Paul Smith* and Robert D. Owen

The subgenus *Micoureus* (Didelphidae: *Marmosa*) in Paraguay: morphometrics, distributions, and habitat associations

Abstract: Two species of *Marmosa* (*Micoureus*) have been documented from Paraguay. Based, in part, on a recently collected series of *Marmosa constantiae*, we review the morphometric relationships, distributions, and habitat associations of the two species in Paraguay. *Marmosa paraguayana* is documented from nine localities, all in eastern Paraguay, in the region originally covered by Upper Paraná Atlantic Forest (UPAF). *Marmosa constantiae* is documented from five localities, all of which are forested areas (generally gallery forest) embedded within Cerrado patches bordering UPAF, or within the Humid Chaco or Dry Chaco ecoregions. Specimens of *M. constantiae* from the Dry Chaco locality Parque Nacional Defensores del Chaco are morphometrically distinct from both *M. paraguayana* and other *M. constantiae* specimens and may represent an unrecognized taxon.

Keywords: Cerrado; Chaco; *Marmosa constantiae*; *Marmosa paraguayana*; Upper Paraná Atlantic Forest.

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Introduction

The subgenus *Marmosa* (*Micoureus*) Lesson, 1842 contains six species of "woolly mouse opossum" distributed from Belize south to northern Argentina. The subgenus is characterized by thick, woolly dorsal pelage; a long (>1.3×HB length) particolored tail with rhomboid scales arranged in a spiral pattern; fine, subequal, and nonpetiolate interscalar tail hairs; prominent supraorbital processes; and small, hemispherical, and widely spaced auditory bullae that lack an anteromedial process on the alisphenoid (Gardner and Creighton 2008). Two species have been documented as present in Paraguay: *Marmosa paraguayana* (Tate, 1931) and *M. constantiae* Thomas, 1904 (Voss et al. 2009).

Marmosa paraguayana was described as *Marmosa cinerea paraguayana* by Tate (1931) with type locality "Villa Rica, Paraguay," and is considered endemic to the Atlantic Forest (Barros et al. 2008). It has a complex nomenclatural history having long been considered conspecific with *Marmosa demerarae* Thomas, 1905. More recently, the names *Micoureus limae* and *Micoureus travassosi* have been used for the species (Patton et al. 2000, Patton and Costa 2003). As currently defined, the species is distributed in the Atlantic Forest zone from northern Minas Gerais south to Rio Grande do Sul in Brazil and west to eastern Paraguay and Provincia Misiones in Argentina (Chebez 1996, Dias et al. 2010).

Marmosa constantiae has only recently been documented as present in Paraguay (Voss et al. 2009). It is a little known but widely distributed species associated with subhumid and semihumid forests, often in otherwise arid areas. The species occurs throughout Bolivia (Departments of Pando, Beni, La Paz, Cochabamba, Santa Cruz, Chuquisaca, and Tarija) (Anderson 1997), east to Mato Grosso and Mato Grosso do Sul states in Brazil (Gardner and Creighton 2008), south to northern Paraguay and into extreme northern Argentina in the Provinces of Jujuy (Díaz and Barquez 2002), Tucumán (Flores and Díaz 2002), Salta (Mares et al. 1989), and Formosa (de la Sancha et al. 2012).

In addition to a valuable systematic study of the entire subgenus, a recent paper (de la Sancha et al. 2012) reviewed locality records and habitat associations of *Marmosa constantiae* and *Marmosa paraguayana* in Paraguay, but contained some factual and interpretational inaccuracies. The availability of a new series of specimens of *M. constantiae* prompted us to review the status of both species of *Marmosa* in Paraguay, in order to provide a clearer understanding of the two species' morphometric relationships, distributions, and habitat associations in the country.

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Materials and methods

One of us (RDO) examined all Paraguayan specimens of *Micoureus* available in the Museo Nacional de Historia Natural del Paraguay (six specimens) and the Colección Zoológica de Para La Tierra (10 specimens). Specimens were identified to species following Gardner (2008), external measurements and weight were recorded from the specimen tag, and cranial and dental measurements were taken following Voss et al. (2004).

Because of wide variability in preparators' measurements of external features of mammalian specimens, only craniodental measurements were included in the morphometric analyses. These were first log-transformed (Ln), to mitigate for indeterminate growth exhibited in didelphids. The measures were then standardized to mean=0, SE=1, to mitigate for unequal influence of characters of different sizes.

For specimens not available for examination, we included cranial measurements taken from de la Sancha et al. (2012; Table 2). Comparability of their cranial measurements and ours was verified by a preliminary analysis including both our measurements and those from de la Sancha et al. (2012) taken on the two specimens (MNHNP 481, TK 121753) that were available to both studies. de la Sancha et al. (2012) provided only eight craniodental measurements for MNHNP 481; thus, this analysis included all specimens (nine *Marmosa constantiae*, six *Marmosa paraguayana*) having these eight measures, regardless of age class. A minimum spanning tree (MST) superimposed onto a plot of the first two principal components showed the two measurement sets as grouped most closely together for both of these specimens, indicating that the variation between the two measurers was less than the actual differences between any two specimens and, thus, that the two measurement sets could be combined. For the two specimens with two sets of craniodental measurements, our measurements were used in all subsequent analyses.

Of the specimens examined by us, only those judged to be adult (age class "A," based on dental eruption and cranial suture closure) were used in morphometric analyses. Specimens judged to be subadult ("S") or juvenile ("J") were not used, except for the initial analysis (described above) done to determine the comparability of our measurements with those of de la Sancha et al. For specimens not examined by us, specimens listed as age class 5 or 6 by de la Sancha et al. (2012) were included in a preliminary analysis. However, this analysis demonstrated clustering of age class 5 specimens together regardless of specific identity; thus, the analyses reported here include only specimens judged by us to be adult ("A") or listed by de la Sancha et al. (2012) as age class 6.

A total of 10 specimens (eight *Marmosa constantiae*, two *Marmosa paraguayana*) met the age criterion, had all 10 craniodental measurements available, and thus were included in the principal component analysis (PCA). Following transformation and standardization as described above, a matrix of product-moment correlations among the characters was calculated. Eigenvectors were extracted from the character correlation matrix, and the standardized character values were projected onto the first two eigenvectors, to visualize the morphometric relationships among the specimens and to evaluate character contributions to differences between species.

A second PCA was conducted using only the five craniodental characters available for TK 121795 (the skull is partially broken), a *Marmosa constantiae* specimen from the Humid Chaco, in order to evaluate its relative placement among all other adult specimens of both species. In addition to this specimen, this analysis included the same 10 specimens used in the previous PCA.

Based on the results of these PCAs, an analysis of variance (ANOVA) was conducted on all adult specimens with craniodental data, evaluating differences among three groups: *Marmosa paraguayana* (2 specimens), *Marmosa constantiae* from Parque Nacional Defensores del Chaco (PNDC) in the Dry Chaco (2), and *M. constantiae* from eastern Paraguay and the Humid Chaco (7). An additional ANOVA was conducted on the seven adult specimens of *M. constantiae* from eastern Paraguay and the Humid Chaco, to evaluate morphometric variation within the species.

PCAs were conducted using NTSYSpc version 2.20x (Applied Biostatistics Inc.). Analyses of Variance were conducted using PROC GLM in SAS 9.2 (SAS Institute Inc.).

Results

Specimens of *Marmosa (Micoureus)* from Paraguay

Table 1 lists all specimens of *Marmosa paraguayana* and *Marmosa constantiae* from Paraguay, which we are aware of, with the available morphometric data. *Marmosa constantiae* has been collected from three localities in the Paraguayan Chaco and two in the eastern part of the country, whereas *M. paraguayana* is known from nine localities, all in eastern Paraguay.

Table 1 Listing of all Paraguayan specimens of *Marmosa* (*Micoureus*) known to us, with external [from specimen tag, or as listed in de la Sancha et al. (2012)], and craniodental measurements, where available. Note that two specimens (MNHNP 481 and TK 121753) are listed twice. Skulls of these two specimens were measured both by de la Sancha et al. (2012) and by one of us (RDO) and are listed twice in order to provide both sets of measurements.

Code	Id.	Sp[2]	Sex	Ag[3]	Lo[4]	Seen[5]	TL	Tail	Ft	Ear	Wt	CBL	NB	LIB	ZB	PL	PB	MTR	LM	M1–M3	WM4
C481F6[1]	MNHNP 481	C	F	6	1							37.0		7.0	20.7	20.5	12.2	15.5	7.7	6.6	
C481FA	MNHNP 481	C	F	A	1	x	352	213	23	26	57	37.6	4.8	7.0	20.6	22.0	12.1	15.3	7.9	6.4	2.6
C659MA	MNHNP 1659	C	M	A	1	x	355	220	25	23	50	36.6	3.0	6.9	20.9	20.9	12.3	15.2	7.9	6.9	2.9
C660FJ	MNHNP 1660	C	F	J	1	x	305	145	21	20	30										
C404MJ	FMNH 54404	C	M	J	2																
C795FA	TK 121795[a]	C	F	A	3	x	412	231	28	27	73		5.4					16.4	8.3	7.0	2.8
C012MS	PLT 012	C	M	S	4	x	382	220	30	28	92							16.7	8.3	7.0	2.9
C013FS	PLT 013	C	F	S	4	x	346	205	24	25	58										
C014FS	PLT 014	C	F	S	4	x	335	200	25	25	52		4.8	7.1				15.8	8.1	7.1	2.1
C015FS	PLT 015	C	F	S	4	x	324	193	23	25	51										
C206MS	PLT 206	C	M	S	4	x	330	192	24.5	25		34.4	4.7	6.3	19.7	19.1	12.7	14.3	8.6	6.6	2.9
C236MA	PLT 236	C	M	A	4	x	395	227	24	24	144	42.6	5.3	7.7	25.1	23.3	13.9	17.0	8.5	6.9	2.6
C256MA	PLT 256	C	M	A	4	x	349	232	28.5	21.5	110	42.4	5.4	7.6	25.1	23.6	13.7	16.6	8.2	6.6	2.7
C261FA	PLT 261	C	F	A	4	x	377	216	21.5	24.5	85	40.5	5.2	6.6	23.4	23.1	13.8	16.8	8.4	7.1	3.1
C438FA	PLT 438	C	F	A	4	x	384	230	22	28	79	40.7	5.2	7.3	23.8	23.2	14.0	17.1	8.6	7.4	3.2
C437MA	PLT 437	C	M	A	4	x	420	233	25	26	125	42.7	6.2	7.8	26.2	23.9	14.4	17.1	8.3	7.2	2.6
C000M6[1]	MSB 67000	C	M	6	5							40.0	4.8	6.2	23.5	21.0	13.6	16.5	8.4	7.1	2.8
P550F4[1]	UMMZ 134550	P	F	4	5		310	183	22	26	53	34.5	4.1	6.2	20.6	18.9	13.1	15.3	8.4	7.3	2.8
P262FU	TK 141262[b]	P	F	U	6	x	335	192	27	24	66										
P753FS	TK 121753	P	F	S	6	x	356	206	25	26	46	38.1	5.2	6.9	21.0	22.2	14.5	16.9	8.8	7.6	2.5
P753U5[1]	TK 121753[1c]	P	U	5	6		356	206	25	26	46	37.4	5.4	7.6	21.2	21.0	13.9	16.9	8.8	7.7	2.8
P462UU	TK 141262	P	U	U	6		335	192	27	24	66										
P551M6[1]	UMMZ 134551	P	M	6	7		380	230	25	29	107	41.6	5.5	7.4	24.2	22.8	14.1	17.7	9.0	7.7	2.8
P416M6[1]	FMNH 211416	P	M	6	8		400	221	26	29	140	40.2	5.7	8.4	23.4	22.4	14.2	17.4	9.2	7.8	3.1
P697UU	TK 129697[d]	P	U	U	8																
P414F3[1]	FMNH 211414	P	F	3	9		275	169	21	21	26	31.0	2.8	6.2	17.2	17.2	11.5	12.5		7.2	
P032UU	MIB 32[d]	P	U	U	10																
	BMNH 2.11.7.17	P	F	A	11																
P115MA	BMNH 25.5.1.15	P	M	A	12																
P415M5[1]	FMNH 211415	P	M	5	13		338	202	24	24	58	40.7	3.8	7.2	23.0	22.8	14.1	17.6	9.2	7.9	3.1
P479F5[1]	TK 129479[e]	P	F	5	13		338	202	24	24	58	36.7	4.1	6.9	21.3	20.6	13.6	16.7	9.1	7.5	2.8
P467MA	TK 129467	P	M	A	13		396	230	26	27	83										

[1]Craniodental measurements taken from de la Sancha et al. (2012), Table 2, rounded to nearest 0.1 mm.

[2]Species. C, *Marmosa constantiae*; P, *M. paraguayana*.

[3]Age. Letters A (adult), S (subadult), J (juvenile) assigned by RDO; numbers assigned by de la Sancha et al. (2012), following Tribe (1990).

[4]Locality. Numbers refer to those in Figure 4 and the legend.

[5]Examined and measured by RDO.

a) de la Sancha et al. (2012) map the locality for specimen TK 121795 (which they list as MNHNP 121795) incorrectly (PY3, p. 232, Figure 2). The field notes list Depto. Boqueron, but the stated locality (km 155 of Trans-Chaco road) is actually well inside Depto. Presidente Hayes, and hence, this is a *lapsus* by the collector. Despite listing Depto. Boquerón as the locality, de la Sancha et al. (2012) mapped the point at the transition between Humid and Dry Chaco, at a location well removed from that stated in the collector's notes, which is well within the Humid Chaco biome (Figure 4). The tail measurement of 213 mm provided by de la Sancha et al. (2012) in Table 2 (p. 233) does not coincide with the field notes, which give 231 mm.

b) Mass of MNHNP 141262 incorrectly stated as 663 g (p. 233, Table 2) by de la Sancha et al. (2012). The specimen number is actually TK 141262, and the field notes show a mass of 66 g.

c) MNHNP 121753 is listed twice in the measurement table by de la Sancha et al. (2012) but with different data (p. 233, Table 2).

d) MNHNP 129697 and MIB 32, cited by de la Sancha et al. (2012) in the text, do not appear in the table of measurements.

e) de la Sancha et al. (2012) provide no locality data for TK 129479. The locality for this specimen is Itapúa: Reserva de Recursos Manejados San Rafael (26.575°S, 55.681°W).

Comparison of our craniodental measurements with de la Sancha et al. (2012)

Measurement sets from each of the two specimens (MNHNP 481 and TK 121753), which were available to both studies, cluster most closely together in the PCA of all specimens having the eight characters which were listed in de la Sancha et al. (2012) for MNHNP 481 (Figure 1). Principal component 1 (PC 1) is a general size component (50.7% of total variance, with 6/8 characters loading strongly and positively – data not shown). The projections along this component indicate that (1) specimens aged 4, 5, and S are typically smaller (thus, they were not used in subsequent analyses); and (2) MNHNP 481 and 1659 (*Marmosa constantiae* from Parque Nacional Defensores del Chaco (PNDC) in the Dry Chaco), although adult are also small. LM3 and M1-M3 load strongly and negatively on PC 2, which accounts for 18.8% of the variance. Among putatively adult age classes (those listed as age classes 5 and 6 by de la Sancha et al. (2012), or as age class A by us), *M. constantiae* generally is smaller in these two characters than *M. paraguayana*.

Interspecific morphometric relationships

When only adult specimens having all 10 characters available are evaluated, PC 1 is a general size component, accounting for 61.2% of the total variance, and with 7/10 characters loading strongly and positively (Table 2). Along this axis, the two specimens of *Marmosa constantiae* from PNDC in the Dry Chaco are considerably smaller than the other specimens attributed to that species, as well as the specimens of *Marmosa paraguayana* (Figure 2), both of which are more similar to each other than either is to the PNDC Dry Chaco *M. constantiae*. Two dental characters load strongly and negatively on PC 2, which generally separates the two specimens of *M. paraguayana* from *M. constantiae* (with the former having larger values for M1–M3 and WM4), although there is considerable variation within *M. constantiae* on this axis.

The three morphometric groups revealed by the PCAs (PNDC Dry Chaco *Marmosa constantiae*, "eastern" *M. constantiae*, and *Marmosa paraguayana*) were evaluated with an ANOVA to determine whether the three groups differ significantly from each other and in which characters. The PNDC Dry Chaco *M. constantiae* average smaller than both other groups in all 10 characters and are significantly different from both other groups in six of the 10 characters (Table 3), whereas the "eastern" *M. constantiae* differ from *M. paraguayana* in only three of the 10 characters. The three groups do not differ significantly in LIB or WM4. The PNDC Dry Chaco *M. constantiae* specimens differ significantly from *M. paraguayana* but not from eastern *M. constantiae* in only one character, the M1–M3 toothrow length.

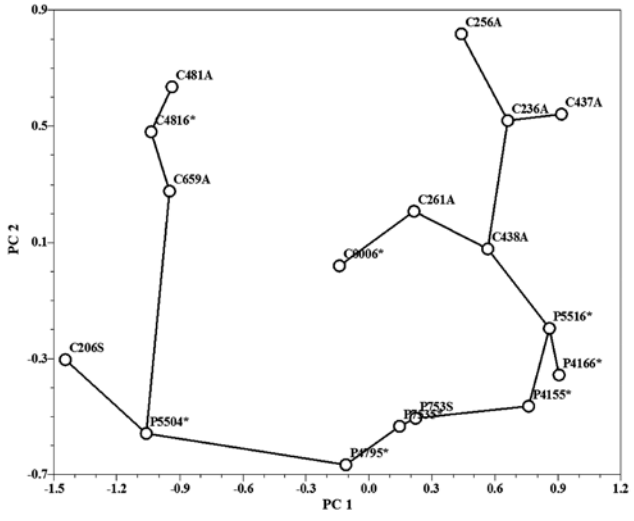

Figure 1 Principal component analysis (PC 1×PC 2, with minimum spanning tree superimposed) of all specimens having the eight craniodental characters listed by de la Sancha et al. (2012) for MNHNP 481, to determine comparability of our measurement sets (by RDO) and those listed in de la Sancha et al. (2012), based on duplicate measurement sets of two specimens (MNHNP 481–C481 in the figure and TK 121753–P753 in the figure). See Materials and methods section for further explanation; see Table 1 for OTU codes.

Table 2 Loadings of 10 or five standardized morphometric characters onto first three or two principal components, plus eigenvalues and percent of total variance explained by principal components.

Character	All adult specimens[1]			*Marmosa constantiae*[2]	
	PC 1	PC 2	PC 3	PC 1	PC 2
CBL	**0.897**	0.374	0.187		
NB	**0.853**	0.253	0.025	0.647	**0.684**
LIB	0.598	0.104	**−0.781**		
ZB	**0.878**	0.330	0.219		
PL	**0.757**	0.458	−0.107		
PB	**0.966**	−0.094	0.187		
MTR	**0.968**	−0.192	0.098	**0.939**	0.261
LM	**0.776**	−0.544	−0.120	**0.962**	−0.038
M1–M3	0.635	**−0.719**	−0.042	**0.902**	−0.298
WM4	0.113	**−0.846**	0.092	0.480	**−0.796**
Eigen value	6.12	2.11	0.77	3.27	1.26
% of variance	61.2	21.1	7.7	65.4	25.4

See text for explanation of the two analyses.

[1]All adult specimens having 10 craniodental characters available (not including TK 121795).

[2]All adult specimens including TK 121795, using five characters only.

Values in bold indicate the highest loading of the character onto a principal component.

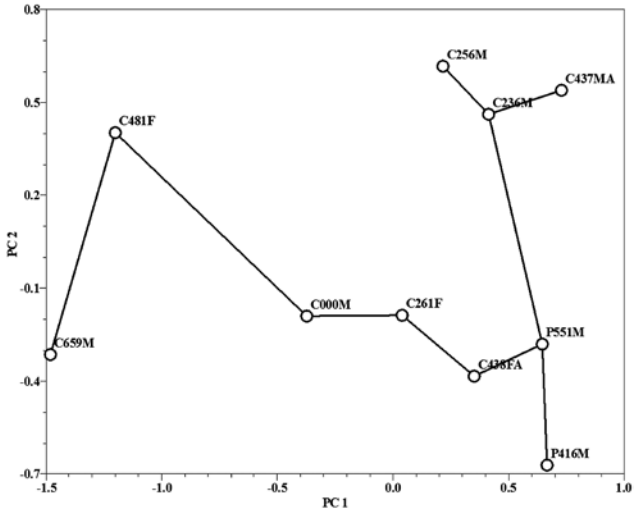

Figure 2 Principal component analysis (PC 1×PC 2, with minimum spanning tree superimposed) of all adult specimens having complete craniodental data (10 characters, see Table 2). See Materials and methods for further explanation; see Table 1 for OTU codes.

Placement of TK121795

Given the wide morphometric and geographic separation of the two PNDC Dry Chaco *Marmosa constantiae* specimens from all others (of both species), the relationship of TK 121795 (*M. constantiae* from the Humid Chaco – Table 1) was evaluated by analyzing it with all specimens having the five craniodental characters available for this specimen. Morphometrically, this specimen falls among the "eastern" *M. constantiae* (Figure 3). In this analysis, PC 1 (65.4% of the variance, Table 2) includes three toothrow length characters, with the PNDC Dry Chaco specimens again being distinctly smaller in these characters, than the remainder of the specimens of this species, and of *Marmosa paraguayana*. Both these specimens and the "eastern" specimens of *M. constantiae* are widely variable along PC 2 (25.4% of the variance).

Variation within *Marmosa constantiae*

An ANOVA of the "eastern" *Marmosa constantiae* specimens (not including the PNDC Dry Chaco specimens), with an evaluation of means for each sex, found that males are larger in five characters (CBL, NB, LIB, ZB, MTR), and females are larger in five (PL, PB, LM, M1–M3, WM4); this difference was marginally significant only in WM4 ($F_{(1,5)}$=9.64, p=0.027) (data not shown). Thus, no sexual dimorphism was detected among the adult specimens of the "eastern" Paraguayan *M. constantiae*.

Discussion

Distributions of *Marmosa constantiae* and *M. paraguayana* in Paraguay

Marmosa paraguayana is distributed throughout the area of eastern Paraguay, which originally represented the western extremity of the Upper Paraná Atlantic Forest ecoregion (Figure 4). Based on the results detailed above and comparisons with the literature, we refer the

Table 3 Means and ranges of 10 craniodental characters for *Marmosa c. constantiae*, *Marmosa paraguayana*, and Dry Chaco *M. constantiae* evaluated in this study.

Character	$F_{(df)}$	Mean (minimum-maximum)[1]		
		constantiae	*paraguayana*	Dry Chaco
CBL	$11.59_{(2,7)}$**	41.48 (40.0–42.7)	40.90 (40.2–41.6)	37.10 (36.6–37.6)
NB	$5.64_{(2,8)}$*	5.36 (4.8–6.2)	5.60 (5.5–5.7)	3.90 (3.0–4.8)
LIB	$1.36_{(2,7)}$	7.20 (6.2–7.8)	7.90 (7.4–8.4)	6.95 (6.9–7.0)
ZB	$11.20_{(2,7)}$**	24.52 (23.4–26.2)	23.80 (23.4–24.2)	20.75 (20.6–20.9)
PL	$2.15_{(2,7)}$	23.02 (21.0–23.9)	22.60 (22.4–22.8)	21.45 (20.9–22.0)
PB	$41.70_{(2,7)}$***	13.90 (13.6–14.4)	14.15 (14.1–14.2)	12.20 (12.1–12.3)
MTR	$40.59_{(2,8)}$***	16.79 (16.4–17.1)	17.55 (17.4–17.7)	15.25 (15.2–15.3)
LM	$45.83_{(2,8)}$***	8.39 (8.2–8.6)	9.10 (9.0–9.2)	7.90 (7.9–7.9)
M1–M3	$10.04_{(2,8)}$**	7.04 (6.6–7.4)	7.75 (7.7–7.8)	6.65 (6.4–6.9)
WM4	$0.39_{(2,8)}$	2.83 (2.6–3.2)	2.95 (2.8–3.1)	2.75 (2.6–2.9)

Significant differences among means tested by Student-Newman-Keuls tests.

[1]Means with the same number of underlines (0, 1, or 2) are not significantly different (SNK).

*0.05≥p>0.01; **0.01≥p>0.001; ***0.001≥p.

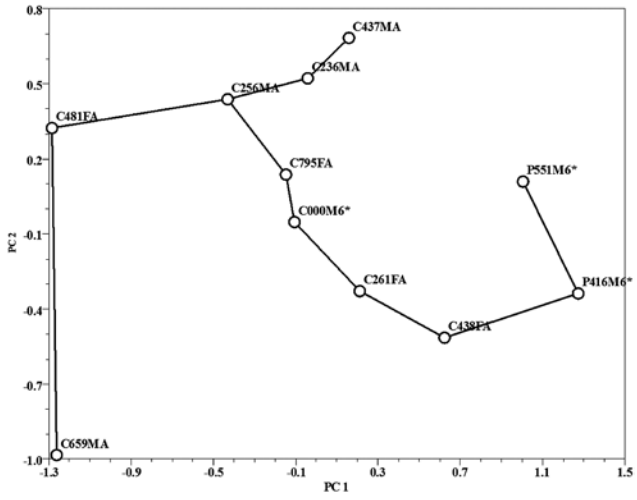

Figure 3 Principal component analysis (PC 1×PC 2, with minimum spanning tree superimposed) of all adult specimens having the five craniodental characters available for TK 121795 (locality 3, see Table 2). See Materials and methods for further explanation; see Table 1 for OTU codes.

"eastern" *Marmosa constantiae* specimens to *M. c. constantiae*. *Marmosa c. constantiae* is known in Paraguay from semihumid semideciduous transitional forest in areas surrounded by Cerrado in the northeastern part of the country (San Pedro and Amambay Departments) and transitional areas of Chaco forest within Palm Savanna in the Humid Chaco ecoregion (Pdte. Hayes and Alto Paraguay Departments).

In addition, a third morphometrically distinct form occurs in the Dry Chaco, where it is currently known only from the area of Parque Nacional Defensores del Chaco (Alto Paraguay Department). Additional specimens are required to fully investigate the nature and geographic distribution of the morphometric variation observed in this population and its relation to other populations currently referred to *Marmosa constantiae*, especially those populations from the Chaco of Paraguay, Argentina, and Bolivia, and the Yungas of Argentina and Bolivia.

In reference to *Marmosa constantiae*, de la Sancha et al. (p. 232) state that "The new locality records fill in the major gaps between the western Brazilian and the northeastern Argentinean records and thus expand its known distribution by more than 530 km to the SW (Figure 2)." However, Flores and Díaz (2002) previously reported the species from as far south as Tucumán, Argentina, and Voss et al. (2009) cited the species from Depto. Amambay, Paraguay. Consequently, the actual distribution extension based on the locality record in de la Sancha et al. (2012) is north easterly within Argentina (p. 231, Figure 2, AR11). This locality, along with two Paraguayan Chaco specimens (this paper, Figure 4, localities 2, 3), confirms that the species occurs within the Humid Chaco ecoregion.

Habitat associations of *Marmosa constantiae* and *M. paraguayana* in Paraguay

As a general rule, *Marmosa paraguayana* occurs in the humid Atlantic Forests of eastern Paraguay and *Marmosa constantiae* in the subhumid and gallery forests of the northern Oriental Region and Chaco. The statement in de la Sancha et al. (2012) that *M. constantiae* occurs in "open areas of Chaco and Cerrado" is contrary to all published data, which clearly describe *M. constantiae* as a forest species (Thomas 1920, Mares et al. 1989, Cáceres et al. 2007, Voss et al. 2009, Sandoval et al. 2010, Alho et al. 2011, Smith et al. 2012).

The largest Paraguayan series of specimens of *Marmosa constantiae* was collected at Reserva Natural Laguna Blanca, San Pedro Department. All were taken in semihumid semideciduous gallery forest with fairly open undergrowth that borders a lake in an area surrounded by Cerrado. Despite intensive year round sampling over several years, no specimens have been taken in islands of dry Cerradón within the Cerrado or in any of the diverse open habitats within the reserve (Smith et al. 2012).

The specimens listed here demonstrate that *Marmosa paraguayana* and *Marmosa constantiae* do occur in sympatry in Amambay Department (Figure 4, locality 5) and that there is at least some marginal distributional overlap. However, no information is available as to whether or not they also overlap ecologically in this area.

The question of the PNDC Dry Chaco specimens

The two *Marmosa constantiae* specimens from Parque Nacional Defensores del Chaco (Dry Chaco) are smaller in all 10 characters than the other specimens of both *M. c. constantiae* and *Marmosa paraguayana*, and they are significantly smaller than *M. c. constantiae* in six of these characters (Table 3). Although it is tempting to refer these specimens to *M. c. budini* Tate 1933, we refrain from doing so because of the conflicting descriptions in the literature (e.g., Thomas 1920, Tate 1933, Anderson 1997) regarding the characteristics and distribution of *M. c. budini*, which together bring into question the distinctiveness of the taxon, and (if it is valid) its morphologic and morphometric characteristics, geographic distribution, and habitat associations.

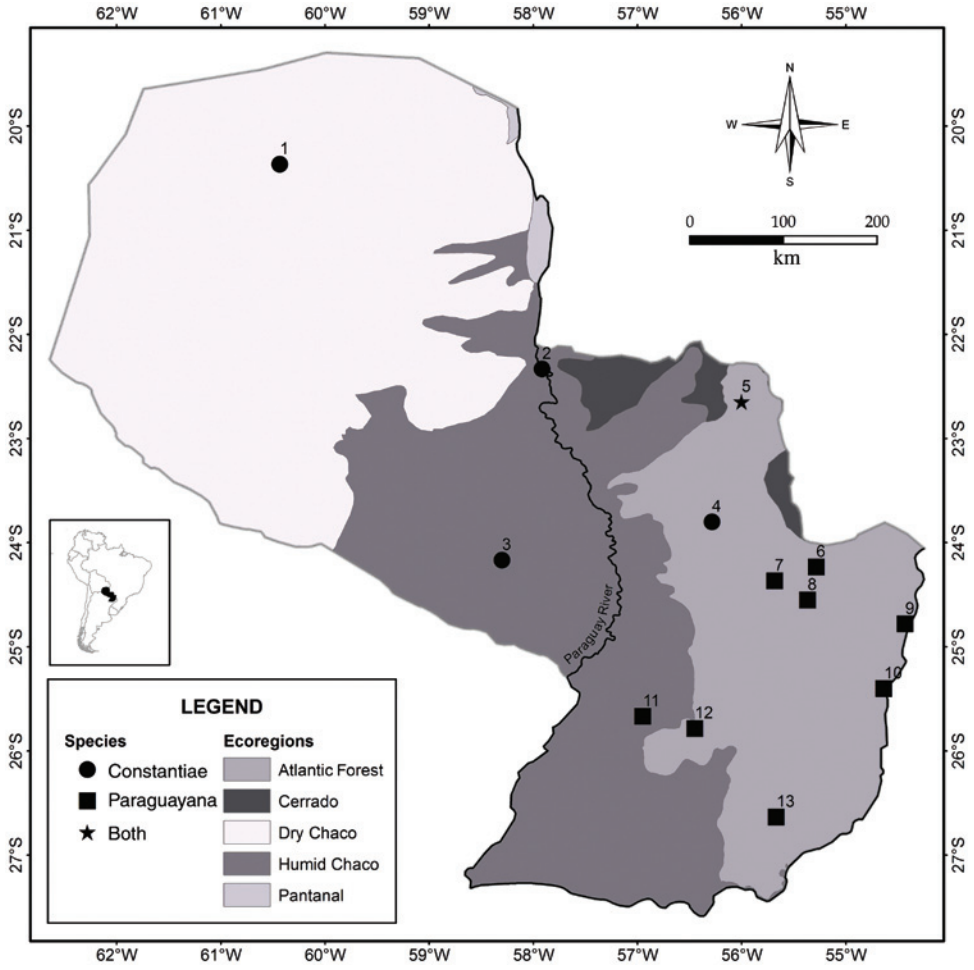

Figure 4 Map of Paraguay, showing known localities for *Marmosa paraguayana* (squares), *Marmosa constantiae* (circles), and both species in sympatry or near sympatry (star). Locality 1 includes the specimens referred to as Dry Chaco *M. constantiae* in this paper; localities 2–5 are represented by *M. c. constantiae*. *Marmosa constantiae* (PNDC Dry Chaco) – 1, Cerro León and Cruce 4 de mayo, Destacamento Militar Patricio Colmán (Parque Nacional Defensores del Chaco, Alto Paraguay). *M. c. constantiae* – 2, Puerto Casado (Alto Paraguay); 3, km 155 Ruta Transchaco (Pdte. Hayes); 4, Laguna Blanca (San Pedro); 5, Cerro Corá (Amambay). *M. paraguayana* – 5, Cerro Corá (Amambay); 6, Britez Cue (Canindeyú); 7, 13.3 km N of Curuguaty (Canindeyú); 8, Morombi (Caaguazú); 9, Limoy (Alto Paraná); 10, Hernandarias (Alto Paraná); 11, Sapucai (Paraguarí); 12, Villa Rica (Guairá); 13, San Rafael (Itapúa).

Though de la Sancha et al. (2012) state that the differences between *M. c. constantiae* and *M. c. budini* are "just size, with the latter being smaller," this is somewhat oversimplified. Tate (1933), in fact, distinguished *budini* on the basis of "small size, proportionately longer tail and smaller teeth" and further by being cranially smaller and "possessing shorter molar tooth rows and less produced supraorbital processes," most of which are characteristics of proportion, rather than size.

Our samples of *Marmosa c. constantiae* and *Marmosa paraguayana* differ significantly in only three toothrow characters (MTR, LM, and M1–M3), and do not differ in either cranial length or breadth characters. Thus, the craniodental morphometric difference between our PNDC Dry Chaco *M. constantiae* and the nominate subspecies is greater than the difference between *M. c. constantiae* and *M. paraguayana*, which are at least marginally sympatric in eastern Paraguay. In contrast, de la Sancha et al. (2012) found high haplotype similarity between two *M. constantiae* from Santa Cruz, Bolivia, and one from Amambay Department (Figure 4, locality 5, eastern Paraguay), suggesting little differentiation among widely separated populations presently referred to as *M. constantiae*. Unfortunately, no molecular analyses have been conducted on the specimens from the Dry Chaco. However, our morphometric results strongly suggest that taxonomic boundaries

within nominal *M. constantiae* are more complex than currently recognized and may present complex phylogeographic patterning, perhaps reflective of ecoregion boundaries.

Our new series of *Marmosa constantiae* from San Pedro enabled us to (1) evaluate the morphometric relationships between *Marmosa paraguayana* and *M. constantiae*; (2) evaluate craniodental sexual dimorphism within *M. constantiae* in the Paraguayan populations, which are near the distributional limit of the species; and (3) detect the presence of a possible third taxon in Paraguay, the identity and relationships of which remain to be clarified. This possible third taxon is currently known from only two specimens (and a possible third specimen, which is a juvenile and not included in the morphometric analyses). These three specimens were collected from near Cerro León in the northern Paraguayan Dry Chaco, in 1983 and 1988, and it is currently unknown whether other populations exist. Although this locality is within a protected area (Parque Nacional Defensores del Chaco), deforestation rates in the Paraguayan Chaco, including areas close to PNDC, have been increasing rapidly during the past 15 years (Caldas et al. 2013) and currently are among the highest in the world (Cardozo et al. 2013). Without additional collecting in PNDC and other similar areas, the taxonomic status of this population may remain undetermined.

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