



First record of *Proechimys pattoni* da Silva, 1998 (Rodentia, Echimyidae) in northwestern Bolivia

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Abstract

Proechimys pattoni da Silva, 1998 is one of the 3 small-bodied species of *Proechimys* and its geographic range is only known in western Brazil and eastern and southern Peru. However, based on morphological and molecular analyses, we report *P. pattoni* from the lowland forest of Bolivia (Pando: Rio Madre de Dios, near San Rosa). This is the first report of *P. pattoni* in Bolivia and extends its distributional range 315 km to the southeast in the Amazon biogeographic region of Bolivia, representing the southeastern most record. Furthermore, we document the karyotype ($2n = 40 / FN = 56$) and morphological variation in diagnostic characters.

Key words

Amazon Basin; Pando; Rio Madre de Dios; karyotype; spiny rats; “*gardneri*” group; mitochondrial DNA.

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Introduction

Spiny rats of the genus *Proechimys* are distinguished from others echimyids by an elongated head and long rostrum, large and erect ears, narrow and long hind feet, and dorsal coloration which varies from reddish-brown to gray-brown, often streaked with black along the mid-line (Patton et al. 2000, Patton and Leite 2015). Some 22 species are now recognized in the genus and these are organized in about 10 groups based on morphological affinities (Patton 1987; Patton and Leite 2015). Only a handful of these groups have been supported by molecular analyses, including the “*gardneri*” group (da Silva 1998; Patton et al. 2000).

The “*gardneri*” group of *Proechimys* includes the only 3 small-bodied species (head and body length < 185

mm) of the genus: *Proechimys gardneri* da Silva, 1998; *P. kulinae* da Silva, 1998; and *P. pattoni* da Silva, 1998. These 3 species are parapatric in western Amazonia (Patton et al. 2000): *P. gardneri* is known from western Amazonian Brazil (right bank of central and lower region of the Jurua River and both sides of Madeira River) and northern Bolivia; *P. kulinae* occurs only on the left bank of the central region of the Jurua River, extending north to the right bank of the Amazon river in northeastern Peru; *P. pattoni* occurs on both sides of the headwaters of the Jurua River in Brazil and extends into eastern and southern Peruvian Amazonia (da Silva 1998, Patton et al. 2000, Schetino 2008). Whereas *P. kulinae* is the most divergent species in the “*gardneri*” group based on morphology, DNA variation, and karyotype; *P. pattoni* and *P. gardneri* share several morphological features and

almost the same karyotype ($2n = 40$, $FN = 56$) because *P. gardneri* from the Madeira river presents $2n = 40$, $FN = 54$ (Eler et al. 2012); however, DNA sequence divergence (Kimura-2p) between these species at the cytochrome-b locus averages about 12% (da Silva 1998, Patton et al. 2000, Patton and Leite 2015).

Currently, *Proechimys gardneri* is the only small-bodied species recorded in Bolivia (Salazar-Bravo et al. 2003, Patton and Leite 2015). In the course of a revision of species of *Proechimys* occurring in Bolivia, we discovered other small-bodied specimens that closely resembled the characteristics of *P. pattoni* instead of *P. gardneri*. Based on those specimens, we examined morphological, chromosomal, and molecular data to test whether *P. pattoni* occurs in Bolivia. In addition, we highlight morphological characters for the Bolivian specimens that differ slightly from those previously considered as diagnostic for *P. pattoni*.

Methods

We examined 2 specimens (skin and skull) of small-bodied *Proechimys* from Bolivia, housed in the Museum of Southwestern Biology (MSB, University of New Mexico). We scored external and craniodental characters following M.N.F. da Silva (1998), Patton et al. (2000) and Patton and Leite (2015); age classification followed Patton and Rogers (1983). External measurements were taken from skin labels and include total length (TOL), tail length (TL), hind foot length (HF), and ear length

(E). In addition, 25 craniodental variables were measured in millimeters with a digital caliper following definitions and endpoints described by Patton and Rogers (1983) and Patton et al. (2000): Greatest skull length (GSL), condyloincisive length (CIL), basilar length (BaL), palatal length “a” (PLa), diastema length (D), palatal length “b” (PLb), maxillary tooththrow length (MTRL), incisive foramina length (IFL), nasal length (NL), rostral length (RL), interorbital constriction (IOC), zygomatic breadth (ZB), mastoid breadth (MB), orbital length (OL), rostral width-1 (RW-1), rostral depth (RD), bullar length (BuL), maxillary greatest breadth (MaxB), mesopterygoid fossa width (MPFW), cranial depth (CD), and cranial depth at M1-M1 (CDM1).

For molecular analyses, DNA was isolated from Bolivian (only the tissue from MSB 57229 was available) and Peruvian specimens of small-bodied *Proechimys*, using IBI Scientific Genomic DNA Mini kit and following the manufacturer’s instructions. Specimens are listed in the Appendix, Table A1. Amplification of a fragment of the cytochrome b gene sequence was performed by the polymerase chain reaction (PCR) using primers MVZ 05 and MVZ 16 (Smith and Patton 1993). Phylogenetic reconstruction included sequences reported by Patton et al. (2000), from GenBank and sequences we obtained in this study (Appendix, Table A1). Alignment of sequences was performed with MEGA v7.0.14 (Kumar et al. 2016) using Clustal W (Thompson et al. 1997) with a total sequence length of 801bp. Phylogenetic analyses were

Table 1. External and skull measurements (in mm) of *Proechimys pattoni* from Pando, Bolivia and measurements of the holotype and other individuals from the Jurua River, Brazil (da Silva 1998, Patton et al. 2000). See text for definition of measurements.

Measurements	Holotype da Silva (1998)	Jurua River (Brazil) Patton et al. (2000)	Pando (Bolivia)	
			MSB 57229 (♂)	MSB 57230 (♀)
TOL	322	305.60 ± 5.37 (278–328) 10	350	321
LT	130	125.3 ± 3.53 (106–141) 10	140	126
HF	41	41.09 ± 0.55 (37–43) 10	43	35
Ear	22	20.82 ± 0.26 (20–22) 11	22	21
GSL	47.1	—	51.43	—
CIL	38.2	37.59 ± 0.35 (36.11–39.53) 11	41.6	39.47
BaL	32.7	—	35.41	33.73
PLa	15	14.84 ± 0.22 (13.97–16.18) 11	16.12	15.5
D	9.4	8.86 ± 0.21 (7.31–9.68) 11	10.38	9.75
PLb	6.2	—	6.69	6.41
MTRL	7.3	7.29 ± 0.06 (6.92–7.54) 11	6.83	7.02
IFL	4.2	3.93 ± 0.14 (3.00–4.56) 11	4.36	3.76
NL	17	15.40 ± 0.31 (15.40–18.37) 11	18.91	—
RL	17.9	18.12 ± 0.22 (16.86–18.93) 11	20	—
IOC	10	9.75 ± 0.18 (8.88–10.90) 11	9.91	11.08
ZB	23	22.3 ± 0.16 (21.52–22.99) 11	22.77	22.86
MB	18.3	17.77 ± 0.15 (16.93–18.55) 11	18.71	18.07
OL	12.5	12.03 ± 0.13 (11.24–12.79) 11	12.55	11.98
RW-1	7.1	7.07 ± 0.12 (6.41–7.92) 11	7.79	7.02
RD	8.3	8.52 ± 0.19 (7.91–9.92) 11	9.38	8.95
BuL	9.9	9.78 ± 0.14 (9.20–10.92) 11	11.54	10.57
MAXB	7.2	7.08 ± 0.13 (6.33–7.98) 11	8.13	8.26
MPFW	3.7	3.86 ± 0.19 (3.1–4.8) 11	3.54	3.33
CD	16.3	15.80 ± 0.11 (15.02–17.07) 11	16.43	15.47
CDM	12.5	12.11 ± 0.10 (11.45–12.46) 11	13.04	12.39

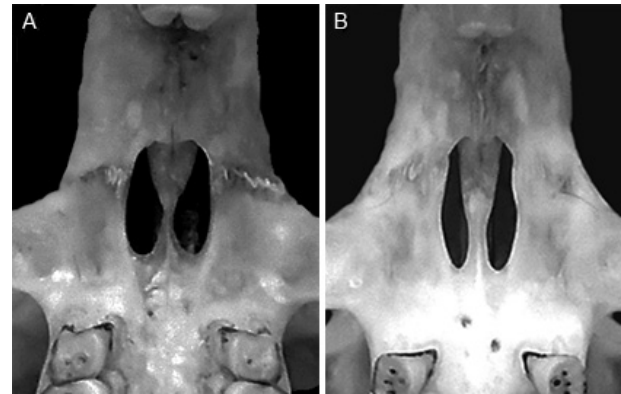


Figure 1. Dorsal and ventral views of the skull of *Proechimys pattoni* (MSB 57229). Scale bar = 10 mm.

conducted using the Maximum Likelihood method with the Randomized Axelerated Maximum-likelihood algorithm (RAxML v. 8.2.7; Stamatakis 2014). Corrected sequence divergence (Kimura-2p, Kimura 1980) among haplotypes was estimated in MEGA v7.0.14 (Kumar et al. 2016). In addition, a non-differentially stained karyotype was prepared from field-prepared slides for one of the 2 specimens (MSB 57230) following protocols described in Anderson et al. (1987).

Results

New record. Bolivia: Pando: left bank of Rio Madre de Dios near Santa Rosa, (12°13'00.01" S, 068°24'00.00" W, 180 m), 3 August 1986 (1 male, MSB 57229; 1 female, MSB 57230). Santa Rosa, a small cluster of ranches, is located in the “bosque húmedo - Subtropical” (= subtropical rainforest; bh-ST) life zone in the Holdridge life zone system modified for Bolivia (Unzueta 1975). The forest consisted of low trees (4–20 cm d.b.h.) with spiny cactus (tacuara), and a few large trees including rubber trees (*Hevea brasiliensis* Müll. Arg.) and Brazil nuts



Figures 2. Presence and variation of the maxillary portion of the septum. **A.** *Proechimys pattoni* from Pando, Bolivia (MSB 57230). **B.** *Proechimys pattoni* from Pando, Bolivia (MSB 57229).

(*Bertholletia excelsa* Humb. and Bonpl.) (L. Ruedas, field notes).

Identification. Two small-bodied specimens (female: MSB 57229, age-class X; male: MSB 57230, age-class IX) agree with the description of *P. pattoni* by da Silva (1998) and Patton et al. (2000) in the following characteristics: dorsal and lateral pelage is uniformly reddish brown and auburn in coloration although it turns slightly darker in the rump; the tail is relatively short (65% of head and body length) with conspicuous scales distributed on rows of about 10 scales per cm; ears are relatively short (< 23 mm, Table 1); hind feet are slim and short with white dorsal surfaces and dark brown bands around the ankles; soles of hindfeet with 6 plantar pads but with weakly developed hypothenars; small but robust skulls with narrow rostra; incisive foramen ovate in shape; postorbital processes of zygoma weakly developed, and small molars (Fig. 1). A morphological variation on tail coloration, the degree of development of the septum of the incisive foramina, the depth of the mesopterygoid fossa, and other characters are evident in Bolivian specimens (Table 2; Fig. 2).

Phylogenetic reconstruction (Fig. 3) including a Bolivian sequence from Pando (MSB 57229) found it to be part of a clade that contained haplotypes of *P. pattoni* from the Jurua River (Brazil) and Madre de Dios (Peru). The intraspecific variation considering all those popula-

Table 2. Morphological variation in Bolivian specimens of *Proechimys pattoni*.

Character	<i>P. pattoni</i> (Patton et al. 2000)	MSB 57229	MSB 57230
Tail	Unicolored (dark brown above, pale brown below)	Sharply bicolored (dark brown above, white below)	Unicolored (dark brown above, pale brown below)
Color around lips	White; usually with white spots at the base of vibrissae	White; without spots at base of vibrissae	Brown; without spots at base of vibrissae
Septum of incisive foramina	Incomplete	Complete, with thinner maxillary portion	Complete, with wider maxillary portion
Depth of mesopterygoid fossa	Reaches midpoint of M2	Only reaches midpoint of M3	Only reaches midpoint of M3
Supraorbital ridge	Well developed, extending above interorbital region	Developed, not extending above interorbital region	Developed, not extending above interorbital region
Floor of infraorbital foramen	Smooth	With a weakly developed groove	Smooth

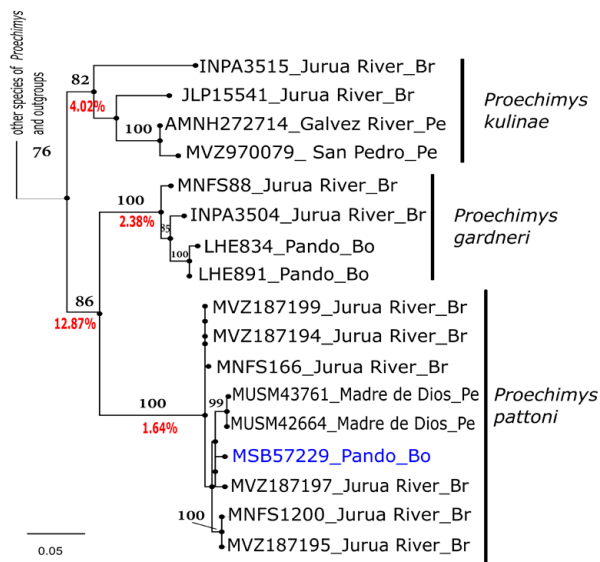


Figure 3. Genealogical relationships of 17 cytochrome-b gene haplotypes from specimens assigned to the “gardneri” group of *Proechimys*. Numbers above branches represent bootstrap support, values below are intraspecific and interspecific variation. Terminal designations are the specimen catalog and locality information (Bo = Bolivia, Pe = Peru, Br = Brazil). The blue tag indicates our *P. pattoni* specimen from Bolivia.

tions (Jurua, Madre de Dios, Pando) is 1.6 ± 0.3 . Genetic divergence between our specimen from Pando and haplotypes from populations of *P. pattoni* from the Jurua River is 1.9% and 1.8%, from Madre de Dios, whereas specimens from Madre de Dios diverge in 2.1% from those of the Jurua River.

The chromosomal analysis shows a karyotype of $2n = 40$ and $FN = 56$ (Fig. 4). The autosome complement comprises 1 medium sized submetacentric chromosome, 7 pairs of medium to small-sized metacentric chromosomes, 3 large pairs of acrocentric chromosomes, 8 pairs of small acrocentric chromosomes. The sex chromosomes are composed of a medium-sized acrocentric X-chromosome.

Discussion

Our results confirm the presence of *Proechimys pattoni* in Bolivia based on morphological, molecular, and karyotype data. This new record corresponds to the Santa Rosa locality (Pando, Bolivia) and extends the current distribution range of *P. pattoni* about 315 km to the southeast from Pakitza (Madre de Dios, Peru).

Although resembling typical *P. pattoni*, these Bolivian specimens also highlight geographic variation in the species. For example, populations assigned to *P. pattoni* from the Jurua River and Ucayali have a deep mesopterygoid fossa that reaches the midpoint of M2 (Patton and Gardner 1972: fig. 3F; Patton et al. 2000: fig. 140); our specimens from Bolivia, on the other hand, show a moderately deep mesopterygoid fossa, reaching almost to the midpoint of M3. In addition, populations from the Jurua River usually have an incomplete septum in the incisive foramen (Pat-

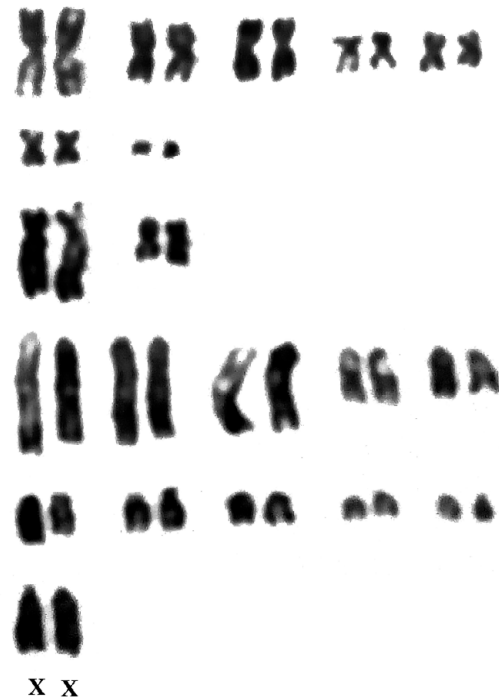


Figure 4. Karyotype of a female individual of *Proechimys pattoni* from Pando, Bolivia (MSB 57230). $2n=40$, $FN=56$.

ton et al. 2000: fig. 141); on the contrary, specimens from Bolivia and Ucayali (Patton and Gardner 1972: figs. 3F, 7, 8) have incisive foramen with complete septa.

We agree with Patton et al. (2000) that the dark band around the ankle and the distinct postorbital processes on the zygomatic arch in *P. pattoni* are the best features to distinguish it from *P. gardneri*. Our analysis of the morphological variation in *P. pattoni* (including the Bolivian samples) suggests, in addition, that the supraorbital ridge in this species is well developed and level with the interorbital region, whereas in *P. gardneri*, the supraorbital ridge is well-developed but lies on a plane or rises above the interorbital region.

Incorporation of haplotypes from Pando raises the percentage of corrected sequence divergence from 1.3% (Patton et al. 2000) to 1.6% (present work) despite adding considerable new geographic range to known populations (Fig. 5). Moreover, in a group where morphological and karyotype variation appears to be the norm, our preliminary work suggests chromosomal stability: all populations of *P. pattoni* present the same karyotype ($2n = 40$ and $FN = 56$) as reported by Patton and Gardner (1972), da Silva (1998), and Patton et al. (2000).

Along its distribution, including the new locality reported herein, *P. pattoni* is sympatric with *P. breviceauda* (Günther, 1876), *P. simonsi* Thomas, 1900, and *P. steerei* Goldman, 1911 (Patton and Gardner 1972, Patton et al. 2000: fig. 133), while only in Brazil is *P. pattoni* in sympatry with *P. cuvieri* Petter, 1978. *Proechimys pattoni* is easily recognized from those species principally by its small body size, but also because it has slim, short, and dorsally mostly white hind feet, with 6 plantar pads. Dif-

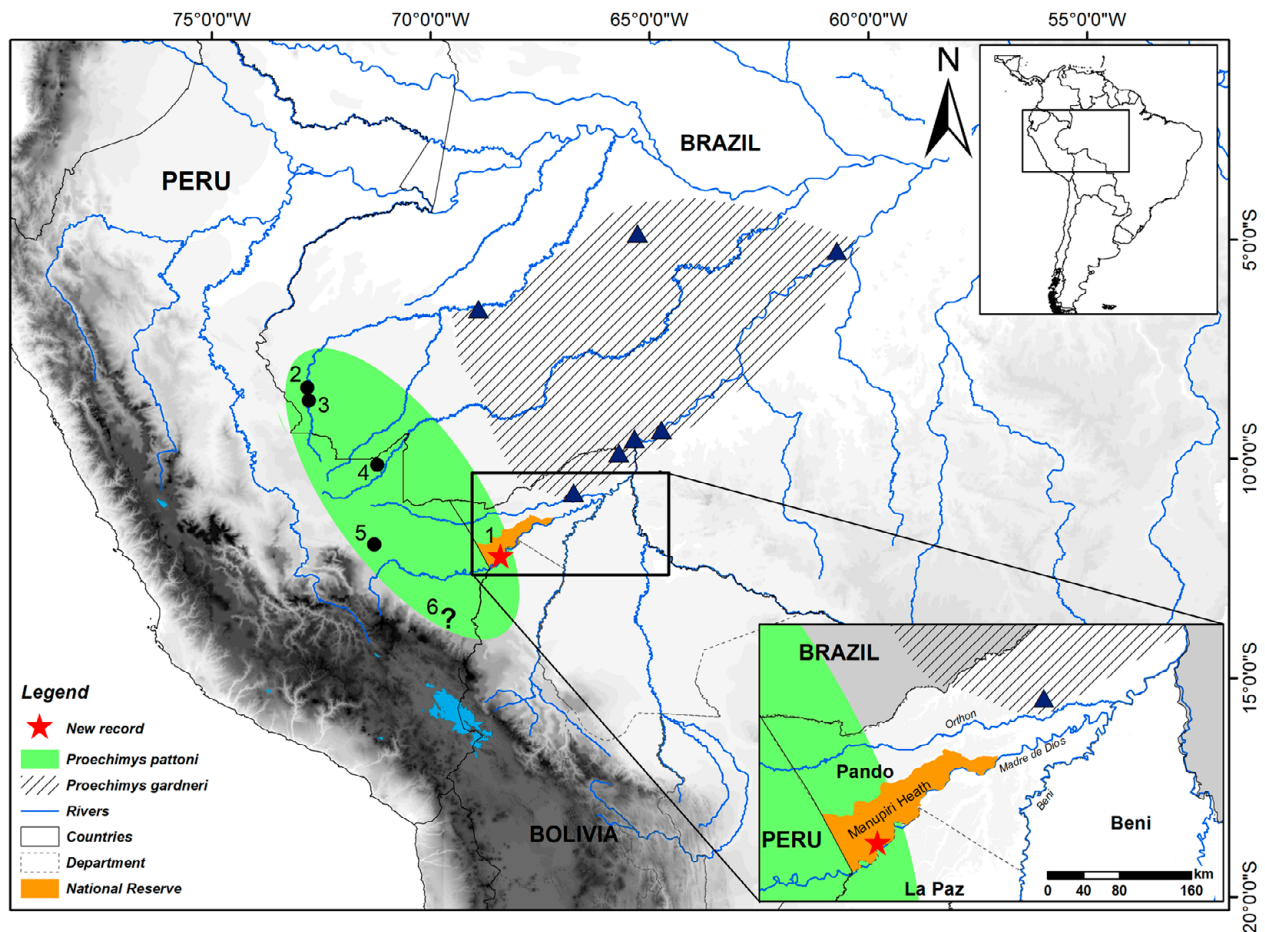


Figure 5. Distribution range of *Proechimys pattoni* and *Proechimys gardneri*. Numbers indicate the localities reported. New record for *P. pattoni* is represented by a red star.

ferences in the skull include narrower molars, the shape of the incisive foramina, and the depth of the mesopterygoid fossa (see other details in Patton et al. 2000).

The new geographic record is about 244 km distant from the nearest, southernmost record of *P. gardneri* (Fig 5), and because there are no significant geographic barriers between these localities, both species may occur in sympatry in northern Bolivia. A meticulous examination of newly collected specimens is needed to avoid any misidentification.

Finally, *Proechimys pattoni* adds to the list of species in Bolivia with unique Amazonian affiliations, a list that includes *Hylaeamys perenensis* (J. A. Allen, 1901), *Oecomys roberti* (Thomas, 1904), *Dasyprocta variegata* Gray, 1842, *Myoprocta pratti* Pocock, 1913, *Dactylomys dactylinus* (Desmarest, 1817), *Isothrix bistrata* Wagner, 1845, *Microsciurus flaviventer* (Gray, 1867), *Cebuella pygmaea* (Spix, 1823), *Saguinus labiatus* (É. Geoffroy in Humboldt, 1812), *S. imperator* (Goeldi, 1907), *Callimico goeldii* (Thomas, 1904), and *Pithecia irrorata* Gray, 1842 (Anderson 1997, Salazar-Bravo et al. 2002a, Miserendino and Azurduy 2005, Martinez and Wallace 2010, Porcel et al. 2010, Romero-Valenzuela and Rumiz 2010, Emmons and Patton 2015, Emmons et al. 2015, Percequillo 2015). This fauna, although more extensively represented in neighboring countries, reaches its southern-most limit

of distribution in the northern part of Bolivia (Anderson 1997, Salazar-Bravo et al. 2002b), and deserves more vigorous conservation efforts by Bolivian authorities.

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Authors' Contributions

PSV, and JSB designed the study, PSV, JC, JW, and JSB wrote the text. JC and JW constructed the karyotypes and

PSV obtained sequences and conducted the molecular analyses.

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Appendix

Table A1. List and localities of the specimens used to molecular analysis.

Species	Catalog Number	Museum Number	Accession or Source	Locality
<i>Trinomys albispinus</i>	AL 3072	—	U34856	Brazil: Fazenda Cruzeiro
<i>Capromys pilorides</i>		MVZ 191417	KM014004	Cuba: Villa Clara
<i>Mesomys hispidus</i>	MNFS 909	INPA 2976	L23398	Brazil: Amazonas, Altamira, right bank Rio Jurua
<i>Thrichomys laurenteus</i>	LBCE 862	—	AY083334	Brazil: State of Piauí, Fazenda Felicidade
<i>Hoplomys gymnurus</i>	JLP 9692	MVZ 162309	AF422922	Colombia: Valle, 6km Buenaventura
<i>Proechimys brevicauda</i>	MNFS 1541	MVZ 190677	Patton et al. 2000	Brazil: Acre, Nova Vida, right bank Rio Jurua
<i>Proechimys cuvieri</i>	MNFS 1077	INPA 3461	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Rio Jurua
<i>Proechimys cuvieri</i>	V 849	—	AJ251400	French Guyana: Petit Saut
<i>Proechimys cuvieri</i>	JAA 215	MUSM 16057	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys longicaudatus</i>	LHE 1419	—	James L. Patton	Bolivia: Santa Cruz, El Refugio
<i>Proechimys steerei</i>	RMW 457	MVZ 166036	present work	Peru: Madre de Dios, Reserva Cusco Amazónico
<i>Proechimys simonsi</i>	JLP 11051	MVZ 166803	U35414	Peru: Madre de Dios, Aguas Calientes
<i>Proechimys pattoni</i>	MNF 1098	MVZ 187194	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Rio Jurua
<i>Proechimys pattoni</i>	MNF 1165	MVZ 187195	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Rio Jurua

Table A1. *Continued.*

Species	Catalog Number	Museum Number	Accession or Source	Locality
<i>Proechimys pattoni</i>	MNFS 1201	MVZ 187199	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Río Juruá
<i>Proechimys pattoni</i>	MNFS 1428	MVZ 187197	Patton et al. 2000	Brazil: Acre, Sobral, left bank Río Juruá
<i>Proechimys pattoni</i>	MNFS 1166	—	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Río Juruá
<i>Proechimys pattoni</i>	MNFS 1200	—	Patton et al. 2000	Brazil: Acre, Igarapé Porongaba, right bank Río Juruá
<i>Proechimys pattoni</i>	MDO 1083	MUSM 43761	V. Pacheco	Peru: Madre de Dios, La Novia
<i>Proechimys pattoni</i>	MDO 469	MUSM 42664	V. Pacheco	Peru: Madre de Dios, La Novia
<i>Proechimys pattoni</i>	.	MSB 57229	present work	Bolivia: Pando, Santa Rosa
<i>Proechimys gardneri</i>	LHE 834	—	Patton et al. 2000	Bolivia: Pando, San Juan de Nuevo Mundo
<i>Proechimys gardneri</i>	LHE 890	USNM 579617	Patton et al. 2000	Bolivia: Pando, Río Negro
<i>Proechimys gardneri</i>	LHE 891	—	Patton et al. 2000	Bolivia: Pando, Río Negro
<i>Proechimys gardneri</i>	JLP 16039	INPA3504	Patton et al. 2000	Brazil: Amazonas, Altamira, right bank Río Juruá
<i>Proechimys gardneri</i>	JLP 16037	MVZ187209	Patton et al. 2000	Brazil: Amazonas, Altamira, right bank Río Juruá
<i>Proechimys gardneri</i>	MNFS 88	—	Patton et al. 2000	Brazil: Amazonas, Alto Río Urucu
<i>Proechimys gardneri</i>	MNFS 121	—	Patton et al. 2000	Brazil: Amazonas, Alto Río Urucu
<i>Proechimys kulinae</i>	JUR 186	INPA 3515	Patton et al. 2000	Brazil: Amazonas, Barro Vermelho, left bank Río Juruá
<i>Proechimys kulinae</i>	JLP 15906	MVZ 187193	Patton et al. 2000	Brazil: Amazonas, Barro Vermelho, left bank Río Juruá
<i>Proechimys kulinae</i>	MNFS 533	INPA 2556	Patton et al. 2000	Brazil: Amazonas, Barro Vermelho, left bank Río Juruá
<i>Proechimys kulinae</i>	JLP 15541	—	Patton et al. 2000	Brazil: Amazonas, Seringal Condor, left bank Río Juruá
<i>Proechimys kulinae</i>	MNFS 541	—	Patton et al. 2000	Brazil: Amazonas, Seringal Condor, left bank Río Juruá
<i>Proechimys kulinae</i>	MV 970059	—	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	MV 970078	—	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	MV 970079	—	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	RSV 2132	AMNH272714	James L. Patton	Peru: Loreto, Río Galvez
<i>Proechimys kulinae</i>	RSV 2026	MUSM13340	James L. Patton	Peru: Loreto, Río Galvez
<i>Proechimys kulinae</i>	MV 970015	MUSM 22409	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	MV 970016	MUSM22410	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	MV 970028	MUSM22364	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	MV 970031	MUSM22418	James L. Patton	Peru: Loreto, San Pedro
<i>Proechimys kulinae</i>	JAA 286	MUSM 16082	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 201	MUSM 16053	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 285	MUSM 16081	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 273	MUSM 16076	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 276	MUSM 16078	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 218	MUSM 16059	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 208	MUSM 16054	present work	Peru: Loreto, Jenaro Herrera
<i>Proechimys kulinae</i>	JAA 284	MUSM 16080	present work	Peru: Loreto, Jenaro Herrera