



## A new species of arboreal rat, genus *Oecomys* (Rodentia, Cricetidae) from Chaco

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A new species of rodent is added to the highly diverse genus *Oecomys* (Cricetidae, Sigmodontinae, Oryzomyini) based on specimens collected in the Argentinian provinces of Chaco and Formosa. The new species is characterized by a derived carotid circulatory pattern, a feature shared with *O. concolor*, *O. mamorae*, and *O. sydandersoni*. A unique combination of morphological, morphometric, and molecular characters, however, provides unambiguous evidence of its validity as a separate entity. Individuals of the new species are larger than other representatives of *Oecomys*, and their skulls have wide and cuneate interorbital regions with well-developed supraorbital shelves, long incisive foramina, long palates, absent alisphenoid struts, and broad Eustachian tubes. This new *Oecomys* appears to be endemic to the Humid Chaco, an ecoregion listed as Vulnerable due to the human impact. Preliminary observations suggest that several specimens from Eastern Paraguay and the Brazilian Pantanal could also be assigned to the new species described herein.

Una nueva especie es adicionada al altamente diverso género de roedores *Oecomys* (Cricetidae, Sigmodontinae, Oryzomyini), sobre la base de especímenes coleccionados en las provincias Argentinas de Chaco y Formosa. La nueva especie se caracteriza por un patrón de circulación carotídea derivado, un rasgo compartido con *O. concolor*, *O. mamorae* y *O. sydandersoni*. Sin embargo, la combinación única de caracteres morfológicos, morfométricos y moleculares provee evidencia inequívoca sobre su validez como una entidad separada. Individuos de la nueva especie son de mayor tamaño en comparación con otros *Oecomys* y sus cráneos tienen una región interorbitaria ancha y acuñada con plataformas supraorbitarias bien desarrolladas, forámenes incisivos largos, paladares largos, ausencia de las barras alisfenoides y tubos de Eustaquio anchos. Este nuevo *Oecomys* parece ser endémico del Chaco Húmedo, una ecorregión considerada como Vulnerable debido al impacto antrópico. Observaciones preliminares sugieren que varios especímenes de Paraguay Oriental y del Pantanal Brasileiro podrían también ser asignados a la nueva especie aquí descrita.

Key words: Argentina, Bolivia, Brazil, *Oecomys mamorae*, Oryzomyini

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Mice of the genus *Oecomys* Thomas, 1906 (Sigmodontinae, Oryzomyini) are small- to medium-sized rodents (combined length of head and body 90–150 mm), moderately arboreal (Hershkovitz 1960), and broadly distributed in lowland forested areas from Costa Rica southward to southern Bolivia and north-eastern Argentina (Carleton and Musser 2015). Morphological and genetic evidence indicate *Oecomys* to be one of the most

diverse genera of the tribe Oryzomyini (Smith and Patton 1999; Weksler 2003, 2006; Rosa et al. 2012). Several contributions have improved our understanding of the alpha taxonomy of the genus in the last 15 years (e.g., Patton et al. 2000; Voss et al. 2001; Andrade and Bonvicino 2003; Carleton et al. 2009; Rocha et al. 2011, 2012; Carleton and Musser 2015), and the limits and content of *Oecomys* have changed substantially since

its recognition as a subgenus of *Oryzomys* by Thomas (1906). Based mostly on body size, Hershkovitz (1960) consolidated almost 25 nominal forms under 2, *Oecomys bicolor* (Tomes, 1860) and *Oecomys concolor* (Wagner, 1845). Recent compilations, however, have recognized at least 16 valid species in *Oecomys* (Musser and Carleton 2005; Weksler and Percequillo 2011; Carleton and Musser 2015).

The knowledge of *Oecomys* in the southern portion of its range is growing rapidly. Carleton et al. (2009), in a keystone contribution to clarify the systematics of the genus, reviewed in detail the taxa from Yungas and associated habitats in Bolivia. These authors emended the diagnoses of *O. concolor* and *Oecomys mamorae* (Thomas, 1906) and added a new form from eastern Bolivia, *Oecomys sydandersoni* Carleton, Emmons and Musser, 2009. On the east side of the Andes, recent revisions involved *Oecomys catherinae* Thomas, 1909 from the Brazilian Atlantic Forest, *Oecomys cleberi* Locks, 1981 from the Brazilian Cerrado, and the description of a new karyological variant from the Brazilian Pantanal (Andrade and Bonvicino 2003; Asfora et al. 2011; Rocha et al. 2011, 2012).

Massoia and Fornes (1964) first reported *Oecomys* from Argentina based on a single specimen trapped in Chaco Province at approximately 27°S. Following Hershkovitz (1960), they referred the specimen to *Oryzomys (Oecomys) concolor*, subspecies *roberti* (Thomas, 1904). Four decades later, the genus was again recorded for this country, this time in Formosa Province (Pardiñas and Ramírez-Llorens 2005). These authors worked with fragmentary material derived from owl pellets and based on several morphological differences among Argentinian populations and other *Oecomys* species, treated them as *Oecomys* sp. This open nomenclature has generally been used subsequently for Argentinian populations of *Oecomys*. Owl pellet analyses and more extensive trapping have provided a better picture of the distribution of *Oecomys* in Argentina (Pardiñas and Teta 2005; Jayat et al. 2006; Teta et al. 2009; Orozco et al. 2014). The taxonomy of these Chacoan populations remains controversial, however, in part due to the scarcity of complete specimens. As was summarized by Carleton et al. (2009:26), “by geographic proximity alone, these samples are plausibly referable to *O. mamorae*, but certain measurements reported for the fragmented crania of the Argentine form seem to run larger than *O. mamorae* proper from Bolivia... Critical review of variation within nominal *O. mamorae* and comparisons with the Argentine populations are required to verify their specific assignment.”

In recent successive field expeditions, we have had the fortune to capture 3 live adult specimens of *Oecomys* in Chaco and Formosa provinces, Argentina, and we have reviewed the entire series of Argentinian *Oecomys* available for study. Viewed in the context of the contributions of Carleton et al. (2009) and Carleton and Musser (2015), these specimens persuade us that Chacoan populations correspond to an unnamed species, which we diagnose and describe in this work. Preliminary observations based on morphology and genetic evidence further suggest that *Oecomys* populations in the Brazilian Pantanal and Paraguay-Paraná river basin can also be referred to the new species described here.

## MATERIALS AND METHODS

Specimens studied consisted mainly of skulls, skeletons, fluid-preserved bodies, and dry skins obtained from field work and systematic collections. Skull fragments recovered from owl pellets were also examined (see Appendix I for a complete list of specimens). Trapped animals were collected following the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Individuals captured were measured and weighed in the field and prepared as skins, skeletons, or fluid-preserved specimens. Vouchers are housed in the following institutions: Colección Elio Massoia (CEM; acquired by Fundación Félix de Azara, Buenos Aires, Argentina); Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina); Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina), Museum of Vertebrate Zoology (MVZ; Berkeley, California), University of Connecticut (UCONN; Storrs, Connecticut), and Museum of Zoology, University of Michigan (UMMZ; Ann Arbor, Michigan). The holotype of *O. mamorae* was studied through photographs kindly provided by P. Cordeiro Estrela. Most of the material retrieved from owl pellets is housed in the Colección de Material de Egagrópilas y Afines “Elio Massoia” of the Centro Nacional Patagónico (CNP-E; Puerto Madryn, Chubut, Argentina). The morphology of other *Oecomys* species recorded in southern South America was assessed through the examination of comparative material housed at the MACN and MVZ mammal collections (see Appendix I) and the literature.

Nomenclature used to describe the skull and its structures follows Carleton and Musser (1989), Weksler (2006), and Carleton et al. (2009), and that of the molars follows Reig (1977). Four relative age classes (juvenile, young adult, full adult, and old adult) were recognized by the degree of molar wear following the criteria of Carleton and Musser (1989). Seven external variables, including total length (TL), length of head and body (HBL), length of tail (T), length of hindfoot with claw (HFL) and without claw (HFLw), length of ear (E), and mass (W; in grams), were retrieved or calculated from original labels. Twenty-two cranial measurements were recorded with manual calipers following the criteria of Musser et al. (1998) and Carleton et al. (2009): occipitonasal length (ONL); greatest zygomatic breadth (ZB); least interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); length of nasals along midline (LN); depth of braincase (DBC); breadth of the zygomatic plate (BZP); width of braincase (WB); breadth of braincase at lateral extremes of lambdoidal ridge (BB); length of diastema (LD); palatilar length (PAL); length of bony palate (BPL); postpalatal length (PPL); breadth of the bony palate across M1s (BBP); length of incisive foramen (LIF); maximum breadth across the incisive foramina (BIF); bullar length (less tube, LBU); breadth across the exoccipital condyles (BOC); coronal length of the maxillary tooththrow (CLM); alveolar length of the maxillary tooththrow (ALM); width of the 1st upper molar (WM1); alveolar length of the mandibular tooththrow (ALm). Descriptive univariate statistics are provided for the new species based on the entire available sample from the Argentinian Chaco. Mean and range

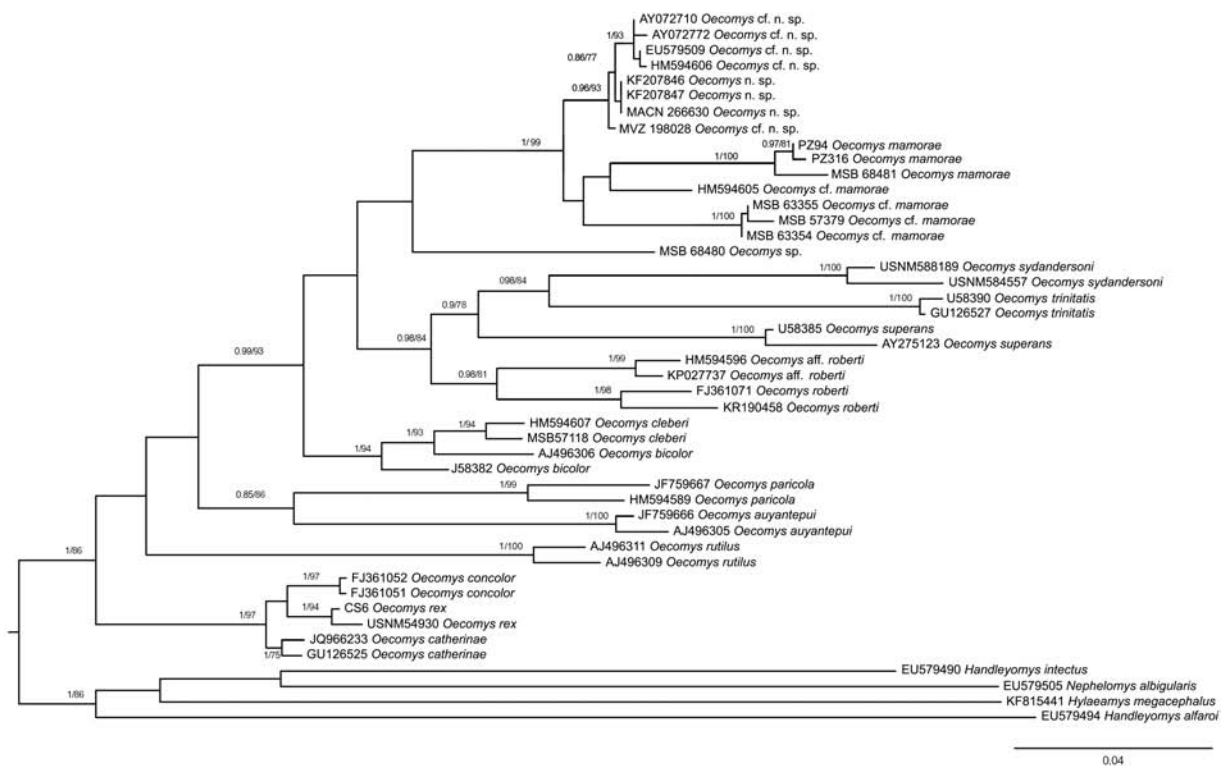
comparisons among larger species of the genus *Oecomys* (those with HBL > 125 mm) employed data tabulated by Carleton et al. (2009:table 4) and Carleton and Musser (2015:415).

Morphometric analyses were performed on a set of 10 (IOB, BR, BZP, LD, BPL, BM1s, LIF, BIF, CLM, WM1) craniodental variables. Included in the analysis were 51 full adult and old adult specimens of *O. mamorae* (measurements provided by M. D. Carleton) and 14 specimens referred here to the new species (see below). Multivariate analyses using principal components (PCs) and size-free canonical discriminant analyses were used to explore the patterns of phenetic differentiation. Size-free canonical discriminant analysis corrects for the misleading influence of ontogenetic growth in intergroup discrimination patterns (dos Reis et al. 1990). Ontogenetic growth was removed by calculating the regression residuals of each of the 10 variables regressed on the 1st PC (computed on a pooled within-group PC analysis), then using the residuals in place of original individual measurements (dos Reis et al. 1990). Canonical variates analysis assumes that all variables are multivariate normal and that groups share similar variance–covariance structure. In our case, a reliable estimate of the variance–covariance structure in the data is guaranteed by a total sample size  $> [(2k - 4) + (G - 1)]$ , where  $k$  is the number of variables measured and  $G$  the number of groups (Webster and Sheets 2010). In a preliminary analysis, specimens from Bolivia were pooled in 4 different geographic subgroups. Subsequent analyses treated Bolivian populations (including some Paraguayan samples from the Dry Chaco) as

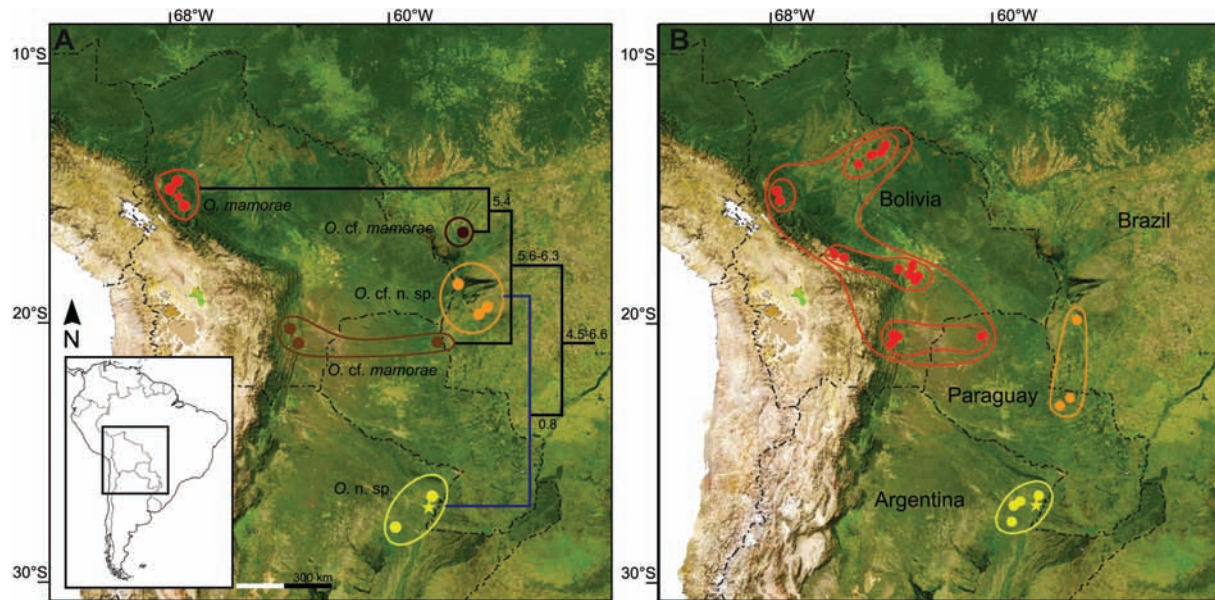
a single taxonomic unit based on the extensive overlap among individuals in multivariate space (Supporting Information S1), morphological homogeneity, and the evidence retrieved from a molecular marker (Figs. 1 and 2). Due to their geographic closeness, environmental continuity, and low sample sizes, *Oecomys* specimens from Brazil and eastern Paraguay were pooled in all statistical analyses. All analyses were run on the log-transformed data set of craniodental measurements using the software InfoStat (di Rienzo et al. 2008).

Genomic DNA was isolated from either frozen or ethanol-preserved tissues with the use of commercial kits (Qiagen) and following the manufacturer's recommendations. A fragment of 801 bp of 1 mitochondrial marker (cytochrome-*b*: *Cytb*) was obtained from several Bolivian and an Argentinian specimen of *Oecomys* (Table 1) using a combination of primers and protocols slightly modified from the literature (Salazar-Bravo et al. 2013). Alignment, visualization, and translation of obtained sequences were performed with modules in Lasergene for Windows (DNASTAR 2003). To place these sequences in a phylogenetic context, we downloaded representative sequences of several species of *Oecomys* from GenBank (Table 1). In addition, specimens of *Handleyomys intectus*, "*Handleyomys*" *alfaroi*, *Hylaeomys yunganus*, and *Nephelomys albigularis* were chosen as outgroup based on results presented by Weksler (2006; Table 1).

MrModeltest (Nylander 2004) was used to estimate the most appropriate model of sequence evolution (GTR+I+G). The data matrix was analyzed using a Bayesian approach in



**Fig. 1.**—Maximum likelihood (ML) analysis of cytochrome-*b* sequences for 42 ingroup terminals and 4 individuals representing outgroup taxa (GTR+I+ $\Gamma_6$ , ln-likelihood = -5573.75833). Node support includes Bayesian posterior probabilities (only values equal or above 0.85) to the left of the diagonal and percentages of 1,000 bootstrap replicates (values above 75%) after the diagonal for nodes recovered in common by ML and BI analyses. GenBank access codes or specimen identification numbers correspond to those of Table 1.



**Fig. 2.**—A) Map of collecting localities of specimens of *Oecomys* included in the *Cytb* phylogenetic analysis. Polygons correspond to the clades identified in the *mamorae* group and relationships among these clades are depicted with black lines. Numbers above black lines are genetic *p*-distances. Type localities are depicted with a star. B) Map showing recording localities for the specimens of *Oecomys* in its southern expression used in morphological analysis; circles = Bolivian and western Paraguayan samples (subgroups, from north to south, correspond to the following geographic groups: Beni, Cochabamba, Santa Cruz, and Chuquisaca; see [Supporting Information S1](#)); triangles = Brazilian and eastern Paraguayan samples; squares = Argentinian samples. *Cytb* = cytochrome-*b*.

MrBayes version 3.2.5 (Ronquist et al. 2012) and a maximum likelihood (ML) approach in PhyML 3.0 (Guindon et al. 2010). Bayesian analysis was performed with the model chosen by MrModeltest, but all model parameters were estimated in MrBayes. Uniform interval priors were assumed for all parameters except base composition and GTR+I+G parameters, which assumed a Dirichlet process prior. Each Bayesian analysis consisted of 2 independent runs, each with 3 heated and 1 cold Markov chains, which were allowed to proceed for 10 million generations and were sampled every 1,000 generations. The first 25% of trees were discarded as “burnin,” and the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade. For the ML analysis, we used the model parameters and variable estimates calculated by the Smart Model Selection (SMS) program of PhyML under the BIC (Bayesian Information Criterion). SMS estimated the same model of evolution as MrModeltest, except that it suggested 6 instead of 4 rate categories. The proportion of invariable sites (I) was fixed at 0.551 and the Gamma shape parameter fixed at 0.991. The number of alternative runs on distinct starting trees was set to 10 in order to avoid entrapment in local maxima. Kimura 2-parameter genetic distances (Kimura 1980) were calculated to assess within- and among-species genetic divergence in MEGA 6.06 (Tamura et al. 2013).

For the *O. mamorae* group (see below), we estimated the hierarchical distribution of genetic diversity through an analysis of molecular variance (AMOVA—Excoffier et al. 1992) using Arlequin version 3.11 (Excoffier et al. 2005). Hierarchical levels were defined on the basis of sampling localities and major clades found in the phylogenetic analysis. Fixation indexes ( $F_{ST}$ ) were estimated with DNAsp v5 (Librado and Rozas 2009).

## RESULTS

Within *Oecomys*, 2 patterns of carotid circulation are especially useful for preliminary taxonomic sorting (Carleton and Musser 2015). Most *Oecomys* species are characterized by a complete circulatory pattern (character state 0 of Carleton [1980] or pattern 1 of Voss [1988]), which is considered the ancestral condition for Muroidea (see Carleton et al. [2009] for a complete description of this pattern). On the other hand, the derived carotid circulatory pattern (character state 3 of Carleton [1980] or pattern 3 of Voss [1988]) is found in only 3 currently recognized species within the genus: *O. concolor*, including *O. marmosurus* (Thomas, 1899) as junior synonym; *O. mamorae*; and *O. sydandersoni*. Specimens from the Argentinian Chaco share with these 3 species the derived carotid circulatory pattern, suggesting a closer morphological relationship. However, as described below, the Argentinian populations are characterized by a unique combination of craniodental characters and differ morphologically and morphometrically from *O. concolor*, *O. mamorae*, and *O. sydandersoni*.

Phylogenetic analysis of *Cytb* sequences recovered highly congruent trees regardless of the analytic method employed. In both topologies, a monophyletic *Oecomys* was recovered with moderate (ML) to strong support (BI; BS = 81, PP > 0.99; Fig. 1), and several groups of species were evident, including a *concolor-catherinae-rex* clade that was the sister group to the remaining species of *Oecomys*. Other species groups included *rutilus*, *paricola-ayantepui*, *bicolor-cleberi*, *roberti*, *superans*, *trinitatis-sydandersoni*, and a group comprising a number of specimens most closely related to *mamorae* (the “*mamorae*” group, below). One animal from northern Bolivia (MSB 68480), representing an unnamed taxon, was retrieved as sister to a

**Table 1.**—List of specimens of *Oecomys* with *Cytb* sequences analyzed in the present study. *Cytb* = cytochrome-*b*.

Species	Voucher	GenBank accession number	Country	Division	Locality	Source <sup>a</sup>
<i>O. mamorae</i>	PZ 316	KT737225	Bolivia	La Paz	Buena Vista	This paper
<i>O. mamorae</i>	PZ 94	KT737226	Bolivia	La Paz	Tumupasa	This paper
<i>O. mamorae</i>	MSB 68481	KT737227	Bolivia	Beni	35 km NW Yucumo	This paper
<i>O. cf. mamorae</i>	MVZ 197505	HM594605	Brazil	Mato Grosso	Base de Pesquisas do Pantanal, 110 km SSW Poconé	Rocha et al. (2011)
<i>O. cf. mamorae</i>	MSB 63354	KT737228	Bolivia	Chuquisaca	Río Limón	This paper
<i>O. cf. mamorae</i>	MSB 63355	KT737229	Bolivia	Chuquisaca	2 km E Chuhuayacu	This paper
<i>O. cf. mamorae</i>	MSB 57379	KT737230	Paraguay	Alto Paraguay	1 km SE Puerto Caballo, Estancia Doña Julia	This paper
<i>O. cf. sp. n.</i>	LBCE 1924	AY072710	Brazil	Mato Grosso do Sul	Corumbá, Fazenda Alegria	Andrade and Bonvicino (2003)
<i>O. cf. sp. n.</i>	LBCE 1941	AY072772	Brazil	Mato Grosso do Sul	Corumbá, Fazenda Alegria	Andrade and Bonvicino (2003)
<i>O. cf. sp. n.</i>	UFMG 2829	EU579509	Brazil	Mato Grosso do Sul	Rio Vermelho, above Passo do Lontra	Rocha et al. (2011)
<i>O. cf. sp. n.</i>	MVZ 197506	HM594606	Brazil	Mato Grosso do Sul	Rio Miranda, above Passo do Lontra	Rocha et al. (2011)
<i>O. cf. sp. n.</i>	MVZ 198028	KT737231	Brazil	Mato Grosso do Sul	Rio Vermelho, above Passo do Lontra	This paper <sup>b</sup>
<i>O. sp. n.</i>	"Parque 224"	KF207846	Argentina	Chaco	Pampa del Indio Provincial Park	Orozco et al. (2014)
<i>O. sp. n.</i>	"Parque 308"	KF207847	Argentina	Chaco	Pampa del Indio Provincial Park	Orozco et al. (2014)
<i>O. sp. n.</i>	MACN 26663	KT737232	Argentina	Formosa	Estación de Animales Silvestres Guaycolec	This paper <sup>b</sup>
<i>O. sp.</i>	MSB 68480	KT737233	Bolivia	Beni	35 km NW Yucumo	This paper <sup>b</sup>
<i>O. trinitatis</i>	MUSM 13320	GU126527	Peru	Loreto	Río Galvez	This paper <sup>b</sup>
<i>O. trinitatis</i>	MVZ 200948	U58390	Brazil	Acre	Opposite Igarapé Porongaba, left bank Jurúá	Percequillo et al. (2011) <sup>c</sup>
<i>O. sydanderi</i>	USNM 588189	KT737235	Bolivia	Santa Cruz	El Refugio, Rio Paragua/Tarvo, right bank	Patton and da Silva (1995)
<i>O. sydanderi</i>	USNM 584557	KT737234	Bolivia	Santa Cruz	PN "Noel Kempff Mercado," El Refugio, 3 km NE	This paper <sup>b</sup>
<i>O. superans</i>	MVZ 155006	AY275123	Peru	Amazonas	Vicinity of Huampami [Aguaruna Village], rio Cenepa	D'Elia (2003)
<i>O. superans</i>	MVZ 200944	U58385	Brazil	Amazonas	Penedo, right bank Jurúá	Patton and da Silva (1995)
<i>O. roberti</i>	UFPB 388	FJ361071	n/d	n/d	n/d	G. Miranda, unpublished
<i>O. roberti</i>	FSF140r	KR190458	Brazil	Pará	Fazenda Santa Fe, Santana do Araguaia	Rocha et al., unpublished
<i>O. aff. roberti</i>	UFMG 2847	HM594596	Brazil	Tocantins	Peixe	Rocha et al. (2011)
<i>O. aff. roberti</i>	RGR404	KP027737	Brazil	Tocantins	Fazenda Lago Verde, Lagoa da Confusão	Rocha et al., unpublished
<i>O. cleberi<sup>b</sup></i>	UFMG 2799	HM594607	Brazil	Minas Gerais	13 km NE Nova Ponte	Rocha et al. (2012)
<i>O. cleberi</i>	MSB 57118	KT737236	Bolivia	Beni	Boca del río Biata	This paper
<i>O. bicolor</i>	V-999	AJ496306	French Guiana	Cayenne	Les Nouragues	J. F. Mauffrey, unpublished
<i>O. bicolor</i>	MVZ 200962	U58382	Brazil	Acre	Sobral, left bank Jurúá	Patton and da Silva (1995)
<i>O. ayanitepui</i>	V 1001	AJ496305	French Guiana	Cayenne	Les Nouragues	J. F. Mauffrey, unpublished
<i>O. ayanitepui</i>	n/d	JF759666	Brazil	n/d	Floresta Estadual do Trombetas	Rocha et al. (2011)
<i>O. paricola</i>	UFES 1438	HM594589	Brazil	Tocantins	Pium	Rocha et al., unpublished
<i>O. paricola</i>	MAJ27	JF759667	Brazil	n/d	Fazenda Tauari, Margem Direita do Baixo Rio Cururu	Rocha et al., unpublished
<i>O. rutilus</i>	MNHN 1995.3236	AJ496309	French Guiana	Cayenne	Saint-Eugene	J. F. Mauffrey, unpublished
<i>O. rutilus</i>	V-889	AJ496311	French Guiana	Cayenne	Les Nouragues	J. F. Mauffrey, unpublished
<i>O. concolor</i>	MN 37763	FJ361051	n/d	n/d	n/d	G. Miranda, unpublished
<i>O. concolor</i>	MN 37764	FJ361052	n/d	n/d	n/d	G. Miranda, unpublished
<i>O. catherinae</i>	MF29	GU126525	Brazil	Espirito Santo	RF C. V. Rio Doce	Percequillo et al. (2011) <sup>c</sup>
<i>O. catherinae</i>	UFES 247	JQ966233	Brazil	Bahia	Reserva Particular do Patrimônio Natural Nova Angélica	Machado et al. (2014)
<i>O. rex</i>	USNM 549530	KT737238	Brazil	Pará	East bank Rio Xingu, 52 km SSW Altamira	This paper <sup>b</sup>
<i>O. rex</i>	CS 26	KT737237	Brazil	Pará	Floresta Nacional Tapirapé-Aquiri, Município de Marabá	This paper <sup>b</sup>

Table 1.—Continued

Species	Voucher	GenBank accession number	Country	Division	Locality	Source <sup>a</sup>
Outgroups						
<i>Nephelemys albigularis</i>	AMNH 268125	EU579505	Peru	Cajamarca	Las Ashtas	D. Hanson, unpublished
<i>Handleyomys inexpectatus</i>	CADY088	EU579490	Colombia	Antioquia	4 km S El Retiro	D. Hanson, unpublished
<i>Hyleamys megacephalus</i>	MN 70000	KF815441	Brazil	Rondonia	Vilhena	Vilela et al. (2014)
" <i>Handleyomys</i> " <i>alfaroi</i>	ROM 101537	EU579494	El Salvador	Santa Ana	PN Montecristo	D. Hanson, unpublished

<sup>a</sup>According to GenBank.

<sup>b</sup>Unpublished sequence provided by Jim Patton.

<sup>c</sup>Sequence not reported in the paper.

<sup>d</sup>Reported as *O. bicolor* in Rocha et al. (2011).

clade containing *O. mamorae* and related specimens; although this unnamed taxon occurs in sympatry with *O. mamorae* at a locality in the Beni department, MSB 68480 is morphologically (e.g., complete carotid circulation), morphometrically, and genetically distinct from species in the *O. mamorae* group.

Three clades comprise the *mamorae* group as defined here (Fig. 2). The 1st clade includes specimens from north-central Bolivia (Tumupasa, Buena Vista and 35 km NW of Yucumo). A Brazilian specimen from Mato Grosso (GenBank accession no. HM594605) falls within this clade although with low to moderate support (BS = 46, PP = 0.6). The 2nd and 3rd clades were retrieved with strong support. These include 1) a group of southern Bolivian and Paraguayan specimens (Río Limón, Chuhuayacu, and Alto Paraguay) and 2) a broadly distributed clade formed by haplotypes recovered from specimens from Mato Grosso do Sul (Brazil) and 3 localities in the provinces of Chaco and Formosa (Argentina). Genetic distances among species of *Oecomys* ranged from about 2.0% (*O. cleberi*–*O. bicolor* pair) to 13.4% (*O. rutilus*–*O. paricola* pair; Supporting Information S2). Distances among members of the *mamorae* group averaged 3.6% (range 0.4–6.6%; Fig. 2). Results from the AMOVA indicate that 73.3% of the genetic variation recovered among members of the *mamorae* group is due to differences among the 3 main clades, suggesting differentiation at the level of species. In addition, an AMOVA comparing the animals from Argentina and Mato Grosso do Sul with Bolivian and Paraguayan samples (*O. mamorae* and *O. cf. mamorae*) indicated a clear pattern of differentiation, with 78.4% of genetic variation due to differences between these groups. Likewise, the estimated value of the Fixation index (Hudson et al. 1992) was  $F_{ST} = 0.7135$  and 0.7294, respectively, suggesting a fairly low level of gene flow among the groups.

In combination, these results provide unambiguous evidence indicating that the specimens from the Argentinian Chaco represent a new species of *Oecomys* that we describe as follows.

Family Cricetidae Fischer, 1817  
 Subfamily Sigmodontinae Wagner, 1843  
 Tribe Oryzomyini Vorontsov, 1959  
 Genus *Oecomys* Thomas, 1906  
*Oecomys franciscorum*, new species  
 Figs. 3 and 4; Table 2

*Oryzomys* (*Oecomys*) *concolor roberti*: Massoia and Fornes, 1964:319; not *Oecomys roberti* (Thomas, 1904).

*Oecomys* sp.: Pardiñas and Ramírez-Llorens, 2005:104.

*Oecomys* sp.: Pardiñas and Teta, 2005:507.

*Oecomys* sp.: Cirignoli et al., 2006:168.

*Oecomys* sp.: Jayat et al., 2006:58.

*Oecomys* sp.: Teta et al., 2009:147.

*Oecomys* sp.: Udriazar Sauthier and Carrera, 2013:55.

*Oecomys* sp.: Orozco et al., 2014:15.

*Holotype*.—CNP 4260, an adult, scrotal male preserved as skull, complete postcranial skeleton, and dry skin, with viscera and tissues in ethanol; collected by G. Panisse and C. Galliari (field number CG 417) on 17 August 2013. External measurements were recorded on the skin label.

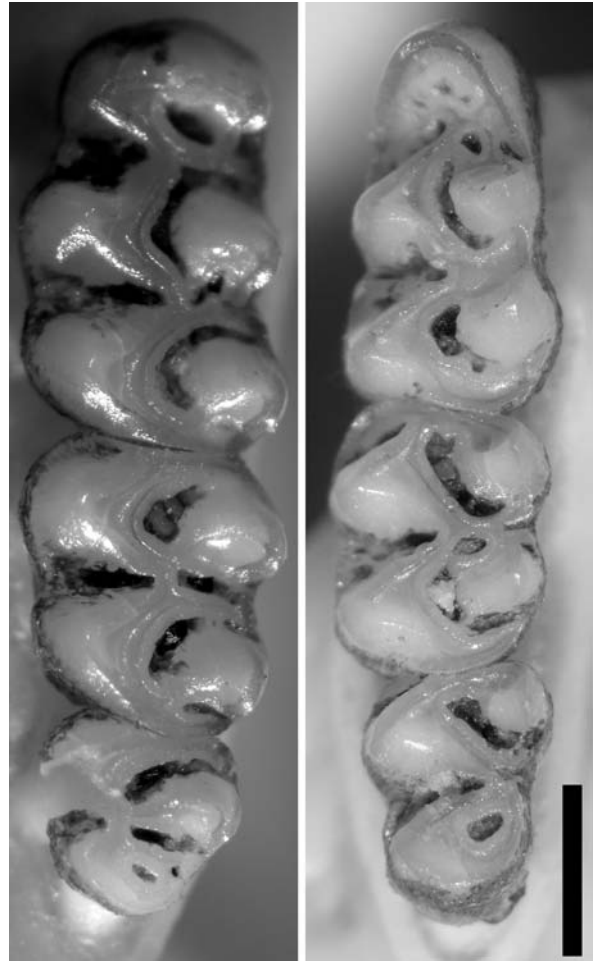


**Fig. 3.**—Holotype of *Oecomys franciscorum*, sp. nov., from Estación de Animales Silvestres Guaycolec, Formosa, Argentina (CNP 4260): skull in right lateral (top), dorsal (left), and ventral (right) views, and left dentary (reversed) in labial view. Scale = 5 mm.

*Paratype.*—MACN 26663, skull, complete postcranial skeleton, and dry skin from adult female trapped by C. Galliari (field number CG 94) on 11 July 2012 at the type locality (see below).

*Type locality.*—Argentina, Provincia de Formosa, Departamento de Formosa, Estación de Animales Silvestres Guaycolec, 0.4 km NW of the junction between Ruta Nacional 11 and Riacho Pilagá (25.982733°S, 58.167781°W [coordinates taken by GPS at the trapsite]), elevation 73 m (Fig. 2).

*Additional material.*—(localities arranged by increasing latitude; specimens with an asterisk were used in morphometric analyses, which also included the holotype and paratype) CNP 700\*, CNP 701\*–709, cranial remains from owl pellets from Estancia Guaycolec (25.976111°S, 58.18°W, Provincia de Formosa, Argentina); CNP 592\*, CNP 594, CNP 598, CNP 603\*, and CNP 680\*, cleaned skulls and bodies preserved in formalin from Reserva Natural El Bagual (26.305165°S, 58.830971°W, Provincia de Formosa, Argentina); CNP 3424\*, CNP 3427\*, and CNP 3428\*, cranial remains from owl pellets collected in RN El Bagual; CNP-E 60 and CNP 4261\*, cranial remains from owl pellets collected at Escuela Provincial de Educación Técnica Agropecuaria N° 8 “Zapallar Norte,” Gral. J. de San Martín (26.531616°S, 59.332543°W, Provincia de



**Fig. 4.**—Holotype of *Oecomys franciscorum*, sp. nov., from Estación de Animales Silvestres Guaycolec, Formosa, Argentina (CNP 4260): upper left (left) and lower left (right) molar tooththrows in occlusal view. Scale = 1 mm.

Chaco, Argentina); CNP 5076, a female with entire body preserved in fluid (field number CG 403) collected on 13 August 2013 at junction between Río de Oro and Ruta Provincial 33 (26.725775°S, 59.048237°W, 75 m elevation, Provincia de Chaco, Argentina); CNP 3425\* and CNP 3426\*, cranial remains from owl pellets collected at Capitán Solari (26.802739°S, 59.561888°W, Provincia de Chaco, Argentina); uncatalogued material, cranial remains from owl pellets collected at Escuela N° 278 “Francisco Joulhe” (26.815319°S, 59.114134°W, Provincia de Chaco, Argentina—Udrizar Sauthier and Carrera 2013); CNP-E 61, cranial remains from owl pellets collected at Escuela Provincial N° 20, General Vedia (26.911476°S, 58.685906°W, Provincia de Chaco, Argentina); CNP-E 58, cranial remains from owl pellets collected at Puerto Bermejo, Pueblo Viejo (26.928685°S, 58.506597°W, Provincia de Chaco, Argentina); CEM 1107\*, skull from adult male trapped on 6 June 1964 in the vicinity of río Negro, Makallé Viejo (27.173814°S, 59.261573°W, Provincia de Chaco, Argentina).

*Diagnosis.*—A large species of *Oecomys* (length of head and body ~147 mm, occipitonasal length ~31.4 mm) characterized by the following combination of characters: a derived carotid circulatory pattern; wide and cuneate interorbital region;

**Table 2.**—Selected external and craniodental measurements (in mm) of *Oecomys franciscorum*, sp. nov., and samples of other larger species of the genus.

	<i>O. franciscorum</i> <sup>a</sup>					<i>O. mamorae</i> <sup>b</sup>				<i>O. concolor</i> <sup>c</sup>	<i>O. rex</i> <sup>d</sup>	<i>O. superans</i> <sup>e</sup>
	Mean	SD	N	Min	Max	Mean	SD	Min	Max	Mean	Mean	Mean
Total length	318.0	8.2	3	311.0	327.0	296.0	18.3			273.2		
Length of head and body	146.7	6.7	3	139.0	151.0	139.8	13.1	120.0	170.0	125.4	128.0	150.0
Length of tail	171.3	5.0	3	166.0	176.0	158.5	10.7	144.0	180.0	147.9	155.0	167.0
Length of hindfoot without claw	27.7	0.6	3	27.0	28.0							
Length of hindfoot with claw	29.5	0.9	3	28.5	30.0	27.3	1.8	23.0	30.0	27.4	28.0	30.0
Length of ear	21.0	1.0	3	20.0	22.0	18.0	1.2	17.0	20.0	17.1		
Mass	72.7	11.0	3	60.0	80.0	73.9	29.9	48.0	120.0	57.8	59.0	85.0
Occipitonasal length	31.4	4.0	6	24.4	35.1	32.5	1.2	30.9	34.5	32.2	34.0	35.8
Greatest zygomatic breadth	16.3	1.5	6	14.8	17.9	17.1	0.7	15.6	18.1	17.7	17.6	18.3
Least interorbital breadth	5.4	0.3	16	4.9	6.1	4.9	0.2	4.6	5.2	5.5	6.5	5.9
Length of rostrum	9.8	2.2	9	6.6	12.9	9.1	0.4	8.6	10.0	9.1		
Breadth of rostrum	6.0	0.6	16	4.8	7.1	5.8	0.3	5.4	6.2	6.1		
Depth of braincase	9.2	0.5	8	8.5	10.0	9.3	0.5	7.7	10.0	9.4		
Breadth of the zygomatic plate	3.3	0.6	16	2.0	3.9	3.4	0.3	2.8	3.9	3.3		
Breadth of braincase at lateral extremes of lambdaoidal ridge	14.7	0.7	2	14.2	15.2	12.6	0.3	12.0	13.2	12.5		
Length of diastema	7.7	1.1	16	5.5	9.4	8.0	0.5	7.2	8.7	8.1		
Length of bony palate	6.3	0.3	14	5.7	6.9	6.1	0.4	5.4	6.9	6.6		
Postpalatal length	11.2	1.1	5	10.0	12.4	11.3	0.5	10.4	12.0	10.6		
Breadth of the bony palate across M1s	6.1	0.4	16	5.2	6.6	5.9	0.3	5.4	6.4	6.1		
Length of incisive foramen	6.0	0.7	15	3.9	7.1	5.8	0.3	5.3	6.3	5.3		
Maximum breadth across the incisive foramina	2.6	0.4	15	1.9	3.3	2.5	0.3	2.0	2.9	2.3		
Coronal length of the maxillary toothrow	5.4	0.2	14	5.1	5.9	5.0	0.2	4.7	5.4	4.9	5.3	5.4
Width of the M1	1.5	0.1	17	1.4	1.7	1.4	0.1	1.3	1.5	1.4		

<sup>a</sup>Specimens from Chaco and Formosa provinces, Argentina (pooled ages and sexes).

<sup>b</sup>Specimens ( $n = 14-16$ ) from Beni Department, Bolivia; after Carleton et al. (2009:table 4).

<sup>c</sup>Specimens ( $n = 23-24$ ) from Amazonas Department, Brazil; after Carleton et al. (2009:table 4).

<sup>d</sup>Specimens ( $n = 8-21$ ) from Brazil, French Guiana, Guyana, and Surinam; after Carleton and Musser (2015:table 1).

<sup>e</sup>Specimens ( $n = 20-86$ ) from Colombia, Ecuador, and Peru; after Carleton and Musser (2015:table 1).

well-developed supraorbital shelf; relatively and absolutely long incisive foramen; palate projected well beyond the posterior margin of the M3 with typically one medium to large posterolateral palatal pit per side; alisphenoid strut absent; broad bony Eustachian tube; large molar toothrow (~5.4 mm).

**Morphological description.**—*Oecomys franciscorum* is large compared to other *Oecomys*, with total length ~318 mm and tail length ~171 mm; its pelage is soft, abundant, and deep (individual hairs are 16 mm long over the middle rump). Dorsal hairs have dark gray bases and terminal yellowish tips (length of the tip ~3 mm). These hairs are finely intermixed with longer black guard hairs projecting ~5 mm beyond the fur over the middle dorsum. General tones are bright on the dorsum and paler on flanks. Dorsal and ventral colors are moderately demarcated and countershading is conspicuous (Supporting Information S3). General appearance of ventral pelage is yellowish; hairs of throat and chest are tinged whitish; perianal and genital areas, abdomen, and the internal surface of the hindlimbs are washed reddish. Pheomelanin pigments are paler toward the rostrum, giving the face a yellowish appearance. Short whitish hairs are present around the lips and rhinarium, and the sides of the rostrum are bordered by small reddish hairs. Mystacial vibrissae are abundant and black, with the longest surpassing the external border of the pinnae. The tail is pale brown, slightly darker on the dorsum, with its dorsal and ventral surfaces finely covered with short, rigid hairs

that do not conceal the fine-scale pattern below. A rudimentary pencil (3 mm) is present at the tip of tail. Caudal hairs are 3 per scale and extend over fewer than 2 scale rows. Ears are comparatively large, oval, and covered by short, delicate reddish hairs, giving a general cinnamon tone and naked appearance. Manus and pes are covered dorsally with dark-brown hairs; sides of both manus and pes and the toes are covered with tawny to whitish hairs. Hind feet are relatively short and broad; unguis tufts are bright white and well developed on digits II–V; claws on these digits are short (1.3 mm) and not keeled; the pollex has a rounded nail and lacks unguis tufts. The distal end of digit I surpasses the 2nd interdigital pad (Supporting Information S4). Palms and plantar surfaces are naked and scutellated; the plantar surface has 6 large, closely positioned pads; the thenar is almost equal to the 4th interdigital pad and the hypothenar is large and broad. The 1st phalanx of digits II, III, and IV is covered by very large scales with crenated margins. Four mammary pairs are present; 1 pair is located in the inguinal region near the midline, 1 is abdominal, 1 is pectoral anterior, and 1 is posterior or axillar.

The skull is robust, with a wide and moderately long rostrum and broad interorbital region (Fig. 3). The nasals are expanded in their distal third, nearly rounded in their anterior end, and inflected downward when viewed in profile; the posterior margins of the nasals are bluntly squared, not surpassing the maxillary-frontal suture and positioned anteriorly to the lacrimal



plane. The supraorbital shelves are well developed and converge forward such that the interorbital constriction is in a relatively anterior position. The zygomatic notches are visible in dorsal view and the zygomatic arches are noticeably expanded. The lacrimal bones contact maxillary and frontal bones equally. The cranial vault is rounded from the interorbit to the occipital border. Temporal ridges are slightly marked and scarcely extend into the parietals. The interparietal is broad, nearly as wide as the posterior border of the frontals in adult individuals. The zygomatic plate is broad, with its anterior border nearly straight and its posterior margin situated anterior to the alveolus of M1. Jugals are present and small; their maxillary and squamosal processes overlap but are not in contact. The posterior orbital wall is without conspicuous relief. The parietals are expanded laterally and extend onto the lateral surface of the braincase. Each subsquamosal fenestra is compressed, nearly a one-half to three-fourths the size of the postglenoid foramen; the hamular process is narrow, straight, and not spatulated distally. Lambdoidal ridges are well developed along the squamosal sutures. The mastoid fenestra is conspicuous and positioned dorsolaterally. Incisive foramina are relatively long, with their posterior margins slightly projecting between the 1st molars in young individuals or terminating just anteriorly of the 1st molar alveoli in adults. The premaxillary septum is inflated and extends posteriorly at least three-fourths the length of the incisive foramen. The palate is long and wide (sensu [Hershkovitz 1962](#)). Posterior palatine foramina exit in the maxillopalatine suture at a level approximately even with the hypoflexus of M2; marked grooves run from the posterior palatine foramina to the posterior borders of the incisive foramina. Posterolateral palatal pits are usually present as medium to large depressions on each side of the palate, sometimes with internal perforations plus 1 or 2 supernumerary foramina immediately anterior. The mesopterygoid fossa is broad, with a blunt U-shaped anterior border and sides that are parallel to slightly divergent posteriorly. The roof of the mesopterygoid fossa is completely ossified. The parapterygoid fossae are slightly excavated but do not reach the level of the mesopterygoid roof. The cranium lacks alisphenoid struts, the buccinator-masticatory foramen and foramen ovale are confluent; the anterior opening of the alisphenoid canal is present and large. A squamosal-alisphenoid groove, sphenofrontal foramen, and posterior opening of the alisphenoid canal are absent. The stapedia foramen persists as a minute pinhole. The posterior suspensory process of the squamosal is absent, and the tegmen tympani do not touch the squamosal. The ectotympanic bullae is intermediate in size, with the exposed wedge of the periotic not contributing to the wall of carotid canal. The bony Eustachian tube is particularly broad and subtriangular in section with its internal border parallel to the basioccipital suture posterior to the opening of a large carotid canal.

The mandible is high and robust ([Fig. 3](#)). Mental foramina are laterally placed, located just in front of the conjunction of the upper and lower ridges of the masseteric crests. The capsular projection of each lower incisor is small but conspicuous, lying just behind the coronoid process. Superior and inferior

masseteric ridges are well developed, converging anteriorly as an open chevron beneath the m1. The anteriormost point of the diastema lies slightly ventral to a line projected forward along the alveolar roots. The coronoid process is triangular in shape, short, and posterodorsally oriented. Angular processes are short with respect to the condyloid process. The sigmoid notch is narrow and subelliptical and the lunate notch shallow. Ventromedial processes of the mandibular rami are moderately expressed. The retromolar fossa is well developed and perforated by just 1 or 2 tiny pits.

Upper incisors are opisthodont and ungrooved with yellowish-orange anterior enamel surfaces. Upper molar rows diverge slightly posteriorly. Molars are pentalophodont, brachyodont, and slightly terraced; labial and lingual cusps are arranged in opposite pairs, with labial and lingual flexi overlapping in the medial molar plane ([Fig. 4](#); [Supporting Information S5](#)). M1 lacks an anteromedian flexus but has an anteromedian fosse-tus (anterocone internal fold sensu [Weksler \[2006\]](#)) separating anterolabial and anterolingual conules, the former slightly larger than the latter. The procingulum of M1 is linked posteromedially to the anterior mure. The anteroloph is well defined, medially connected to the anterior mure, and merges with the anterocone in old individuals. The paracone is linked posteromedially to the posterior part of the protocone, defining a long and obliquely oriented paraflexus; a protolophule is sometimes present. The protocone joins the anterior mure anteriorly and is separated from the anterocone by a protoflexus and from the paracone by a paraflexus. The mesoloph is long, reaching the labial margin of the molar; in some individuals, the mesoloph is connected in its distal third to an enamel lophule from the paracone (a paralophule?), enclosing an internal metafossetus. The metacone is linked posteriorly to the hypocone, defining a long metaflexus. The posteroloph is short and the posteroflexus is reduced to a subtle fossetus in old individuals. The proto- and hypocones are subequal in size; the hypoflexus is broad and penetrates to the medial molar plane. An enterostyle is usually present ([ICZN 1999](#)).

M2 is nearly square in outline and closely resembles the comparable portion of M1; the anteroloph is the only remnant structure of the procingulum. A mesoloph is well developed. Both M1 and M2 have wrinkled enamel cingula closing the lingual flexi. M3 is nearly triangular in outline with a short mesoloph unrelated to the paracone; the paracone is connected directly to the metacone by an enamel lophule (metalophule?) in old individuals. Metacone, hypocone, and posteroloph are all reduced. Upper molars have 3 large, externally visible roots (anterior, posterior, and lingual); between the labial roots of the M1 typically a small accessory rootlet is present ([Supporting Information S5](#)).

The lower molars have moderately terraced crowns and alternating main cusps ([Fig. 4](#); [Supporting Information S5](#)). The m1 lacks an anteromedian flexid; the anteriorly-posteriorly compressed procingulum contains a slotted anteromedian fossetid. The procingulum is extended posteriorly by an anterolabial cingulum, which touches the protoconid in old individuals. The mesolophid is long, distally spatulate, and completely confluent

with the entoconid in old animals. The posterolophid is well developed, and its lingual opening persists even with intensive wear in old individuals. Proto- and hypoconid are subtriangular in outline, the latter slightly larger than the former. The hypoflexid is very broad and is divided by an ectolophid that contacts an enlarged ectostylid at the molar labial border. The m2 is subrectangular in outline, with a broad, well-developed anterolabial cingulum that closes the labial opening of the protoflexid where it contacts the protoconid. The ectolophid and ectostylid are clearly distinguishable. A mesolophid is well developed.

The m3 is subtriangular in outline and slightly shorter than the m2; both protoflexid and anterolabial cingulum are conspicuous. The hypoflexid is broad and extends more than half of the molar surface. The mesolophid is reduced to a spur of enamel. Both entoconid and ectolophid are absent. An ectolophid is present as a creased enamel border at the base of the hypoflexid. Lower molars each have 1 anterior and 1 posterior large subcylindrical roots (Supporting Information S5).

The axial skeletal in CNP 4260 includes 13 ribs, 12 thoracic vertebrae, 8 lumbar vertebrae, 3 fused sacral vertebrae, and 40 or 41 caudal vertebrae. The paratype MACN 26663 has 12 ribs, 12 thoracic vertebrae, 7 lumbar vertebrae, 3 fused sacral vertebrae, and 37 caudal vertebrae. As it is typical in *Oryzomyia*, the neural spine on the 2nd thoracic vertebra is enlarged and about 3 times the length of the 3rd thoracic. Based on the 3 livetrapped individuals, the stomach is unilocular-hemiglandular, which is a widespread condition in sigmodontines and was previously reported for *Oecomys* (Carleton 1973). The bordering fold approximately bisects the stomach on a line from the incisura angularis to a point opposite it on the greater curvature (Supporting Information S6).

*Measurements (in mm) of the holotype.*—TL 311; T 172; HFL 30; HFLw 28; E 22; ONL 33.6; ZB 17.6; IOB 5.5; LR 10.1; BR 6.6; LN 11.9; DBC 10; BZP 3.7; WB 14.2; BB 12.8; LD 8.3; PAL 14.2; BPL 6.1; PPL 11.4; BBPs 6.6; LIF 6.3; BIF 2.9; LBU 4.3; BOC 7.9; ALM 5.5; CLM 5.3; WM1 1.5; ALM 5.8; CLM 5.7. Body mass of the holotype, 60 g. Measurements for additional specimens are given in Table 2.

*Comparisons.*—*Oecomys franciscorum* can be distinguished from most other species of *Oecomys* by the presence of a derived circulatory pattern (see above). One of the key cranial features of *O. franciscorum* is the absence of alisphenoid strut. Within the 3 currently recognized species of *Oecomys* with a derived carotid circulatory pattern, an alisphenoid strut is present in *O. concolor* and *O. sydandersoni*, and absent in *O. mamorae*. In addition, both *O. concolor* and *O. sydandersoni* are smaller than *O. franciscorum* (cf. Table 2; Carleton et al. 2009:table 4) and have shorter incisive foramina and narrower upper tooththrows (width of M1 < 1.5). The shape of the incisive foramina is also different. In *O. concolor*, it is acute in its anterior and posterior ends, curved along the lateral edges and widest near the middle; in *O. sydandersoni*, it is acute in its anterior end and wider to the rear; and in *O. franciscorum*, it is acute in its anterior end and nearly round to the rear with almost parallel borders (Carleton et al. 2009:figure 4). Further, current knowledge of their distributions suggest that large geographical gaps

separate the ranges of *O. concolor* in northern South America, *O. sydandersoni* in northeastern Bolivia, and *O. franciscorum* in northeastern Argentina (see Carleton et al. 2009:figure 6; Carleton and Musser 2015).

Like *O. franciscorum*, *O. mamorae* is also a large species (Table 2) with long incisive foramina and absent alisphenoid strut. *O. mamorae* can be distinguished from *O. franciscorum*, however, by 5 main cranial morphological features (Fig. 5): 1) its shorter rostrum and shorter incisive foramina terminating just anterior to the anterior face of the M1s, including a less developed and shorter premaxillary septum; 2) its narrow, more amphoral shaped interorbital region with much less prominent supraorbital shelves (Supporting Information S7) and consequently posteriorly displaced interorbital constriction; 3) its V-shaped coronal suture; 4) its shorter bony palate that terminates more or less even with the caudal margin of the M3; and 5) its narrower bony Eustachian tubes. In addition, posterolateral palatal pits are less developed in *O. mamorae*, while in *O. franciscorum*, the posterior portion of the bony palate is typically more foraminated (but see “Variation” below). The external appearance of both species is also different (Supporting Information S3 and S8). *O. mamorae* has a fulvous dorsal coloration, with a sharply defined pure white belly (Thomas 1906). In *O. franciscorum*, the line between dorsal and ventral regions is not obvious. The dorsal coloration is grayish-brown with a yellowish tinge and the belly is yellowish. The ears of *O. mamorae* do not contrast strongly with the dorsal fur (Thomas 1906; Osgood 1916), while those of *O. franciscorum* are ochraceous or orange in strong contrast with the grayish head.

Multivariate analyses of cranial measurements reveal that *O. mamorae* and *O. franciscorum* are well separated in multivariate space. PC1, PC2, and PC3 accounted for 51.0%, 20.8%, and 7.2% of the total variation, respectively (Table 3). In bivariate plots of PC1 and PC2 (Fig. 6), *O. mamorae* from Bolivia and western Paraguay does not overlap with Argentinian specimens of *O. franciscorum*, nor with specimens from Brazil and eastern Paraguay here treated as *O. cf. franciscorum* (Fig. 6). Overlap between the clusters of specimens from Argentina versus those from Brazil and eastern Paraguay is limited, suggesting that specimens from Brazil and eastern Paraguay may also differ from Argentinian specimens. Bivariate plots of PC2 and PC3 depict a moderate overlap between samples from Argentina versus Brazil and eastern Paraguay, with specimens of *O. mamorae* strongly separated (Fig. 6). The size-free canonical analysis shows an almost complete separation of those samples identified as *O. mamorae* from Bolivia and western Paraguay, but it failed to separate Argentinian individuals from those from Brazil and eastern Paraguay (Fig. 6; Tables 4 and 5), suggesting that differences between the latter 2 last groups are in size, not in shape. In synthesis, *O. franciscorum* appears larger in most cranial dimensions than *O. mamorae*. The Brazilian and eastern Paraguayan populations that may correspond to *O. franciscorum* (see “Discussion” below) differ slightly in size from Argentinian populations of that species, but not in shape. Whether these differences are indicative of clinal variation from north to south or the existence of more



**Fig. 5.**—Selected qualitative anatomical traits differentiating *Oecomys mamorae* and *Oecomys franciscorum*, sp. nov. Photographs of *O. franciscorum* are of MACN 26663 except the palate, which is CNP 4260. *O. mamorae* is represented by MACN 50.387. A) and B) Interdiastemal palate of *O. mamorae* and *O. franciscorum*, respectively; note posterior end of incisive foramen with respect to the plane defined by the anterior face of the M1. C) and D) Interorbital region of *O. mamorae* and *O. franciscorum*, respectively: note the position of the constriction. E) and F) Posterior palate region of *O. mamorae* and *O. franciscorum*, respectively. G) and H) Ectotympanic of *O. mamorae* and *O. franciscorum*: note the bony Eustachian tube and the petrosal expression.

**Table 3.**—Results of the principal components (PCs) analyses comparing full and old adult specimens of *Oecomys franciscorum*, sp. nov. and *O. mamorae* ( $n = 51$ ). Results are based on 10 log-transformed craniodental variables (see “Materials and Methods” for abbreviations).

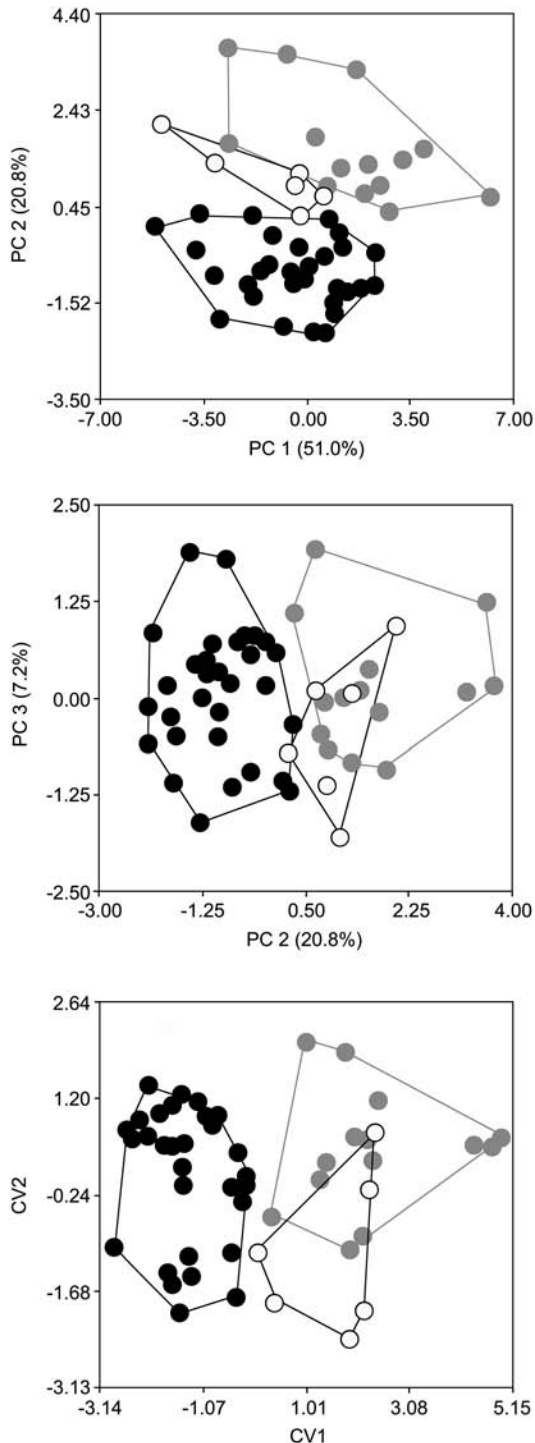
Variables	PC1	PC2	PC3
IOB	0.35	0.19	0.08
BR	0.41	0.07	0.05
BZP	0.32	-0.26	-0.47
LD	0.37	-0.31	0.09
BPL	0.29	0.14	-0.43
BM1s	0.34	0.08	-0.40
LIF	0.36	-0.11	0.40
BIF	0.35	-0.16	0.48
CLM	0.16	0.59	0.12
WM1	0.06	0.62	0.05
Eigenvalue	5.10	2.08	0.72
% Variance	0.51	0.21	0.07

than 1 entity within *O. franciscorum* cannot be resolved with the limited evidence at hand.

*Oecomys franciscorum* can be differentiated from other congeneric species whose range extends (at least potentially) into the Paraguay-Paraná basin (Asfora et al. 2011; Rocha et al. 2011, 2012; Carleton and Musser 2015) by its derived carotid circulatory pattern. *O. bicolor*, *O. cleberi*, and *O. paricola* (Thomas, 1904) can also be set apart because they include animals clearly smaller than *O. franciscorum* (i.e., with head and body length < 110 mm), with pure white to pale cream underparts, relatively shorter tail (i.e., < 110% of the head and body length), and tails well covered with hairs obscuring scale rows

(except in *cleberi*). *O. catherinae* and *O. trinitatis* (J. A. Allen and Chapman 1893) are very similar to each other, with soft and dense dorsal fur varying from brownish-orange to tawny brown, venter generally dark grayish-white, tail longer than combined head and body (> 115%) with caudal hairs short and revealing the scale rows. Both differ from *O. franciscorum* in that they are slightly smaller, lack a strong demarcation between dorsal and ventral coloration along the sides of their bodies, and typically lack a discrete tuft at the tip of their tails.

**Variation.**—The cranial fragments derived from owl pellets revealed variation in some morphological traits in *O. franciscorum*. Most important was the number and size of the posterolateral palatal pits. We typically recorded 2 pits, a single minute pit anterior to a moderately large posterior pit that is located almost even the anterior border of the mesopterygoid fossa. However, some individuals have only a large posterior pit (as the holotype) or, less frequently, 3 pits. A few specimens show 2 posterolateral palatal pits recessed in a shallow depression (Supporting Information S9). We also recorded minor variation in the posterior limit of the incisive foramina and the width of the palatal process of the maxillary. This variation may be related to age, as those individuals with the incisive foramina reaching the protoflexus of the M1 are younger than those in which this structure is even with the anterior face of the M1s (Supporting Information S9). It is important to note that variation in the number and expression of the posterolateral palatal pits is widespread in oryzomyines (e.g., Musser et al. 1998; Weksler 2006; Chiquito et al. 2014). Nonetheless, the number of pits was recently used as a diagnostic trait for



**Fig. 6.**—Projection of individual scores on PC1 × PC2 (top) and PC2 × PC3 (middle) extracted from PC analyses comparing samples of fully adult specimens of *Oecomys* ( $n = 51$ ; black circles = *O. mamorae*; gray circles = *O. franciscorum*; white circles = *O. cf. franciscorum*); and size-free discriminant analysis (bottom) for the same samples. See also Tables 3 and 4. PC = principal component.

a new *Cerradomys* (see Bonvicino et al. 2014). The available sample of *O. franciscorum* is insufficient to assess sexual dimorphism.

**Etymology.**—This species is dedicated to 2 Franciscos: the surgeon Francisco Maldonado da Silva (San Miguel de

**Table 4.**—Results of the 3-group size-free discriminant function analysis of full and old adult specimens of *Oecomys* from Argentina, Bolivia, Brazil, and Paraguay ( $n = 51$ ); see “Materials and Methods” for abbreviations. CV = canonical variate.

Variables	CV1	CV2
IOB	0.17	0.61
BR	−0.30	−0.03
BZP	0.09	−0.74
LD	−0.48	−0.18
BPL	−0.13	−0.25
BM1s	−0.29	0.29
LIF	−0.17	0.16
BIF	−0.20	0.06
CLM	0.46	−0.44
WM1	0.51	−0.17
Eigenvalue	3.12	0.22
% Variance	93.55	6.45

**Table 5.**—Classification matrix determined by the size-free discriminant function analysis. AR = *Oecomys franciscorum*, n. sp.; BO = *O. mamorae*; PG = *O. cf. franciscorum*.

Group	Predicted group membership				
	AR	BO	PG	Total	Error (%)
AR	11	0	3	14	21.43
BO	0	30	1	31	3.23
PG	2	0	4	6	33.33
Total	13	30	8	51	11.76

Tucumán, 1592–Lima, 1639); and the current Pope of the Catholic Church, Francisco (Jorge Mario Bergoglio; Buenos Aires, 1936). Maldonado da Silva was persecuted and burned by the Inquisition because he defended his freedom to practice the Jewish religion. Pope Francisco is championing a powerful discourse of understanding and reconciliation; in addition, his Encyclical *Laudato Si'* (the “Green Encyclical” 24 May 2015) is viewed as a strong document in defense of the environment. The conjunction of both “Franciscos” in this specific epithet reflects our hope for a more inclusive and peaceful world. The epithet is formed from the Latin name “Franciscus” in the genitive plural, with the stem “francisc” plus the Latin suffix “orum” (ICZN 31.1.1).

**Nomenclatural statement.**—A life science identifier (LSID) number was obtained for the new species (*Oecomys franciscorum*): urn:lsid:zoobank.org:pub:4F59D73F-5522-4A98-8C53-30C6F90E60FA.

**Distribution.**—*Oecomys franciscorum* is known from several localities in the Humid Chaco in the eastern portions of the provinces of Chaco and Formosa, Argentina (see above). According to our preliminary observations, sequence data and morphological characters gleaned from literature, several specimens from eastern Paraguay and Mato Grosso do Sul, Brazil, may also represent this new species (see above), and it is likely that *O. franciscorum* ranges along the Pantanal-Paraguay river and neighboring regions from about 19°S to 27°S.

**Parasites.**—A preliminary inspection of ectoparasites (M. Lareschi, CEPAVE-CONICET, pers. comm.) from the live-trapped specimens of *O. franciscorum* revealed the presence

of mites (Mesostigmata, Laelapidae) of 2 different species (*Gigantolaelaps* sp. and *Laelaps furmani*). *L. furmani* was previously reported from *O. bicolor* from Brasília (Brazil—Gettinger 1992; although the reference to *bicolor* should be checked in the current taxonomy of the genus). The only endoparasite recorded was the nematode *Syphacia* sp. (Nematoda, Oxyurida; R. Robles, CEPAVE-CONICET, pers. comm.).

*Natural history.*—Capture localities are all in the Humid Chaco, a transitional area between the Dry Chaco ecoregion to the west and the Alto Parana Atlantic Forest ecoregion to the east. The landscape of the Humid Chaco comprises a mosaic of wetlands, humid grasslands, palm savannas, and gallery forests (Olson et al. 2001).

The holotype of *O. franciscorum* was captured in gallery forest along the Riacho Pilagá, in a trap set 1.60 m above the ground on a tree (*Patagonula americana*). The paratype was obtained at the same locality in a trap set on the forest floor in a dense bromeliad (*Bromelia serra*) understory. Additionally, an adult female was trapped along the Rio de Oro on the floor of a gallery forest with a dense cover of the bromeliad *Pseudananas sagenarius*, at the base of a large tree (*Phyllostylon rhamnoides*). Four juveniles were captured in Reserva Natural El Bagual in pitfall traps placed in gallery forests, and 1 was obtained in a grassland of espartillo (*Elionurus muticus*) and chajapé (*Imperata brasiliensis*). These gallery forests are dense, closed, and tall (Supporting Information S10). The structure and species composition of these forests is related to small topographic differences along the riverbanks, periodicity and permanence of flooding, and groundwater availability (Maturó et al. 2005; Placci and Holz 2005).

Other cricetids captured inside of gallery forest where *O. franciscorum* was collected included *Oligoryzomys nigripes*, *Sooretamys angouya*, and less frequently, *Akodon toba* and *Graomys chacoensis*. *Akodon azarae*, *Necomys lasiurus*, and *Oligoryzomys* cf. *fornesi* were common in neighboring grasslands and open areas, and *Holochilus chacarius*, *Pseudoryzomys simplex*, and *Scapteromys aquaticus* were found in nearby marshes and their edges.

The distribution of *O. franciscorum* extends to the interior Chaco, probably as a result of dispersal along the riparian corridors produced by gallery forests surrounding main rivers and creeks. Animals recently captured and released by Orozco et al. (2014), which were identified through *Cytb* sequencing and blastn comparisons, revealed *O. franciscorum* populations deeply placed in Chaco woodlands > 150 km west of the Paraguay River (see also Orozco et al. 2013). These studies suggest the likely role of this arboreal rodent as a reservoir of *Trypanosoma cruzi* (Trypanosomatidae), a relationship previously detected for Brazilian Pantanal populations (see Rademaker et al. 2009).

*Biogeography.*—*Oecomys franciscorum* is distributed in the Humid Chaco ecoregion. Most of the large mammals occupying this ecoregion have widespread distributions in other open to forested areas of South America, such as maned wolves (*Chrysocyon brachyurus*), black howler monkeys (*Alouatta caraya*), Azara's night monkeys (*Aotus azarae*),

peccaries (*Tayssu pecari* and *Pecari tajacu*), giant anteaters (*Myrmecophaga tridactyla*), capybaras (*Hydrochoerus hydrochaeris*), deer (*Mazama* spp.), marsh deer (*Blastocerus dichotomus*), pumas (*Puma concolor*), and jaguars (*Panthera onca*—The Nature Conservancy et al. 2005). In contrast, among small mammals of this ecoregion some endemic species are found, such as the rare didelphid *Chacodelphys formosa* or the large rat *Gyldenstolpia fronto chacoensis* (Voss et al. 2004; Pardiñas et al. 2008).

The closest relative to *O. franciscorum* is *O. mamorae*, a species found in the eastern forested slopes of the southern Yungas. Among mammals, other examples also suggest a connection between Yungas and Chaco biomes, both at the genus and species levels. The distribution of genus *Cryptonanus* mirrors that of *O. mamorae* and *O. franciscorum*, with *C. chacoensis* living mostly on humid Chaco environments and *C. unduaviensis* on forested areas of Bolivia. At the species level, several medium-sized species are found both in eastern Bolivia and in the Humid Chaco, including the 4-eyed opossum *Philander opossum canus* (Chemisquy and Flores 2012; de la Sancha and D'Elía 2015), the mouse opossum *Marmosa (Micoureus) constantiae* (de la Sancha et al. 2012), Azara's agouti *Dasyprocta azarae* (Patton and Emmons 2015), and Azara's capuchin *Sapajus cay* (Rylands et al. 2005). These species have distributional ranges that lie in a horseshoe pattern, with populations present in the Yungas and other forested areas of eastern Bolivia and connected to the north through the Chiquitano Dry forests and Pantanal with the Humid Chaco. They are mostly absent from the Dry Chaco. At the genus level, *Oecomys* conforms to this pattern, being present in the humid Chaco (*O. franciscorum*) and Yungas (*O. mamorae*) but apparently absent from most of the Dry Chaco of Argentina.

*Conservation.*—*Oecomys franciscorum* appears to be moderately abundant in some localities, particularly as suggested by its frequent occurrence in pellet assemblages produced by forest owls (e.g., Riacho Pilagá, Estancia Guaycolec—Pardiñas and Ramírez-Llorens 2005). Its scarcity in mammal collections may be related to its arboreal habits and the failure of traditional trapping to detect those species that live in the canopy. Its distributional range is close to 20,000 km<sup>2</sup>. Nevertheless, its restriction to forested riparian habitats, combined with the fact that its Chacoan environments, especially those of the Humid Chaco, are being extensively converted to agroecosystems (The Nature Conservancy et al. 2005), lead us to suggest that this species be designated Vulnerable [Vu B1ab(iii)] under the criteria defined by the International Union for the Conservation of the Nature (IUCN 2001). If those populations of Paraguay and Brazil also correspond to this species, then its conservation status will be in need of reevaluation. Teta and Pardiñas (2012) characterized the species, as *Oecomys* sp., as Data Deficient.

## DISCUSSION

“New species descriptions form the keystone to all biological hypotheses” concluded Carleton et al. (2009:21) after naming a new entity from the complex assembly of *Oecomys* species that

inhabit the Bolivian lowlands. Here, we add another species from the southern range of the genus. Paradoxically, in a genus with more than 45 available names (cf. Carleton and Musser 2015), a new one is needed.

The recognition of *O. franciscorum* as a species distinct from *O. mamorae* reduces the complexity of the current view of *O. mamorae* as a polytypic species ranging broadly across extremely diverse biomes including Amazonian plains, Yungas, Chaco, and Pantanal (Carleton et al. 2009). *O. mamorae* and *O. franciscorum* are phenetically very close. In fact, we first explored the hypothesis that Humid Chaco *Oecomys* specimens belonged to a southern, slightly differentiated population of *O. mamorae*. The hypothesis of subspecific differentiation of a widespread *O. mamorae* (living from Amazonian Bolivia to northeastern Argentinian Chaco) is plausible, and this scenario was partially advanced by Carleton et al. (2009). These authors examined *O. mamorae* specimens from the Cerrado in Bolivia, the Chaco in Paraguay, and from the Paraguay River in Brazil and Paraguay (see also Carleton and Musser 2015). Argentinian specimens were cautiously treated as "...plausibly referable to *O. mamorae*..." (Carleton et al. 2009:26). A similar conclusion was reached by previous students; for example, a specimen of *Oecomys* from the Paraguayan Chaco was linked to "Bolivian populations (known as *Oecomys mamorae* Thomas...)" (Myers and Wetzel 1979:640). Our results agree with the early and astute perception of Carleton et al. (2009) that Argentinian populations are very similar to those of Bolivian *O. mamorae*. However, with a much larger sample available to us than was available to those authors, we also found that the Argentinian specimens show a unique combination of qualitative and quantitative differences. In addition, this set of differentiating traits is also present in animals collected along the Pantanal and Paraguay River and neighboring regions referred in the literature as *O. concolor* (Myers 1982:87), *O. mamorae* (Gamarra de Fox and Martin 1996:545; Carleton et al. 2009:27), or *Oecomys* sp. (Andrade and Bonvicino 2003:196).

Genetic distances among representatives of the *mamorae* group (which includes *O. franciscorum*, *O. mamorae*, and related forms; Figs. 1 and 2) are under 7%, while distances for most (74%,  $n = 91$ ) pairs of species of *Oecomys* are above 10% (mean value for this subsample is 12%; Supporting Information S2). Similar patterns of variation are found in many other oryzomyine genera. Within *Zygodontomys*, reported *Cytb* distances varied from 2% to 9% (González et al. 2010:662), while among 8 species of *Cerradomys*, they ranged from 0.6% to 9% (Bonvicino et al. 2014:530) and for several clades of *Holochilus*, 7% to 15% (D'Elía et al. 2015). In contrast, a supposedly monotypic *Sooretamys* revealed *Cytb* distances only from 0% to 3%, although measured on a sample of short sequences (675 bp—Chiquito et al. 2014:857). Even more strikingly, *Cytb* fragments from *Megalomys desmarestii* and *M. luciae* differ by only 0.6% (Brace et al. 2015:table 2; there rounded to 0% but recalculated here using GenBank sequences). While the relatively small differences separating members of the *mamorae* group are suggestive of a close relationship among its members, we conclude that other speciose

oryzomyines show a large range of hierarchical *Cytb* variation, and the genetic evidence provided by levels of differentiation based on a fragment of 1 mitochondrial marker alone is insufficient to produce a solid taxonomic hypothesis.

Our concept of *O. mamorae* is clouded by confusion over its type locality. According to Thomas (1906:446), the holotype of *O. mamorae* was obtained in "Mosetenes, Upper Mamoré, Yungas, Bolivia" (this locality was presented erroneously by Tate [1932:21] as "Mostenes"). Hershkovitz (1960:562) listed it as "Mosetenes" but noted without explanation that this was probably a misspelling, and he placed the type locality in the modern Cochabamba department. Anderson (1997:102) put it near "Cordillera de Mosetenes" in Cochabamba department, provided geographic coordinates (ca. 16°40'S/66°03'W), and noted several alternative spellings. Carleton et al. (2009) reported the type locality of *O. mamorae* as "Bolivia, Cochabamba, Yungas, upper Rio Mamore, Mosetenes."

The original linkage between "Mosetenes" and "Upper Mamoré" may be incorrect, however, and it is uncertain that the type locality should be in Cochabamba department. The holotype of *O. mamorae* was collected by Luigi Balzan, an Italian naturalist who traveled extensively throughout Bolivia between 1890 and 1892. Balzan wrote a detailed diary of his activities, published as successive letters (Balzan 1892; López Beltrán 2008). He described 3 Missions formed for the Mosetén populations, 1 in Santa Ana, 1 in Covendo, and 1 in Muchanes, all located about 30 km downstream from the confluence of the Bopi and Beni rivers. We are confident that Balzan obtained the type of *mamorae* from this general area, i.e., the Upper Beni River, and not from the Upper Mamoré River, ~300 km east, for several reasons: 1) there are no Mosetén missions along the Mamoré River; in fact, the Atlas Sociolingüístico de Pueblos Indígenas en América Latina maps the distribution of the Mosetén linguistic group proper to the west of the Beni River (Crevels 2009:284); 2) Balzan highlighted the diversity of mammals, especially bats and rodents, particularly in reference to the Mosetén missions; 3) when visiting Muchanes, Balzan (1892:253) secured "350 pipistrelli di 3 specie... un piccolo marsupiale nuovo e vari topi" (freely translated, "350 bats of 3 species... one small new marsupial and several mice"). Therefore, we restrict the type locality of *O. mamorae* to Muchanes, with approximate coordinates 15.18°S and 67.58°W, on the right forested side of the Beni River, department of Beni, Bolivia. In this context, the concept of *O. mamorae* is here limited to the Bolivian populations that inhabit the riverine forest of the Amazonian drainage and the Yungas, excluding Bolivian and Paraguayan samples from Chiquitano and Chaco biomes (cf. Carleton et al. 2009:figure 6).

Few collections of *Oecomys* connect Amazonian and Yungas populations of *O. mamorae* (under our restricted concept of the species) with those populations of *Oecomys* that live along the Pantanal-Paraguay river basin (i.e., *O. franciscorum*; Fig. 2). This huge territory encompasses about 4° of latitude and is mostly covered by Chaco woodlands. The 1st *Oecomys* specimen reported for this region is an adult male, UMMZ 125456 (HBL = 149, TL = 182, HFL = 29 [in mm]), with scrotal testes

captured 50 km WNW Fortín Madrejón, Paraguay (Myers and Wetzel 1979:640). Three additional specimens came from a neighboring locality, Colonia San Alfredo, about 90 km NNW, in the same Chacoan environment; these animals (UCONN 19187, UCONN 19188, UCONN 19189) are large adults (HBL =  $147.3 \pm 4.0$ , TL =  $172 \pm 10.5$ , HFL =  $27.7 \pm 2.1$ , E =  $21.0 \pm 1.0$ , W =  $81.3 \pm 8.5$  [measurements in mm]). All these western Chaco *Oecomys* are characterized by large skulls, broad interorbital regions with marked constrictions (except UCONN 19187), V-shaped coronal sutures, frontals with sharp margins, incisive foramina just reaching the anterior face of the M1, and long palates with 1 or 2 posterolateral palatal pits sometimes recessed in large paired fossae (UMMZ 125456). These animals are more robust than typical *O. mamorae* and show some of the diagnostic traits cranially useful for separating *O. mamorae* from *O. franciscorum* (e.g., broad interorbit coupled with sharp frontal borders). Their inclusion as representatives of *O. franciscorum* in the interior of Chaco woodlands is a plausible hypothesis, which receives biogeographic support from the recent discovery of “inland” populations of this species well within the Argentinian Chaco (Orozco et al. 2014, there designated *Oecomys* sp.). Moreover, the western Chacoan animals discussed above were treated as an example of morphological variation by Carleton et al. (2009:13), who wrote “In some individuals of *O. mamorae* (UMMZ 125456, 133793; UCONN 19187–19189)...a vestige of a squamosal-alisphenoid groove can be detected...Such occasional atavistic reminders of the ancestral character state...” These details acquire, in the context of the taxonomic hypothesis advanced here, a new significance pointing to the morphological differentiation of Chacoan populations rather than random variation.

About a decade ago, a new karyotype was described for *Oecomys* based on animals from the Brazilian Pantanal. Those specimens, treated at that time as *Oecomys* sp., show diploid (2n) and fundamental numbers of 72 and 90, respectively (Andrade and Bonvicino 2003). The cytogenetic uniqueness of this population is in agreement with its divergent *Cytb* sequences (Andrade and Bonvicino 2003; Rosa et al. 2012). A 2nd set of specimens of *Oecomys* from the Brazilian Pantanal was associated with the epithet *mamorae*, surely following Hanson (2008; based on a voucher—JLP [= James L. Patton] 16961—from Brazil, Mato Grosso do Sul, Rio Vermelho). We had the opportunity to examine 2 specimens from the Rio Vermelho, MVZ 197504 and MVZ 197506, the 2nd one with *Cytb* sequenced and referred to *O. mamorae* (Rocha et al. 2011). These individuals are indistinguishable from *O. franciscorum*, averaging slightly smaller than Argentinian representatives (see above). Andrade and Bonvicino (2003) provided detailed morphological description of the animals they karyotyped from Corumbá. Significant traits include the general dorsal coloration “grey-yellow and grey-orange... The head is more greyish... The inner and outer sides of the pinnae are covered with short orange hairs... In live specimens, the rump was notably more strongly orange coloured...,” size “head-body length,  $147.20 \pm 8.17$  mm; tail length,  $164.75 \pm 13.40$  mm; hindfoot (without nail)  $28.20 \pm 2.17$  mm; hindfoot (with nail)

$29.40 \pm 1.82$  mm; internal ear length,  $20.00 \pm 0.71$  mm. The mean mass was  $102.00 \pm 17.89$  g...” The specimen has a wide interorbital region, a well-defined supraorbital crest, and a relatively long palatal bridge. These traits are also characteristic of Argentinian populations here referred to *O. franciscorum*. Further, a Paraguayan specimen (UMMZ 133793) also deserves mention. An adult female collected in the eastern side of the Paraguay River ( $25^{\circ}30'S$ ), about 130 km NE the type locality of *O. franciscorum*, this animal has a broad and cuneate interorbital region with well-developed supraorbital shelves; U-shaped coronal suture; long incisive foramina slightly surpassing the plane defined by both M1 anterior faces; palate well projected beyond the posterior margins of the M3s with 2 posterolateral palatal pits; no alisphenoid struts; large molar tooth rows (> 5 mm) and broad bony Eustachian tubes. All these traits agree with our description of *O. franciscorum*.

In summary, we recognize 2 species of *Oecomys* in the southernmost geographic range of the genus (Fig. 2). One of them appears to be restricted to Amazonian and Yungas environments mostly in the Bolivian departments of Beni, Cochabamba, and Santa Cruz and corresponds to the original description of *O. mamorae*. The other, here described as *O. franciscorum*, is associated mainly with the Humid Chaco with populations from Pantanal in Brazil to the Argentinian provinces of Chaco and Formosa. Among *Oecomys* whose karyotypes are known, *O. franciscorum* is unique with  $2n = 72$ , but the diploid complement of *mamorae* is still unknown. Finally, *O. franciscorum* has been retrieved in several phylogenetic analyses as a well-defined clade sister to *O. mamorae* (Fig. 1; Rocha et al. 2011, 2012; Orozco et al. 2014). A 3rd group of specimens, comprising animals from the Paraguayan Chaco, eastern Paraguay, and the Brazilian Pantanal, shows traits that strongly link it to *O. franciscorum*, but its taxonomic status remains uncertain pending additional study.

*Oecomys franciscorum* joins a perhaps surprisingly small group of Chacoan endemic rodents. However, Chacoan sigmodontines are still poorly known and those of the Humid Chaco are clearly no exception. The main aspects of the fauna have been described in scattered contributions from Argentina (e.g., Shamel 1931; Massoia 1971a, 1971b, 1971c, 1973; Contreras 1982a, 1982b, 1984; Contreras and Berry 1983; Pardiñas and Teta 2005) and Paraguay (e.g., Myers and Wetzel 1979; Myers 1982). Neither extensive trapping efforts nor revisionary studies, however, have been conducted for the small mammal assemblages in the Paraguay-Paraná gallery forest and associated grasslands. Forested corridors along the main affluents of the Paraguay River, such as Montelindo, Guaycolec, Pilagá, or Negro, include dense blocks of trees in many cases over 1.5 km wide along the river course. To date, only 3 large scansorial sigmodontines have been recorded from these forests, the oryzomyines *O. franciscorum* and *S. angouya* and the phyllotine *G. chacoensis*. Caviomorphs are apparently absent. Why are these riparian forests apparently so rodent-poor? Is it because a small number of species is actually present, or does it simply reflect lack of careful study? Alternatively, why have rodents failed to colonize the arboreal niche in these southernmost

forests? Can this taxonomic poverty be related to ecological constraints such as unstable habitats and/or forest size-fragments? Or does the depauperate fauna reflect the patchy nature, marginality, and scattered distribution of these southern forest environments? Recent literature emphasizes the importance and value of seasonally dry tropical and subtropical forest (e.g., Werneck 2011; Werneck et al. 2011). However, studies based on mammals are still few. Could the apparent low richness in arboreal rodents in these southern forests be linked to their mostly postglacial development (cf. Mayle 2004)? A similar pattern of poverty was highlighted by de la Sancha (2014) regarding Eastern Paraguayan sigmodontine forest assemblages. This parallelism invites the search of common explanations.

*Oecomys franciscorum* was recognized based on evidence aggregated from a number of fields. It provides an excellent example of the flow of information among researchers, cementing small pieces of morphological, karyological, epidemiological, molecular, and distributional evidence in a single taxonomic hypothesis (an example of “integration by cumulation” sensu Padiál et al. 2010).

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#### SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online ([jmmammal.oxfordjournals.org](http://jmmammal.oxfordjournals.org)). The materials consist of data provided by the author that are published to benefit the reader.

The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

**Supporting Information S1.**—Quantitative morphological analyses on *Oecomys* from Argentina, Bolivia, Brazil, and Paraguay.

**Supporting Information S2.**—Observed genetic *p* distance of the cytochrome-*b* gene within and among species level clades in *Oecomys*.

**Supporting Information S3.**—External appearance of *Oecomys franciscorum*, sp. nov.

**Supporting Information S4.**—Cheiridia of *Oecomys franciscorum*, sp. nov.

**Supporting Information S5.**—Occlusal view of right molar rows and alveoli in *Oecomys franciscorum*, sp. nov.

**Supporting Information S6.**—Stomach gross morphology in *Oecomys franciscorum*, sp. nov.

**Supporting Information S7.**—Comparison of interorbital regions between *Oecomys mamorae* and *Oecomys franciscorum*, sp. nov.

**Supporting Information S8.**—External appearance of *Oecomys mamorae*.

**Supporting Information S9.**—Palatal region in *Oecomys franciscorum*, sp. nov., morphological variation.

**Supporting Information S10.**—General view of the gallery forest where *Oecomys franciscorum*, sp. nov., was recorded.

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## APPENDIX I

Specimens studied belong to the following mammal collections: The Natural History Museum (BM; London, United Kingdom); Colección Elio Massoia (CEM; acquired by the Fundación de Historia Natural Félix de Azara, Buenos Aires, Argentina); Colección de Mamíferos del Centro Nacional Patagónico (CNP; Chubut, Argentina); Colección de Material de Egagrópilas y Afines “Elio Massoia,” Centro Nacional Patagónico (CNP-E; Chubut, Argentina); Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina); Museu Nacional (MN; Rio de Janeiro, Brazil); Museum of Vertebrate Zoology (MVZ; Berkeley, California); University of Connecticut (UCONN; Storrs, Connecticut); University of Michigan Museum of Zoology (UMMZ; Ann Arbor, Michigan). Materials examined through photographs are indicated by an \*.

*Oecomys bicolor* ( $n = 2$ ): PERU: Amazonas, vicinity of Huampami, Aguaruna village (MVZ 153519, MVZ 154989).

*Oecomys catherinae* ( $n = 1$ ): BRAZIL: São Paulo, Base do Carmo, Fazenda Intervalos (MVZ 182087).

*Oecomys franciscorum*, sp. nov. ( $n = 28$ ): ARGENTINA: Formosa, Riacho Pilagá, Estancia Guaycolec (CNP 700–CNP 709); Formosa, Riacho Pilagá, Estación de Animales Silvestres

Guaycolec (CNP 4260 [holotype], MACN 26663 [paratype]); Formosa, Riacho Pilagá, Reserva Natural El Bagual (CNP 592, CNP 594, CNP 598, CNP 603, CNP 680, CNP 3424, CNP 3427, CNP 3428); Chaco, Escuela Provincial de Educación Técnica Agropecuaria N° 8 “Zapallar Norte” (CNP-E 60, CNP 4261); Chaco, conj. between Río de Oro and Ruta Provincial 33 (CNP 5076); Chaco, Capitán Solari (CNP 3425, CNP 3426); Chaco, Escuela N° 278 “Francisco Joulhe” (uncatalogued material); Chaco, Escuela Provincial N° 20, General Vedia (CNP-E 61); Chaco, Puerto Bermejo, Pueblo Viejo (CNP-E 58); Chaco, Makallé Viejo (CEM 1107).

*Oecomys* cf. *O. franciscorum*, sp. nov. ( $n = 5$ ): BRAZIL: Mato Grosso do Sul, rio Miranda, above Passo do Lontra (MVZ 197504, MVZ 197506). PARAGUAY: Alto Paraguay, Estación Biológica Los Tres Gigantes (2 uncatalogued specimens

from owl pellets); Alto Paraguay, edge río la Garenza (= río Timanes); Alto Paraguay, Colonia San Alfredo, 28 km WNW Mayor Pablo La Garenza (UCONN 19187, UCONN 19188, UCONN 19189); Alto Paraguay, 50 km WNW Fortín Madrejón (UMMZ 125456); Paraguairí, Saltos de Piraretá (UMMZ 133793).

*Oecomys mamorae* ( $n = 4$ ): BOLIVIA: Beni, Marbán (MACN 50.373, MACN 50.377, MACN 50.387); Beni, “Yungas, Mosetenes” (BM 0.5.3.21\* [holotype]).

*Oecomys phaeotis* ( $n = 1$ ): BOLIVIA: Cochabamba, Chapare (MACN 50.361).

*Oecomys superans* ( $n = 1$ ): PERU: Amazonas, vicinity of Huampami; Amazonas, Aguaruna village (MVZ 153524).

*Oecomys trinitatis* ( $n = 1$ ): VENEZUELA: Bolivar, 132 km SE (by road) río Cuyuni (MVZ 160081).