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I am submitting herewith a thesis written by Corey Shepard Sparks entitled "Reassessment of Cranial Plasticity in Man: A Modern Critique of Changes in Bodily Form of Descendants of Immigrants." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Masters of Arts, with a major in Anthropology.

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REASSESSMENT OF CRANIAL PLASTICITY IN MAN: A MODERN CRITIQUE OF CHANGES IN BODILY FORM OF DESCENDANTS OF IMMIGRANTS

A Thesis

Presented for the

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Degree

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Corey Shepard Sparks

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DEDICATION

This thesis is dedicated to the life of Edwin Claude Sparks Jr. (1943-2000), who taught me more about life than I can ever express in words.

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ABSTRACT

The reconstruction of biological relationships in humans using the cranium relies on the assumption that the multivariate distances derived from cranial data have a genetic component. This notion has been criticized by some authors based mainly upon one study of Franz Boas. This study focused on the idea that within one generation the cranial form of a population can be significantly altered by a sudden change in the environment. Boas's original study has been cited for the past ninety years as evidence of cranial plasticity.

A modern critique of Boas's original study has been long overdue and is pursued herein using modern genetic and statistical methods. Heritabilities of cranial traits derived from Boas's data reveal a high genetic component to the traits. Multivariate distances between parents and their American-born offspring are small, and when Boas's original comparisons are conducted using modern statistical methods, the significant changes witnessed by Boas are often due to random chance. While small differences do exist between parents and offspring, these differences are negligible when compared to inter-ethnic differences.

Findings indicate that the genetic component of the human cranium is substantial, and cranial data can be used as a proxy for genetic data. Critiques of studies based upon population comparisons based on

craniometric data need to be reconsidered in biological anthropology based on the small environmental component contained in cranial variation.

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Chapter 1

Introduction

Craniometric data in biological anthropology has a long history and has been utilized in a variety of studies. Many of these studies focus on the reconstruction of prehistoric human populations (Carlson, 1976; Jantz and Owsley, 2001; Key and Jantz, 1981; Sokal and Uytterschaut, 1987) or on the diversity of the human species in regards to the evolution of modern humans (Howells, 1973; Relethford, 1994; Relethford and Harpending, 1994). The findings of many of these studies point to the idea that the patterns of variation seen in human cranial variation can be generalized to patterns of genetic variation. In other words, cranial data are very often utilized as a proxy to understand genetic similarity or differentiation between human groups, past and present. This idea is often acceptable in the literature on the subject, but criticisms of craniometry run far back into the history of our discipline. Many critiques are based on the idea that human cranium exhibits such a plastic response to the environment that studies utilizing craniometric data for population studies are biologically meaningless due to such a profound environmental effect (Armelagos and Goodman, 1998; Goodman, 1995). The basis of the arguments for cranial plasticity focus on a number of early twentieth century studies by Franz Boas and his students (Boas, 1911; Goldstein, 1943; Shapiro, 1939). These studies consist of anthropometric

observations on a parental generation of immigrants and their offspring, who are born in a new environmental setting, usually America. The arguments contained in these studies focus on the amount of differentiation between the immigrant parents and their offspring. The conclusion is that the plasticity of the human body, especially the cranium, in response to a new environment is so great that the proxy use of anthropometric/craniometric data should be utilized with extreme caution in population comparisons. The arguments of these studies were well conceived in their day, but none of them utilizes any statistical methodologies except for direct subtraction of means. In modern biological anthropology, which was once called the proving grounds of multivariate statistics (van Vark and Howells, 1984), most modern studies utilize often complex statistical methodologies. The fact is that when the early studies were performed, the analytical techniques and the raw computer power were still sixty to seventy years in the future. The modern analysis of data collected many years ago is not a new idea (see Jantz, 1995; Jantz et al., 1992; Szathmary, 1995), but the data from these studies, while being public record for as much as seventy years, have been untouched by modern methods. The analysis of the data gathered in these early studies is paramount to the understanding of the nature of human variability.

The purpose here then is to perform a thorough modern statistical analysis of the first, and largest, of these studies, that of Franz Boas (1910). Boas's study and its findings will be described in detail in the next chapter.

With multivariate quantitative genetic methods, estimates of heritability of anthropometric traits are performed; these are intended to show the overall genetic component of the phenotypic variation of the cranial complex. Several multivariate distance analyses are performed showing the low degree of differentiation caused by the American environment and the proportionality of phenotypic and genotypic data. Some of the procedures used in Boas (1910) are replicated using univariate linear modeling and t-tests. These analyses are intended to examine the relative stability of the human cranium in response to one generation of environmental change and the degree of genetic information contained in cranial data.

Chapter 2

Literature Review

Changes in Bodily Form of Descendants of Immigrants

Between 1909 and 1910 Franz Boas, under the auspices of a congressional committee referred to as the Immigration Commission, conducted a study entitled “Changes in Bodily Form of Descendants of Immigrants (Boas, 1910; 1912a).” The ultimate goal of this massive undertaking was to determine if the American environment had any effect on the physical form of the increasing European immigrant population. The underlying motive of the commission, while not stated directly, concerned the notion that the European immigrants would change their social, psychological, and political way of life upon immigrating to the United States (Boas, 1910). The study of Boas then examined another aspect of the suspected societal change expected by the commission, an effort to show any change in the bodily form of immigrants and their descendants in response to the American environment such that they formed a new American type. The data collection was accomplished by Boas and a team of thirteen anthropometrists trained by Boas. The team went around to schools in the New York area and measured children, and made follow up visits to the homes of many immigrants in the area (Boas, 1910). Data on

nearly 15,000 individuals of Hebrew, Sicilian, Bohemian, Hungarian, Polish, Italian, and Scotch ancestry were collected during this period.

In what must have been a massive computational undertaking, the data on segments of the sample were analyzed, tabulated and discussed in a series of reports for the Immigration Commission (Boas, 1910; 1912a). The findings dealt mainly with the fact that the cranial index, once thought to be a distinctive feature of the major human races, changed dramatically between European-born parents and their American-born offspring. The findings were condensed and discussed in Boas (1912b). The conclusions were as follows: American-born descendants of immigrants differ in type from their European-born parents, and the difference varies by magnitude and direction between populations. The effect of the American environment makes itself felt with increasing intensity according to the time elapsed between arrival of the mother and the birth of the child (Boas, 1912b). There exists a difference in the parental races (Hebrew and Sicilian) in Europe, but their American-born children do not exhibit this difference (Boas, 1912b). There was also a dramatic increase in stature of the American-born children compared to their European-born brethren, and this difference varied with family size, in that larger families tended to have shorter children (Boas, 1912b). These findings were considered unequivocal evidence of both cranial and bodily plasticity as well as proof of the misgivings of the concept of race (Cole, 1931). As an interesting note, all of the findings of Boas's study were discussed without regard or mention of any statistical testing of the differences observed. This

seems rather uncharacteristic for Boas, who's other studies (1899a; 1908; 1933) often focused very heavily on mathematics and statistics.

Following the lead of Boas (1910; 1912a), studies were conducted by students of Boas dealing with the problem of environmental effects on bodily dimensions. Shapiro (1939) undertook a large study on the differences that exist between Japanese immigrants living in Hawaii and Japanese sedentes in Japan. While the scale of Shapiro's study was smaller as far as sample size, his findings were similar to Boas's (1910; 1912a) in that he detected differences between the sedente portion of the sample and the American-born segment of the sample, allegedly due to the effect of the environment. Shapiro's (1939) study collected many more anthropometric measures than did Boas's, and among the changes seen the most dramatic involved stature and facial height, while the length and breadth of the cranium and the bizygomatic breadth exhibited little change. Similarly, a study conducted by Goldstein (1943) on Mexican immigrants to the United States and their American-born descendants looked at the effects of the American environment on bodily proportions. The findings of this study found changes similar to those observed by Boas (1910; 1912a) and Shapiro (1939) concerning stature, but the cephalic index and other raw cranial dimensions exhibited little to no change between foreign and American-born family members. Lasker (1946) likewise found no significant changes between American-born and immigrant Chinese in regards to cranial measurements,

while observing significant changes in variables such as stature, nasal height, arm span, and foot length.

Modern studies by Bogin (1988; 1991; 1995) have confirmed the increase in stature, weight, and skinfold measurements in American-born offspring of Mayan immigrants living in the United States. These studies, however do not deal with head measurements, so it is impossible to say if the environmental effects of migration and environment are seen in this population. The findings of these studies represent the major studies performed on this topic, and as a whole seem quite similar in regards to the plasticity of stature and measurements dealing with weight and body composition, however they vary with regard to the environmental effects on the cranio-facial complex.

While many authors have cited the work of Boas and his students as evidence of human cranial plasticity, relatively few have attempted to critique the studies (e.g. Armelagos and Goodman, 1998; Cole, 1931; Lasker, 1946; 1969; Mascie-Taylor and Bogin, 1995; Mascie-Taylor and Lasker, 1988). Morant and Samson (1936) make several well-founded criticisms of Boas's (1910; 1912a) study. They note that since the samples studied by Boas are so variable regarding date of arrival that any secular change that was occurring in the populations could lead to the differences Boas observed (Morant and Samson, 1936). In addition, they note that Boas, in order to make many of his comparisons, pooled individuals of different ages in order to obtain sufficient sample sizes. This is indeed an unwise practice due to

the possible effects of growth and even old age. Boas (1940b) alluded to this age effect and the possibility of a secular trend on the cephalic index after the fact. Even after the discussion of the age changes discussed in Boas (1940b), later responses to the critiques of Morant and Samson (1936) by Boas (1940c) ignore the question of secular trends altogether, and never answer the age effect question except the Hebrews in which he notes the age factor, but offers no statistical solution for it. To date, the article of Morant and Samson (1936) remains the only thorough critique of Boas's work, and there are no criticisms of the studies of Goldstein (1943) or Shapiro (1939).

Heritability of Anthropometric Traits

The heritability or proportion of phenotypic variance due to a genetic component, of anthropometric traits has received a considerable amount of coverage in anthropological literature. The concept of heritability is important to consider in studies attempting to describe population history. This is because the heritability of a trait has implications for the response of a trait to selective pressures (Hartl and Clark, 1997). Likewise, it represents the transmissible component of a trait, or the degree to which offspring resemble their parents.

A variety of methods are utilized to determine the heritability of a trait. Traditionally, parent or mid-parent-offspring correlation or regression has been utilized to estimate heritability. This represents the regression of

offspring onto parent or mid-parent, and the value produced from the ratio is the beta parameter of a regression and $\beta_{op} = ½ h^2$, where β_{op} is the regression described above and h^2 is the narrow sense heritability (Lynch and Walsh, 1998). Using this method, Sjovold (1984) estimates the heritability of a variety of cranial dimensions from a series of historic Austrian crania. This study made use of a novel situation where family lines are estimated by family specific decoration or family names on the individual crania. However, this method has problems due to the uncertain nature of some of the crania not having names on them and small sample sizes (Sjovold, 1984). Using the same methodology to estimate heritabilities, Devor et. al. (1986a) and Susanne (1975; 1977) produced estimates of a variety of anthropometric traits on the living. Devor et. al. (1986) using data from a sample of Alexanderwohl Mennonites produced heritabilities ranging from .3 to .17 for a variety of head dimensions and higher values for bodily measurements. Susanne (1975; 1977) produced heritability values around .5 for head dimensions, with values approaching .8 for other bodily dimensions from a sample of Belgian families.

Another method for estimating heritabilities is path analysis developed by Rice et. al.(1978; 1980), which expands the familial correlation to include non-genetic effects in the path of transmission from parent to offspring. The basic model expresses the standardized phenotype as a linear, additive function of the transmissible component and a nontransmissible component (Rice et. al., 1978; 1980) . The transmissible component is then comparable

to the heritability of the trait, or traits, in question. The advantage of this model over simple parent or midparent-offspring correlation is the ability to estimate the environmental component of transmission and the ability to analyze multiple traits. Using this methodology, Devor (1987) and Devor et. al. (1986b) estimated the transmissible component of head dimensions from .45 to .6 in the Alexanderwohl Mennonite sample. Using the same model, Poosha et. al. (1984) estimated the transmissible component of craniofacial dimensions ranging from .35 to .75 in a sample of Indian Brahmins. The results from the studies utilizing either familial correlation or path analysis seem consistent in their estimates of craniofacial heritability. However, the disadvantage to using these methods is the ability to only consider one parent-offspring correlation at a time, and the use of complex pedigrees is computationally tedious.

The method proposed by Elston and Stewart (1971) revolutionized the analysis of complex pedigrees in quantitative genetics. The procedure proposed by Elston and Stewart (1971) not only allowed for complex pedigree information to be incorporated based on a kinship matrix, but it also allowed for tests to be constructed for multiple modes of inheritance. The idea proposed by Elston and Stewart (1971) forms the basis of complex segregation analysis. This type of analysis allows for the components of phenotypic variance for a single or multiple traits to be estimated under various models of inheritance. Paganini-Hill et. al. (1981) utilized this method for deriving heritability estimates under a major-gene model of inheritance,

and found thirteen out of fifty-five bodily dimensions to possibly be influenced by a major-gene effect. Total facial height was the only variable found by Paganini-Hill et. al. to be significantly influenced by a major gene. Using the premises set forth in Elston and Stewart (1971) and Hasstedt (1982), Blangero and Konigsberg (1991) devised a method that approximates the multivariate variance component likelihood calculation using a series of univariate likelihoods (see Chapter 3). Using a reduced version of the Blangero and Konigsberg method, Konigsberg and Ousley (1995), estimated the variance components on a series of anthropometric measurements from the Boas Native American database (Jantz et. al., 1992; Szathmary, 1995). Although the heritabilities of the traits are not directly stated in their findings, the ranges can be extrapolated from Table 3 in Konigsberg and Ousley (1995, p489), and range between .35 and .55, with an average of .4.

It is evident from a number of studies that heritabilities of cranio-facial traits are rather homogeneous and range from .3 to .6. This indicates a significant contribution of genetics in the expression of the cranio-facial phenotype. This is common, as most complex phenotypes have non-zero heritabilities (Cheverud, 1988; Kohn, 1991).

Reconstructing Genetic Relationships from Anthropometrics

The use of the cranial/anthropometric phenotypes as a proxy for genetic data has had wide acceptance in modern biological anthropology. Although some authors have criticized the use of cranial/anthropometric data

due to the high degree of plasticity involved in the growth process (Armelagos and Goodman, 1998; Goodman, 1997; 1995), many authors have utilized cranial/anthropometric data without reservation (Crawford ed., 1976; Jantz and Meadows, 1995; Konigsberg and Blangero, 1993; Relethford and Lees, 1982; Wescott and Jantz, 1999; Williams-Blangero and Blangero, 1989; Williams-Blangero et. al., 1990). This is because anthropometric and craniometric data generalize well in quantitative genetic models (Williams-Blangero et. al., 1989). In fact, many recent articles dealing with notions of population relationship have utilized anthropometric and craniometric data within model-based approaches to estimate the genetic heterozygosity of populations (e.g. Relethford, 1994; Relethford and Crawford, 1995; Schillaci and Froehlich, 2001; Tatarek and Sciulli, 2000; Wescott and Jantz, 1999). These types of approaches have great advantage over traditional model-free approaches because the heritability of traits can be factored into them (Relethford and Blangero, 1990). These studies often utilize the R-matrix method of Harpending and Jenkins (1973), which provides estimates of genetic distances from phenotypic data, as well as estimates of F_{ST}, or subpopulation heterozygosity in relation to total population heterozygosity. The genetic distances are often computed with heritability estimates of $h^2=1$ in order produce minimum estimates of F_{ST} (see Harpending and Jenkins, 1973; Relethford and Blangero, 1990 for descriptions of the R-matrix method).

The use of phenotypic data such as anthropometrics in the calculation of multivariate distances has been shown to closely approximate distances derived from genetic data (Konigsberg and Ousley, 1995). In general, phenotypic data will underestimate the actual genetic distance between groups because the phenotype has portions of variance due to both genetic and environmental effects (Konigsberg and Ousley, 1995). Harding (1990) building on the work of Sokal and Uytterschaut (1987) and Sokal et. al. (1989) showed that blood polymorphism data and craniometric data show nearly identical patterns of spatial autocorrelation, indicating similar results in terms of detecting the Neolithic colonization of Europe. Likewise, sample relationships derived from blood group data and anthropometrics show similar patterns in Tlaxcaltecan populations (Crawford ed., 1976). Evidence such as this lends credence to the idea that cranial or anthropometric variables offer good approximations to genetic data, and since both show similar patterns when put into direct comparison, there must be some support for the genetic value of phenotypic data.

This thesis intends to deal with issues concerning the reliability of the results of Boas (1910; 1912a) in a framework that includes biological distance, the relationship of phenotypic and genetic distances in population studies, and the quantitative genetics of the cranio-facial complex. It also will deal with the criticism of biodistance studies that focus on the notion of cranial plasticity and environment as the only mechanism affecting human variation (Goodman, 1995).

Chapter 3

Materials and Methods

Background

The data for this study were collected under the auspices of Franz Boas and co-workers between 1909 and 1910 in New York City, New York for a now famous study on the plasticity of human beings in response to environmental change (Boas, 1910). Anthropometric and anthroposcopic data were collected from several populations of European immigrants and their American-born children (Boas, 1928). The data set utilized in this study is drawn from Boas's (1928) work *Materials for the Study of Inheritance in Man*. The variables collected were as follows: maximum head length (HL), maximum head breadth (HB), bizygomatic or facial breadth (FB), and stature (ST)(Boas, 1928). From these measurements, two indices were also constructed including the cranial and facial indices. The cranial (or cephalic) index represents cranial breadth as a percentage of cranial length (Boas, 1899a) and is commonly given as:

$$CI = (HB/HL)*100$$

and the facial index is given as:

$$FI=(FB/HL)*100$$

and represents bizygomatic breadth as a percentage of cranial length. In addition to the anthropometric data, a series of anthroposcopic traits was collected including eye color and hair color. The data set could be considered sparse in comparison to the protocol established by Boas for the

World Colombian Exposition, which consisted of twelve anthropometric dimensions, and over twenty anthroposcopic traits (Jantz et al., 1992). The small number of quantitative traits gathered by Boas and colleagues from the European sample presents one disadvantage to this analysis. Fortunately, another protocol established for the European study was the collection of detailed pedigree information for each family. As will be discussed later, without accurate pedigree information, quantitative genetic analyses must resort to often computationally complex simulation procedures (Konigsberg and Blangero, 1993).

Samples

The populations from which data were collected are as follows: Sicilians, Central Italians, Bohemians, Hungarians, Slovakians, Poles, Scotch, and Hebrews (Boas, 1910; 1912). Table 1 lists the total sample sizes used in this study. The complete data set listed many families with only one parent, or no parents. These families were not included in this analysis; likewise, any individual with missing values for any of the cranial dimensions was also excluded. Table 2 lists the population specific sample sizes for the different geographic/ethnic affiliations. Unfortunately, the exact hometowns or precise regions were not listed for the Bohemians, Poles, Scotch, Hungarians, or Slovakians.

Table 1 Immigrant Family Data Subjected to Analysis.

Total Individuals	Males	Females	Pedigree Number	Average Pedigree Size
4668	2194	2474	1063	4.4

Table 2 Sample Sizes for Regional Populations.

Population	N	Males	Females
Bohemian	1227	564	663
Central Italian	1248	609	639
Polish	180	84	96
Scotch	204	94	110
Sicilian	1445	665	780
Hungarian/Slovakian	373	187	186

Statistical Methods

Variance Components and Pedigree Analysis

The variance of quantitative traits, such as anthropometric measures, under the assumption of no epistasis or interaction between components of variation can be decomposed into additive genetic and random environmental components such that:

$$\mathbf{V_P = V_A + V_E}$$

where $\mathbf{V_P}$ is the total phenotypic variance, $\mathbf{V_A}$ is the proportion of the variance attributable to additive genetic effects, and $\mathbf{V_E}$ is a random environmental component (Falconer and McKay, 1996). The additive genetic component is of importance because it is the proportion of the trait that is transmissible from parent to offspring. The ratio of additive genetic variance to phenotypic variance is often referred to as the narrow-sense heritability of a trait (Konigsberg, 2000). This value is typically given as:

$$h^2 = \frac{V_A}{V_A + V_E} = \frac{V_A}{V_P}$$

The heritability of a trait is often thought of as the degree of resemblance between parents and their offspring, and is a key idea in studies of evolution, as it highly affects the response of a trait to selection. Traits with little or no additive genetic component are not expected to respond to either natural or artificial selection (Ousley, 1997).

The estimation of the variance components is a complex task, and several methods have been employed to perform it. Parent-offspring regression methods were originally employed to estimate heritabilities (Lynch

and Walsh, 1998). These methods, as well as similar correlation methods, are not particularly well suited to the Boas data because the methods can only deal with one set of familial relationships at a time. Therefore, parent-offspring and sib pair relationships may be computed, but these effects cannot be easily combined through these methods. The method of maximum likelihood has come to be the method of choice for the estimation of variance components. The usefulness of maximum likelihood estimation (MLE) is easily seen, as the rules of its construction are not hindered by special demands on the design or balance of data sets (Lynch and Walsh, 1998). The likelihood function utilized here was originally employed by Blangero and Konigsberg (1991) and Konigsberg et al. (1991), and is based on the generalized multivariate mixed model likelihood derived by Hasstedt (1982). Konigsberg and Ousley (1995) utilize a form of this algorithm in their analysis of anthropometric traits from Boas's Native American data, and the methods employed here are based on their methods.

Prior to analysis, the three traits (head length, head breadth, bizygomatic breadth) are mean centered by age to alleviate the effects of growth, as well as by sex to reduce any dimorphism that exists. This process is not considered z-scoring the variables, as it does not constrain the variances for the traits. Ages are pooled into yearly intervals up to age 20, at which point young (20-39), middle (40-59), and old (60+) classes were defined. In order to preserve any morphological differences between the

regional populations, the data were pooled across the subpopulations. Following mean centering, the maximum likelihood estimates are obtained for the group means for the three variables and the variance components. Following Konigsberg and Ousley (1995), the general model specifies the probability density function for X_i (where X_i is the 1 x 3 row vector of measurements for individual *i*) as the multivariate normal $N(\mu_j, \Omega)$, where μ_j is the vector of means for population *j* and Ω is the 3n x 3n matrix of expected phenotypic covariances among pedigree members for the pedigree containing individual *i.* If all phenotypic variances and covariances for traits are due to additive genetic and environmental components, Ω is given as:

$$\Omega = G \otimes 2\Phi + E \otimes I, \qquad (1)$$

where *G* and *E* are the 3 x 3 additive genetic and environmental variance-covariance matrices among traits, Φ is the *n x n* matrix of kinship coefficients among the *n* relatives, *I* is an *n x n* identity matrix, and $\otimes$ represents a Kronecker product operator. The log-likelihood across the *n* individuals in the pedigree is then:

$$\ln L(\mu, G, E|X) = -\frac{1}{2}\ln|\Omega| - \frac{1}{2}[vec(X-\mu_j)'\Omega^{-1}vec(X-\mu_j)] - \frac{p}{2}n\ln(2\pi), \qquad (2)$$

where *vec* stacks columns of the matrix into a 3n x 1 column vector.

The log-likelihood shown in (2) can be maximized using a variety of methods. Due to the intricate task of maximizing the log-likelihood rather

than performing the maximization for (2), a transformation developed by Blangero and Konigsberg (1991) to break the likelihood calculation into the sum of 3 univariate likelihoods is employed. Following Blangero and Konigsberg (1991), if *P* is the phenotypic variance-covariance matrix among the traits (where *P* = *G* + *E*) then the transformation matrix *T* is defined as:

$$T = S(S'PS)^{-\frac{1}{2}}, \qquad (3)$$

where *S* is the 3 x 3 matrix of eigenvectors of $P^{-1}G$ and the negative exponent indicates a Cholesky decomposition of an inverse. By applying the transformation matrix to the data to form *X** = *T'X*, the phenotypic variance covariance matrix of the transformed traits (*P**) will be an identity matrix and the additive genetic and environmental variance-covariance matrices (*G** = *T'GT* and *E** = *T'ET*) will be diagonal. The log-likelihood from (2) can then be written as :

$$\ln L(\mu, G, E|X) = \sum_{k=1}^{p} \ln L(\mu_{jk}^{*}, g_{kk}^{*}, e_{kk}^{*}|x^{*}) + n\ln(abs|T'|), \qquad (4)$$

where the log-likelihoods on the right-hand side are for univariate trait analyses and the second term on the right-hand side is an adjustment to the log-likelihood to account for the transformation (Konigsberg and Ousley, 1995). The resulting log-likelihood for the multivariate likelihood can be obtained through the summation of the univariate likelihoods (Blangero and Konigsberg, 1991). The log-likelihood is then maximized across all

pedigrees until convergence is reached, indicating the likelihood of the estimated parameters has reached the maximum and no further improvement is possible. The maximum likelihood estimate will then represent the best estimate for the parameters among all individuals in every pedigree.

Evaluation of the log-likelihood from (4) will be accomplished through the Multfsh program written in FORTRAN by Lyle Konigsberg. The output from the program includes the phenotypic, additive genetic and environmental variance-covariance matrices for the three variables.

In addition to the heritabilities calculated from the method of maximum likelihood, multivariate heritabilities will be estimated by multiplying the inverse of the phenotypic variance-covariance matrix **P** by the genetic variance-covariance matrix **G**. The diagonal of the matrix $\mathbf{P}^{-1}\mathbf{G}$ will then represent the multivariate heritabilities for the three traits. If the matrices were perfectly proportional then the matrix $\mathbf{P}^{-1}\mathbf{G}$ would be a matrix with proportionality constants on the diagonal and zeros on the off-diagonals.

Multivariate Distance Analysis

Based on the estimated phenotypic and additive genetic variance-covariance matrices, Mahalanobis distances will be calculated from the group means and each respective variance-covariance matrix using the traditional method given as

$$D^2 = (x_i - x_j)\Sigma_P^{-1}(x_i - x_j)' \quad , \qquad (5)$$

where Σ_P is the pooled phenotypic variance-covariance matrix, and x_i and x_j represent the vectors of means for the i^{th} and j^{th} population. The analysis will subsequently be performed using the pooled additive genetic variance-covariance matrix Σ_G. The pooled matrices, Σ_P and Σ_G, will be calculated from the group specific phenotypic and genetic covariance matrices using the formula:

$$\Sigma_P = \frac{\sum_{i=1}^{C}(N_i - 1)\Sigma_i}{N - C} \qquad (6)$$

, where N_i is the sample size of the N^{th} group and V_i is the group specific variance-covariance matrix. If the matrices are proportional, and $P = cG$, where c is a constant of proportionality, such as described by Konigsberg and Ousley (1995), then the Mahalanobis distances should likewise be equal, except for a scaling constant of $1/h^2$. The two resulting distance matrices will then be compared using a least squares Procrustes fit to determine the nature of the relationship between the phenotypic and additive genetic variance-covariance matrices and the distance coefficients derived from each. The Procrustes superimposition, or generalized least squares method, is commonly used in biology to superimpose one species consensus, or mean, configuration onto another in order to ascertain morphological differences between the two (Bookstein, 1997; Slice, 1994). The Procrustes fit is a three-step process, which translates, rotates, and scales one configuration into the same coordinate system as the other (Bookstein, 1997; Slice, 1994). This process is modeled by the equation,

$$\mathbf{X}' = \rho\mathbf{X}\mathbf{H} + \mathbf{1}\boldsymbol{\tau}, \qquad (7)$$

where $\mathbf{X}'$ is the result of scaling, rotating, and translating **X** by ρ, **H**, and $\boldsymbol{\tau}$, respectively. Here, **X** and $\mathbf{X}'$ are p x̣ k matrices of the k coordinates of the p points in a configuration before and after fitting, ρ is a scalar, **H** is a *k* x *k* transformation matrix, **1** is an p x 1 matrix of ones, and $\boldsymbol{\tau}$ is a 1 x *k* matrix of translation parameters (Slice, 1994). Estimates of all of the parameters are made with respect to a reference specimen **Y**, another p x̣ k matrix that might represent another specimen or a mean configuration, so that the coordinates of points in $\mathbf{X}'$ can be used to assess shape differences relative to **Y** (Slice, 1994). This technique has been used to likewise compare distance matrices in biological anthropology (Konigsberg et al., 1993; Konigsberg and Herrmann, 2001; Konigsberg and Ousley, 1995). In order to perform the Procrustes superimposition of distance matrices, the matrices must first be converted to a coordinate system. This is done by first double-centering the individual distance matrices, which transforms a distance matrix to a scalar product so the latent roots and vectors may be computed resulting in a principal coordinates analysis, or metric multidimensional scaling analysis (Gower, 1966). The transformation of the distance matrix involves first transforming the elements of the matrix to $-1/2d_{ij}$, then the row and column means of the matrix are subtracted from each element and the grand mean is added on (Gower, 1966). The product of the transformation is the ***A*** matrix of Gower (1966) and has elements:

$$a_{ij} = a_{ij} - \bar{a}_i - \bar{a}_j + \bar{a}. \qquad (8)$$

, as described above. In the transformed matrix, the diagonal elements can be considered the squared distance from each group to the centroid of the space. When the roots and vectors of this matrix are found, the elements of the eigenvectors corresponding to positive eigenvalues can be interpreted as the coordinates of each point in a Cartesian space. This technique reduces the dimensionality of often-multidimensional distance matrices in order to summarize the information contained therein. Once this method is performed, the individual groups can be plotted in a two-dimensional plane as Cartesian coordinates. The Procrustes fit is then performed on these coordinates for the genetic and phenotypic coordinate systems.

The final multivariate method utilized here utilizes the double-centered matrix described above. Since the diagonal elements of the matrix represent the squared distance of each group to the centroid, the trace of the matrix should be equal to the total variation among the samples. Using this idea, three matrices were constructed for both the genetic and phenotypic variance-covariance matrices. The first of the three matrices is the Mahalanobis distance matrix of all parent-offspring groups for each of the subsamples, in this case a 12x12 matrix. The second matrix is taken from the total 12x12 Mahalanobis distance matrix and represents the distances between the parental groups, a 6x6 matrix. The third matrix is the Mahalanobis distance matrix between offspring groups, another 6x6 matrix. The trace of the 12x12 matrix should represent the total variation of the

sample with both a genetic (ethnic group) and environmental (parent-offspring) component. The two individual 6x6 matrices should then represent the ethnic component of variation for the parental and offspring groups. It is proposed then that the ratio:

$$\frac{tr(A_P) + tr(A_O)}{tr(A_{total})} \qquad (9)$$

, where $tr(A_p)$ and $tr(A_O)$ are the traces of the double-centered 6x6 distance matrices for parental and offspring pairs respectively, and $tr(A_{total})$ is the trace of the double-centered 12x12 distance matrix of all possible distances. This ratio will be the proportion of the total variation in the sample due to an ethnic component.

Univariate Methods

Two Sample t-test

In order to investigate the original findings of Boas concerning the environmental effect on American compared to European born siblings a series of two-sample t-tests are performed. These tests, which simply test for differences of univariate means, are what Boas would have used in his original study if the computational facilities had been available. This test is important because these univariate comparisons formed the backbone of the original study (Boas, 1910). t-tests were applied to same age American born and European born individuals of each region to assess Boas's claim that there were "strong effects of the American environment" (Boas, 1910, p17) on each of the variables (HL, HB, FB). Two hundred eighty-eight of these tests are performed to replicate Boas's findings.

Regression Analysis

In order to investigate the possible effects of secular change acting on the immigrant parents and any possible links between ongoing change and environmental influences, a series of first-order regression analyses are performed. Using linear and polynomial regression, (Jantz and Meadows Jantz, 2000) show in the American population the process of secular change acting on several cranial vault dimensions over the past 100 years. The possibility of similar effects in the parental generation of immigrants as well as the possible continuance of the secular change in the American-born generation could have major implications for Boas's findings. A series of least-squares regressions is employed on each sub-sample of the data in order to evaluate any secular change occurring in these populations. The regression model is constructed such that each of the three cranial variables and stature are regressed onto birth year. The birth year for each individual was estimated as: birth year = (1910-age), since all individuals were measured between 1909 and 1910. The regression coefficient produced from this model will be the sub-population specific amount of secular change.

Regression analysis will also be employed to assess the idea presented in Boas's (1910) original study that the cranial index in American born children changed with prolonged exposure to the American environment. In order to test this, the cranial index is regressed onto the time of exposure to the environment defined as 1910 – birth year for American-born children and 1910 – immigration year for European-born

children. The cranial index will likewise be regressed onto age to determine if the effect observed by Boas is in fact due to exposure to the environment or if it is simply an effect of growth. Since the American born offspring's environmental exposure variable, denoted YIC (years in country), is equal to their age that is the only variable considered in the analysis. The European-born children however have different values for both variables so both age and YIC are considered in the model. In order to assess the individual regression effects, the Type 2 sums-of-squares are utilized, providing partial regression coefficients.

In order to directly investigate the possible differences between parents and offspring, an analysis of variance design is employed. Using the mean-centered data that effectively removes any effect of age or sex, the model will be constructed that regresses the three variables on birth decade. Using the average age of the parents, their values in that birth decade will be compared with the values of the children born in the appropriate birth decade. A Bonferroni adjustment is applied to the tests of significance due to the multiple pairwise tests necessary to examine this model. The data will be limited to European-born parents and American-born offspring in order to control for the possible effects of the American environment and maximize the potential of the model to detect any differences. This model should address the question of changes in head form of the children relative to their parents.

Chapter 4

Results

Descriptive Statistics

Anthropometric data are generally considered quite normal in their distributions (Mascie-Taylor, 1994); this is fortunate due to the assumptions of many statistical tests. The distribution of head lengths in the sample is given in Figure 1. The distribution of head lengths appears normally distributed, without any significant skewness. Figure 2 gives the distribution of head breadth in the sample. The distribution of head breadths likewise appears normal. Figure 3 gives the distribution of bizygomatic breadth in the sample. The distribution of bizygomatic breadth also appears normal, but is slightly more skewed than both head length or head breadth. The assumption of multivariate normality also must be addressed. Multivariate normality will be assessed with the MNPP macro for the SAS system (Johnson, 1998; SAS Institute, 2000). Figure 4 gives the multivariate normal probability plot for the three variables in the analysis. This plot represents the quantiles of the data in comparison with the expected multivariate normal quantiles. Large deviations from the multivariate quantiles, given in red in the plot, can mean that normality of the data is suspect (Johnson and Wichern, 2000).

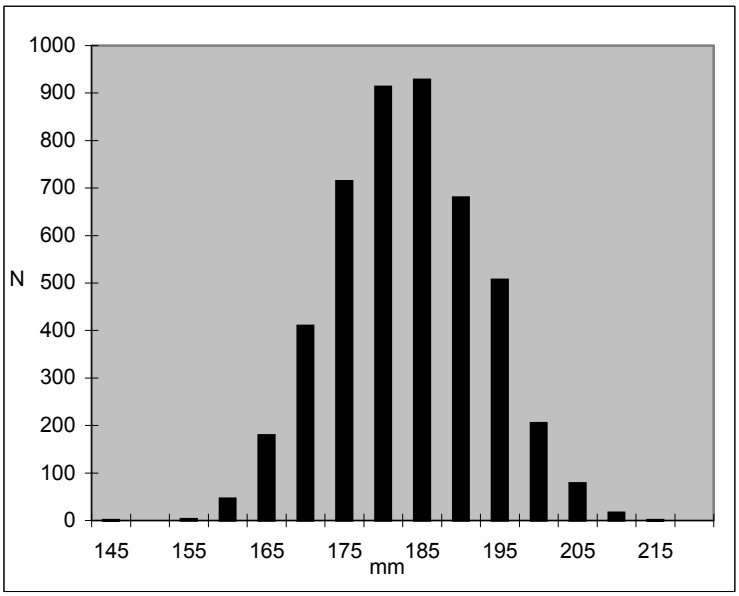


Figure1 Distribution of Head Length in the Immigrant Sample.

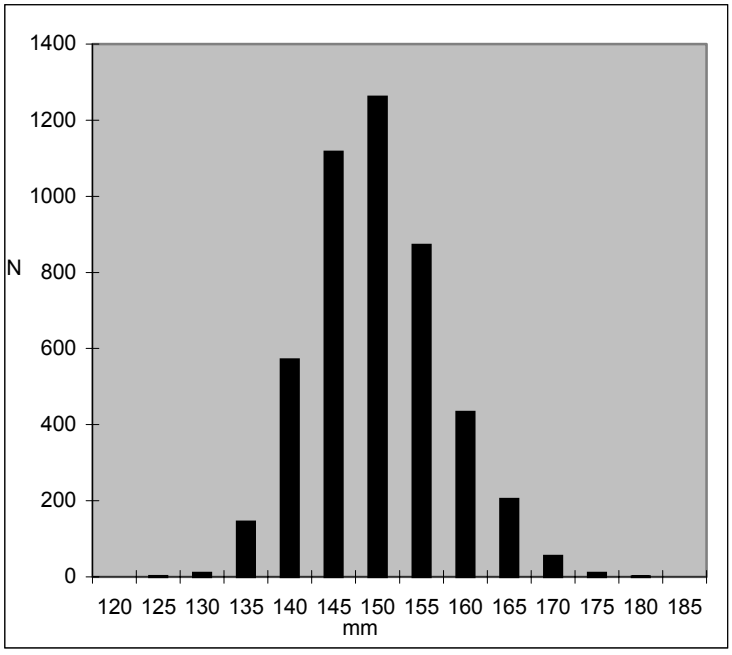


Figure 2 Distribution of Head Breadth in the Immigrant Sample.

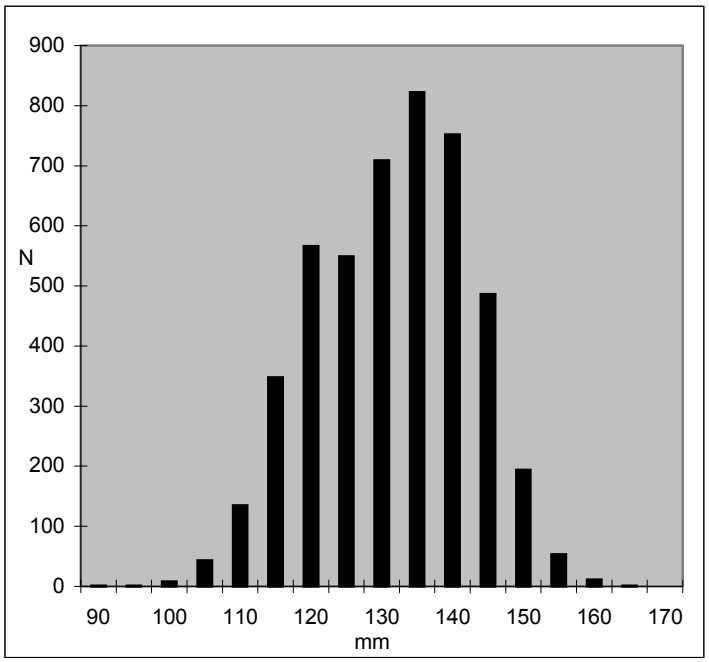


Figure 3 Distribution of Bizygomatic Breadth in the Immigrant Sample.

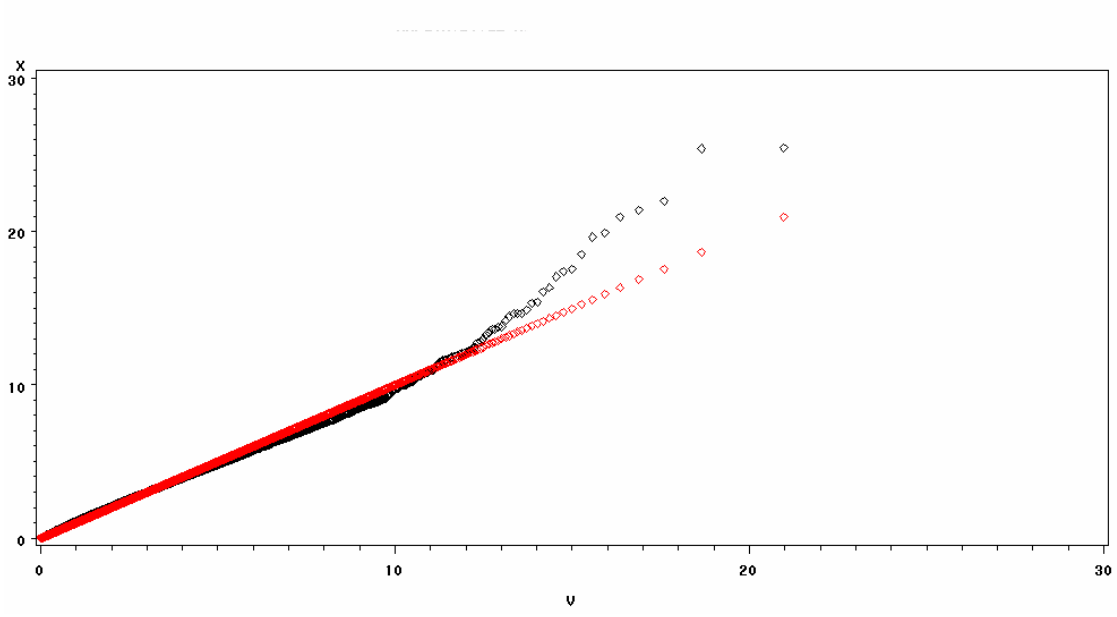


Figure 4 Multivariate Normal Probability Plot for the Three Traits.

There appears to be a slight departure from normality toward the upper tail, but this is not considered a dramatic departure. Since the data appear to be nearly normal in the univariate and multivariate sense, they are more likely to represent a biological meaningful group of variables. Table 3 gives the population specific means and variances for the three traits following the mean-centering process.

Components of Variation

The purpose of multivariate quantitative genetics in this setting is to partition the amount of phenotypic variation accounted for by genetic and environmental effects acting on the three traits in question. Table 4 gives the population specific and total sample univariate heritabilities and standard errors for the three traits. All population specific heritabilities are significantly different from zero at $p < .05$ based on likelihood ratio tests, indicating that there is a significant genetic component to all of the traits, in some cases nearly 70%. These heritabilities are, on average higher than the heritabilities found by Konigsberg and Ousley (1995) using the same methodology, but with less pedigree information. The heritabilities are also higher than those found by Devor et al. (1986b) and Devor (1987) using path analysis and those of Devor et al. (1986a) using factor analysis and, and on average higher than the average heritability of quantitative traits of .35 proposed by Cheverud (1988).

Table 3 Population Specific Means and Phenotypic Variances.

Population	N	Head Length μ σ^2	Head Breadth μ σ^2	Bizygomatic Breadth μ σ^2
Bohemian	1227	-1.31 51.37	4.09 37.29	1.61 36.48
Central Italian	1248	-1.15 48.18	-1.08 32.48	-0.72 34.81
Polish	180	-1.10 49.00	1.51 29.93	2.80 28.73
Scotch	204	5.68 45.09	-0.89 32.59	-1.36 35.18
Sicilian	1445	2.13 47.46	-3.43 29.07	-1.54 30.27
Hungarian/Slovakian	373	-2.63 40.52	3.13 30.95	2.41 30.87
Total Sample		0 52.25	0 41.70	0 35.69

Table 4 Population Specific and Total Sample Univariate Heritabilities.

Population	Head Length h^2 s.e.	Head Breadth h^2 s.e.	Bizygomatic Breadth h^2 s.e.
Bohemian	0.527 .048	0.598 .045	0.600 .044
Central Italian	0.600 .043	0.561 .045	0.570 .042
Polish	0.611 .117	0.691 .113	0.582 .137
Scotch	0.429 .135	0.382 .108	0.530 .115
Sicilian	0.542 .045	0.585 .043	0.596 .043
Hungarian/Slovakian	0.544 .091	0.613 .082	0.541 .089
Average h^2	.542	.572	.570
Total Sample	.631 .022	.699 .018	.629 .021

In order to form the genetic variance-covariance matrix for use in the biological distance portion of the analysis, the population specific correlations were each subjected to :

$$\Sigma_i = s_i R_i s_i \qquad (9)$$

, where Σ_i is the population specific variance-covariance matrix, s_i is a diagonal matrix of genetic standard deviations for the three traits, and R_i is the population specific genetic correlation matrix. The associated pooled phenotypic variance-covariance matrix is easily estimated from the raw data. The pooled within group phenotypic, genetic, and environmental variance-covariance matrices, the matrix $\mathbf{P}^{-1}\mathbf{G}$, and the multivariate heritabilities are given in Table 5, also the differences between the multivariate and univariate heritabilities are given. It is evident that the univariate and multivariate heritabilities are very close for all three traits.

The total sample genetic correlation matrix between traits is given in Table 6, and the total sample phenotypic correlation between traits is given in Table 7. It is evident that the two correlation matrices are closely related to one another. This is expected due to the relatively high total sample heritabilities (Cheverud, 1988). It is also evident that two elements of the genetic correlation matrix exceed the phenotypic values. In order to estimate the total sample correlation matrix difference between the two matrices, Cheverud (1988) proposes a method based on the average matrix R^2. The specific correlation matrices are first squared, and then the off-diagonal elements are averaged to produce the average matrix R^2. The difference

Table 5 Pooled Phenotypic, Genetic, and Environmental Variance-Covariance Matrices and the P-1G Matrix.

Matrix	HL	HB	FB
Phenotypic			
HL	48.077	15.728	16.802
HB	15.728	32.475	21.388
FB	16.802	21.388	33.314
Genetic			
HL	26.567	12.196	8.981
HB	7.180	16.258	9.867
FB	6.577	11.680	19.422
Environmental			
	21.510	3.532	7.821
	8.547	16.217	11.521
	10.225	9.708	13.892
$P^{-1}G$			
HL	0.587	0.104	-0.003
HB	0.003	0.440	-0.138
FB	-0.100	0.016	0.673
Multivariate h^2	0.587	0.440	0.673
Univariate h^2	0.553	0.501	0.583
Difference	0.034	-0.061	0.090

Table 6 Total Sample Genetic Correlation Matrix.

Trait	HL	HB	FB
HL	1		
HB	.124	1	
FB	.147	.693	1

Table 7 Total Sample Phenotypic Correlation Matrix.

Trait	HL	HB	FB
HL	1		
HB	.100	1	
FB	.186	.618	1

produced is then a scalar and represents the total difference between the two matrices. The value produced from this procedure in this case is .03, very close to the average difference of .06 observed from forty-one such comparisons in Cheverud (1988). The similarity of the two matrices indicate proportionality, and hence the ability to use phenotypic correlation matrices when genetic correlation matrices are unavailable, which is often the case. This aspect of proportionality in the immigrant data will be discussed further below.

Multivariate Distance Analysis

The Mahalanobis D^2 matrix produced from the genetic variance-covariance matrix is given in Table 8. Despite the use of only three variables, there appears to be structure to the distance matrix. Following Gower (1966), the distance matrix is double-centered, and the roots and vectors are found. Each group is then represented as coordinates in Euclidean space lying along the eigenvectors associated with positive eigenvalues from the double-centered matrix. The average values of D^2 derived from the genetic and phenotypic variance covariance matrices are presented in Table 9. The parent-offspring differences represents less than 10% of the between ethnic group distances between both parental and offspring groups. This points to the small degree of differentiation between intra-ethnic group parents and offspring caused by an environmental effect. A comparison of Fst derived from the phenotypic and genetic distances, presented in Table 10, however

Table 8 Mahalanobis D^2 Matrix Derived from Genetic Variance-Covariance Matrix.*

	BOMF	BOSD	HMF	HSD	PMF	PSD	SCMF	SCSD	SIMF	SISD	CMF
BOSD	0.15										
HMF	0.24	0.12									
HSD	0.50	0.15	0.09								
PMF	1.09	0.46	0.71	0.32							
PSD	1.10	0.55	0.53	0.20	0.17						
SCMF	4.16	3.42	4.70	3.99	2.25	3.42					
SCSD	5.00	3.93	5.28	4.41	2.48	3.85	0.25				
SIMF	5.37	3.91	4.94	3.86	2.02	3.12	1.21	0.53			
SISD	4.29	3.08	4.11	3.19	1.52	2.58	0.68	0.27	0.10		
CMF	2.20	1.21	1.70	1.09	0.32	0.86	1.87	1.58	0.89	0.68	
CSD	1.53	0.77	1.27	0.85	0.29	0.87	1.85	1.68	1.31	0.94	0.10

*BOMF=Bohemian mother-father mean vector, BOSD= Bohemian son-daughter mean vector, HMF=Hungarian mother-father mean vector, HSD=Hungarian son-daughter mean vector, PMF=Polish mother-father mean vector, PSD=Polish son-daughter mean vector, SCMF=Scottish mother-father mean vector, SCSD=Scottish son-daughter mean vector, SIMF=Sicilian mother-father mean vector, SISD=Sicilian son-daughter mean vector.

Table 9 Average D^2 Values Between Parents and Offspring.

Matrix Type	Average D^2 Between Parents	Average D^2 Between Children	Average D^2 Between Parents and Children
Phenotypic	1.874	1.271	0.127
Genetic	2.470	1.649	0.149

Table 10 Fst Comparison of European and American-born Subsamples.

Matrix Type	Fst Between European-born Subpopulations (s.e.)	Fst Between American-born Subpopulations (s.e.)	t (p<t)
Phenotypic	.110 (.0062)	.087 (.0079)	2.275 (.023)
Genetic	.180 (.0069)	.145 (.0093)	3.019 (.006)

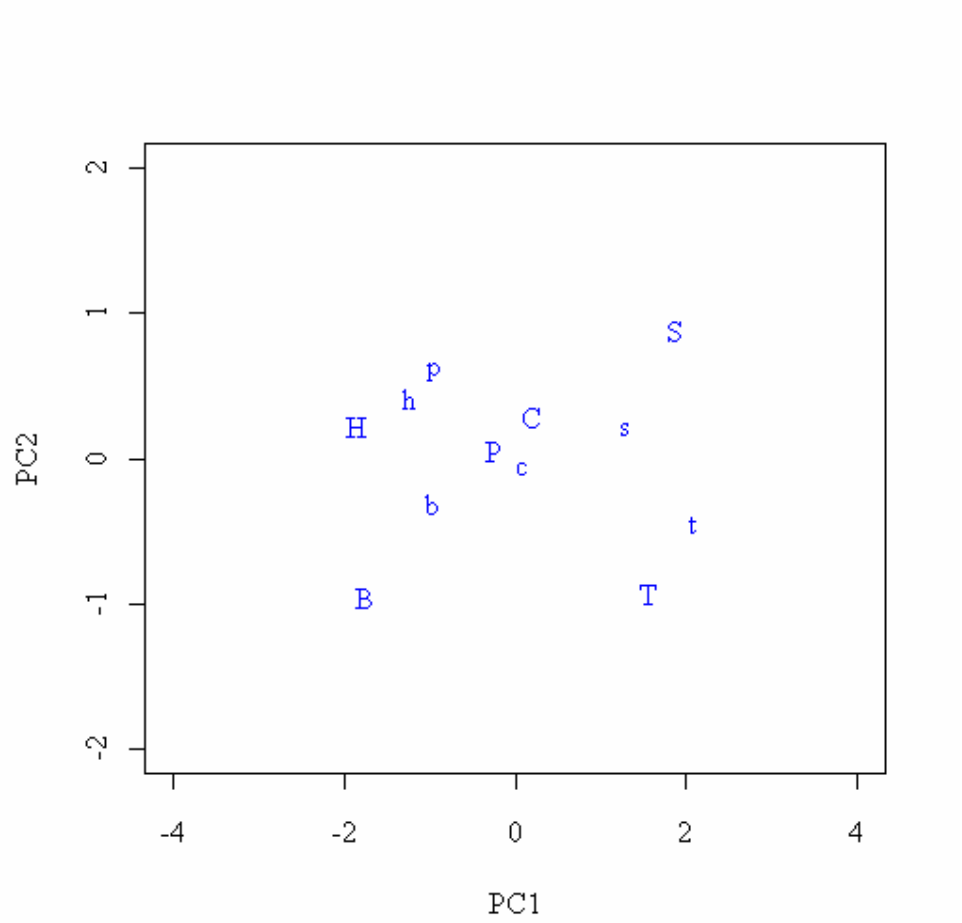
points to a significant reduction in heterozygosity in the American-born segment of the sample compared to the European-born segment. The reduction is not unexpected because differences exist between parent-offspring groups.

In order for distance matrix comparison, the phenotypic Mahalanobis D^2 -matrix is also calculated and is presented in Table 11. A noticeable difference exists between the two distance matrices. Since the genetic variance-covariance matrix represents a portion of the total phenotypic variance, the distances corresponding to that matrix should be slightly greater than those derived from the original phenotypic variance-covariance matrix. However, due to the large amount of variance in the phenotype accounted for by genetic effects, the distances do not vary greatly. Similar to the genetic D^2 matrix, the phenotypic D^2 matrix is also double-centered and the roots and vectors are found. Since both matrices are now represented as coordinate systems in a Cartesian plane (Gower, 1966), they can be subjected to a Procrustes fit to compare their proportionality (Konigsberg and Ousley, 1995). The Procrustes fit between the genetic and phenotypic coordinate systems is accomplished using the algorithm provided in Konigsberg and Herrmann (2001) and implemented in the package R® - version 1.2.3 (CRAN, 2000). Figure 5 presents the results of the principal coordinates analysis of the distance matrix derived from the phenotypic variance-covariance matrix.

Table 11 Mahalanobis D2 Matrix Derived from Phenotypic Variance-Covariance Matrix.*

	BOMF	BOSD	HMF	HSD	PMF	PSD	SCMF	SCSD	SIMF	SISD	CMF
BOSD	0.13										
HMF	0.24	0.10									
HSD	0.49	0.16	0.07								
PMF	0.89	0.36	0.51	0.23							
PSD	1.01	0.50	0.41	0.15	0.15						
SCMF	2.97	2.49	3.51	3.11	1.86	2.89					
SCSD	3.64	2.89	3.95	3.40	2.00	3.17	0.20				
SIMF	4.04	2.88	3.62	2.85	1.51	2.39	1.13	0.53			
SISD	3.17	2.23	2.99	2.36	1.16	2.03	0.63	0.26	0.09		
CMF	1.76	0.95	1.27	0.82	0.25	0.69	1.60	1.32	0.64	0.51	
CSD	1.20	0.59	0.97	0.67	0.24	0.75	1.43	1.26	0.94	0.65	0.09

*BOMF=Bohemian mother-father mean vector, BOSD= Bohemian son-daughter mean vector, HMF=Hungarian mother-father mean vector, HSD=Hungarian son-daughter mean vector, PMF=Polish mother-father mean vector, PSD=Polish son-daughter mean vector, SCMF=Scottish mother-father mean vector, SCSD=Scottish son-daughter mean vector, SIMF=Sicilian mother-father mean vector, SISD=Sicilian son-daughter mean vector.

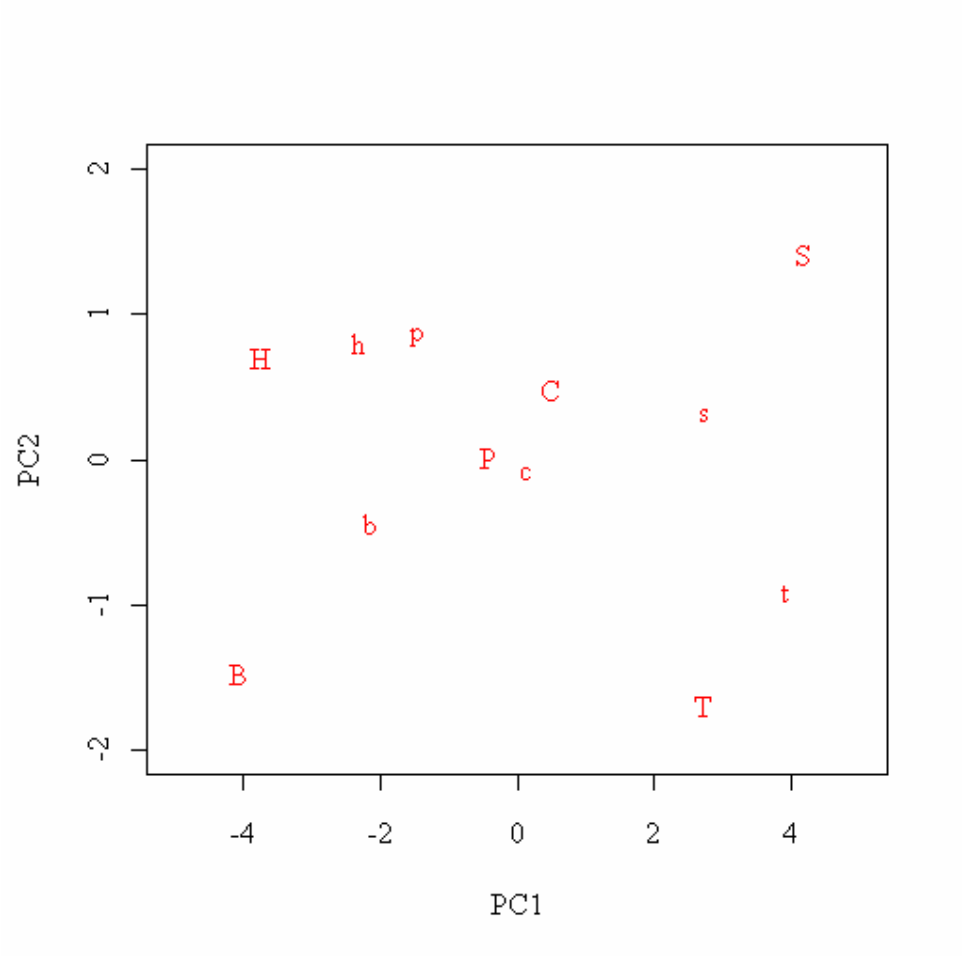


B=Bohemian, C=Central Italian, H=Hungarian/Slovakian, P=Polish, S=Sicilian, T=Scottish. The capital letters represent parental groups, and the lower case letters represent offspring groups.

Figure 5 Principal Coordinates Plot of Phenotypic Distance Matrix.

The first principal coordinate represents 83.98% of the total variation, and the second principal coordinate represents 16.01%. The plot shows marginal differentiation of groups with the first principal coordinate probably representing geography, as more Eastern European group (Bohemian, Hungarian, Polish) are low on the axis, and the Western European groups are positive on the axis. The Scottish and Sicilian groups are perhaps the most different from the other cluster. There exists a difference between parent-offspring pairs, but in the majority of cases, this distance is less than that of the parental groups to one another. There is also a tendency for the Eastern European offspring groups to cluster with one another; this is also seen in the Western European offspring groups.

The principal coordinates plot of the double centered distance matrix derived from the genetic variance-covariance matrix is presented in Figure 6. A similar picture to the phenotypic distance matrix is seen in the plot of the genetic distance matrix. The first principal coordinate represents 90.09% of the total variance, and the second represents 9.91%. The interpretation from the phenotypic distance matrix holds true for this plot. It is noticeable that the genetic distance plot has a larger spread on both the first and second principal coordinates. This is expected since the genetic variance-covariance matrix is proportional to, but not equal to the phenotypic variance-covariance matrix by the factor $1/h^2$ (Konigsberg and Ousley, 1995). It is evident that the findings of Konigsberg and Ousley (1995) are supported, since the genetic distances are greater than the phenotypic distances.



B=Bohemian, C=Central Italian, H=Hungarian/Slovakian, P=Polish, S=Sicilian, T=Scottish. The capital letters represent parental groups, and the lower case letters represent offspring groups.

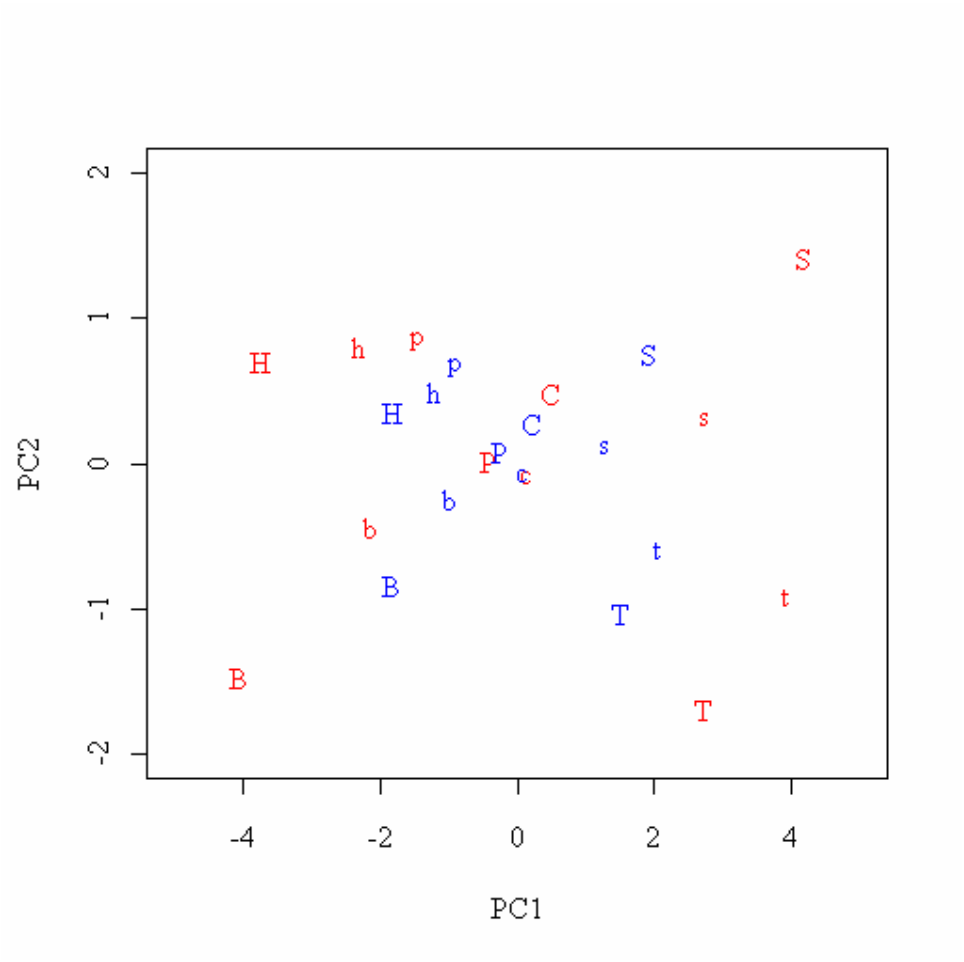
Figure 6 Principal Coordinates Plot of Genetic Distance Matrix.

Figure 7 presents the result of the Procrustes fit of the two distance matrices. While Figure 7 shows the proportionality of the distance matrices, a more accurate representation of the two matrices is produced when the phenotypic distance matrix is dilated onto the genetic distances. This is accomplished by undoing the scaling effect in the Procrustes fit, in effect removing the 'size' component of the distances leaving just the 'shape' component (Rohlf and Slice, 1990). If the genetic distance matrix and the genetic variance-covariance matrix were perfectly proportional to the phenotypic matrices, then the two matrices would coincide perfectly. The dilated fit of the genetic and phenotypic principal coordinates is presented in Figure 8. It is clear that the two distance matrices are not equal, but the phenotypic distances provide a good proxy for genetic distances (Konigsberg and Ousley, 1995).

Table 12 presents the comparison the traces of the double-centered distance matrices. Due to the properties of the matrix **A**, the amount of the total variance in the distances due to ethnic differences between groups is 99.79% for the phenotypic distance matrix and 99.83% for the genetic distance matrix. This indicates that the effect of the American environment on the children of European immigrants is very slight at best.

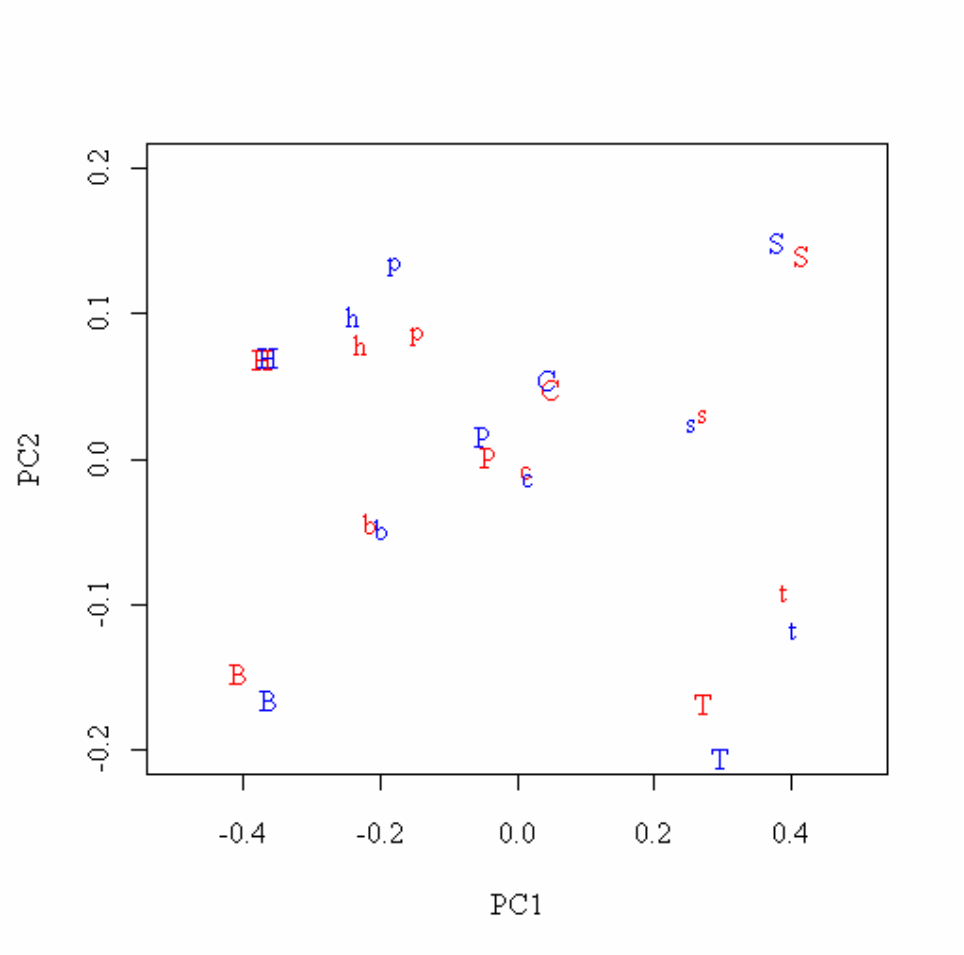
Univariate Statistical Results

The results of the 288 t-tests are not presented in detail due to space constraints. The results are tabulated in Table 13 to facilitate their



(Blue points indicate phenotypic coordinates and red points indicate genetic coordinates)

Figure 7 Procrustes Fit of Genetic and Phenotypic Principal Coordinates.



(Blue points indicate phenotypic coordinates and red points indicate genetic coordinates)

Figure 8 Procrustes Fit of Dilated Genetic and Phenotypic Principal Coordinates.

Table 12 Results of Trace Comparison.

D^2 Matrix Type	$tr(A_P)+tr(A_O)$	$tr(A_{total})$	%
Phenotypic	7.8363	7.8527	99.79
Genetic	10.1896	10.2073	99.83

Table 13 Results of Two-Sample t-tests for Differences Between European-Born and American-Born Children.

Sex	Variable	Number of Tests	Number of Tests with Significant t	% Significant Difference at α=.05	Number of Tests Significant at α=.001	Average Difference Between Means
Male	HL	31	0	0.0	0	-
	HB	31	0	0.0	0	-
	FB	31	4	12.9	0	-6.39
Male Total		93	4	4.3	0	-6.39
Female	HL	28	7	25.0	1	-7.32
	HB	28	2	7.1	0	-0.74
	FB	28	5	17.8	1	-4.96
Female Total		84	14	16.7	2	-4.34
Total		177	18	10.1	2	-4.85

understanding. It is worth noting that only 177/288 were capable of being performed due to sample size constraints and many of the tests included in the results are considered liberal in their interpretation should be considered with caution due to limited sample sizes. This type of analysis is what Boas (1910) would have used if the tests had actually been formulated, and represents the main foundation of his original argument. There is a pattern in the analyses that females show more significant differences at $p<.05$ than males. The difference between males and females is significant when compared with a chi-square test (X^2=7.38, p=.006, df=1). Table 14 presents the results of the t-tests by ethnic group. The variable with the most cases (9/18) of significant differences is FB, followed by HL (7/18) while the least number of significant differences concern the variable HB (2/18). As seen in Table 13 and 14, a small amount of the actual pair wise differences is actually significant. This points to a small difference between European born and American born children. Indeed the findings are even less significant since an alpha significance level of .05 is used. There would be almost 9 significant tests by chance alone using this level of significance. If an alpha significance level of .001 is used, then there are no significant differences among males, only 2% of the female differences are significant, and 1% of the total tests are significant. This indicates a very low amount of differentiation between European-born and American-born children. If the findings of Boas (1910) held true then all of the tests would have to be significant, and they appear not to be in the majority of cases.

Table 14 Results of t-tests by Ethnic Group.

Ethnic Group	Sex	Variable	Number of Tests	Number of Tests with Significant t at α=.05	Number of Tests Significant at α=.001	% With Significant Difference at α=.05
Bohemian	Male	HL	3	0	0	0
		HB	3	0	0	0
		FB	3	1	0	33.3
	Female	HL	3	0	0	0
		HB	3	0	0	0
		FB	3	0	0	0
Central Italian	Male	HL	13	0	0	0
		HB	13	0	0	0
		FB	13	0	0	0
	Female	HL	14	3	1	21.4
		HB	14	1	0	7.1
		FB	14	1	0	7.1
Hungarian/Slovakian	Male	HL	5	0	0	0
		HB	5	0	0	0
		FB	5	2	0	40.0
	Female	HL	5	0	0	0
		HB	5	1	0	20.0
		FB	5	0	0	0
Polish	Male	HL	1	0	0	0
		HB	1	0	0	0
		FB	1	0	0	0
	Female	HL	-	-	-	-
		HB	-	-	-	-
		FB	-	-	-	-
Scottish	Male	HL	-	-	-	-
		HB	-	-	-	-
		FB	-	-	-	-
	Female	HL	-	-	-	-
		HB	-	-	-	-
		FB	-	-	-	-
Sicilian	Male	HL	9	0	0	0
		HB	9	0	0	0
		FB	9	1	0	11.1
	Female	HL	13	4	0	30.7
		HB	13	0	0	0
		FB	13	4	1	30.7

The results of the secular trend analyses are presented in Table 15. The results of the regression analyses show a secular trend occurring in the European immigrant groups. The trend tends to be expressing itself most profoundly on bizygomatic breadth, with males and females being nearly identically affected. In males, the only variable being affected is facial breadth. Females show a higher degree of secular change on bizygomatic breadth than other head dimensions, but head length and breadth are also affected. Males and females show a slight difference in degree of change in bizygomatic breadth, with males having an average of .051, and females .064. Females show a slightly higher secular change in head length with an average R^2 of .037 compared to the male average of .008. Females also show a slightly higher value of R^2 for head breadth, .023, compared to the male value of .009. The trends that exist are all negative, in that there tends to be a reduction over time. These findings are consistent with those of Jantz and Meadows Jantz (2000), which also show a significant secular decrease in bizygomatic breadth in American white males, females, and black females. One difference exists in this sample, in that males have a lower degree of secular change on head length than females, while the sample used by Jantz and Meadow Jantz (2000) shows the opposite.

The results of the regression of the cranial index on time of environmental exposure reveal no statistically significant effects of environmental exposure in any of the sub-samples. The results of the

Table 15 Results of Linear Regression Analysis of Individual Variables on Birth Year.

Ancestry	Sex	Variable	R^2	p
Bohemian	Male	HL	0.008	0.113
		HB	0.008	0.105
		FB	0.066	**<.0001**
	Female	HL	0.047	**<.0001**
		HB	0.020	**0.008**
		FB	0.087	**<.0001**
Central Italian	Male	HL	0.004	0.276
		HB	0.006	0.181
		FB	0.029	**0.003**
	Female	HL	0.011	0.074
		HB	0.000	0.795
		FB	0.021	**0.011**
Hungarian/Slovakian	Male	HL	0.010	0.319
		HB	0.010	0.331
		FB	0.005	0.461
	Female	HL	0.005	0.485
		HB	0.060	**0.017**
		FB	0.053	**0.026**
Polish	Male	HL	0.000	0.939
		HB	0.000	0.901
		FB	0.006	0.583
	Female	HL	0.014	0.420
		HB	0.002	0.730
		FB	0.019	0.338
Scottish	Male	HL	0.026	0.243
		HB	0.026	0.244
		FB	0.124	**0.009**
	Female	HL	0.135	**0.003**
		HB	0.052	0.071
		FB	0.159	**0.001**
Sicilian	Male	HL	0.001	0.529
		HB	0.006	0.119
		FB	0.073	**<.0001**
	Female	HL	0.009	**0.062**
		HB	0.001	0.595
		FB	0.043	**<.0001**

regression analysis for the European-born children are presented in Table 16 and the results for the American-born children are presented in Table 17. The European-born children exhibit some change due to age that is not present in the American-born children, but neither group exhibits change due to environmental exposure (YIC). These findings contradict the findings of Boas (1910; 1940a), which indicates a large effect due to environmental exposure.

The results of the analysis of variance model show no significant differences between the European-born parental sample and the American-born children when considered as a whole or when analyzed separately by sex. The average age of the parents is 42.5 years for males and 38.1 years for females, while the average ages for the children are 9.4 for males and 11.1 for females. The comparisons of interest focus on the decades 1860-1870 (average parent) and 1900-1910 (average child). The sub-sample specific results of this comparison are presented in Table 18. When the individual subsamples are considered separately, three significant differences emerge. These represent 16.7% of the total number of pairwise comparisons. This indicates that there exist differences in a limited number of cases between European-born parents and American-born offspring. This is to be expected because multivariate distances exist between parent-offspring pairs as seen in Table 9.

Table 16 Results of Environmental Exposure Regression Analysis (European-born Children).

Ancestry	Variable	Variable t (p>t)	Total Model F (p>F)	R^2
Bohemian	YIC	.69 (.494)	4.55 (.016)	.17
	Age	-2.90 (.006)		
Central Italian	YIC	-1.03 (.306)	.86 (.426)	.01
	Age	-.36 (.719)		
Hungarian/Slovakian	YIC	1.78 (.079)	2.37 (.100)	.05
	Age	-1.49 (.139)		
Polish	YIC	.83 (.415)	1.82 (.186)	.15
	Age	-1.91 (.070)		
Scottish	YIC	-1.84 (.098)	1.70 (.236)	.27
	Age	.92 (.380)		
Sicilian	YIC	.97 (.331)	7.84 (.0005)	.04
	Age	-3.96 (<.0001)		
Total Sample	YIC	-.52 (.61)	15.5 (<.0001)	.04
	Age	-5.04 (<.0001)		

YIC (Yeas in Country) = 1910 – age.

Table 17 Results of Environmental Exposure Regression Analysis (American-born Children).

Ancestry	t (p>t)	R^2
Bohemian	-1.2 (.232)	.003
Central Italian	-.58 (.574)	.001
Hungarian/Slovakian	-1.72 (.089)	.03
Polish	-.91 (.355)	.02
Scottish	1.35 (.177)	.03
Sicilian	-.87 (.387)	.003
Total Sample	.0 (.999)	.00

Table 18 Results of Sample Specific Parent-Offspring Pairwise Comparisons.

Ancestry	Variable	t	*p*
Bohemian	HL	-1.87	1.00
	HB	-6.66	**<.0001**
	FB	-1.51	1.00
Central Italian	HL	0.21	1.00
	HB	1.65	1.00
	FB	-3.22	**.04**
Hungarian/Slovakian	HL	0.57	1.00
	HB	-1.96	1.00
	FB	0.18	1.00
Polish	HL	-2.27	.37
	HB	0.87	1.00
	FB	1.52	1.00
Scottish	HL	0.28	1.00
	HB	-3.13	.07
	FB	-2.79	.21
Sicilian	HL	0.99	1.00
	HB	3.47	**.02**
	FB	-0.41	1.00

Chapter 5

Discussion

The value of the heritabilities derived in this study is that they are based on very complete, often large pedigrees. Schork and Schork (1993) discuss the power of estimating the heritability of a quantitative trait under varying sibship sizes. They conclude that when possible it is best to use analytical methods based on a kinship matrix, which utilizes all available family information, as opposed to methods based on pairs of family members (Schork and Schork, 1993). The large sample sizes of the subpopulations in this study, and the relatively high degree of available pedigree information make it ideal for estimation of variance components. The heritabilities derived in this study are considered good estimates based on these factors, as well as the large effective population size (Cheverud, 1988). The total sample heritabilities on average represent 65.3% of the variance in the phenotype. The high heritabilities imply that the distances derived from phenotypic data are close approximations to genetic distances. The proportionality of the distance matrices in this study is seen in Figure 7. The findings here mirror those of Konigsberg and Ousley (1995) and represent an important consideration in studies of biological distance. The constant of proportionality proposed by Cheverud (1988) of $G=h^2P$ where h^2 is .35 could be a conservative estimate in this case however. The fact remains that distances derived from phenotypic variances will represent an approximation

to the distances derived from genetic variances. This represents an important consideration in studies that consider the biological relationship between human groups using model-based methods (Relethford and Lees, 1982), as well as model free methods such as the Mahalanobis distance. The assumption of heritabilities of h^2=1 in model based methods such as suggested by Relethford and Blangero (1990), can be reduced to accommodate reasonable heritabilities in the .5 to .6 range such as in Schillaci and Froehlich (2001). The resulting relationships could be considered more meaningful, minimum values of F_{ST} would most likely be closer to actual values, and relationships that are more meaningful could be established. In order to establish values of F_{ST} for the immigrant data, the program RMET 4.0 for Windows (Relethford, 1996; Relethford and Blangero, 1990) is utilized. In this case, the value of F_{ST} assuming a heritability of 1 is .103. If the average heritability of .567 derived from the three traits in this analysis is used in the calculation of F_{ST}, the value increases to .168. This increase is slight, but represents an increase in average heterozygosity. If the constant suggested by Cheverud (1988) is used to calculate F_{ST}, then the value increases to .247, and represents a major increase in heterozygosity. It is proposed that heritabilities in the .4-.6 range be used when estimating considering the notion of population structure using anthropometric data. This will most likely yield values of F_{ST} that more closely represent reality, without compromising the minimum value of $F_{ST.}$

The fact that heritabilities approaching .6 can be estimated from the Boas immigrant data has implications for the usage of anthropometric and skeletal data in population studies. Criticisms of biodistance studies have focused on the original report of Boas (1910), on the basis that radical changes can take place in human head form in as little as one generation. The findings of this analysis do not support these criticisms. The replication of Boas's original study performed herein shows that upon statistical reanalysis of the data there is actually very little differentiation caused by the American environment. The results or the trace comparison analysis presented in Table 12 shows that 99.75% of the total phenotypic and 99.83% of the genetic variation is due to an ethnic component, leaving very little of the variation to be accounted for by an effect of the environment. Differences do exist between American-born children and their European-born parents, but these differences are small in comparison with the distances between ethnic parental groups and children. In addition, the results of the replication of Boas's original tests on differences between American and European-born children reveal a small amount of differentiation occurring due to the effect of the American environment. The results are clear that 10.1% of the 177 t-tests capable of being performed produced significant differences. The differences amongst males represent 2.3% of the total number of tests, and females represent 7.9% of the significant differences. These numbers are very low when one considers the amount of citations that Boas's original (1910) work has received concerning the differences he observed concerning

this very set of comparisons. The only variable affected by the American environment in males is bizygomatic breadth, interestingly enough this is the only variable on which secular change appears to be occurring in males. This variable also represents the majority of instances of secular change in females (40%). This trend is evident in the American population, with a slightly higher degree of secular change occurring in females than in males (Jantz and Meadows Jantz, 2000). The trend in the immigrant data of reduced general vault and facial size is seen in females, while facial size appears to be the only variable undergoing a secular change in males. The secular trends that are present in the data could represent the differentiation seen between European-born parents and their American-born offspring seen in Table 16. In all instances, but the case of Sicilian head breadth, the parent-offspring differences coincide with variables that are under significant amounts of secular change. The differences seen by Boas (1910) could then be interpreted as the continuation of the secular trend in the American-born children. American-born children on average tend to resemble segments of the sample born as early as 1830-40 more than their own parents who were born around 1860-70. This has implications for the ideas surrounding the notion of cranial plasticity in the immigrant sample, because if American-born children resemble the individuals born some sixty to seventy years before them then the relative shape of the vault and face must be considered rather stable with regard to time and environment.

The findings of the regression analysis of the cranial index on environmental exposure indicate the lack of any significant change in the cranial index. The findings presented in Boas (1911; 1912a; 1940a) discuss the effect of exposure to the American environment in regards to change in the cranial index. However, if these findings were indeed accurate then the regression analysis would detect them.

If the American environment is the causal mechanism in operation on the samples analyzed here and cranial plasticity is the end result of such a mechanism, and the findings of Boas (1910; 1912a) are accurate, then one would expect to have the following null hypotheses: 1. American-born children should be quite different form European-born children, 2. American-born children should be quite different from their European-born parents, 3. If the findings of Boas concerning the increased differentiation of the cranial index with respect to amount of time exposed to the American environment, then there should be a linear increasing or decreasing trend present, 4. There should be a homogenization amongst the samples of American-born children in a principal coordinates plot due to a common result of the American environment, 5. The differences should be great enough to reduce the cranial trait heritabilities due to a large component of variance represented by an environmental component. If one considers the findings of this thesis, then the null hypotheses stated above are all rejected.

It has been seen that the differences present between American-born and European-born children of the same age are few and most are isolated

in the female segment of the sample. There is not a widespread significant difference between offspring born in Europe and America. The parent-offspring differences observed in the data are on the order of ten times less than ethnic group differences in a multivariate sense.

The direct comparison of parents and offspring using an ANOVA model indicates the relative likeness of American-born offspring to their European-born parents. In only 3/18 comparisons was a significant difference between parent and offspring observed. Like the comparisons between children, this does not represent a large proportion of the total amount of possible tests.

The regression analysis of cranial index and time of exposure to the American environment points to the fact that there is no significant increase or decrease in the cranial index amongst any of the samples. This indicates that the conclusions of Boas (1910; 1912a) are not accurate for the samples considered here. The findings of this analysis, in conjunction with the results of the t-tests performed on the same-age children born in America and Europe go directly against the findings of Boas (1910; 1912a). They provide as much proof as any of the analyses performed here that the amount of change that occurred in the immigrant samples is poor evidence of cranial plasticity.

As seen in Figures 5 and 6, there appears to be a slight cross-sample homogenization among the offspring toward an Americanoid form but, the geographic groups remain close to their relative group centroids. In other

words, the groups from Eastern Europe remain close to the Eastern European groups, and the same holds true for the Western European groups.

Finally, the reduction of heritabilities is not seen in the data. The heritabilities are on average higher than those observed elsewhere (Devor et al, 1986a, 1986b; Konigsberg and Ousley, 1995) and are nearly the same as those derived by other researchers (Paganini-Hill et al., 1981, Sharma and Sharma, 1984; Poosha et al. 1984). This indicates a relatively high degree of the phenotypic variation due to genetic factors, and a lower amount than one would expect if the American environment had a major effect on head form. Since the pedigrees in the analysis include both European-born parents and children and American-born children one would suggest that if an environmental component of the phenotypic variance would be maximized if there are indeed differences between the European and American-born groups. This suggestion is not upheld in light of the analyses performed here, indicating the diminutive effect of the American environment on head form.

Chapter 6

Conclusions

The evidence presented herein concerning the changes in bodily form of descendants of immigrants should not be considered irrefutable proof of the fallacy of cranial plasticity. It should be considered as evidence of the relatively low degree of change that occurred in one generation of parents and offspring. The findings presented in this thesis represent only a portion of the possibilities present in the Boas data set (Boas, 1928). The nature of science demands reinvestigation of previous work in order to aid in confirmation of or disproval of some previous hypothesis. This thesis has attempted to do such. Since the original publication of segments of this data some ninety-one year ago, (Boas, 1910) the findings of that report have been quoted many times as irrefutable proof of cranial plasticity. However, authors who attempted to critique the data (e.g. Fisher, (1938) and Morant and Samson (1936)) have been cited rarely if ever in reports that cite Boas's study. This thesis joins the authors who have attempted to shed light on the controversy surrounding this extraordinary data set and this vital issue in biological anthropological research.

The findings presented here have reaching implications for studies of biological distance and population structure. The evidence with regard to the relative stability of the human cranial vault in situations of environmental

change lends credence to biological reconstructions of both prehistoric and historic population relationships based on the human crania. The use of phenotype data, due to relatively high degrees of heritability, in the light of genetic data provides a good proxy due to the proportionality of the variance-covariance matrices.

The reconstruction of population relationships is a complex process with many assumptions, and without understanding the assumptions of any model-based methods, the result will have any number of possible critiques. The goal of this thesis was to possibly alleviate one the strongest critiques of biodistance and population structure analyses: cranial plasticity. If the differences observed by Boas (1910; 1912a) are considered evidence of cranial plasticity, these accounts need to be reconsidered in the light of modern reassessment of his data.

The study of Boas (1910) represents only one, while perhaps the main, of the studies of human cranial and bodily plasticity. If the question of cranial plasticity is to be answered, then the findings of other studies (Goldstein, 1943; Lasker, 1946; Shapiro, 1939) likewise need to be considered. Since the data for these studies are available, this problem is not beyond the means of modern biological anthropology. The only obstacle to overcome is the political and ideological hurdles that many in our field have constructed that make it difficult for these issues to be evaluated.

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