

Biodiversity of South American Indians. A collation of multifactorial and single gene marker systems between Andean and tropical forest tribes

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ABSTRACT

This article represents an effort to summarize very briefly some of the main findings obtained during 25 years of work among South American Indian populations. Patterns of variation of multifactorial traits such as dental traits, dermatoglyphics, anthropometrics and craniometrics, as well as migration data and single marker gene loci variation, are examined. Whenever possible, results obtained in Andean groups are compared with similar findings derived from tropical forest Indian data. It is concluded that the differences in magnitude of genetic variation encountered are ultimately the result of different cultural adaptations to regional environmental conditions.

INTRODUCTION

Our group in Santiago has been concerned with describing and interpreting the biological variability of South American populations, specially Andean Indians, for the last 25 years. So far, emphasis has been given to the study of multifactorial characters, such as dental traits, dermatoglyphics and anthropometrics (Rothhammer, 1987), as well as single gene marker systems, including blood groups, serum proteins, erythrocyte enzymes, HLA antigens, mtDNA haplotypes and VNTR's. (Rothhammer *et al.*, 1990, Deka *et al.*, 1992; Bailliet *et al.*, 1994; Merriwether *et al.*, 1995). Since some of these traits can also be identified in ancient human remains, our studies were extended to prehistoric populations, including craniometric and dental trait variability (Rothhammer and Silva, 1990) and, more recently, also the distribution of mtDNA haplotypes (Merriwether *et al.*, 1994; Rothhammer and Bianchi, 1995). In what follows, we shall briefly review some of our results and compare these, when available, with similar findings obtained in tropical forest tribes.

Dental traits and dermatoglyphics

The usefulness of dental traits and dermatoglyphics in contributing substantially to the understanding of population structure is limited by their relatively low genetic determination. Despite this fact we established that the congruence of these traits with gene markers appears to vary with levels of populations differentiation. The association remains insignificant until the racial level of differentiation is considered. Below this level (i.e. at the tribal or intratribal level) distance matrices based on dental traits or dermatoglyphics depart from a similar genetic marker analysis, which reflects more accurately the patterns of biological relatedness among South American tribal subpopulations. (Rothhammer *et al.*, 1977; Palomino *et al.*, 1977).

Anthropometric variation

The anthropometric among-village variability was studied by us in the Aymará, an Andean population inhabiting altitudinal gradients in northern Chile. (Rothhammer and Spielman 1972). We were able to show that in this particular environment, anthropometric differences

are primarily related to altitudinal differences among villages, whereas in tropical forest populations living in more homogenous environments (such as the Yanomama) inter-village anthropometric differences reflect the intra-tribal genetic microdifferentiation (Rothhammer, 1976).

Craniometric variability

The independent contribution of climate, altitude, chronology, and geographic location of archeological sites to craniometric variation, were analyzed in a sample of 1,119 prehistoric skulls from South America. Geographic location was responsible for the highest proportion of craniometric variation, followed by climate and altitude. It was concluded that in pre-Columbian South America, geographic isolation has partially prevented gene flow from counterbalancing craniometric microdifferentiation produced by founder effects (Rothhammer and Silva, 1990).

Migration data and variable marker gene loci

Bodmer and Cavalli-Sforza (1968) suggested summarizing migration data in the form of migration matrices, where the birthplaces of parents are given as columns and those of offspring as rows. Each scalar of the matrix is divided by the row totals, including the birthplaces of parents located outside the geographic area considered in the analysis. The resulting "backward stochastic migration matrix" can be manipulated algebraically to generate an estimate of the expected Wahlund variance in a given population.

Bodmer and Cavalli-Sforza's (1968) algorithm was applied by us to the Aymará and generated a Wahlund variance of 0.0106, which is approximately reached after 12 generations. The observed Wahlund variance for variable marker gene loci is 0.0116. This value is reduced 10%, that is to 0.0104, if gene frequencies are adjusted for the inclusion of relatives (Rothhammer *et al.*, 1990).

According to these findings the bulk of genetic variation encountered among the Aymará is the result of chance, despite the fact that this population is exposed to contrasting, rigorous environmental conditions. The small number of inhabitants of most villages reduces drastically the probability that all alleles are transmitted from one generation to the next. Given the actual village sizes, this process would theoretically lead to the fixation of alleles after approximately 200 generations. In practice the random loss has been compensated for by intervillage migration and gene flow from adjacent areas, probably giving rise to a "steady state". Although chance is also responsible for most genetic variation in tropical forest Indians, the mechanisms originating and maintaining it are somewhat different. Instead of genetic drift counteracted by intervillage migration, "founder" and "lineal" effects are only partially offset by gene flow resulting from village fusions.

Several authors found in Yanomama Indians a good correspondence of among-village biological distances,

particularly genetic ones, with geographic locations. It was suggested that the tendency of Yanomama villages to progressive fissioning and the recent centrifugal expansion of the tribe may result in unusually large intervillage distances, factors which may play a role in the degree of correspondence observed (Neel *et al.*, 1974). In contrast with these findings, previous reports have failed to detect the same tendency among the Aymará. Only a very low, statistically not significant correlation was obtained by us between electrophoretically determined marker genes and geographic distances among 14 Aymará villages studied. On the basis of gene frequencies for 24 loci published by several authors, we computed estimates for seven Aymará and seven Yanomama villages, located in an area of similar dimensions, as well as for 12 Amerindian tribes (Rothhammer *et al.*, 1990). It is noteworthy that tropical forest aborigines exhibit, on average, higher Wahlund variances and lower heterozygosity values than Andean Indians. When comparing Wahlund variance estimates with those obtained in 12 Amerindian tribes, it turned out that the seven Yanomama villages are 36% and the Aymará villages 15% as variable as the Central and South American Indians.

This notable difference in the magnitude of the genetic variation encountered between Andean and tropical forest tribes is directly attributable to different migration patterns, which in turn are a consequence of different social organizations. The constant fissioning of villages (and kinship subgroups) in the tropical forest, which is the direct result of social tensions, but more generally of the practice of a slash and burn technology, results in higher homozygosity and intervillage variation. Andean tribes are sedentary. Moreover, their migration patterns reflect zonal complementarity and regional interactions rather than a search for independent cultivating ground.

We may conclude that although chance is largely responsible for the genetic variation observed in indigenous Andean populations as well as tropical forest tribes, there are observable differences in magnitude between the two groups. Furthermore, the differences seen are the result of different migration patterns, which are part of their social structures and represent in each case adaptations to regional environmental conditions.

mtDNA variation

Recently, in collaboration with colleagues from the University of Pittsburgh, we obtained the distribution of mtDNA lineages for six Aymará villages (Merriwether *et al.*, 1994). The frequencies varied greatly between villages. Lineage A exhibit a range of 0.10, lineage B of 0.50, lineage C of 0.32 and finally lineage D of 0.18. In order to compare among-village with among-tribal variation, we computed the coefficients of variation of G_{st} (for details please see Nei, 1973). G_{st} is defined as D_{st}/H_t where D_{st} is the between sub-population and H_t the total variation encountered. The computed value of G_{st} for the Aymará villages was 0.186. That means that 19% of the variation for mtDNA lineages was found between villages and 81% within villages. Using

Table I - Variation of multifactorial and single gene marker systems at the village and tribal levels.

| | Villages | | | Tribes | | |
|---------------------|----------------|----------------|-----------------|----------------|----------------|-----------------|
| | H _t | H _s | G _{st} | H _t | H _s | G _{st} |
| Dental traits | 0.331 | 0.294 | 0.112 | 0.361 | 0.319 | 0.116 |
| Dermatoglyphics | 0.379 | 0.367 | 0.029 | 0.362 | 0.349 | 0.036 |
| Traditional markers | 0.311 | 0.299 | 0.038 | 0.372 | 0.342 | 0.080 |
| mtDNA | 0.437 | 0.355 | 0.186 | 0.733 | 0.592 | 0.192 |

the published data for mtDNA lineages in South American tribes, we obtained an estimate of 0.192, which is not significantly different. It seems interesting to point out that mtDNA lineages are more variable at village and tribal levels than the other morphological and genetic traits traditionally employed in population studies (Table I) probably as a consequence of drift due to reduced effective population number. We note that this higher variability of mtDNA haplotypes must be taken into account when comparing extinct with extant populations. It may erroneously be concluded that two populations have an independent origin, despite the fact that both are closely related or vice-versa.

RESUMO

Este artigo representa um esforço para resumir muito rapidamente algumas das principais descobertas obtidas durante 25 anos de trabalho entre a população indígena da América do Sul. Padrões de variação de traços multifatoriais tais como dermatoglifos e características dentárias, antropométricas e craniométricas, bem como os dados de migração e variação de "gene loci marcadores", são examinados. Sempre que possível, resultados obtidos em grupos Andinos são comparados com dados similares de índios da floresta tropical. Concluiu-se que as diferenças em magnitude da variação genética encontrada são o resultado de diferença na adaptação cultural às condições regionais de ambiente.

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