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Author(s): Juan A. Martínez-Lanfranco , David Flores , J. Pablo Jayat , and Guillermo D'Elía

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Sección Mamíferos, Museo Nacional de Historia Natural, Dirección de Innovación, Ciencia y Tecnología para el Desarrollo, Ministerio de Educación y Cultura, 25 de Mayo 582, Montevideo, Uruguay (JAM-L)
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Av. Angel Gallardo 470, Buenos Aires, Argentina (DF)
Consejo Nacional de Investigaciones Científicas y Técnicas, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (DF, JPJ)
Universidad Nacional de Chilecito, Campus Los Sarmientos, Ruta Los Peregrinos s/n, Los Sarmientos, 5360 Chilecito, Argentina (JPJ)
Instituto de Ecología Regional, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (JPJ)
Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja s/n, Valdivia, Chile (GD)

* Correspondent: guille.delia@gmail.com

This study presents the most comprehensive systematic revision of the genus *Lutreolina* to date, by means of genetic (mitochondrial DNA of 22 specimens) and morphologic (assessment of 262 specimens) evidence. Molecular analyses were based on cytochrome-*b* gene sequences from 22 individuals collected at 18 localities from Argentina, Bolivia, Brazil, Paraguay, and Uruguay, which are currently allocated to *L. crassicaudata*. Results indicate that *Lutreolina* has sharp phylogeographic structure, with 2 reciprocally monophyletic groups (2.7% divergent, whereas intraclade variation is minimal) occurring east and west of the Dry Chaco, where *Lutreolina* is absent. The eastern clade includes populations from eastern Paraguay, northeastern central Argentina, southern Brazil, and Uruguay. These populations were traditionally allocated to the subspecies *L. c. crassicaudata* and *L. c. paranalis*, whose monophyly is not supported in our study. Therefore, eastern populations are all assigned here to the nominotypic subspecies. The western clade is restricted to montane Yungas forests of northwestern Argentina and southern Bolivia, a very different environment from those inhabited by *Lutreolina* elsewhere (i.e., lowland savannah grasslands). The populations from the Yungas also are morphologically distinct, in size, shape, and in discrete characters of the skull and dentition. We found that these populations belong to a different species than that of the eastern lowlands. Because no taxonomic name is available to apply to these populations, we name and describe a new species of lutrine opossum to encompass them.

Key words: Didelphimorphia, Didelphini, marsupial, Massoia's lutrine opossum, taxonomy, South America, Yungas

Didelphid marsupials are conspicuous members of South American mammal assemblages, covering the whole continent except the southern portion of Patagonia and inhabiting all major habitats (Gardner 2007 [2008]). Among Didelphidae, the genus *Lutreolina* Thomas, 1910, represents a distinct ecomorphological type, because of its terrestrial habits and weasel-like appearance derived from its middle-sized and elongated body, short, stout limbs, small, round ears, and short rostrum (Stein and Patton 2007 [2008]). The genus is considered among the most carnivorous of the family (Santori and Astúa de Moraes

2006) and it has a more specialized swimming gait than other terrestrial didelphids (Santori et al. 2005).

Lutreolina is currently considered to comprise a single living species (Cabrera 1957; Marshall 1978; Stein and Patton 2007 [2008]), *Lutreolina crassicaudata* (Desmarest, 1804); meanwhile, the extinct species *L. materdei* Goin and de los Reyes, 2012, was recently described. The distribution of *L. crassi-*
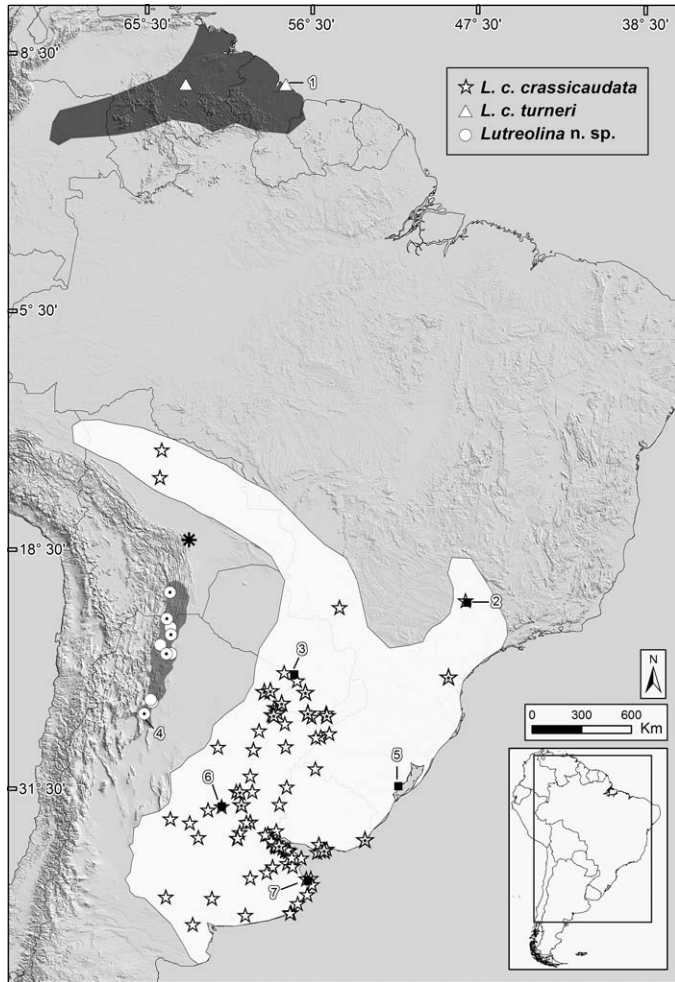
FIG. 1.—Map of collecting localities of the specimens of *Lutreolina* used in the present study. Symbols with a dot in the middle indicate recording localities of sequenced specimens. Numbers identify type localities of the living nominal forms assigned to *Lutreolina* (1.— *turneri*: Better Hope; 2.—*travassosi*: Guariba; 3.—*crassicaudata*: Asunción; 4.—the new species described here: Arroyo El Saltón, Remanso del Gallego, Reserva Provincial Santa Ana, 455 m; 5.— *lutrilla*: São Lourenço do Sul; 6.—*paranalis*: Las Rosas; 7.—*bonaria*: Los Yngleses). Shaded areas represent the approximate distribution of the as here delimited subspecies *L. c. crassicaudata* and *L. c. turneri* (following Brown [2004] and Stein and Patton [2007 {2008}]), and the new species of *Lutreolina* here described. The asterisk indicates the Bolivian locality of San Jose mentioned in the text.

caudata has been described as consisting of 2 main disjunct areas in South America isolated by the Amazon Basin. The northern distribution includes eastern Colombia, Venezuela, and western Guyana, where populations have been traditionally referred to as *L. c. turneri* (Günther, 1879), the type locality of which is Better Hope, Demerara, Guyana. The southern portion of the distribution is broad, encompassing northern and central and eastern Argentina, southern Brazil, Bolivia, Paraguay, southernmost Peru, and Uruguay. All of these populations are assigned to the nominotypical subspecies (Marshall 1978; Luna et al. 2002; Stein and Patton 2007 [2008]), the type locality of which has been restricted by Cabrera (1957) to

Asunción, Paraguay. However, some authors (e.g., Graipel et al. 1996) have argued that at least 2 subspecies are present in southern South America, *L. c. crassicaudata* and *L. c. paranalis* Thomas, 1923, the latter with its type locality in Las Rosas, Santa Fe, Argentina. In addition, 3 other nominal forms, with type localities in the eastern range of *Lutreolina*, *bonaria* Thomas, 1923 (Los Yngleses, Buenos Aires, Argentina), *lutrilla* Thomas, 1923 (São Lourenço do Sul, Rio Grande do Sul, Brazil), and *travassosi* Miranda-Ribeiro, 1936 (Guariba, São Paulo, Brazil), are considered synonyms of *L. crassicaudata* (Fig. 1).

The presence of *L. crassicaudata* is well documented for northwestern Argentina (e.g., Olrog 1976, 1979; Mares et al. 1996, 1997; Flores et al. 2007). Massoia (1973) considered populations from northwestern Argentina taxonomically closer to the typical subspecies than to *L. c. paranalis*, but referred those to *L. c.* ssp. Likewise, Olrog (1976, 1979) considered specimens collected in northwestern Argentina as distinctive because of their smaller size and suggested that the same form also could be present in the contiguous montane forests of Bolivia. Accordingly, Emmons (1997) considered specimens from southern Bolivia as distinctive, and Flores et al. (2007) suggested that montane populations are taxonomically different from pampean populations based on their small size and darker coloration.

Although comprehensive reviews on the taxonomic history and synonymy of the forms associated to *L. crassicaudata* are available (Thomas 1923; Cabrera 1957; Ximénez 1967; Marshall 1978; Graipel et al. 1996; Stein and Patton 2007 [2008]), their taxonomic status remains poorly understood. Although partial assessments of morphological variation have been conducted (e.g., Graipel et al. 1996), to date no morphological study has included populations from the montane Yungas forest of northwestern Argentina and southwestern Bolivia, nor has any analysis of DNA sequence variation been published.

Here we present a taxonomic study of *L. crassicaudata* in southern South America based on genetic and morphologic evidence. First, we analyze the genetic variation and phylogeographic structure within the largest (southern) fraction of the distributional range of *L. crassicaudata* (i.e., samples from Argentina, Bolivia, Brazil, Paraguay, and Uruguay). Second, we evaluate the agreement between the uncovered phylogroups with the pattern of morphological variation and current taxonomy. In light of the results gathered, we describe a new species to encompass populations from the Yungas montane forest from northwestern Argentina and southern Bolivia.

MATERIALS AND METHODS

Study specimens.—We studied 262 specimens of the genus *Lutreolina* from Argentina, Brazil, Paraguay, Uruguay, Bolivia, Venezuela, and Guyana, deposited in museum collections indicated in Appendix I (museum acronyms are defined in Appendix I; see Fig. 1). The sample includes the type specimens of the forms *bonaria*, *lutrilla*, *paranalis*, and *turneri*. No type material exists for *crassicaudata*; but our

sampling includes Paraguayan specimens, the country where the type locality of this form has been restricted (Cabrera 1957). We also examined specimens coming from Jaboticabal (São Paulo, Brazil), near the type locality of the form *travassosi* (Guariba, São Paulo, Brazil). All parts of the study involving live animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

DNA sequence analyses.—Genetic comparisons and phylogenetic analyses were based on partial (the first 801 base pairs) cytochrome-*b* gene (hereafter *Cytb*) DNA sequences. Analyses included 22 sequences gathered from specimens of *Lutreolina* collected at 18 localities in Argentina, Brazil, Bolivia, Paraguay, and Uruguay (Fig. 1). DNA sequences were mostly generated by us, but we also included unpublished sequences kindly provided by S. Jansa (Bell Museum of Natural History, University of Minnesota, St. Paul, Minnesota), J. Salazar-Bravo (Texas Tech University, Lubbock, Texas), and J. L. Patton (Museum of Vertebrate Zoology, University of California, Berkeley, California) as well as 1 downloaded from GenBank. Sequences obtained from representatives of the remaining genera of the tribe Didelphini were used to form the outgroup. As such, the DNA sequence matrix analyzed included 26 sequences. Specimens from which DNA sequences were gathered are listed in Appendix I.

The *Cytb* sequences acquired in this study were gathered using primers MVZ 05 and MVZ 16 and following the polymerase chain reaction protocols of Cañón et al. (2010) and using an external sequencing service (Macrogen, Inc., Seoul, Korea). We edited DNA sequences using CodonCode Aligner software (CodonCode Corporation, Dedham, Massachusetts). All new sequences were deposited in GenBank (accession numbers KF684296–KF684317).

Sequences were aligned using the default parameter values in Clustal X (Thompson et al. 1997); no adjustment by eye was needed. Observed genetic distances (p-distances) were calculated in MEGA5 (Tamura et al. 2011). Phylogenetic relationships among haplotypes were inferred using maximum-parsimony (Farris 1982) and Bayesian (Huelsenbeck et al. 2001) analysis. Maximum-parsimony analyses were carried out in PAUP* (Swofford 2000) with characters states treated as unordered and equally weighted, 500 replicates of heuristic searches with random addition of sequences, and tree-bisection-reconnection branch swapping. Relative support of the recovered clades was calculated by performing 1,000 bootstrap replications (B) with 5 random sequence additions per replicate. Bayesian analysis was conducted using MrBayes 3.1 (Ronquist et al. 2005), with 2 independent runs, each with 3 heated and 1 cold Markov chains. The model used included 6 categories of base substitution rates, a gamma-distributed rate heterogeneity parameter, and a parameter for the proportion of invariant sites, which was selected with MEGA5 under the Bayesian information criterion. All model parameters were estimated in MrBayes. Uniform-interval priors were assumed for all parameters except base composition and GTR parameters, which assumed a Dirichlet prior. Runs were

allowed to proceed for 20 million generations with trees sampled every 1,000 generations per chain. To check for convergence on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each. The first 25% of the trees were discarded as burn-in and the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

Morphology-based analyses.—In our comparisons and description we followed Ridgway (1912) for coloration, Wible (2003) for terminology of skull morphology, Reig et al. (1987) for tooth morphology nomenclature, and Tribe (1990) for dental eruption terminology.

The morphometric analyses are based on the following 9 cranial measures: condylo-incisive length (CIL), from the anterior tip of the incisive foramina to the posteriormost projection of the occipital condyle; zygomatic breadth (ZB), the greatest distance across the outer margins of the zygomatic arches; length of nasals (LN), the distance from the posterior border to the anterior border of the nasal; breadth of the braincase (BB), greatest external distance of the braincase; mastoid breadth (MB), greatest distance across outer margin of mastoid processes; rostral length (RL), distance between anterior margin of the orbit to the anterior tip of the rostrum; canine–canine breadth (CC), distance between the outer margin of upper canines; upper molar toothrow length (UML), distance from the anterior margin of the upper 1st molar to the posterior margin of the upper last molar; and breadth of the palate (BP), distance between the outer margin of the upper last molars. To assess size differences between populations, comparisons were made only between individuals of adult age; specimens were considered as adults if the permanent 2nd premolar and last molar were completely erupted (Regidor et al. 1999; Flores et al. 2003). Following the current subspecific composition of the unique living species in the genus, *L. crassicaudata* (Stein and Patton 2007 [2008]), and the results of the genealogical analysis (see below) we consider for morphometric analyses 3 groups: a group from central and eastern Argentina, Brazil, Paraguay, and Uruguay, which represents the nominotypic subspecies *L. c. crassicaudata* ($n = 67$); a group of northern populations, which are allocated to *L. c. turneri* ($n = 4$), from Venezuela and Guyana; and a 3rd group ($n = 6$) from montane forest from northwestern Argentina and southern Bolivia (western group) that also is geographically disjunct from the others (Appendix I).

Statistical analyses were performed using the software PAST (Hammer et al. 2001). Measurements were log_{10} transformed and used to perform a principal components analysis (see Cudeck 2000) using a variance–covariance matrix. Statistical differences between groups were assessed using a discriminant function analysis (see Brown and Wicker 2000) and multivariate analysis of variance (MANOVA—see Huberty and Petoskey 2000). We performed MANOVAs between the lowland and western groups, and between the lowland and northern groups. We excluded the comparison between the northern and western groups, because our sample size was insufficient for this approach. In the MANOVA, Wilks'
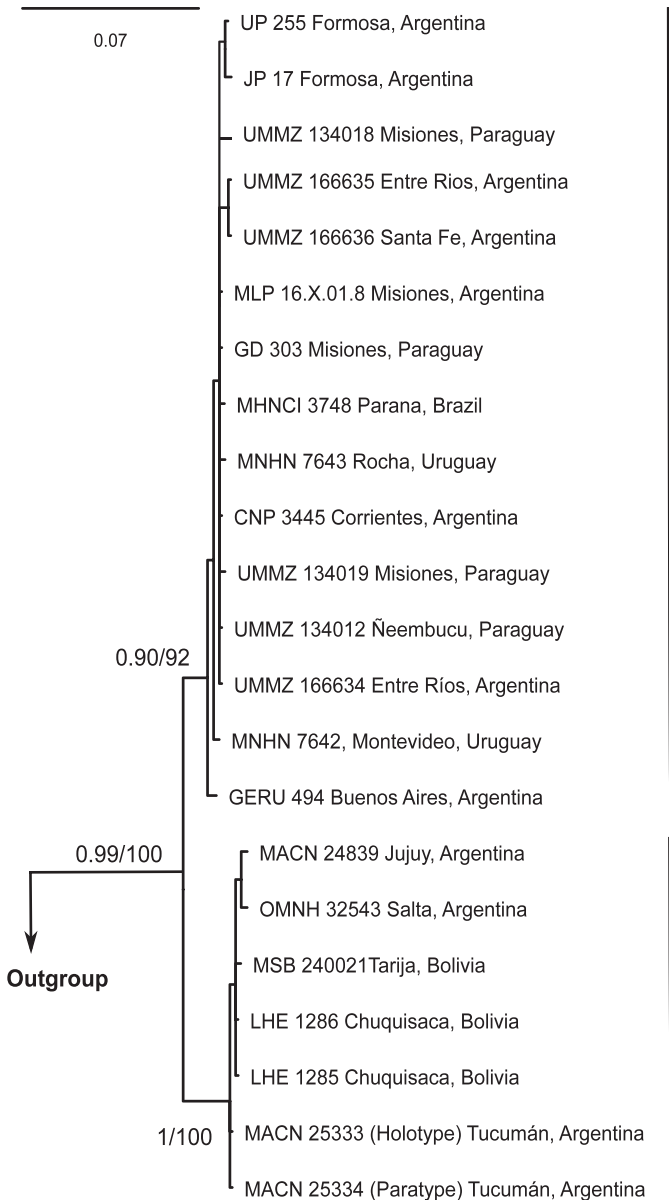
FIG. 2.—Majority-rule consensus tree obtained in the Bayesian analysis of cytochrome-*b* gene sequences of *Lutreolina* specimens collected in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Numbers indicate posterior probability (PP; left of the slash) and maximum-parsimony bootstrap (right of the slash) values of the adjacent nodes. For simplicity, only the values for the *Lutreolina* clade and its 2 main clades are shown. For the other nodes, a black dot indicates that that particular node has more than PP = 0.90 of support value (none of these 3 nodes has 75 or greater of bootstrap support). For each terminal, museum of field catalog number, province or department, and country are provided. For specific localities see Appendix I.

lambda was used to check the significance of pairwise differences. In the discriminant analysis, all the groups had the same probability, so a specimen could be assigned to any group independently of the size of the group. Cross validation was performed using the option "leave out" in PAST. The

percentage of correct posterior classification was used as an indicator of the performance of the function.

RESULTS

Phylogenetic analyses.—The analyzed DNA sequence matrix had 247 variable characters. Maximum-parsimony (139 informative sites) analysis recovered 64 trees of 378 steps (consistency index = 0.772; retention index = 0.753). The strict consensus maximum-parsimony tree (not shown) and the Bayesian tree (Fig. 2) were highly congruent. Both analyses showed a strongly supported *Lutreolina* clade (B = 100; PP = 0.99). Within the clade of *Lutreolina* 2 strongly supported clades sister to each other were recovered. One clade (B = 92; PP = 0.90) groups sequences recovered from specimens collected in the eastern and southern lowland in northeastern and eastern Argentina, southeastern Brazil, Paraguay, and Uruguay. Within this clade average pairwise divergence is 0.3%. The 2nd main clade (B = 100; PP = 1.0) groups haplotypes gathered from specimens collected in the Yungas of northwestern Argentina and southern Bolivia. Average pairwise divergence within the Yungas clade is 0.2%. Observed divergence between main clades of *Lutreolina* is 2.7%.

Morphometric analyses.—Bivariate plots of principal components I (83.4% of the total variance) and II (5.2% of the total variance) resulting from the principal components analysis (Fig. 3) showed that the specimens assigned to *L. crassicaudata crassicaudata* (southern lowland) and *L. c. turneri* (northern) are closer on the space but with little overlap. The western group from the mountain forests of the Yungas falls at the negative side of principal component I, well separated from the other 2 groups. Variables with higher loadings on principal component I include several affecting the breadth of the skull, such as zygomatic, mastoid, and canine–canine breadth, but also some linked to the longitudinal dimension of the skull (e.g., rostral and nasal length). The discriminant function analysis showed an almost complete separation between the southern lowland and western groups, with 99% of the specimens correctly classified ($F = 9.15$; $P < 0.000001$). A similar result was obtained comparing the northern and southern groups ($F = 9.94$; $P < 0.000001$), where 97% of the specimens were correctly classified (the same result was obtained using cross validation; data not shown). The MANOVA was significant between western and lowland groups (Wilks' $\lambda_{62} = 0.43$; $P < 0.000001$), as well as between northern and lowland groups (Wilks' $\lambda_{60} = 0.4$; $P < 0.000001$).

DISCUSSION

The morphological and genetic comparisons guided by the results of the phylogeographic analyses provide unambiguous evidence indicating that the specimens of *Lutreolina* from the Yungas forests belong to an undescribed species of the genus *Lutreolina* that is described below.
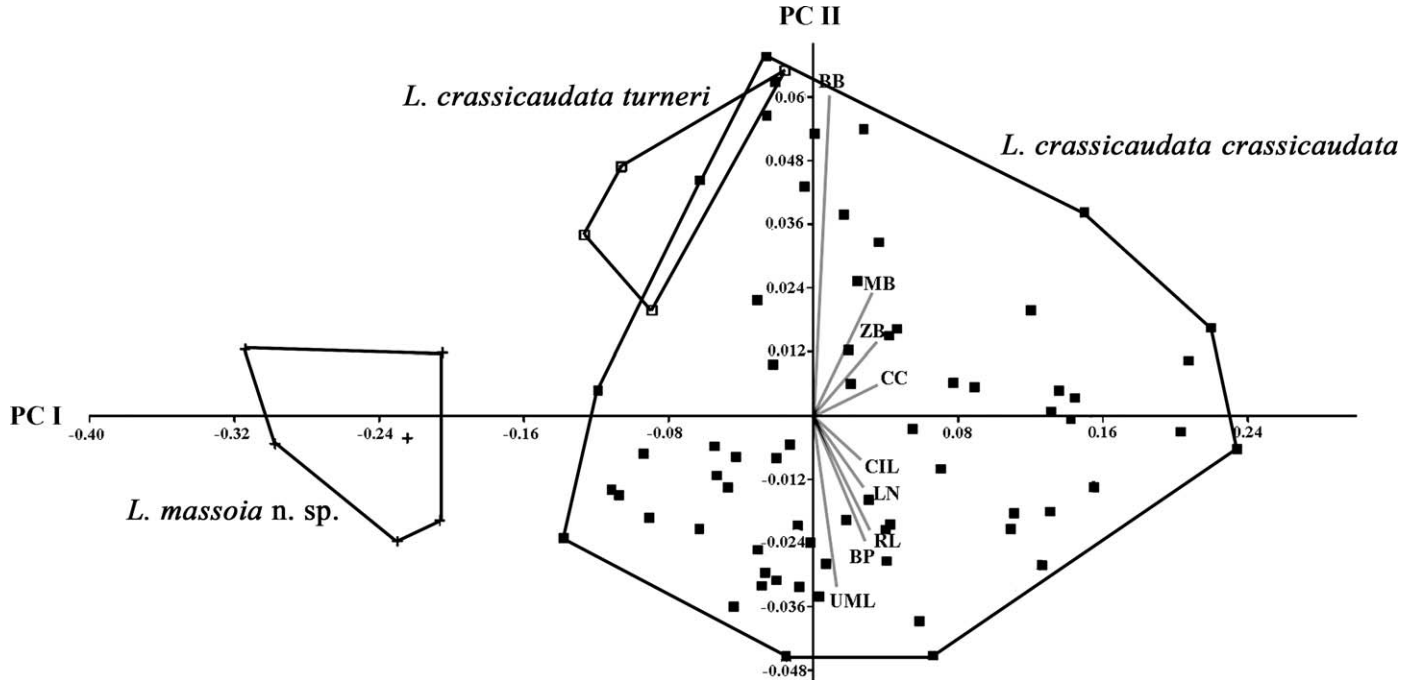
Fig. 3.—Specimen scores of adult individuals of *Lutreolina* for principal components I and II, extracted from the variance–covariance matrix (see text for abbreviations of variables). Crosses, Yungas or western clade (which is here described as a new species). Black squares, *Lutreolina crassicaudata crassicaudata*. White squares, *Lutreolina c. turneri*.

Didelphimorphia Gill, 1872
Didelphidae Gray, 1821
Lutreolina Thomas, 1910
Lutreolina massoia, new species

Urn:lsid:zoobank.org:act:A155F686-D022-462C-BA1E-C907295C45DE

Holotype.—Adult female, skin and skeleton (MACN 25333; Figs. 4 and 5) and tissue (MACN-MA-CT 485) collected on 8 May 2013, by J. P. Jayat (original field number JPJ 2490).

Type locality.—Argentina, Tucumán Province, Río Chico Department, Arroyo El Saltón, Remanso del Gallego, Reserva Provincial Santa Ana, 455 m above sea level (27°26′16.26″S, 65°46′33.6″W).

Diagnosis.—Size small for the genus (Table 1). Fur short; pelage unpatterned, dorsal coloration uniform brownish olive, head and sides similar to the dorsum; rhinarium sooty black in the upper one-half and orange-pink on its lower half (Fig. 5). Ears bone-brown, without any pattern. Tail tricolored; basal 1st one-third cinnamon-brown, the middle sooty black, and an orange-citrine distal tip (15 mm). Hands with short hairs dorsally, darker than dorsum (Prout's brown); toes clearer (orange-pink, as rhinarium). Feet with hairs of similar coloration as hands on dorsal side (Fig. 5).

Skull (Figs. 4 and 6) with rostrum short and wide. Nasals wider anteriorly at two-thirds of its length, expanded abruptly at the level of the frontomaxillary suture. Supraorbital processes present but poorly developed. Interorbital and postorbital borders parallel in dorsal view, with almost the same width in transversal section, including in adult specimens.

Zygomatic arches not well expanded, poorly divergent in dorsal view, and almost straight in ventral plane. Temporal crests short and barely perceptible; sagittal and nuchal crests present but not strongly developed. Braincase globose, with its breadth similar to rostrum length. In lateral view, occipital plate protrudes posteriorly, with condyles well developed, strongly broader. Exoccipital contacts the rostral tympanic process (Fig. 7a). Alisphenoid process of the bulla well developed, surpassing ventrally the level of the postglenoid process. On the inner and lateral region, the sphenoparietal suture extends anteriorly to the level of the foramen rotundum.

Second and 3rd upper premolars without labial and lingual cingulum. Lower molars with talonids relatively wider than trigonids, by lateral extension of the hypoconid; entoconid and hypoconulid notably separated, and the talonid of the last lower element not strongly reduced (Fig. 7c).

Measurements of the holotype.—External measurements (in mm): length of head and body, 238; tail length, 212; length of hind foot (with claw), 38; ear length, 24. Cranial measurements (in mm): condyloincisive length, 54.0; zygomatic breadth, 26.7; braincase breadth, 16.5; rostral length, 17.0; nasal length, 18.6; upper molar toothrow length, 10.9; breadth of the palate, 17.4; mastoid breadth, 17.3; upper canine–canine breadth, 8.50.

Description and comparison.—Total length, 397–494 mm; tail length, 209–255 mm; hind foot length, 38–40 mm; ear length, 24–25 mm; body mass, 284 g. Pelage of *L. massoia* n. sp. (Fig. 5) is similar to that of *L. crassicaudata* (i.e., unmarked) but darker. Externally, *L. massoia* n. sp. is clearly smaller in body and cranial size. Rostrum short, sooty black on
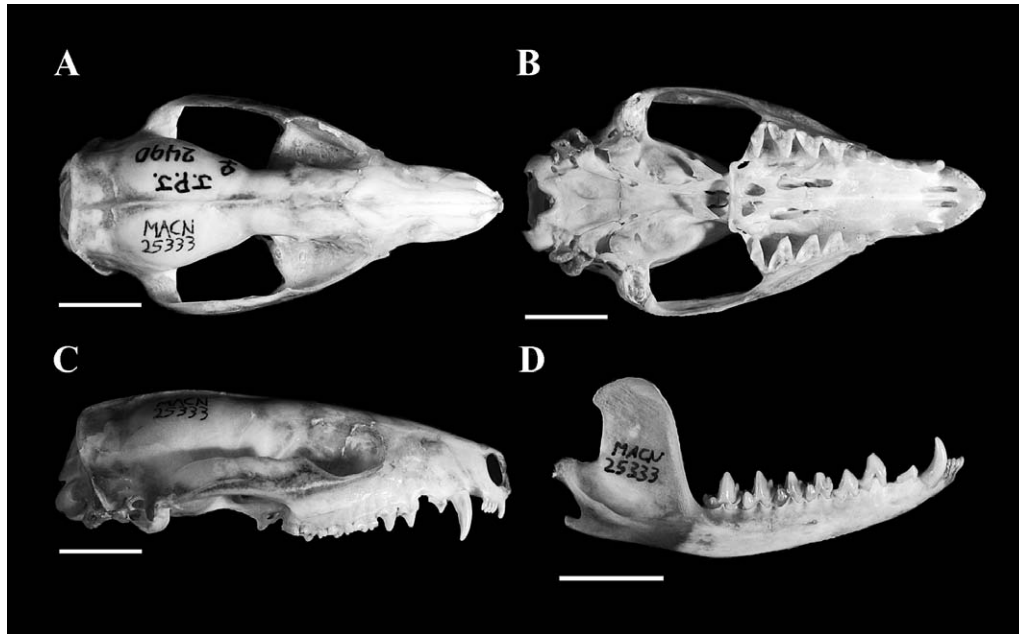
FIG. 4.—*Lutreolina massoia*, new species (holotype, MACN 25333): dorsal (upper left), ventral (upper right), and lateral (middle) views of skull and labial view (bottom) of mandible. Scale: 10 mm.

dorsal and lateral margins, extended to the anterior tip of the eyes. Dorsum (including head) of the new species brownish olive, with some hairs dark olive-buff, which are more abundant on the sides. Venter orange-cinnamon, which extends to the throat, cheeks, and posterior parts of legs. Hair of venter with dark gray bases absent; hairs on sides with gray bases. Throat gland absent. Hairs of dorsum gray-based, but those of the sides and venter are unicolored. Vibrissae well developed, the longest extended almost to the ear level. Ears rounded, uniform and slightly furred with brown short hairs. Hand dorsally darker than the rest of the arm; manual claws longer than apical pads of digits. Forelimbs short and bicolored, dark olive-buff anteriorly, but posteriorly with the same color as the dorsum. Strong claws (except in the hallux) surpassing the tips of the toes; 4 plantar tubercles are present: 2 interdigital, thenar, and interdigital pad between hallux and 2nd digital joins with the hypothenar pad. Pouch present. Tail thick, furred dorsally and ventrally. Proximal one-third of the tail with long hairs, similar to dorsum in general coloration (although more cinnamon), and the remaining with short hairs blackish brown (except the distal tip, which is orange-citrine).
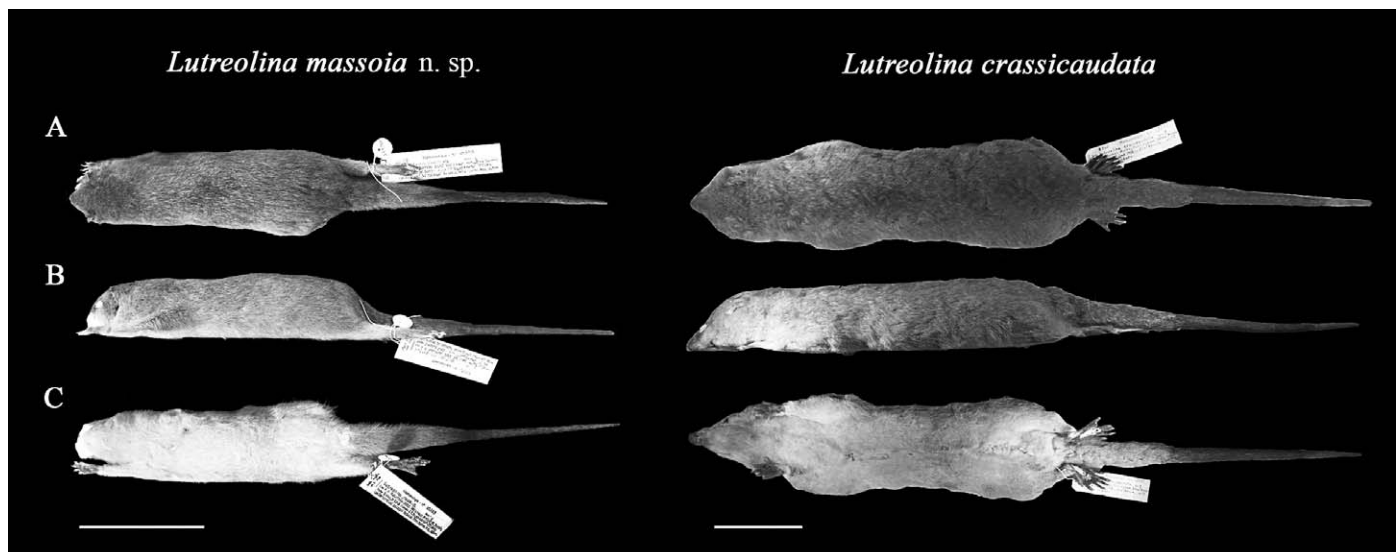

FIG. 5.—Dorsal (top), lateral (middle), and ventral (botton) view of skin of *Lutreolina massoia*, new species (holotype, MACN 25333) and *L. crassicaudata* (MACN 13285). Scale: 10 cm.

TABLE 1.—Summary statistics ($\bar{X}$, range, standard deviation) of cranial measurements (in mm) of *Lutreolina crassicaudata crassicaudata*, *L. c. turneri*, and *L. massoia*, new species. For definitions of measurement abbreviations see the "Materials and Methods."

Measurement	*Lutreolina c. crassicaudata* (n = 64)		*Lutreolina c. turneri* (n = 4)		*Lutreolina massoia*, new species (n = 6)	
CIL	70.32	(60.6–83.6) 5.2	62.8	(61.6–66.2) 2.57	56.25	(52.4–58.8) 2.53
BB	18.44	(16.1–21.9) 1.26	18.7	(17.1–20.2) 0.85	16.75	(16.4–17) 0.25
ZB	36.69	(30–46.1) 3.39	33.8	(31.6–35.8) 1.76	28.5	(26.4–31.5) 2.05
MB	23.64	(20–26.1) 2.08	20.03	(20.8–24.3) 1.96	17.7	(16.9–19.6) 1.02
RL	22.5	(19–26.54) 1.74	20.68	(19.8–21.9) 1.05	18.4	(17–19.6) 1
LN	24.33	(19.2–30.9) 2.09	22.01	(20–24.3) 1.41	20.5	(18.6–21.6) 1.17
CC	11.74	(10–14.9) 1.19	10.67	(10.1–11.7) 0.53	8.8	(8.2–9.3) 0.42
UML	12.29	(11.1–13.9) 0.59	11.33	(11–11.5) 0.23	10.7	(9.7–11.5) 0.61
BP	20.9	(18.1–23.5) 1.21	17.33	(17.3–17.4) 0.04	17.3	(16.5–17.8) 0.44

Caudal scales arranged in spiral series, each scale with 4 subequal hairs.

Skull (Figs. 4 and 6): Cranium robust, with similar general characteristics to that of *L. crassicaudata*, although smaller. Rostrum wide; short nasals, with lateral margins not pointed, and posteriorly not reaching the level of the supraorbital process, but beyond the anterior margin of orbits, and anteriorly not beyond the I1 level. Premaxilla without rostral process, caudally extended to the canine level, although without the wedge between nasal and maxillar, as observed in *L. crassicaudata*. Paracanine fossa well developed; its anterior half limited by the premaxilla and the posterior half limited by the maxillae. Infraorbital foramen well developed and located at the P2 level. Lacrimal well exposed laterally, with 2 small lacrimal foramina in each side. No contact between nasal and lacrimal (due to the contact between maxillar and frontal). Postorbital process small and not pointed, even lesser than those observed in *L. crassicaudata*. Temporal ridge poorly developed, and convergent anteriorly to a point anterior to frontoparietal suture, in a not strongly developed sagittal crest (which also involves the parietals). Postorbital breadth similar to the interorbital breadth. This character clearly differentiates the new species from *L. crassicaudata*, where the interorbital breadth is broader than that of the postorbital (Fig. 6). Infraorbital foramen well developed at the level of P2. Lacrimal anteriorly extended outside from the
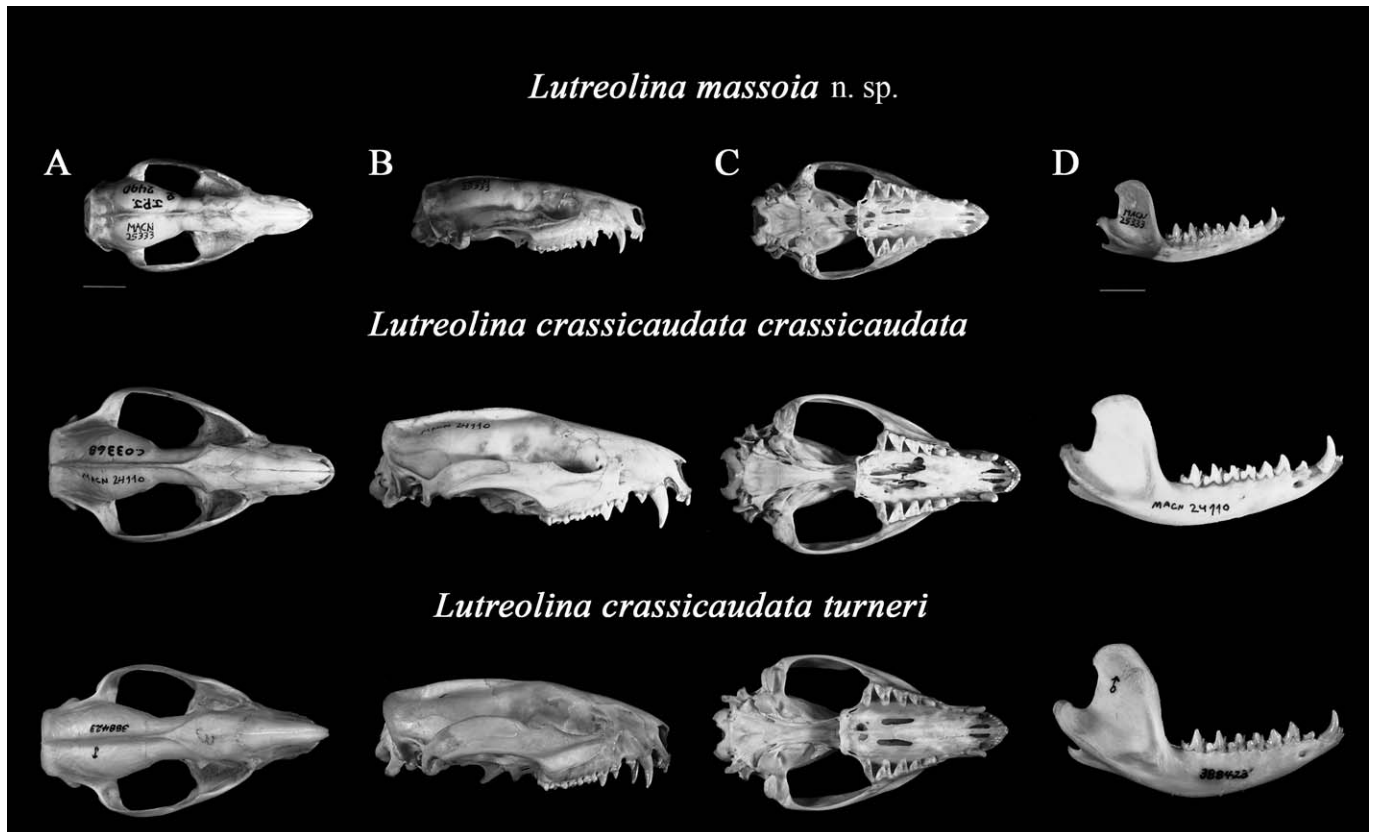

FIG. 6.—A) Dorsal, B) lateral, and C) ventral views of skulls and labial view of the D) right jaw in *Lutreolina massoia*, new species (holotype MACN 25333), *L. crassicaudata crassicaudata* (MACN 24.110), and *L. c. turneri* (USNM 388423). Scale: 10 mm.
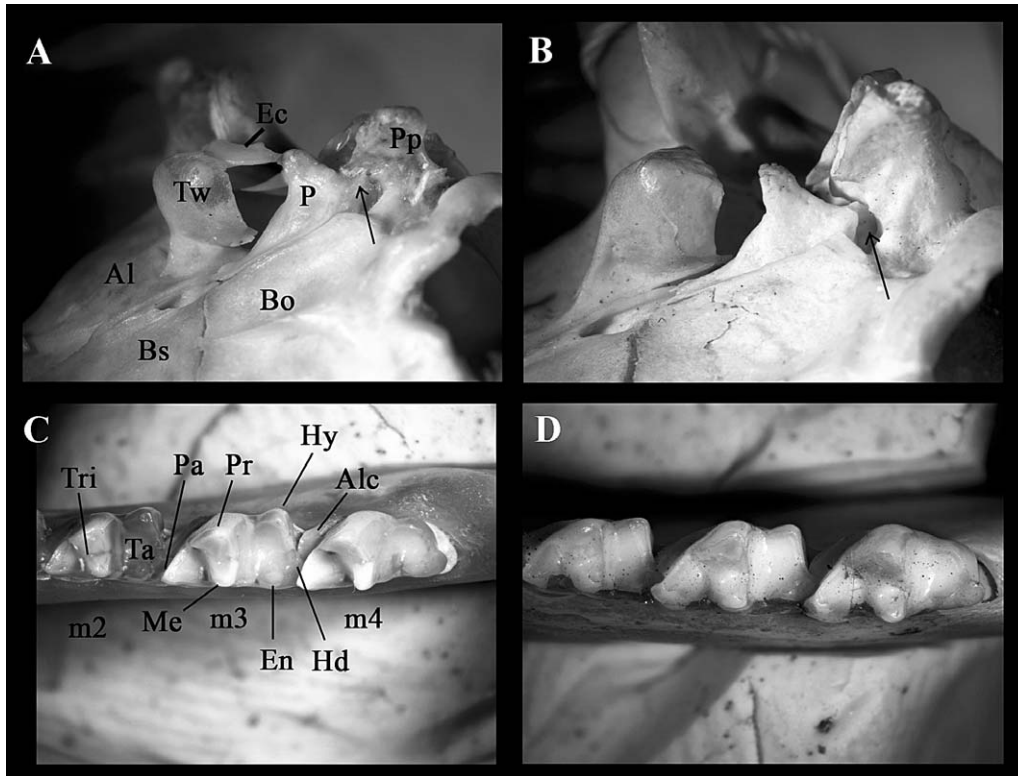
Fig. 7.—Comparison of *Lutreolina massoia*, new species (holotype MACN 25333) and *L. crassicaudata* (MACN 45.101). Partial view of the basicranial region of A) *L. massoia*, new species and B) *L. crassicaudata* showing the contact of the exoccipital and the rostral tympanic process in *L. massoia*, new species, whereas in *L. crassicaudata* both bones are separated (arrows). C) m2–m4 of *L. massoia*, new species with talonids relatively wider than trigonids; whereas, D) in *L. crassicaudata* talonids and trigonids are about the same width. Abbreviations: Al, alisphenoid; Alc, anterolabial cingulum; Bo, basioccipital; Bs, basisphenoid; Ec, ectotympanic; Hd, hypoconulid; Hy, hypoconid; m2, 2nd lower molar; m3, 3rd lower molar; m4, 4th lower molar; Me, metaconid; P, petrosal; Pa, paraconid; Pp, paraoccipital process; Pr, protoconid; Ta, talonid; Tri, trigonid; Tw, tympanic wing of the alisphenoid.

orbit, beyond the level of the frontomaxillar suture. Infraorbital process present, located at the same level as the last upper molar. Postglenoid process well developed, but less than in *L. crassicaudata*, not extending beyond the level of the tympanic wing of the alisphenoid. In ventral view, pterygoid region narrow. Although the nuchal crest is evident, it is not as strongly developed as in *L. crassicaudata*. Mastoid process well developed, as well as paraoccipital process, which is clearly oriented in a posteroventral direction. As observed in *L. crassicaudata*, the occipital plate and occipital condyles protrude posteriorly. However, in *L. massoia* n. sp. the occipital condyles are proportionally broader, compared with *L. crassicaudata* (Fig. 6). Palate slender, with incisive foramen extended from I3 to upper canine level, maxillopalatine fenestra from M1 to M3, and palatine fenestra placed on M4 level. Palatine torus well developed, inflected ventrally, more or less straight with projecting lateral corners. Tympanic wing of the alisphenoid globose, with a medial lamina of the alisphenoid, which defines a secondary foramen ovale, located at the same level as the carotid canal. Petrosal ventrally exposed, with a small tympanic process, which does not contact the tympanic wing of the alisphenoid. Exoccipital contacts the rostral tympanic process, whereas in *L. crassi-*

caudata both bones are separated (Fig. 7b). The basioccipital presents a midline Y-shaped crest (pharyngeal tubercle) forming the medial border of paired oval muscular depressions. Mandible slender, with mandibular condyles laterally expanded, coronoid processes wide, and angular processes short. Mental foramina well developed and placed at the same level as the small diastema separating lower p1–p2.

Dentition: Upper incisive similar to *L. crassicaudata*. The 1st element taller than the remaining, which are asymmetrical and with their anterior cutting edge longer than the posterior one. Canines well developed, without additional cusps. First upper premolar shorter than P2 and P3, which lack the lateral and lingual cingulum observed in *L. crassicaudata*. Anterior margin of the 2nd upper premolar straight, not convex as in *L. crassicaudata*. Upper molars (Fig. 6) comparatively smaller than in *L. crassicaudata*. Anterolabial cingulum present but not well developed. Stylar shelf broad, with stylar cusps B and D more developed; paracristae becoming sequentially more developed from M1 to M4. Ectoflexus of M3 well developed, and protocone of this element and M4 notably bladelike, compared with the more bulbous protocone of M1 and M2. Paracristae confluent with stylar cusp B in M1 and M2, but in M3 the paracristae is confluent between cusps A and B. As in

L. crassicaudata, the metacrista is notably elongated, and the centrocrista is V-shaped. Metacone is taller than paracone and protocone, which are subequals. Lower incisive without accessory cusps. The 1st element wider and taller than the remaining. Canines well developed, without accessory cusps. First lower element smaller and separated from p2 by a short diastema. Second premolar taller and all elements with a posterior cingulum. Second and 3rd premolar with an inconspicuous anterior cingulum. Lower molars (Fig. 7c) with an anterior cingulum, elevated approximately at the same level as the talonid, which is relatively wider than the trigonid by lateral extension of the hypoconid (whereas in *L. crassicaudata* the trigonid is wider than the talonid [Fig. 7d]). Protoconid taller than metaconid and paraconid. In the 1st and 2nd element, the metaconid is slightly taller than paraconid, but in p3 and p4 both cusps are subequals. Talonid of the last lower molar reduced, but as strongly as observed in *L. crassicaudata*; entoconid and hypoconulid well separated, proportionally more than in *L. crassicaudata*.

Paratype.—Young male collected on 10 May 2013 (MACN 25334; tissue: MACN-MA-CT 486) by J. P. Jayat (original field number JPJ 2497).

Distribution.—*Lutreolina massoia* n. sp. is distributed in Yungas forest from southern Bolivia (Tarija and Chuquisaca departments) to northwestern Argentina (Jujuy, Salta, and Tucuman provinces), in the so called "Tucumano-Boliviana" montane forests (Hauman 1931; Navarro and Maldonado 2002; Malizia et al. 2012—see gazetteer and map in Supporting Information S1, DOI: 10.1644/13-MAMM-A-246.S1).

The northern distributional limit of *L. massoia* n. sp. is so far unclear. Although there are some isolated records of *Lutreolina* from northern Bolivia (Beni Department—see Anderson 1997:149), these fall outside the Yungas ecoregion. One adult specimen examined by us from San Javier, Beni (AMNH 210420; Appendix I) and others with published measurements (Anderson 1997) of such northern populations are larger than those of *L. massoia* n. sp. In addition, specimen AMNH 210420 presents the morphological characters observed in *L. crassicaudata* (i.e., lower molar morphology and petrosal and basioccipital without contact). Given this, we assign those populations from Beni, as well as those from Pampas del Heath, southern Peru (Luna et al. 2002), to *L. crassicaudata*. It remains an open question if these populations belong to *L. c. crassicaudata* or to another subspecies (i.e., *L. c. turneri* or one not yet described). The locality "San Jose" from Santa Cruz Department (Bolivia) cited for 1st time by Krumbiegel (1941; but omitted by Anderson 1997) was mapped by Brown (2004) at the position of "San Jose de Chiquitos," which also was followed by Stein and Patton (2007 [2008]); this constitutes an isolated locality (17°50′S, 60°43′W) for *Lutreolina*. However, the recording locality of Krumbeigel (1941), "San Jose" [sic], seems to correspond to a place approximately 300 km west of "San Jose de Chiquitos," in the montane forest of western Santa Cruz (17°57′S, 63°21′W). If this is correct, this population could represent the northernmost locality of *L. massoia* n. sp. (i.e., approximately 300 km north of our northernmost confirmed record [Fig. 1]). Unfortunately, Krumbiegel (1941) did not detail the specimens that constitute the basis of this record; as such, it is not possible to study them to assess their morphology. Additional survey efforts in this area of montane forests are needed to test if *Lutreolina* inhabits it, and if this proves to be the case, to see if that population belongs to the new species here described.

On the other hand, the southern limit of *L. massoia* n. sp. seems to be clearer, because it is placed near the austral limit of the Yungas ecoregion (Burkart et al. 1999). Although Brown (2004) cited *Lutreolina* further south, in Catamarca Province, Argentina, living *Lutreolina* specimens have not been registered for that province (Mares et al. 1997). The records from Catamarca Province cited by Brown (2004) correspond to fossil specimens (see Marshall 1978; Flores 2004). Moreover, fossils coming from such deposits in northwestern Argentina (Huayquerian—Riggs and Patterson 1939) correspond to a species of the extinct genus *Hyperdidelphys* (i.e., *H. pattersoni*—see Goin and Pardiñas 1996). However, because surveys at the southern end of the Yungas forests are still scarce, future fieldwork may show that *L. massoia* n. sp. inhabits Catamarca Province.

Etymology.—The species name is constructed as a noun in apposition based on the name of a man. Dedicated to the memory of Elio Massoia (1936–2001), author of numerous key contributions that significantly expanded our knowledge of the alpha diversity of South American mammals. In particular, Massoia (1973) was among the 1st researchers noticing the distinctiveness of the specimens of *Lutreolina* from the Yungas forests. We suggest for the new species the common name Massoia's lutrine opossum.

Natural history.—*Lutreolina massoia* n. sp. is restricted to Yungas forest, from premontane areas, at 450 m, to the upper forested belts, at 2,000 m. Most authors (e.g., Olrog 1976, 1979; Mares et al. 1981, 1996; Anderson 1997; Capllonch et al. 1997; Mares and Braun 2000; Flores et al. 2007) mentioned areas with dense ground cover and aquatic environments (including marshy or swampy areas, and permanent watercourses) as the habitat most frequently used by this species (Fig. 8).

Massoia's lutrine opossum is crepuscular and nocturnal, feeding mostly on small mammals, fish, and invertebrates, but it also consumes bird eggs, and fruits (Mares et al. 1989; Flores et al. 2007). Olrog (1979) suggested that the high abundance of this species in Cerro Calilegua, Jujuy Province, for certain years, could be related to the population peaks of sigmodontine rodents. This opossum also has been mentioned as a good climber, as agile on the ground, and as an excellent swimmer (Anderson 1997; Díaz and Barquez 2007; Flores et al. 2007). The home ranges of 2 specimens in Tucuman Province were found to be 650 m^2 and 950 m^2 (Mares and Braun 2000; fide Cajal 1981). The nematodes *Travassostrongylus yungaensis* and *Hoineffia simplicispicula* are known to parasitize the gut of *L. massoia* n. sp. (Navone et al. 1991).

Conservation.—Massoia's lutrine opossum is endemic to the Yungas forested areas of northern Argentina and southern Bolivia, an ecoregion that extends over 56,000 km^2 (Brown

Fɪɢ. 8.—General view of the environment at Remanso del Gallego, the collecting locality of the type and paratype specimens of *Lutreolina massoia*, new species.

and Kappelle 2001). Presently, the Yungas are extremely fragmented and under great anthropic pressure (e.g., Malizia et al. 2012). Notwithstanding, specimens of this species are frequently captured in the distributional range of the Yungas and have been registered in several Argentinean protected areas, including Parque Nacional Calilegua in Jujuy Province (Heinonen and Bosso 1994); Parque Nacional Baritú (Gil and Heinonen 2003) and Parque Nacional El Rey (Flores et al. 2007) in Salta Province; and Reserva Provincial Aguas Chiquitas, Reserva Provincial La Florida, Reserva Provincial Santa Ana, Reserva Provincial Los Sosa, and Parque Biológico Sierra de San Javier in Tucumán Province (Mares et al. 1996; Capllonch et al. 1997; Flores et al. 2007).

Taxonomic and biogeographic considerations.— Cytochrome-*b* gene sequence divergence between *L. crassicaudata* and *L. massoia* n. sp. is 2.7%. Similarly low values of interspecific variation have been observed in other pairs of sister species in the tribe Didelphini, such as *Didelphis marsupialis* and *D. aurita* (3%—Patton and Costa 2003) and *Philander opossum* and *P. mcilhennyi* (Tamura 3 parameters values: 3.6–5.4%—Chemisquy and Flores 2012). Interestingly, comparisons involving species of small didelphid genera (e.g., *Marmosa*, *Marmosops*, *Monodelphis*, and *Thylamys*) generally show much larger genetic distances (e.g., Teta et al. 2009; Giarla et al. 2010; Gutiérrez et al. 2010; Carvalho et al. 2011; de la Sancha et al. 2012; Voss et al. 2013). The cause of this difference in observed genetic distance between large and small didelphids is unclear. Futures studies would clarify if it is

due to cryptic species diversity (e.g., Giarla et al. 2014), to distinct substitution rates among lineages, to difference in lineage ages, or a combination of these.

The *Cytb* genealogy of *Lutreolina* shows that populations from the lowlands of Argentina, Brazil, Paraguay, and Uruguay lack phylogeographic structure. As such, no haplogroups match the distributions of *L. c. crassicaudata* and *L. c. paranalis*, which are recognized by several authors (e.g., Cabrera 1957; Ximénez 1967; Massoia 1973; Graipel et al. 1996). This result supports the scheme of Marshall (1978), Stein and Patton (2007 [2008]), and Gardner (2005), who considered a single subspecies (*L. c. crassicaudata*) for the lowlands of southeastern South America (which also included the populations here described as *L. massoia* n. sp.). Nevertheless, Graipel et al. (1996) noted that specimens of *L. c. crassicaudata* from southern populations (e.g., Buenos Aires Province in Argentina and Uruguay) are larger than those from northern populations of this subspecies (e.g., Misiones and Corrientes provinces in Argentina, Paraguay, and Brazil—see Graipel et al. 1996). Unfortunately, our molecular analysis does not include sequences from populations from northern South America, which are assigned to *L. c. turneri*. This subspecies inhabits open environments (northern savanna grasslands) with similar landscapes to those from the southern pampasic regions (Cabrera and Willink 1973) where *L. crassicaudata* occurs. However, our morphometric analyses indicated that specimens of *turneri* are mostly distinct from *L. c. crassicaudata* (Fig. 3). In addition, the general skull

morphology of *L. c. turneri* exhibits several differences from *L. c. crassicaudata*, such as nasals not posteriorly extended (in *L. c. turneri* they extend anteriorly), a more robust interorbital region and zygomatic arches, and pterygoid region notably broader (Fig. 6). However, until genetic data of specimens assigned to *turneri* are analyzed, we prefer not to innovate in relation to the taxonomic status of this form.

Lutreolina shows a complex distribution pattern with different degrees of disjunction. Even though species of *Lutreolina* present affinity and dependence for humid environments (e.g., Stein and Patton 2007 [2008]), the genus is not found in Amazonia (Marshall 1978; Stein and Patton 2007 [2008]). Other mammal groups (e.g., the hystricognath *Cavia aperea* [Dunnum and Salazar-Bravo 2010] and the sigmodontine genera *Calomys* and *Necromys* [Salazar-Bravo et al. 2001; D'Elía et al. 2008]), and examples of other vertebrate groups (i.e., amphibians, reptiles, and birds—see Quijada-Mascareñas et al. 2007), have disjunct distributions that exclude Amazonia. For the moment, it is not clear whether the current distribution of *L. crassicaudata* is the remainder of a larger distributional range that included Amazonia or if during the glacial cycles of the Pleistocene, with the suggested fragmentation of Amazonia (see Haffer 1969), *L. crassicaudata* used open-area corridors to cross south or north into its current distribution (Cerqueira 1982). A comprehensive phylogeographic study of *L. crassicaudata* (i.e., including samples from *L. c. turneri*) may shed light on this issue.

Our sampling for *L. c. crassicaudata*, although sparse, mostly covers the distributional range of the subspecies. As in other taxa that occur in northeastern and eastern Argentina, southeastern Brazil, Paraguay, and Uruguay (e.g., *Calomys musculinus* [González-Ittig et al. 2007], *Necromys lasiurus* [D'Elía et al. 2008], *Oligoryzomys nigripes* [Francés and D'Elía 2006], and *Scapteromys aquaticus* and *S. tumidus* [D'Elía and Pardiñas 2004]), *L. c. crassicaudata* lacks phylogeographic structure. This fact does not necessarily imply that the occurrence of *L. c. crassicaudata* in the area is recent, but may indicate that current populations are relatively young (i.e., there may have been cycles of population expansions and retractions). Additional studies are needed to further assess the biogeographic history of *L. crassicaudata*.

Isolated localities in the arid region of central-western Argentina were mentioned for *L. crassicaudata* by Cabrera (1957), but these seem to be misidentifications of specimens and localities. For instance, Cabrera (1957) and subsequent authors (e.g., Olrog and Lucero 1981; Flores et al. 2007) included Mendoza Province (central-western Argentina) in the distribution of *Lutreolina*, based on a specimen deposited at the Museo de La Plata (MLP 1688 from San Rafael, Mendoza). Our examination of this specimen indicates that it corresponds to a breeding specimen of *Didelphis albiventris*. In this regard the specimen of *L. crassicaudata* reported by Massoia and Pardiñas (1988) from Cueva Epullán Grande, Neuquén Province, is of interest; this site is very distinct given that it is the only record of the genus in the Patagonian steppe, and is approximately 625 km southwest from the closest recorded

locality of the genus (i.e., Algarrobo, Buenos Aires Province; see Appendix I). In addition, it is unclear if the specimen, for which no collection number is provided (it is likely housed in the Colección Elio Massoia, Fundación de Historia Natural Felix de Azara, Buenos Aires; U. F. J. Pardiñas, pers. comm., Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina) and that has been ignored by subsequent authors (but see Massoia et al. 2000), constitutes a recent or a fossil record. Additionally, another specimen of *Lutreolina* from "La Rioja" (central-western Argentina) deposited at the Museo Argentino de Ciencias Naturales (MACN 28201) corresponds to a juvenile, and may represent an erroneous transcription of the original locality, because the extremely arid environment in this area makes the presence of this genus unlikely. As such, no specimen of *Lutreolina* has been recorded for the arid Chaco region, suggesting a geographic gap between *L. crassicaudata* and *L. massoia* n. sp.

The Chacoan distributional gap seen in *Lutreolina* in southern South America mirrors that of several other mammals that have counterparts at both humid sides of the dry Chaco (i.e., Yungas in the west and humid Chaco–Atlantic Forest–Pampas toward the east). Some examples are *Sciurus ignitus* and *S. aestuans*, *Cavia tschudii* and *C. aperea*, *Dasyprocta punctata* and *D. azarae*, and *Leopardus wiedii boliviae* and *L. w. wiedii* (see Barquez et al. 2006). Similarly, several species or subspecies pairs of birds show the same distributional pattern (Nores 1992). Similar to what we found for *Lutreolina* in southern South America, the passerine species *Thamnophilus ruficapillus* showed allopatric mitochondrial lineages structured geographically in the same manner (Kerr et al. 2009). Nores (1992, 1994) suggested that most of these bird species pairs have origins prompted by climatic changes that caused vegetation expansion along the Pilcomayo and Bermejo rivers, allowing ancestral bird species to cross the dry Chaco. Then, when forests retreated to their current distribution, isolated populations differentiated, leading to the patterns of diversity observed today. Future phylogeographic studies would clarify if this model (which has been criticized by da Silva [1994]) fits the history of *L. crassicaudata* and *L. massoia* sp. n., as well as that of other codistributed taxa.

Finally, it is worth noting that the alpha taxonomy of didelphids has greatly changed in the last decade. Several new species (e.g., *Marmosops pakaraimae* Voss et al., 2013; *Monodelphis handleyi* Solari, 2007; *Monodelphis reigi* Lew and Peréz-Hernandez, 2004; *Philander olrogi* Flores et al., 2008; *P. deltae* Lew et al., 2006; and *P. mondolfii* Lew et al., 2006) and genera (e.g., *Hyladelphys* Voss et al., 2001; *Tlacuatzin* Voss and Jansa, 2003; *Chacodelphys* Voss et al., 2004; and *Cryptonanus* Voss et al., 2005) have been described. Similarly, the status of several already available specific (e.g., Teta et al. 2009; Gutiérrez et al. 2010) and generic (e.g., Voss and Jansa 2009) names has changed. As such, the description of *L. massoia* n. sp. is part of a recent and extensive series of taxonomic studies of didelphid marsupials where formal nomenclatorial acts are proposed. We expect this trend to continue with the same intensity for the next decade.

Resumen

Este estudio es la revisión taxonómica más comprensiva del género *Lutreolina*. Se analizaron datos genéticos (ADN mitocondrial de 22 especimenes) y morfológicos (evaluación de 262 especimenes). Los análisis moleculares emplearon secuencias del gen que codifica para el citocromo *b* de 22 individuos colectados en 18 localidades de Argentina, Bolivia, Brasil, Paraguay y Uruguay; actualmente estas poblaciones se incluyen en *L. crassicaudata*. Los resultados indican que *Lutreolina* tienen una marcada estructura filogeográfica, con 2 grupos recíprocamente monofiléticos (2,7% divergentes entre si y con mínima variación interna) distribuidos, respectivamente, al este y oeste del Chaco seco, en el cual *Lutreolina* no se distribuye. El clado oriental incluye poblaciones de Paraguay oriental, centro y noreste de Argentina, sur de Brasil y Uruguay. Estas poblaciones tradicionalmente fueron referidas a las subespecies *L. c. crassicaudata* y *L. c. paranalis*, cuya monofília no es corroborada en este estudio. Por lo tanto, todas las poblaciones del clado oriental son aquí asignadas a la subespecie nominotípica. El clado occidental se distribuye en las selvas de montaña o Yungas del noroeste de Argentina y suroeste de Bolivia, un ambiente marcadamente diferente del habitado por *Lutreolina* en otras áreas (i.e., pastizales en tierras bajas). Las poblaciones de las Yungas son también morfológicamente distintas, tanto en tamaño y forma como en caracteres discretos del cráneo y la dentición, de aquellas de las áreas abiertas del este. Por lo tanto, concluimos que las poblaciones de las Yungas pertenecen a una especie diferente de aquella que habita las tierras bajas del este. Debido a que no hay un nombre disponible para las poblaciones de las Yungas, nominamos y describimos una nueva especie de comadreja para contener a estas poblaciones.

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APPENDIX I

Specimens examined.—Acronyms for institutions and personal catalogs are as follows. Argentina: American Museum of Natural History (AMNH), New York; British Museum of Natural History (BMNH), London; Centro Nacional Patagónico (CNP), Puerto Madryn, Argentina; Colección Mamíferos Lillo (CML), Tucumán, Argentina; Colección Mastozoológica del Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Mendoza, Argentina; Grupo de Ecología de Roedores Urbanos (GERU), Universidad de Buenos Aires, Argentina; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires; Museo de la Plata (MLP), La Plata, Argentina; Museo Nacional de Historia Natural de Montevideo (MNHN), Montevideo, Uruguay; Smithsonian National Museum of Natural History (USNM), Washington, D.C.; Museum of Southwestern Biology (MSB), New Mexico; Museum of Zoology, University of Michigan (UMMZ), Michigan; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Brazil; and Sam Noble Oklahoma Museum of Natural History (SNOMNH). JP: field number of Javier Pereira; GD: field number of Guillermo D'Elía; LHE: field number of Louise H. Emmons; and UP: field number of Ulyses F. J. Pardiñas. Localities are listed in alphabetic order. GenBank accession numbers for cytochrome-b gene DNA sequences are provided between square brackets ([ ]) next to collection numbers. Asterisks (*) indicates specimens used in the principal components analysis.

Lutreolina crassicaudata crassicaudata (244).—ARGENTINA: Buenos Aires Province: Algarrobo (MACN 32.233); Arroyo Tapalqué (MACN 17.63); Ayo Pereyra, Pereyra (AMNH 254511*, 254512*); Bella Vista (MACN 43.73*); Berazategui, Parque Pereyra Iraola (MACN 17268*); Berisso, A. El Pescado (MLP 19.VI.97.2); Berisso-La Balandra (MLP 4.IV.00.9); Buenos Aires (AMNH 838, 36923, 36924, 36925; MACN 167; MNHN 1121*, 1122*, 1123*, 1124*, 1291*, 1292*, 1293*, 2484*); Castelar (MACN 50.477); Chapadmalal (MACN 13066); Chascomús (MACN 15365*); Chascomús, Los Libres del Sur (MACN 49.213, 52.76*); Dock Sur (MACN 92, 93); Ecia. El Tuyú (MLP 9.VIII.71.16); Escobar (MACN 30.404, 30.405, 30.406); General Belgrano (MLP 1569, 1571, 1570, 1591, 17.VI.44.7, 17.VI.44.8, 17.VI.44.9, 17.VI.44.10, 25.XI.41.1, 25.XI.41.2); General Lavalle (MLP 1676, 6.VII.40.3, 6.VII.40.4, 6.VIII.40.1, 6.VIII.40.2, 6.VIII.40.5, 20.I.41.3); Isla Retama, Delta del Paraná (CML 802*, 803*, 804*, 805*, 806*, 807*, 808, 809*, 810*, 811, 919*, 918*); Jardín Zoo La Plata (MLP 10.XII.37.1); La Plata (MLP 620, 10.VI.44.4, 11.VI.42.1, 17.VI.44.2, 17.VI.44.3, 17.VI.44.4, 17.VI.44.5, 17.VI.44.6, 21.X.35.2, 27.V.44.9); La Plata, Punta Lara

(CML 1353*); La Plata–Villa Elisa (MLP 21.X.35.1, 21.X.35.4, 21.X.35.5); Las Flores (MACN 31.258, 52.79); Los Yngleses (BMNH 20.2.7.44 [holotype *L. crassicaudata bonaria*]); Magdalena–Ecia San Isidro (MLP 5.IX.4.9); Mar Chiquita (MACN 13069*); Mar de Ajó (MACN 18.12, 18.13); Matheu (MACN 34.547*); Miramar (MLP 15.II.96.50); Morón (MACN 13.70); Morón, Hurlingam (MACN 13265*, 13266, 13285*); Pergamino (MACN 19191*, 19190*, 19202, 18735); Pigüe–Curamalan Chico (MLP 21.X.35.6); Punta Lara (AMNH 254513*; MACN 17267); Pta Indio, Estancia San Isidro (MLP 22.VI.41.1, 22.VII.41.2); Quilmes (MACN 30.248*); Ramallo (CML 4114, 4115, 4116, 4117); Reserva Ecológica Costanera Sur, Ciudad Autónoma de Buenos Aires (GERU 494 [KF684303]); Roberto Payró (MACN 42.108); Rojas (MACN 14407); Rojas-R 188 Km 116 (MLP 22.III.72.2, 22.III.72.3, 22.III.72.4); San Fernando (MACN 33.282); San Nicolás (MLP 20.IX.49.16); Tres Arroyos (MACN 24.160); Villa Gesell (IADIZA 3301, 3745); Zárate, Isla Talavera (MLP 10.V.87.10); Zelaya (MACN 31297). Chaco Province: Las Palmas (MACN 39.466*); Río de Oro (MACN 14.343); Villa Ana (MLP 707). Córdoba Province: Barreto (MLP 7.XI.41.1); Leones (MACN 49.37*, 49.242*); Río Cuarto–Puente Olmos (MLP 1509, 1.VII.37.1, 1.VII.37.2). Corrientes Province: Capital, Ituzaingó, Pto. Valle (IADIZA 3435); Capital, Finca La Adelita, Laguna Paiva (CNP 3445 [KF684308]); Capital, Las Lomas, Lag. Paiva (IADIZA 3744, 3743, 3428*, 3427*, 3430); Capital, Pirayuí (IADIZA 3296, 3297, 3298*, 3300, 3429*, S/N*); Estancia San Nicolás, 22 Km al SE de San Miguel (CNP 3483); Mercedes, Isleta Caabo Estancia (USNM 331053*); Cañada de Pirayuí (IADIZA S/N); Corrientes, SE, at Centro Argentino de Primates (USNM 536827, 536828, 536829, 536830, 536831, 536832, 536833, 536834, 536835); Ea. El Cedro (MLP 28.IV.50.2); Laguna Grande (MLP 28.IV.50.1); Laguna Paiva (IADIZA 3305, 3304); Manantiales (MACN 13713*); Paso de la Patria (MACN 40.161); Pirayuí (IADIZA 3299, 3302); San Cosme, 8 km N El Palmar (IADIZA 3303). Entre Ríos Province: Brazo Largo (MLP 22.I.44.1); Concordia (MACN 48.282); María Grande (MACN 14904); Las Cuevas (UMMZ 166634 [KF684315], 166635 [KF684316]); Pronunciamiento (MACN 31.269). Formosa Province: 17 km WSW Cnia. Mayor Villafañe (UP 255 [KF684307]); Parque Nacional Pilcomayo, Brazo Norte (MACN 20809); Reserva El Bagual (JP 17 [KF684305]). La Pampa Province: 5 km E Gral. Acha (IADIZA S/N); Fco. Pampa (MLP 21.X.35.7, MLP 21.X.35.8). Misiones Province: Arroyo Garupá (MACN 17270); Estancia Santa Inés, km 10 de la Ruta N° 105 (MLP 16.X.01.8 [KF684306]); Posadas (MACN 17923*). Santa Fe Province: 12 km E Santa Fe (UMMZ 166636 [KF684317]); Colonia Mascias (MACN 43.21); Gral. Obligado, Malabrigo (MACN 36.101, 36.882, 36.884, 36.886, 36.888, 36.889); Las Rosas (BMNH 17.5.2.24* [holotype *L.*

crassicaudata paranalis]); Rufino (MLP 1694, 22.VII.41.3); Santo Tomé (MLP 669, 703); Tostado (MACN 45.101*); Villa Guillermina (MACN 33.175). BOLIVIA: Beni Department: about 23 km W San Javier, Rio Mamore (AMNH 210419, 210420*, 210421, 210422, 210423, 210424, 210425); Mamoré, San Joaquín (USNM 364720). BRAZIL: Paraná State: Curitiba, Rua Vicente Migueleto (MHNCI 3748 [KF684309]). Matto Grosso State: Maracaju (AMNH 133249*, 133250*, 133251, 133252, 133253, 133254, 133255, 133256); Rio Grande do Sul State: São Lourenzo do Sul (BMNH 85.6.26.26* [holotype *L. crassicaudata lutrilla*]); not specific locality (AMNH 202727). São Paulo State: Jaboticabal (AMNH 139825*). Brazil, not specific locality (AMNH 235822; USNM 9046, 9047). PARAGUAY: Central Department: Colonia Nueva Italio, near Villeta (AMNH 143884, 143885, 143886*). Misiones Department: San Ignacio, Santa Teresa, 30 km W San Ignacio de Misiones (USNM 390041*); 2 km NE Ayolas (UMMZ 134018 [AJ628364], 134019 [KF684314]); Centu-cué (GD 303 [KF684304]); Neembucú Department: 4 km NW Pilar (UMMZ 134012 [KF684312]). URUGUAY: Artigas Department: Artigas (MNHN 1296*). Canelones Department: 36 km Interbalnearia, E. Montevide (AMNH 205378, 205379, 205380); A° Las Brujas (IADIZA 2530); Canelones (MNHN 716*, 717*, 718*, 1247*, 1248*, 1249*, 1251*, 1294*, 1295*). Montevideo Department: Montevideo (MNHN 1297*); Parque Roosvelt (MNHN 7642 [KF684310]). Rocha Department: Balneario Aguas Dulces (MNHN 7643 [KF684311]); Rocha (MNHN 885*). San José Department: San José (MNHN 2837*).

Lutreolina crassicaudata turneri (4).—VENEZUELA: Bolivar Department: Hato San Jose, 20 Km W La Paragua (USNM 388420*, 388422*, 388423*). GUYANA: Better Hope, Demerara (BMNH 79.5.1.3* [holotype]).

Lutreolina massoia n. sp. (14).—ARGENTINA: Jujuy Province: Santa Bárbara, Finca El Piquete, aproximadamente a 3 km del cruce del Río Tamango con la senda maderera, 820 m (MACN 24839 [KF684296]); Valle Grande, Abra de Cañas, El Monolito, 1,707 m (CML 1759*); El Duraznal, Santa Bárbara, 1,800 m (CML 1596*, 1597*); "Jujuy" (MACN 34.634). Salta Province: Aguas Blancas (MACN 17269); Orán (OMNH 32543 [KF684302]). Tucumán Province: La Cocha, Dique San Ignacio (CML 2895*); Río Chico, Arroyo El Saltón, Remanso del Gallego, Reserva Provincial Santa Ana, 455 m (MACN 25333* [holotype] [KF684297], 25334 [paratype] [KF684298]); Yerba Buena, Cerro San Javier (CML 1357*); Raco (CML 465). BOLIVIA: Chuquisaca Department: Rinconada del Bufete, 2,000 msnm (LHE 1285 [KF684301], 1286 [KF684300]). Tarija Department: 3 km SE de Cuyambuyo, 900 msnm (MSB 240021 [KF684299]).