Analysis of Uniparental Lineages in Two Villages of Santiago del Estero, Argentina, Seat of Pueblos de Indios *in Colonial Times*

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Abstract Based on the analysis of the mitochondrial control region and seven biallelic markers of the Y chromosome, we investigated the genetic composition of two rural populations of southern Santiago del Estero, Argentina, that were seats in colonial times of *pueblos de indios*, a colonial practice that consisted of concentrating the indigenous populations in organized and accessible settlements, to facilitate Christianizing and policing.

We found the Native American Y chromosome haplogroup Q1a3a in only 11% (3 of 27) of the males. Haplogroup R, common in European populations, is the most frequent haplogroup in Santiago del Estero (55%). In contrast, the persistence of Native American maternal lineages is extremely high (95%). This finding is most likely due to the low incidence in that region of the 20th-century European wave of migration and to the existence of pueblos de indios from 1612 to the first decades of the 19th century. In contrast to archeological records that suggest Santiago del Estero late pre-Hispanic groups were strongly influenced by the Andean world, we did not find genetic evidence in support of significant gene flow. On the other hand, these populations share many mitochondrial DNA hypervariable region I (HVRI) haplotypes with other populations from the Sierras Pampeanas (particularly with Córdoba) and the Gran Chaco regions.

Santiago del Estero, founded by Francisco de Aguirre in 1553, is the oldest city that is definitely rooted in the current territory of Argentina. Located on the border between the western farmers of the Andean valleys and the hunter-gatherers of the Gran Chaco, this settlement was part of the Spanish colonization process of the northwestern region of Argentina during the 16th century.

The landscape of Santiago del Estero Province is dominated by plains, crossed

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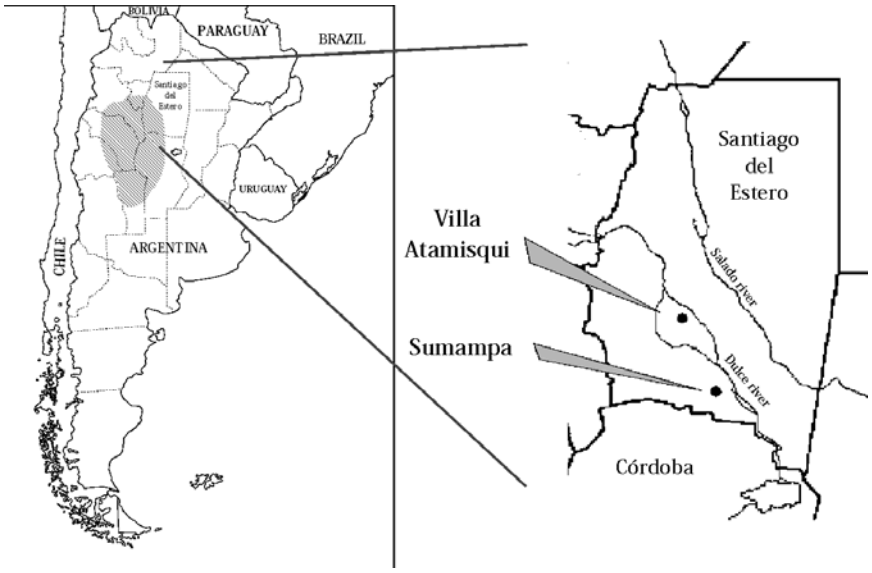

Figure 1. Map of the Southern Cone of South America and geographic location of the populations studied in Santiago del Estero Province. The shaded area corresponds approximately to the Sierras Pampeanas geographic region.

diagonally by the Dulce and Salado Rivers, which originate in the Andean foothills. The south is the only portion of the province that includes low hills, connected to the Sierras Pampeanas, a mountain system that occupies the central-northwestern portion of Argentina (see Figure 1).

In pre-Hispanic times, the valleys between these rivers were centers of sedentary groups related to the Andean world (Bonnin and Laguens 2000; Taboada and Angiorama 2010). Archaeological evidence suggests that these groups collaborated with the Inca Empire in the late pre-Hispanic period (Palomeque 2000).

Despite this unquestionable cultural influence, craniometric evidence suggests low biological affinities between Santiago del Estero and ancient Andean populations that inhabited northwestern Argentina. However, a close resemblance was observed with other human groups that inhabited the central region of Argentina, in the current territory of Córdoba Province (Cocilovo 1984; Cocilovo and Di Rienzo 1984–1985; Fabra and Demarchi 2012).

The historical records show that the Spanish Conquest and colonization began a series of transformations that affected the whole "Indian" world. While most of the populations were unstructured and even "disappeared" quickly (Piana 1992), others survived and persisted reduced in *pueblos de indios* (Indian villages) within the system of colonial domination (Castro Olañeta 2003). As expressed by Faberman (2008), the Indian villages under the encomienda regime became

colonial corporations as pueblos de indios, when Francisco de Alfaro's ordinances were enacted in 1612. The most important measures were the creation of *reducciones* with communal lands and of traditional Indian authorities and alcaldes (village officials), as well as the replacement of the personal service for *tributo* (taxes). Briefly, this colonial practice consisted in the concentration of the native population in organized and accessible settlements, to facilitate both Christianizing and policing.

In Argentina, the first half of the 19th and beginning of the 20th century was marked by a population expansion as result of massive European immigration (Pellegrino 2002). Between 1880 and 1935, about 3.4 millions of Europeans, mainly from Spain and Italy, arrived to the ports of Buenos Aires. It is estimated that between 50% and 75% of them settled in the country, mainly in the cities of the Pampean and Patagonian regions (Sánchez Albornoz 1994). In contrast, this massive European migration had little impact in Santiago del Estero. In 1928, only 3.5% of its population were foreigners (Grosso 2008).

Molecular markers, particularly those located on mitochondrial DNA (mtDNA) and the nonrecombinant portion of the Y chromosome, are useful for the study of the genetic composition and biological history of neo-American populations, in which it is possible to infer the substantial contribution of the Native American component but where its members have lost their ethnic identity as a result of dramatic historical, cultural, and social changes (García and Demarchi 2009). Thus, it is possible to observe the preservation of a substantial proportion of the original gene pool in contemporary populations, despite the disappearance of a large number of American ethnic groups after centuries of European colonization (Sans 2000; Rocco et al. 2002; Wang et al. 2008; García and Demarchi 2009; Pauro et al. 2010; Bobillo et al. 2010; Corach et al. 2010; Cardoso et al. 2013).

Currently, there is no information about the incidence and distribution of parental Native American lineages for the human population of Santiago del Estero. This province of northwestern Argentina has a large archeological tradition and documented settlements of several ethnic groups that survived for centuries after the arrival of the Spaniards.

In this study we investigated the genetic composition of two rural populations of southern Santiago del Estero, Villa Atamisqui and Sumampa, based on the analysis of mtDNA sequences and Y chromosome markers. Our particular interest in the study of the genetic history of these two villages lies in the fact that both populations were seats in colonial times of pueblos de indios. Additional interest arises in the fact that the census records of 1778, ordered by King Carlos III, were particularly contrasting for these two parishes: while the Soconcho parish (currently Villa Atamisqui) was composed of an Indian majority, most of the inhabitants of Sumampa were of African origin (Grosso 2008).

The objectives of this study were to investigate (1) whether or not the contrasting composition of both populations, recorded in the census of 1778, would be reflected in the genetic composition of the contemporary populations; (2) the proportion of Native American lineages that still survive in these villages; (3)

whether or not the pattern of biological relationships, observed from craniometric analyses, relating Santiago del Estero and the ancient populations of Córdoba, is supported by molecular evidence; and (4) the phylogeographic and phylogenetic relationships of the Santiago del Estero population with other Native American groups from the Southern Cone of South America, based on the analysis of mtDNA hypervariable region I (HVRI).

Materials and Methods

The Sample. A total of 85 samples from unrelated individuals were collected at public hospitals of Sumampa (S 29.38°, W 63.47°; $n = 29$, 11 males and 18 females) and Villa Atamisqui (S 28.48°, W 63.8°; $n = 56$, 16 males and 40 females). All participants were informed of the objectives of this study and consented to donate buccal swabs to be used anonymously in the execution of this nonprofit scientific investigation. With the aim of defining and limiting the sample, we considered only individuals with at least three generations at the specific birthplaces. The information gathered in the field regarding the birthplaces of subjects and their parents indicated that the inhabitants of these villages present low to moderate mobility, limited to their region of origin.

In order to investigate the affinities in mtDNA lineages distribution between the studied populations and other Native American populations from the Southern Cone of South America, we selected from the literature 38 population samples representing different geographic-ecological regions (Table 1).

Laboratory Methods. Genomic DNA was extracted from cheek swabs using the Accuprep Genomic DNA Purification Kit (GenBiotech). The 27 male samples were analyzed with seven biallelic markers located in the nonrecombinant region of the Y chromosome. These polymorphisms were defined by the presence or absence of the characteristic mutation for the following markers: M3 (Underhill et al. 1996), M207 (Su et al. 1999), M168 and M9 (Underhill et al. 2001), M89 (Karafet et al. 1999), M2 (Seielstad et al. 1994), and YAP (Hammer 1995). All polymorphisms were analyzed using standard polymerase chain reaction (PCR) protocols with minor modifications and then digested with restriction enzymes (except for the insertion YAP). The amplification strategy was carried out following a hierarchical amplification protocol (Hammer et al. 2001; Jobling et al. 2004; Karafet et al. 2008), which means that each subject was not genotyped for all markers. The genotyped samples were assigned to haplogroups, useful for identifying geographic origins (Karafet et al. 2008; Jobling and Tyler-Smith 2003).

The mtDNA noncoding control region was amplified for all 85 samples using the specific primers F15811 (5′ TCATTGGACAAGTAGCATCC 3′) and R698 (5′ GCATGTGTAATCTTACTAAGAG 3′). The amplification reaction was performed in a Biometra T-Personal thermocycler in a volume of 50 μl under the following conditions: an initial denaturation step of 94°C for 5 min, followed by 40 cycles

with temperatures of 94°C for 1 min, 52°C for 1 min, and 72°C for 1.5 min, and a final extension step of 72°C for 5 min. Verification and quality control of PCR amplification were performed by gel electrophoresis on 2% agarose, stained with GelStar (Lonza), and visualized with ultraviolet light. The amplified products were sent to Macrogen Inc. (Seoul, Korea) for purification and automatic sequencing, using primers F15811 and F16475 (5′ TAGCTAAAGTGAACTGTATCC 3′). The sequences were corrected manually and then aligned and compared with the revised Cambridge Reference Sequence using the program MEGA, version 4.0 (Tamura et al. 2007). Haplogroups were defined by the presence of specific mutations in the control region following Tamm et al. (2007) for Native American lineages, and HaploGrep (Kloss-Brandstaetter et al. 2010) and Phylotree (van Oven and Kayser 2008) for nonnative American lineages.

Data Analysis. Heterogeneity in mtDNA and Y chromosome haplogroups distribution between both Santiago del Estero samples was evaluated using the exact test of population differentiation (Raymond and Rousset,1995). Population genetic structure was further investigated by mean of the analysis of molecular variance (AMOVA) (Excoffier et al. 1992), as implemented in the program Arlequin, version 3.11 (http://cmpg.unibe.ch/software/arlequin3). This program was also used to calculate Kimura two-parameter pairwise genetic distances (Kimura 1980), with nonzero significance evaluated by a randomization test. From the distance matrix, a genetic map was constructed by means of multiple dimensional scaling (Kruskal 1964). For the analyses including Santiago del Estero and the other 38 Southern Cone population samples (Table 2), we considered the mtDNA sequences of HVRI between nucleotide pairs (np) 16051 and np 16362.

A median-joining network for each haplogroup was constructed using the technique of Bandelt et al. (1995) with the program Network (version 4.6.1.1), including mtDNA sequences between np 16027 and np 16362 (HVRI) from the 13 populations of Argentina (Table 1). After a careful screening of published data representing populations from the Southern Cone, we observed that the Santiago del Estero samples only share haplotypes with other Argentinian populations, excepting in the case of nodal haplotypes. As the full median network can contain unnecessary median vectors and links, it was subjected to a maximum parsimony analysis to resolve ambiguities in the dataset, using the three criteria proposed by Crandall and Templeton (1993), frequency, topology, and geography, based on predictions from the coalescent theory.

Results

Paternal Lineages. The Native American haplogroup Q1a3a is present in only 11.1% (3/27) of the males of the total sample (1/11 from Sumampa, and 2/16 from Villa Atamisqui). Haplogroup R, the most frequent haplogroup in Europe (Jobling and Tyler-Smith 2003), and in Argentinian urban populations (Corach et al. 2010;

Table 1. Southern Cone Populations Included in the Analysis, by Geographic Region

POPULATION	ABBREVIATION	*n*	REGION
Santiago del Estero	SGO	81	Sierras Pampeanas, Argentina
Córdoba	CBA	180	Sierras Pampeanas, Argentina
San Luis	SL	60	Sierras Pampeanas, Argentina
Wichí–Formosa	WFOR	67	Gran Chaco, Argentina
Wichí–Chaco	WCH	32	Gran Chaco, Argentina
Toba–Chaco	TCH	43	Gran Chaco, Argentina
Toba–Formosa	TFOR	24	Gran Chaco, Argentina
Pilagá	PIL	38	Gran Chaco, Argentina
Catamarca	CAT	25	Sierras Pampeanas, Argentina
Azampay–Catamarca	AZA	118	Sierras Pampeanas, Argentina
Guarani–Misiones	GUAM	121	Subtropical Forests, Argentina
Mapuche	MAPAR	90	Patagonia, Argentina
Tehuelche	TEH	29	Patagonia, Argentina
Fueguinos	GUE	36	Patagonia, Chile
Mapuche	MAPCH	53	Patagonia, Chile
Pehuenche	PEH	66	Patagonia, Chile
Kawesqar	KAW	13	Patagonia, Chile
Atacama	ATA	28	Central Andes, Chile
Aymara	AYMC	39	Central Andes, Chile
Huilliche	HUI	58	Patagonia, Chile
Guaraní M´byá	MBYA	24	Subtropical Forests, Brazil
Guaraní Kaiowá	KAI	120	Subtropical Forests, Brazil
Guaraní Ñandeva	NAN	56	Subtropical Forests, Brazil
Kaingang Rio	KRIO	53	Subtropical Forests, Brazil
Kaingang Paraná	KPAR	21	Subtropical Forests, Brazil
Ayoreo	AYO	91	Gran Chaco, Paraguay
Aché	ACHE	63	Subtropical Forests, Paraguay
Ignacianos	IGN	15	Lowlands, Bolivia
Movima	MOV	12	Lowlands, Bolivia
Trinitare	TRI	11	Lowlands, Bolivia
Yuracaré	YUR	15	Lowlands, Bolivia
Aymara–Titicaca	AYM	96	Central Andes, Bolivia
Quechuas–Potosi	QUE	93	Central Andes, Bolivia
Arequipa	ARE	22	Central Andes, Peru
Tayacaja	TAY	60	Central Andes, Peru
Quechua–Puno	QPNO	30	Central Andes, Peru
Aymara–Puno	APNO	14	Central Andes, Peru
Quechuas–Titicaca	QTT	37	Central Andes, Peru
Aymara–Titicaca	ATT	20	Central Andes, Peru

LATITUDE (S)	LONGITUDE (W)	REFERENCE
28.75	63.38	Present study
31.23	64.11	García 2011
32.61	65.24	García 2011
24.00	62.20	Cabana et al. 2006
24.60	61.50	Cabana et al. 2006
26.00	60.60	Cabana et al. 2006
26.20	58.30	Cabana et al. 2006
24.40	59.60	Cabana et al. 2006
28.28	65.46	Tamm et al. 2007
27.36	67.05	Ramallo 2009
25.83	54.33	Sala et al. 2010
40.36	68.82	Ginther et al. 1993; de Saint Pierre et al. 2012
42.21	66.36	de Saint Pierre et al. 2012
55.02	67.40	Moraga et al. 2000; de Saint Pierre et al. 2012
39.29	72.80	Moraga et al. 2000; de Saint Pierre et al. 2012
37.43	71.16	Moraga et al. 2000; de Saint Pierre et al. 2012
53.08	70.55	Moraga et al. 2000
23.45	68.17	de Saint Pierre et al. 2012
17.22	68.90	de Saint Pierre et al. 2012
40.50	73.35	de Saint Pierre et al. 2012
25.18	52.32	Marrero et al. 2007
23.06	55.12	Marrero et al. 2007
23.48	54.30	Marrero et al. 2007
27.00	52.00	Marrero et al. 2007
24.30	55.50	Marrero et al. 2007
19.00	60.30	Dornelles et al. 2004
23.70	55.90	Schmitt et al. 2004
15.10	66.40	Bert et al. 2004
14.26	65.53	Bert et al. 2004
14.00	65.00	Bert et al. 2004
17.00	65.00	Bert et al. 2004
16.30	68.80	Gaya-Vidal et al. 2011
19.30	65.44	Gaya-Vidal et al. 2011
16.23	71.32	Fuselli et al. 2003
12.23	74.52	Fuselli et al. 2003
15.50	70.01	Lewis et al. 2007
15.50	70.01	Lewis et al. 2007
15.88	69.92	Barbieri et al. 2011
15.85	69.96	Barbieri et al. 2011

Table 2. Native American mtDNA Haplogroup Distributions in the Population Samples Used in This Study

HAPLOGROUP	SUMAMPA	VILLA ATAMISQUI	TOTAL
A2	0.207 (6)	0.161 (9)	0.185 (15)
B2	0.069 (2)	0.107 (6)	0.098 (8)
C1	0.310 (9)	0.482 (27)	0.444 (36)
D1	0.379 (11)	0.196 (11)	0.272 (22)

Numbers in parenthesis are the absolute frequencies. Exact p-value = 0.245 ± 0.006 (after 100,000 Markov steps).

Bailliet et al. 2011), is also frequent in Sumampa and Villa Atamisqui (63.6% and 50%, respectively). Haplogroup F, common in both European and Middle Eastern/North African populations, is well represented in Villa Atamisqui (6/16) but not in Sumampa (1/11). Finally, two individuals from Sumampa carry the haplogroup DE, but do not represent the derivative state for M2, being therefore most likely of European origin. Observed differences in Y Chromosome haplogroups distribution between samples are not statistically significant ($p = 0.156$).

Maternal Lineages

Mitochondrial Haplogroups Distributions. Two individuals from Villa Atamisqui and one from Sumampa represent European lineages, whereas only one subject, from Villa Atamisqui, represents mtDNA of African origin. The other 81 subjects possess Native American mtDNAs. It is interesting to highlight the extremely high incidence of Native American mitochondrial haplogroups in these two rural towns (96.6% in Sumampa, and 94.6% in Villa Atamisqui), particularly in contrast with what we found for paternal haplogroups. Table 2 presents the Native American mtDNA haplogroups distributions by sample. The most frequent haplogroups in both samples are C1 and D1. Although haplogroup C1 is more frequent in Villa Atamisqui and haplogroup D1 has the highest incidence in Sumampa, differences are not statistically significant ($p = 0.245$). For this reason, in further analyses both samples were combined and considered as one, Santiago del Estero population (SGO).

Analysis of mtDNA Sequences. Fifty-nine different haplotypes were found among the 81 subjects that possess Native American mtDNAs (see appendix 1). Below we provide a description and comments about the distribution and phylogeographic relationships of the mtDNA haplotypes found in Santiago del Estero and 12 other populations from Argentina, based on HVRI sequences (Table 3). Networks for haplogroups C1 and D1 are presented in Figures 2 and 3. Networks for haplogroups A2 and B2 are not shown because they do not present any geographic structure that could help in clarifying phylogeographic relationships.

Table 3. Haplotypes Representing the HVRI mtDNA Sequences between np 16027 and np 16362, Present in the Population Samples of Santiago del Estero and Shared with Other Populations from Argentina

HAPLOGROUP/ HAPLOTYPE	*n*	SHARED WITH	POLYMORPHIC SITES
A2			
h1 (nodal)	8	Most of populations	16111 16223 16290 16319 16362
h2	1	1 CBA, 5 AZA	16111 **16189** 16223 16290 16319 16362
h3	4	4 CBA, 6 MAP, 1 PIL	16223 16290 16319 16362
h4	1	—	16111 16290 16319 16362
h5	1	—	**16086** 16111 16223 16290 16319 16362
B2			
h6	1	—	**16092 16145 16156 16157** 16189 16217 **16295**
h7	1	3 CBA	16189 16217 **16357**
h8 (nodal)	3	Most of populations	16189 16217
h9	1	—	**16145 16156 16157** 16189 16217 **16362**
h10	1	—	16189 16217 **16247 16261**
h11	1	—	**16092 16126** 16189 **16214** 16217 **16355A**
C1			
h12	11	12 CBA, 1 CAT, 3 WFOR	**16051** 16223 16298 16325 16327
h13 (nodal)	7	Most of populations	16223 16298 16325 16327
h14	5	1 TFOR	**16136** 16223 16298 16325 16327
h15	2	3 CBA	**16051 16129** 16223 16298 16325 16327
h16	2	4 CBA, 1 WFOR	**16092** 16223 16298 16325 16327
h17	1	—	16223 16298 16325 16327 **16343**
h18	1	—	**16037 16092** 16223 **16260** 16298 16325 16327
h19	1	—	**16051 16189** 16223 16298 16325 16327
h20	1	—	16223 **16291** 16298 16325 16327
h21	2	3 WFOR	**16051** 16223 **16259 16271** 16298 **16311** 16325 16327
h22	2	—	**16136** 16223 **16256** 16298 16325 16327
h23	1	—	**16172** 16298 16325 16327
D1			
h24 (D1j)	11	26 CBA, 1 MAP, 6 CAT, 1 PIL, 2 WFOR	16223 **16242 16311** 16325 16362
h25 (D1j)	3	—	16223 **16242 16286 16311** 16325 16362
h26	5	3 CBA, 1 PIL, 2 WFOR	16223 **16311** 16325 16362
h27 (D1j)	1	2 CBA	**16157** 16223 **16242 16311** 16325 16362
h28	1	2 CBA, 1 MAP	**16126** 16223 16325 16362
h29 (nodal)	1	Most of populations	16223 16325 16362

Boldface indicates polymorphic sites that differ from the nodal motif.

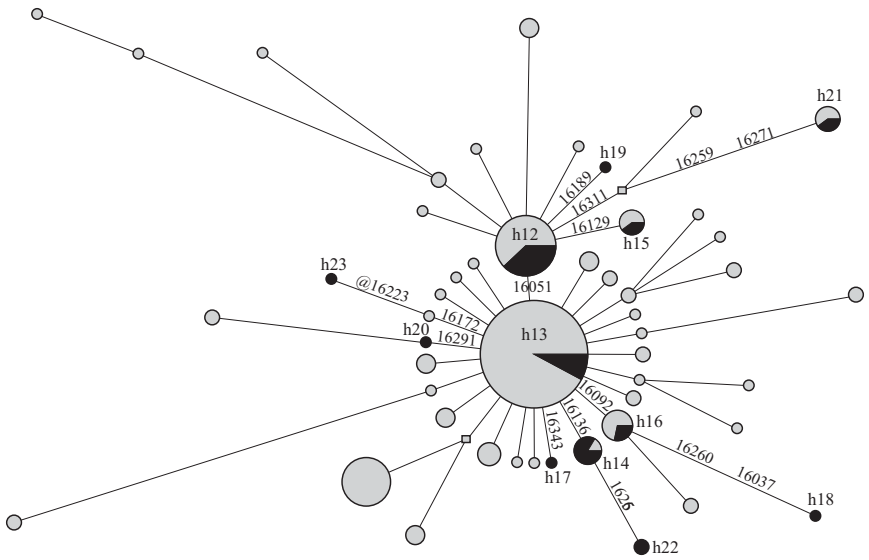

Figure 2. Median-joining network for haplogroup C1 of 230 haplotypes observed in population from different regions of Argentina. mtDNA motifs of hypervariable region I between 16,027 and 16,362 positions were used to draw the tree. Each circle represents a different haplotype, and the relative size reflects the frequency of each haplotype. The gray squares represent hypothetical haplotypes not found in this study. The black circles are the haplotypes present in Santiago del Estero populations. The nodal haplotype h13 is characterized by 16223–16298–16325–16327 mutation positions. Haplotypes present in individuals from Santiago del Estero are detailed in Table 3.

Haplogroup A2. Most of the individuals (8 of 15) represent the nodal motif A2. Two haplotypes are shared with other populations: h2 shows a transition in site 16189 (considered a hotspot; Soares et al. 2009), and h3 lacks the diagnostic site 16111, a pattern already observed in individuals from Córdoba (García 2011), Mapuche individuals from the Argentinian Patagonia (Ginther et al. 1993), and one Pilagá from the Gran Chaco region (Cabana et al. 2006).

Haplogroup B2. Three individuals present the nodal haplotype, and the other five present several mutational steps from the nodal. One haplotype (h7) is shared with three individuals from Córdoba (García 2011). Partial matches for h6 and h9 were found in six individuals from Azampay (province of Catamarca; Ramallo 2009) and in 7 of the 19 ancient samples from the Pampa Grande site (province of Salta), dated at 1,300 BP (Carnese et al. 2010; not included on the network). Two other partial matches (at one mutational step) were found for h11 in one Toba and one Wichí from the Gran Chaco (Cabana et al. 2006).

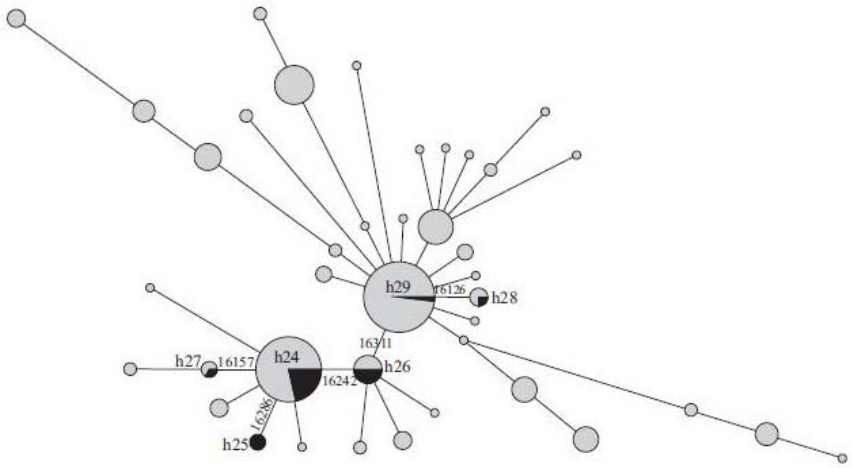

Figure 3. Median-joining network for haplogroup D1 of 249 haplotypes observed in population from different regions of Argentina. mtDNA motifs of hypervariable region I between 16,027 and 16,362 positions were used to draw the tree. Each circle represents a different haplotype, and the relative size reflects the frequency of each haplotype. The black circles are the haplotypes present in Santiago del Estero populations. The nodal haplotype h29 is characterized by 16223–16325–16362 mutation positions. Haplotypes present in individuals from Santiago del Estero are detailed in Table 3.

Haplogroup C1. Most of the individuals included in haplogroup C1 (n = 36) present nodal haplotypes for C1b (seven individuals; transition at 493 is not included in the network) and C1d (11), widely shared with other South American populations (see Figure 2). Two haplotypes (h14 and h21) are shared with individuals from Gran Chaco populations (Cabana et al. 2006), one is shared with Córdoba (h15, García 2011), and another (h16) is shared with both populations.

Haplogroup D1. The nodal haplotype D1 was found in only one individual. Most of the subjects (15 of 22; 68%) assigned to the haplogroup D1 belong to the recently defined subhaplogroup D1j (Bodner et al. 2012) that is characteristic of other populations of central Argentina, such as Córdoba and San Luis (García et al. 2012) and Catamarca (Tamm et al. 2007) (see Figure 4). H26, found in five individuals from Santiago del Estero, was already observed in three individual from Córdoba (García 2011) and two individuals from Gran Chaco populations (Cabana et al. 2006). Finally, h28 is shared with two inhabitants of Córdoba (García et al. 2012) and one Mapuche from the Argentinian Patagonia (de Saint Pierre et al. 2012).

In summary, except in the case of nodal haplotypes, the samples from Santiago del Estero share several haplotypes with populations from the Sierras Centrales (mostly from Córdoba) and a few haplotypes with the Gran Chaco populations, revealing a strong geographic structure.

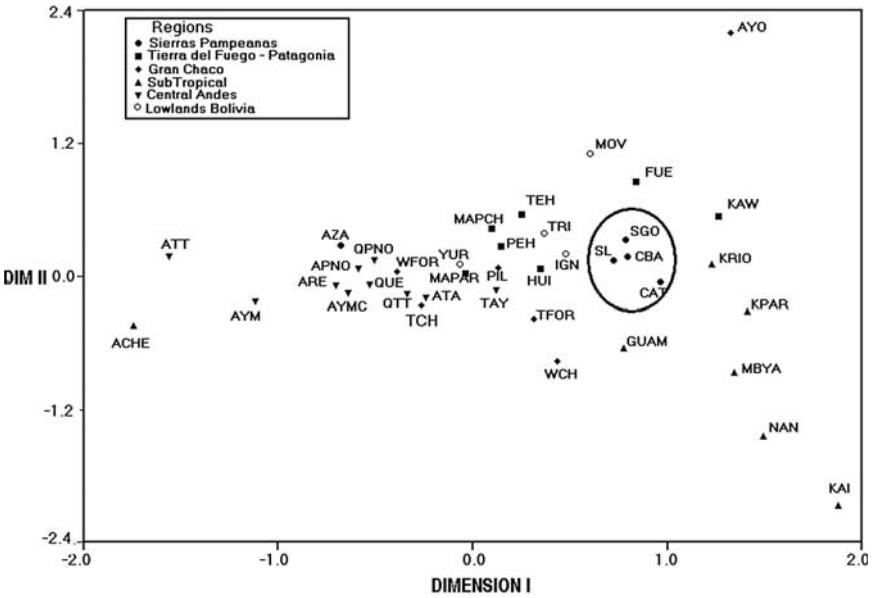

Figure 4. Bidimensional plot showing relative affinities between population samples across the Southern Cone of South America based on Kimura two-parameter distances calculated from mtDNA HVRI (stress = 0.110). For abbreviations, see Table 1.

Distance Analysis The bidimensional plot representing variation in mtDNA HVRI among 39 population samples from the Southern Cone, based on the Kimura two-parameter distances (Figure 4), reveals some geographic structure. The subtropical forest tribes, with high frequencies of haplotypes included in haplogroup A2, are scattered along the second axis at the extreme right side of the plot. The Gran Chaco, lowlands of Bolivia, and Tierra del Fuego–Patagonia samples fall along the first axis, more or less around the center of the cluster but also exhibiting some geographic structure. Ayoreo (AYO) and Aché (ACHE), two populations that have experienced marked diversity reduction, most probably due to founder effects, are outliers on the left and the top borders of the plot, respectively. Of the particular interest in this study, we observe that four of the five samples from the Sierras Pampeanas region cluster close to each other, showing that the sample of Santiago del Estero has the shortest distance with Córdoba. On the left side of the plot, the fifth sample of the region (Azampay, AZA) is close to its neighbor Andean populations, all characterized by high incidence of B2 lineages.

Analysis of Molecular Variance. The analysis of molecular variance for Native American lineages based on mtDNA HVRI sequences among Southern Cone populations is presented in Table 4. In first place, we introduced in the analysis all populations together, separating them into six cultural-geographic groups: Sierras

Table 4. Analysis of the Molecular Variance for Native American Based on mtDNA HVRI Sequence Distribution among Southern Cone Populations by Geographic Region

REGION	*n*			% VARIANCE COMPONENTS*		
	SEQUENCES	SAMPLES	GROUPS	WITHIN POPULATIONS	AMONG POPULATIONS/ WITHIN GROUPS	AMONG GROUPS
Southern Cone	2,016	39	6	75.03	16.00	8.97
Southern Cone minus Ayoreo and Aché	1,864	37	6	78.45	8.95	12.60
Sierras Pampeanas	464	5	—	87.91	12.09	—
Tierra del Fuego–Patagonia	345	7	—	94.06	5.94	—
Gran Chaco	295	6	—	68.52	31.48	—
Gran Chaco minus Ayoreo	204	5	—	92.44	7.56	—
Subtropical forests	458	7	—	62.39	37.61	—
Subtropical forests minus Aché	395	6	—	76.53	23.47	—
Central Andes	439	10	—	95.17	4.83	—
Lowlands	53	4	—	97.23	2.77 (NS)	—

*All values are significant at the 1% level except that marked with (NS).

Pampeanas, Tierra del Fuego–Patagonia, Gran Chaco, subtropical forests, Central Andes, and lowlands of Bolivia, using data from the populations listed in Table 1. As is a rule in human populations, most of the variance observed was due to the intrapopulation variability. At the first geographical level, considering all the 39 population samples, the among-groups variation is smaller than the among-population/within-groups variance. Both values are relatively high and statistically significant. When we removed from the analysis the two outliers observed in the distance analysis (Ayoreo and Aché), the among-group variation became larger than the among-population/within-group variance, since the extreme differentiation of these two populations inflate the within-group variance. Separate analyses for each region reveal that the subtropical forest populations are substantially more variable than the other Southern Cone groups, which has previously been observed (Demarchi et al. 2005; Tarazona-Santos et al. 2001). On the other extreme, the populations from the lowlands of Bolivia show small, nonsignificant differentiation. The Sierras Pampeanas populations present intermediate, statistically significant differentiation. However, a more detailed analysis reveals that the F_{ST} value between Santiago del Estero and Córdoba is extremely low (0.0016, $p = 0.291$), less than 10-fold that observed between Santiago del Estero and the other populations of the region (data not shown).

Discussion

This work constitutes the first study that examines the genetic variability of human populations in the province of Santiago del Estero. In agreement with what has

already been found in numerous other studies carried out in Latin American populations, the survival of indigenous paternal lineages in this population is relatively low. In contrast, the persistence of maternal lineages of Native American origin is extremely high. This is the typical pattern found in Latin American populations, a consequence of asymmetric gene flow, resulting in a population composed of a paternal component mostly European and a predominantly Native American maternal component (see Wang et al. 2008 and literature cited therein). However, in spite of this precedent, it is still remarkable to find that the maternal gene pool of the populations of southern Santiago del Estero is almost exclusively of American origin (95%), a proportion even higher than that found in some Native American settlements. This finding is most likely due to the relatively low incidence of the 20th-century European migratory wave in this region and the survival for a long time—from 1612 to the early 19th century—of pueblos de indios in these two villages (Palomeque 2000; Grosso 2008).

The census ordered by Carlos III, in 1778, recorded the population using the categories "Spaniards," "Indians," "free Negroes, Zambos, and Mulattoes," and "Slaves." The records show that Soconcho (currently Villa Atamisqui) and Sumampa parishes were particularly contrasting: while Soconcho parish was composed of an Indian majority (94%), Sumampa presented a majority of African descents (90%, mostly within the category "free Negroes, Zambos, and Mulattoes") (Grosso 2008). Despite this apparently contradictory history, at present we did not observe genetic differences between the two populations. Whereas Villa Atamisqui shows an incidence of maternal Native American lineages (similar to that recorded as Indians in the 1778 census in the former Soconcho parish), the high incidence of African descendants in Sumampa reported in that census is not reflected in the gene pool of the current population. Trying to shed light on that marked lack of agreement, Grosso (2008) states that, in colonial times, those Indians who did not pay tribute to the Spanish crown (because they were free or were not living at the time in their village of origin) were usually included in the loosely defined census category "free Negroes, Zambos, and Mulattoes." Under the same scenario, the absence of African lineages found in the current population of Sumampa could reflect an inaccurate categorization that denied the existence of free Indians, incorporating them into the category "free Negroes, Zambos, and Mulattoes." Even though the censuses carried out in colonial times enable us to obtain valuable information, they should be considered with extreme care (Faberman 2008).

At the regional level, and in despite the archeological record suggesting that Santiago del Estero late pre-Hispanic groups were strongly influenced by Andean cultures (Bonnin and Laguens 2000; Palomeque 2000; Taboada and Angiorama 2010), we did not find any genetic evidence that this relationship was associated with a significant gene flow—at least in the populations that occupy the southern portion of the province. On the other hand, these populations share many haplotypes with other Sierras Pampeanas populations, particularly with Córdoba. There are no significant statistical differences for considering them as separate populations, although Santiago del Estero populations, unlike Córdoba, share several haplotypes

with the Gran Chaco populations—probably as result of gene flow due to the closer geographic distances.

It is particularly interesting to note the high incidence of the recently described subhaplogroup D1j in the Santiago del Estero population (19%). The high frequency of this lineage across central and northwestern Argentina was already reported by our group (García et al. 2012). That study, which included the same D1 sequences analyzed in the present study strongly supported the hypothesis of a local origin for subhaplogroup D1j. The existence of a putative ancestral lineage, carrying the transitions 152 16311, present in four of the other D1 haplotypes and found only in this region, gives additional support for a scenario of local origin for D1j. As mentioned in that study, the restricted geographical distribution of D1j in other regions of South America suggests the existence of an ancient metapopulation (with this lineage serving as its genetic signature) covering the Sierras Pampeanas (García et al. 2012). This close genetic relationship is reflected in the bidimensional plot among four of the five populations of the Sierras Pampeanas region (Figure 4).

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Appendix 1. mtDNA Control Region Haplotypes Found in Both Santiago del Estero Population Samples

			CONTROL REGION	
ID	HAPLOGROUP	*n*	16024–16569	01–576
SGO1	A2	3	111 223 290 319 362	64 73 146 153 235 315+C 523–524d
SGO2	A2	2	111 223 290 319 362	64 73 146 152 153 235 263 315+C
SGO3	A2	1	111 223 290 319 362	64 73 146 153 235 263 309+C 315+C 523–524d
SGO4	A2	1	111 189 223 290 319 362	44+C 64 73 146 153 235 263 309+CC 315+C 523–523d
SGO5	A2	3	223 290 319 362	64 73 146 153 235 263 309+CC 315+C 523–524d
SGO6	A2	1	223 290 319 362	64 73 146 153 235 263 309+C 315+C 523–524d
SGO7	A2	1	111 290 319 362 519	64 73 146 151 153 235 315+C 523–524d
SGO8	A2	1	111 223 290 319 362 519	64 73 146 153 210 235 263 315+C 523–524d
SGO9	A2	1	086 111 223 290 319 362 526	64 73 146 150 153 235 263 309+C 315+C
SGO10	A2	1	111 223 290 319 362 512 547 550 551+G	73 146 153 263 309+CC 315+C 523–524d
SGO11	B2	1	183C 189 217 357 519	73 195 263 315+C 499
SGO12	B2	1	092 145 156 157 182C 183C 189 217 295 519	73 263 309+C 315+C // 499
SGO13	B2	1	145 156 157 182C 183C 189 217 362 381	73 263 309+CC 315+C 499
SGO14	B2	3	182C 183C 189 217 519	73 143 146 165 263 315+C 499
SGO15	B2	1	182C 183C 189 217 247 261	73 146 263 309+CC 315+C
SGO16	B2	1	092 126 182C 183C 189 214 217 355A 519	73 152 309+CC 315+C // 499
SGO17	C1d	2	051 223 298 325 327	73 194 195 249d 263 290–291d 309+C 315+C 489 523–524d
SGO18	C1d	2	051 223 298 325 327	73 194 195 204 249d 263 290–291d 309+C 315+C 489 523–524d
SGO19	C1d	1	051 223 298 325 327	73 194 195 249d 263 290–291d 309+C // 523–524d

SGO20	C1d	2	051 223 298 325 327
SGO21	C1d	1	051 223 298 325 327
SGO22	C1d	2	051 129 223 298 325 327
SGO23	C1d	1	051 223 298 325 327 519
SGO24	C1d	1	051 223 298 325 327 519
SGO25	C1d	1	051 223 298 325 327 519
SGO26	C1d	1	051 189 223 298 325 327
SGO27	C1d	1	051 223 259 271 298 311 325 327
SGO28	C1d	1	051 223 259 271 298 311 325 327 519
SGO29	C1b	1	223 298 325 327 519
SGO30	C1b	1	223 298 325 327 519
SGO31	C1b	2	223 298 325 327 519
SGO32	C1b	1	223 298 325 327 519
SGO33	C1b	1	223 298 325 327 519
SGO34	C1b	3	136 223 298 325 327 519
SGO35	C1b	1	136 223 298 325 327 519
SGO36	C1b	1	136 223 298 325 327 519
SGO37	C1b	2	136 223 256 298 325 327 519
SGO38	C1b	2	092 223 298 325 327
SGO39	C1b	1	037 092 223 260 298 325 327
SGO40	C1b	1	223 291 298 325 327 519
SGO41	C1b	1	223 298 325 327 390

73 194 195 249d 263 290–291d 315+C 489 523–524d
73 195 204 249d 263 290–291d 309+CC 315+C 489 523–524d
73 194 195 249d 263 290–291d 309+C 315+C 489 523–524d
73 194 195 249d 263 290–291d 309+CC 315+C 489 523–524d
73 194 195 204 249d 263 290–291d 309+CC 315+C 489 523–524d
73 194 195 249d 263 290–291d 309+C 315+C 489 523–524d 573+CCC
73 194 195 249d 263 290–291d 309+C 315+C 489 523–524d
73 194 195 249d 263 290–291d 315+C 489 523–524d
73 151 194 195 249d 263 290–291d 315+C 489 523–524d
73 146 150 207 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 146 249d 263 290–291d 309+C 315+C 489 493 523–524d 574
73 146 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 146 249d 263 290–291d 309+CC 315+C 489 493 523–524d
73 150 207 249d 263 290–291d 309+CC 315+C 489 493 523–524d
73 146 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 94 146 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 146 249d 263 290–291d 315+C 489 493 523–524d
73 146 153 249d 263 290–291d 309+C 315+C 489 493 523–524d 549
73 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 150 249d 263 290–291d 309+C 315+C 489 493 523–524d
73 150 194 249d 263 290–291d 309+C 315+C 489 493

SGO42	C1b	1	172 298 325 327 526	73 153 249d 263 290–291d 315+C 489 493 523–524d
SGO43	C1c	1	(15930) 223 298 325 327 343	73 146 249d 263 290–291d 315+C 489
SGO44	D1	1	223 325 362	73 185 263 315+C 489
SGO45	D1j	4	223 242 311 325 362	73 152 263 315+C 489 524+AC
SGO46	D1j	1	223 242 311 325 362	73 152 263 309+C 315+C 489
SGO47	D1j	1	223 242 311 325 362	73 152 263 309+C 315+C 489 524+AC 538C
SGO48	D1j	2	223 242 311 325 362	73 152 235 263 315+C 489
SGO49	D1j	1	223 242 311 325 362	73 152 235 263 309+CC 315+C // 489
SGO50	D1j	1	223 242 311 325 362	42+G 73 106–111d 152 212 263 309+C 315+C 489
SGO51	D1j	1	223 242 311 325 362	73 106–111d 152 212 263 309+C 315+C 489
SGO52	D1j	2	223 242 286 311 325 362	73 106–111d 152 212 263 309+C 315+C 489
SGO53	D1j	1	223 242 286 311 325 362	73 106–111d 152 212 263 309+C 315+C 374 489
SGO54	D1j	1	157 223 242 311 325 362	73 152 263 309+CC 315+C 489
SGO55	D1	1	223 311 325 362 391	73 152 200 225 263 309+C 315+C 489 523–524d
SGO56	D1	1	223 311 325 362 391	73 152 263 309+C 315+C 489 523–524d
SGO57	D1	2	223 311 325 362 391	73 152 200 263 309+C 315+C 489 523–524d
SGO58	D1	1	223 311 325 362 391 519	73 152 200 263 309+C 315+C 489 523–524d
SGO59	D1	1	126 223 325 362	10 55 56 64 73 263 279 309+C 315+C 489
SGO60	K	1	224 311 519	//
SGO61	H	1	162 192	263 315+C
SGO62	U7-Y?	1	126 231 318T 519	73 146 152 263 309+C 315+C 523–524d
SGO63	L1c4	1	37 129 140 184 187 189 223 274 278 294 301 311 360 519	73 152 182 186A 189C 195 198 247 263 297 315+C 316