CHAPTER 15
ADIMIXTURE ESTIMATES AND SELECTION IN TLAXCALA

by

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Estimates of genetic admixture in human populations, based upon allelic frequencies, can be traced back to the original formulations of Bernstein (1931). Bernstein's formula, based upon the proportionate contribution of one population to the genetic makeup of the hybrid, may be expressed as follows:

\[ m = q_x - Q, \]

\[ q - Q \]

where \( m \) is the proportion of admixture, \( Q \) and \( q \) are the allelic frequencies in two parental populations and \( q_x \) is the frequency of the same allele in the hybrid population. This method of estimating admixture was first applied by da Silva (1949) and Ottensooser (1944) on populations of Brazil; by Glass and Li (1953), and Roberts (1955) on Afro-American groups; and by Matson (1970), Nagel and Soto (1964), and Saldhana (1968) on Amerindian peoples. These investigations based their estimates of admixture (\( m \)) in Afro-American populations on a number of different alleles—including \( F_y^a, R^C (cDe), R^C (CDe) \) and more recently the \( Gm^{ab} \) haplotype. Similarly, \( D^b \), brittle cerumen, and \( Gm^{fb} \) have been described as useful markers that can be used to distinguish hybrid groups of Indian and European ancestry.

Instead of basing estimates of admixture upon information from a single locus or allele, a number of investigators have combined information from various loci for the computation of a composite \( m \). Roberts and Hjorns (1962, 1965) proposed a least-squares measure of \( m \) which assumes \( p \) parental populations with known gene frequencies, and no selection or drift. Similarly, Krieger, et al. (1963) computed \( m \) for a large triracial hybrid population in north-eastern Brazil utilizing a maximum likelihood solution. These methods were compared, contrasted and modified by Elston (1971), and using the same data sets he demonstrated that roughly similar results may be obtained irrespective of the method of computation. Chakraborty (1975) has recently presented a promising new method for estimating racial admixture based upon the probability of gene identity.

A number of investigators have attempted to detect the action of natural selection by searching for loci with seemingly anomalous \( m \) values. For example, Workman, Blumberg, and Cooper (1963) used 14 polymorphic traits from Claxton, Georgia, to show that this approach identified certain loci such as \( G-6-PD \) and \( HbS \) otherwise believed to be subjected to natural selection. Hertzog and Johnston (1968), noting elevated estimates of \( m \) utilizing the \( d \) allele of the Rhesus system, concluded that selection is operating against the \( D \) allele and in favor of \( d \). A recent critical re-evaluation of the evidence for selection by Adams and Ward (1973) concluded on a more cautionary note arguing that errors in estimating the gene frequencies of the parental populations may explain many of the observed deviations at certain loci.

The purpose of this chapter is four-fold: (1) to quantify the rate of gene flow from the Spanish into the Mexican Indian gene pools during the creation of a Mestizo population; (2) to estimate the genetic affinities of two Mexican populations to the surrounding populations through the use of various genetic distance measures; (3) to determine if the various measures of genetic distance reflect the estimated proportion of hybridization experienced by a population; (4) to determine if the admixture estimates for Mestizo populations can be employed as indicators of the actions of natural selection on the specific loci controlling the blood groups and proteins.

The Tlaxcalan Valley was chosen for the
study because of the historically documented low rates of gene flow into the Valley. This was partially the result of a military alliance between the Tlaxcaltecans and the Spanish directed against the Aztecs of the adjoining valley, and partially because of the cultural integrity of the populations in the Valley. While the more isolated populations within the Valley experienced little, if any, intermixture with the Spanish, the administrative towns of the state of Tlaxcala underwent considerable miscegenation.

METHODS

The proportion of Spanish admixture with the Indians of Tlaxcala was estimated by five different methods. Three of these methods, Roberts and Hiorns', true least squares and maximum likelihood, were analyzed by means of a computer program written by R. C. Elston (1968). Biracial hybridization was also computed through a weighted multiple regression analysis (using assumed parental frequencies) and through the summation of $m$ values for individual loci weighted by variance. The regression method assumes that only sampling errors are involved, examines $X = a\sqrt{n} + b$, and if $a$ is not significantly different from zero, $b$ provides an estimate of intermixture. These methods are based upon Bernstein's formula which assumes $q_s = \text{Spanish}$, $q_t = \text{Indian}$, and $q_m = \text{Mestizo (Tlaxcala-hybrid)}$ gene frequencies. By standard method:

$$X = \frac{q_m - q_s}{q_t - q_s},$$

where $X$ is the proportion of Indian ancestry, and

$q_m = Xq_t + (1 - X)q_s = X(q_t - q_s) + q_s$

if we assume that:

$$\sigma^2q_m = \frac{q_m(1 - q_m)}{2N_m},$$

$$\sigma^2q_t = \frac{q_t(1 - q_t)}{2N_t},$$

and $\sigma^2q_s = 0$. PUBLICATIONS IN ANTHROPOLOGY

If it is further assumed that Spanish gene frequencies are known without error (i.e., they represent "true" or parametric values in ancestors), then it can be shown that, approximately

$$1\sigma^2_m = m^2 \left\{ \frac{\sigma^2q_m}{(q_m - q_s)^2} + \frac{\sigma^2q_t}{(q_t - q_s)^2} \right\}$$

In particular it derives from the approximate variance ($V$) of a ratio:

$$V_{(r)} = r^2 \left\{ \frac{V_x}{x^2} + \frac{V_y}{y^2} - \frac{2\text{cov.}(xy)}{xy} \right\}$$

where $r = x/y$

The covariance (cov.) of $x$ and $y$ is only due to the appearances of similar terms in $x$ and $y$. In particular, if $m = \frac{q_m - q_s}{q_t - q_s}$, then

$$\text{cov.}[(q_m - q_s), (q_t - q_s)] = \sigma^2_s.$$

If Spanish values are not subject to sampling error, covariance $= \sigma^2 = 0$. We use formula

$$1\sigma^2_q = \frac{pq}{2N}$$

for codominant loci

and $\frac{1 - q^2}{4N}$ for dominant loci.

This method further obtains the weighted mean of the estimates $m_i$ by

$$m_i = \frac{\sum m_i \frac{1}{V_{m_i}}}{\sum \frac{1}{V_{m_i}}}$$

and the variance of the weighted mean is

$$\frac{1}{\sum \frac{1}{V_{m_i}}}$$

Mahalanobis' generalized distances (1936) are computed between pairs of populations in this study using gene frequency data as de-
The rationale for utilizing the method of Mahalanobis (1936) is described by Crawford et al. (1974). Allelic frequencies used in the computation of genetic distances between pairs of Mexican populations were compiled from various publications. The frequencies of the Tlaxcaltecan, Spanish, and Ahican populations used in the calculation of the $D^2$ are summarized in Table 75 (Crawford et al. 1974).

### RESULTS

Table 76 summarizes the proportion of Spanish admixture with the Indians of Tlaxcala estimated by five different methods, four of them utilizing 39 different alleles and the 5th method described above utilizing 12 alleles. Three of the methods, multiple regression, Roberts and Horr's, and least squares, provide the most similar estimates of hybridization. This is not surprising, since the last two methods are based upon a least squares solution to the problem of the estimation of parental contribution using random sets of independently assorting loci. In contrast to Elston's (1971) findings, maximum likelihood estimates differ most from the other methods even when all alleles are used in the formula. Significant differences in the estimates of hybridization can also result from the use of particular loci and alleles.

A composite Nahua population, based upon the gene frequencies from eight Indian tribes, was substituted for San Pablo del Tlapa. Table 76 contains the proportions of Indian ancestry, standard deviations, and differences in Spanish and Indian gene frequencies by loci. Using all 12 alleles and the formula described in Crawford et al. 1974, the proportion of hybridization can also result from the use of particular loci and alleles.
Monte as a parental population in a multiple regression analysis. The computed \( m \) for Tlaxcala was identical to the value estimated when San Pablo allelic frequencies were used to represent the parental Indian population \( (q_I) \). The only detectable difference between the two estimates was in the standard deviation, which was .034 when San Pablo was utilized and .070 when the eight Nahua tribes were grouped to represent \( q_I \). The high standard deviation for the composite Nahua population reflects the heterogeneous nature of the grouping.

### Table 77. Proportion of Indian ancestry in the hybrid population presented by locus.

<table>
<thead>
<tr>
<th>Gene</th>
<th>Proportion Indian Ancestry</th>
<th>Standard Deviation</th>
<th>( q_I - q_A )</th>
</tr>
</thead>
<tbody>
<tr>
<td>FY'</td>
<td>.769</td>
<td>.0580</td>
<td>.554</td>
</tr>
<tr>
<td>E</td>
<td>.730</td>
<td>.1130</td>
<td>.278</td>
</tr>
<tr>
<td>M</td>
<td>.661</td>
<td>.1366</td>
<td>.221</td>
</tr>
<tr>
<td>O</td>
<td>.643</td>
<td>.1663</td>
<td>.280</td>
</tr>
<tr>
<td>P'</td>
<td>.719</td>
<td>.1899</td>
<td>.153</td>
</tr>
<tr>
<td>Hp'</td>
<td>1.053</td>
<td>.2519</td>
<td>.150</td>
</tr>
<tr>
<td>C</td>
<td>.518</td>
<td>.3699</td>
<td>.085</td>
</tr>
<tr>
<td>D'</td>
<td>1.357</td>
<td>.3762</td>
<td>.056</td>
</tr>
<tr>
<td>Gc'</td>
<td>1.750</td>
<td>.5028</td>
<td>.072</td>
</tr>
<tr>
<td>Jk</td>
<td>1.197</td>
<td>.7291</td>
<td>.071</td>
</tr>
<tr>
<td>PGM'</td>
<td>1.625</td>
<td>1.5876</td>
<td>.024</td>
</tr>
<tr>
<td>S</td>
<td>5.750</td>
<td>32.4147</td>
<td>.004</td>
</tr>
</tbody>
</table>

Because some African admixture has been detected in a number of Mexican populations by Lisker, Zarate, and Loria (1966) and Cordova, Lisker, and Loria (1967), and because of the elevated presence of the \( R_4(cD_e) \) chromosomal segment, a triracial hybrid analysis was attempted for Tlaxcala. Spanish, West African and Tlaxcaltecan (represented by San Pablo) frequencies were utilized initially for a multiple regression estimate of hybridization. This analysis suggested a small proportion of African admixture (6.7 percent), which reduced the estimate of the Caucasian component, but did not affect the Indian contribution to the Mestizo population (see Table 78).

With the exception of the maximum likelihood method, which consistently but mildly overestimated the Indian contribution to the Mestizo gene pool, the results of the triracial analysis, irrespective of methods, were fairly consistent. Fewer alleles were used to represent the parental populations in the triracial model because of the paucity of reliable data on some systems.

One test of the accuracy of each method of estimating admixture is the degree of agreement of the observed and expected values of gene frequencies in the hybrid group. This test is accomplished by multiplying the estimated contributions from each parental population by the frequency of the gene in that population. The sum of the two products in a biracial hybrid (or three in a triracial), which is the expected frequency of a gene, is then compared with the observed value of that gene frequency in the hybrid group to form a chi-square statistic. A total chi-square value for all genes is also obtained (Pollitzer 1964). There are no significant differences in the chi-square values between the five methods employed. However, Table 78 indicates that Duffy, Lewis, and the group specific components (GSC) are the most deviant loci, while Diego and PTC tasting observed frequencies differ slightly from the expected values (at \( P < 0.05 \)).

Four of the five loci found to deviate from the expected values in dihybrid analysis are also significantly deviant in the trihybrid

### Table 78. Estimates of triracial hybridization based upon four different methods.

<table>
<thead>
<tr>
<th>Methods</th>
<th>Number of Alleles*</th>
<th>Percentage of Contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Spanish</td>
</tr>
<tr>
<td>1. Roberts and Hoens</td>
<td>26</td>
<td>24.43</td>
</tr>
<tr>
<td>2. Least Squares</td>
<td>26</td>
<td>23.87</td>
</tr>
<tr>
<td>3. Maximum Likelihood</td>
<td>26</td>
<td>15.93</td>
</tr>
<tr>
<td>4. Multiple Regression</td>
<td>23</td>
<td>22.90</td>
</tr>
</tbody>
</table>

* Hybridization estimates are based upon nine loci: ABO, Duffy, Kidd, Diego, MNS-CHRM, MN, Rhesus, Kell, and Lewis.
model. However, the PTC locus, significantly deviant in the biracial hybrid, falls within the expected values in the triracial model. In contrast, the Kidd locus does not deviate in the biracial model, but does deviate significantly in the triracial analysis. Most important in this analysis is a comparison of the sums of the chi-square values for all loci; those in the dihybrid model are almost twice the values observed in the trihybrid sum (See Tables 79 and 80). These differences suggest that the trihybrid model better fits these data than the assumption that the Mestizo population resulted only from the admixture of Spanish and Indian parental groups.

If the admixture with the Spanish began in the Valley of Tlaxcala at the time of contact, A.D. 1519, and continued until the present time i.e., 1969 when gene frequencies were first calculated for Tlaxcaltecan populations, then 18 generations of 25 years each must have transpired. Assumming that 30% of the Mestizo gene pool is of Spanish and West African origin and that 18 generations of continuous hybridization have transpired, then the rate of gene flow can be computed as follows:

$q_M - q_S = (1 - m)^k = 1 - q_S$, where $k$ is the number of generations during which admixture has occurred. Let $M = 30\%$, the contribution of Spanish to Hybrid Tlaxcaltecan, so that $m = 1 - \frac{k}{1} - M$. Thus, where $K = 18$ generations, $m = 1.96\%$ per generation. However, the period of actual gene flow from the Spanish administrators into the Valley of Tlaxcala ended in 1750 (Halberstein, Crawford and Nutini, 1973). Thus, most of the gene flow took place in approximately nine generations followed by a period in which the Spanish and African alleles segregated throughout the urban Tlaxcalan centers. Using nine generations of gene flow, the rate per generation becomes 3.88% per generation—a sizeable rate of gene flow!

**GENETIC DISTANCES**

Genetic distances were computed to determine to what extent hybridization and gene flow affect the affinities of geographically proximal populations. The genetic distances, summarized in Table 81, indicate that a "gross" relationship exists between genetic and geographical distances in Mexican populations. Two exceptions to this purported relationship between geography and genetics appear in San Pablo-Tabasco and Puebla-Chiapas. San Pablo population exhibits a closer genetic affinity to that of the State of Tabasco than geography would dictate, while the Puebla/Chiapas genetic distances suggest populations separated by considerable geographic separation. Deviations from the isolation-by-distance model can, in part, be accounted for by the various degrees of Spanish and African admixture and the possible action of genetic drift or similar selective forces (as well as social factors). It is interesting to note that the Mestizo (Tlaxcala) population has a genetic distance to the Spanish (Caucasian) centroid which is less than one-half the distance to the Indian population (San Pablo). These distances are in agreement with the admixture estimates, which suggest that approximately 30% of the Mestizo gene pool is of "foreign" origin.

**DISCUSSION**

The five methods of estimating admixture indicate that from 23 to 32% of the Mestizo gene pool is of Spanish and/or West African origin. The gene flow, which undoubtedly began with Spanish contact in 1519, continued until 1750, the latest recorded date for the influx of Spanish administrators. Spanish gene flow into the Mestizo gene pools probably ceased about 1750, after 230 years or more than nine generations of admixture. In light of the small number of Spanish residents in the three administrative centers at any one time, it is surprising to note that close to 30% of the Mestizo gene pool is of Spanish and West African origin. Several interrelated demographic factors have been advanced by Halbertstein, Crawford, and Nutini (1973) to explain this excessive parental contribution of the Spanish. (1) The Valley of Tlaxcala underwent considerable depopulation, from approximately 300,000 persons in 1519 to its all-time low of 100,000 in the year 1600. This
Table 79. Biracial analysis: comparison of Chi-square values for different methods of calculating proportions of admixture.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Degrees of Freedom</th>
<th>Methods</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Roberts and Horn's</td>
<td>Least Squares</td>
<td>Maximum Likelihood</td>
<td>Multiple Regression</td>
<td>Bernstein's M</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hiorn's</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>1. ABO</td>
<td>2</td>
<td>2.4580</td>
<td>2.5658</td>
<td>5.3137</td>
<td>2.4720</td>
<td>3.4203</td>
</tr>
<tr>
<td>2. Duffy</td>
<td>1</td>
<td>23.0492*</td>
<td>23.9745*</td>
<td>38.1999*</td>
<td>23.1715*</td>
<td>29.6239*</td>
</tr>
<tr>
<td>3. Kidd</td>
<td>1</td>
<td>1.7398</td>
<td>1.6516</td>
<td>0.7142</td>
<td>1.7242</td>
<td>1.9575</td>
</tr>
<tr>
<td>4. Diego</td>
<td>1</td>
<td>5.6011*</td>
<td>5.4040*</td>
<td>3.9971</td>
<td>5.5642*</td>
<td>4.3934*</td>
</tr>
<tr>
<td>5. MN</td>
<td>1</td>
<td>0.1102</td>
<td>0.1538</td>
<td>1.4170</td>
<td>0.1168</td>
<td>0.5397</td>
</tr>
<tr>
<td>7. HP</td>
<td>1</td>
<td>2.7056</td>
<td>2.6193</td>
<td>1.4540</td>
<td>2.6929</td>
<td>2.1170</td>
</tr>
<tr>
<td>8. AP</td>
<td>2</td>
<td>5.6011</td>
<td>5.4040°</td>
<td>3.9971°</td>
<td>5.5642°</td>
<td>4.3934°</td>
</tr>
<tr>
<td>9. PGM</td>
<td>1</td>
<td>0.6910</td>
<td>0.6834</td>
<td>0.5878</td>
<td>0.6894</td>
<td>0.6411</td>
</tr>
<tr>
<td>11. PTC</td>
<td>1</td>
<td>5.1078°</td>
<td>4.8329°</td>
<td>1.9139</td>
<td>5.0590°</td>
<td>3.4158</td>
</tr>
<tr>
<td>12. Cerumen</td>
<td>1</td>
<td>0.9451</td>
<td>1.1101</td>
<td>4.2775°</td>
<td>0.9697</td>
<td>2.2597</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>5.2610</td>
<td>5.2426</td>
<td>5.4360</td>
<td>5.2527</td>
<td>5.2247</td>
</tr>
</tbody>
</table>

* P < .05.

The founding population of the City of Tlaxcala probably had a high proportion of foreign genes. (2) According to Snow (1969), the precontact settlements in Tlaxcala were situated on bluffs and valley walls because of the poor drainage in the low-lands. The City of Tlaxcala was founded by the Spaniards as an administrative center after the valley floor was drained.

Table 80. Triracial analysis: comparison of Chi-square values for different methods of calculating proportions of admixture.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Degrees of Freedom</th>
<th>Methods</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Roberts and Horn's</td>
<td>Least Squares</td>
<td>Maximum Likelihood</td>
<td>Multiple Regression</td>
<td>Bernstein's M</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hiorn's</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td>1. ABO</td>
<td>2</td>
<td>0.9859</td>
<td>1.0838</td>
<td>3.2116</td>
<td>1.8315</td>
<td></td>
</tr>
<tr>
<td>2. Duffy</td>
<td>1</td>
<td>10.2739*</td>
<td>10.8486*</td>
<td>22.0033*</td>
<td>17.8481*</td>
<td></td>
</tr>
<tr>
<td>4. Diego</td>
<td>1</td>
<td>5.6649*</td>
<td>5.4253*</td>
<td>3.5431</td>
<td>5.0147*</td>
<td></td>
</tr>
<tr>
<td>5. MN</td>
<td>1</td>
<td>5.6649*</td>
<td>5.4253*</td>
<td>3.5431</td>
<td>5.0147*</td>
<td></td>
</tr>
<tr>
<td>6. Rhesus</td>
<td>6</td>
<td>2.6128</td>
<td>2.5303</td>
<td>1.4930</td>
<td>2.1681</td>
<td></td>
</tr>
<tr>
<td>7. HP</td>
<td>1</td>
<td>1.1384</td>
<td>1.0394</td>
<td>0.5094</td>
<td>1.5756</td>
<td></td>
</tr>
<tr>
<td>8. AP</td>
<td>2</td>
<td>2.4747</td>
<td>2.4415</td>
<td>2.2016</td>
<td>2.5576</td>
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</tr>
<tr>
<td>9. PGM</td>
<td>1</td>
<td>24.6928*</td>
<td>24.2078*</td>
<td>18.2047*</td>
<td>21.3304*</td>
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</tr>
<tr>
<td>10. Lewis</td>
<td>1</td>
<td>0.9908</td>
<td>0.8432</td>
<td>0.2244</td>
<td>1.9415</td>
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</tr>
<tr>
<td>11. PTC</td>
<td>1</td>
<td>0.9106</td>
<td>1.0915</td>
<td>3.7399</td>
<td>1.4888</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>3.5564</td>
<td>3.5212</td>
<td>3.5566</td>
<td>3.7120</td>
<td></td>
</tr>
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</table>

* P < .05.
Table 81. Genetic distances (D') from San Pablo del Monte, Tlaxcala, Caucasian and African populations to multivariate centroids representing six Mexican states (Crawford et al., 1974).

<table>
<thead>
<tr>
<th>Populations</th>
<th>San Pablo</th>
<th>Tlaxcala</th>
<th>Nayarit-Jalisco</th>
<th>Vera Cruz</th>
<th>Puebla</th>
<th>Oaxaca</th>
<th>Chiapas</th>
<th>Tabasco</th>
<th>Caucasian</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Tlaxcala</td>
<td>78.705</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Vera Cruz</td>
<td>11.982</td>
<td>54.485</td>
<td>32.543</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Puebla</td>
<td>16.928</td>
<td>137.842</td>
<td>33.499</td>
<td>37.714</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Oaxaca</td>
<td>51.015</td>
<td>78.044</td>
<td>94.727</td>
<td>49.549</td>
<td>107.193</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Chiapas</td>
<td>15.990</td>
<td>87.869</td>
<td>28.608</td>
<td>13.130</td>
<td>34.953</td>
<td>55.162</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Tabasco</td>
<td>19.532</td>
<td>37.022</td>
<td>41.612</td>
<td>11.618</td>
<td>58.970</td>
<td>22.783</td>
<td>12.903</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Caucasian</td>
<td>394.925</td>
<td>145.496</td>
<td>478.020</td>
<td>342.244</td>
<td>491.271</td>
<td>448.569</td>
<td>658.665</td>
<td>469.249</td>
<td>341.628</td>
</tr>
</tbody>
</table>

Valley experienced little or no admixture with the Spanish, the gene pool of the administrative cities contained a disproportionate percentage of "Spanish" genes. (4) The Spanish contact with the City of Tlaxcala lasted for 230 years. During eight or nine generations, constant gene flow of high magnitude could account for 50 percent of the estimated admixture. A fourth possible cause for the high incidence of "Spanish" genes in the Mestizo gene pool is assortative mating based upon Spanish morphological features. Individuals with Spanish ancestry may have constituted preferred mates and thus contributed disproportionately to the genetic composition of the hybrids.

On the basis of total chi-square values for the blood loci (see tables 79 and 80), it appears that the triracial model of hybrid origin for the Mestizo gene pool provides a better fit than does the biracial model. The sum of the chi-square values for the various blood loci, assuming a triracial origin of the Mestizos, are almost one half the values of the chi-square totals for the biracial model. These values suggest that the Mestizo population received gene flow from an African component as well as a Spanish parental population. Historically, the Spanish conquest of Mexico is well documented; however, there is no evidence for the existence of slave populations in the highlands of Tlaxcala. The "African" genes may have come into Tlaxcala in one or both of the following ways:

1. With the "Spanish genes," carried by the soldiers of Moorish ancestry, or
2. By Indians from the coast or from Puebla whose ancestors had interbred with slaves.

The evidence is strongly in favor of the first alternative, because the population is in genetic equilibrium for all 23 loci, and because a fitting of the multiple regression curve for a trihybrid population, when compared to a bihybrid population, results in a change in the contribution of the Caucasians but not the Indians. However, the presence of eight or nine percent African genes in the Mestizo gene pool is considerable. The demographic data suggest that gene flow from outside the valley is a recent phenomenon. If the African genes were constantly flowing into the community then the equilibrium might be disrupted.

Santiago Genoves, who led the formal discussion at the symposium in Mexico City, argued that the African genes probably flowed into Tlaxcala from Puebla, which had a large Mulatto and West African slave population. The answer probably lies somewhere between the two positions, and it is likely that both hypotheses are correct.

Workman (1968) has suggested that if estimates of ancestral frequencies are reasonably accurate, the admixture studies may be used to detect the action of natural selection. He computed admixture estimates "m" (Bernstein, 1931) for a number of blood loci in American Black populations and suggested that the data indicate that selection may be operating on the Hb^a, Hb^b, HP^a, G-6-PD, and A^1 alleles. Although the hemoglobin and G-6-PD loci were not tested in the present study, because African admixture was not suspected,
the ABO and haptoglobin loci have been tested for possible selection. The chi-square analysis illustrated in Table 5 and 6, however, suggest that selection does not appear to be acting on these loci in the Tlaxcalan population. However, the Duffy locus exhibits exceptionally high chi-square values, suggesting the possible action of natural selection. Reed (1969) has suggested that the Duffy blood group system Fy" gene may be the best available marker for estimating "m" in American Blacks, but judging from these data, the Duffy system cannot be recommended for calculation of \( m \) in Mexican Indian populations.

In sum, while there is minor disagreement in the results based upon the various methods of calculating admixture, the geographic and genetic distances show some agreement. It appears that geographic distance and admixture with the Spanish are the primary factors involved in determining the distribution of the allelic frequencies in Mexico.

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