*, and *R. wetzeli*), only found in high elevation cloud forests and lowland rainforests. Because collections to date do not represent a thorough sampling of their geographic range, taxonomic arrangement of some taxa (*e. g.*, *Rhipidomys venustus*), has been controversial. However, new specimens collected in recent years provide novel insights into the biogeographic variation of the genus *Rhipidomys*. In this article, we evaluate the taxonomy and geographic distribution of *R. venustus* based on a morphometric and morphological review that included integument, skull, teeth and post-cranial skeleton. Specimens examined cover the entire geographic range of this species. The results showed significant differences between populations, and supports the recognition of a new species inhabiting cloud forests in the Cordillera de la Costa Central and the Sistemas de colinas Lara-Falcón, Venezuela. The new species is larger than any of its congeners in the *R. fulviventer* group in this country. It shows dorsal and ventral coloration differences and unique qualitative characters associated with integument, skull and post-cranial skeleton. The geographic distribution of *R. venustus* is updated, and restricted to the Cordillera de Mérida. Remarks on the ecology and conservation status of the new taxon are also presented.

Key words: Andes, climbing rats, *Rhipidomys venustus*, Serranía del Litoral, Sierra de Aroa, Venezuela.

RESUMEN

Las ratas arborícolas del género *Rhipidomys*, pertenecen a un grupo taxonómico de distribución Neotropical, incluidas en la Tribu Thomasomyini. En Venezuela, el grupo *Rhipidomys fulviventer* está conformado por cuatro especies (*R. fulviventer, R. tenuicauda*, *R. venustus* y *R. wetzeli*), las cuales se encuentran en áreas boscosas, tanto en selvas nubladas de altura como en bosques lluviosos de tierras bajas. Debido a que hasta la fecha las colecciones de estos roedores no representan la totalidad de sus distribuciones geográficas, la ubicación taxonómica de algunas especies (*e. g.*, *Rhipidomys venustus*), ha sido

controversial. Sin embargo, muestras biológicas obtenidas en años recientes ofrecen una nueva percepción de la variación biogeográfica del género *Rhipidomys*. En este trabajo evaluamos la taxonomía y la distribución geográfica de *R. venustus* basados en una revisión morfométrica y morfológica que incluye integumento, cráneo, dientes y esqueleto post-craneal. Los ejemplares examinados cubren la totalidad de la distribución geográfica de esta especie. Los resultados mostraron diferencias significativas entre las distintas poblaciones y apoyan el reconocimiento de una nueva especie que habita los bosques nublados de la Cordillera de la Costa Central y del Sistema de colinas Lara-Falcón, en Venezuela. Esta nueva especie es la de mayor talla dentro de las otras que conforman el grupo *Rhipidomys fulviventer* en este país. Posee diferencias de coloración dorsal y ventral y caracteres cualitativos únicos asociados con el integumento, el cráneo y el esqueleto post-craneal. Finalmente, actualizamos la distribución geográfica de *R. venustus*, la cual se restringe a la Cordillera de Mérida. Se enfatiza además sobre la ecología y el estado de conservación del nuevo taxón.

Palabras clave: Andes, ratas arborícolas, *Rhipidomys venustus*, Serranía del Litoral, Sierra de Aroa, Venezuela.

INTRODUCTION

Arboreal rats of the genus *Rhipidomys* Tschudi, 1895, belong to a taxonomic group of Neotropical distribution, included in the tribe Thomasomyini Steadman & Ray, 1982 (Musser & Carleton 2005). Their geographic distribution extends from Panama to Southeastern Brazil and Northern Argentina, with records from some islands in the Caribbean Sea: Bonaire (Netherlands Antilles), Margarita (Venezuela) and Trinidad and Tobago (Tribe 2015).

The genus contains 23 species in South America, of which nine are reported for Venezuela (Tribe 2015). Of all the species occurring in the country, only two are endemic: *R. tenuicauda* (J. A. Allen, 1899) and *R. venustus* Thomas, 1900 (Tribe 2015). *Rhipidomys tenuicauda* was described from "Los Palmales" in the Macizo de Turimiquire, Sucre State, and it was considered as a subspecies of *R. fulviventer* Tate, 1939 (Tribe 1996). *Rhipidomys venustus* was described from "Las Vegas del Chama", in the Cordillera de Mérida, and its geographic distribution was restricted to that area, however, it has since been found in cloud forests of the Cordillera de la Costa Central and in the Sistemas de colinas Lara-Falcón (Handley 1976, Linares 1998, Rivas & Salcedo 2006, Anderson *et al*. 2012, García *et al*. 2013).

Because specimens of *R. venustus* are very scarce throughout its distributional range and there is no molecular evidence to support any phylogenetic arrangement of this species within the genus *Rhipidomys* (Costa *et al*. 2011, de la Sancha *et al*. 2011, Tribe 2015), it has been considered as a synonym of *R. latimanus* Tomes, 1860, or as a subspecies of that taxon (*R. l. venezuelae* Thomas 1900), and also of *R. fulviventer* (*R. f. venustus*) (Eisenberg 1989, Tribe 1996).

Recently, using geometric morphometrics on skulls of Venezuelan specimens assigned to the *Rhipidomys fulviventer* group, García & Sánchez-González (2013), suggested a more detailed taxonomic study in populations of *R. venustus* from the Sierra de Aroa, since they could represent a different species from its Andean counterpart.

Based on an expanded analysis that included integument, skull, post-cranial skeleton and morphometry on a greater number of specimens collected in recent years by different researchers in the Sierra de Aroa (Cordillera de la Costa Central, Venezuela), together with new records from the Cordillera de Mérida (Andes), Serranía del Litoral (Cordillera de la Costa Central) and Sierra de San Luis (Sistemas de colinas Lara-Falcón), housed in Venezuelan museums, we did a more exhaustively review of the taxonomic and geographic status of *R. venustus*, which resulted in the recognition of a new species inhabiting cloud forests from the Cordillera de la Costa Central and the Sistemas de colinas Lara-Falcón.

MATERIALS AND METHODS

Our description and comparisons between the new species and specimens from others species used in this work came from biological material stored in Venezuelan museums, generated as a result of several authors and laboratory projects (*e.g*. Handley 1976). Therefore, we declare that there was not manipulation of live animals in any of the different stages of the work.

We examine 84 specimens considered adults (age classes 2-4; Appendix), following the criteria of Tribe (1996) and Costa *et al*. (2011). Specimens cover the geographic range of four species with three subspecies of the *Rhipidomys fulviventer* group reported for Venezuela (Fig. 1): *R. fulviventer elatturus* Osgood, 1914 (n=7), *R. f. javiersanchezi* García *et al*., 2015 (n=6), *R. f. bisbali* García *et al*., 2015 (n=2), *R. tenuicauda* (n=13), *R. venustus* (n=43) and *R. wetzeli* Gardner, 1989 (n=13). Additionally, we reviewed morphological descriptions available in the literature (Tribe 1996, 2015, Pacheco & Peralta 2011) for four species of the *R. fulviventer* group not present in Venezuela: *R. f. fulviventer*, *R. ochrogaster* J. A. Allen, 1901, *R. similis* J. A. Allen, 1912, and *R. caucensis* J. A. Allen, 1913.

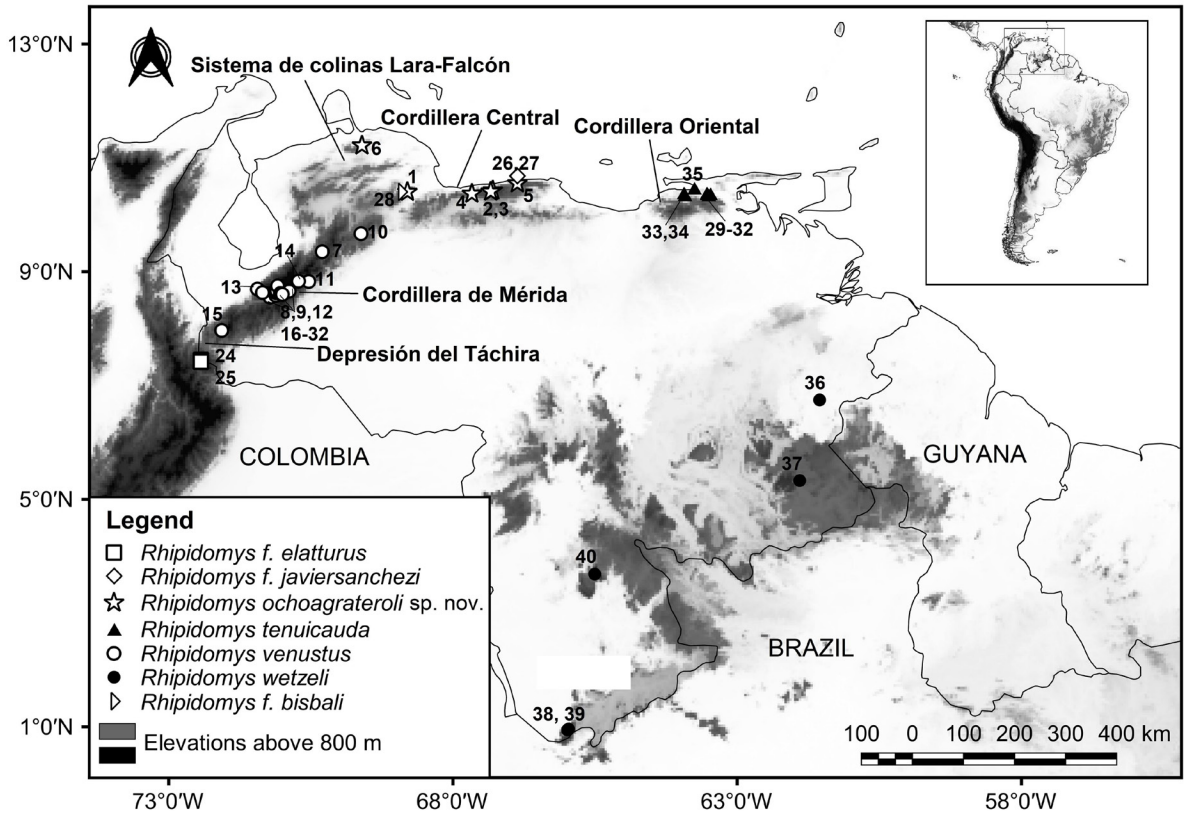

Figure 1. Map of Venezuela showing the geographic distribution of the species of the *Rhipidomys fulviventer* group. Numbers correspond with examined and reported localities (Appendix).

Morphological analyses

For each specimen available of *Rhipidomys venustus*, we investigated variations in their integument (dorsal and ventral pelage coloration; dorsal and ventral pelage of manus, hind feet and ears; vibrissae; scales, caudal coloration and mammae), skull and teeth. Additionally, we compared theses qualitative aspects with other taxa of the *R. fulviventer* group from Venezuela, Peru and Colombia.

Statistical analyses

We used descriptive and multivariate statistics both to document differences in means, ranges, intra-specific variations, as well as integrating multiple variables between species recorded in the Venezuelan territory. However, our bivariate statistical analysis was restricted to comparing the populations previously named as *R. venustus* from the Andes with populations inhabiting the Cordillera de la Costa Central and the Sistemas de Colinas Lara-Falcón. Since species in the genus *Rhipidomys* do not show sexual dimorphism (Tribe 1996, Costa *et al*. 2011), males and females were pooled in all analyses.

We conducted a Ryan-Joiner test on the relevant residuals to test for any departure from normality in our quantitative data. Additionally, we used the Levene's test for homogeneity of variances. To avoid an increase in the proportion of false positives (Type I error), we determined significance within families of tests (*e. g*., within a series of t-tests, each comparing the mean between two samples for one of several variables), using Holm's (1979) modification of the Bonferroni procedure. For cranial measurements, we did a transformation for natural logarithms and used a two-sample t-test to compare, separately the means (external or cranial measurements) of *R. venustus* from the Andes with the corresponding mean of its most similar congener (*Rhipidomys* sp., from the Cordillera de la Costa Central and the Sistemas de Colinas Lara-Falcón). For external measurements, we conducted a non-parametric test (Mann-Whitney U-test), due to non-normality and non-homogeneity of variance.

Additionally, we applied a Discriminant Function Analysis (DFA), with only 18 log-transformed cranial measurements (Jolicoeur 1963), to compare mean cranial measurements and to discriminate between the several groups of *Rhipidomys* previously known. All statistical analyses were performed using SPSS, version 8.0.

We obtained the following external and cranial measurements used by Tribe (1996) for each specimen available: Head and Body Length (HBL), Tail Length (TL),

Hind-Foot Length (HFL), Ear Length (EL), Nasals Length (NL), Rostral Length (RL), Rostral Breadth (RB), Interorbital Breadth (IOB), Zygomatic Breadth (ZB), Braincase Breadth (BCB), Occipito-Nasal Length (ONL), Condylo-Incisive Length (CIL), Post-Palatal Length (PPL), Palatal Length (PL), Diastema Length (DL), Palatal Bridge Length (PBL), Incisive Foramina Length (IFL), Incisive Foramina Breadth (IFB), First Upper Molar Breadth (M1B), Palatal Breadth at M1 (PB1), Palatal Breadth at M3 (PB3), Mesopterygoid Fossa Breadth (MFB),Temporal Fossa Length (TFL), Zygomatic Plate Length (ZPL), Rostral Height (RH), Upper Molar Row Alveolar Length (UMR), Greatest Length of Mandible (GLM), Mandibular Molar Row Alveolar Length (MMR) and Depth of Ramus (DR). The body mass (weight), was recorded in grams (g). External measurements and weight were obtained from museum specimen tags. Cranial measurements were obtained with digital calipers (accuracy = 0.02 mm). All measurements are reported in millimeters (mm).

Specimens examined are preserved in the following Venezuelan institutions (Appendix): Museo de la Estación Biológica de Rancho Grande (EBRG, Maracay), Museo de Historia Natural La Salle (MHNLS, Distrito Capital), Museo de Biología de la Universidad Central de Venezuela (MBUCV, Distrito Capital), Colección de Vertebrados de la Universidad de Los Andes (CVULA, Mérida) and Laboratorio Museo de Zoología de la Universidad de Carabobo (MZUC, Carabobo).

In our study, we follow the Biological Species Concept proposed by Mayr (1942), which postulates that "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". In addition to the evidence of the geographical isolation produced by the Lara depression, which separates populations defined as *Rhipidomys* sp., from the Cordillera Central and the Sistemas de Colinas Lara-Falcón of *Rhipidomys venustus* from the Andes, there is another geographical barrier known as the Táchira depression, which separates *R. venustus* from the remaining *Rhipidomys* species of the Andes of South America. There is also clear evidence of phenotypic and morphometric differentiation, which are our basics for the description of the new species as new evolutionary linage (Baker & Bradley 2006).

RESULTS

Results indicate that the studied populations currently referred to *R. venustus* have intra-specific variations both in external features, as well as skull and post-cranial skeleton. These differences were most notable for Andean populations compared with the Cordillera de la Costa Central and the Sistemas de Colinas Lara-Falcón. In addition, a set of external, cranial and post-cranial characters were found to be different from the Andean population (*Rhipidomys venustus*) with respect to the Cordillera de la Costa Central and the Sistemas de Colinas Lara-Falcón (*Rhipidomys* sp.).

Quantitative comparisons showed significant differences between *R. venustus* with respect to *Rhipidomys* sp., in the following external measurements (P<0.005 for significant comparisons): HBL (P<0.01), TL (P< 0.005) and Weight (P< 0.005). In cranial measurements, the following variables were significant (after correction for multiple comparisons): ONL (P< 0.005), CIL (P< 0.005), PL (P< 0.02), DL (P< 0.005), TFL (P< 0.005), UMR (P< 0.005), RB (P< 0.005), RD (P< 0.005) and ZB (P< 0.005).

Multivariate analyses also supported differences between *Rhipidomys* sp., *R. venustus* and the other five taxa of *Rhipidomys* evaluated. The first two axes, showed the separation between the seven groups in a multi-dimensional morphological space. The discrimination capacity was statistically significant (F=6.97; P< 0.0000), with a 100% of discriminant function correctly classified and accumulated total variance of 86.05% (Fig. 2). The RL, IFB, TFL, UMR and MMR were the principal variables responsible of the differentiation (P< 0.004), followed by DL, RB and GLM (P< 0.01).

These results allow us to propose a new name for the populations from the Cordillera de la Costa Central and the Sistemas de Colinas Lara-Falcón, which differ in morphometry, phenotype, cranial structure and post-cranial skeleton of its Andean counterparts.

Rhipidomys ochoagrateroli sp. nov.

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Rhipidomys venustus: Handley, 1976: 49 [in part].

Holotype: Male (MZUC-977, age class 2), preserved as skin, skull and post-cranial skeleton, collected by Franger J. García (field number: FG-2150) on November 13th 2011, at cloud forest, Yurubí National Park, Sierra de Aroa, Yaracuy State, Venezuela. Skin, skull (Figs. 3A; 4A, B, C), and post-cranial skeleton were in excellent condition. Measurements of holotype are listed in Table 1.

Paratype: One female (MZUC-970, age class 2), preserved in ethanol (70%), with skull extracted (Fig. 4C, D), collected by Franger J. García (field number: FG-1937), Douglas Mora and Luis Aular on April 21st 2011, at cloud forest, Yurubí National Park, Sierra de Aroa, Yaracuy State,

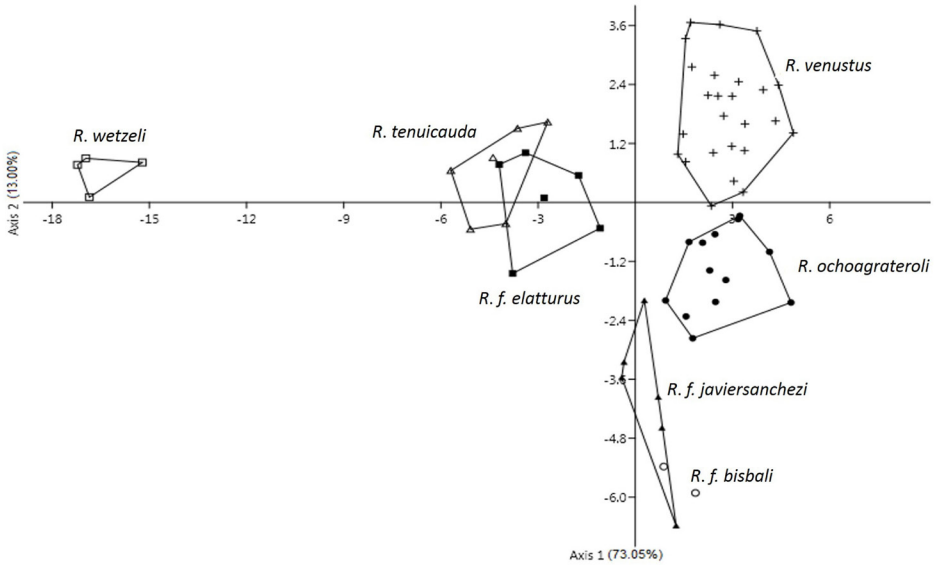

Figure 2. Discriminant function analysis (DFA), using 18 cranial measurements taken from adult specimens of the *Rhipidomys fulviventer* group in Venezuela.

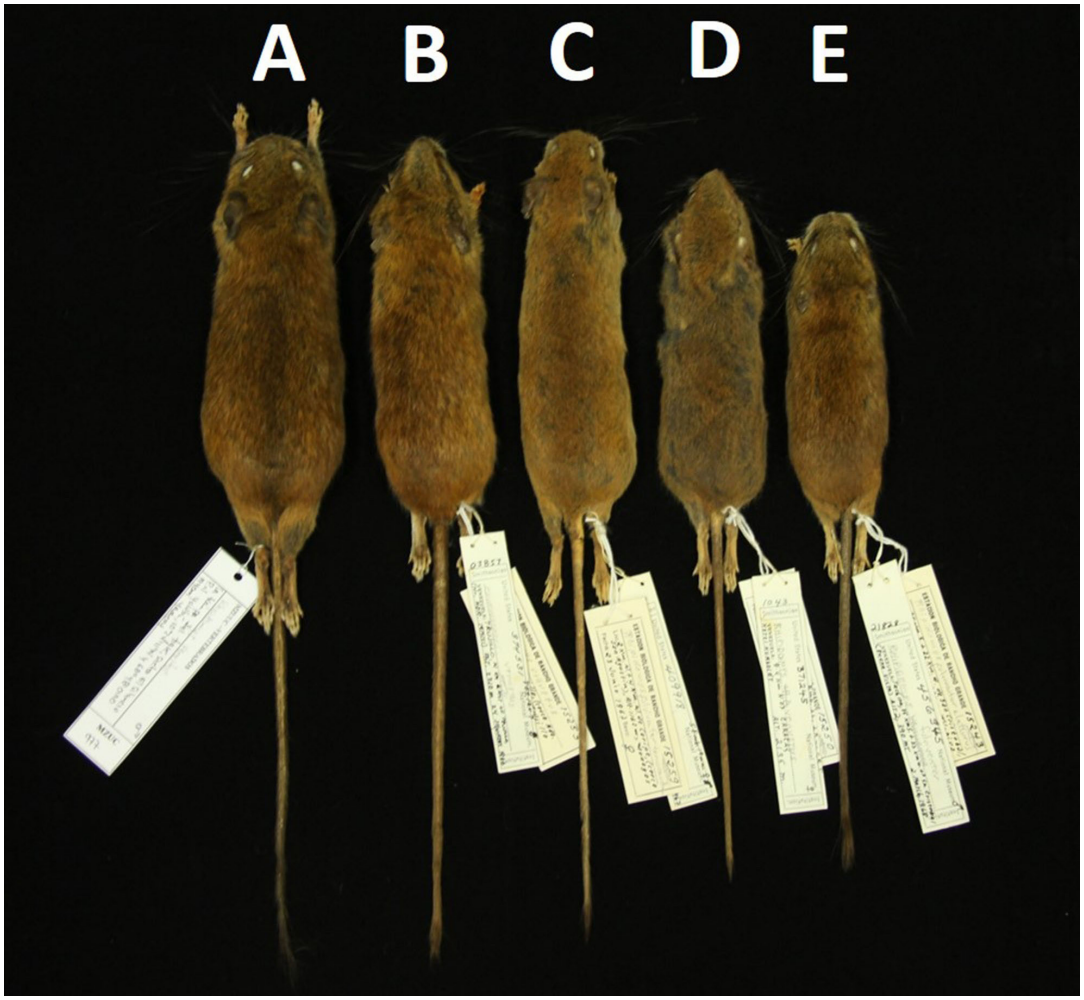

Figure 3. Skins from five taxa of the *Rhipidomys fulviventer* group in Venezuela. A) *Rhipidomys ochoagrateroli* **sp. nov.**, (MZUC–977), *Rhipidomys venustus* (EBRG–15253), *Rhipidomys tenuicauda* (EBRG–15259), *Rhipidomys fulviventer javiersanchezi* (EBRG–15250) and *Rhipidomys fulviventer elatturus* (EBRG–15243).

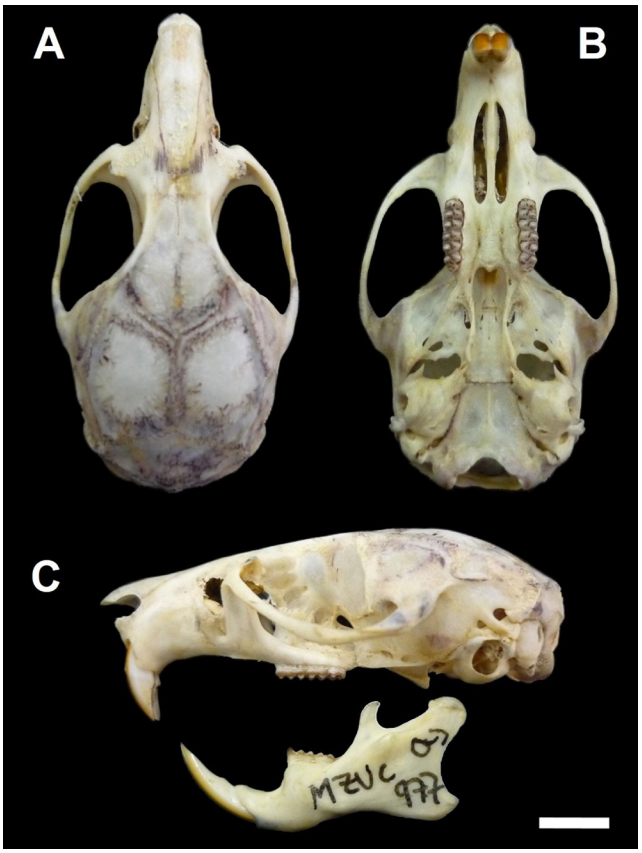

Figure 4. Dorsal (**A**), ventral (**B**) and lateral (**C**) views of the skull and mandible of the holotype of *Rhipidomys ochoagrateroli* **sp. nov.**, (MZUC–977). Scale = 5 mm.

Venezuela. Skull and body were in excellent conditions. Measurements of Paratype are listed in Table 1.

Type locality: La Trampa del Tigre (10°24'11"N, 68°48'01"W; 1940 m asl), sector El Silencio, Parque Nacional Yurubí, Sierra de Aroa, Estado Yaracuy, Venezuela (Fig. 6A, B, C).

Distribution: Cordillera de la Costa Central (Sierra de Aroa and Serranía del Litoral) and in Sistemas de colinas Lara-Falcón (Sierra de San Luis, Juan Crisóstomo Falcón National Park), Venezuela.

Etimology: This species is dedicated to José Rafael Ochoa-Graterol, an outstanding taxonomist and ecologist, whose contributions to the knowledge of the mammals of Venezuela has helped to document the great taxonomic diversity of this group in this country, particularly for marsupials, bats and rodents.

Diagnosis: *Rhipidomys ochoagrateroli*, **sp. nov.**, is a large sized rodent distinguished from its congeners by the combination of the following characters: large body with a long and soft dorsal pelage; bright chestnut brown in color; long tail with small scales, imbricated and squarish in shape, dark brown triplet of small hairs covers two scales in length; long terminal tuft of hairs present; large and robust skull with a long and wide rostrum; inflated nasolacrimal capsule; long and parallel incisive foramina; robust and broad hamular process of squamosal bone; and alisphenoid strut frequently bifurcated.

Table 1. External and cranial dimensions of the type series of *Rhipidomys ochoagrateroli* **sp. nov.**

Measurements	(Holotype MZUC-977)	(Paratype MZUC-970)
HBL	140.00	132.00
TL	176.00	165.00
HFL	23.00	26.00
EL	18.00	20.00
NL	12.30	10.70
RL	10.40	8.80
RB	5.20	5.00
IOB	4.80	4.80
ZB	18.20	17.60
BCB	13.00	12.60
ONL	34.00	31.90
CIL	31.30	29.70
PPL	12.60	12.10
PL	15.70	14.90
DL	9.30	8.60
PBL	4.50	4.40
IFL	6.70	6.50
IFB	2.50	2.30
M1B	1.30	1.30
PB1	3.50	3.40
PB3	3.70	3.70
MFB	2.20	2.20
TFL	9.90	9.40
ZPL	2.80	2.50
RH	6.40	5.60
UMR	5.00	4.90
GLM	19.90	16.40
MMR	5.20	4.90
RD	3.90	3.80
Weight	81.00	65.00

Description: *Rhipidomys ochoagrateroli*, **sp. nov.**, is an arboreal rat of large size, compared with other species from the *Rhipidomys fulviventer* section in Venezuela (Table 2). The mistacial, superciliary and genal vibrissae are long (mistacials reaching the posterior edge of the ears). The in-

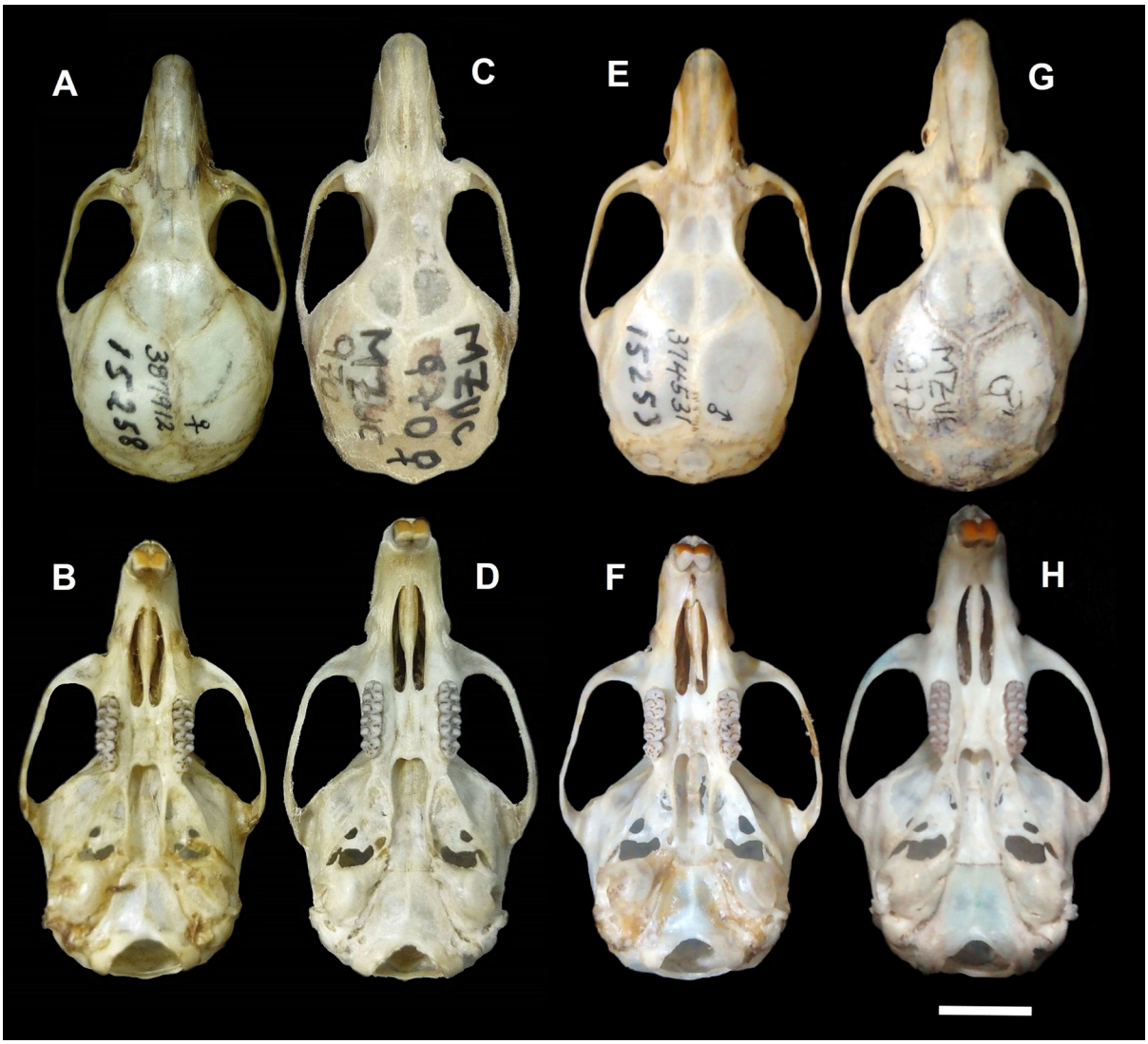

Figure 5. Dorsal and ventral views of four skulls of two species of *Rhipidomys* (age classes 2, respectively), showing the differences in size. Two females: **A** and **B**: *R. venustus* (EBRG-15258); **C** and **D**: *R. ochoagrateroli* **sp. nov.**, (Paratype, MZUC-970). Two males: **E** and **F**: *R. venustus* (EBRG-15253); **G** and **H**: *R. ochoagrateroli* **sp. nov.**, (Holotype, MZUC-977). Scale = 5 mm.

terramal and submental vibrissae are short and white. The ears are brown.

The manus are yellowish in specimens preserved both in ethanol as well as dry skins, and have very short brown hairs on the dorsal surface of the metacarpals. The metacarpals and digits have silver hairs on their dorsal surface. The ungual tufts are white and extend to the tips of the claws or beyond. The claws are elongated. In dorsal view, the scales on the manus are granular in shape, small, and reach the second phalange from every digit. Five palmar pads are present: three inter-digitals, closely joined to each other; one large hypothenar and one thenar, robust and larger than the hypothenar. The ulnar-carpal vibrissae are short in size and white in color.

The dorsal pelage is long and soft, bright chestnut brown, not contrasting with the flanks and hairs are gray-based (the gray band covers more 50% of the hair length). The length of the mid-dorsal hairs is approximately 5-7 mm and the length of the guard hairs is 9-12 mm. The ventral pelage is white, but gray-based (the gray band covers at least 50% of hair length). The length of the mid-venter hairs is approximately 7-8 mm. Females have the following mammary formula: one post-axial pair; one abdominal pair, and one inguinal pair.

The hind feet are broad (frequently narrower compared with individuals of *R. venustus* of the same age class) and long, with a dark patch of short brown hairs on the dorsal surface of the metatarsals (except MZUC-980). The meta-

Figure 6. **A**. Cloud forests in the Yurubí National Park, Yaracuy State, Northern Venezuela. **B** and **C**. Habitats (canopy and understory) of *R. ochoagrateroli* **sp. nov.**, in the cloud forest from the Trampa del Tigre (type locality).

tarsals and digits have silver hairs on their dorsal surface. The ungual tufts are white and extend to the tips of the claws or beyond. In dorsal view, the scales on the hind feet are granular in shape, small and reach the second phalange from each digit, and then they are arranged in a single scale, rectangular in shape. Six well developed plantar pads are present: four inter-digitals, closely joined to each other; one small hypothenar with a broad base, and one large thenar with a reduced base.

The tail is much longer than the combined head and body length (Tables 1 and 2) and is uniformly-colored. The scales on the tail are small, imbricated and squarish in shape. Scales have a triplet of small dark brown hairs of equal size at the base (length approximated=3 mm; Fig. 7A, C); these hairs can reach two scales in length but are longer at the tip of the tail forming a long terminal tuft.

The skull is large size and robust. The rostrum is long and broad with nasals long, expanded anteriorly and in contact with the maxillary-frontal suture. The zygomatic arches, posterior root of the zygomatic arches, braincase and occipitals are broad. The lacrimal bones are elongated and laterally expanded. The nasolacrimal capsule is inflated and clearly visible in dorsal and ventral view. A gnathic process is present but poorly developed. The zygomatic spine on the anterior edge of the zygomatic plate is absent. The zygomatic notch is concave.

The interorbital region is convergent anteriorly. The supraorbital ridges are weakly developed. The ethmoid foramen is present. The hamular process of squamosal bone is robust, uniformly broad and clearly separating a distinct subsquamosal fenestra and postglenoid foramen (Fig. 8A); although in two specimens the postglenoid foramen is almost precluded (paratype and MZUC-973), which is smaller than subsquamosal fenestra (Fig. 8A). A broad alisphenoid strut is frequently present (except EBRG-15251) and bifurcated (Fig. 8C), separating the masticatory–buccinator foramen of the alisphenoid canal; when not is bifurcated (MZUC-900, 971, 975, 979), the alisphenoid canal and masticatory-buccinator foramen are fused. The sphenofrontal foramen is small.

The incisive foramina are long, convergent anteriorly and parallels in the medial part. These foramina reach

Table 2. External and cranial dimensions of *Rhipidomys ochoagrateroli* **sp. nov.**, and its congeners from the *Rhipidomys fulviventer* group from Venezuela. The descriptive statistic included the sample size (n), mean and range (minimum and maximum).

Measurements	*Rhipidomys ochoagrateroli* **sp. nov.**	*Rhipidomys venustus*	*Rhipidomys tenuicauda*	*Rhipidomys fulviventer javiersanchezi*	*Rhipidomys fulviventer bisbali*	*Rhipidomys fulviventer elatturus*	*Rhipidomys wetzeli*
EXTERNAL	n=17	n=26	n=13	n=5	n=2	n=7	n=13
HBL	140.41 111.00-190.00	120.65 94.00-198.00	114.00 100.00-130.00	117.80 108.00-133.00	109.00 93.00-125.00	105.14 92.00-112.00	88.77 63.00-103.00
TL	164.88 137.00-190.00	139.74 74.00-168.00	147.20 125.00-160.00	143.20 125.00-161.00	146.00 132.00-160.00	117.71 107.00-133.00	123.77 82.00-140.00
HFL	27.41 23.00-31.00	26.14 22.00-30.00	25.80 25.00-27.00	26.20 22.00-30.00	26.50 25.00-28.00	24.28 22.00-26.00	22.77 21.00-24.00
EL	19.52 16.00-21.00	19.87 16.00-25.00	20.50 19.00-22.00	18.40 17.00-20.00	17.50 17.00-18.00	19.14 17.00-21.00	17.15 15.00-21.00
Weight	64.37 37.00-81.00	49.24 26.00-95.00 (n=24)	35.10 22.00-48.00	53.50 (n=1)	—	32.71 23.00-39.00	25.56 18.00-32.00
Cranials	n=13	n=26	n=8	n=6	n=2	n= 6	n=4
NL	11.49 10.60-12.80	11.05 9.60-12.50	9.56 9.80-11.70	9.86 9.20-10.70	10.30 9.70-10.90	10.23 9.80-10.60	8.87 8.30-9.10
RL	10.00 8.80-10.90	9.86 8.70-11.50	9.20 8.80-10.10	8.61 7.90-9.70	9.80 9.70-9.90	8.45 8.10-8.90	7.47 7.00-7.80
RB	5.20 4.70-6.50	4.38 3.70-5.70	5.15 4.50-5.60	5.20 4.50-5.70	5.50 5.10-5.90	4.73 4.30-5.20	4.52 4.40-4.70
IOB	4.85 4.60-5.00	4.74 4.20-5.10	4.41 4.30-4.50	4.66 4.40-4.90	4.65 4.60-4.70	4.30 4.10-4.50	4.12 4.00-4.20
ZB	17.67 16.60-18.20	16.50 14.60-18.20	15.80 15.20-16.40	16.16 14.40-17.70	15.95 15.40-16.50	15.13 14.50-15.60	13.30 13.20-13.40
BCB	12.88 12.20-14.20	12.94 12.00-14.10	11.86 11.00-12.90	12.91 12.20-13.40	13.15 13.10-13.20	12.03 11.70-12.30	11.40 11.10-11.80
ONL	32.95 31.90-34.40	31.69 29.30-38.40	30.00 29.40-30.90	30.72 28.20-33.30	30.25 29.10-31.40	28.48 28.10-29.40	25.00 24.50-25.50
CIL	30.23 29.20-31.90	28.70 25.60-31.90	27.33 26.80-27.70	27.76 25.20-30.10	26.85 25.70-28.00	25.83 25.30-26.90	22.17 21.70-23.20
PPL	12.46 11.00-13.30	11.95 10.10-13.40	11.08 10.60-11.40	11.30 10.10-12.20	10.20 9.60-10.80	10.58 10.40-10.90	9.02 8.70-9.60
PL	15.16 14.70-16.30	14.51 12.40-16.30	13.53 13.30-13.80	13.61 12.40-15.10	13.85 13.20-14.50	12.83 12.60-13.10	10.97 10.60-11.40

Table 2. (*Continuation*)

Measurements	*Rhipidomys ochoagrateroli* **sp. nov.**	*Rhipidomys venustus*	*Rhipidomys tenuicauda*	*Rhipidomys fulviventer javiersanchezi*	*Rhipidomys fulviventer bisbali*	*Rhipidomys fulviventer elatturus*	*Rhipidomys wetzeli*
DL	8.74 8.10-9.30	8.17 6.90-9.20	7.73 7.20-7.90	7.51 7.00-8.50	7.60 7.00-8.20	7.18 7.00-7.40	6.40 6.00-6.80
PBL	4.56 4.10-5.10	4.57 3.80-5.20	4.11 3.80-4.40	4.13 3.70-4.60	4.20 4.00-4.40	4.01 3.70-4.60	3.15 2.50-3.50
IFL	6.72 6.20-7.30	6.47 5.10-7.40	5.64 5.00-5.90	6.17 5.70-6.70 (n = 4)	6.30 6.10-6.50	5.46 5.20-5.60	3.95 3.30-4.90
IFB	2.54 2.30-3.10	2.39 1.90-3.00	2.32 2.20-2.50	2.32 2.20-2.50 (n = 4)	2.50 2.50-2.50	1.98 1.80-2.10	2.10 1.90-2.20
M1B	1.34 1.20-1.40	1.34 0.70-1.40	1.18 1.10-1.30	1.30 1.20-1.40	1.30 1.30-1.30	1.23 1.20-1.30	0.90 0.80-1.00
PB1	3.32 3.20-3.50	3.17 2.70-3.60	2.94 2.50-3.20	2.96 2.70-3.30	3.25 3.20-3.30	2.81 2.60-2.90	2.60 2.30-2.90
PB3	3.69 3.40-3.90	3.57 2.90-4.10	3.21 3.00-3.40	3.48 3.10-3.90	3.60 3.40-3.80	3.20 3.10-3.30	3.00 2.90-3.20
MFB	2.13 1.90-2.50	2.20 1.80-2.50	2.07 1.70-2.30	1.98 1.80-2.20	2.05 1.90-2.20	1.98 1.80-2.20	1.90 1.70-2.10
TFL	9.70 9.30-10.00	9.29 8.20-10.30	8.36 7.80-9.40	8.85 8.50-9.70	10.05 9.90-10.20	8.51 8.10-9.70	6.92 6.80-7.30
ZPL	2.60 2.30-3.00	2.52 2.10-3.40	2.28 1.80-2.50	2.16 2.00-2.40	2.15 2.00-2.30	2.30 2.10-2.50	1.92 1.80-2.10
RH	6.06 5.60-6.40	5.76 5.00-6.70	5.32 4.70-5.70	5.34 4.80-6.30	5.40 5.10-5.70	5.13 5.00-5.30	4.55 4.40-4.70
UMR	5.02 4.80-5.20	4.86 4.60-5.10	4.43 4.30-4.60	4.91 4.70-5.10	5.20 5.10-5.30	4.41 4.30-4.80	3.37 3.20-3.50
GLM	17.12 15.90-17.90	16.69 15.00-18.60	15.88 15.30-16.40	16.21 14.50-17.90	16.00 15.30-16.70	14.65 13.90-15.40	12.62 12.30-13.00
MMR	5.17 4.90-5.60	5.20 4.90-5.80	4.61 4.50-4.80	5.00 4.80-5.10	5.05 5.00-5.10	4.58 4.50-4.70	3.62 3.60-3.70
DR	3.92 3.60-4.20	3.56 2.90-4.40	3.30 3.10-3.70	3.76 3.20-4.90	3.55 3.40-3.70	3.26 3.20-3.40	2.75 2.70-2.90

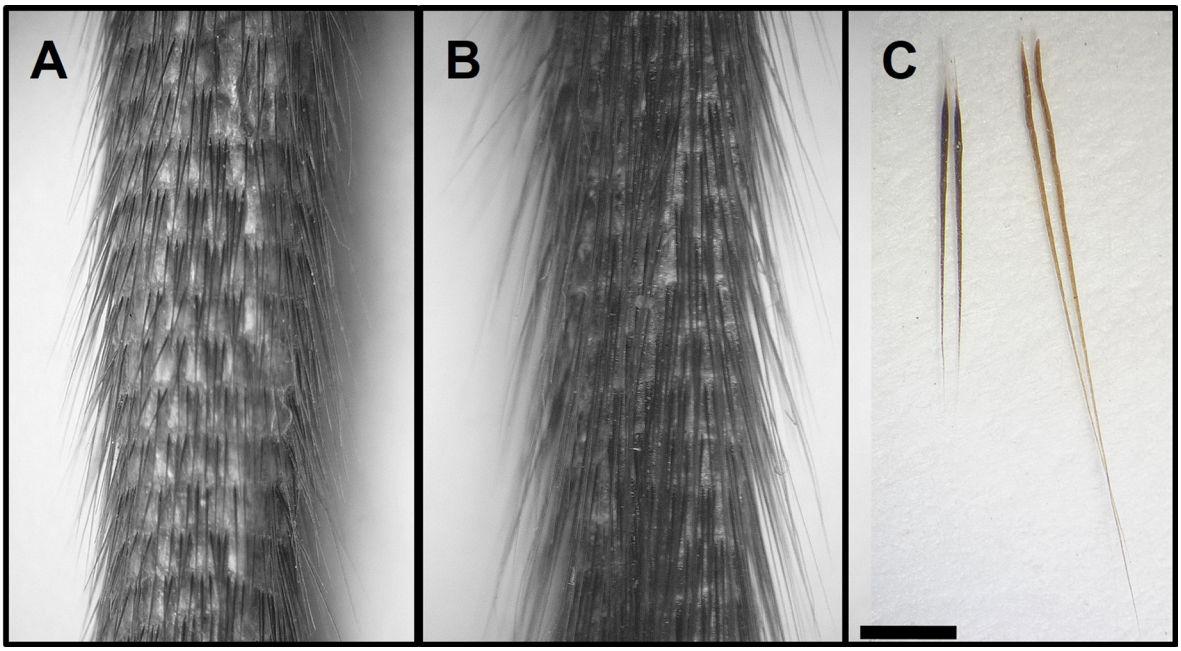

Figure 7. Medial sections of the tails of two species of *Rhipidomys* showing the differences related with density and size of hairs (**A**): *Rhipidomys ochoagrateroli* **sp. nov.**, (Holotype, MZUC-977) and (**B**): *Rhipidomys venustus* (EBRG-28303). (**C**): individual hairs of *Rhipidomys ochoagrateroli* **sp. nov.**, (left) and *Rhipidomys venustus* (right). Scale = 1 mm.

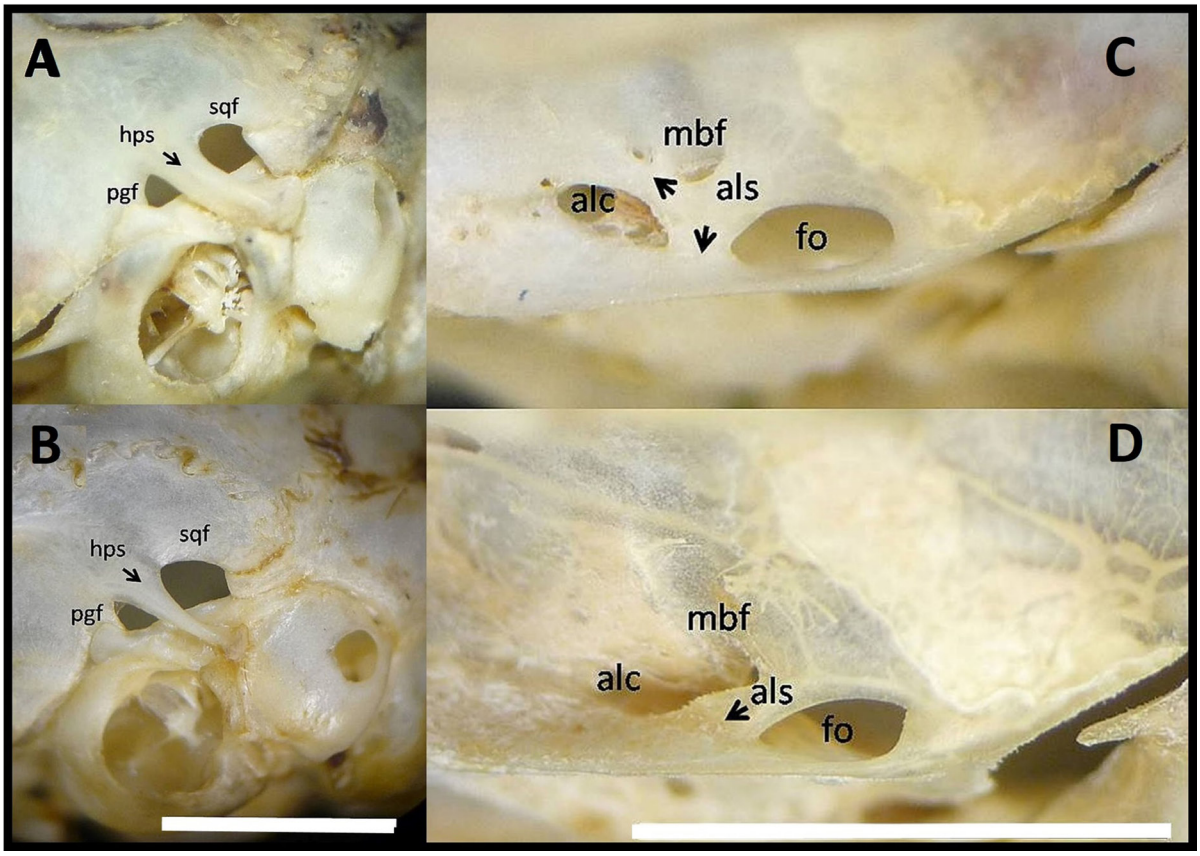

Figure 8. Morphology of the hamular process of the squamosal (hps) in *Rhipidomys ochoagrateroli* **sp. nov.**, (**A** = Holotype, MZUC-977) and *Rhipidomys venustus* (**B** = EBRG-15255). In addition, we report the variation in the alisphenoid strut (als); frequently bifurcated in *Rhipidomys ochoagrateroli* **sp. nov.**, (**C** = Holotype, MZUC-977) and not bifucarted in *Rhipidomys venustus* (**D** = EBRG-1255). Scales = 5 mm.

anterior roots of the first upper molars. The palate is long (compared with other species in the *R. fulviventer* section from Venezuela) and broad on M1 and M3. Two longitudinal grooves are present on the palate. The palatal foramina are small, usually present in three pars on each side. The lateral postpalatal foramina are present. The mesopterygoid fossa is deep and with a small postpalatal projection. The sphenopalatine fissures are long and frequently are present (except in the paratype and MZUC-971, which lack these fissures). The parapterygoid fossae are frequently fenestrated (except MZUC-970). The foramen ovale is large. The carotid circulatory pattern is of primitive type, with a stapedial foramen large; and the supraorbital ramus of the stapedial artery following groove across inner surface of alisphenoid to sphenofrontal foramen; Pattern 1 of Voss (1988).

The upper incisors are robust and opisthodont. The upper molars are pentalophodont, large and robust. The first upper molars have protocone, hypocone, paracone and metacone developed. The anterolingual and anterolabial conules frequently are divided by an anteromedian flexus (except MZUC-971, 973). The anteromedian style is present and well developed. The anteroflexus and anteromedian flexus are separated. The protoflexus, mesoflexus, hypoflexus, paraflexus, metaflexus and posteroflexus are long. The anterior and median mures are present and are developed. The medial and labial fossettes on the second upper molars are long and are separated.

The mandible is long, broad and high in the condylar region and coronoid processes. The sigmoid notch is shallow. The first lower molars have metaconid, entoconid, protoconid and hypoconid. The anterolingual and labial conulids are not frequently divided by an anteromedian flexid (except MZUC-974). The anteroflexid, and protoflexid are present. The mesoflexid, hypoflexid, entoflexid and posteroflexid are long. The second lower molars have metaconid, entoconid, protoconid and hypoconid. The mesoflexid, entoflexid, hypoflexid and protoflexid are present, and are long. The posteroflexid is bifurcated.

The scapula (Fig. 9A), is high and straight; the acromion is developed, rounded and elongated toward the scapular crest; the acromial angle is slightly curved (approximately 110°). The medial edge is slightly convex; the lateral edge is almost straight and the upper edge is slightly concave. The scapular notch is shallow. The upper angle is less curved than lower angle. The infraspinous fossa is larger than supraspinous. The infraglenoid tubercle is developed.

The humerus (Fig. 9C), is large with the head developed and larger than greater tubercle. The deltoid process is developed. The olecranon and coronoid fossa are very deep. The medial epicondyle is more developed than lateral epicondyle. The capitulum is large. The humeral trochlea is shallow.

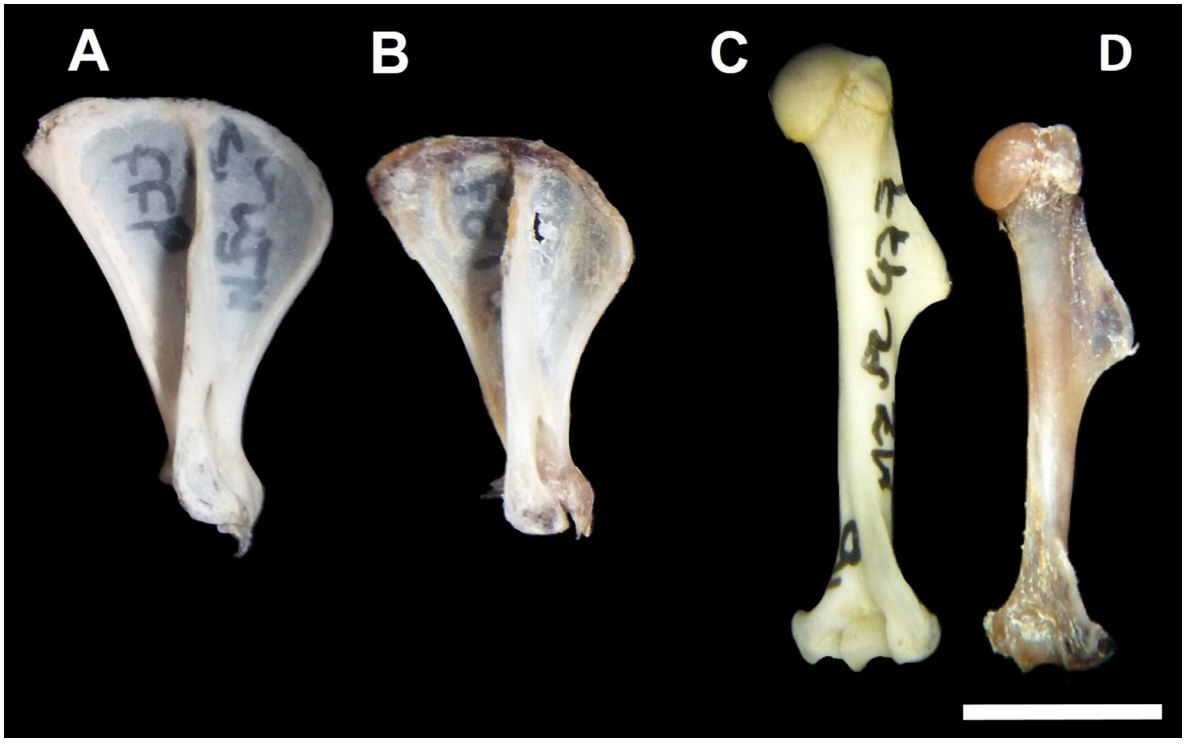

Figure 9. Posterior views of the morphology of right scapula and right humerus of adult *Rhipidomys ochoagrateroli* **sp. nov.**, (**A**, **C**; Holotype: MZUC-977) and *Rhipidomys venustus* (**B**, **D**; CVULA-I-6157), showing the differences in size. Scale = 5 mm.

Comparisons: Externally, *R. ochoagrateroli* **sp. nov.**, can be easily distinguished from *R. leucodactylus* Tschudi, 1844, *R. couesi* J. A. Allen & Chapman, 1893, *R. venezuelae* Thomas, 1896 and *R. nitela* Thomas, 1901 (*Rhipidomys leucodactylus* group), because of its smaller size and from *R. macconnelli* De Winton, 1900 (*Rhipidomys macconnelli* group), because of its comparatively large size. The ventral coloration is also different; the species in the *R. leucodactylus* and *macconnelli* groups have a venter pure white or cream (unicolored hairs), but *R. ochoagrateroli* **sp. nov.**, although it has a venter white, the hairs are gray-based (bicolored).

In cranial features, the carotid circulatory pattern is primitive in *R. ochoagrateroli* **sp. nov.** (Pattern 1, Voss 1988), against a derived pattern for species in the *R. leucodactylus* and *macconnelli* groups (Patterns 2 and 3, Voss 1988).

Compared with the species of the *R. fulviventer* group from Venezuela, *R. ochoagrateroli* **sp. nov.**, is larger than *R. tenuicauda*, *R. f. javiersanchezi*, *R. f. bisbali*, *R. f. elatturus* and *R. wetzeli* in most external and cranial measurements, as well as body mass and qualitative features (Table 2). In addition, *R. ochoagrateroli* **sp. nov.**, has a skull and mandible different in shape with respect to its congeners of the *R. fulviventer* group from Venezuela (García & Sánchez-González 2013; named in that study as *Rhipidomys venustus* Aroa).

Regarding external and cranial features, *R. ochoagrateroli* **sp. nov.**, is different of *R. tenuicauda* in the following aspects: dorsal pelage coloration (bright chestnut brown *vs.* bright orange-brown agouti); ventral pelage coloration (white hair tips *vs.* cream hair tips); hind feet (long and broad *vs.* small and narrow); hair colors on the dorsal surface of the metatarsals (dark brown *vs.* pale brown); terminal tuft of tails length (15.38 mm [n=17] *vs.* 11.64 mm [n=13]); skull and palate (large and long *vs.* small and short); palatal foramina (3–4 pairs *vs.* 1–2 pairs); parapterygoid fossae (fenestrated *vs.* not fenestrated).

Rhipidomys ochoagrateroli **sp. nov.**, is different of *Rhipidomys f. javiersanchezi* in the following features: dorsal pelage coloration (bright chestnut brown *vs.* brown agouti); ventral pelage coloration (white hair tips *vs.* cream hair tips); hind feet (broad *vs.* narrow); hair colors on the dorsal surface of the metatarsals (dark brown *vs.* pale brown); terminal tuft of tails length (15.38 mm [n=17] *vs.* 8.50 mm [n=5]); skull and palate (large and long *vs.* medium and short); Parapterygoid fossae (fenestrated *vs.* not fenestrated); accessory sphenofrontal foramen in the alisphenoid (absent *vs.* present).

Rhipidomys ochoagrateroli **sp. nov.**, differs of *R. f. bisbali*, in the dorsal pelage coloration (bright chestnut brown *vs.* brown agouti); hind feet (broad *vs.* narrow); hair colors on the dorsal surface of the metatarsals (dark brown *vs.* brown); terminal tuft of tails length (15.38 mm [n=17] *vs.* 6.04 mm [n=1]); skull and palate (large and long *vs.* small and short); parapterygoid fossae (fenestrated *vs.* not fenestrated); alisphenoid strut (frequently bifurcated *vs.* not bifurcated).

Rhipidomys ochoagrateroli **sp. nov.**, is different of *Rhipidomys f. elatturus* in the dorsal pelage coloration (bright chestnut brown *vs.* pale brown); ventral pelage coloration (white hair tips *vs.* cream hair tips); hind feet (long and broad *vs.* short and narrow); hair colors on the dorsal surface of the metatarsals (dark brown *vs.* pale brown); skull and palate (large and long *vs.* small and short); sphenopalatine fissures (long *vs.* short); parapterygoid fossae (fenestrated *vs.* sometimes fenestrated).

Rhipidomys ochoagrateroli **sp. nov.**, is different of *Rhipidomys wetzeli* in the dorsal pelage coloration (bright chestnut brown *vs.* bright orange agouti); ventral pelage coloration (white hair tips *vs.* cream or orange hair tips); hind feet (long and broad *vs.* short and narrow); hair colors on the dorsal surface of the metatarsals (dark brown *vs.* pale brown); terminal tuft of tails length (15.38 mm [n=17] *vs.* 13.30 mm [n=4]); skull size (large *vs.* small); palatal foramina (small and 3-4 pairs *vs.* one pair large).

Rhipidomys ochoagrateroli **sp. nov.**, is morphologically similar to *R. venustus,* but is larger both in external and cranial morphometry, as well as body mass (Table 2). The following measurements are statistically significant: HBL, TL, Weight, RB, ZB, ONL, CIL, PL, DL, TFL, DR and UMR.

The mistacial vibrissae are less abundant in *R. ochoagrateroli* **sp. nov.**, (*R. venustus* has densely abundant mistacial vibrissae); the tail is less furry in *R. ochoagrateroli* **sp. nov.**, with a triplet of short hairs dark brown on each scale covering approximately two scales in length (*R. venustus* has a very furry tail and a triplet of small hairs, frequently light brown, covering approximately six scales; Fig. 7); dorsal hairs in *R. ochoagrateroli* **sp. nov.**, are shorter than *R. venustus*; *R. ochoagrateroli* **sp. nov.**, has a venter pure white, versus frequently yellowish (cream) in *R. venustus*; *R. ochoagrateroli* **sp. nov.**, has a larger skull than *R. venustus* (Fig. 5); the incisive foramina are parallel in *R. ochoagrateroli* **sp. nov.**, whereas is mostly laterally expanded in *R. venustus*); the nasolacrimal capsule is more inflated and developed in *R. ochoagrateroli* **sp. nov.**, than in *R. venustus*; the hamular process of the squamosal bone is uniformly broad and robust in *R. ochoagrateroli* **sp. nov.**, whereas is comparatively narrow in *R. venustus* (Fig. 8). Although in *R. ochoagrateroli* **sp. nov.**, the alisphenoid strut is variable (bifurcated or not), in all examined specimens of *R. venus-*

tus the alisphenoid strut is not bifurcated; therefore, the alisphenoid canal and masticatory-buccinator foramen are fused (Fig. 8). The scapula and humerus are larger in *R. ochoagrateroli* **sp. nov.**, than in *R. venustus* (Fig. 9).

Compared with other taxa belonging to the *R. fulviventer* group from Colombia and Peru (*R. caucensis*, *R. similis*, *R. f. fulviventer* and *R. ochrogaster*), *R. ochoagrateroli* **sp. nov.**, is larger than *R. caucensis* in the HBL (140.41 mm *vs.* 110.00 mm) and upper molar row (5.20 mm *vs.* 4.50 mm) (Tribe 2015). Additionally, *R. caucensis* has a derived carotid circulation pattern (Tribe 1996, 2015) and *R. ochoagrateroli* **sp. nov.**, has a primitive carotid circulation pattern. *Rhipidomys similis* has a dorsal pelage coloration reddish to orange brown or yellowish rufous, lined with black and the ventral pelage is cream or orange (Tribe 1996, 2015); in *R. ochoagrateroli* **sp. nov.**, the dorsum is chestnut brown, without a line black, and the venter is white; the supraorbital ridges are slightly developed in *R. similis* and in *R. ochoagrateroli* **sp. nov.**, are weakly developed or absent; the sphenopalatine fissures in *R. similis* are small to medium, opposite at large and long in *R. ochoagrateroli* **sp. nov.**,; the upper molar row is larger in *R. similis* than in *R. ochoagrateroli* **sp. nov.**, (5.25 mm *vs.* 5.02 mm) (Tribe 2015).

Rhipidomys f. fulviventer is medium-sized with a dorsal pelage coloration tinged with olive (Tribe 1996, 2015) and not so bright chestnut brown as in *R. ochoagrateroli* **sp. nov.**,; ventral pelage usually has an orange suffusion (Tribe 2015) and in *R. ochoagrateroli* **sp. nov.**, is white; flanks are paler than dorsum (flanks not are contrasting in *R. ochoagrateroli* **sp. nov.**,) and it has small sphenopalatine fissures (long in *R. ochoagrateroli* **sp. nov.**,). *Rhipidomys ochrogaster* is larger than *R. ochoagrateroli* **sp. nov.**, in the HBL (> 150.00 mm *vs.* 140.41 mm), tail (> 190.00 mm *vs.* 164.88 mm) and the upper molar row (> 6.00 mm *vs.* 4.50 mm) (Pacheco & Peralta 2011, Tribe 2015). *Rhipidomys ochrogaster* has a dorsal pelage bright orange-brown and a ventral pelage pale-orange (Tribe 1996, Pacheco & Peralta 2011); in *R. ochoagrateroli* **sp. nov.**, the dorsal pelage is chestnut brown and the ventral pelage is white.

DISCUSSION

The recognition of *Rhipidomys ochoagrateroli* **sp. nov.**, is based exclusively on a morphologic analysis and metric comparisons; methodology previously used in descriptions of other taxa of thomasomyines, as *Thomasomys* Coues, 1884, or *Rhipidomys* (Leo & Gardner 1993, Gardner & Romo 1993, Tribe 2005). Although the identification of this new species is clear and unambiguous, it is necessary to evaluate its phylogenetic history and position in the future, including molecular data from all taxa of the genus *Rhipidomys* from Venezuela.

Rhipidomys ochoagrateroli **sp. nov.**, inhabits high elevations (1300-2223m asl) in the Cordillera de la Costa Central and in the Sistemas de Colinas Lara-Falcón. It has been recorded in four National Parks (Yurubí, Waraira Repano [El Ávila], Henri Pittier and Juan Crisóstomo Falcón) and in the Pico Codazzi Natural Monument (Handley 1976, Rivas & Salcedo 2006, Anderson *et al.* 2012, García *et al*. 2013, 2016). All records are from cloud forests with a low degree of disturbance, suggesting it may be vulnerable to habitat fragmentation. Throughout its geographic range, *R. ochoagrateroli* **sp. nov.**, was captured on vines and branches in mature forests (Handley 1976, Rivas & Salcedo 2006, Anderson *et al*. 2012, García *et al*. 2013, 2016).

Rhipidomys ochoagrateroli **sp. nov.**, is sympatric with the following species of small non-volant mammals: *Caluromys trinitatis* Thomas, 1894, *Didelphis marsupialis* L., 1758, *Gracilianus marica* Thomas, 1898, *Marmosa demerarae* (Thomas, 1905), *Marmosops carri* J. A. Allen & Chapman, 1897, *M. fuscatus* Thomas, 1896, *M. ojastii* García, Sánchez & Tenedo, 2014, *Cryptotis aroensis* Quiroga-Carmona & Molinari, 2012, *C. venezuelensis* Quiroga-Carmona, 2013, *Notosciurus granatensis* (Humboldt, 1811), *Heteromys anomalus* Thompson, 1815, *H. catopterius* Anderson & Gutiérrez, 2009, *Necromys urichi* (J. A. Allen & Chapman, 1867), *Microryzomys minutus* Tomes, 1860, *Neacomys tenuipes* Thomas, 1900, *Nephelomys caracolus* (Thomas, 1914), *Olygoryzomys delicates* (J. A. Allen & Chapman, 1897), *Oecomys bicolor* (Tomes, 1860), *O. flavicans* Thomas, 1894, *O. trinitatis* (J. A. Allen & Chapman, 1893), and *R. f. javiersanchezi* (Handley 1976, Rivas & Salcedo 2006, Anderson *et al*. 2012, García *et al*. 2013, 2014, 2015, 2016).

On the other hand, to date, *Rhipidomys venustus* has been documented to have a wide geographic distribution in the Cordillera de Mérida (Handley 1976, Tribe 1996). In that region, it is known almost exclusively in cloud forests at elevations above 1000 meters and in páramo ecosystems (Handley 1976, Díaz de Pascual 1988, Durant & Díaz de Pascual 1995, Tribe 1996, Soriano *et al*. 1999a, b, Ochoa *et al*. 2001).

Throughout its geographic distribution range, *R. venustus* is sympatric with the following species of small non-volant mammals: *Caluromys trinitatis* Thomas, 1894, *Didelphis marsupialis*, *D. pernigra* Allen, 1900, *Gracilianus dryas* Thomas, 1898, *Marmosops fuscatus*, *Marmosa demerarae*, *Cryptotis meridensis* Thomas, 1898, *Notosciurus granatanesis*, *Heteromys anomalus*, *H. australis* Thomas, 1901, *Ichthyomys hydrobates* (Winge, 1891), *Neusticomys mussoi* Ochoa & Soriano, 1991, *Necromys urichi*, *Mela-*

nomys colombianus (Allen, 1899), *Microryzomys minutus*, *Neacomys tenuipes*, *Nectomys rattus* Petter, 1979, *Nephelomys meridensis* (Thomas, 1894), *Oecomys bicolor, O. flavicans*, *O. trinitatis*, *Oligoryzomys delicatus*, *Sigmodontomys alfari* J. A. Allen, 1897, *Sigmodon hirsutus* Burmeister, 1854, *Aepeomys lugens* Thomas, 1896, *A. reigi* Ochoa, Aguilera, Pacheco & Soriano, 2001, *Rhipidomys couesi*, *R. venezuelae, Thomasomys emeritus* Thomas, 1916 and *T. vestitus* Thomas, 1898 (Handley 1976, Díaz de Pascual 1988, Soriano *et al.* 1999a, b, Durant & Díaz de Pascual 1995, Ochoa *et al.* 2001).

Our discovery of a new species has biogeographic implications for *R. venustus*, now restricted to the Andes (Cordillera de Mérida). Thus, it is necessary to increase efforts to conserve *R. venustus*, which is isolated of its sister species by the Táchira and Lara depressions, in an area that has suffered systematic fragmentation since pre-Columbian times (Soriano *et al.* 1999a, b).

Warm and dry climatic conditions, together with a belt of deciduous vegetation in the Táchira depression are postulated as important barriers that restrict the dispersal in some forest mammalian taxa (Soriano *et al.* 1999b, Gutiérrez *et al*. 2015). However, some studies in Colombia, have recorded species of non-volant small mammals, known previously only from the Cordillera de Mérida in Venezuela (*Neusticomys mussoi* and *Nephelomys meridensis*) (Rodríguez-Posada 2014, Villamizar-Ramírez *et al*. 2017). Also in Venezuela, some authors have documented the presence of taxa with geographic distributions in the Colombian Cordillera Oriental (*Heteromys australis* Thomas, 1901 and *Marmosa waterhousei* Tomes, 1860) (Anderson & Soriano 1999, Gutiérrez *et al*. 2011), and others have shown that between these ranges, there is not morphological and molecular differentiation of two red brocket deer species, *Mazama bricenii* Thomas, 1908 and *Mazama rufina* (Pucheran, 1851) (Gutiérrez *et al*. 2015). This evidence indicates that the Táchira depression should not be assumed as an absolute barrier for species apparently restricted to habitats of high elevations of the northern Andes (Gutiérrez *et al.* 2015).

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APPENDIX

Gazetteer and specimens examined. Collection localities for species of the *Rhipidomys fulviventer* group examined. Numbers correspond with records shown in Fig. 1. Localities of specimens not examined in this study are reported with their reference.

Rhipidomys ochoagrateroli **sp. nov.**

1. La Trampa del Tigre (type locality: 10°24'N - 68°48'W; 1940 m asl), sector El Silencio, Parque Nacional Yurubí, Sierra de Aroa, Estado Yaracuy (MZUC-970-75; 978-81, 1539); 2. Monumento Natural Pico Codazzi, Sector La Florida (10°25'N - 67°18'W; 2000 m asl), carretera vía El Limón, Estado Aragua (MZUC-900); 3. Monumento Natural Pico Codazzi (10°24'N - 67°20'W; 1827 m asl), Estado Aragua (MZUC-901); 4. Parque Nacional Henri Pittier, El refugio, Pico Guacamaya (10°22'N - 67°40'W; 1720 m asl), Estado Aragua: includes: Parque Nacional Henri Pittier, La Cumbre, Estado Aragua (EBRG-28304, 28305, 28306, 28307); 5. Parque Nacional El Ávila (10°33'N - 66°52'W; 2135 m asl), 9.4 km, Norte de Caracas, Distrito Federal (EBRG-15251): includes: Distrito Capital, Pico Ávila, near Hotel Humboldt (Tribe, 2015); 6. San Luis, Parque Nacional Juan Crisóstomo Falcón, sector Cumbre de Uría (11°13.581'N - 69°36.932'W; 1320 -1370 m asl), 9 km de Cabure (EBRG-24865).

Rhipidomys venustus

7. Hacienda Misisí (09°21'N - 70°18'W; 2210 m asl), 14 km E Trujillo, Estado Trujillo (EBRG-15253, 15254, 15255, 15256); 8. 5.5 km E and 2 km S Tabay (08°36'N - 71°01'W; 1530-2077 m asl), Parque Nacional Sierra Nevada, Estado Mérida (EBRG-15258); 9. Monte Zerpa (8°38'N - 71°09'W; 2100 -2160 m asl), 3 km N de Mérida, Estado Mérida (CVULA-1114, 1231, 1930, 2779; EBRG-28300, 28301, 28302, 28303). 10. El Blanquito (09°40'N - 69°37'W; 1600 m asl), 9 Km SE de Sanare, Parque Nacional Yacambú, Estado Lara (CVULA-2737); 11. Cerro Alto (8°49'N - 70°32'W; 1460 m asl), 2 km NO de la Soledad, Parque Nacional Sierra Nevada, Estado Barinas (CVULA-5937, 5938, 6135); 12. Laguna Brava, Páramo de Mariño (8°39.20'N - 70°53.56'W; 2090 m asl), Parque Nacional Sierra Nevada, Estado Mérida (CVULA-3282); 13. Mirabel (8°41'N - 71°26'W; 1500 m asl), 3 km SSE de la Azulita, Estado Mérida (CVULA-6073, 6074); 14. El Baho (8°50'N - 7 0°43'W; 3010 m asl), 5 km SO de Santo Domingo, Estado Mérida (CVULA-6145, 6157, 6158); 15. El Zumbador (7°58'N - 72°04'W; 2650 m asl), 8 km SSO de El Cobre, Parque Nacional General Juan Pablo Peñaloza, Estado Táchira (CVULA-5740); 16. Río Chama (08°33'N - 71°13'W; 1400 -2020 m asl): includes: Cafetos de Chama; montañas de Chama; Las Vegas del Chama [type locality]), Estado Mérida (Tribe 1996); 17. Mérida (08°35'N - 71°07'W; 2600 m asl), 3.1 km SE, 4.1 km SE de Mérida, Estado Mérida (Tribe, 1996); 18. Río Milla (08°38'N - 71°07'W; 1700 -3050 m asl): includes: Río Mucujún, ladera del Páramo San Antonio, Estado Mérida (Tribe 1996); 19. Montes del Valle (08°40'N - 71°06'W; 2000 m asl), Estado Mérida (Tribe 1996); 20. Monte Culata (08°45'N - 71°05'W; 4000 m asl), Parque Nacional Sierra de la Culata, Estado Mérida (Tribe 1996); 21. Tabay (08°37'N - 71°02'W; 2450-3160 m asl): includes: 4 km S and 6.5 km E Tabay; 6 km ESE of Middle Refuge; 2.9 km E, Mérida; 7 km SE Coromoto; La Mucuy, camino a la Coromoto, primer refugio, Estado Mérida (MBUCV-322; Handley 1976, Tribe 1996); 22. Lourdes (08°36'N - 71°00'W; 1630 m asl), Estado Mérida (Tribe 1996); 23. La Carbonera (08°38'N - 71°21'W; 2200 m asl), San Eusebio, Estado Mérida (MBUCV-323).

Rhipidomys fulviventer elatturus

24. 35 km S + 22 km O de San Cristóbal (Buena Vista) (07°27'N - 72°26'W; 2405 m asl), Parque Nacional El Tamá, Estado Táchira (EBRG-15241, 15242, 15243, 15244, 15245, 15246, 15247); 25. Páramo del Tamá (type locality: 07°25'N - 72°26'W; 2133 m asl), Parque Nacional El Tamá, Estado Táchira (Tribe 1996).

Rhipidomys fulviventer javiersanchezi

26. Hotel Humboldt (type locality: 10°33'N - 66°52'W; 2095 -2135 m asl; García *et al*. 2015), 9.4 km N de Caracas, Distrito Capital: includes: Pico Ávila, 5 km NNE de Caracas, cerca del Hotel Humboldt (EBRG-15248, 15249, 15250, 15252; Handley 1976, Tribe 1996). 27. Lagunazo (10°32'N - 66°50'W; 2100 m asl), Parque Nacional El Ávila, Distrito Capital (MHNLS-10619, 10618).

Rhipidomys fulviventer bisbali

28. La Trampa del Tigre (type locality: 10°24'N - 68°48'W; 1940 m asl; García *et al*. 2015), sector El Silencio, Sierra de Aroa, Estado Yaracuy (MZUC-1125, 1126).

Rhipidomys tenuicauda

29. 2 km N + 4 km W Caripe (cerca de San Agustín) (10°12'N - 63°32'W; 1170 -1340 m asl), Estado Monagas: includes: 2 km N + 4 km O de Caripe (La Laguna); Serranía de Turimiquire, cumbre cerro La Laguna, Estado Anzoátegui; Cueva del Guácharo, Caripe; San Agustín, 5 km NO de Caripe; Hacienda San Fernando;

Monagas, San Agustín (EBRG-15259, 15260,15261, 15262, 15263, 15264, 22872; MNHLS-8926; Tribe 1996); 30. Cerro Espejo (10°11'N - 63°32'W; 1600 m asl), Caripe, Estado Monagas (MBUCV-318); 31. Las Delicias (10°11'N - 63°28'W; 1400 m asl), Caripe, Estado Monagas (MBUCV-319, 320); 32. Caripe (10°10'N - 63°30'W; 100 - 500 m asl), cerca de San Agustín, Estado Monagas (MBUCV-321, 324); 33. Carapas (10°12'N - 63°56'W; 1710 m asl), Cerro Turimiquire, Estado Sucre (Tribe 1996); 34. Latal (10°10'N - 63°55'W; 945 m asl), Estado Sucre (Tribe 1996); 35. Los Palmales [= Palmares] (type locality: 10°17'N - 63°45'W; Tribe, 1996), Estado Sucre.

Rhipidomys wetzeli

36. 85 km SE de El Dorado (06°38'N - 61°33'W; 75 m asl), Estado Bolívar (EBRG-15236, 15237, 15238, 15239; Gardner 1990, Tribe 1995, 2015); 37. Churi-tepui (05°13'N - 61°54'W; 1495 m asl), Estado Bolívar (Tribe 1996, 2015); 38. Cerro Neblina, campamento II (00°50'N - 65°59'W; 2200 m asl), 2.5 km NE del Pico Phelps, Estado Amazonas (MBUCV-3311; serie tipo); 39. Cerro Neblina, campamento VII (type locality: 00°51'N - 65°58'W; 1800 -2000 m asl; Tribe 1996), Estado Amazonas (MBUCV-3519 to 3526; serie tipo); 40. Cerro Duida, cabecera del caño Culebra (03°34'N - 65°30'W; 1140 -1480 m asl; Tribe 2015), Estado Amazonas.