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Genetic variability at 14 STR loci in the Puna population of north western Argentina

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Abstract Frequency data of the short tandem repeat (STR) loci D3S1358, vWA, FGA, D8S1179, D21S11, D18S51, D5S818, D13S317, D7S820, HUMTH01, D4S243, D18S535, HUMF13A1 and D12S391 were determined in the Puna population (Andean region from north western Argentina). In this study, 5 out of the 14 loci did not meet Hardy-Weinberg expectations. The excess of homozygotes observed in most of the markers could be due to a Wahlund effect and/or inbreeding. The frequencies were significantly different from those of other compared populations from Europe and America. Forensic parameters indicated that the 14 loci studied in the Puna region are highly discriminating, but the lack of Hardy-Weinberg equilibrium in some of the markers must be taken into account in the application of these results to paternity and forensic casework.

Keywords Short tandem repeats (STRs) · Profiler · Population genetics · Andean populations · Puna · North western Argentina (NOA)

Introduction

Different methodologies have been used in studies on genetic variability in human populations to assess their genetic composition, their relationships and the evolutionary factors to which they are subjected, as well as for forensic

purposes. Among these, short tandem repeats (STRs) have been increasingly used in the last decade because of their high level of informativeness (Tautz 1989; Edwards et al. 1991; Gill et al. 1995; Brinkmann 1996; Pérez-Lezaun et al. 2000; Tomàs et al. 2000, among others).

The Puna region in the Province of Salta (NW Argentina) is a typical Andean plateau at high altitude with arid or semi-arid conditions. The populations in this region have extremely marginal conditions, characterised by low temperatures, low oxygen pressure and poor soils. In addition, they are separated from other urban populations by poor and difficult roads. All these factors contribute to the isolation of these populations. There is little reliable information on the structure of the population in north western Argentina before contact with Europeans in the late fifteenth century. In addition, the lack of historical data for the post-contact period means that the exact origin or the degree of admixture of the inhabitants of this region (Lorandi 1992; Acreche and Smith 2001) is also unknown.

The settlement model in the Puna region is a disperse one with a low population density. In this Andean area, San Antonio de los Cobres (altitude 3,880 m) is the most populated locality (approx. 3,000 inhabitants) and it has public services such as health and education that people from the whole Puna region attend. Additionally, Cobres is a locality 71 km away from San Antonio de los Cobres, at an altitude of 3,850 m and with a total population of 141 individuals when the samples were collected.

Demographic and a few genetic data for these populations, based on blood groups and cytogenetic techniques, have been published elsewhere (Acreche et al. 1996, 1999; Acreche and Smith 2001; Caruso et al. 1999a, 1999b) but no data on STRs have been published to date.

The purpose of the present study was to report data on the STR frequencies in the population living in the Puna region for the application of these markers in forensic investigations and in population studies. Moreover, a comparison with European and other American populations was performed and forensically relevant parameters were calculated.

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Table 2 Statistical parameters for the STRs studied in the Puna population (*H* heterozygosity, *PD* power of discrimination, *CE* chance of exclusion, *CE2* chance of exclusion if only one parent and child are typed)

System	Number of alleles	H obs/exp	Deficiency of heterozygotes	<i>P</i> exact test	PD	CE	CE2
D3S1358	7	0.600/0.633	0.3653	0.1199	0.797	0.363	0.212
vWA	8	0.629/0.693	0.0000	0.0234	0.855	0.452	0.281
FGA	16	0.827/0.862	0.0005	0.0000	0.968	0.731	0.575
D8S1179	10	0.778/0.808	0.0002	0.2824	0.934	0.620	0.444
D21S11	13	0.796/0.843	0.0020	0.1953	0.954	0.681	0.513
D18S51	14	0.837/0.876	0.0014	0.2769	0.970	0.742	0.587
D5S818	7	0.613/0.723	0.0000	0.0002	0.886	0.503	0.321
D13S317	7	0.750/0.794	0.0087	0.0025	0.926	0.594	0.415
D7S820	8	0.728/0.705	0.0000	0.0000	0.862	0.460	0.289
HUMTH01	5	0.610/0.685	0.0087	0.0001	0.847	0.432	0.262
HUMF13A1	6	0.711/0.713	0.4199	0.9422	0.881	0.493	0.310
D4S243	8	0.794/0.732	0.9372	0.1705	0.839	0.444	0.277
D18S535	7	0.727/0.770	0.0790	0.0074	0.909	0.552	0.374
D12S391	9	0.738/0.737	0.6068	0.2603	0.883	0.497	0.323
Average	8.9	0.723/0.755	–	0.0000	1/3.217 E+14	0.999988	0.998816

Materials and methods

Blood samples from 107 unrelated individuals were collected and frozen at -20°C . Samples were collected in Cobres (at the school) ($n = 17$) and in San Antonio de los Cobres ($n = 90$, most of them at the hospital). According to genetic demographic information, these 90 samples were taken from individuals from different localities of the Puna area (Salta).

DNA was organically extracted by a standard protocol (Sambrook et al. 1989) and quantified spectrophotometrically. The STRs studied were D3S1358, vWA, FGA, D8S1179, D21S11, D18S51, D5S818, D13S317, D7S820, HUMTH01, D4S243, D18S535, HUMF13A1 and D12S391. The co-amplification of the first nine STR loci was performed using the AmpF/STR Profiler Plus PCR amplification kit (PE Applied Biosystems) following the manufacturer's instructions. PCR amplification of the other five tetrameric STR systems (HUMTH01, D4S243, D18S535, HUMF13A1 and D12S391) was achieved in singleplex under standard conditions. HUMF13A1 and D12S391 were analysed by using fluorescently labelled primers (JOE and 5-FAM, respectively). The HUMTH01 system was analysed using a GenePrint STR Systems kit (Promega). All loci were amplified in a GeneAmp PCR System 2400 (PE Applied Biosystems).

The nine markers amplified with the Profiler Plus, as well as the HUMF13A1 and D12S391, were analysed on an ABI Prism 310 DNA sequencer (PE Applied Biosystems). Samples (0.5 μl) were mixed with formamide (20 μl) and the internal standard size (GS-350 ROX) and denatured at 97°C for 5 min. GeneScan 2.1 analysis software was used for the interpretation of the results. Allele resolution of the HUMTH01, D4S243 and D18S535 systems was undertaken in non-denaturing conditions using 6% PAGE on a 0.75 mm thick gel. Alleles were visualised after gel staining with an ethidium bromide solution (Pérez-Lezaun et al. 1997). In all cases, standard size markers and specific allele ladders were used for allele designation.

The sequence analysis of one novel allele was carried out by isolating the amplified alleles from heterozygous individuals using the "crush and soak" method (Sambrook et al. 1989). Isolated fragments were reamplified and purified by using the QIAquick PCR purification kit (Qiagen). The sequence reaction was carried out using the BigDye Terminator Cycle Sequencing Ready Reaction kit (PE Applied Biosystems). Sequences were analysed on an ABI Prism 310 DNA sequencer (PE Applied Biosystems). Sequencing Analysis version 3.0 was used for the automatic analysis of the sequenced data.

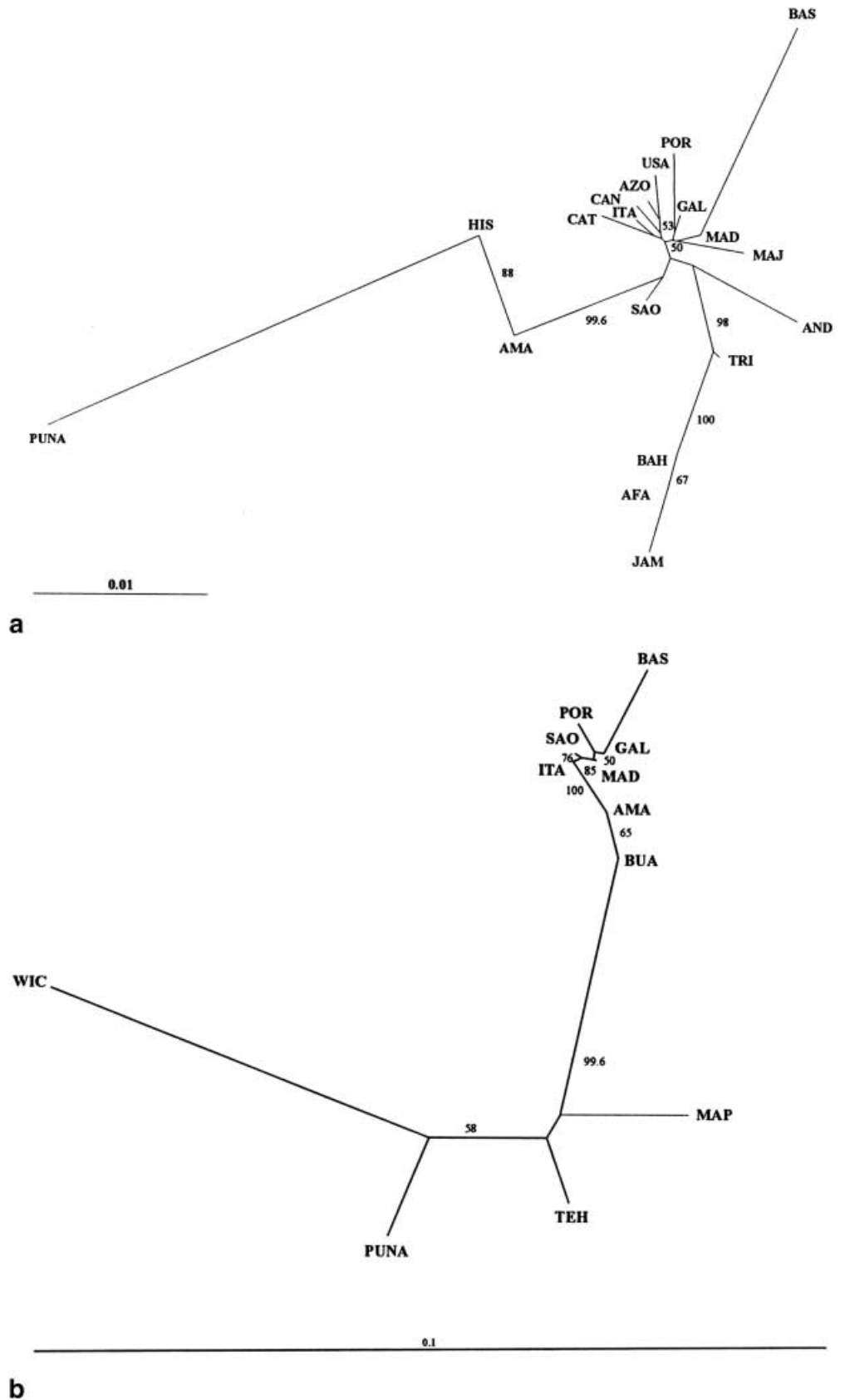
Statistical analyses

Allele frequencies were estimated by the gene counting method. The Hardy-Weinberg (HW) equilibrium was tested by calculating the exact *p*-values as proposed by Guo and Thompson (1992) and the deficiency of heterozygotes with the GENEPOP programme (Raymond and Rousset 1995). Independence among loci was estimated by means of genotype disequilibrium for each locus pair using Fisher's method (Raymond and Rousset 1995). When appropriate, the Bonferroni procedure (Weir 1996) was used to correct for multiple analyses.

The following European and American populations from the literature were used for comparisons: Italy (Garofano et al. 1998); Spain: Majorca (Tomàs et al. 2001a, 2001b), Catalonia, Andalusia, Basques (Gené et al. 1997; Gamero et al. 1998; García et al. 1998; Pérez-Lezaun et al. 2000), Galicia (Gusmão et al. 2000), Canary Isles (Gamero et al. 2000), Central Spain (Instituto Nacional de Toxicología-GEP); Portugal, Azores (Souto et al. 1998; Corte-Real et al. 1999; Anjos et al. 2000; Pérez-Lezaun et al. 2000); USA (Kupferschmid et al. 1999); Colombia (Yunis et al. 2000); Chile (Figueroa et al. 2000); Uruguay (Pagano et al. 2001); Hispanics, Bahamians, Jamaicans, Trinidadians, African Americans (Budowle et al. 1999); Brazil: Sao Paulo, Amazonas (Corte-Real et al. 2000) and Argentina: Buenos Aires, Mapuches, Tehuelches, Wichis (Sala et al. 1999; Gangitano et al. 2001). Due to the lack of data in the literature on D4S243, D18S535 and D12S391, these markers were not included in these analyses. Comparisons between populations were calculated by means of the F_{ST} statistic (Wright 1951) with the BIOSYS-1 program (Swofford and Selander 1989), using the maximum number of loci available for every pair of populations. Two neighbor-joining dendrograms (Saitou and Nei 1987) based on Reynolds' genetic distance (Reynolds et al. 1983) were built. Dendrogram robustness was assessed by carrying out 1,000 bootstrap iterations using the PHYLIP package (Felsenstein 1993).

Furthermore, the potential usefulness of the markers from a forensic point of view was evaluated by means of the power of discrimination (PD) following Fisher's method (Fisher 1951), the observed and expected heterozygosity ($1 - \sum p_i^2$ where p_i is the frequency of the *i*th allele in the locus), the a priori chance of exclusion if the mother is known and typed (CE) (Chakravarti and Li 1983) and the probability of paternity exclusion if only one parent and child are typed (CE2) (Chakraborty and Jin 1993).

Fig. 1 **A** Neighbor-joining dendrogram based on Reynolds' genetic distance for 19 European and American and American populations and the 9 STRs markers of the Profiler kit. The numbers indicate the bootstrap values (>50) in percentages (*ITA* Italy, *MAJ* Majorca, *CAT* Catalonia, *AND* Andalusia, *BAS* Basques, *GAL* Galicia, *CAN* Canary Islands, *MAD* Central Spain, *POR* Portugal, *AZO* Azores, *USA* USA, *HIS* Hispanics, *BAH* Bahamians, *JAM* Jamaicans, *TRI* Trinidadians, *AFA* African Americans, *SAO* Sao Paulo, *AMA* Amazon and *PUNA* Puna region). **B** Neighbor-joining dendrogram based on Reynolds' genetic distance for 12 European and South American populations and 5 STRs (TH01, F13A1, vWA, D7S820, D13S317). The numbers indicate the bootstrap values (>50) in percentages (*ITA* Italy, *BAS* Basques, *GAL* Galicia, *MAD* Central Spain, *POR* Portugal, *SAO* Sao Paulo, *AMA* Amazon, *BUA* Buenos Aires, *MAP* Mapuches, *TEH* Tehuelches, *WIC* Wichis and *PUNA* Puna region)



Results and discussion

Allele frequencies of the 14 STR loci investigated are shown in Table 1. In the D18S51 marker, one new allele not yet described in the literature was found in the Puna population which had an electrophoretic mobility corresponding to an allele 7. Sequencing data have confirmed that it had seven units of the repetitive motif (AGAA). When the Hardy-Weinberg equilibrium test (Table 2) was calculated by the exact p -values, 7 out of 14 tests were significant. When the Bonferroni correction for multiple tests was applied, five out of the seven previous p -values remained significant. Moreover, the test for deficiency of heterozygotes was also significant for these five markers (FGA, D5S818, D13S317, D7S820 and HUMTH01).

Taking into account that 10 out of the 14 markers studied showed an excess of homozygotes, the lack of equilibrium could be due to inbreeding (the coefficient of inbreeding F in these 10 systems ranged from 0.04 to 0.15). Moreover, demographic data and previous studies on blood groups in localities of the Puna region have also indicated high inbreeding coefficients (Acreche and Smith 2001). However, it must be pointed out that the number of alleles and other parameters of variability (PD and CE) (Table 2) were, in general, within the range of those found in other Caucasian populations studied. Thus, these parameters were not as low as we could have expected due to endogamy. The fact that most of the samples were collected in San Antonio de los Cobres from individuals living in smaller localities, in conjunction with the conclusions of Acreche and Smith (2001) that the Puna region could be composed of semi-isolated demes with differences between frequencies in some blood groups, could lead to the conclusion that the deficiency of heterozygotes observed in this study may be the result of the Wahlund effect. Nevertheless, it is not always easy to determine if a deficit of heterozygotes is due to inbreeding or to the Wahlund effect (Hedrick 2000). However, the heterozygote frequency of all the loci should be affected by inbreeding, whereas only the heterozygote frequency of those loci with allelic frequency variation in subpopulations should be reduced by the Wahlund effect. In the markers studied in the Puna region, 10 showed a deficit of heterozygotes, 2 showed an excess of heterozygotes and 2 the number of expected heterozygotes. Therefore, we cannot discard the conclusion that the lack of equilibrium is due to the Wahlund effect. Moreover, and supporting this hypothesis, when the samples collected from Cobres are excluded, the rest of samples are still in disequilibrium, while that from Cobres agrees with HW equilibrium. It would be convenient to study the frequency of STRs in different localities of this region in greater depth in order to understand the possibly complex genetic structure of the population of the Puna area better and unravel the different evolutionary factors that could have affected it.

When the pair-wise comparisons between loci were carried out, 7 out of 91 tests were significant. When the Bonferroni procedure was applied, there was no evidence

of significant allele association, with the exception of the D3S1358-FGA and D3S1358-D12S391 pairs.

The comparisons between this population and other American and European populations were calculated by means of the F_{ST} values. Statistically significant differences were found between the Puna population and all the other populations. Figure 1 A shows the neighbour-joining tree based on Reynolds' genetic distance. It can be seen that most of the European and USA populations occur in a central cluster with no internal structure, as reflected by the short interpopulation branches and low bootstrap values. Basques (who are known to differ genetically from other Spanish and European populations) were linked to the tree through a longer branch. The Caribbean populations, together with African Americans, clustered in a second and significantly differentiated branch (98%) and the South American populations included in this analysis clustered on a third group with the Hispanics. In this group, the Sao Paulo population was closer to European and USA populations, while the populations of Amazonia, Hispanics and Puna were on the longest and most robust branch (99.6% of the bootstrap replications) with the Puna clearly being the most differentiated population. In Fig. 1 B it can be seen that most of the South American populations were linked to the tree through a longer and robust (100%) branch. Puna is grouped with Amerindians, reflecting the Amerindian component that this population must have, although considerable distance between them can be observed.

Statistical parameters of genetic variability, such as heterozygosity and the number of alleles, are presented in Table 2. All the systems showed heterozygosity values $\geq 60\%$, with a mean value of 0.723, which is lower than the average detected in Caucasians (approx. 0.8). The number of alleles ranged from 5 to 16. Some parameters of forensic interest are also shown in Table 2. The 14 loci showed a combined discrimination power (PD) of 1 in 3.217×10^{14} individuals and a combined chance of exclusion (CE) of 0.999988. Even when only one parent and child were typed the CE was 0.998816.

Therefore, the a priori statistical power of this set of STRs in the Puna region indicated that they were very informative, although the lack of Hardy-Weinberg equilibrium in some of the markers must be taken into account in the application of these results in paternity and forensic casework. The genetic differences found between different South American populations support the importance of developing more detailed local databases for forensic DNA purposes, based on reference data from each of the appropriate populations and not on general databases based on random or combined samples.

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Samples were collected with informed consent and this study was approved by the University of the Balearic Islands.

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