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The taxonomic status of *Oligoryzomys brendae* Massoia, 1998 (Rodentia, Cricetidae), with comments on the availability of this name

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Abstract

Oligoryzomys brendae was poorly described by Massoia in 1998 to include populations of the large form of *Oligoryzomys* that inhabits the Yungas and high altitudinal grasslands of northwestern Argentina, which were previously referred as *O. longicaudatus*, *O. stolzmanni*, *O. destructor* or *Oligoryzomys* sp. Contrary to some interpretations, we state that the name *O. brendae* is available, given that it fully accomplishes the requirements of the International Code of Zoological Nomenclature. We also present morphologic and genetic evidence showing that this taxon represents a distinct species and provide an emended diagnosis and re-description of it. In addition, the evidence at hand indicates that *O. brendae* is the only large-sized species of *Oligoryzomys* inhabiting northwestern Argentina.

Key words: Brenda's pigmy rice rat, Oryzomyini, Sigmodontinae, Tucumán, Yungas

Introduction

The genus *Oligoryzomys* Bangs, 1900 includes at least 19 species of small-sized, long tailed mice, widely distributed in the Neotropical Region (Musser & Carleton 2005). The alpha taxonomy of this genus is complex, being subject of constant changes in the taxonomic status of some nominal forms (e.g., Francés & D'Elía 2006; González Ittig *et al.* 2010; Agrellos *et al.* 2012) and descriptions of new species being moderately frequent (e.g., Weksler & Bonvicino 2005). At the same time, the alpha taxonomy of *Oligoryzomys* is full of dubious statements about the taxonomic status of several nominal species, especially those from forested tropical and subtropical areas. A clear example of the latter scenario is that concerning populations of a large-sized form that inhabits the Yungas and high altitudinal grasslands of northwestern Argentina (Cirignoli *et al.* 2006; Jayat *et al.* 2008, 2009; González Ittig *et al.* 2010). At first, these animals were included within the concept of *O. longicaudatus* (Bennet 1832) (e.g., Cabrera 1961; Mares *et al.* 1981; Ojeda & Mares 1989). However, morphological, karyological and phylogenetically analyzed molecular data clearly separate northwestern Argentinean populations from *O. longicaudatus* (e.g., González Ittig *et al.* 2002; Rivera *et al.* 2007). Espinosa & Reig (1991), mostly based on karyological analysis, provisionally referred these populations to *O. stolzmanni* (Thomas 1894), a form included under *O. destructor* (Tschudi 1844) by Carleton & Musser (1989). In consequence, subsequent authors have used the name of *O. destructor* to allocate these large-sized populations of *Oligoryzomys* from northwestern Argentina (e.g., Capllonch *et al.* 1997; Díaz & Barquez 2007). An additional quote of complexity was established with the description of a new species to encompass these populations. The binomial form *Oligoryzomys brendae* was

erected by Massoia (1998), with type locality on "...Tucumán (localidad típica: Cerro San Javier, Dpto. Tafí Viejo) (aprox. 1000 m. de altura)...". The description of this form is, unfortunately, extremely poor for current and even for those days' standards (see Appendix 1). It includes only four external measurements and mentions only two cranial character states. *Oligoryzomys brendae* was considered as a distinct species, and as such, as nomenclatorially available, by Musser & Carleton (2005), Pardiñas & Jayat (2008), Reeder *et al.* (2007) and Jayat *et al.* (2011a). A different view was expressed by Cirignoli *et al.* (2006) and Palma *et al.* (2010), which considered the possible condition of *O. brendae* as a *nomen nudum*. Cirignoli *et al.* (2006), who did not develop their argument about the availability of the name, used the name. In turn, Palma *et al.* (2010) considered the name *O. brendae* as not available in nomenclatural terms and referred those populations from northwestern Argentina as *Oligoryzomys* sp. 1. To further complicate this scenario, several authors recognized the presence of both *O. brendae* and *O. destructor* (e. g., Musser & Carleton 2005; Cirignoli *et al.* 2006) or *O. destructor* and *O. longicaudatus* (e. g., Braun & Díaz 1999; Díaz 2000; Díaz *et al.* 2000) in northwestern Argentina, leaving doubts about the presence of one or more large-sized species of *Oligoryzomys* in this area.

The clarification of the taxonomic status of populations of *Oligoryzomys* inhabiting the Yungas and high altitudinal grasslands of northwestern Argentina is not only of importance for basic biological issues (e.g., biogeography, ecology), but also for epidemiological reasons given that *Oligoryzomys* is the main reservoir of hantavirus in the New World (e.g., Delfraro *et al.* 2008), which is known to cause severe cases of Hantavirus pulmonary syndrome (HPS; Rivera *et al.* 2007). Moreover, in northwestern Argentina there are records of several strains of this virus, such as Bermejo and Oran, which are known to cause HPS (Levis *et al.* 1998).

In this work, we present evidence showing that *O. brendae* Massoia, 1998 represents a distinct species of *Oligoryzomys*, and provide an emended diagnosis and a re-description of this taxon. In addition, we made some comments about the nomenclatural availability of this name.

Material and methods

Nomenclature used to describe the skull follows Carleton & Musser (1989), Musser *et al.* (1998) and Weksler (2006) and that of the molars corresponds to Reig (1977). For comparative purposes, we studied large series of specimens of *Oligoryzomys* from northwestern Argentina (Appendix 2), including the holotype (Colección Elio Massoia [CEM] 482: skin and skull without mandible) and paratype (CEM 483; skin and skull without mandible) of *O. brendae*. Individuals were classified according to the age criterion delineated by Myers & Carleton (1981), based on tooth wear. Four external and 12 cranial dimensions were recorded (see Table 1 for measurements definitions and abbreviations); external measurements were obtained from specimen labels and collector catalogues, while craniodental dimensions (following the landmarks defined and illustrated by Musser *et al.*, 1998) were taken with a manual caliper (to the nearest 0.1 mm). A principal component analysis was conducted using the software STATISTICA (StatSoft 2001), performed on the 12 craniodental measurements, and considering specimens (n = 32) of age class 2-3 without missing values; this sample included representatives of *O. flavescens* (Waterhouse) given it is the only species of *Oligoryzomys* sympatric with the large-sized form at northwestern Argentina. Principal components were extracted from a variance-covariance matrix and computed by using the craniodental variables after transformation to their natural logarithms.

Phylogenetic analyses and genetic comparisons were based on the first 801 base pairs of the mitochondrial gene that codes for cytochrome *b*. Sequences of 49 specimens belonging to 23 forms of *Oligoryzomys* were analyzed (Table 2). This sampling includes 11 sequences recovered from large-sized *Oligoryzomys* specimens collected at northwestern Argentina. All sequences, except seven, were retrieved from GenBank. Sequences produced by us were obtained following the laboratory protocol outlined in Cañon *et al.* (2010) using the Wizard Genomic DNA Purification Kit (Promega) and primers MVZ 05 and MVZ 16 (da Silva & Patton, 1993) with the following conditions: 94°C for 3 min; 35 cycles of 94°C for 20 s, 45°C for 15 s, 72°C for 60 s, and 72°C for 7 min. Amplicons were sequenced using an external sequencing service (Macrogen, Inc. Korea). New sequences were deposited in Genbank with accession numbers JX154129 to JX154135. Outgroups included sequences from *Microryzomys minutus* (AF108698), *Neacomys spinosus* (EU579504), *Oreoryzomys balneator* (EU579510), and *Pseudoryzomys simplex* (EU579517); the former three taxa belongs to genera that together with *Oligoryzomys* form a strongly supported clade within the oryzomyine radiation; while the later falls in the sister clade of the clade containing *Oligoryzomys* (Weksler 2003). Sequence alignment was done with Clustal X (Thompson *et al.* 1997)

using the default parameter values. Reported genetic distances correspond to observed (p) distances calculated with MEGA 5 (Tamura *et al.* 2011). Phylogenetic analyses were done using the Maximum likelihood (ML; Felsenstein 1981) and parsimony (MP; Farris 1982) criteria. ML analysis was conducted in Treefinder (Jobb *et al.* 2004; Jobb 2008). The best fitting model of nucleotide substitution (a transition model [Rodriguez *et al.* 1990] noted in Treefinder as J2[Optimum,Empirical]:G[Optimum]:5; see Jobb 2008) was selected with the Akaike information criterion in Treefinder using the “propose model” routine. We estimated the best tree under the model of nucleotide substitution previously selected using the most exhaustive search algorithm implemented in Treefinder (level 2; see Jobb 2008: 44) as implemented in Treefinder version March 2011; nodal support was estimated with 1000 bootstrap pseudoreplicates (BL). MP analysis was done in PAUP* (Swofford 2000) with characters treated as unordered and equally weighted, 500 replicates of heuristic searches with random addition of sequences, and tree bisection reconnection (TBR) branch swapping. Relative support of the recovered clades was calculated with 1000 bootstrap pseudoreplicates (BP) with three random sequence additions per pseudoreplicate.

TABLE 1. External and craniodental measurements (in mm) of *Oligoryzomys brendae* from northwestern Argentina of age class 2 (mean \pm standard deviation and [range]).

	CEM 482 (holotype)	CEM 483 (paratype)	<i>Oligoryzomys brendae</i> (n = 21)
Head and body length [HBL]	87	108	89.7 \pm 5.7 [78–101]
Tail length [TL]	130	143	126 \pm 6.9 [112–135]
Hind foot length (with claw) [HFL]	25*	24*	26.5 \pm 0.9 [24–28]
Ear length [EL]	18	19	18.2 \pm 0.8 [17–20]
Condylolincisive length [CIL]	22.8	22.1	22.9 \pm 0.9 [21.5–24.5]
Diastema length [DL]	6.1	6.1	5.8 \pm 0.3 [5.1–6.4]
Palatal bridge [PB]	4.30	4.20	4.3 \pm 0.2 [3.9–4.8]
Maxillary toothrow length [MTL]	3.80	3.90	3.9 \pm 0.1 [3.5–4.1]
Incisive foramina length [IFL]	4.80	4.90	4.7 \pm 0.3 [4.3–5.1]
Zygomatic plate breadth [BZP]	2.70	2.40	2.6 \pm 0.3 [2.2–3.1]
Zygomatic breadth [ZB]	13.80	13.80	13.7 \pm 0.4 [12.8–14.5]
Braincase breadth [BB]	11.90	12.10	12.1 \pm 0.3 [11.5–12.6]
Interorbital constriction [IOB]	3.80	3.70	3.8 \pm 0.1 [3.4–4.0]
Mid rostral width [RW2]	4.80	4.90	4.6 \pm 0.2 [4.3–4.9]
Nasal length [NL]	9.10	9.50	9.1 \pm 0.6 [8.1–10.8]
Breadth across exoccipital condyles [BOC]	6.10	6.10	5.9 \pm 0.1 [5.7–6.3]

*Massoia (1998) do not explained if these measurements include or not the claw; usually, Massoia reported the length without claw.

TABLE 2. List of specimens included in the phylogenetic analysis. For each terminal species, catalog and GenBank accession numbers are provided. Taxonomy follows that of Agrellos *et al.* (2012), except for the three unnamed forms that are listed here as 1, 2, and following Palma *et al.* (2010) as B. Sequences marked with asterisks were gathered in this study.

	Species	Catalog number	Accession number
1	<i>Oligoryzomys andinus</i>	AMNH 230986	L37400
2	<i>Oligoryzomys brendae</i>	PIDBA 986	GU185900
3	<i>Oligoryzomys brendae</i>	Jy 1245	GU185901
4	<i>Oligoryzomys brendae</i>	MIC 210	EU192167
5	<i>Oligoryzomys brendae</i>	MIC 211	EU192168
6	<i>Oligoryzomys brendae</i>	JPJ 1311	JX154129 *

.....continued on the next page

TABLE 2. (Continued)

	Species	Catalog number	Accession number
7	<i>Oligoryzomys brendae</i>	JPJ 1055	JX154130 *
8	<i>Oligoryzomys brendae</i>	JPJ 2163	JX154131 *
9	<i>Oligoryzomys brendae</i>	JPJ 2375	JX154132 *
10	<i>Oligoryzomys brendae</i>	JPJ 2423	JX154133 *
11	<i>Oligoryzomys brendae</i>	JPJ 2219	JX154134 *
12	<i>Oligoryzomys brendae</i>	JPJ 1188	JX154135 *
13	<i>Oligoryzomys chacoensis</i>	TK 62932	EU258543
14	<i>Oligoryzomys chacoensis</i>	Or 22498	GU185904
15	<i>Oligoryzomys costaricensis</i>	TK 163369	GU393988
16	<i>Oligoryzomys costaricensis</i>	NK 101588	EU192164
17	<i>Oligoryzomys delicatus</i>	TK 138080	DQ227457
18	<i>Oligoryzomys delicatus</i>	AMNH 257262	GU126529
19	<i>Oligoryzomys destructor</i>	TEL 1481	GU393991
20	<i>Oligoryzomys destructor</i>	TEL 1479	EU258544
21	<i>Oligoryzomys destructor</i>	NK 22846	EU192171
22	<i>Oligoryzomys flavescens</i>	UP 51	GU185924
23	<i>Oligoryzomys flavescens</i>	PV 27	GU185921
24	<i>Oligoryzomys fornesi</i>	MN 36746	DQ826022
25	<i>Oligoryzomys fornesi</i>	MN 36928	DQ826023
26	<i>Oligoryzomys fulvescens</i>	ASNHC 1665	EU294233
27	<i>Oligoryzomys fulvescens</i>	ASNHC 1666	EU294234
28	<i>Oligoryzomys longicaudatus</i>	MVZ 154463	GU393998
29	<i>Oligoryzomys longicaudatus</i>	NK 95268	AY275697
30	<i>Oligoryzomys magellanicus</i>	IPAT	AY275705
31	<i>Oligoryzomys messorius</i>	MN 37751	DQ826024
32	<i>Oligoryzomys microtis</i>	MVZ 190401	HM594624
33	<i>Oligoryzomys microtis</i>	BYU 19014	AY439000
34	<i>Oligoryzomys moojeni</i>	MN 36832	DQ826019
35	<i>Oligoryzomys moojeni</i>	MN 50287	JQ013772
36	<i>Oligoryzomys nigripes</i>	MN 37531	DQ825996
37	<i>Oligoryzomys nigripes</i>	UFPB 357	DQ826004
38	<i>Oligoryzomys rupestris</i>	MN 50322	JQ013763
39	<i>Oligoryzomys rupestris</i>	MN 50326	JQ013764
40	<i>Oligoryzomys</i> sp. 1	TK 17858	EU258546
41	<i>Oligoryzomys</i> sp. 1	MN 37756	DQ826025
42	<i>Oligoryzomys</i> sp. 2	UFES 1442	HM594618
43	<i>Oligoryzomys</i> sp. B	MUS A2625	EU192159
44	<i>Oligoryzomys stramineus</i>	UFPB 1827	DQ826027
45	<i>Oligoryzomys stramineus</i>	MN 46410	JQ013747
46	<i>Oligoryzomys utiaritensis</i>	MN 75612	JQ013776
47	<i>Oligoryzomys utiaritensis</i>	MN 75598	JQ013760
48	<i>Oligoryzomys vegetus</i>	BYU 15215	EU294252
49	<i>Oligoryzomys vegetus</i>	BYU 15217	EU294251
50	<i>Oreoryzomys balneator</i>	AMNH 268144	EU579510
51	<i>Microryzomys minutus</i>	MVZ 173975	AF108698
52	<i>Neacomys spinosus</i>	MVZ 155014	EU579504
53	<i>Pseudoryzomys simplex</i>	GD 065	EU579517

Results and discussion

Maximum likelihood analysis recovered a well-resolved topology (lnL = -6500.1432; Fig. 1), as the maximum parsimony analysis (70 shortest trees of 1224 steps; consistency index = 0.362; retention index = 0.666) did. There is only one polytomy involving lineages of species level; however, as indicated by Bootstrap values, there are several interspecific relationships weakly supported. Not surprisingly, topologies of both analyses disagree in these weakly supported relationships (Fig. 1). All species, but *O. longicaudatus* in the MP analysis that collapse to a polytomy with *O. magellanicus*, are recovered monophyletic. *Oligoryzomys* appears well supported (BL = 94; BP = 87). Haplotypes of northwestern Argentinean large-sized *Oligoryzomys* form a strongly supported clade (BL = 93; BP = 100). To this clade belongs one haplotype recovered from a specimen collected at Parque Biológico Sierra de San Javier (JPJ 1188), type locality of *O. brendae* (Tucumán, Cerro San Javier, Dpto. Tafí Viejo), and one additional haplotype recovered by González-Ittig et al. (2010) from one individual taken at El Siambón, less than 10 km of that locality and in the same Yungas habitat. The clade of Argentinean haplotypes is sister to an haplotype recovered from a Bolivian specimen from Tinkusiri (Depto. Cochabamba) identified as *O. destructor* by Palma et al. (2010). This clade has good support (BL = 81; BP = 80), but observed divergence between Argentinean and Bolivian samples reaches the high value of 9.8 %. Remarkably, haplotypes of two Ecuadorian specimens identified as *O. destructor* by Hanson et al. (2011) are distantly related to the just mentioned clade and appear as sister (BL and BP < 50) to *O. rupestris*. The clade of Ecuadorian *O. destructor* and *O. rupestris* is nested in a large clade (BL and BP < 50) that encompass other 14 forms of *Oligoryzomys* (16 including *O. destructor* and *O. rupestris*) of which the northwestern Argentinean large-sized *Oligoryzomys* is not part. In other words, the large-sized form of northwestern Argentina is distantly related to Ecuadorian *O. destructor* (Fig. 1). In addition, observed percentage of sequence divergence between the northwestern Argentinean sample of large-sized *Oligoryzomys* and Ecuadorian *O. destructor* is 9.9 %; this value is 13.4 % when the comparison involves the Bolivian and Ecuadorian samples of *O. destructor*. As such, phylogenetic analysis based on cytochrome *b* gene sequences suggests that, in its present conception (e.g., Musser & Carleton, 2005), *O. destructor* is a complex of two or more morphologically similar forms.

TABLE 3. Results of a Principal Components Analysis of 11 craniodental measurements of adult specimens of *Oligoryzomys* (age class 2; n = 32). See Table 1 for the explanation of the abbreviations.

	PC 1	PC 2	PC 3
CIL	-1.63525	-0.027318	0.129267
DL	-0.40764	-0.058170	0.113285
PB	-0.24654	-0.010592	0.055498
MTL	-0.20453	0.083645	-0.066084
IFL	-0.33044	0.019215	0.029277
BZP	-0.37953	0.004760	0.031099
ZB	-0.88211	0.110590	-0.047466
BB	-0.54411	0.233159	-0.129923
IOB	-0.09184	0.078284	-0.049558
RW2	-0.38348	0.054496	-0.065742
NL	-0.69539	-0.297347	-0.196841
Eigenvalue	4.909296	0.175737	0.103472
% variance	90.86589	3.25270	1.91516

Our examination of the holotype and paratype of *O. brendae* and its comparison with large series of *Oligoryzomys* from northwestern Argentina, including those referred in the literature as *O. destructor* (e.g., Capllonch et al. 1997; Díaz & Barquez 2007) or *Oligoryzomys* sp. (Jayat et al., 2008, 2011a), as well as with sympatric species (i.e. *O. flavescens*), and other supposedly related forms now allocated under *O. destructor* indicates that *O. brendae* is morphologically distinct from all other congeneric and that only one form of large-

sized *Oligoryzomys* inhabits northwestern Argentina. The PCA analysis (Fig. 2) shows no overlap on multivariate space between the large and small (*O. flavescens*) forms of *Oligoryzomys* present in northwestern Argentina, nesting the holotype and paratype of *O. brendae* within the multivariate space of the large form. First three principal component summarize 96 % of the total variation but only the first (PCI, 90.8 % of the explained variance) was statistically significant (Table 3). This was clearly a size component, as the variables with the heaviest load on PCI were CIL and NL. The second component separated individuals mainly by BB and ZB.



FIGURE 1. Maximum likelihood tree (ln = -6500.1432) resulting from the analysis of cytochrome *b* gene sequences of *Oligoryzomys* species. Numbers indicate bootstrap values of the adjacent node retrieved in the maximum likelihood (left to the diagonal) and maximum parsimony (right to the diagonal) analyses. A less-than sign (<) indicates that the given clade receives less than 50 % of Bootstrap either in the ML and/or MP analyses. A dash (-) indicates that in the MP analysis that clade was not recovered. GenBank accession numbers of analyzed sequences are included at terminal labels; in addition, specimen numbers are provided for *O. brendae*.

Peruvian specimens collected near the type locality of *O. destructor* (= haciendas along the “Río Chinchao, Huanuco Province”, 900-1000 m [see the discussion in Hershkovitz 1940:81]; according to Musser & Carleton [2005] a formal fixation is pending), are characterized by a diploid complement of $2n = 60$ and $FN = 76$ (reported by Gardner & Patton [1976] as *Oryzomys longicaudatus* variant [4]; see Musser & Carleton 2005). This karyotype differs from that of individuals from Jujuy and Tucumán (including specimens collected near the type locality of *O. brendae*) in Argentina that present a $2n = 58$, $FN = 74$ (Espinosa & Reig 1991; these karyotyped specimens are now housed at the MMPMa, see appendix 2 [D. Romero, com. pers.]).

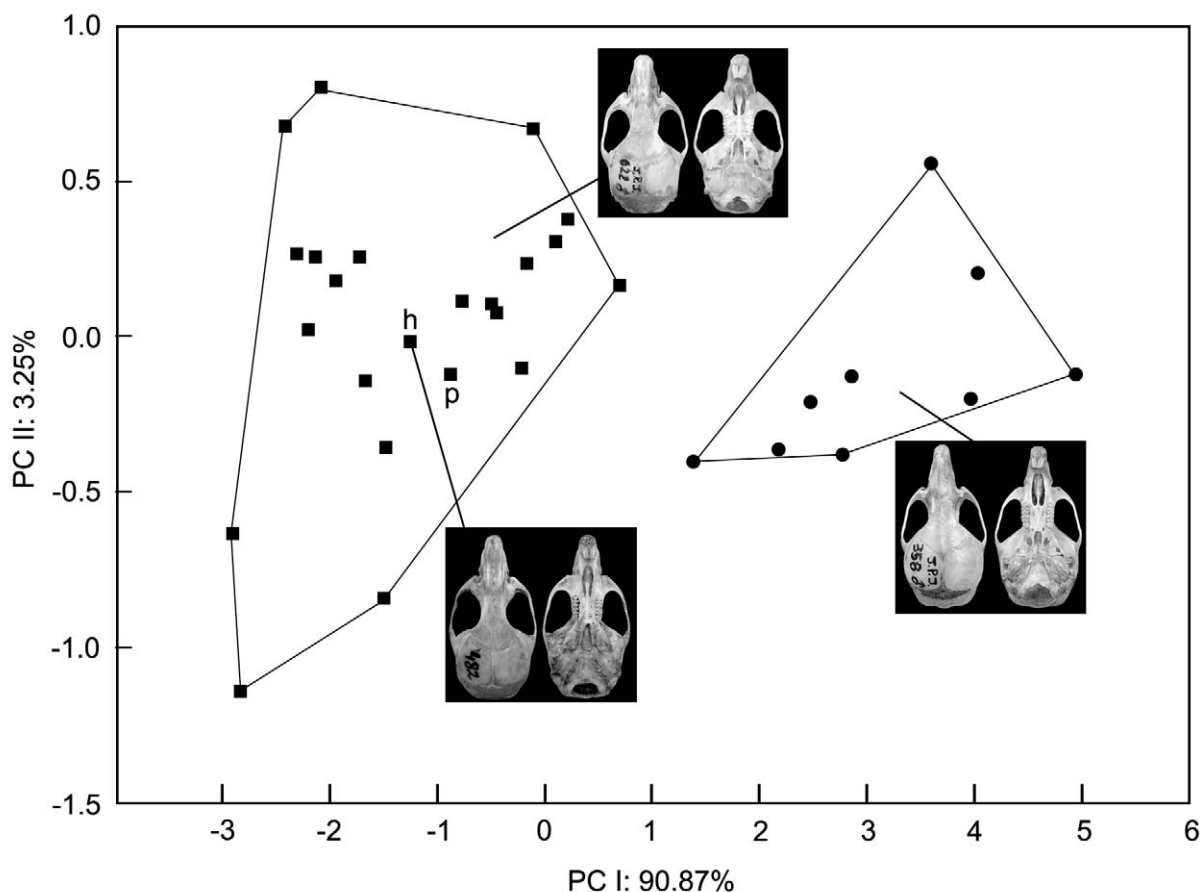


FIGURE 2. Specimen scores of individuals of *Oligoryzomys* (age class 2) for principal components 1 and 2 extracted from a variance-covariance matrix of 12 craniodental distances (see Table 1). Symbols are: squares = *O. brendae*; circles: *O. flavescens*. Abbreviations: h = holotype of *O. brendae* (CEM 482); p = paratype of *O. brendae* (CEM 482).

Taking all of these antecedents together, we consider that only one form of large-sized *Oligoryzomys* is present in northwestern Argentina and that it is distinct from other species of *Oligoryzomys*. For these reasons detailed below we use the name *O. brendae* to this form.

Nomenclatural remarks. In a recent contribution, Palma *et al.* (2010: 561) referred large-sized populations of *Oligoryzomys* from northwestern Argentina under the informal concept of “*Oligoryzomys* sp. 1” and stated that “no formal description for *O. brendae* is yet available (the citation in Musser & Carleton refers to a meeting presentation), and hence this name as published constitutes a *nomen nudum*”. However, the description of *O. brendae* was published on a book edited by the *2do. Congreso Argentino de Zoonosis, 1er Congreso Argentino y Latinoamericano de Enfermedades Emergentes y Asociación Argentina de Zoonosis* (the first of a series that now has four volumes; see Cacchione *et al.* 2008), entitled *Temas de Zoonosis y Enfermedades Emergentes*, and not in the volume of the meeting abstracts (i.e., Libro de Resúmenes of 2° Congreso Argentino de Zoonosis, 1° Congreso Argentino de Enfermedades emergentes, 1° Congreso Latinoamericano de Enfermedades Emergentes 1998). Therefore, the binomial *O. brendae* accomplishes the basic premises for publication criteria indicated in the International Code of Zoological Nomenclature (ICZN 1999; see Articles 7 to 9). Even when the given diagnosis of *O. brendae* is brief and scarcely informative (see Appendix 1), Massoia (1998: 243–244 and Cuadro 1) clearly stated that he was coining a new name of species rank and that it was applied to the large-sized species of *Oligoryzomys* that inhabits the Yungas of northwestern Argentina. In turn, if published after 1930 a name is unavailable if does not accomplish the statements of Article 13 of the Code (ICZN 1999); clearly, this is not the case of *O. brendae*. Therefore, as already mentioned by Musser & Carleton (2005), we state that the name *Oligoryzomys brendae* Massoia, 1998 is (contra Palma *et al.* 2010) available for use in zoological nomenclature. As such, we use it for the single large-sized long-tailed mouse that inhabits the extreme south of the neotropical montane cloud forest or Yungas. Given that *O. brendae* was poorly described by Massoia (1998), we provide an emended diagnosis and a re-description of it.

Oligoryzomys brendae Massoia, 1998

Type locality: "...Tucumán (localidad típica: Cerro San Javier, Dpto. Tafí Viejo) (aprox. 1000 m. de altura)..." = Argentina, Tucumán, Tafí Viejo, Cerro San Javier (ca. -26.78°, -65.37°).

Emended diagnosis. A member of the sigmodontine genus *Oligoryzomys* characterized by the following combination of characters: size large for the genus (HBL: 90 mm; CIL: 22.9, MTL: 3.9, BB: 12.1; all measurements in average); dorsal coloration orangish brown, with somewhat grizzled appearance; ventral hairs basally grey and whitish to ochraceous at the tip; ears short, rounded, and dark brown; tail longer than head and body and sharply bicolored; skull (Fig. 3) relatively robust, with a short and broad rostrum, well expanded zygomatic arches and a braincase inflated and broad; interorbital constriction narrow and hourglass shaped, with slightly defined supraorbital ridges; incisive foramina relatively long, posteriorly extended to the anterior border of M1; karyotype with $2n = 58$, $FN = 74$.

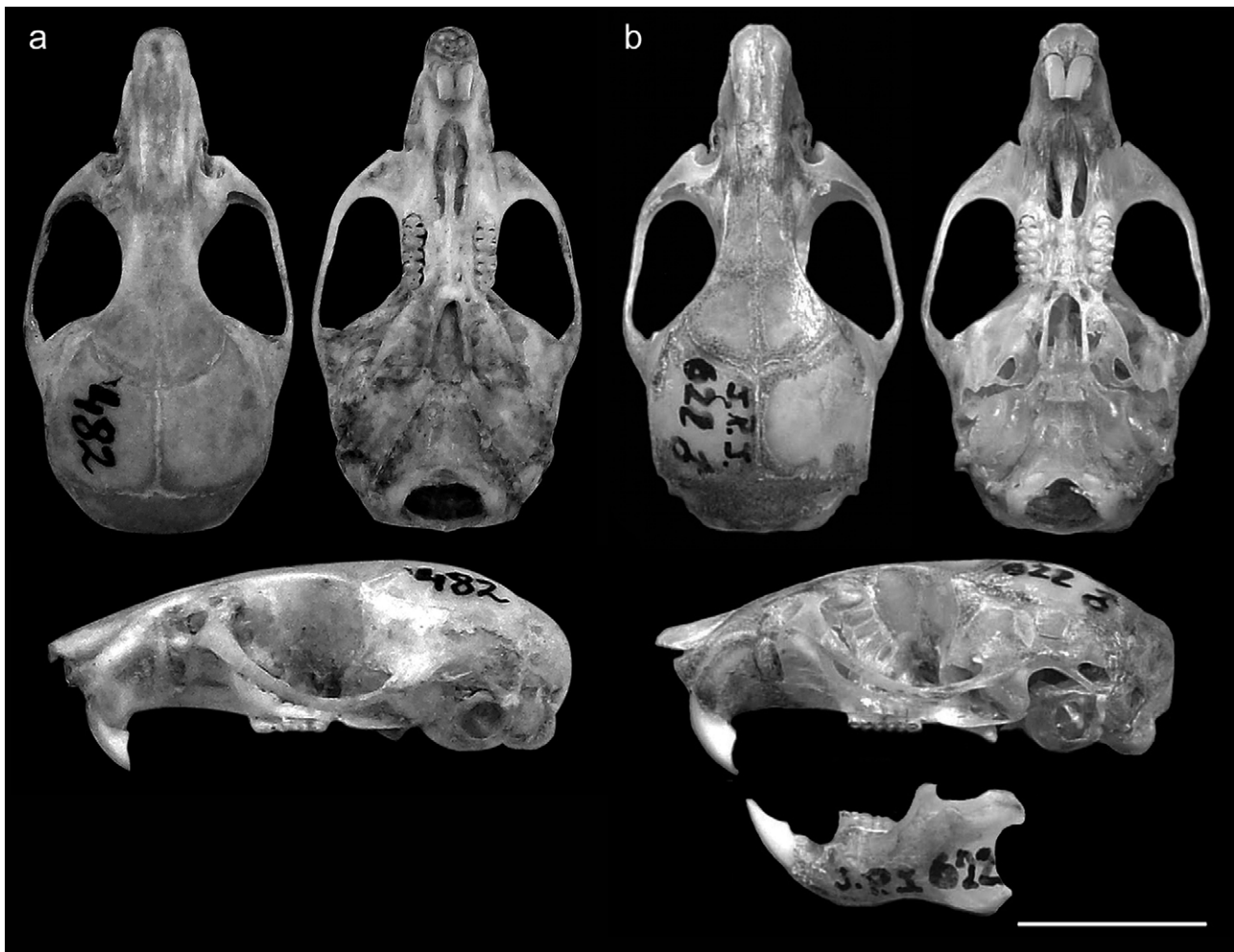


FIGURE 3. Dorsal, ventral and lateral views of the skull and labial view of the mandible of two specimens of *Oligoryzomys brendae* (a, holotype, CEM 482; b, JPI 622). Scale = 10 mm.

Distribution. *Oligoryzomys brendae* is mainly found in forested and highland grassland environments of the Yungas between 700 and 2900 m elevation, from northernmost Salta province southward to Catamarca, Argentina. Additionally, we recently recorded the species further south in La Rioja province where it is restricted to isolated humid ravines at the ecotone between the xeric Chaco Seco and Monte desert formations. Jayat *et al.* (2011b) cited a large species of *Oligoryzomys* for the Famatina range in La Rioja province; nevertheless, the specimens from Pampa de la Viuda reported here (see Appendix 2) constitute the first unequivocal mention of *O. brendae* for the province of La Rioja.

Description. *Oligoryzomys brendae* is a large-sized species within the genus (Figs. 3, 4; Table 1); its dorsal pelage is soft, and dense; individual hairs have gray bases and ochraceous to reddish tips, giving a general grizzled

orangish-brown appearance, slightly darker at the head and midline and orangish towards the cheeks and flanks. Cover hairs are 10 to 12 mm long, being larger in the mid rump region; guard hairs are longer and darker, projecting 3–4 mm beyond the fur in the rump. Ventral hairs are basally grey and whitish to ochraceous at the tip. Ears are short, rounded, and dark brown in coloration; its inner surface is covered by short brown hairs with yellowish tips. Eyes are large and are surrounded by a conspicuous ring of dark brown hairs. Mystacial vibrissae are abundant and moderately long, reaching or slightly surpassing the base of the ear. Interamial and submental vibrissae are short and white. Fore and hindfoot are dorsally covered by short white hairs. Ungueal tuft are whitish and slightly larger than claws. The tail is longer than head and body and sharply bicolored, dark grey dorsally and whitish in the belly.

The skull (Fig. 3) is relatively robust, with a short and broad rostrum, well expanded zygomatic arches and braincase inflated and broad. Nasals are slightly expanded in its distal third. The interorbital constriction is narrow and hourglass shaped, with slightly defined supraorbital ridges. Temporal and mastoid crests are scarcely developed. The zygomatic notches are wide and deep. The dorsal profile of the skull is nearly convex. Zygomatic plate is broad, with its anterior margin nearly straight and the upper root slightly slanted. Long and delicate hamular process separates a well developed postglenoid foramen from a small subsquamosal fenestra. Incisive foramina are relatively long, posteriorly extended to the anterior border of M1. Mesopterygoid fossa is broad, with straight and slightly divergent lateral borders; its anterior margin is well behind the posterior plane defined by the M3. Posterolateral palatal pits are rounded and large, located nearly the anterior border of the mesopterygoid fossa. Parapterygoid fossae are wide and relatively deep, with convex external borders. Auditory bullae are inflated and with relatively broad and long eustachian tubes. The associate foramina of the otic capsules and cephalic arterial patterns do not differ from the typical condition seen in other *Oligoryzomys* species and fully described by Carleton & Musser (1989). Both specimens lack alisphenoid strut, sphenofrontal foramen and the accompanying squamosal-alisphenoid groove.

The mandible is robust and comparatively deep. The masseteric crest is well developed, with their anterior end situated above the mental foramen and extending at the level or slightly beyond the anterior border of m1. The capsular projection is strongly developed and situated below a shallow sigmoid notch. The coronoid process is comparatively broad and very short, extending slightly above the level of the condyle. The angular process is also heavily constructed and does not surpass posteriorly the level of the condyle.

Upper incisors are ungrooved and opistodont, with orange enamel in its anterior surface. Molars are pentalophodont and brachyodont, with the lingual cusps slightly anterior to the labial ones; the anteromedian flexus is deep and defines prominent anterolingual and anterolabial conules; the anteroloph and parastyle are comparatively short and broad; the mesoloph and mesostyle are well developed and the posteroloph is near to metacone. The M2 is nearly as a truncate oval and closely resembled M1 except for the lack of a well developed procingulum. The M3 is small and in both specimens it has a large inner enamel island. Procingulum and anterolabial cingulum on m1 are well developed; anteromedian flexid is expressed only in young specimens. The anterolophid-metastylid and mesolophid-mesostylid are very short and the posterolophid is well developed. In the m2 the procingulum is vestigial, the mesostylid is small and the posterolophid is well developed. The m3 is large, reaching 50% of the m2, with anterolabial cingulum and ectostylid vestigial.

Morphological comparisons. Our examination of the holotype and paratype of *O. brendae* and large series of *Oligoryzomys* from northwestern Argentina allow us to state that there are only one large-sized form of *Oligoryzomys* inhabiting forested and high altitudinal grasslands areas of northwestern Argentina. This species is *Oligoryzomys brendae*, which differs from the sympatric *O. flavescens* by its larger size, darker ears, absence of white hairs in chin and throat, broader rostrum, broader zygomatic notches and more expanded zygomatic arches.

Oligoryzomys chacoensis (Myers & Carleton, 1981), that is found at lower elevations and Chacoan environments, has conspicuously posteriorly divergent interorbital edges, being intermediate in size between *O. brendae* and *O. flavescens*, and having a more strong orangish dorsal fur that contrast with the whitish underside. A small but distinctive tuft of orangish hairs are anterior to the relatively larger ears. Furthermore, hairs on chin and throat are white to the base. Compared with specimens from populations referred to *O. destructor*, *O. brendae* has longer ears (17–20 mm, vs. 12–14 mm [Peru], 14–17 [Ecuador] and 15–17 [Bolivia]), larger hindfeet (24–28 mm, vs. 22.5–24.5 [Peru], 22–25 [Ecuador] and 19–25 [Bolivia]) and a wider braincase (11.5–12.6 mm, vs. 11.4 mm [Peru], 10.4–11.2 [Ecuador] and 10.4–11.8 [Bolivia]; see Osgood, 1914; Hershkovitz, 1940; Olds & Anderson, 1987; Anderson, 1997). Bolivian populations have more grayish venters (cf. Olds & Anderson, 1987), while

Peruvian and Ecuadorian forms (including true *O. destructor*, and the nominal forms *stolzmanni*, *spodiurus* and *melanostoma*) are more reddish to ochraceous dorsally and brighter colored (Thomas, 1926a, 1926b; Hershkovitz, 1944; Olds & Anderson, 1987). It is worth noting that specimens referred by Hanson *et al.* (2011) to *O. destructor* (TEL 1479, 1481; assessed via photographs), and included in our phylogenetic analysis, match the description of the Ecuadorian populations made by Hershkovitz (1944) under *Oryzomys (Oligoryzomys) spodiurus* (= *O. destructor*, see Musser & Carleton, 2005) in having narrow nasals, expanded palatine foramina, long molar tooththrows, wide palates and mesopterygoid fossae, narrow zygomatic arches and grayish tails.



FIGURE 4. Dorsal (a) and ventral (b) external views of the holotype (CEM 482, at the right) and paratype (CEM 483, at the left) of *Oligoryzomys brendae*.

Genetic variation. Our sampling of *O. brendae* was not large enough to constitute a phylogeographic analysis, but our results provide a preliminary view on the geographic structure of the genetic variation of this species. We analyzed 12 sequences gathered at six localities from the Yungas of Catamarca, Tucumán, Salta and Jujuy provinces and two from Monte-Chaco Seco ecotone of La Rioja province, in northwestern Argentina. These haplotypes are quite similar, differing on average by an observed value of only 0.9 %. In addition, despite of the large geographic coverage of the sample covering more than 700 km (ca. six latitudinal degrees), and several environmental discontinuities (e.g., large rivers, xeric habitats) among the analyzed populations, there is a lack of phylogeographic structure in the analyzed sample (Fig. 5). These two facts reinforce the notion that only one species of large-sized *Oligoryzomys*, *O. brendae*, inhabits eastern mountain ranges of northwestern Argentina. The lack of phylogeographic structure of *O. brendae* resembles the pattern of *A. spegazzini* (Jayat *et al.* 2010), that has a similar distributional pattern, while contrasts with that shown by *Necromys lactens* (D'Elía *et al.* 2008) over roughly the same distributional range but mainly restricted to the high altitudinal grasslands of the Yungas. The clarification of causes behind these similitude and difference awaits further studies with larger samplings. Notwithstanding, the environmental history of the region (Iriondo, 1993; Ortiz *et al.*, 2011 and references therein) and the ecological requirements of these species, with *N. lactens* inhabiting open and isolated highland habitats (Jayat & Pacheco, 2006), and *O. brendae* (Jayat *et al.*, 2008, as *Oligoryzomys* sp.) and *A. spegazzinii* (Jayat *et al.*, 2010) occurring in more continuous forested habitats, can explain, at least in part, the observed phylogeographic differences.

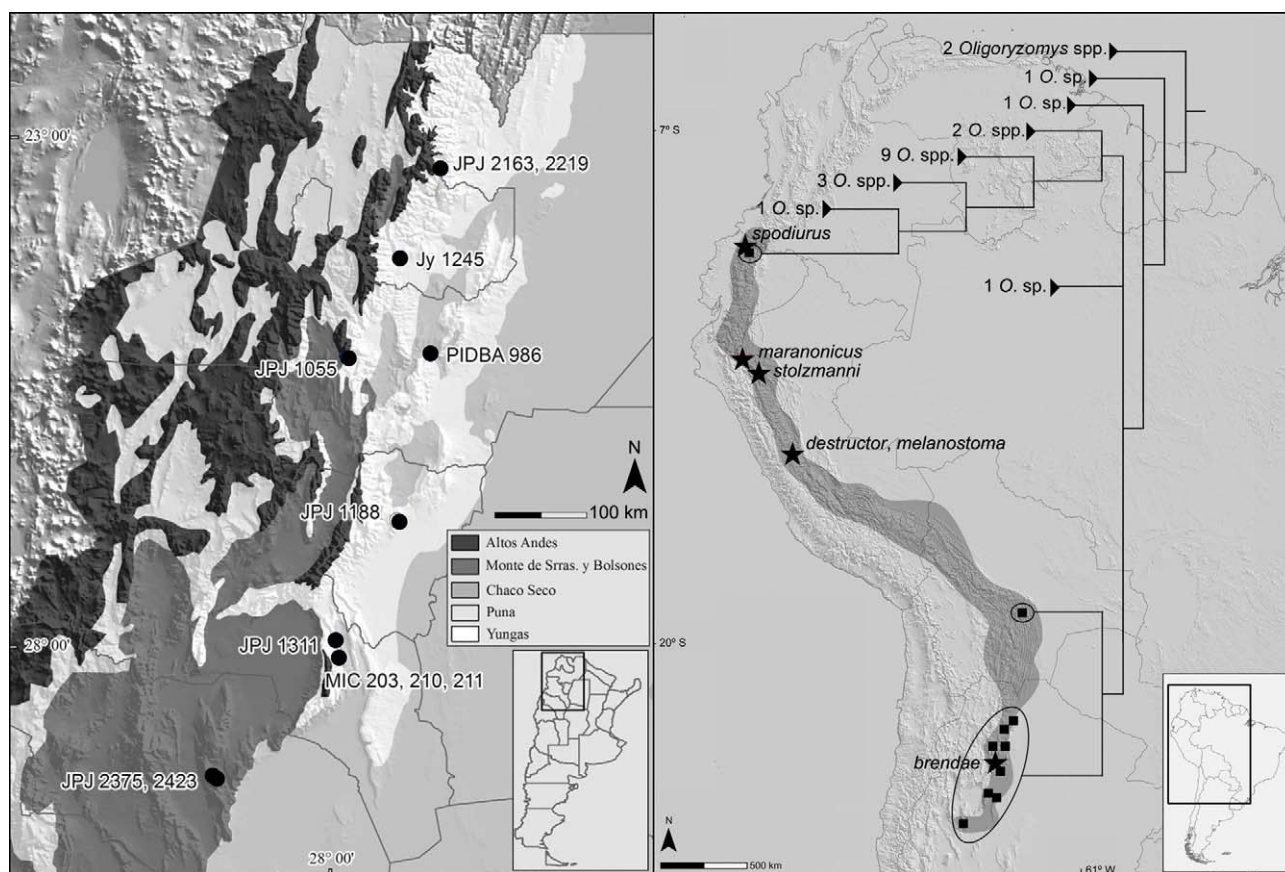


FIGURE 5. Left: partial map of northwestern Argentina where collection localities of specimens of *Oligoryzomys brendae* included in the phylogenetic analysis are shown (circles). Right: partial map of South America showing the distribution of *Oligoryzomys destructor* as understood previously to this study (see text); squares correspond to collection localities of individuals associated to *O. destructor* and of *O. brendae* used in the phylogenetic analysis; stars signal the type localities of taxa associated to *destructor* (i.e., *spodirus*, *maranonicus*, *stolzmanni*, *melanostoma*, and *destructor*) and of *O. brendae*. A simplified version of the most likely tree (see Fig. 1) is superimposed in the map; the only branches signalling recording localities (indicated with squares) are those leading to *destructor* and *brendae*.

Final considerations. Given the results of the phylogenetic analysis, a re-evaluation of northern nominal taxa, such as *Hesperomys melanostoma* Tschudi, 1844, *Oryzomys stolzmanni* Thomas, 1894, *Oryzomys stolzmanni maranonicus* Osgood, 1914 and *Oryzomys (Oligoryzomys) spodiurus* Hershkovitz, 1940 is needed to completely clarify the taxonomic scenario within large-bodied *Oligoryzomys* of the forested foothills of the eastern Andean region. It is also a pending task to determine the northern distributional limit of *O. brendae*, until now confidently established on northern Salta province, northernmost Argentina. Anderson (1997) referred many specimens coming from several localities of Bolivia (from the northern La Paz department to southern Tarija) to *O. destructor*, but the correct identity of these specimens remains to be resolved. In fact, given our phylogenetic results, these populations perhaps correspond to an unnamed form of this genus.

Finally, by showing that a distinct species of *Oligoryzomys*, *O. brendae*, inhabits the Yungas of northwestern Argentina, this study reinforces the biodiversity value of this eco-region, which counts with two recently discovered endemic species of Sigmodontinae, *Oxymycterus wayku* and *Phyllotis anitae* (Jayat *et al.* 2007, 2008). Our finding emphasizes the need to intensify field work in this biome, which unfortunately is being highly modified by human activities (Brown *et al.* 2001).

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APPENDIX 1.

Original description of *Oligoryzomys brendae* (after Massoia, 1998).

Oligoryzomys brendae sp. nov.¹

N.v. [nombre vulgar]: "Colilargo del San Javier" – D.g.c. [distribución general conocida]: Tucumán (localidad típica: Cerro San Javier, Dpto. Tafí Viejo), (aprox. 1.000 mts. De altura), Salta y Catamarca.

Diagnosis preliminar: colilargo de tamaño exterior muy similar al de *O. longicaudatus philippi*, de éste y de *O. flavescens* se diferencia especialmente por caracteres craneanos, que no admiten considerarlos en grado subespecífico. Es decir, la caja cerebral es casi circular y mucho más ancha. Designamos como *Holotypus* al ♂ adulto CEM 482, cuyas medidas externas son las siguientes: Longitud total 217 mm., cola 130 mm., oreja 18 mm. y pié 25 mm. y como *Allotypus* a la ♀ CEM 483, cuyas medidas, homólogas a las anotadas, son las siguientes: 251, 143, 19 y 24.

¹Nombre dedicado a mi queridísima nieta Brenda Paulina Tomasini.

APPENDIX 2.

Specimens of *Oligoryzomys* examined in this study; acronyms for institutions are as follow: Argentina, Buenos Aires: Colección Elio Massoia (CEM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN); Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" (MMPMa); Tucumán, Field catalog of Jorge Pablo Jayat (JPJ). An asterisk indicates specimens used in morphometric analysis, and two asterisks those used in molecular analysis.

Oligoryzomys brendae (n = 92): ARGENTINA, CATAMARCA: aprox. 10 km al W de Los Varela, sobre Ruta Provincial Nº 4, Sierra de Humaya, 2006 m, 27° 56' 12.1" S; 65° 56' 52.8" W (JPJ 1311*, **); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial Nº 1, 1888 m, 27° 42' 24.2" S; 65° 54' 40.6" W (JPJ 563*, 564*, 565); Mogote Las Trampas, aprox. 15 km al NW de Chumbicha, 2300 m, 28° 44' 30.66" S; 66° 19' 14.05" W (JPJ 1464); unión entre las rutas provinciales Nº 9 y 18, 3.4 km al S, sobre Ruta Provincial Nº 18, 1529 m, 27° 49' S; 65° 47' W (JPJ 25, 46, 1118, 1122, 1130*, 1136, 1138, 1139*, 1140*, 1154*). JUJUY: Arroyo La Tablada, León (MMPMa 1237, 1240, 1250, 1252, 1253, 1261, 1265, 1266, 1268, 1269); León (MMPMa 2133, 2149, 2153, 2154, 2189, 2221); Bárcena, aprox. 3 km al S, sobre Ruta Nacional Nº 9, 1808 m, 24° 00' 02.0" S; 65° 26' 51.6" W (JPJ 643*, 644, 645*, 653*, 660-662*, 665*); La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial Nº 6, 1428 m, 24° 18' 05.7" S; 64° 29' 38.7" W (JPJ 595, 597, 598*, 599*, 607*, 613, 614*, 616, 618*, 619*, 621, 622); León, Arroyo La Tablada (MMPMa 1252, 1261, 1265, 1268, 1269); Parque Nacional Calilegua (MACN 23549); Quebrada Alumbrijo, aprox. 8 km al NE de Santa Ana, 2900 m, 23° 19' 16" S; 64° 55' 3.7" W (JPJ 2163**, 2175, 2219**); Termas de Reyes, aprox. 15 km al N, sobre Ruta Provincial Nº 4, 24° 7' 4.5" S; 65° 29' 19.5" W (JPJ 329); Termas de Reyes, mirador, sobre Ruta Provincial Nº 4, 24° 9' 46.5" S; 65° 29' 58.5" W (JPJ 297, 298, 304, 319). LA RIOJA: Km 14 de la ruta provincial Nº 73, aprox. 1 km de Pampa de la Viuda, 2100 m, 29° 17' 1.7" S; 67° 7' 8.2" W (JPJ 2423**); km 19 de la ruta provincial Nº 73, Pampa de la Viuda, 2150 m, 29° 16' 12.9" S; 67° 8' 34.7" W (JPJ 2375**); SALTA: aprox. 15 km al W de Escoipe, sobre Ruta Provincial Nº 33, 2680 m, 25° 10' S; 65° 49' W (JPJ 1055*, **); aprox. 1.6 km al W de Los Toldos, sobre la senda a Santa Victoria, 1621 m, 22° 16' 41.2" S; 64° 42' 45.9" W (JPJ 1584, 1608, 1690); aprox. 5 km (por ruta) al S de Los Toldos, sobre camino a Vallecito, 1705 m, 22° 19' 06" S; 64° 43' 08" W (JPJ 1618, 1630, 1705, 1708); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 m.s.n.m., 24° 53' S; 65° 40' W (JPJ 133); El Corralito, aprox. 23 Km al SO de Campo Quijano, sobre ruta Nac. Nº 51, 24° 58' S; 65° 48' W (JPJ 144, 149). TUCUMÁN: Alberdi (MACN 20651); aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m, 26° 19' 20.2" S; 65° 36' 45.5" W (JPJ 760, 981, 982, 986, 1000*, 1009, 1222); Concepción (MACN 33346); cumbre del Taficillo, al NE de Las Agüitas, Parque Biológico Sierra de San Javier, 26° 41' 51.7" S; 65° 20' 20.4" W (JPJ 112, 114, 116, 118); Horco Molle, Taficillo (CML 3999); Hualinchay, sobre el camino a Cafayate, 1861, 26° 18' S; 65° 36' W (JPJ 209, 243, 249); La Cruz, Cumbre del Taficillo, Parque Biológico Sierra de San Javier, 1907 m, 26° 41' 11.7" S; 65° 19' 56.4" W (JPJ 870, 894*, 911, 920); Parque Biológico Sierra de San Javier, área de la Residencia Universitaria, a metros del LIEY, 711 m, 26° 46' 36" S; 65° 19' 31" W (JPJ 1187, 1188**); Tafi Viejo, Cerro San Javier (CEM 482* [holotype], 483* [paratype]); Villa Nougues, aprox. 2 km al N, sobre Ruta Provincial Nº 338, a la altura de la antena repetidora del Canal 10 de televisión, 26° 52' S; 65° 23' W (JPJ 282); Quebrada de Los Sosa (MMPMa 2398, 2866, 2868, 2869).

Oligoryzomys destructor (n = 2): ECUADOR, Pichincha (TEL 1479, 1481).

O. flavescens (n = 32): ARGENTINA, CATAMARCA: aprox. 10 km al W de Los Varela, sobre Ruta Provincial Nº 4, Sierra de Humaya, 2006 m, 27° 56' 12.1" S; 65° 56' 52.8" W (JPJ 1306, 1307, 1310); aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial Nº 42, al E del Portezuelo, 1992 m, 28° 25' 10.9" S; 65° 32' 40.5" W (JPJ 424, 802); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial Nº 1, 1888 m, 27° 42' 24.2" S; 65° 54' 40.6" W (JPJ 525, 541); unión entre las rutas provinciales Nº 9 y 18, 3.4 km al S, sobre Ruta Provincial Nº 18, 1529 m, 27° 49' S; 65° 47' W (JPJ 9, 11, 13, 1112). JUJUY: La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m, 24° 17' S; 64° 23' W (JPJ 965); La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial Nº 6, 1428 m, 24° 18' 05.7" S; 64° 29' 38.7" W (JPJ 620); Termas de Reyes, aprox. 15 km al N, sobre Ruta Provincial Nº 4, 24° 7' 4.5" S; 65° 29' 19.5" W (JPJ 294). SALTA: Pampa Verde, aprox. 8 km al OSO de Los Toldos y al S del Cerro Bravo, 2400 m, 22° 17' S; 64° 48' W (JPJ 344, 347, 353, 354, 358, 365). TUCUMÁN: aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m, 26° 19' 20.2" S; 65° 36' 45.5" W (JPJ 987, 997, 998, 1005); aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m, 22° 23' S; 65° 05' W (JPJ 818, 841, 851-853); Cumbre del Taficillo, al NE de Las Agüitas, Parque Biológico Sierra de San Javier, 26° 41' 51.7" S; 65° 20' 20.4" W (JPJ 120); Hualinchay, sobre el camino a Cafayate, 1861, 26° 18' S; 65° 36' W (JPJ 247); Villa Nougues, aprox. 2 km al N, sobre Ruta Provincial Nº 338, a la altura de la antena repetidora del Canal 10 de televisión, 26° 52' S; 65° 23' W (JPJ 256).