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Laura Angela Glesmann

Instituto Multidisciplinario de Biología Celular, La Plata, Buenos Aires, Argentina

Pablo Francisco Martina

Universidad Nacional de Misiones, Argentina

Cecilia Inés Catanesi

Instituto Multidisciplinario de Biología Celular, La Plata, Buenos Aires, Argentina, ccatanesi@imbice.gov.ar

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Genetic variation of X-STRs in the Wichí population from Chaco province, Argentina

Laura Angela Glesmann ¹

Pablo Francisco Martina ²

Cecilia Inés Catanesi ¹

1: Laboratory of Molecular Genetics, Instituto Multidisciplinario de Biología Celular, La Plata, Buenos Aires, Argentina.

2: Facultad de ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Argentina.

ccatanesi@imbice.gov.ar

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XSTR Variation in Wichí.

Corresponding Author:

Cecilia I. Catanesi

Laboratory of Molecular Genetics - IMBICE

C.C. 403 - 1900 La Plata

Argentina

Tel./Fax: +54-221-421 0112

E-mail: ccatanesi@imbice.gov.ar

Abstract

The Wichí people from Chaco province inhabit the region called Impenetrable Chaqueño, where the climatic conditions are extreme. Besides the scarce communication with the main urban centers, the cultural patterns of the Wichí cause these communities to live in certain degree of isolation. The effect of this situation is an increased genetic differentiation from other populations, as it was observed through autosomal and Y chromosome markers. However, the genetic variation of X chromosome has not been fully analyzed yet. The patterns of allele distribution of different markers of X chromosome can be highly informative in comparative studies, because its special features make this chromosome a potential source to uncover ethnic differences.

The aim of this study was to assess the variation of X chromosome present in the Wichí population living around Misión Nueva Pompeya, in the Chaco province, and to identify particular variation of X-repetitive markers (X-STRs) in Chaco Amerindians. We genotyped Wichí for ten non-coding X-STRs and compared them with a Mocoví population and with published data on individuals coming from European immigration.

We found high homozygote proportion and linkage disequilibrium values for X chromosome in the Wichí population. The Wichí showed to be more distant from non-native people than the Mocoví population analyzed for comparison. We also found certain differences with Mocoví, possibly due to a higher genetic flow of the latter with non-natives. A process of genetic drift seems to be enhanced by the social behavior of the Wichí, since they live apart from other native and non-native groups. The geographic isolation and the extreme environmental conditions can also be considered as major factors contributing to the population differentiation. Although we found no new allele or undescribed variation, the whole pattern of variation for these markers gives the Wichí a particular population identity.

Most of Amerindian people living in Argentina have been driven to a drastic reduction in the number of individuals due to epidemics, forced labor, malnutrition, rigors of nomadic life, and poverty (Franceschi & Dasso 2010). In the present time, some of them live in Amerindian neighborhoods, while others live in isolated regions, far from urban centers. The latter generally retain their language, culture and traditions, especially the populations living in the western region of the province of Chaco, called “Impenetrable Chaqueño” (Argentina) (De Pompert de Valenzuela 2008; Solá 2009).

The province of Chaco is part of the vast Gran Chaco phytogeographic region, an extensive wooded plain, still inhabited by people of the Mataco-Mataguayo, Guaycurú, Lule-Vilela, Arawak and Tupi-Guaraní linguistic groups (Martínez-Sarasola 2004). These ethnic groups have no written language; therefore, the historical record prior to the arrival of the Spanish conquerors comes only from oral sources. In fact, the current written record has been mostly written by non-native authors, who gave some distortion to the information (Martínez-Sarasola 2004; Tissera 2008; Franceschi & Dasso 2010).

The Wichí people are a group of hunters, gatherers, and fishermen who inhabit the provinces of Salta, Formosa and Chaco in Argentina. At present, they are mainly located in the Impenetrable Chaqueño, where many of them still preserve some of their practices, and sometimes join the forestry activities of timber mills or work as temporary harvesters (Solá 2009).

The distinctive cultural patterns of the Wichí cause these communities to live in certain degree of isolation, which is exacerbated by the lack of means of communication with the main urban centers and the typical severe climatic conditions of the geographical region (Altamirano & Salvay 1996).

Through autosomal Short Tandem Repeats (STRs), the Wichí population of Chaco province was found to be genetically different from Toba and Pilagá populations, and relatively similar to the Wichí population from Formosa (Crossetti et al. 2008). On the other hand, the occurrence of gene flow among Wichí, Chorote, and Toba has been suggested in a study of native groups from Salta province (Dejean et al. 2004).

Our previous work with X-STRs in Wichí from Salta province showed them grouping with the Chorote population living in the same location (Catanesi et al. 2007), and significant differences were described when comparing with more distant Amerindian groups (Sala et al. 1998).

The genetic variation of X chromosome has not been fully analyzed among this and other Amerindian populations of Gran Chaco. The patterns of allele distribution of different markers of X chromosome can be highly informative in comparative studies because the special features of X chromosome make this a potential source to uncover ethnic differences (Szibor 2007, Bourgeois et al. 2009).

The aim of this study was to assess the variation of X chromosome present in the Wichí population of the Chaco province. In this way, this is the first contribution on X-STRs analysis on Wichí from Chaco province. We also intended to identify distinctive variation in Chaco Amerindians, by comparing the X-STR data from Wichí with those from a Mocoví population and from individuals coming from European immigration.

Subjects and Methods

Populations studied

Blood samples were obtained from 94 unrelated volunteer Wichí people, including 55 women and 39 men. For comparison purposes, blood samples from 32 Mocoví men were also analyzed. All donors signed an informed consent statement.

At the moment of sampling, the Wichí were living around the town of Misión Nueva Pompeya, in the province of Chaco (60.88°W, 25.44°S, Fig. 1), and the Mocoví were living at Colonia Dolores, San Justo, in Santa Fe province (60.31°W, 30.38°S, Figure 1).

DNA extraction

Genomic DNA was obtained from peripheral blood by the cell lysis technique with Proteinase-K, and by using either phenol-chloroform or lithium chloride extraction, as described elsewhere.

Genotyping

Samples were genotyped for ten non-coding X-STR markers (DXS8378, DXS9902, DXS7132, DXS9898, DXS6809, DXS7133, DXS6789, GATA172D05, GATA31E08, and DXS7423) in a single multiplex reaction, according to Gusmão et al. (2008). PCR fragments were separated and detected through capillary electrophoresis in an ABI PRISM 3130 genetic analyzer (Applied Biosystems, Foster City, USA). Allele assignment was confirmed by participating in the GHEP-ISFG control exercises 2010-2012.

Statistical analyses

Allele frequencies, gene diversities, exact test of Hardy-Weinberg equilibrium (only for female samples), molecular variance (AMOVA), and pairwise genetic distances (FST-RST) were analyzed with Arlequin v. 3.5 (Excoffier et al. 2010). For comparison with the Wichí and Mocoví samples (this work) we selected Argentinean data from Gusmão et al. (2009) including Buenos Aires province (N= 383), and three provinces geographically close to Chaco province, Córdoba (N=132), Entre Ríos (N=28), and Misiones (N=44).

For the linkage disequilibrium (LD) analysis, exact test was calculated for all possible pairs of X-STRs in the Wichí, Mocoví, and Buenos Aires haplotypes (only male). In order to correct the possible influence of multiple testing, D' values of linked markers were compared with a mean D' baseline for each population, assessed as the average of all unlinked markers, as in Leite et al. 2009. These calculations were also performed with Arlequin software.

Population stratification was tested with the Bayesian model implemented in Structure v. 2.1 (Pritchard et al. 2000) for the Wichí, Mocoví, and Buenos Aires data, using the geographic location as the criterion of sample grouping, and assuming an admixture model. We performed independent runs of 500 iterations for each K value between 2 and 5, following a burn-in period of 10,000.

Results

The allele and genotype frequencies of the Wichí and Mocoví populations for the ten X-STRs are shown in Tables 1 and 2. It can be seen that the modal allele of each marker generally showed a much higher frequency than the rest of the alleles, and it is remarkable that for all markers except for DXS6789, the modal genotype was a homozygous one. The effective allele number was always lower than the observed allele number. The average gene diversity over ten loci was 0.61464 +/-0.32538 for Wichí, and 0.64812 +/-0.38089 for Mocoví (values for each separate marker are in Tables 1 and 2 respectively). Only three markers (DXS9898, DXS6789, and GATA172D05) fit the Hardy-Weinberg equilibrium (Table 1) with 21% as the highest difference between observed and expected heterozygosity values.

The Wichí LD exact test rendered significant values for three pairs of X-STRs: DXS6809-DXS6789 ($P=0.01732 \pm 0.00097$), DXS6789-GATA172D05 ($P=0.03762 \pm 0.00127$), and DXS8378-GATA31E08 ($P=0.04831 \pm 0.00076$), and the D' values for the mentioned pairs were between 0.73200 and 0.77860, exceeding the baseline D' of 0.62069. The Mocoví LD analysis was significant for four pairs of markers: DXS7132-DXS6789 ($P=0.00623 \pm 0.00082$), DXS9898-DXS6809 ($P=0.00960 \pm 0.00076$), DXS9898-GATA172D05 ($P=0.00000 \pm 0.00000$), and DXS8378-DXS6789 ($P=0.03059 \pm 0.00109$). But the last pair of markers did not exceed the D' baseline of 0.67400 (exceeding values between 0,78866 and 0,87694). On the contrary, among the three pairs of markers with significant values of LD of Buenos Aires data, only one pair exceeded D' baseline (data not shown).

The two Amerindian groups (Wichí and Mocoví) shared modal alleles for DXS8378, DXS9902, DXS7132, DXS7133, DXS6789, GATA31E08 and DXS7423 markers, but were not coincident for the other three markers. The Wichí shared five modal alleles with Buenos Aires data by Gusmão et al. (2009) (DXS9898, DXS7133, DXS6789, GATA172D05, DXS7423). Besides, certain Wichí and Mocoví alleles for DXS6809 and DXS7133 were not found among Buenos Aires people.

We performed an AMOVA analysis for the ten markers using FST and RST distances, which resulted in 3.75% (FST) and 6.18% (RST) of variation among Wichí, Mocoví, and samples from the provinces of Buenos Aires, Córdoba, Entre Ríos, and Misiones from Gusmão et al. (2009). On the other hand, when we grouped natives (Wichí-Mocoví) and non natives (including the samples from the four mentioned provinces) the comparison showed higher values: 6.47% (FST) and 12.26% (RST). The FST and RST values for the whole set of markers are detailed in Table 3.

The clustering results (Figure 2) showed partial differentiation with the data from Buenos Aires, while it did not clearly separate the two Amerindian groups. The clustering did not fit the geographic labels, grouping the Wichí and the Mocoví together with some individuals from Buenos Aires.

Discussion

The Wichí community included in this work inhabit the Impenetrable Chaqueño region, near Misión Nueva Pompeya town, which was founded in 1900. Before its foundation, a Franciscan mission was already established, for evangelizing the Wichí community. The mission grouped about 76 Wichí families who, at that moment, began to work in the mills and farms in the frontline of Salta province (De Pompert de Valenzuela 2008). The lands corresponding to the mission are owned today by the native people, while the non-native people, mainly coming from European immigration, live closer to the center of the town.

The Mocoví community included for comparison is located in Santa Fe province. In the 1960s, the Mocoví from Chaco and Santa Fe provinces started a process of migration to urban centers, a behavior also adopted by the Toba (Qom) population, but not by the Wichí. Mocoví people arrived in large cities like Santa Fé, Rosario, La Plata, and Buenos Aires, and settled there with certain social and cultural cost, since they changed some of their habits, learned the Spanish language, and have to take their children to common schools (Franceschi & Dasso 2010).

The Wichí, as well as the Native people of Gran Chaco region in general, have been previously analyzed for autosomal and Y chromosome repetitive polymorphisms (Tourret et al. 1999, 2000, Demarchi & Mitchel 2004, Catanesi et al. 2006, Crossetti et al. 2008, Demarchi 2009, Parolin & Carnese 2009) and a marked reduction in genetic variability has been found. In the present study, we found a similar situation for repetitive markers in X chromosome, where the modal alleles showed frequencies over 40%-70% and some rare alleles had probably been lost. Over 50% of the alleles described for Buenos Aires were found in the Wichí population, although some of them in a very low frequency, suggesting a loss of variability. The AMOVA analysis and the significant F_{ST}/R_{ST} values found in the comparison with non-native populations from three provinces neighboring Chaco (Table 3), might be caused by this reduction of variation.

The departure from the Hardy-Weinberg equilibrium in seven markers is clearly caused by the high proportion of homozygous genotypes. A high level of homozygosity in Wichí women might be interpreted as the consequence of null alleles not detected, but this possibility can be discarded because we found a similar allele distribution among men (hemizygotic) and we were able to genotype all of them. Moreover, an excess of homozygosity has also been described among the Wichí population for autosomal repetitive markers (Tourret et al. 1999). On the other hand, the values of LD found in Wichí people, compared to non-native data would suggest certain degree of consanguinity.

An explanation of the high homozygosity and LD might be related to their way of life. The Wichí people of Chaco province currently live in community settlements around the region of Misión Nueva Pompeya, within allocated territories. Extensive matrilineal families form a household, where individuals share certain degree of consanguinity and can be considered far relatives (Franceschi & Dasso 2010). The households are exogamic among them, and to some extent matrilineal, since the man usually moves to the household where his wife lives, and in this way, a related extensive family can emerge and establish in the same area (Franceschi & Dasso 2010). This way of life may be driving the Wichí population to a

higher level of homozygosity. However, it is possible that different households might be slightly different from each other in their allele and genotype frequencies, causing a population sampling effect or substructure, as it was proposed by Diegoli & Coble (2011) even for non-native populations. In fact, our previous work on X-STRs in Gran Chaco showed the existence of a genetic structure separating the Wichí living in Salta province from the Mocoví population living in Santa Fe province (Catanesi et al. 2007), while the present work showed certain similarities between the Wichí living in Chaco province and the same Mocoví population, as seen in Figure 2, where differences between the two Amerindian groups are fewer than with non-native people from Buenos Aires. The different patterns of variation in Salta and Chaco populations suggest a geographic differentiation within the two Wichí communities, possibly due to local genetic flow within Chaco province. In this way, Leite et al. (2009) supports the importance of geographic distribution for the genetic structuring of Amerindian populations.

The average Wichí gene diversity was similar to that found in Mocoví. However, gene diversity differed for some of the individual markers between the two Amerindian groups (see Tables 1 and 2), in agreement with a process of genetic drift currently acting on both native groups. This process probably contributed to some differences between them, as suggested by the significant values found only in the analysis of F_{ST} (marking drift or migration processes) but not of R_{ST} (marking mutational processes). Moreover, it is considered that the Wichí and Mocoví populations passed through a drastic reduction of their effective population sizes in the recent past, reinforcing a possible action of genetic drift (Martínez Sarasola 2004, Demarchi 2009, Glesmann et al. 2011).

Conclusions

This is the first contribution of X-STR marker analysis in a Wichí community from Chaco province. The Wichí population living around Misión Nueva Pompeya presents a particular genetic diversity for X chromosome, with high homozygote proportion and linkage disequilibrium values. These findings might

be caused by a process of genetic drift that seems to be enhanced by their social behavior, since they live in households apart from other native and non-native groups. The geographic isolation and the extreme environmental conditions can also be considered as major factors contributing to the population differentiation, which might be higher than for the Wichí living in Formosa (Crossetti et al. 2008) and Salta (Goicoechea et al. 2001, Dejean et al. 2004) provinces.

Although we found no new allele or variation undescribed in other groups, the whole pattern of variation for these markers gives the Wichí a sense of population identity.

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C. Catanesi is a CONICET researcher, and P. Martina and L. Glesmann are CONICET fellows.

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Appendix

Table 1. Allele frequency distribution, gene diversity with standard deviation (GD), and P values for Hardy-Weinberg Equilibrium test (P-HWE) for the Wichí sample from Misión Nueva Pompeya. Asterisks indicate significant P-HWE values ($\alpha=0.05$).

DXS8378	Allele frequency	DXS9902	Allele frequency	DXS7132	Allele frequency	DXS9898	Allele frequency	DXS6809	Allele frequency
10	0.1409	11	0.1258	11	0.0265	8.3	0.0066	30	0.1060
11	0.6443	12	0.5298	12	0.0397	10	0.0066	31	0.0132
12	0.1745	13	0.1192	13	0.3576	11	0.0993	32	0.0927
13	0.0336	14	0.1921	14	0.3113	12	0.4437	33	0.2781
14	0.0067	16	0.0331	15	0.1987	13	0.2450	34	0.3576
GD	0.6146 +/- 0.3253	GD	0.5283 +/- 0.4913	16	0.0530	14	0.1988	35	0.0927
P-HWE	0.00005*	P-HWE	0.00373*	17	0.0132	GD	0.6741 +/- 0.5746	36	0.0463
				GD	0.742876 +/- 0.612630	P-HWE	0.04756	37	0.0067
				P-HWE	0.00003*			38	0.0067
								GD	0.7938 +/- 0.6404
								P-HWE	0.00378*
DXS7133	Allele frequency	DXS6789	Allele frequency	GATA172D05	Allele frequency	GATA31E08	Allele frequency	DSX7423	Allele frequency
7	0.02	15	0.04	6	0.1788	9	0.0265	14	0.1589
8	0.0397	16	0.0794	7	0.0132	10	0.1391	15	0.5431
9	0.7152	19	0.0132	9	0.0332	11	0.053	16	0.0728
10	0.1126	20	0.543	10	0.404	12	0.7086	17	0.2252
11	0.0993	21	0.298	11	0.1854	13	0.0464	GD	0.6328 +/- 0.5514

12	0.0132	22	0.0132	12	0.1854	14	0.0264	P-HWE	0.00169*
GD	0.4266 +/- 0.4303	23	0.0132	GD	0.7565 +/- 0.6201	GD	0.5003 +/- 0.4748		
P-HWE	0.00037*	GD	0.6197 +/- 0.5440	P-HWE	0.18547	P-HWE	0.00031*		
		P-HWE	0.37768						

Table 2. Allele frequency distribution, and gene diversity with standard deviation (GD) for the the Mocoví from Santa Fe, sampled for comparison.

DXS8378	Allele frequency	DXS9902	Allele frequency	DXS7132	Allele frequency	DXS9898	Allele frequency	DXS6809	Allele frequency
10	0.406	11	0.1562	11	0.0625	8.3	0.0312	31	0.1875
11	0.4375	12	0.7813	12	0.0312	10	0.0312	32	0.0937
12	0.1562	13	0.0625	13	0.2500	12	0.3438	33	0.5938
GD	0.6327 +/- 0.5642	GD	0.3729 +/- 0.4066	14	0.2813	13	0.5000	34	0.0937
				15	0.2188	14	0.0626	36	0.0313
				16	0.1250	15	0.0312	GD	0.5544 +/- 0.5192
				17	0.0312	GD	0.6167 +/- 0.5549		
				GD	0.7647 +/- 0.6391				
DXS7133	Allele frequency	DXS6789	Allele frequency	GATA172D05	Allele frequency	GATA31E08	Allele frequency	DSX7423	Allele frequency
9	0.5333	16	0.0625	6	0.0312	9	0.0625	14	0.4062
10	0.0667	19	0.0625	8	0.0625	10	0.0312	15	0.4062
11	0.4000	20	0.4375	9	0.0312	11	0.1875	17	0.1876
GD	0.5701 +/- 0.5297	21	0.3438	10	0.1563	12	0.6563	GD	0.6720 +/- 0.5867
		22	0.0937	11	0.5938	13	0.0625		
		GD	0.6370 +/- 0.5677	12	0.1250	GD	0.5543 +/- 0.5182		
				GD	0.5947 +/- 0.5431				

Table 3. *Fst/Rst* values over ten X-STR loci. Asterisks indicate significant *P* values ($p < 0.005$ with Bonferroni correction)

FST RST	Wichí	Mocoví	BsAs	Córdoba	Entre Ríos	Misiones
Wichí	-	0.04982 *	0.07484 *	0.07593*	0.09571*	0.10063*
Mocoví	0.02846	-	0.06598*	0.06152*	0.09926*	0.07857 *
Buenos Aires	0.12668*	0.12234*	-	0.00202	0.00449	0.00500
Córdoba	0.12104*	0.11354*	-0.00054	-	0.00329	0.00875*
Entre Ríos	0.18278*	0.19098*	0.00804	0.00010	-	0.01940*
Misiones	0.15822*	0.12805*	0.00225	0.00213	0.01308	-

Figure legends:

Figure 1: Geographical localization of the two Amerindian populations included in this work. The province of Buenos Aires is also included for comparison

Figure 2: Clustering obtained with Structure for Wichí, Mocoví and Buenos Aires samples

Figure 1.

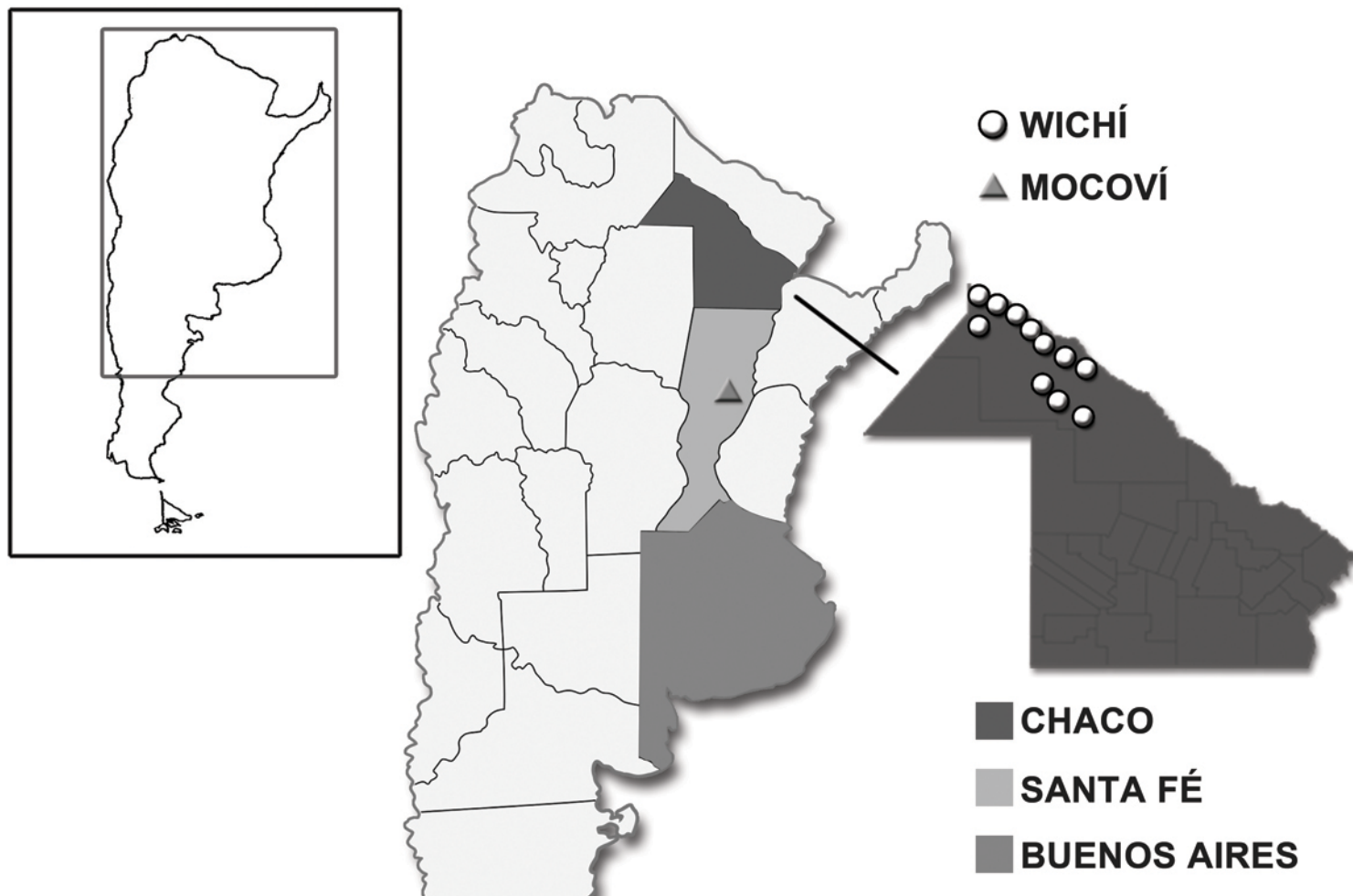


Figure 2.

