Human Biology

Volume 83 | Issue 1 Article 4

2011

Mitochondrial DNA in Basque Descendants from the City of Trinidad, Uruguay: Uruguayan- or Basque-like Population?

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Recommended Citation

Sans, M.; Figueiro, G.; Ackermann, E.; Barreto, I.; Egana, A.; Bertoni, B.; Poittevin-Gilmet, E.; Maytia, D.; and Hidalgo, P. C. (2011) "Mitochondrial DNA in Basque Descendants from the City of Trinidad, Uruguay: Uruguayan- or Basque-like Population?," *Human Biology*: Vol. 83: Iss. 1, Article 4.
Available at: http://digitalcommons.wayne.edu/humbiol/vol83/iss1/4

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Abstract

Like other countries in the Americas, during its colonization Uruguay was the recipient of immigrants from several ethnic groups from Europe, as well as of enslaved Africans. After its independence in 1830, Basques were the first group of Europeans to arrive in the country. In this paper, we aim to contribute to the understanding of the process of integration of these migratory waves into the Uruguayan society. For that purpose, individuals of Basque origin from the city of Trinidad, Uruguay, were chosen to participate in this study. Particularly, we wanted to determine if Basque descendants in Uruguay remained relatively isolated or if they mixed with other ethnic groups. Mitochondrial DNA (mtDNA) of 60 self-identified Basque descendants, taken from a larger sample of subjects with Basque ancestors, was analyzed. The origin of mtDNA haplogroups was 77.8% European, 20.4% Amerindian, and 1.8% African, showing similar frequencies to other Uruguayan regions. Very few sequences showed a clear Basque origin, although other sources such as the Canary Islands are likely. Moreover, genetic distances clearly show that Basque descendants are genetically closer to other Uruguayan groups than to European populations, including Basques. It is possible to conclude that Basques and their descendants in the region of Trinidad did not remain isolated and that their marriage behavior was similar to that of other Uruguayan populations. However, to have a more accurate picture of the way Basques intermarried with other populations in Uruguay, new analyses are needed that take into account paternal lineages as well as biparental genetic markers.

Keywords

maternal origin, mtDNA haplogroups, HVRI, surnames, genetic structure

Cover Page Footnote

This work was made possible thanks to the collaboration of the Association Haize Hegoa, the people, authorities and media of Trinidad, and the students of Anthropology at the Facultad de Humanidades y Ciencias de la Educacion. We specially thank Maite Bengoa, Lucía Pe´rez, Renee Ferna´ndez, Egle Vera, Alvaro Fagalde, Gloria Oholeguy, Soledad dos Santos, Ana Irazabal, Mirentxu Saralegui, and Florencia Sevrini. We also thank Carolina Bonilla for their language revision and clarifications. We gratefully acknowledge many helpful comments and suggestions that we have received from three anonymous reviewers of this paper. The project was supported by Eusko Itaskuntza-Donostia, San Sebastian, Spain.

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Mitochondrial DNA in Basque Descendants from the City of Trinidad, Uruguay: Uruguayan- or Basque-like Population?

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Abstract Like other countries in the Americas, during its colonization Uruguay was the recipient of immigrants from several ethnic groups from Europe, as well as of enslaved Africans. After its independence in 1830, Basques were the first group of Europeans to arrive in the country. In this paper, we aim to contribute to the understanding of the process of integration of these migratory waves into the Uruguayan society. For that purpose, individuals of Basque origin from the city of Trinidad, Uruguay, were chosen to participate in this study. Particularly, we wanted to determine if Basque descendants in Uruguay remained relatively isolated or if they mixed with other ethnic groups. Mitochondrial DNA (mtDNA) of 60 self-identified Basque descendants, taken from a larger sample of subjects with Basque ancestors, was analyzed. The origin of mtDNA haplogroups was 77.8% European, 20.4% Amerindian, and 1.8% African, showing similar frequencies to other Uruguayan regions. Very few sequences showed a clear Basque origin, although other sources such as the Canary Islands are likely. Moreover, genetic distances clearly show that Basque descendants are genetically closer to other Uruguayan groups than to European populations, including Basques. It is possible to conclude that Basques and their descendants in the region of Trinidad did not remain isolated and that their marriage behavior was similar to that of other Uruguayan populations. However, to have a more accurate picture of the way Basques intermarried with other populations in Uruguay, new analyses are needed that take into account paternal lineages as well as biparental genetic markers.

Uruguay was initially populated by three or four Native ethnic groups, the extermination and extinction of which shaped the Uruguayan national identity (see, for example, Ministerio de Instrucción Pública 1925). During colonial times Spaniards and Portuguese started settling in the current Uruguayan territory, bringing

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Human Biology, February 2011, v. 83, no. 1, pp. 55–70

KEY WORDS: MATERNAL ORIGIN, MTDNA HAPLOGROUPS, HVRI, SURNAMES, GENETIC STRUCTURE.

in slaves from Africa or Brazil. After independence in 1830, migration from Europe became continuous. Between 1835 and 1838, 14,600 Europeans entered the country, mostly Basques and Canary Islanders (Zubillaga 1997). In total, this first migratory wave involved more than 40,000 immigrants (Barrán and Nahum 1979). Subsequent migration waves included Brazilians, Spaniards (mostly Galicians and Catalonians), Italians, and most recently, during the 20th century, Eastern Europeans, and Western Asians. Census data show that in 1908 the population was composed of 861,464 Uruguayans and 181,222 foreigners (INE 1908).

The integration of natives and immigrants in a new territory is a culturally and biologically complex process. As Yinger (1985) points out, linguistic, religious, or "racial" barriers can delay the process of amalgamation or biological assimilation. Little is known about this process in Uruguay. Classical Uruguayan historiography illustrates immigration as a linear process in which immigrants were quickly assimilated (Oddone 1966). However, the Uruguayan society did not integrate migrants easily. As opposed to I. I. Zangwill's "melting pot," studies based on church registers showed that immigrants preferred to marry their compatriots, or their daughters, and this is true at least for the first two generations after entering the country (Barreto and Sans 2000, 2003; Barreto et al. 2004; Barreto 2008; Sans and Barreto 1997; Sans et al. 1996).

The genetic structure of the population can give clues about the historical process of peopling. Genetic studies performed during the last 20 yrs show that the present-day population was conformed by unequal contributions of Native Americans, Europeans, and Africans (Hidalgo et al. 2005; Sans et al. 1997, 2006). When uniparental contributions are analyzed, percentages by origin change, showing not only regional differences but directional matings between European men and native or African women (Bertoni et al. 2005; Bonilla et al. 2004; Gascue et al. 2005; Pagano et al. 2005a and b; Sans et al. 2002, 2006).

In 2004, the Department of Biological Anthropology (Universidad de la República) together with the Association of Basque descendants Haize Hegoa, began a multidisciplinary study about Basque immigrants to Uruguay that involved the use of historical, demographic, genealogical, cultural, and genetic sources. The primary aim of studying this ethnic group was to understand the process of integration of European migratory waves to the Uruguayan society. The Basques are a unique group, not only because of its language, but also due to other cultural characteristics such as its cuisine and sports (for instance, "jai alai," or Basque ball game; MacClancy, 2008).

Basque immigration started as soon as Montevideo was founded in 1724 and increased after 1825, with two clearly identifiable periods: the French period (1825–1842) and the Spanish period (1842–1876; Marenales and Luzuriaga 1990). The migrants settled mainly in the center and south of the country, where conditions were favorable for the raising of sheep (Campal 1969). Different hypotheses have been proposed about the origin of the Basque, and genetic and molecular information about this ethnic group is extensive (Aguirre et al. 1991; Alfonso-Sánchez et al. 2008; Alonso and Armour 1998; Alonso et al. 2005;

Arnaiz-Villena et al. 1999; Bertranpetit et al. 1995; Calderón et al. 2003; Comas et al. 2000; de Pancorbo et al. 2001; García-Obregón et al. 2007; Iriondo et al. 2003; Izagirre and De la Rúa 1999; Pereira et al. 2005; Rodríguez-Ezpeleta et al. 2010).

In this paper, we analyze the way in which a group of European descendants integrated to the Uruguayan society and became part of its present-day population. Particularly, we aim to determine if Basque-descendants in Uruguay remained relatively isolated or if they mixed with other ethnic groups. We selected Trinidad, a city in the southwest, because it shows a high percentage of Basque descendants, and analyzed its maternal lineages.

Materials and Methods

Sample. Trinidad, the capital city of the Department of Flores, is located 200 kilometers away from Montevideo (Figure 1). In 2004, its population consisted of 20,982 inhabitants, 83.6% of the total population of the department (INE 2004). The city was founded in 1804, whereas its cathedral, named "de la Santísima Trinidad," was founded in 1802, and ecclesiastical archives started in 1820. At the moment of the first population census in 1834, only a few families were registered as of Basque origin (AGN 1834). However, it has been pointed out that a high percentage of individuals of Basque origin live there at present (Marenales y Luzuriaga 1990).

We interviewed 139 self-identified Basque descendants living in the city of Trinidad. Another 31 Basque descendants, also self-identified, were recruited from a sample of 100 individuals from Trinidad who were selected across several different neighborhoods (data not analyzed in this paper). All participants were asked for personal and familial information (including the origin of their ancestors and the date of their arrival in Uruguay), as well as about their familiarity with Basque culture. Genealogies, built using both parish records and interview data, were drawn using GenoPro version 2.0.1.1 (Morin 2007).

After explaining the study, 60 apparently nonconsanguineous individuals gave written consent to participate in the DNA analysis. Fifty-seven samples of peripheral blood and three hair samples were collected for that purpose.

Laboratory Techniques

DNA Extraction. Whole blood samples were collected in EDTA vacutainer tubes. Total genomic DNA was extracted from blood samples according to the "salting out" method of Miller et al. (1988). DNA from hair samples was isolated based on the acid extraction protocol from Hidalgo et al. (2009).

PCR Amplification and Sequencing. PCR amplification reaction conditions followed those described by Martinez-Cruzado et al. (2001), with minor modifications. The PCR reaction profile was performed with an initial denaturation step at 95°C for 5 min, followed by 45 cycles with denaturation at 95°C for 40 sec, annealing at 50°C for 40 sec, and extension at 72°C for 1 min, and a final 5-min

Figure 1. Map of South America (partial) and Uruguay, indicating the city of Trinidad, Department of Flores.

extension step at 72°C. The amplification products were verified by electrophoresis on a 2% agarose gel with ethidium bromide staining. PCR products were purified using silica columns (Illustra GFX™ PCR DNA and Gel Band Purification Kit, GE Healthcare) for sequencing. MtDNA hypervariable region I (HVRI) was amplified using primers 15997°F (5′-CACCATTAGCACCCAAAGCT-3′) and 16498R (5′-CCTGAAGTAGGAACCAGATG-3′). DNA was sent to be sequenced to an external service provider (Macrogen Inc., Seoul, South Korea).

Sequence Analysis and Haplogroup Assignment. A primary haplogroup was assigned to the samples by identifying the diagnostic HVRI mutations for each haplogroup, following mainly the criteria of Achilli et al. (2004, 2008), Macaulay et al. (1999), Salas et al. (2002), Simoni et al. (2000), Tamm et al. (2007), and van Oven and Kayser (2009). Dubious haplogroup assignments were confirmed using RFLP determination as in Martínez-Cruzado et al. (2005), with the exception of haplogroup L that was analyzed by also testing site 10871MnlI, or by sequencing the hypervariable region II (HVRII). Primers 10814°F (5′-ACCACTGACATGACTTTCC-3′) and 10912R (5′-GAGGAAAAGGTTGG-GGAACAG-3′), designed by one of us (G.F.), and primers 29F (Vigilant et al. 1989) and 397R (5′-CATACCGCCAAAAGATAAAAT-3′) were used to amplify the corresponding fragments.

Data Analyses. Sequences were visualized using Chromas Lite 2.01 (Technelysium Pty Ltd., 1998–2005, Queensland, Australia) and aligned using Genedoc 2.7.000 (Nicholas and Nicholas 1997). To evaluate the quality of our mtDNA sequence data, the ratio of the number of weighty transitions to the number of transversions plus indels (WTTI, Bandelt et al. 2002) was calculated. R × C contingency tables (Miller 1997) were used to test differences between frequencies. Two parameters were used to measure haplogroup diversity in the sample: h (Nei 1987), defined as $(N/N-1)(1-\sum x_i^2$, where x_i is the haplogroup frequency and N is the sample size, and Shannon diversity index (Magurran 1988), defined as $H = -\sum p_i \log_2 p_i$, where p_i is the sample frequency of the ith haplogroup.

Nei′s D_A genetic distances (Nei 1972) between Basque descendants in Uruguay and other Uruguayan and European populations were calculated using the DISPAN software (Ota 1993), with haplogroup frequencies. European populations used for comparison belong to countries where the majority of immigrants came from, i.e., Spain, Italy, Portugal, and France (Vidart and Pi Hugarte 1969; Barrán and Nahum 1979; Zubillaga 1997). See references in Figure 2.

Sequences were compared with others of the same origin, found in GenBank or published elsewhere.

Results

General Data. From the 170 interviews, 150 Basque immigrants, or founders, were identified. Most of them (75%) arrived in Uruguay in the second half of the 19th century, while 6% arrived in the first half. About 16% entered the country in the first half of the 20th century, but the date of arrival of the remaining 3% could not be determined. In 63% of the cases, the country of origin was known, 34% having arrived from France and 29% from Spain.

Genealogical Data. The genealogical reconstruction of the 60 individuals who were part of the mtDNA study showed some interesting facts. Twenty-eight of 60 individuals were included in the same genealogy, i.e., they are connected by at least one member in their families. This genealogy includes up to 6 generations back from the interviewee and two generations forward, with a total of 1064 individuals. In one case, 4 individuals shared their maternal ancestor (great-grandmother or great-great-grandmother), and in two cases, 2 individuals shared

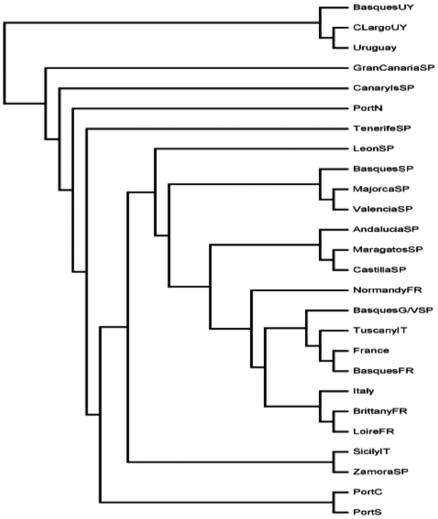

Figure 2. Neighbor-joining tree with D_A distances (Nei 1972) computed by DISPAN method (Ota 1993). Haplogroups considered: H/HV, V, U*, U2, U3, U4, U5, U6, K, T, J, I, W, X, M, L1, L2, L3, ABCD, and others. Populations considered: Spain (SP): Maragatos, Leon, Castilla, Andalusia (Larruga et al. 2001), Majorca, Valencia (Picornell et al. 2005), Zamora (Alvarez et al. 2010); Tenerife, Gran Canaria (Maca-Meyer et al. 2005), Canary Islands (Rando et al. 1999); Basques (Alzualde et al. 2005); Basques G/V (Guipuzcoa and Vizcaya; Alfonso-Sánchez et al. 2008); France (FR): Normandy, Périgord (Dubut et al. 2004), Brittany, Basques (Richard et al. 2007); Portugal (PORT): North, Center, South (Pereira et al. 2000); Italy (IT): Tuscany (Torroni et al. 1996), Sicily (Achilli et al. 2007); Italy (Alzualde et al. 2005); Uruguay (UY): CerroL (Cerro Largo) (Sans et al. 2006), Uruguay (Pagano et al. 2005a modified); Basques (present study).

their maternal ancestor (grandmother). Only one of each remained in the sample, and consequently, the total number of individuals analyzed diminished. As another case was discarded because of technical problems with its biological sample, the final study population is composed of 54 individuals. The analysis of surnames of these 54 individuals showed that 49 (90.7%) had a Basque paternal last name, but only 22 (40.7%) had a Basque maternal last name. It is important to point out that Uruguayan legal naming practices, that extend to all Uruguayan citizens, require two last names, being the first, the paternal, and the second, the maternal last name. Two individuals do not have any of their paternal last names of Basque origin: in one case, the maternal grandmother was from the Basque country, and in the other, the paternal grandmother had a Basque surname. Concerning the four last names (two paternal, two maternal), most individuals have two Basque surnames (23 cases, 42.6%), followed by those with one Basque surname (18 or 33.3%), three Basque surnames (9 or 16.8%, and four Basque surnames (3 or 5.6%), and one undetermined (one unknown surname). The maternal origin could be verified only in 13 cases: 8 were from Euskal Herria

(Basque region, 4 grandmothers, 4 great-grandmothers), 2 from Italy, 1 from Switzerland, and 2 from the Canary Islands (Spain). All individuals mentioned before that shared maternal ancestors (and consequently, were excluded from mtDNA analysis) have a maternal Basque ancestor.

Mitocondrial DNA Data. The WTTI ratio of the DNA sequences (9.8) is higher than the one suggested by the authors (Bandelt et al. 2002) but is consistent with that found before in Cerro Largo (10.0; Sans et al. 2006). When speedy transitions are compared with weighty transitions, the number obtained is similar to that reported by Bandelt et al. (2002; 10.7 vs. 9.2); therefore the difference is due to a lower presence of transversions plus indels in our analysis, as opposed to the existence of artifacts, which validates the sequences obtained in our study. Haplogroup diversity indexes in our sample were h: 0.865 and H: 2.207, lower than the estimates based on a sequence data set from Uruguay (Pagano et al. 2005a, modified).

As previously indicated, only 54 sequences were finally used for the analysis. The haplogroups were 42 (77.8%) European, 11 (20.4%) Native American, and 1 (1.8%) African (Table 1). Haplogroup H was the most frequent, representing 35.2% of the whole sample and 45.2% of all European haplogroups. Interestingly, the 8 relatives who shared 3 Basque ancestors belonged to haplogroup H: two who shared one ancestor exhibited subhaplogroup H5, whereas the others' subhaplogroup was non-H2 because of the presence of 263G and 315+C. Consequently, if the present-day population of Trinidad is considered without accounting for consanguinity, the frequency of haplogroup H would be much higher than calculated in this study. The second most frequent haplogroup was U, 13.0% and 16.7%, respectively, in the global sample and among European haplogroups. Regarding the origin of the sequences, over a half of those belonging to haplogroup U (4 in 7) were from the Canary Islands (subhaplogroup U6b1, 7.4%). Besides the sequences with Canary Island origin, it was possible to assign a potential origin to some of the other sequences (Table 1). One, B03, had mutations that are typically Basque, whereas a second one, A18, was found only in the French, although its exact origin is undetermined (Pierron et al. 2008). Most of the sequences had mutations common in European populations or had not been identified in any population studied so far. Other sequences were found in Eastern European or Asian populations: C12 in one Russian and one Croatian individuals, C45 in Russians, and C46 in Hungarians (see Table 1 for details).

With respect to Native American haplogroups, all four major founding haplogroups were detected. The most frequent was D1, with a frequency of 7.4% in the whole sample and 36.4% among the Native American haplogroups, followed by B2 (5.6 and 27.3%, respectively). An African haplogroup, L3b, was also found (1.8%).

Consistently, all individuals whose European ancestry was confirmed in the genealogies had European haplogroups (Table 2). When compared with those

Table 1. HVRI Sequences, Selected Coding Region RFLPs, Selected HVRII Mutations, and Haplogroups, in the 54 Basque Descendants from Trinidad, Uruguay

#	*N*	*16025–16390, 16000 Minus*	*RFLP Sites*	*Haplo-group*	*Origin*
B06, C41, C26, A01, A11, A26, B13, C02b	8		−7025 AluI	H	Eu[a]
A18	1	260, 357	−7025 AluI	H	Eu[b]
A03	1	183C, 189, 260	−7025 AluI	H	Eu[c]
B05	1	266	−7025 AluI	H	Eu[a]
C46	1	129, 189, 355, 356, 362	−7025 AluI	H	Eu[d]
C10	1	362	−7025 AluI	H	Eu[a]
B01	1	189	−7025 AluI	H	Eu[a]
EG	1	189, 356, 390	−7025 AluI	H	Eu[a]
C14	1	051, 162	−7025 AluI	H	Eu[a]
C07	1	176	−7025 AluI	H	Eu[a]
C09, B02	2	304	−7025 AluI	H	Eu[a]
C06	1	189, 298 (72, 263, 309.1, 315.1)	+7025 AluI	V	Eu[a]
B19	1	274, 298, 311 (72, 263, 309.1, 315.1)	+7025 AluI	V	Eu[c]
A39	1	298 (72, 263, 309.1, 315.1)	+7025 AluI	V	Eu[a]
C31	1	298, 335G (72, 263, 309.1, 315.1)	+7025 AluI	V	Eu[c]
C40	1	192, 270	+7025 AluI	U5	Eu[a]
C03	1	192, 270, 319	+7025 AluI	U5	Eu[e]
C12	1	189, 192, 256, 270	+7025 AluI	U5	Eu[f]
C13	1	163, 172, 219, 311	+7025 AluI	U6b1	Eu[g]
B12	1	163, 172, 219, 293, 311	+7025 AluI	U6b1	Eu[g]
A06, C18	2	92, 163, 172, 219, 311	+7025 AluI	U6b1	Eu[g]
A09, B24	2	224, 311	+7025 AluI	K	Eu[a]
C49	1	93, 172, 224, 311	+7025 AluI	K	Eu[c]
A20	1	69, 126	+4216 NlaIII	J	Eu[a]
A28, A08	2	69, 126, 311	+4216 NlaIII	J	Eu[a]
C45	1	126, 140, 189, 294, 296, 311	+4216 NlaIII	T2	Eu[h]
C36	1	126, 294, 296, 304	+4216 NlaIII	T2	Eu[a]
B10, A10, C19	3	126, 220, 292, 294	+4216 NlaIII	T2	Eu[c]
C22	1	129, 223, 304, 391	+7025 AluI	I	Eu/Asia[i]
JA	1	124, 223, 278, 362	−10871MnI, −3592HpaI, −del regV	L3b	Af
C21	1	111, 223, 290, 319, 356	+663 HaeIII	A2	Na
B15	1	111, 193, 223, 290, 319, 320, 362	+663 HaeIII	A2	Na
B14	1	189, 217, 274	+10871MnlI, −3592HpaI, +del regV	B2	Na
C11	1	183C, 189, 217, 241	+10871MnlI, −3592HpaI, +del regV	B2	Na
A25	1	182C, 183C, 189, 217, 220, 241	+10871MnlI, −3592HpaI, +del regV	B2	Na
B38	1	223, 325, 327	+13262 AluI, +5176 AluI	C1	Na

Table 1. (*continued*)

#	*N*	*16025–16390, 16000 Minus*	*RFLP Sites*	*Haplo-group*	*Origin*
B11	1	51, 140, 223, 288, 298, 325, 327	+13262 AluI, +5176 AluI	C1	Na
A16, RI	2	223, 311, 325, 362	−13262 AluI, −5176 AluI	D1	Na
A23	1	223, 242, 311, 325, 362	−13262 AluI, −5176 AluI	D1	Na
A35	1	223, 242, 311, 325, 362	−13262 AluI, −5176 AluI	D1	Na

Eu: European, Af: African, Na: Native American. All mutations are transitions at least it is specified. Only selected mutations of HVRII are shown. HVRII mutations are in parentheses in column 3.

a. Sequences common in Western Europe.

b. Sequence found in two French (Pierron et al. 2008).

c. Sequences not found in databases.

d. Sequence found in three Hungarians (Brandstaetter et al. unpublished; GenBank #EF185698, #EF185680; #EF185662).

e. Sequence common in Basques (Bertranpetit et al. 1995, Côrte-Real et al. 1996, Alfonso-Sanchez et al. 2008).

f. Sequence found in one Russian (Malyarchuk et al. 2010) and one Croatian (Harvey et al. unpublished; GenBank #AY005679).

g. Sequence common in the Canary Islands (Rando et al. 1999; Maca-Meyer et al. 2003).

h. Sequence found in Pomor, Russia (Tonks et al. unpublished; GenBank #AY959591).

i. Sequence common in Europe and Asia.

whose origin was not determined, the difference is significant ($p < 0.05$), due to the latter showing Native American and African haplogroups (Table 3a). When the first two surnames were considered, i.e., having a paternal, maternal or both Basque surnames, the difference was not significant (Table 3b). However, if the four surnames were considered, the difference between having 1 or 2, or having

Table 2. Individuals Whose European Ancestry Was Confirmed by Genealogies and Their mtDNA Haplogroups

#	*Haplogroup*	*Origin of the Maternal Ancestor*
C02	H	Basque
A26	H	Basque
B02	H5	Basque
C09	H5	Basque
B24	K1c	Basque
C40	U5b1	Basque
C03	U5b2	Basque
A39	V	Basque
C22	I	Italian
B01	H	Italian
C18	U6b1	Canarian
B10	T2	Canarian
B06	H	Swiss

Table 3. Comparisons and p Values Using R × C

	Haplogroup Origin	
	Native + African	*European*
A) Origin of the maternal ancestor		
Basque	0	9
Other European	0	4
Undetermined	12	29
R × C (European vs. undetermined origin), $p = 0.048^a$		
B) Origin of two first surnames		
Basque paternal	9	21
Basque maternal	0	3
Both Basques	2	17
R × C, $p = 0.248$, N.S.		
C) Quantity of Basque surnames		
1	5	13
2	6	16
3 or 4	0	13
R × C (1 or 2 vs. 3 or 4 Basque last names), $p = 0.049^a$		

A) Origin of the maternal ancestry and origin of the mtDNA haplogroup; B) origin of the first two surnames and origin of the mtDNA haplogroups; and C) quantity of Euskal surnames among the first four and origin of the haplogroups.

a. p value is significant at the 5% level.

3 or 4, was significant ($p < 0.05$), due to the lack of non-European haplogroups in the latter (Table 3c).

Distance analysis of the haplogroup frequencies showed two main clusters. Uruguayan populations conformed one cluster and all the European populations a separate one (Figure 2).

Discussion

Participants in our study were self-identified Basque descendants who had learned about the study through the media or, for the most part, by word-of-mouth from other citizens. Even though in Uruguay two last names (one paternal and one maternal) are used in all legal documents, people are usually known by their paternal surname. This fact, together with the way people learned about the study, may explain the unequal numbers of individuals with paternal (91%) or maternal (41%) Basque last names that volunteered for the study. However, because their Basque ancestors lived at least two generations ago, having a paternal or maternal Basque surname does not seem to significantly affect their genetic background, as evidenced from the lack of difference in the origin of mtDNA haplogroups (Table 3b). On the other hand, individuals who have three or four Basque last names, which reflects a strong Basque ancestry, show all European mtDNA haplogroups, as opposed to those with fewer Basque surnames (Table 3c).

The genealogical data indicates that the paternal Basque contribution is 91%, whereas the matrilineal Basque contribution is only 15% (8 cases).

However, the apparent absence of a matrilineal Basque origin may be due to the loss of maternal last names after two generations or at the moment of arrival of the immigrants in the country. Because it is possible to estimate paternal contributions based on last names due to the link between them and the Y-chromosome (Bowden et al. 2008), we are able to determine that the paternal Basque contribution is 91%, and therefore, the paternal European contribution should be at least as much. The maternal European contribution is 78%, whereas the maternal Basque contribution represents a lower percentage (see Table 1). These data also show that, as reported for other Uruguayan populations, there has been directional mating between non-European women and European men (Bertoni et al. 2005; Bonilla et al. 2004; Bravi et al. 1997; Sans et al. 2002, 2006). Moreover, it reveals that matings between non-Basque women and Basque men have taken place, as shown by parish records (Barreto y Sans, 2000, 2003; Sans et al. 1996). Thus, Basque and Basque descendants in Trinidad exhibited a similar marriage behavior to other ethnic groups that settled in Uruguay. Directional matings are common in all Latin American countries, as a direct consequence of the characteristics of the immigration in the region, which involved mainly male migrants (see Sans et al. 2006 for references).

Basque descendants have a lower percentage of Native American ancestry (20.4%) compared with the Northeast (Tacuarembó 62%, Cerro Largo 30.2%), and also with Uruguay as a whole (31%, calculated from Pagano et al. 2005a), but identical to the capital city of Montevideo (20.4%, Gascue et al. 2005). This supports historical data that indicates that Montevideo and its surrounding region were the main receptors of the European immigration that took place during the late 19th century and the first half of the 20th century (Vidart and Pi Hugarte 1969). Basque descendants show a low African contribution (1.8%) with respect to the Northeastern region: Tacuarembó 16.7% (Bonilla et al. 2004), and Cerro Largo 16,3% (Sans et al. 2006), yet, this percentage is similar to that reported for a sample of the whole country (1.7%, calculated from Pagano et al. 2005a). Haplogroup U6b was not included as African in the above calculations (see discussion below). Figure 2 clearly shows that Uruguayan populations, including individuals of Basque descent, are more similar to each other than to European populations.

When the global European contribution is considered, the frequency of haplogroup H reaches 45.2% among European lineages, and a similar frequency (44.4%) among maternal Basque lineages. Present-day populations from Euskal Herria have a frequency of haplogroup H around 62%, whereas Aldieta, a historical population, had 49% (Alzualde et al. 2005, 2006) and prehistoric populations in the region showed frequencies between 38 and 44% (Izagirre and De la Rúa 1999). Given that Basques entered Uruguay mostly during the second half of the 19th century, they could be more closely related to historical Basque populations than to contemporary ones. More research on Basque descendants in Uruguay could shed light on this subject.

The presence of haplogroup U6b1 in Basques from Trinidad (7.4%) is noteworthy. This subhaplogroup probably originated in the Near East (as pre-U6), spreading first to North Africa and subsequently, to West Africa. It became U6b and U6c in the Canary Islands, revealing the presence of North Africans in the islands during prehistoric times and has also been identified in the ancient Guanches (Maca-Meyer et al. 2003, 2004; Rando et al. 1999). Additionally, this subhaplogroup is present, with frequencies a little lower than in Trinidad, in Cerro Largo (4.7%, Sans et al. 2006), and it shows a frequency of 4.2% in the country as a whole (Pagano et al. 2005a), highlighting the extent of the migration and admixture from the Canary Islands that the country experienced.

Finally, a mention to non-European haplogroups should be made. As in other parts of the country, all four main Native American haplogroups were found among Basques from Trinidad, but with different frequencies. In other regions haplogroups B and C show the highest frequencies, with the exception of Montevideo, where A and B are the most frequent (Bonilla et al. 2004; Gascue et al. 2005; Sans et al. 2002, 2006). In the present study the most frequent haplogroup was haplogroup D. Two facts may account for these differences: the small number of Native American haplogroups considered, related to the small total sample size, and the lack of information about the west and central regions of Uruguay. Historical sources state that the Uruguay river region was occupied by Chaná groups, unlike other regions of the territory where Charrúa/Guenoa or Guaraníes predominated (Bracco 1998; Cabrera 1992; Pi Hugarte 1993). At present, there are no genetic studies about the descendants of the Chaná Indians, or about historical Chaná Indians, neither for the west region of Uruguay nor the neighboring province of Entre Ríos in Argentina. It is interesting to note that haplogroup D is also present in high frequencies in the Chaco, Pampa, Patagonia, and Tierra del Fuego regions in Argentina and Chile (Demarchi et al. 2001; Goicoechea et al. 2001; Lalueza et al. 1997; Moraga et al. 2000).

In conclusion, Basque descendants from Trinidad, Uruguay, show the same origin as other Uruguayan ethnic groups or geographical regions, with a closer similarity to the south of the country. However, some haplogroup frequencies are somewhat different from other reported Uruguayan samples, which could be attributed to the small size of the Trinidad sample but also to local events. Further studies on Basque descendants in Uruguay as well as on populations around the city of Trinidad should answer this and other questions.

Acknowledgments This work was made possible thanks to the collaboration of the Association Haize Hegoa, the people, authorities and media of Trinidad, and the students of Anthropology at the Facultad de Humanidades y Ciencias de la Educación. We specially thank Maite Bengoa, Lucía Pérez, Renée Fernández, Eglé Vera, Alvaro Fagalde, Gloria Oholeguy, Soledad dos Santos, Ana Irazabal, Mirentxu Saralegui, and Florencia Sevrini. We also thank Carolina Bonilla for their language revision and clarifications. We gratefully acknowledge many helpful comments and suggestions that we have received from three anonymous reviewers of this paper. The project was supported by Eusko Itaskuntza-Donostia, San Sebastián, Spain.

Received 10 June 2010; revision accepted for publication 7 September 2010.

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