

Admixture and Relationships of the Population of Jacobina, Bahia, Brazil

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ABSTRACT As part of the Cornell-Bahia project on leishmaniasis, the people of Jacobina in the state of Bahia in northeastern Brazil were studied for five genetic polymorphisms: ABO blood groups, hemoglobin variants, PGM1, 6PGD, and adenylate kinase. A maximum likelihood method of calculation of frequency of genes for these traits indicates that the ancestry of the people is 45% African, 43% Portuguese, and 12% Brazilian Indian. This estimate is similar to previous estimates of admixture in the people of northeastern Brazil, except for more African and less Caucasian ancestry. Previous distance relationships, based upon physical traits only, showed the population of Jacobina to be similar to Seminole Indians of Florida and equally distant from Whites and Blacks. While not strictly comparable, the genetic and morphologic pictures of relationships are compatible and show concordance with surnames. The presence of Hemoglobin C and the frequencies of alleles of PGM1 and 6PGD in the Jacobina population are consistent with the greater importation of Africans into Brazil from Costa de Mina on the Guinea Coast than from Angola. © 1996 Wiley-Liss, Inc.

The search for genetic factors underlying the tropical parasitic disease leishmaniasis provided an opportunity to observe physical features and determine genetic polymorphisms in the people of Jacobina, a town in Bahia in northeastern Brazil. Their morphology and pigmentation, the relationship of physical traits to surnames and to reproductive fitness, and their implications for admixture have been the subject of previous reports on this population (Pollitzer et al., 1982; Pollitzer, 1983; Pollitzer and Barefoot, 1984; Pollitzer et al., in press).

The people of northeastern Brazil have significant ancestry from Whites (especially Portuguese), Blacks, and Indians, and their biological and cultural heritage has been the subject of extensive investigation. The present article reports phenotype and gene frequencies of the Jacobina people for five polymorphic genetic systems, estimates admixture, and compares these with previous estimates of admixture in northeastern Bra-

zil. These genetic findings are related to morphologic studies of Jacobinans and other populations and to the geographic origin of African slaves. The results are also of potential value for evaluating genetic predisposition to disease.

MATERIALS AND METHODS

Jacobina, 225 km (135 miles) northwest of Salvador, was chosen for research conducted jointly by the Medical School of Cornell University and the Federal University of Bahia. Its location is shown in Figure 1. Of 493 families in the study area, 200 were selected for study by complete ascertainment of parents on the basis of duration of residency, cohabitation time, and age of mother. The

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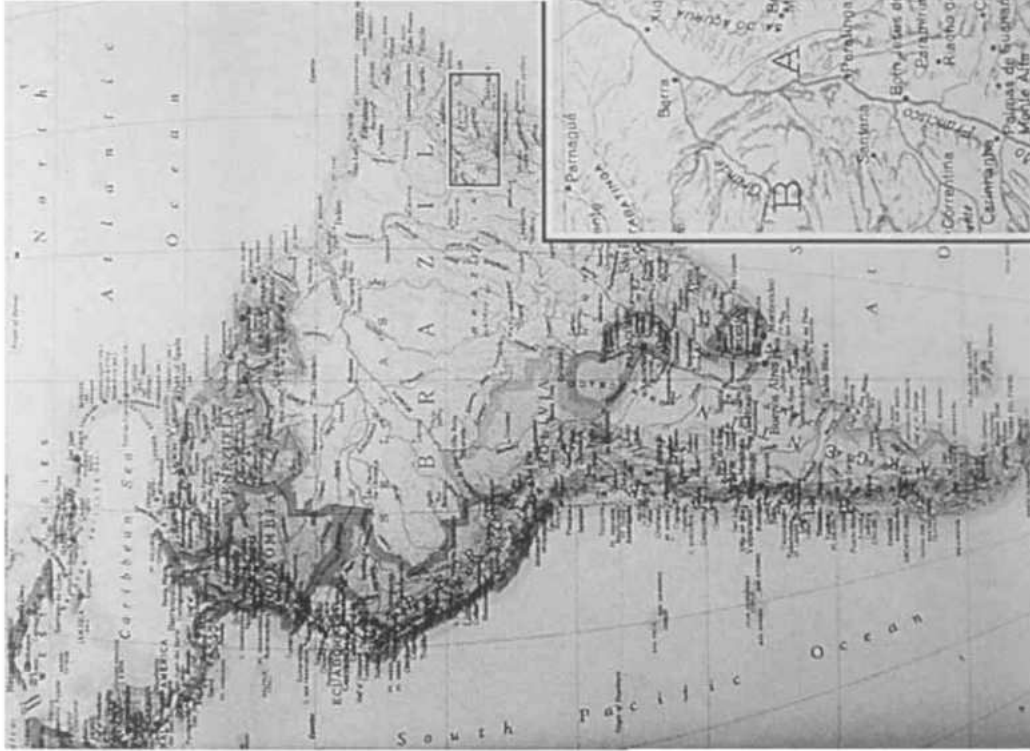


Fig. 1. Location of Jacobina.



TABLE 1. Phenotype frequencies in Jacobina and comparative gene frequencies in three ancestral populations

System	Phenotype	No.	Frequency	Allele	Jacobina	White	Black	Indian
ABO	A	89	.3346	A	.2010	.3040	.1570	0
	B	31	.1165	B	.0963	.0660	.1500	0
	AB	12	.0451	O	.7027	.6300	.6930	1.0000
	O	134	.5038					
Total		266						
Hb.	AA	257	.9245	A	.9591	1.0000	.9100	1.0000
	AS	19	.0683	S	.0300	0	.0660	0
	AC	2	.0072	C	.0109	0	.0240	0
Total		278						
PGM1	1-1	160	.5755	1	.7548	.7357	.7566	.8161
	2-1	101	.3633	2	.2452	.2643	.2434	.1839
	2-2	17	.0612					
Total		278						
6PGD	AA	251	.9061	A	.9639	.9864	.9333	1.0000
	AC	26	.0939	C	.0361	.0136	.0667	0
Total		277						
AK	1-1	267	.9604	1	.9760	.9530	.9912	1.0000
	2-1	11	.0396	2	.0240	.0470	.0088	0
Total		278						

current report is on 278 adults of the parent generation only, as the heterogeneity of family size in the filial generation significantly disturbed genetic equilibrium. Genetic loci analysed are ABO blood groups, hemoglobin variants, PGM1, 6PGD, and adenylate kinase (AK). G6PD, also determined, was not included in the present analyses, since phenotype identification was somewhat disturbed among females. All enzymes were determined by methods described in Harris and Hopkinson (1976).

For calculating admixture, White, Black, and Indian groups are identified as recognized locally. Gene frequencies for these three hypothetical parent populations vary with different systems. Those for Whites are from Portuguese data; those for Blacks are both Bantu and Sudanese Africans; and those for Indians are Brazilian, chiefly of the Ge-Pano-Carib linguistic group. ABO and hemoglobin allele frequencies are the same as those of a previous study of admixture in northeastern Brazil that used 17 genetic systems (Krieger et al., 1965). PGM1, 6PGD, and AK frequencies, not then available, are in Roychoudhury and Nei (1988). All frequencies are averages weighted by sample size.

The maximum likelihood method of Krieger et al. (1965) was used to calculate admixture. It assumes that the initial matings giving rise to the ethnic classes are not assortative with respect to the loci involved, that the Hardy-Weinberg equilibrium holds,

that the immediate effect of selection is negligible, and that gene frequencies of the sample are derived from and representative of the three parent populations only.

Following the notation of Morton (1964), let N, I, and C be the proportions of Negro, Indian, and Caucasian admixture, respectively. Therefore $C = 1 - N - I$. Let m_ϕ = observed number of individuals of phenotype ϕ , determined by locus G with alleles G^1, G^2, \dots, G^k in frequencies p_1, p_2, \dots, p_k . Then the expected frequency of ϕ is $P(\phi) = c_{ij}p_i p_j$ and $c_{ij} = 0, 1, \text{ or } 2$. On the further assumption that $p_{iN}, p_{iI}, \text{ and } p_{iC}$ are the frequencies of G^i in the ancestral populations, known without error, $p_i = Np_{iN} + Ip_{iI} + Cp_{iC}$. Then the Maximum Likelihood Scores are

$$U_N = \sum m_\phi \sum_{i=1}^k \frac{\partial \ln P(\phi)}{\partial p_i} \{p_{iN} - p_i\}$$

$$U_I = \sum m_\phi \sum_{i=1}^k \frac{\partial \ln P(\phi)}{\partial p_i} \{p_{iI} - p_i\}$$

RESULTS

The number and frequency of phenotypes in each of the five genetic systems in Jacobina, the allele frequencies calculated from them, and the comparable allele frequencies in each of the three parent populations are shown in Table 1. The Jacobinans are predominantly in Group O, followed by Group

TABLE 2. Estimate of racial admixture in Jacobina

Group	Proportion	Standard error
White	.4265	.0623
Black	.4545	.0602
Indian	.1190	.0490

TABLE 3. Homogeneity of estimates

System	Goodness of fit	D.F.	Departure from overall model	D.F.
ABO	1.899	3	1.205	2
Hb	3.540	3	0.156	1
PGM1	0.057	2	0.018	1
6PGD	2.856	2	1.516	1
AK	0.501	2	0.531	1
Total	8.853	12	3.426	6

A and then Group B. They have 7% sickle cell hemoglobin, and less than 1% Hemoglobin C; no other abnormal hemoglobins were found. In the PGM1 system, 1-1 predominates as in most populations; the great majority are 6PGD A and AK 1-1. No rare variants were detected in any of the systems. In the 12 alleles shown, the Jacobina sample is intermediate between Blacks and Whites in all alleles except that for Group O.

The maximum likelihood estimate of proportion of admixture is shown in Table 2, along with its standard error. Black predominates with 45%, followed closely by White with 43%; Indian is only 12%. The maximum likelihood scores for racial admixture by each genetic system and analysis of variance both between and within systems indicate a good homogeneity among systems as shown in Table 3.

DISCUSSION

Soon after the Portuguese settled Bahia in northeast Brazil in the 1530s, slaves were imported from Africa. Of the some four million brought to Brazil over three centuries, those who entered Bahia came early and constituted about one-third of the total (Curtin, 1969; Goulart, 1975; Eltis, 1987a,b). Of these, some 850,000 came from the "Costa da Mina" around the Bight of Benin on the Guinea Coast, and another 350,000 from Angola (Goulart, 1975). As they spread from the port at Salvador into the interior, the Portuguese settlers and their African slaves encountered native Indians, and both conflict and interbreeding occurred among the three groups.

Studies of northeastern Brazil have revealed much information of genetic, medical, and anthropologic value (Morton, 1964; Krieger et al., 1965; Krieger, 1970). Beginning in 1962, 1,068 migrant families, consisting of 6,864 people, were examined as they passed through the Hospedária do Imigrantes in São Paulo on their way to the interior states. Most were from Bahia and Minas Gerais. Selected on the basis of high fertility, genetic variability, consanguinity, and infant mortality, they were interviewed, given medical examinations, and had blood and saliva collected. Interethnic crossing was responsible for only a slight increase in genetic heterozygosity, and no significant increase occurred in pathological conditions and abnormalities over that expected by chance alone (Krieger, 1970). Analysis of gene frequencies revealed 59% White, 30% Black, and 11% Indian admixture (Krieger et al., 1965).

Azevêdo and colleagues (Azevêdo, 1980; Tavares-Neto and Azevêdo, 1977) demonstrated the concordance of morphology, genetics, and surnames among the people of Bahia. Since Blacks adopted devotional names related to the Catholic church, Indians took names of plants and animals, and Whites had Portuguese names, these surnames, inherited like the Y chromosome, are a guide to ancestry. Surnames along the route of migration from the coast to the interior, like physical features and gene frequencies, reflect the decline of both Black and White and the increase in Indian influence. The analysis of surnames and physical traits in the Jacobina population sample bears out this association (Pollitzer et al., 1982).

Division of the sample of 398 Jacobinans of the current study into four classes on the basis of pigmentation and physical traits showed some expected morphological differences from lightest to darkest individuals in facial features, notably an increase in nose width and lip thickness. In stature and in lower segment length in both sexes, "White" and "Dark" were greater than the intermediate classes of "Light" and "Medium" (Pollitzer et al., 1982).

Factor analysis of physical traits revealed a Body Size factor that accounts for 50% of the variance, an Ethnic Factor that accounts for 35%, and a third or Facial Factor more difficult to interpret. Only the Ethnicity Factor is significantly associated with surnames (Pollitzer and Barefoot, 1984).

Assortative mating between "heads of households" (usually but not necessarily mates) is highly significant for skin color and lip thickness as well as age. Those with lighter skin color reported more conceptions but also greater reproductive loss through miscarriages, stillbirths, and child mortality; darker mothers appear to have a higher percentage of surviving offspring (Pollitzer et al., in press). Such trends, if consistent and widespread, could have a selective significance. The estimate of a greater percentage of Black admixture in the Jacobina sample than in the earlier study of northeastern Brazil could reflect the ethnic composition of the city which houses a large number of mine laborers of low socioeconomic status. It could also reflect the use of different genetic polymorphisms as markers of the ancestral populations. It is doubtful that selection operating for 20 years would be responsible for this difference.

To gain some idea of the physical nature of the Jacobina population, Mahalanobis's Distance, based on stature, nose length and width, and face length and width, was used to compare the Jacobina sample with three unrelated populations: Old American Whites measured by Hrdlička (1925), Gullah Blacks of coastal South Carolina and Seminole Indians of Florida both measured by Pollitzer and coworkers (1958, 1970), and Sioux Indians of the North American Plains measured by Sullivan (1920). The Jacobinans are most similar to the Seminoles, slightly more like the Black than the White population, and farthest removed from the Sioux (Pollitzer et al., 1982). Given the history of the Seminoles, with their close association with runaway slaves from South Carolina and Georgia, their similarity to the Jacobina population is not surprising, if we assume that west African ancestry in both groups is responsible for a seeming morphological convergence. The dissimilarity of the Jacobinans to the Sioux Indians in physical traits is consistent with the minimal admixture of the Jacobinans with full-blood Brazilian Indians as revealed by gene frequencies. Their approximately equal distance from Old American Whites and from Gullah Blacks in morphology also parallels their almost equal admixture from Whites and Blacks as indicated by gene frequencies.

Knowledge of gene frequencies in Africa invites comparison with those of Jacobina for any indications of the influence of the

volume of slave trade from the Guinea coast vs. that from Angola. Some genetic loci are uninformative. Alleles for ABO groups are fairly similar in both coastal regions; both A and B run around 15% (Mourant et al., 1976). Hemoglobin S is not helpful for comparison either as both African areas have four or five times as much of the sickle cell allele as Jacobina (Livingstone, 1985). However, the presence of Hemoglobin C in Jacobina indicates probable ancestry from the Benin region as the allele is about 5% there and virtually absent in Central Africa. The Jacobina frequency of the PGM1 1 allele (.755) is much closer to those of the Yoruba tribe of Nigeria (.769) and the people of the Camerouns (.745) than to that of the Angola population (.849) (Roychoudhury and Nei, 1988). Similarly, the 6PGD A allele in Jacobina (.964) is nearer to that of the Yoruba tribe (.945) and Camerouns people (.954) than to that of the population of Angola (.917) (Roychoudhury and Nei, 1988). The AK-1 allele in Jacobina (.976) is slightly below both that for the people of the Guinea Coast (1.000) and Angola (.995) (Roychoudhury and Nei, 1988).

Thus, the available informative gene frequencies are at least consistent with the far greater importation of Africans into Bahia from the Costa da Mina than from Angola. Data from Cavalli-Sforza et al. (1994) further support this conclusion.

Since both genetic disease and genetic predisposition to infectious disease may be dependent upon population ancestry, gene frequency data that relate modern people to their likely ancestors are of importance.

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