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CHAPTER 17

HOW GENETIC ARE HUMAN BODY PROPORTIONS?

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L INTRODUCTION

Children tend to resemble their parents in stature, body proportions, body composition, and rate of development. It may be assumed that barring the action of obvious environmental influences on growth (such as chronic illness or long-term malnutrition) these resemblances reflect the influence of genes that parents contribute to their biological offspring. A study published by Prokopec and Lhotská (1989), based on a sample of 81 boys and 78 girls, is an example of this view. The subjects, all from Prague, were measured annually from birth to age 20 years. The Preece-Baines growth curve was fit to the longitudinal data of each subject. From these fitted curves for all the boys and girls, the three tallest, the three shortest, the three slowest maturing, and the three fastest maturing of each sex were selected. None of these extreme cases was known to have any major chronic or acute diseases. Neither the subject's history of common childhood diseases, nor the occupation of the fathers had an effect, positive or negative, on growth and development. In contrast, the midparent height did predict the adult stature of offspring. Mid-parent height is the average of the stature of the mother and the father. Inspection of the Prece-Baines curves showed that tall or short stature at age 20 could be predicted from stature at age four years. The positive impact of mid-parent stature on offspring growth and the predictability of adult height from stature at age four are prima facia evidence for the role of heredity. Moreover, these findings attest to the early establishment of individual patterns of growth and their stability over time.

Other well-known research strategies are used to demonstrate the genetic determination of human growth. These strategies include the study of monozygotic and dizygotic twins, correlations in growth between biological relatives (non-twins), and the effects of genetic abnormalities on growth (reviewed in Bogin 1999). Studies such as these lend support to the concept of a "genetic potential" for body size, body composition and body proportions. The term "genetic potential" usually means that every human being has a genetically determined upper limit to adult stature, the ratio

of leg-length to sitting-height, and other anthropometric dimensions. It is further assumed that an individual may achieve this "genetic potential" if the environment is free of insults that delay or retard growth.

The origin of the idea of "genetic potential" in human development may be found in the theory of epigenesis. In 1651 the English physician and anatomist William Harvey hypothesised that the specialised tissues, organs, and structures of the individual develop from unspecialised and undifferentiated cells in the ovum. Experimental support for this hypothesis came only in 1759 with the research of the German anatomist Kaspar Friedrich Wolff. He was able to show that the development of the organs of the chick in the egg did indeed develop from undifferentiated cells and tissues. Further research into embryology during the 19th century came to view prenatal development as largely fixed, or predetermined, in nature. With the rediscovery of Mendel's principles of heredity in 1900, the mainstream view within developmental biology was that, "the basic potential nature and organisation of the structures of the organism are determined by the genetic constitution of the fertilised egg" (Roche and Boell 1999). The quoted material is from a popular electronic encyclopaedia. Note that the authors of this quote link the words "potential nature," "determined," and "genetic" to describe how developmental biology operates. This is one more example of the way in which the concept of "genetic potential" is ingrained in scientific and popular literature.

Some scholars extend the concept of "genetic potential" from the individual to populations. Body-proportion differences between populations and ethnic groups are well known, and are often used to exemplify the concept of "genetic potential." Norgan (1998), for example states that, "The largest differences between ethnic groups, when all are growing up in good environments, are those of shape rather than size." Eveleth and Tanner (1990, p. 186) state, "These differences are certainly genetic in origin...." Both Norgan and Eveleth and Tanner reinforce these statements with a good deal of compelling data from growth research conducted on diverse human populations. The data are, however, circumstantial as no genetic basis for body shape is provided in any of the studies cited. Indeed, there is no known basis for the determination of human body proportions.

In addition to the use of circumstantial data to support the belief in a genetic determination of body proportions, several authors use a series of somatotype-like photographs of men of European or African origin. One version of these photographs, from the *Cambridge Encyclopedia of Human Growth and Development* (1998, p. 360), is reproduced here as Figure 1. The caption for this version of the figure reads, "Comparison of European and African physiques, showing the relatively longer legs of Africans." The implication of this statement, and the accompanying article on body proportions, is that population differences in body shape are genetically determined. Note that the photographs of each man are reduced or enlarged in size so that all of the men have the same sitting height, as this makes the differences in leg length more clear.



Figure 1. Comparison of European and African Olympic athlete physiques showing the relatively longer legs of Africans. In each of the four comparisons the European athlete is on the left. This figure was re-imagined from a photograph in The Cambridge Encyclopedia of Human Growth and Development (Ulijaszek 1998, p. 360). Professor Tanner supplied the original photograph).

The photographs were originally published in Tanner (1964), and are of Olympic athletes. Olympic athletes are a highly selected group of people. The body shape of Olympic athletes, including the ratio of leg length to sitting height, is strongly correlated with the type of sport performed. Moreover, Olympic athletes constitute only a very small segment of humanity, far smaller in number than would be required for reliable and accurate statistical analysis. Olympic athletes, then, are in no way representative of the general population in terms of biology or behaviour. Yet, a version of the original photographs has been reprinted in several textbooks, including both editions of Eveleth and Tanner's *Worldwide Variation in Human Growth* (1976, 1990), and is used to demonstrate genetic differences in growth potential between human populations.

The concept of "genetic potentials" in growth and body shape of human populations is well entrenched in the field of human growth research. Some scholars take the concept of "genetic potentials" as a given and use it without definition or justification from research, that is, without reference to the scientific literature. Interested readers may peruse recent issues of journals dealing with human biology, physical anthropology, paediatric medicine, and related fields, where they will find the concept of "genetic potential" used in this way.

The problem with this casual usage is that the assumption upon which it is based is not true. Existing research shows that adult stature, body proportions, and body composition are highly plastic. One of the clearest examples of the plasticity of human body proportions comes from Tanner et al.'s (1982) studies of relative lag length of Japanese children. In 1957 the relative leg length of adult Japanese was significantly less than that of Northern Europeans, and it was assumed that this difference was due mostly to genes. By 1977 the two ethnic groups had become virtually identical in shape. This invalidated the genetic explanation, which was replaced by an explanation favouring improvements in the physical and social environment of Japan. Research conducted in China (Zhang and Huang 1988), Argentina (Bolzan et al. 1993), Poland (Wolanski 1979), and Mexico (Gurri and Dickinson 1990, Wolanski et al. 1993, Wolanski 1995, Siniarska 1995) shows that the development of body proportions during the growing years is exquisitely sensitive to the quality of the local environment (reviewed in Bogin 1999 and discussed below). In these studies boys and girls of identical ethnicity and genetic background are compared, and children from lower SES families are significantly shorter in leg length than children of higher SES families.

In this article we re-examine the existing literature to see to what extent ethnic and population differences in body-proportions which are assumed to be of a genetic nature are, in fact, better explained by environmental plasticity in growth. We also present the findings of a new study of body proportion change in the children of Guatemalan immigrants now living in the United States. Finally, we make use of experimental findings on the determinants of fluctuating asymmetry in insects to develop an ecological model of body-proportion development.

2. WORLD-WIDE VARIATION IN HUMAN BODY PROPORTIONS - A NEW ANALYSIS

The first and second editions of the book Worldwide Variation in Human Growth (Eveleth and Tanner 1976, 1990) provide the most comprehensive compendia of

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human growth studies. The authors present data for several measures of body proportions. Here we re-analyse the data for relative sitting height, which is calculated as [(sitting height/stature) x 100]. Relative sitting height is a ratio that expresses the percent contribution of sitting height -- the length of the head, neck and trunk -- to total stature (Lohman, Roche, and Martorell 1988). In practice, this ratio is most often used as an indication of leg length differences between individuals or populations. The reason for this is due to the cephalo-caudal gradient of growth, which means that during the years of growth the head and trunk are always closer to their final adult size relative to the legs. The sitting height ratio changes with age as the legs begin to grow relatively faster than the head and trunk of the body.

From the data found in Eveleth and Tanner (1976, 1990) we analysed a total of 874 samples of relative sitting height of boys and girls, measured at different ages and representing populations from many countries. The samples include people living on most of the major continents and islands of the world. When discussing the relative sitting height data, Eveleth and Tanner focus on only a few of these samples, which they consider to be representative of four major geographic regions of the world. The 1976 edition of their book presents samples from London (Europe), from Ibadan, Nigeria (Africa), Hong Kong (Asia), and of Australian Aborigine origin (Australia). In proportion to sitting height, the Australians had the longest legs followed, in order by Africans, Europeans, and Asians. Expressed quantitatively. "at a sitting height of 60 cm, for example, London boys have leg lengths averaging 43 cm, Ibadan boys 53 cm and Australian Aborigine boys 61 cm" (Eveleth and Tanner 1976 p. 229). In the 1990 edition of their book they analyse data from Bergen (Europe), the People's Republic of China (Asia), "Afro-Americans" (Africa) measured for the NHANES II study (a national study of health and nutrition in the United States), and the Australian Aborigines from 1976 (Australia). The 1990 analysis finds almost the same differences in leg length as found in 1976.

By organising the samples in this way, Eveleth and Tanner are employing a geographic "racial" typology (Garn and Coon 1955, Garn 1971). Garn (1971, p. 17-18) states that, "To a large extent the geographical races of mankind coincide with the major continents and...may also be spread over major island chains, as is evident in the Pacific today." Over the past century, many researchers have assumed that the body proportion differences between geographic populations are explainable only in terms of a genetic or "racial" model. The population difference in body proportions is usually considered to be an adaptation to regional climates, for example, long arms and legs in hot and humid regions and short appendages in cold regions. There is considerable evidence to support the correlation between climate and body proportions (Roberts 1953 is the classic study). However, no genes for the determination of body proportions are known and a plausible genetic mechanism that might account for population differences in body shape has never been formulated.

We use quote marks when writing the word "race" because that term implies a biologically definable group of people. Definable biological distinctions between socalled "races" do not exist at the genotypic or phenotypic level (Bogin 1993, Lasker 1999). "Race" does have some value as a shorthand term to categorise people into groups that differ in economic opportunities, social organisation and resources, and political power. In the United States those people who are classified as "white" enjoy, on average, greater socio-economic opportunities and political power than those classified as "black." These differences have an impact on social resources that

often translate into biological effects, such as patterns of growth and development (see Bogin 1999 for a more general and comprehensive discussion of "race" and human growth).

The analysis presented by Eveleth and Tanner compares four samples from different geographic areas. These areas conform to the four major world regions defined by many of those researchers using a "racial" typology to divide humanity --Africa, Asia, Australian, Europe. Eveleth and Tanner (1990, p. 188) attribute the differences in relative sitting height and other body proportions to "racial differences." Indeed, all of the growth data presented in both editions of Worldwide Variation in Human Growth are organised into categories based upon geographical "races." These "races" are Europeans, Africans, Asian, Australian Aborigines and Pacific Islanders (including New Guineans and Maoris of New Zealand). Indo-Mediterraneans (includes Algeria, Egypt, Ethiopia, India, Iran, Israeli Kurds and Yemenites, Pakistan, Saudi Arabia, Turkey, and Yugoslavian gypsies), and a final group of "inter-racial crosses", such as Cuban mulattos, South African Coloureds, and Mexican Mestizos. The geographic "racial" classification is reinforced in their work in that Eveleth and Tanner are more concerned with the putative geographic origin of the samples than with the location at which they were measured. For example, Black children measured in Tanzania and Black children measured in Washington, DC are considered to be "African race." Native Canadians (Indians of Canada), the Maya of Guatemala, and Chilean Indians are considered to be "Asian race." Any samples of children in the United States with light skin colour and claiming European origin are considered to be of the "European race."

2.1 Materials and methods of the re-analysis

We retain the geographical "race" scheme employed by Eveleth and Tanner in our reanalysis of their data on relative sitting height and we add several new variables. In all, we assigned an AGE, SEX, RACE, REGION, WORLD, SES, and SES x WORLD variable to each sample. The numeric values assigned to sub-samples within each variable are given in Table 1. These new variables are defined as follows. AGE is the chronological age of a sample. Whole years are used to define AGE, meaning that AGE 7 included all individuals between 7.00 and 7.99 years old and so on for all other ages. Any individuals age 20 or older were considered adults and were assigned the AGE score of 20. The SEX variable indicates the biological sex of an individual, that is, either male or female.

RACE is the geographical "race" categorisation as found in Eveleth and Tanner (1976, 1990). As stated above, this means that Tanzanians and fifth generation Blacks living in the United States are "Africans." REGION is the geographic location where each sample was measured regardless of "race" categorisation. This means that Blacks and Whites measured in the United States and Canada are coded as North American REGION, and any sample measured in Africa are African REGION. The RACE variable assesses variability in body proportions by sorting people into purported historical populations. The REGION variable provides an assessment of the effect of current geographic location on body proportions of a sample.

 Table 1. Variables used to re-analyse Eveleth and Tanner's data, the scores assigned to each variable and the meaning of these scores.

Variable	Score			
AGE	1 to 18 - indicates the chronological age of a sample; e.g. a score of 7 is for individuals between 7.00 and 7.99 years old. A score of 20 indicates age 20 years old or older.			
SEX	1 = male and 2 = female			
RACE	= Origin in Australia, New Zealand, or Papua New Guinea, 2 Origin in Africa, 3 = Origin in Europe, 4 = Origin in Asia, cludes Native Americans (North, Central, and South merican Natives).			
REGION	I = Europe, $2 = North America (Canada and United States)$, $3 = Central America (Mexico to Panama)$, $4 = South America$, $5 = Africa$, $6 = Asia$, $7 = Indo-Mediterranean$, $8 = Australia$, New Zealand, Papua New Guinea, and Pacific Islands			
WORLD	1 = Industrialised/developed nations, $2 =$ former Soviet Union and its satellites, $3 =$ non-industrialised/lesser developed nations, $1.5 =$ Hong Kong, Singapore, Southern Europe			
SES	1 = very high SES, $2 =$ high SES, $3 =$ middle SES in the industrialised nations, $4 =$ urban poor/working poor, $5 =$ rural poor			
SES x WORLD	Multiplication product of SES and WORLD			

The WORLD variable indicates that a sample was measured in a first world, second world, or third world country. First world countries in the Eveleth and Tanner database are those of North-western Europe, the United States, Canada, Japan, Australia, and New Zealand. Second world nations in the database are those that belonged to the former Soviet Union and its satellite republics. Third world nations in the database are those of Africa, Asia (except Japan), Latin America, the Pacific Islands, New Guinea, and India. Some nations in Eveleth and Tanner's database were most difficult to categorise. We assigned the value of 1.5 to Hong Kong, Singapore, and southern Europe (Spain, Italy, and Greece) indicating that these nations were halfway between first and second world in development indicators at the time the growth data were collected. The WORLD variable is intended to assess the effect of the general level of industrial development and standard of living on body proportions.

The SES variable is an estimate of socio-economic status for each sample varying from a high of 1 to a low of 5. Scores of 1 or 2 were assigned to samples living in any country if the sample was described as "very high" or "high" SES. A score of 3 is for middle SES samples in the industrialised nations of the first and second world. A score of 4 is for urban poor and a score of 5 is for rural poor. Parental occupation and parental education, especially of the father of a child, are usually used to estimate SES. But, such information is not always known, and this

makes the SES variable the most difficult to assign with accuracy. We tried to use the SES information provided in each of the original publications cited by Eveleth and Tanner. Most often, the authors of these papers describe their samples as "low SES," "middle SES," or "high SES." However, not all of the original papers included measures of SES for their sample. Also, we could not locate all of the original papers. Our assignment of a SES score to each sample is, therefore, a mixture of quantifiable information and qualitative assessment based on our best estimate of the general socio-economic status of the sample.

The SES x WORLD variable is the multiplication product of the variables SES and WORLD. We included this variable based on existing empirical research showing an interaction between SES and WORLD on human growth (e.g. Henneberg and Van Den Berg 1990, Bogin 1999). For example, low SES Maya children growing up in the United States, a first world nation, are significantly taller and heavier than low SES Maya children of the same ages growing up in their third world homeland of Guatemala (Bogin and Loucky 1997).

For analysis, each of these variables was entered into a ridge regression model. Ridge regression is used when multicollinearity exists between the independent variables. A test for multicollinearity found that the variables WORLD and SES x WORLD were highly correlated with the other variables. Ridge regression reduces the effects of such high correlations by adjusting the regression model for more reliable *beta* coefficients.

2.2 Results

A summary of the regression analysis is presented in Table 2. We find that AGE explains 42% of the variance in relative sitting height of the 874 samples in the Eveleth and Tanner database. As is well known, relative leg length increases from infancy to adulthood. The geographical RACE organisation of the samples explains 3.6% of the variance and SES variable accounts for an additional 1.0% of the total variance. The SEX variable explains only 0.002% of the variance, which is not statistically significant. The other variables did not enter the regression model.

Table 2. Summary of the stepwise ridge regression model for relative sitting height (lambda set at 0.10). R = 0.684, $R^2 = 0.465$, F(4, 869) = 191.03, p < 0.000, Standard error of estimate = 2.083

	Step	Multiple R	Multiple R ²	R ² change	p-level
AGE	1	.648	.420	.420	.000
RACE	2	.675	.456	.036	.000
SES	3	.682	.466	.010	.000
SEX	4	.684	.468	.002	.120

2.3 Discussion

Eveleth and Tanner state that, "The ultimate size and shape that a child attains as an adult is the result of a continuous interaction between genetical and environmental

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influences during the whole period of growth" (1990, p.176). We agree with this statement. Our re-analysis of Eveleth and Tanner's data helps to refine the role of "genetical and environmental influences." Our regression analysis shows that geographic RACE does contribute to variation in body proportions, but at a relatively low level. Explaining only 3.6% of the total variation, RACE contributes much less to the variability in body proportion than is assumed by many researchers and the general public. The socio-economic variable SES, also contributes a small and significant amount to the variance in body proportion. Indeed the relative contribution of RACE and SES to the variance in body proportion are statistically equal in our analysis, as a test for equality of slopes of their regression coefficients (the unstandardised *betas*) shows no differences (t = 0.94). It is important to note that, due to the imprecise definition of both RACE and SES in our re-analysis, our results must be taken with caution.

To better understand variation in body proportions it is necessary to have more accurate control of genetic and environmental variables. Some studies of body proportion have such control. For example, Ramos-Rodriguez (1981) shows that Mexico City children of middle SES have relatively longer legs than low SES Mexican children from Oaxaca. She also shows that genetics cannot account for this difference. Genetics played no role in the secular trend of Japanese body proportions studied by Tanner *et al.* (1982). Prior to 1960, the Japanese were considered to be both a short stature and short-legged "race." Between 1960 and 1977 the Japanese, on average, gained 10 cm in stature and almost all of this increase was in leg length. After 1977, the average height of Japanese men and women continued to increase, but at a slower rate (Takaishi 1995), and both leg length and sitting height seem to have increased at about the same rate, at least for young women (Hojo *et al.* 1981). Since 1990 there is little evidence for further increase in stature. Today, Japanese have, on average, virtually the same body proportions as many European populations.

Several researchers working in Argentina, Poland and Mexico report similar findings on the plasticity of body proportions. A team of researchers working in small towns located in the Province of Buenos Aires measured 569 boys and girls, seven to 13 years old, attending several schools (Bolzan et al. 1993). The sample was divided into groups according to age, sex, and occupational status of the father. Both boys and girls with fathers of lower occupational status (lower SES) were shorter, and especially shorter in leg length, than subjects of higher family SES. In Poland (Wolanski 1979), improvements in living conditions in towns and villages, such as nutrition and health care, are associated with increases in leg length relative to stature. Similar results are reported from a series of Mexican studies that find that the body proportions of boys and girls vary according to relatively small differences in family SES. The authors of these studies (Wolanski et al. 1993, Wolanski 1995, Siniarska 1995) measured children living in the Yucatan region, including both ethnically Maya and non-Maya populations. All of the families were of, generally, low SES, but children from families of slightly better economic means were longerlegged than children from lower SES families. Other studies from Mexico find even more subtle influences of life style on body proportions. The leg-length-to-stature proportions of women living in Chiapas Mexico, all of low SES, differ according to socio-economic status, ecological region, and demography (Gurri and Dickinson 1990). All of the 421 women studied were 20 years old or older and all were of

generally low SES. The sample was divided into four SES regions: 1) a region of intensive export agriculture, 2) a region of cattle for meat production, 3) a region of mixed agriculture and dairy herding, both for national consumption, and 4) a region of subsistence agriculture. The authors also divided the sample into four ecological regions: 1) Pacific coastal plain, 2) Sierra Madre mountains. 3) Central Valleys, and 4) Central Plateau. Finally a demographic division was made between those women living in rural or urban areas. The authors found that 80% of the variance in stature in the sample was due to SES region and that 20% of the variance was due to ecological region. Almost all of the differences in stature within the sample were due to variation in growth of the leg. Women from the SES regions of export agriculture and the cattle raising area were the tallest. Women from the highland ecological regions were, generally, the shortest. Similar findings are reported for children and adults living in the Yucatan (Murguia *et al.* 1990, Dickinson *et al.* 1990). These Mexican studies indicate that even within a generally low SES population, life style differences exist and exert influence on body proportions.

3. RAPID CHANGE IN THE BODY PROPORTIONS OF MAYA CHILDREN

3.1 Materials and methods

Since 1992, we have studied the growth of samples of Maya children living in the United States (Bogin and Loucky 1997). These children are the offspring of Maya adults who immigrated from Guatemala to the United States, mostly from the late 1970s to the early 1990s. Some of the Maya children measured in our 1992 survey were born in Guatemala or Mexico and some were born in the United States. Our 1992 survey shows that the children of Maya immigrant parents are significantly taller than Maya children living in Guatemala (Bogin and Loucky 1997). We did not measure body proportions in that study, but we hypothesised that an increase in relative leg length accompanies the increase in stature.

A new study of the growth of Maya children in the United States began in 1999. We measured the height, weight, and sitting height of 360 Maya children ages 6 to 12 years old, living in south central Los Angeles in February 1999 and in Indiantown, Florida in March, 2000. With these data we computed the sitting height ratio. We compared these newer data with the data for height of the 1992 samples and with the data for height and sitting height ratios of a sample of Maya schoolchildren living in rural Guatemala measured in 1998 (n = 1297). The Guatemalan data were kindly supplied by Luis Rios of the Universidad Autónoma de Madrid.

3.2 Results

Mean values for height and sitting height ratio for each sample are shown in Figures 2 and 3. Anthropometric reference data from the NHANES I and II surveys of the United States (Frisancho 1990) are used as a baseline for comparison in each graph. Analysis of variance (ANOVA) was used to evaluate differences between samples.



Figure 2. Mean height of Maya children living in the United States measured in 1992 (Maya-USA 1992) and in 1999-2000 (Maya-USA 2000) compared with Maya children living in Guatemala measured in 1998 (Maya-Guat) and the United States reference data from NHANES 1 and II.



Figure 3. Mean sitting height ratio of Maya children living in the United States measured in 1999-2000 (Maya-USA 2000) compared with Maya children living in Guatemala measured in 1998 (Maya-Guat) and the United States reference data NHANES I and II.

After adjusting for the effect of age and sex, our results show (Figure 2) that the Maya children of the 1999 and 2000 samples (abbreviated as "Maya-USA 2000") are significantly taller (Figure 1) than the Maya samples measured in 1992 (abbreviated as "Maya-USA 1992") and Maya children living in Guatemala (abbreviated as "Maya-Guat"). The Maya living in the USA also have smaller sitting height ratios than Maya living in Guatemala (Figure 3). All differences are significant at p < .01. A smaller sitting height ratio generally indicates a child with relatively longer legs. Compared with the NHANES references, all of Maya are shorter and have higher sitting height ratios, i.e., relatively shorter legs.

3.3 Discussion

Our findings add further support to the literature on developmental plasticity in body proportions. The results indicate that between 1992 and the present, there is a clear, and positive, trend in growth of Maya children living in United States. The reasons for this trend are likely due to improvements in the environment for growth. All Maya in the USA have access to clean drinking water, health care, and education. The Maya children living in Indiantown, Florida participate in school breakfast and lunch programs. Nearly all of the Maya children have at least one parent with a wage-carning job. All of this provides the Maya in the United States with a higher standard of living than that found in Guatemala, as clean water, health care, education and wage paying employment often do not exist for Maya living in rural Guatemala. These health, economic, social, and nutritional changes are known to result in greater stature. Our findings support the hypothesis that the increase in stature is due mostly to relatively longer legs. We predict that the positive trend in height and sitting height ratio seen between 1992 and 2000 will continue for the Maya in the United States. Eventually heights and body proportions should achieve values that approximate those for long-term residents of the United States.

4. CONCLUSION

In this article we have taken a critical look at the concept of genetic potential or genetic determination of human body proportions. We find that population differences in body proportions are influenced very little by genetic background, at least as imputed from geographic, ethnic, or "racial" categorisations. Our findings stand in sharp contrast to the opinion found in several of the most widely consulted books on human growth. In a more general sense, the whole concept of "genetic determination" in human growth is seriously flawed. That notion implies that the flow of information about how any human trait is developed, be it height, body fatness, personality, or intelligence, originates in the DNA and then unfolds into the phenotype. Within this scenario, one may allow for a greater or lesser amount of environmental influence on the phenotype, but the flow of information basically begins with the DNA and moves one way.

The roles of DNA in human development are much more complex, and often much less direct, than this. Genes do not directly cause growth and development. Rather, the many proteins that genes produce, which are mediated by the endocrine and neurological systems, regulate the expression of a genetically inherited pattern of

growth. The physical and social environment also mediates growth. In the case of the Prague study discussed in the introduction of this article, it is important to note that the parents and children were living in the same households and, therefore, shared a very similar environment. It is too simplistic, therefore, to ascribe the similarities in growth between parents and offspring to genes alone.

The interactions between genes, hormones, and the environment may flow in all directions. A marvellous example of the interaction of genes, proteins, and the endocrine system may be seen in the action of homeobox genes and *Hox* genes. The description and elucidation of homeobox and Hox genes is one of the most important advances of molecular biology of the past two decades. The homeobox is sequence of 180 DNA base pairs that codes for a 60 amino acid segment of a protein. First discovered in the genome of the fruit fly, Drosophila, homeobox sequences are found in all eukaryote organisms so far examined. These highly conservative DNA sequences -- the same homeobox sequences are found in organisms as diverse as hydra, nematodes, all arthropods (the group that includes insects) and all chordates (the group that includes human beings) -- produce proteins that regulate the expression of other genes, "...and control various aspects of morphogenesis and cell differentiation" (Mark et al. 1997, p. 421). Hox genes are a category of homeobox genes that encode transcription factors (Holland and Garcia-Fernandez 1996), which are proteins that initiate and regulate the conversion of the DNA code to the RNA sequence that is used to make amino acid polypeptide chains.

In multicellular animals, homeobox genes act to delimit the relative positions of body regions, for example the head, thorax and abdomen of insects, or the general body plan and limb morphology of vertebrates. Homeobox genes seem to have their greatest impact during the earliest stages of development. The proteins that homeobox genes produce are needed to regulate the expression of other DNA to, "...sculpt the morphology of animal body plans and body parts" (Carroll 1995, p. 479). The DNA affected by homeobox proteins will, in turn, produce other proteins that mediate cellular differentiation, growth, and development. These "down stream" proteins do not act alone. Some of them must combine via a process called molecular zipping before they have any effect on a given segment of DNA (McKnight 1991). These and other proteins need an appropriate environment to have any effect. In placental mammals, the biochemical environment of the egg cell and, a bit later in time, of the mother's womb and the placenta, provide a host of factors needed for growth, including nutrients and hormones.

Throughout life, the endocrine system often provides the necessary biochemical environment for gene action. The human adolescent growth spurt, for example, requires adequate amounts of two hormones, growth hormone and testosterone (boys) or oestradiol (girls), to be secreted into the blood stream. Without these two hormones the genes that regulate growth of skeletal, muscle, and adipose tissue will not increase enough in activity to produce the growth spurt. The endocrine system also responds to the influence of many environmental factors that affect human development. Under-supply or over-supply of many nutrients, such as vitamin A or D and folate, can have major effects on the growth and development of tissues, organs, and the body as whole. These nutrients influence growth via their effect on the regulation of DNA expression, protein synthesis, and hormonal regulation (see Bogin 1999 for several additional examples). Because it is situated between the action of genes and the external environment, the endocrine system serves as a

mechanism that unifies the genes we inherit and the environments in which we live to shape the pattern of growth of every human being.

Fluctuating asymmetry and human body proportions

Animal models are beginning to clarify the underlying biological processes of the development of body proportions. Here we describe one experiment that manipulated the size of forewings and hindwings in the buckeye butterfly (*Precis coenia*). The authors of this study (Klingenberg and Nijhout 1998) were interested in the control of fluctuating asymmetry (FA), that is, departures from the anticipated or normal symmetry between the parts of growing organisms. In bilateral organisms one measure of FA is to measure and compare the left and right sides of an individual. In organisms with fore and hind limbs, wings, or other appendages it is possible to measure FA by comparing the size of the distal and caudal segments. "Fluctuating asymmetry... is increasingly being discussed as a potential indicator of environmental stress" (Wilsey and Saloniemi 1999, p. 341). The working hypothesis is higher level of FA are indicators of greater developmental instability and greater environmental stress (Klingenberg and Nijhout 1998). The search for the factors underlying FA, in both plants and animals, is an active area of developmental biology research.



Figure 4. Regression of dry weight per forewing (the average of left and right sides) on dry weight of the body for butterflies from which one, both, or no hindwing imaginal discs had been removed (from Klingenberg and Nijhout 1998, p1136, with permission of the author)

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In their experiments with the butterflies, Klingenberg and Nijhout (1998, p. 1135) "...removed the hindwing imaginal discs from one or both body sides of caterpillars. Emerging butterflies were thus missing one or both hindwings, but had heavier forewings, midlegs, and hindlegs than untreated controls. When only one hindwing was removed, the forewing and hindleg on the treated side were heavier than the untreated side." The results of these experiments for the growth of the forewing are shown graphically in Figure 4. The authors note that the degree of asymmetry and increase in weight of the growing forewings or legs diminished with greater physical distance between the removed imaginal disc and the remaining tissue.

Imaginal discs are embryonic structures of insects that provide the basic information and the tissue structures to form body segments in adult organisms. The developmental biology of imaginal discs are best known from the fruit fly *Drosophila*, where the limbs and eyes arise from discrete imaginal discs. The imaginal discs of *Drosophila* are epithelial sacs composed of a "...columnar cell monolayer covered by a squamous epithelium known as the peripodial membrane" (Gibson and Schubiger 2000). During the fly's development the peripodial cells are able to send biochemical information to the imaginal disc via microtubule connections. Experiments by Gibson and Schubiger (2000) demonstrate that biochemical communication between the peripodial cells and the imaginal discs influences the control of growth and pattern formation of cells that will become the eye and wing in the adult fly.

Based on the results of their experiments with butterflies, Klingenberg and Nijhout (1998, p. 1135) concluded that, "Our findings are consistent with the hypothesis that the growing imaginal discs compete for a haemolymph-borne resource, such as a nutrient or growth factor. Such competition is a possible mechanism for feedback interactions and may thus participate in the developmental control of asymmetry." This hypothesis is strengthened by the work of Gibson and Schubiger which finds that a physical connection, via microtubules, exists between the imaginal disc and the peripodial cells, which can transmit information and resources to the disc cells.

These findings, while based on work with insects, strongly indicate that the development of human body proportions is more complex than can be accounted for by any simple "racial" or genetic model. The known and hypothesised function of homeobox and *Hox* genes in human development is compatible with the insect models. This means that there is a role for genetic, environmental, and hormonal interactions in the regulation of the growth of human body segments. Human body proportions are important determinants of the biomechanical efficiency of movement and performance in many daily activities and in sport. Body proportions are also increasingly used as primary indicators of healthy growth and development (Bogin 1999). Accordingly, more sophisticated research on the regulation of development of body proportions needs to be done. The new research must discontinue the use of alleged geographic origin, skin colour, and other markers of "race." The new research must also discontinue the uncritical use of the concept of genetic potential. The new research must instead make use of better-defined, bioculturally valid, samples of people and the independent variables that may influence their body proportions.

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