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Short Note

Molecular and morphometric evidence validates a Chacoan species of the grey leaf-eared mice genus *Graomys* (Rodentia: Cricetidae: Sigmodontinae)

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Since its formal definition, the genus *Graomys* (Thomas 1916) has been the subject of numerous taxonomic changes, both at the generic (Tate 1932, Osgood 1947, Pearson 1958, Hershkovitz 1962) and specific level (Cabrera 1961, Hershkovitz 1962, Pearson and Patton 1976, Williams and Mares 1978, Steppan 1995). Currently, four extant species are recognized: *G. centralis* (Thomas 1902a), *G. domorum* (Thomas 1902b), *G. edithae* (Thomas 1919), and *G. griseoflavus* (Waterhouse 1837) (Musser and Carleton 2005, Díaz et al. 2006). *G. centralis* is the name used for the populations of Central Argentina characterized by 2n=41–42 cytotype (Musser and Carleton 2005, Díaz et al. 2006). *G. domorum* is distributed in the eastern slopes of the Andes from Central Bolivia to northwestern Argentina. The karyotype of this species is 2n=28 (Pearson and Patton 1976) and includes *G. taterona* (Thomas 1926) as synonymous (Musser and Carleton 2005). *G. edithae* is only known from its type locality (Otro Cerro, Catamarca province Argentina) and it is maintained as a valid species pending on more detailed studies of the original type series and additional specimens from the type locality (Musser and Carleton 2005). Finally, the most widely distributed species, *G. griseoflavus* (2n=34–38), ranges from Paraguay and Bolivia to southern Argentina, and includes as synonymous *G. cachinus* (Allen 1901), *G. chacoensis* (Allen 1901), *G. lockwoodi* (Thomas 1918), and *G. medius* (Thomas 1919) (Musser and Carleton 2005). However, the validity of these species, currently considered as synonymous of *G. griseoflavus*, is not fully understood.

The name *G. centralis* was used for populations with 2n=41–42 cytotype, based on strong evidence indicating that these populations represent a different biological species from those with 2n=36–38 cytotype (Theiler 1997). Experimental breeding performed under laboratory conditions have demonstrated the existence of a reproductive barrier between *G. centralis* (2n=42) and *G. griseoflavus* (2n=36–38) (Theiler and Blanco 1996a,b, Theiler et al. 1999b). There is also an apparent spatial segregation between the 2n=41–42 cytotypes, which are mainly distributed in the Chaco and Espinal biome of Central Argentina, and the 2n=36–38 cytotypes, mainly inhabiting the Monte desert biome of North-Western and Southern Argentina; the two forms are found together in the borderlines of these phytogeographical regions (Zambelli et al. 1994, Theiler and Blanco 1996a, Tiranti 1998). Additionally, molecular studies based on allozyme polymorphism (Theiler et al. 1999a) and mtDNA (Catanesi et al. 2002, 2006) support the specific status of *G. centralis*. Nonetheless, the nomenclatural situation of the species characterized by 2n=41–42 cytotypes should be addressed under a wider geographic sampling; including other named putative taxa in order to apply the proper specific epithet.

Recently, Lanzone et al. (2007) studied specimens of *Graomys* collected at the type locality of *G. medius* (Chumbicha, Catamarca Province, Argentina). They suggested, based on their morphological and cytogenetic results, that *G. medius* must be considered as a synonymous of *G. centralis* instead of *G. griseoflavus*. Moreover, they note the occurrence of specimens 2n=42 from 460 km to NW of Villa Hayes (Boquerón Department, Paraguay). The unexpected wide geographic range of this cytotype, together with the result of a phylogenetic analysis (Steppan et al. 2007), where a specimen from the Bolivian Chaco assigned to *G. griseoflavus* grouped closely with *G. centralis* (2n=42) from Central Argentina led the authors to hypothesize that *G. medius* and *G. centralis* are actually synonymous of *G. chacoensis* (Lanzone et al. 2007). Furthermore, *G. chacoensis* was considered as a valid species by Díaz (1999) based on the examination of type material. However, in a recent contribution it was listed as a subspecies of *G. griseoflavus*, but it was pointed out that further study would be required to support the specific recognition of this entity (Díaz and Barquez 2007).

In this note, we provide new data of *Graomys* from a poorly known region in the Northern Argentinean Chaco. Our original data are based on mitochondrial DNA sequences obtained from specimens collected in the province of Formosa. In addition, we compare our spec-

imens with the original descriptions of *Graomys* species. Also, we made comparative morphometrics of our specimens with the 2n=42 and 2n=36–38 specimens from Central-Western Argentina.

During a field trip in July 2004, we collected two specimens of *Graomys* from two localities in Eastern Formosa province, Patiño department: 1) Cruce entre ruta 95 y Riacho Pilaga, 7 km N de cruce entre ruta 81 y 95 (7 km N jct. Hwy. 95 and 81, along Hwy 95 near Riacho Pilaga; 25°13′ S–59°42′ W), and 2) Estancia Poguazu, 8 km N de cruce entre ruta 81 y 95, 6 km E de ruta 95 (8 km N jct. Hwy. 95 and 81, along Hwy 95 and 6 km E from Hwy 95; 25°12′ S–59°38′ W) (Figure 1). Our two specimens were preserved as skin and complete skeletons, and deposited in the Colección Mamíferos Lillo (CML), Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán with collection numbers CML 7539 and CML 7540, and original field numbers LIF 078 and LIF 118, respectively. The collecting area belongs to the Humid Chaco ecoregion (Burkart et al. 1999) characterized by xerophytic forests (*Schinopsis balansae*, *Apidosperma quebracho-blanco*, *Prosopis* spp., *Acacia* spp., *Gleditsia amorphoides*) mixed with palm savannas (*Copernicia australis*) (Cabrera 1976).

We compared our specimens from Formosa with the original description of *G. cachinus* (Allen 1901), *G. chacoensis* (Allen 1901), *G. centralis* (Thomas 1902a), *G. domorum* (Thomas 1902b), *G. edithae* (Thomas 1919), *G. lockwoodi* (Thomas 1918), and *G. medius* (Thomas 1919). Additionally, a multivariate approach was used to assess the morphometric affinity of the specimens from Formosa with those of *G. centralis* 2n=42 and *G. griseoflavus* 2n=36–38 from Central-Western Argentina analyzed by Martínez et al. (2009 in press). We recorded the

Figure 1 Geographic distribution of the *Graomys* specimens with available Cyt*b* sequences superimposed on the phytogeographic provinces. Localities: 1 – Comarapa, 5 km E; Santa Cruz de la Sierra department, Bolivia. 2 – Boyuibe, 26 km E; Santa Cruz de la Sierra department Bolivia. 3 – Comandante Fontana, 7 km N; Formosa province, Argentina. 4 – Salicas, La Rioja province. 5 – Chamical, La Rioja province, Argentina. 6 – General Belgrano department, La Rioja province, Argentina. 7 – Santiago Temple, Cordoba province, Argentina. 8 – Ñacuñan, Mendoza province, Argentina. 9 – Beazley, San Luis province, Argentina. 10 – Playa Fracaso, Chubut province, Argentina. Circles indicate geographic distribution of the "Chacoan clade". Squares indicate geographic distribution of the "Andean-Patagonic clade". Triangles indicate the Cyt*b* sequence geographic origin of *Graomys domorum*.

same 19 cranial measurements used by these authors with a 0.02 precision caliper. The measurements are as follows: greatest length of skull (GLS), basal length (BL), palatal length (PL), diastema length (DL), zygomatic breadth (ZB), least interorbital breadth (LIB), breadth of braincase (BB), rostral breadth (RB), nasal length (NL), nasal width (NW), length of incisive foramen (LIF), length of maxillary tooth row (LM), length of mandibular tooth row (Lm), mastoidal breadth (MB), postpalatal length (PPL), length between molars (LBM), condylo-first molar length (C1ML), length of tympanic bulla (LTB), and width of tympanic bulla (WTB). Detailed definition of these measurements can be found in Gallardo and Palma (1990). We used the software package PAST (Hammer et al. 2001) to perform principal component analysis on a correlation matrix in order to reduce the dimensionality of data. Then, the first eight principal components (90.32% of total variation) were used to perform a discriminant analysis to obtain the rates of correct classification of previously karyotyped animals (Theiler and Gardenal 1994, Theiler and Blanco 1996a,b, Theiler 1997, Martínez et al. 2009 in press). The values of the discriminant function were used to examine the morphometric similarity of the specimens from Formosa.

Tissue samples of the two specimens were preserved in 96% ethanol; DNA was extracted following the standard phenol-chloroform protocol (Maniatis et al. 1982), precipitated in absolute ethanol, and dried and stored in TE buffer (Tris-EDTA) pH 8. The mitochondrial gene that codifies for cytochrome *b* (Cyt*b*) was amplified by polymerase chain reaction (PCR) using the primers Mus 14095 (5′ GAC ATG AAA AAT CAT CGT TGT AAT TC 3′) and Mus 15398 (5′ GAA TAT CAG CTT TGG GTG TTG RTG 3′) (Anderson and Yates 2000). PCR reactions were performed in a final volume of 50 μl: 1× buffer [75 mM Tris-HCl pH 8.8, 20 mM $(NH_4)SO_4$, 0.01% Tween-20], 24 nM each dNTP (dATP, dCTP, dGTP, dTTP), 0.2 pmol/μl Mus14095, 0.2 pmol/μl Mus15398, 2.0 mM $MgCl_2$, 1.5 U *Taq* polymerase (Fermentas, St.Leon-Rot, Germany) and 5–15 ng of template DNA. The thermal protocol was as follows: one initial denaturation of 94°C for 3 min, followed by 35 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min, and final extension of 72°C for 5 min. Then, the same primers were used to obtain the 1140-pb sequences of Cyt*b*. Double-stranded PCR products were purified and sequenced by Macrogen USA (www.macrogenusa.com). Sequences were deposited in GenBank under the following accession numbers: FJ573153 and FJ573154. Additionally, in order to perform phylogenetic analyses, 24 *Graomys* sequences were obtained from GenBank: *G. griseoflavus* (AF159290, AF268101, AF281211, AF281212, AF281213, AF281214, AF281215, AF281216, AF281217, AF281218, AF281219, AY275117, and AY705089), *G. centralis* (AF268100, AF281202, AF281203, AF281204, AF281205, AF281206, AF281207, AF281208, AF281209, and AF281210), *G. domorum* (AF159291). The specimens of *G. centralis* that exhibit 2n=42 (AF281203, AF281204, AF281205, AF281208, AF281209) and individuals of *G. griseoflavus* with 2n=36–38 (AF281211, AF281212, AF281214) were incorrectly located in Villa General Belgrano (Córdoba province) in the original paper by Catanesi et al. (2002). According to the collector, Gerardo Theiler, those specimens were collected in General Belgrano department of La Rioja province (30°39′ S–66°00′ W) (Theiler and Gardenal 1994, G. Theiler personal communication). We also could not correctly situate the collecting locality of the specimen AF268101, because it was not listed in the published source (Catanesi et al. 2002). Three species were selected as outgroup: *Calomys laucha* (AY033190), *Eligmodontia typus* (AF108692), and *Eligmodontia puerulus* (AF159289). The Cyt*b* sequences were aligned using the default parameters of Muscle program version 3.6 (Edgard 2004). We performed a maximum parsimony analysis to the aligned sequences using the TNT program (Goloboff et al. 2003a, 2008). Character states were equal weight and gaps were treated as missing. The heuristic search consisted of 250 random addition sequences, keeping 5 trees by replicate and tree bisection recombination branch swapping. Robustness of the nodes was evaluated by 1000 bootstrap replicates (Felsenstein 1985). Also, Bremer support (BS) values were calculated for each node (Bremer 1994). Finally, we calculated the average amount of genetic divergence within *G. griseoflavus* (2n=36–38) and *G. centralis* (2n=42). Then, we evaluated the average genetic distance between *G. griseoflavus* (2n=36–38), *G. centralis* (2n=42), *G. domorum* and our specimens from Formosa together with the specimen (AF159290) from the Bolivian Chaco. Genetic distances were inferred by using the MEGA 3.1 program (Kumar et al. 2004) employing K2P distances including transitions, transversions and uniform rates of substitution among sites.

The specimens from Formosa clearly match the description of *Graomys chacoensis* better than all other species descriptions. Our specimens are adult animals of great size, yellowish brown above, pure white belly and tail with a terminal tuft. Dorsally, the yellowish coloration differ from the grayish coloration mentioned for *G. cachinus*, *G. centralis*, *G. domorum*, *G. lockwoodi*, and *G. medius*, while the pure white to the base hairs of the ventral surface differs from the basally plumbeous or slaty ventral hairs of *G. cachinus*, *G. domorum*, and *G. lockwoodi*, according to the original descriptions. These traits also differentiate our specimens from *G. griseoflavus* (Waterhouse 1837, Allen 1901). The skull of *G. chacoensis* was described as long and narrow with large bullae and narrow braincase (Allen 1901). Afterwards, Thomas (1902a) described *G. centralis* under *Eligmodontia griseoflavus centralis*, and noted that this species has larger bullae than *domorum* but smaller than *chacoensis* and that the diminutive molars distinguish *centralis* from all members of the group. *G. lockwoodi* was described as large feet *Graomys*, very opisthodont, approximately the same size as in *G. domorum* and *G. cachinus*, but with bullae larger than the former and smaller than the latter (Thomas 1918). Finally, in the description of *G. medius* and *G. edithae*, Thomas (1919) pointed out that this form can be distinguishable almost entirely by size; the skull in *G. medius* is always smaller than in *G. cachinus*, with shorter nasals and smaller tympanic bullae, while in *G. edithae* the skull is a miniature of that of the other species. The measurements of CML 7539 and CML 7540, and those of the type specimen of *G. cachinus*, *G. cha-*

Table 1 External and cranial measurements (mm) of the type specimen of *Graomys cachinus* (Allen 1901), *Graomys centralis* (Thomas 1902a), *Graomys chacoensis* (Allen 1901), *Graomys domorum* (Thomas 1902b), *Graomys edithae* (Thomas 1919), *Graomys lockwoodi* (Thomas 1918), and *Graomys medius* (Thomas 1919) taken from the original descriptions and the two specimens from Formosa province, Argentina.

	G. cachinus	*G. centralis*	*G. chacoensis*	*G. domorum*	*G. edithae*	*G. lockwoodi*	*G. medius*	CML 7539	CML 7540
Total length	296	286	327	286	235	289	274	317	320
Head and body	137	130	142	140	108	131	124	148	145
Tail	159	156	185	146	127	158	150	169	175
Hind foot	29	29	33	31	25	32	27	30	33
Ear	24	26	24	25	20	25	25	25	23
Length of the skull	35	33.5	38	35.4	28.5	35	31.2	36.2	35.1
Basilar length	27	26	29	27.5	–	–	–	30.3	30.1
Condilo-incisive length	–	–	–	–	26.5	31.7	28.5	32.7	32.4
Nasal length	15.5	14	16	15	10.5	14.7	11.8	14.4	14.6
Zygomatic breadth	17	–	18	18.4	15	18	16.1	17.8	17.7
Mastoid breadth	14.5	–	14	–	–	–	–	13.6	13.3
Breadth of braincase	–	13.5	–	–	13.5	15	14.2	14.9	13.6
Interorbital breadth	5	5.4	6	5.6	4.5	–	5.2	5.6	5.6
Palatal length	6.8	–	7.2	–	–	–	–	7.5	7.7
Palatilar length	–	14.7	–	15.3	12.8	15.7	14.1	15.5	15.4
Palatal foramina	7.2	–	8	7.6	6.7	7.3	7	7.7	7.7
Upper toothrow	5.4	4.5	5	5.1	4.7	5.4	5.2	5.8	5.4
Length of bullae	7.3	6	–	6.2	6	6.7	6.4	7.0	6.8

coensis, *G. centralis*, *G. lockwoodi*, *G. medius*, and *G. edithae* taken from the original description are provided in Table 1. Unambiguously, our specimens from Formosa match the external measurements of *G. chacoensis* better than all other species, while the cranial dimension of our specimens matches very well either with *G. chacoensis* or *G. lockwoodi*. Furthermore, the collecting localities in Formosa province are quite close to the border with Paraguay, approximately 200 km West of Asuncion (Figure 1). The type locality of *G. chacoensis*, Waikthlatingwayalwa, is cited to be located in "the northern Chaco country of Paraguay, Northwest of Asunción" (Allen 1901 p. 408).

The discriminant analysis correctly classified 95.35% of the specimens previously identified according to their karyotypes. Based on morphometrics, two specimens were misclassified (one of each species): one from Chamical (La Rioja province) and the other from Papagayos (San Luis province). Therefore, considering the high rate of accurate classification, the morphometric similarity of specimens from Formosa was demonstrated based on discriminant function analysis. The centroids in the discriminant space were -8.96 (-13.77–0.89) and 8.96 (-1.43–19.02) for *G. centralis* (2n=42) and *G. griseoflavus* (2n=36–38), respectively. The results of discriminant function, -2.83 and -6.82 for CML 7539 and CML 7540, respectively, reveal that the specimens from Formosa are more similar to *G. centralis* 2n=42 from Central-Western Argentina than to *G. griseoflavus* 2n=36–38. Therefore, the two specimens from Formosa were considered together with the *G. centralis* (2n=42) specimens to evaluate which measurement differ significantly from the *G. griseoflavus* (2n=36–38) analyzed by Martínez et al. (2009 in press). The t-test revealed significant differences in the mean of 13 measurements. Six measurements were very highly significant ($p<0.001$): length of incisive foramen, postpalatal length, condylo-first molar length, length of tympanic bullae, width of tympanic bullae, and basal length. Three measurements were highly significant ($p<0.01$): greatest length of skull, diastema length, and breadth of braincase. Four measurements were just significant ($p<0.05$): zygomatic breadth, nasal length, mastoidal breadth, and length between molars. The mean of all these measurements were significantly greater in *G. griseoflavus*.

In the phylogenetic analysis we obtained 81 most parsimonious trees (CI: 0.782; RI: 0.837), each 555 steps long, summarized by a strict consensus tree (Figure 2). Besides the low support for the relationship between *G. domorum* and *G. griseoflavus* (16% of bootstrap and BS=1), two very well supported clades are apparent. One clade was formed by the specimens of *G. griseoflavus* mainly distributed in Monte desert and Patagonian steppe ecoregions (99% bootstrap and BS=9). The other lineage, also very strongly supported (99% of bootstrap and BS=9.8), encompasses specimens of *G. centralis* (2n=42) from Cordoba and La Rioja provinces in Argentina, the specimen from Santa Cruz in the Bolivian Chaco assigned to *G. griseoflavus* and the two specimens from Formosa sequenced in this work.

The genetic divergences estimated using the K2P model are presented in Table 2. The average genetic distance within 2n=42 and 2n=36–38 specimens was 0.47% and 0.61%, respectively; while between them the average genetic distance was 9.62%. The specimens from Formosa together with the specimen from the Bolivian Chaco (AF159290) diverge at 9.31% from *G. griseoflavus* 2n=34–38, at 11.1% from *G. domorum*, and at 1.32% from the Central Argentina 2n=42 karyomorph. These values of divergence suggest that our specimens from Formosa are conspecific with the 2n=42 karyomorph of Central Argentina and with the specimen from the Bolivian Chaco. Moreover, the monophyletic nature of the two major clades, the Andean-Patagonic and the Chacoan, are very strongly supported (Figure 2), and therefore a nomenclatural problem became evident. This

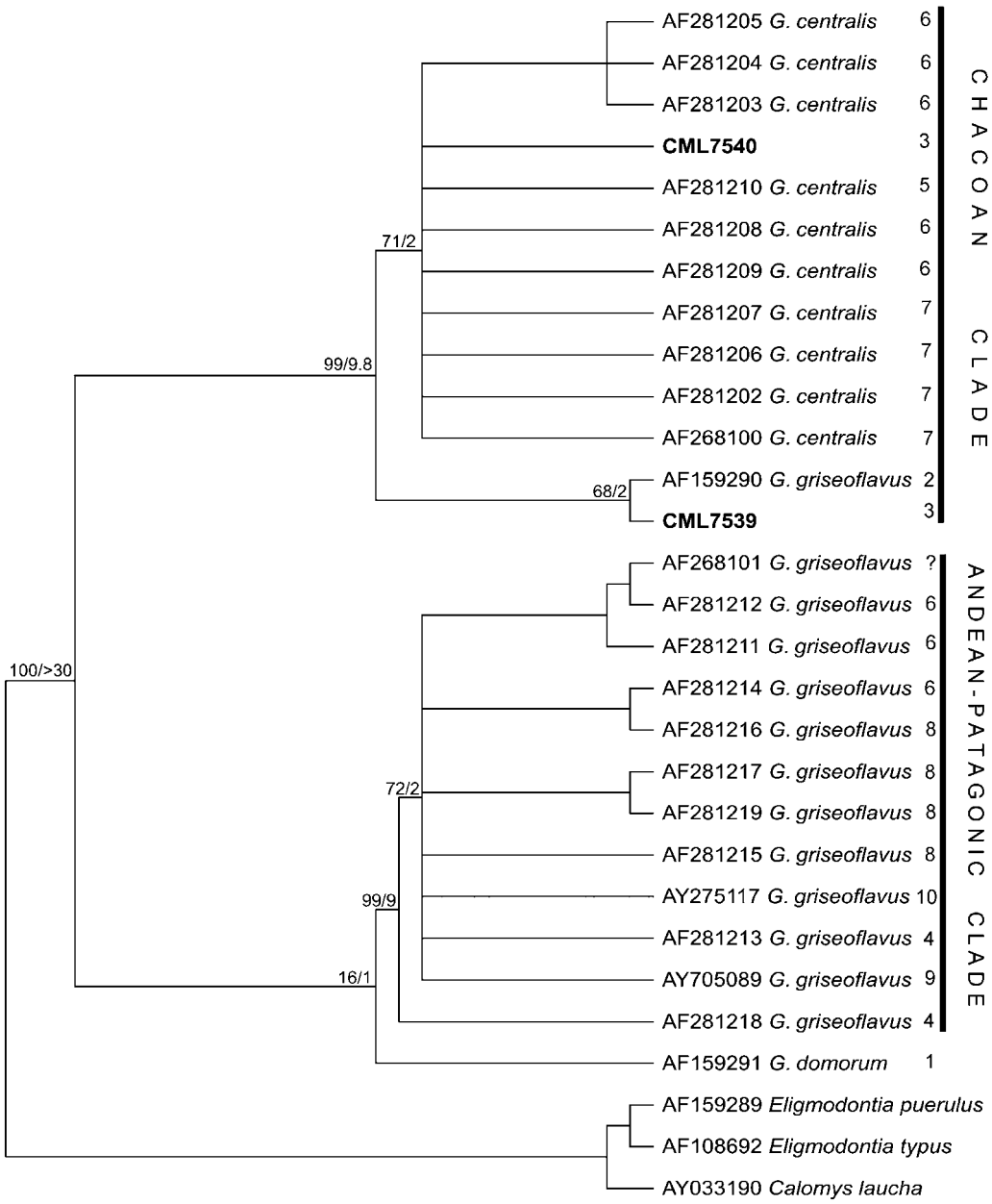

Figure 2 Maximum parsimony consensus tree for *Graomys* Cyt*b* sequences. The values to the left and right of the crossbar represent 1000 bootstrap pseudo-replicates and relative Bremer support, respectively. The bootstrap supports are expressed as GC values following Goloboff et al. (2003b). Numbers following names of species indicate the localities from Figure 1.

problem regarding *Graomys* species has already been detected by Steppan et al. (2007) when they found that *G. griseoflavus* from the Bolivian Chaco clusters with *G. centralis* from Central Argentina and tentatively attributed this problem to the premature separation of *G. centralis* from *G. griseoflavus*. Also, they pointed out that their data support the presence of at least three species in *Graomys*, but its resolution awaits further study.

Our analyses indicate that the same species inhabit the northernmost and the southernmost portions of the Cha-

Table 2 Average amount of genetic divergence calculated using the Kimura 2 parameter model within and between groups.

	G. domorum	*G. centralis*	*G. griseoflavus*	CML 7539–7540 and NK23331
G. domorum	**nc**			
G. centralis	0.119915	**0.004793**		
G. griseoflavus	0.099390	0.096229	**0.006189**	
CML 7539–7540 and NK23331	0.110870	0.013254	0.093120	**0.013545**

Values on the diagonal line in bold font are within group average calculations; nc: not calculated within group distance. CML 7539–7540 correspond to specimens from Formosa province, Argentina and NK23331 (AF159290) corresponds to specimens from Santa Cruz department, Bolivia.

co biome. The fact that the two specimens from Formosa have different haplotypes, one closely related to the Central Argentina populations and the other related to the specimen from Bolivia, as well as the reference of a 2n=42 cytotype for specimens from Paraguay, reinforces the hypothesis of a Chacoan species in *Graomys* (Lanzone et al. 2007). Besides, based on the perfect concordance of our specimens from Formosa with the original description of *G. chacoensis*, in addition to wide geographic sampling within the Chacoan populations and the proximity of our collecting localities to the border with Paraguay, a country where the type locality of *G. chacoensis* occur, we suggest that the name *G. chacoensis* (Allen 1901) should be applied to these populations instead of *G. centralis* (Thomas 1902a). However, much work must still be done within this species, including a comprehensive and detailed morphological study in order to accurately define its geographic range limits and geographic variation. Our morphometrics results can provide clues for further morphological analysis. Also, the status of other named putative taxa, such as *G. cachinus* (Allen 1901), *G. edithae* (Thomas 1919), *G. taterona* (Thomas 1926) or *G. lockwoodi* (Thomas 1918), should be assessed in order to clarify the taxonomy of this genus.

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