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Pedro C. Hidalgo

*Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la Educación. Universidad de la República, Uruguay, drpedro.hidalgo@gmail.com*

Patricia Mut

*Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la Educación. Universidad de la República, Uruguay*

Elizabeth Ackermann

*Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la Educación. Universidad de la República, Uruguay*

Gonzalo Figueiro

*Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la Educación. Universidad de la República, Uruguay*

Monica Sans

*Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la Educación. Universidad de la República, Uruguay*

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**Questioning the “melting pot”: Analysis of Alu inserts in three population samples  
from Uruguay**

Pedro C. Hidalgo<sup>1\*</sup>, Patricia Mut<sup>1</sup>, Elizabeth Ackermann<sup>1</sup>, Gonzalo Figueiro<sup>1</sup>, Monica  
Sans<sup>1</sup>

1. Departamento de Antropología Biológica. Facultad de Humanidades y Ciencias de la  
Educación. Universidad de la República, Uruguay.

\*Correspondence to: Pedro C. Hidalgo, Departamento de Antropología Biológica,  
Facultad de Humanidades y Ciencias de la Educación, Universidad de la República,  
Magallanes 1577. 11200. Montevideo, Uruguay.

E-mail: drpedro.hidalgo@gmail.com

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polymorphisms.**

**Abstract.** The way that immigrants integrate to recipient societies has been discussed for decades, mainly from the perspective of the social sciences. Uruguay, as other American countries, received different waves of European immigrants, although the details of the process of assimilation, when occurred, are unclear. In this paper, we use genetic markers to understand the process experienced by the Basques, one of the major migration waves that populated Uruguay, and its relation to other immigrants as well as to Native American and African descendants. For this purpose, we analyze the allele frequencies of ten ALU loci (A25, ACE, APOA1, B65, F13B, PV92, TPA25, HS2.43, and HS4.65) in three samples from Uruguay (two of Basque-descendants, one of non-

Basque-descendants) from two locations: Montevideo and Trinidad. No departure from Hardy-Weinberg expectations was observed, with the exceptions of the APO and D1 loci in the non-Basque descendants' sample. Our data show that the maximum genetic contribution in the three samples comes from Europe (78% to 88%) with minor African (10% to 15%) and Native American (0% to 10%) contributions to the present-day Uruguayan population. Genetic distances reveal that Basque-descendants from Trinidad cluster with Europeans, while both Montevideo samples cluster together and separate from other populations, showing two different ways of integration, related to the general characteristics of each regional population.

## **Introduction**

According to the 2011 National Census, Uruguay has a population of 3,286,314 inhabitants, 1,319,108 of them living in the capital city, Montevideo (INE 2012). The present population is the consequence of various processes, several of them shared with other Latin American countries. However, there are some differences that make the Uruguayan population unique, such as the variety of European source populations and the lack of Native American and African descendant communities.

In general terms it is possible to recognize several origins for European migratory waves, most of them occurring during the 19th and 20th centuries, that originate with the Iberians (mostly from the Canary Islands but also several Basques, and Portuguese) that occupied the region during colonial times (Pi Hugarte and Vidart 1969). The first wave of immigrants (1825-1842) came during the early times of Uruguayan independence and includes 40,000 to 45,000 individuals, mostly French Basques. More Basques came in a second wave (1842-1876), in this case mainly from Spain (Barrán and Nahum 1990; Marenales Rossi and Luzuriaga 1990). These two

“foundational” waves were composed mostly by males (81.8%, compared to 18.2% females). A third, “forced” wave occurred during the Spanish Civil War (1936-1939), and does also include several Basques (Arocena and Aguiar 2007). It should be emphasized that during the 19th century, migrants to Uruguay were mostly of Spanish, Portuguese and Italian origin, while during the 20th century, origins diversified, adding several thousands of Armenians, Jews from Western Europe, Central Europe and the Middle East, Russians, Swiss, and others (Vidart and Pi Hugarte 1969). In 1908 the proportion of foreigners in the population was approximately 18%, decreasing to 8% in 1963 and to a present-day minimum of 3% (INE 2012).

The process of assimilation, when it occurred, is unclear, and the coexistence in a common social space, shared by the immigrants and other ethnic groups (Africans, Natives, and their descendants), does not necessary imply a “melting pot”, a model inspired in 1907 I. Zangwill’s play about immigrants in the United States of America, in which immigrants quickly amalgamated with the receiver population. This model is opposed to “cultural pluralism”, in which ethnic groups retained some individuality. According to Yinger (1985), the process of assimilation includes four threads, which can be termed as structural, cultural, psychological, and biological (amalgamation). The amalgamation, which results in the gene pools being indistinguishable, depends on the characteristics of both the migrants and the recipients, and various barriers have been observed (linguistic, religious, or "racial") that can restrain the process. However, in general terms, the coexistence of different groups does not occur in conditions of equality. Nowadays in Uruguay, Native American-descendants and Afro-descendants claim for cultural diversity. As Olivera Chirimini (2004) said, Natives American as well as African descendants have been forgotten, occulted, and erased from the history of the Rio de la Plata region.

Since the mid-1980s the Uruguayan population has been studied in terms of their genetic structure and how it reflects the prehistoric and historic processes of the population. The tri-hybrid origin composed of Native Americans, Africans, and Europeans has been proven through blood polymorphisms and DNA, with estimates of around 10% (1% to 20%) Native American and 6% (4% to 15%) African contribution (Sans et al. 1997, 2006; Hidalgo et al. 2005). Different studies have shown that the matrilineal contributions to be between 20% and 62% Native American and between 7% and 15% African in different parts of the country (Bonilla et al. 2004; Gascue et al. 2005; Pagano et al. 2005a; Sans et al. 2006). Few studies have analyzed the Y-chromosome, showing low proportions (<7%) of Native American and African contribution (Bertoni et al. 2005, Pagano et al 2005b). These data are poorly correlated with the information given in the last Census (INE 2012), as only 4.9% of the population believes to have at least one Native American ancestor, and 7.8% believe to have at least an African one.

Recently, we analyzed the maternal contribution in a self-defined Basque-descent sample from the city of Trinidad, Flores, Uruguay (Sans et al. 2011). Unexpectedly, it showed that the Native American contribution was similar to the one found in a general sample of mixed ancestry from Montevideo (20%), with a smaller African contribution (2%). The analyses of surnames showed a different picture, with 91% of the individuals having a Basque paternal surname, while 41% had a Basque maternal surname.

To improve the comprehension of the ways of integration of European ethnic groups, we analyzed nuclear DNA markers in the above mentioned self identified Basque-descendant subpopulation from Trinidad, and we extended the study to Basque-descendants and non-Basque descendants from Montevideo, to answer two research

questions: 1) is it possible to observe significant differences among Basque descendants living in different areas of Uruguay? 2) are there differences between Basques and non-Basques living in the same area or does amalgamation occur?

For this purpose we selected Alu inserts, which comprise approximately 10% of human DNA (Rowold and Herrera 2000; Batzer and Deininger 2002). In the course of human evolution, the number of Alu type transposons has grown through a mechanism of self-copy (Batzer and Deininger 2002), being a testimony of both ancient and recent evolutionary processes. As the insertion of Alu elements is produced by a single mutational event, it is possible to establish the ancestral state (Rowold and Herrera 2000). Alu elements have the advantage of being easily identified and some of them have been characterized in many populations, including the Basque (Batzer et al. 1994; Comas et al. 2000; González-Pérez et al. 2003; García-Obregón et al. 2006; Romualdi et al. 2002; Stoneking et al. 1997; Terreros et al. 2005). In addition, Alu insertions have been validated for the estimation of the degree of mixing in hybrid populations, based on yielding a correct classification of 91.5% of individuals using discriminant functions (Gómez-Pérez et al. 2007).

## **Materials and Methods**

The first sample is composed by 58 subjects originally ascertained for anthropological studies, all of them descendant from Basques living in the city of Trinidad (BTD), Department of Flores, located 200 kilometers away from Montevideo in the southwest of Uruguay (described in Sans et al. 2011). A second sample is composed by 55 individuals of self-defined Basque descent from the city of Montevideo (BMVD), having at least one Basque grandparent or with a recognized Basque surname. The third sample is a subset of 70 individuals of European ancestry but without known Basque

ancestry, that is, without a known grandparent of Basque origin and lacking surnames identified as such, also taken from Montevideo (MVD). All individuals were asked for information regarding parental and grandparental place of birth. None of the individuals were close biological relatives at least at third grade, and all have at least two generations born in the country.

After a complete description of the study was provided, written informed consent was obtained from all subjects, and confidentiality was assured. The project was approved by the Facultad de Humanidades (Universidad de la República) Ethics Review Board.

### **DNA typing**

The genetic characterization of the Uruguay population was carried out by analyzing the polymorphism of 10 autosomal Alu insertions (A25, ACE, APOA1, B65, D1, F13B, PV92, TPA25, HS2.43, and HS4.65), typed using DNA isolated from peripheral venous blood, buccal swab and hair. The extraction of genomic DNA from the leukocyte fraction of the blood and buccal swab samples was carried out using the Miller et al. (1988) “salting out” technique, while DNA from hair was extracted following the protocol of Hidalgo et al. (2009). The extracted DNA was stored at -20°C.

### **PCR amplification**

The 10 *Alu* insertions were typed according to the conditions previously established for A25, ACE, APOA1, B65, F13B, PV92, and TPA25 loci by García-Obregón et al. (2006), while for HS2.43 and HS4.65, the conditions published by Ray et al. (2005) were used. The genotyping was carried out through electrophoresis in 2% agarose gel and staining using ethidium bromide, and visualizing the gels under UV light. In some

cases the results were confirmed in polyacrylamide gel electrophoresis (PAGE) with silver staining.

### **Population Affinities**

For the analysis of the genetic affinities of our samples, 16 populations from a broad continental context, typed for the same ten Alu loci used in our study, were selected from the literature (Table 1). We also included two admixed populations from the United States of America for comparative purposes.

### **Statistical Methods**

Allele and genotype frequencies of the Alu-insertion loci were obtained by direct gene counting (Li 1976). Divergence from the Hardy-Weinberg equilibrium (HWE) was determined at each locus by Chi-square, Levene's correction and exact test with the Biosys 2 program (Swofford and Selander 1997). The heterogeneity in allele frequencies among Uruguayan samples were performed with an exact test using the Genepop 4.2.2 package (Rousset 2008).

Genetic differentiation was measured by  $G_{ST}$  (Nei 1987) by using the gene diversity for the entire population ( $H_T$ ) and the average gene diversity for samples ( $H_S$ ) with the Dispan computer program (Ohta 1983). The significance of the allele heterogeneity in each locus among Uruguayan samples was calculated according to Srikumari et al. (1986).

Analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed to test the presence of genetic structure among samples with the GenAlEx 6.5 software (Peakall and Smouse 2012).



Genetic admixture was estimated by Elston's method (1971). We used the average allele frequencies for the European, African and Native American populations listed in Table 1. Allele frequencies for Native Americans were complemented using data for seven loci in Amazonian Indians (Battilana et al. 2006). The allele frequencies for each individual locus were pooled and weighted by arithmetical means.

Nei's  $D_A$  distance (Nei et al. 1983; Nei 1987) and Reynolds et al. (1983)  $F_{ST}$  distance among Uruguayan samples were computed. We also estimated Nei's  $D_A$  genetic distances between the Uruguayan samples and the populations listed in Table 1.  $D_A$  genetic distances were represented in Unweighted Pair Group Method with Arithmetic Mean (UPGMA) trees (Sneath and Sokal 1973) by means of the Neighbor program, generating 1,000 bootstrap replicates with Seqboot, and a consensus tree was obtained with Consense as implemented in the PHYLIP package (Felsenstein 2002).

## **Results**

The distribution of Alu insertion frequencies in the ten loci typed for the three Uruguayan samples is shown in Table 2. The highest allele frequency corresponds to the APOA1 locus in all samples. The lowest frequencies were observed for the HS2.43 and the HS4.65 loci. Table 3 shows the departure from HWE. Significant deviations from HWE ( $p < 0.05$ ) were observed for the loci APOA1, D1 and TPA25 in MVD, for locus D1 in BMVD, and for loci B65, D1 and F13B in BTD. Significant deviation from HWE using the Dunn-Sidak correction (Sokal and Rohlf 1995) were only found for APO and D1 loci in the MVD sample, at the 0.16% level.

For the ten Alu loci genetic heterogeneity for each paired sample was calculated, showing that both samples from Montevideo (MVD and BMVD) exhibit significant

differences with respect to Basques from Trinidad, but not between one another (Table 4).

The gene diversity and the coefficient of differentiation analysis are given in Table 5. The intrapopulational gene diversity ( $H_s$ ) for the Uruguayan samples ranged from 0.041 (HS4.65) to 0.458 (F13B) with a mean value of 0.302. The average value of  $D_{st}$  a measure of the gene diversity among samples, is 0.01 with large variation among loci (0.001 to 0.028). The gene differentiation coefficient relative to the total population ( $G_{ST}$ ) shows large variation from locus to locus (0.004 to 0.063), being the highest differentiation found for the B65 locus, and the least for PV92. The mean  $G_{ST}$  over all 10 loci is 3.1% (slightly lower than Wright's  $F_{ST} = 0.034$ ), with significant differences in five loci. The mean estimate of  $G_{ST}$  indicates modest but definite differentiation in Alu polymorphisms.

The result of the  $G_{ST}$  indicates that the fraction of the total gene diversity is fundamentally attributable to differences within the samples. Our analysis indicates that even with ten loci, reliable estimation of genetic variation could be obtained.

Hierarchical analysis of molecular variance (AMOVA) across individuals from the three samples revealed most of the genetic diversity to be due to the variation within samples (88%), while the variation among samples (12%) was small but significant (Table 6).

Genetic distances, based on Nei's  $D_A$  and using the 10 Alu loci, range from 0.87% to 3.6%, being the highest value between BTD and the Montevideo samples (Table 7). Similar results were obtained using Reynolds's distance (Table 7).

Using Elston's (1971) admixture method we estimated an average of 4% Native contribution and 12% African contribution (Table 8). The level of admixture estimated indicates a substantial European ancestry in the samples. In addition, these data show that the percentage of African alleles ranges from 9.6% to 15% in the Uruguayan

samples with a relatively low level of Native American contribution, albeit higher in BTD.

The UPGMA tree (Fig.1), clearly shows that the Uruguayan samples are placed in the cluster formed by the European populations and separated from the clusters formed by Africans and by Native Americans. However, the Montevideo samples (MVD and BMVD) appear separate within the European cluster, while the BTD sample is more related to the Spanish populations.

## **Discussion**

The pattern of genetic variation defined by the Alu insertion/deletion polymorphism in the Uruguayan population shows higher differentiation than the one observed when considering other systems as HLA, ABO and Rh (CDE) loci in the Uruguayan population as a whole (Hidalgo et al. 2007). Three statistics showed significant departure from HWE in several comparisons (7 in 30), leading to the conclusion that loci APO and D1 are not in HWE in the MVD sample. One possible explanation could be the occurrence of microevolutionary process that affected Uruguayan populations, such as founder effects, external and internal migrations, and consanguinity, as discussed below.

The Native American contribution found in Montevideo is similar to the one found by Sans et al. (1997) based on classical markers, while the estimate for Trinidad is close to the estimates for Uruguay as a whole according to the data by Hidalgo et al. (2005) based on Polymarkers. However, the African contribution determined using Alu insertions is slightly higher than the one found in previous work (Sans et al. 1997; Hidalgo et al. 2005). Differences in African contribution can be due to different factors, as sampling, lack of adequate data on parental populations for the estimates and/or

changes in the frequencies in the parental populations during time. It is interesting to note that Montevideo as a whole as well as Basque descendants from Trinidad have been studied for Native American maternal contributions showing similar results (21% and 20% Native, respectively) (Gascue et al. 2005; Sans et al. 2011).

The two samples from Montevideo form a tight cluster that could be explained by different patterns of mating and amalgamation inside this city, concordant with the concept of “melting pot”. On the other side, the sample of Basque-descendants from Trinidad forms a separate cluster. Moreover, comparisons of Nei’s and Reynolds’ distances showed that the distances between the MVD and BMVD samples are not significant but the distances between BTD and MVD, as well as between BTD and BMVD, are statistically significant. When including different world populations, the three samples formed a large cluster with the European populations, Trinidad being closer to West European populations, and all three samples apart from “United States Hispanics”, as well as from African and Native American populations. As mentioned before, the magnitude of Native American or African contributions cannot be the explanation, as Trinidad has more non-European contribution than the other two samples. Other reasons need therefore to be explored.

Local genetic structures are determined not only by the amount of gene flow but also by the characteristics, including size, of the populations that get in contact. During the last part of the *19th* Century and first half of the *20th* Century, Uruguay received a large amount of migrants from Europe and surrounding regions, process that ended soon after the end of World War II (Vidart and Pi Hugarte 1969). However, after 1910, internal migrations had an important role, being mainly from the countryside to the capital city, Montevideo (Campiglia 1968). When analyzing the population growth during the 20th. Century, while from 1908 to 1996 Montevideo multiplied its population

by 4.3 (probably as an effect of both types of migration), the population of Trinidad multiplied by 2.4, and a pronounced decline in growth rate is observed when considering years 1963 to 1996, when external migrations had finished (data from INE 2012): during this period, the population of Trinidad multiplied by 2.1 and 1.3 respectively. It is then possible to hypothesize that Montevideo became more exogamous due to incoming migrations, while Trinidad continued being relatively endogamous. A study about patterns of endogamy in Montevideo showed that Italians and French (mostly Basques) have the highest rates of endogamy, followed by the Spaniards, including in this last group a broad variety of origins. In all three cases, the endogamy of these groups is higher than in the population of Montevideo taken as a whole (Barreto and Sans 2000).

As a conclusion, it is possible to answer the two questions asked in the introduction of this study. The first question was related to the possibility of observing significant differences among Basque descendants living in different areas of Uruguay, and it has been proven that there are differences between the ones living in Trinidad related to the ones living in Montevideo. The second question, relative to differences between Basques and non-Basques living in the same area or the occurrence of amalgamation, it is possible to say that, in Montevideo, amalgamation has indeed occurred. However, we are not able to either confirm or dismiss the occurrence of amalgamation in Trinidad, as there is no data available for non-Basque descendants in the city or the surrounding region. Moreover, our data show that each population, with a different history and inhabiting a different region, need to be studied, as two populations with an apparent same origin (Basques) were found to differ in their present-day genetic structure. Consequently, we emphasize the importance of prospective analyses of the ancestral characteristics of the populations to be studied, especially when admixture

occurs as it is the case in Latin America. We strongly suggest the necessity of developing holistic views to deal with tri-hybrid population complexities. Multiculturalism is a reality in Uruguay, and it is not only related with sociocultural aspects, but it also affects the genetic structure of the populations and the effective amount of gene flow interchange (Harrison and Boyce 1972; Stobart 2005; Stone and Lurquin 2007)

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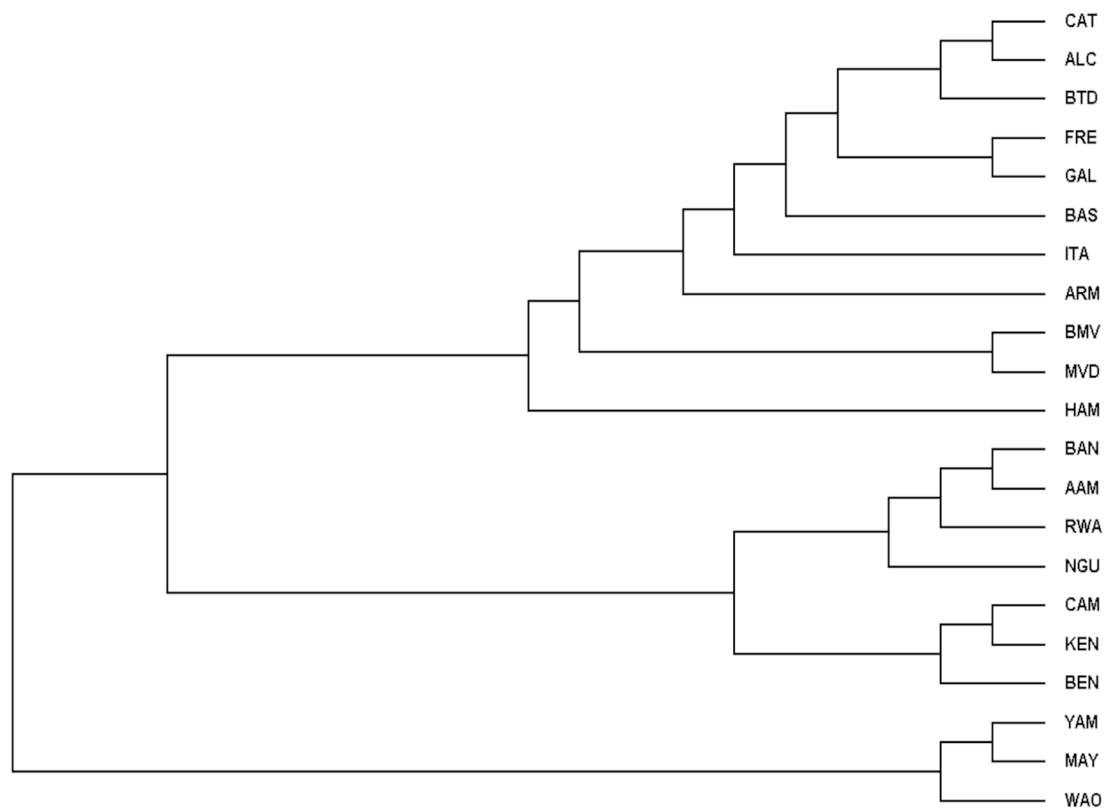


Figure 1. UPGMA tree of the Nei's  $D_A$  genetic distance matrix for the ten Alu insertions in the ten loci analyzed. Sample codes in Table 1.