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Artículo

CHROMOSOMAL VARIABILITY IN TUCO-TUCOS (*Ctenomys*, RODENTIA) FROM THE ARGENTINEAN NORTHEASTERN WETLANDS

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ABSTRACT. Chromosomal diversity is a key feature for understanding the evolution of mammalian species. Rodents, the most diverse taxon among mammals, exhibit a wide chromosomal diversity; the study of their karyomorphs has contributed greatly to understand the evolution in this group. South American subterranean rodents of the genus *Ctenomys* (tuco-tucos) are one of the most speciose mammalian genera. Chromosomal variability in several lineages of *Ctenomys* has been characterized; however, the description of the karyomorphs of the tuco-tucos that inhabit the broad area under the influence of the Iberá marsh in the northeast of Argentina (the Corrientes group) is incomplete. This work provides new chromosomal information of the *Ctenomys* Corrientes group that includes the description of 3 new and 5 previously undescribed karyomorphs. We found four fundamental numbers (FNs): 76, 78, 80 and 84 and chromosomal numbers (2n) that ranged between 41-44, 44-46, 48 and 50-70, respectively. In addition, we found a new sampling site of *C. roigi*, a critically endangered species.

RESUMEN. Diversidad cromosómica en tuco-tucos (*Ctenomys*, Rodentia) de los humedales del noreste argentino. La diversidad cromosómica es clave para entender la evolución de las especies de mamíferos. Los roedores, el taxón más diversificado de los mamíferos, presentan una gran diversidad cromosómica; el estudio de sus cariomorfos ha contribuido mucho a la comprensión de su evolución. Los roedores subterráneos del género *Ctenomys* (tuco-tucos) son uno de los géneros de mamíferos con mayor número de especies. En muchos linajes de *Ctenomys* la variabilidad cromosómica ha sido caracterizada; sin embargo, la descripción de los cariomorfos de los tuco-tucos que habitan en una amplia área bajo la influencia de los esteros del lberá en el noreste de Argentina (grupo Corrientes) está incompleta. El presente trabajo brinda nueva información cromosómica del grupo *Ctenomys* de Corrientes, que incluye la descripción de 3 cariomorfos nuevos y 5 no descriptos previamente. Encontramos cuatro números fundamentales (NFs): 76, 78, 80 y 84 y números cromosómicos (2n) que varían entre 41-44, 44- 46, 48 y 50-70, respectivamente. Además, identificamos un nuevo sitio de muestreo de *C. roigi*, especie en peligro de extinción.

Key words: Chromosomal variability. Ctenomys. Iberá marsh. Tuco-tucos.

Palabras clave: Ctenomys. Esteros del Iberá. Tuco-tucos. Variabilidad cromosómica.

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INTRODUCTION

Subterranean rodents of the genus Ctenomys (commonly named tuco-tucos) have been considered a clear example of chromosomal evolution since the seminal work of Reig and Kiblisky (1969) because of their broad range of chromosomal numbers (from 2n = 10 to 70) (Cook et al., 1990; Ortells et al., 1990). Among mammals, the genus Ctenomys is characterized by having one of the highest numbers of living species, about 60 as registered by Woods y Kilpatrick (2005). Most of the species present quite distinctive karyotypes, a characteristic that was called to be an example of chromosomal speciation (Reig y Kiblisky, 1969). However, chromosomal polymorphisms or polytypisms also occur in Ctenomys. For instance, C. pearsoni is considered a single species although its karyotypes range between 2n = 56 to 2n = 70 as reviewed by Tomasco and Lessa (2007). Similar cases have been recently reported in the Brazilian tuco-tuco species C. lami (2n = 54 to 58) and C. minutus (2n = 42)to 50) that also depict large intraspecific karyotypical variability, mainly due to centric fusions/fissions and pericentric inversions (Freitas, 2007; Lopes et al., 2013).

The present work deals with chromosomal variability of the Ctenomys Corrientes group that exhibits one of the widest ranges of diploid numbers within the genus. Demes of tuco-tucos from this group are patchily distributed in a vast area under the wide influence of the Iberá marsh and its natural channels and lagoons, in the Argentinean province of Corrientes, between the Paraná and Uruguay rivers. Sandy soils, predominant in this area, are favorable habitats for tuco-tucos, though their proximity to the wetlands makes these habitats temporary and spatially fragmented. The dynamics of habitat availability (via expansions and contractions) imposes putative contacts between neighboring populations and/or splitting and divergence of demes.

The pioneering works of Contreras y Scolaro (1986), Ortells et al. (1990) and Ortells y Barrantes (1994) initiated chromosomal studies in the *Ctenomys* Corrientes group. Ortells et al. (1990) showed that high karyotypical variabil-

ity, with chromosomal numbers ranging from 2n = 42 to 2n = 70, characterized this group. Chromosomal numbers and morphology have been described for some karyomorphs in the mentioned contributions, as well as in subsequent ones (García et al., 2000; Argüelles et al., 2001). However, for several karyomorphs only chromosomal (2n) and fundamental (FN) numbers have been published without any data on chromosomal morphology (Giménez et al., 2002; Lanzone et al., 2007). The purpose of the present work is to expand the chromosomal information of the Ctenomys Corrientes group, particularly of the Iberá subgroup that comprises the tuco-tucos that inhabit the margins of the Iberá marsh (Caraballo et al., 2012). We found 3 new karyomorphs, described another 5 from which only 2n and FN values were available. and confirmed chromosome number and morphology of another 6 previously published karyomorphs.

MATERIALS AND METHODS

Specimens

This study included 47 individuals from 15 localities of the province of Corrientes (Argentina). Animals were live-captured with modified Oneida Victor Nr. 0 snap traps. Guidelines of the American Society of Mammalogists (Gannon et al., 2007) were followed. Well-preserved skulls were deposited in the Colección de Mastozoología of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Trapping localities with their geographical location (Fig. 1) as well as field / catalog numbers (when available) were recorded: Estancia la Tacuarita (27° 58' 42.7" S; 56° 33' 40.6" W), specimens 203, 204 and 205; Saladas Centro (28º 14' 20.3" S; 58º 37' 40.4" W), specimens 128 and 129; Saladas Sur (28° 17' 37.5" S; 58° 41' 19.2" W), specimen 134; San Alonso (28° 17' 76" S; 57° 24' 45" W), specimens 186, 187, 188 and 190; Estancia San Luis (28° 6' 43.7" S; 58° 51' 48.1" W), specimens 236/ 26484, 237/26485, 238/26486 and 239/26487; Goya (29° 11' 17.2" S ; 59° 12' 36.7" W), specimens 181 to 184; San Roque (28° 41' S; 58° 42' W), specimens 135 to 137; Chavarría (28° 58' S; 58° 35' W), specimens 149 to 153; Curuzú Laurel (27° 55' 24.4" S; 57° 29' 23.5" W), specimens 220 to 222; Loreto (27° 44' 43.7" S ; 57º 14' 35.2" W), specimens 156, 223/26479 and 224; Contreras Cué (28° 5' 28.6" S ; 56° 33' 53.7" W), specimens 199, 207, 208, 210

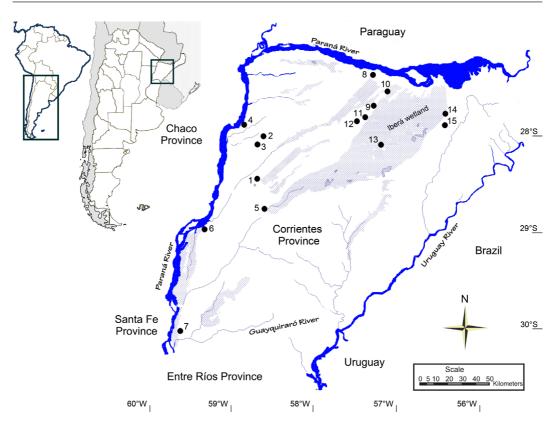


Fig. 1. Map showing sampling localities. Numbers correspond to the following localities: 1-San Roque, 2-Saladas Centro, 3-Saladas Sur, 4-Estancia San Luis, 5-Chavarría, 6-Goya, 7-Paraje Sarandicito, 8-Mbarigüí, 9-Curuzú Laurel, 10-Loreto, 11-San Miguel, 12-Paraje Caimán, 13-San Alonso, 14-Estancia La Tacuarita, 15-Contreras Cué.

and 211; Mbarigüí (27° 33' S; 57° 31' W), specimen 174; San Miguel (28° 0' 58.6" S; 57° 36' 19.2" W), specimens 214/26478, 216 and 217; Paraje Caimán (28° 3' 3.1" S ; 57° 40' 38.4" W), specimens 225, 226/26480, 227/26481 to 228/26482, and Paraje Sarandicito (30° 14' 43.1" S; 59° 33' 46.1" W), specimens 212/26476 and 213/26477.

Chromosome preparations

Metaphase preparations were obtained from bone marrow following Ford and Hamerton (1956) and stained with Giemsa. Chromosomes were classified according to Levan et al. (1964) and FNs were computed considering autosomes and sexual chromosomes. For each specimen a minimum of 20 metaphases was analyzed. For each specimen a karyogram was considered reliable when at least five different metaphases yielded the same assembly. Chromosomes were classified into three groups: sexual chromosomes (see Results), and biarmed and telocentric autosomes. Chromosomes were joined in pairs according with their morphology and size, in decreasing order.

RESULTS

In **Table 1** we present a summary of the karyomorphs of the *Ctenomys* Corrientes group published in the literature. In the present paper, we described a total of 15 karyomorphs. The sexual chromosome system for the Corrientes group is XX/XY; both sexual chromosomes were biarmed, as was characterized by Ortells et al. (1990). The identification of sexual chromosomes was based on the differences between males and females from each population, as well as contrasting our karyomorphs with previously reported ones (Ortells et al., 1990). In each karyomorph the sexual pair was included in a third group apart from the classification of biarmed and telocentric chromosome pairs (**Figs. 2-6**).

Table 1

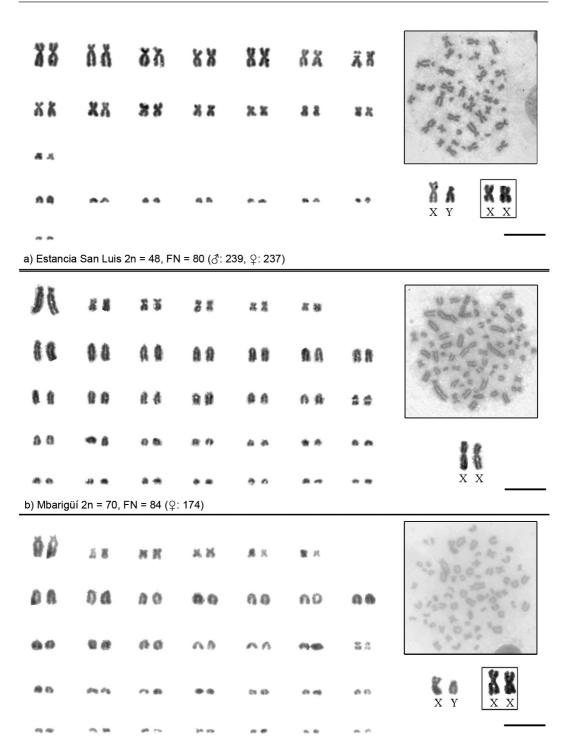
Karyomorphs of the *Ctenomys* Corrientes group. 1: Ortells et al. (1990), 2: Argüelles et al. (2001), 3: Giménez et al. (2002) and 4: Lanzone et al. (2007).

Locality	2n/FN values (Published in)	Giemsa-stained karyomorph (Published in)	
Costa Mansión	48/80 (1, 3, 4)	1	
Estancia San Luis	48/80 (this paper)	This paper	
Colonia Brougnes	48/80 (3)	-	
Estancia Rosarito	51-52/80 (4)	-	
Mbarigüí	70/84 (1, 2, 3, 4, this paper)	1, this paper	
Paraje Angostura	70/84 (4)	-	
Paraje Sarandicito	70/84 (2, 3, this paper)	2, this paper	
San Roque	62/84 (1, 3, this paper)	1, this paper	
MF Mantilla	62/84 (1)	1	
Santa Rosa	65-66/84 (3, 4)	-	
Chavarría	56/84 (this paper), 58/84 (3, 4)	This paper , -	
Saladas Centro	54/84 (this paper), 55-56/84 (1, 3, 4)	This paper, 1	
Saladas Sur	51/84 (this paper)	This paper	
Ruta Saladas-Mburucuyá Km 10-12	54-58/84 (3)	-	
Ruta Saladas-Mburucuyá Km 7	54-56-58/84 (1, 3)	1	
Goya	50/84 (1, 2, this paper)	1, this paper	
Colonia 3 de abril	50/84 (2)	-	
Rincón de Ambrosio	50/84 (2)	-	
Pago Alegre	56/84 (3, 4)	-	
Mburucuyá	58/84 (1)	1	
Pago de los Deseos-Km 10	56/84 (4)	-	
Yataytí-calle	53-54/84 (1)	1	
Paraje Santo Domingo	54-55/82 (4)	-	
San Alonso	44/78 (this paper)	This paper	
Paraje Caimán	45-46/78 (this paper) 46-47/78 (3)	This paper	
San Miguel	44/76 (3, 4, this paper)	This paper	
Contreras Cué	41-42/76 (3, this paper)	This paper	
Estancia La Tacuarita	42/76 (3, this paper)	This paper	
Curuzú Laurel	42/76 (1, 3, 4, this paper)	1, this paper	
Loreto	42/76 (3, this paper)	This paper	

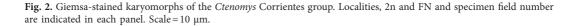
Estancia San Luis

The four individuals, two females (236 and 237) and two males (238 and 239) sampled at estancia San Luis were homozygous 2n = 48 and FN = 80 (**Fig. 2a**). The autosomal complement comprises 15 biarmed and 8 telocentric

pairs. On the 7th biarmed pair, a secondary constriction was observed. The X chromosome is a large metacentric, while the Y chromosome is a medium-sized submetacentric. The karyomorph found in Estancia San Luis is indistinguishable from that found in Costa Mansión, *Ctenomys roigi*'s type locality (Ortells



c) Paraje Sarandicito 2n = 70, FN = 84 (♂: 213, ♀: 212)



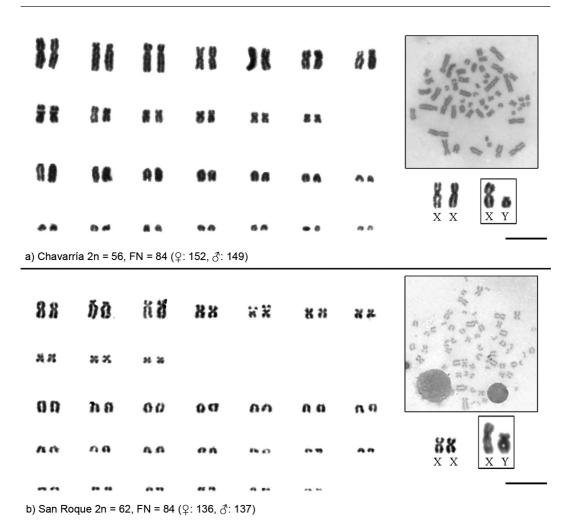


Fig. 3. Giemsa-stained karyomorphs of the *Ctenomys* Corrientes group. Localities, 2n and FN and specimen field number are indicated in each panel. Scale = $10 \ \mu m$.

et al., 1990), less than 10 km from Estancia San Luis.

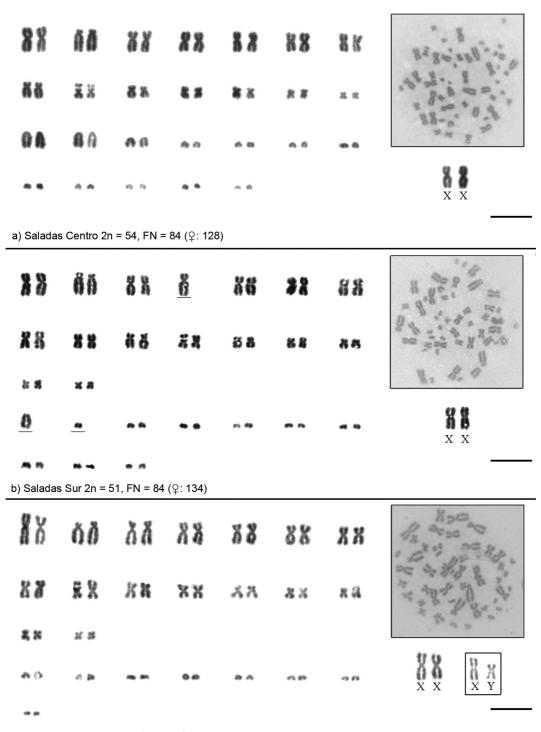
Mbarigüí

The chromosome complement of a female (174) from Mbarigüí, the type locality of *Ctenomys dorbignyi* was 2n = 70 FN = 84, confirming the characteristic karyotype of this species, which possesses the highest diploid number of the genus (**Fig. 2b**). The autosomal complement consists of 6 biarmed and 28 telocentric pairs. The 14th monobrachial pair presents a secondary constriction. This karyomorph shows the

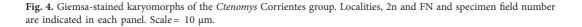
same morphology and chromosome number as the one described by Ortells et al. (1990), corresponding to the same locality. We identified the X chromosome as a large metacentric, also in accordance with Ortells et al. (1990).

Paraje Sarandicito

A male (213) and a female (212) captured at the locality of Paraje Sarandicito had a 2n=70 FN=84 karyomorph (**Fig. 2c**) distinguishable from the one found in Mbarigüí (**Fig. 2b**) for having a submetacentric second pair instead of metacentric, in agreement with Argüelles et al. (2001). The Y



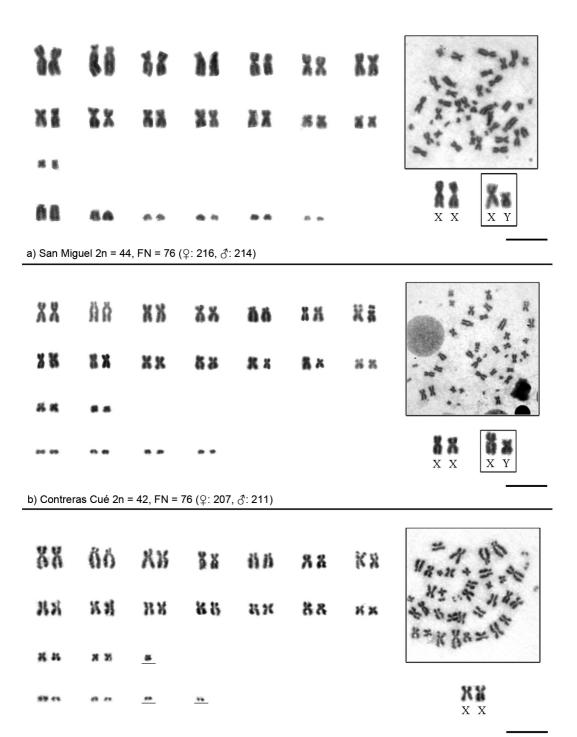
c) Goya 2n = 50, FN = 84 (♀: 183, ♂: 181)



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a) Paraje Caimán 2n = 46, FN = 78 (♀: 226, ♂: 227)									
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b) Paraje Caimán 2n = 45, FN = 78 (♀: 225)									
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c) San Alonso 2n = 44, FN = 78 (♀: 190, ♂: 188)

Fig. 5. Giemsa-stained karyomorphs of the *Ctenomys* Corrientes group. Localities, 2n and FN and specimen field number are indicated in each panel. Scale = $10 \ \mu m$.



c) Contreras Cué 2n = 41, FN = 76 (♀: 199)

Fig. 6. Giemsa-stained karyomorphs of the *Ctenomys* Corrientes group. Localities, 2n and FN and specimen field number are indicated in each panel. Scale = $10 \ \mu m$.

chromosome is a medium-sized submetacentric, in agreement with previous descriptions (Ortells et al., 1990; Argüelles et al., 2001).

Chavarría

Specimens sampled in Chavarría depicted the same karyomorph. Three males (149, 150 and 153) and two females (151 and 152) shared a karyomorph 2n = 56 and FN = 84 (**Fig. 3a**). The autosomal complement of the 2n = 56 FN = 84 comprises 13 biarmed and 14 telocentric pairs, while the sexual pair consists of a medium-sized metacentric X chromosome and a small submetacentric Y chromosome. A secondary constriction was found in the 8th biarmed pair. For the same locality, Giménez et al. (2002) and Lanzone et al. (2007) mentioned a karyomorph 2n = 58 FN = 84. However, these publications did not include any photographic material to corroborate chromosome number.

San Roque

Two females (135 and 136) and one male (137) from San Roque were analyzed. The 3 specimens had a karyomorph 2n = 62 and FN = 84, consisting of 11 biarmed and 30 telocentric autosomal pairs (**Fig. 3b**). A secondary constriction was observed in the 5th biarmed pair. The X chromosome is a medium-sized submetacentric, while the Y chromosome is a medium-sized metacentric. This karyomorph matches the one described for the same population by Ortells et al. (1990).

Saladas Centro

The two females (128 and 129) sampled in the locality of Saladas Centro had 2n = 54 FN = 84. A total of 14 biarmed and 12 telocentric pairs compose the autosomal complement (**Fig. 4a**). The 9th biarmed pair bears a secondary constriction, and the X chromosome is a large metacentric, in correspondence with an identical karyomorph found in this population by Ortells et al. (1990). These authors found two additional karyomorphs 2n = 55 and 2n = 56, both with FN = 84, which correspond to heterozygous and homozygous morphs originated by a centric fusion/fission event comprising the 7th biarmed pair.

Saladas Sur

Saladas Sur is a previously undescribed locality placed 7.3 km far from Saladas Centro in southwest direction. The karyomorph of a female (134) was 2n = 51 FN = 84 constituting a new 2n record for the Corrientes group (Fig. 4b). The autosomal complement consists of 15 biarmed pairs plus one biarmed chromosome in heterozygosis, and 8 telocentric pairs plus two telocentric chromosomes in heterozygosis. One of the chromosomes of the biarmed pairs—probably the 4th—was "orphan" and could be involved in a fusion/fission event with two telocentric chromosomes. This Robertsonian rearrangement should be confirmed by banding techniques. The X chromosome is a large metacentric, identified in comparison with the karyomorph found in the neighboring population of Saladas Centro. The 11th biarmed pair bears a secondary constriction.

Goya

The chromosome complement of the 2 females (183 and 184) and 2 males (181 and 182) sampled in Goya, the type locality of *C. perrensi*, was 2n=50 FN=84, in accordance with the karyotype previously published (Ortells et al., 1990). This karyomorph comprises 8 telocentric and 16 biarmed autosomal pairs (**Fig. 4c**). A secondary constriction was observed in the 9th biarmed pair. The X chromosome is a large metacentric while the Y chromosome is a medium-sized submetacentric.

Paraje Caimán

In the population sampled at Paraje Caimán, from a total of 4 specimens, 2 females (225 and 228) were heterozygous with 2n=45 (**Fig. 5b**) while a female (226) and a male (227) had 2n=46 (**Fig. 5a**), all of which had FN = 78. In the morph with 2n=46 the autosomal complement consists of 15 biarmed and 7 telocentric pairs. The sexual pair is heteromorphic; the X chromosome is a large submetacentric, whereas the Y chromosome is a small submetacentric. The 6th biarmed pair, a medium-sized submetacentric, bears a secondary constriction. In the 2n=45 morph, the 3rd biarmed and the first two major

telocentric chromosomes resulted "orphans", being probably involved in a fusion/fission event that originated the heterozygous condition. The 2n=44, FN=78 morph was not found in this population, likely due to insufficient sampling. However, the occurrence of this karyomorph is highly probable in this population, and it would be indistinguishable from the one found in San Alonso (**Fig. 5c**). In a previous article Giménez et al. (2002) stated that in Paraje Caimán, in addition to the 2n=46, a 2n=47 morph was found. But, like in the case of Chavarría, these karyomorphs cannot be compared because there is no photographic material available.

San Alonso

San Alonso is a sandy patch located in the central area of the Provincial Reserve Esteros del Iberá. It is an island surrounded by shallow marshes that could eventually reconnect with the mainland. Two males (186 and 188) and two females (187 and 190) sampled in San Alonso had 2n = 44 and FN = 78, previously undescribed karyomorph for the Corrientes group. The autosomal complement consisted of 16 biarmed and 5 telocentric pairs, with a secondary constriction observed in the 7th biarmed pair (**Fig. 5c**). The sexual pair was heteromorphic, including a large submetacentric X chromosome and a small submetacentric Y chromosome.

San Miguel

The sample from San Miguel consisted of two males (214 and 217) and one female (216), with a 2n=44 and FN=76 karyomorph (**Fig. 6a**). In this case, the autosomal complement presented 15 biarmed and 6 telocentric pairs. Within the telocentric group, the two major pairs resemble the ones found in Paraje Caimán. The sexual pair was heteromorphic, including a large submetacentric X chromosome and a small submetacentric Y chromosome. This karyomorph was already published by Giménez et al. (2002) as well as by Lanzone et al. (2007) for this locality but again lacking photographic support.

Contreras Cué

A total of 5 specimens were sampled at Contreras Cué. Four of the individuals, two females (207 and 208) and two males (210 and 211) had 2n=42 and FN=76 (**Fig. 6b**) while a female (199) was heterozygous with 2n=41 and the same fundamental number (**Fig. 6c**). The autosomal complement of the 2n=42 karyomorph consists of 16 biarmed and 4 telocentric pairs. The sexual pair is submetacentric: the X is a large chromosome, while the Y is small. The female with 2n=41 had one extra small metacentric chromosomes of the autosomal complement. When compared with the karyomorph 2n=42, these differences are most probably due to a centric fusion.

Curuzú Laurel

Two females (220 and 221) and a male (222) captured at the locality of Curuzú Laurel were homozygous with 2n = 42 and FN = 76, in agreement with the karyomorph published by Ortells et al. (1990) corresponding to the same locality. This karyomorph is indistinguishable from the 2n = 42 described for Contreras Cué (**Fig. 6b**).

Loreto

A total of three tuco-tucos were captured in Loreto, two males (156 and 224) and a female (223) that were homozygous with a karyomorph that was identical to the 2n = 42 found in Contreras Cué (**Fig. 6b**). The 2n and FN found in this locality coincide with the ones previously published by Giménez and collaborators (2002).

Estancia La Tacuarita

Cytogenetic analyses were carried out for three individuals sampled at Estancia La Tacuarita, two females (203 and 204) and a male (205), The karyomorph was homozygous and indistinguishable from the other 2n = 42 described in this paper (**Fig. 6b**), and also reported by Giménez et al. (2002) although without photographic support.

DISCUSSION

In the present work we characterized 3 new karyomorphs: 2n = 44 FN = 78 from San Alonso (Fig. 5c) plus two heterozygous 2n = 51 FN = 84 from Saladas Sur (Fig. 4b) and 2n = 45 FN = 78

from Paraje Caimán (Fig. 5c). We also showed another 5 karyomorphs from which only 2n and FN numbers have been published but without photographs depicting the morphology and size of the chromosomes: those from Chavarría (Fig. 3a), Paraje Caimán (Fig. 5a), San Miguel (Fig. 6a), Contreras Cué (Fig. 6b and c), Loreto (see Results) and estancia La Tacuarita (see Results). We also reanalyzed the previously described karyomorphs, confirming those from Mbarigüí, the type locality of C. dorbignyi (Fig. 2b), Paraje Sarandicito (Fig. 2c), Goya, the type locality of C. perrensi (Fig. 4c), San Roque (Fig. 3b), Saladas Centro (Fig. 4a) and Curuzú Laurel (see Results). The finding of a new population of C. roigi (Estancia San Luis) is important because this is a critically endangered species (Bidau et al., 2008).

New chromosomal data from the Corrientes group confirm that FNs 76, 78, 80 and 84 characterize the karyomorphs of the group. Fundamental numbers 76 and 78 were found in the Iberá subgroup; FN = 80 was only found in the karyomorph from Estancia San Luis (which is indistinguishable from that of Costa Mansión, the type locality of *C. roigi*) and FN = 84 was found in the remainders.

The karyomorphs of the Iberá subgroup that share FN = 76 are very similar (see **Results**) with 2n = 41, 42 and 44. The same occurs with those that share FN = 78 that depict 2n = 44, 45 and 46. Differences in 2n without changes in FN might be mainly explained by Robertsoninan events, although banding techniques are required to confirm it and to identify the chromosomes involved. Since within each FN, 2n range is limited, the rearrangements involved might be easy to track by G-banding techniques.

The karyomorphs that share FN = 84, on the contrary, include a broader range of chromosomal numbers, from 2n = 56 to 2n = 70. In these cases, although Robertsonian changes are also probably the most frequent rearrangement, as those described by Lanzone et al. (2002) and Lanzone et al. (2007), the relationships among the karyomorphs might be more difficult to establish. The ample range of chromosomal numbers suggests a more complex scenario that may include parallelisms, reversions and/ or convergences.

New chromosomal data shown in this paper broaden the chromosomal information of the *Ctenomys* Corrientes group, essential to understand the role of chromosomal variability in speciation and hybridization processes. However, phylogeny (Caraballo et al., 2012), population genetics (Gómez-Fernández et al. 2012), morphology and ecology should also be taken into account to establish species boundaries in this interesting group of tuco-tucos.

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