This paper was presented at the session "Exploring the Nature of Human Biological Diversity: Myth v. Reality" at the American Anthropological Association (AAA) 2003 Annual Meeting on November 21, 2003 in Chicago, Illinois. The session was sponsored by the AAA *Understanding Race and Human Variation* project, organized by AAA's Society for Medical Anthropology and Committee on Minority Affairs, and funded by the Ford Foundation. The *Understanding Race and Human Variation* project is funded by the National Science Foundation and the Ford Foundation. This paper represents the views of the author and not the AAA *Understanding Race and Human Variation* project.

THE MEANING AND CONSEQUENCES OF MORPHOLOGICAL VARIATION

Richard L. Jantz
Professor of Anthropology
Department of Anthropology
University of Tennessee
Knoxville, TN 37996

INTRODUCTION

Morphological variation is an exceedingly broad topic with correspondingly complex causes. Since it is impossible to cover the topic in any comprehensive manner, this presentation will focus on cranial morphology, arguably the most controversial because of its historical connection to race. In this presentation, I will review some of the historical contributions to the meaning of cranial morphology, and then move into recent research with designs capable of revealing components of cranial variation that could not be uncovered in the earlier research. Much of the controversy revolves around cranial plasticity, the following issues central to the discussion:

1). How large is the effect?
2). What environmental factors are involved?
3). Does it mask genetic variation.
4). What ontogenetic processes are involved?

ENVIRONMENTAL EFFECTS AND CRANIAL PLASTICITY

Boas's Immigrant Study

Any consideration of plasticity must start with Boas's classic immigrant study, conducted on behalf of the U.S. Immigration Commission in 1909 and 1910 (Boas 1910; summarized in Boas 1940). In the 19th and early 20th century, cranial morphology was widely viewed as a stable "race" marker. It was Boas's work on immigrants and their children that brought about the realization that plasticity was a factor in cranial morphology. It would be difficult to overemphasize the importance of

Boas's work. In Boas's own time it began the demise of use of cranial morphology in racial typology. Boas's work has led to general acceptance of environmental influences on body morphology. Boas's study inspired several other immigrant studies: His own student, Marcus Goldstein (1943) studied Mexican immigrants, and two of Hooton's students, Shapiro (1939) and Lasker (1946) studied Chinese and Japanese. All of these demonstrated a number of changes, most notably, American born are taller and heavier. Cranial index, however, changes little. Differences in cranial index are small, variable in direction, and not statistically significant.

One of the most methodologically sophisticated studies is that of Hulse also a student of Hooton's, published in French in 1957 and English in 1964. Hulse examined non-random migration (sedents vs. migrants), immigration (Swiss born vs. California born), and exogamy vs. endogamy.

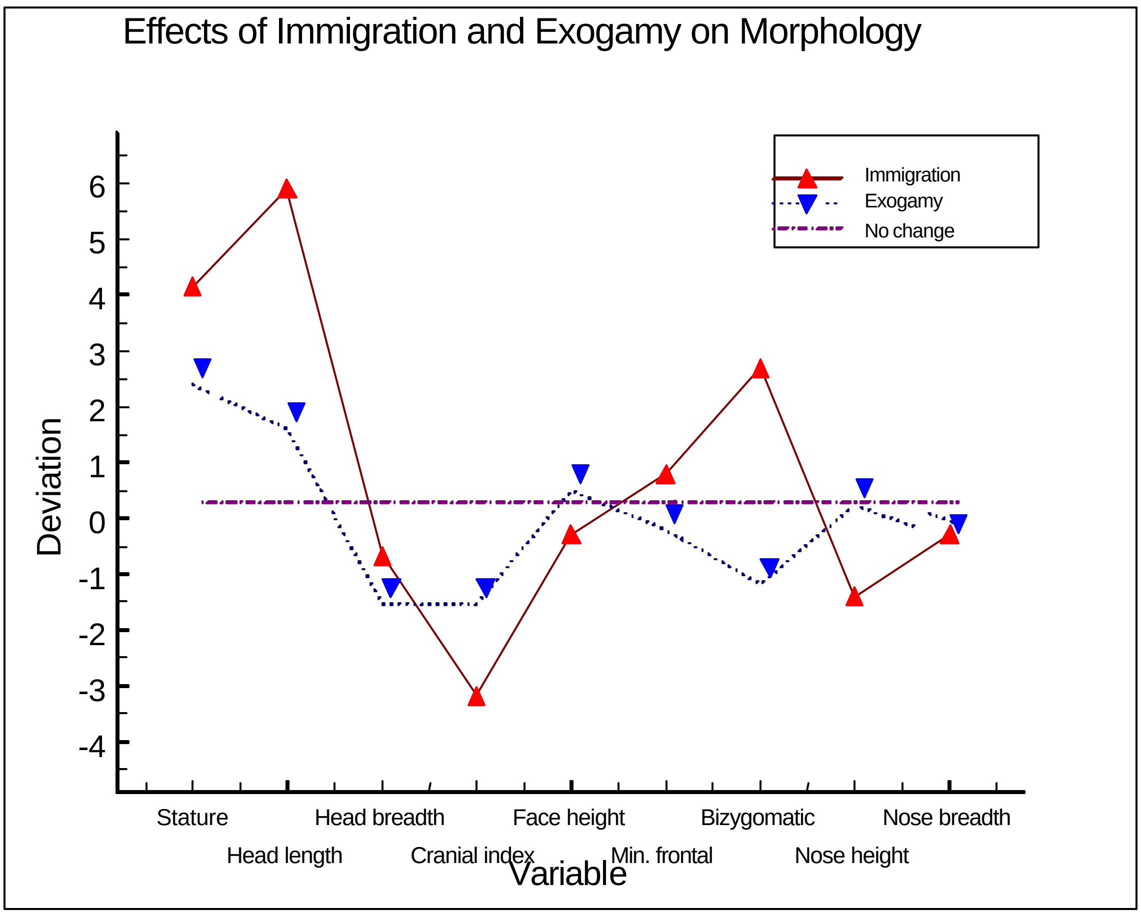

Figure 1. Graphical presentation of the effects of exogamy and immigration on various measurements in Swiss. After Hulse (1964).

Figure 1 shows the immigration and exogamy effect as deviations (in original units) of Hulse's data. It shows that both immigration and exogamy have an effect on certain variables, most prominently stature and head length. Head breadth is more strongly influenced by exogamy than by immigration. Hulse's research, as well as that of others, demonstrates that population structure can influence cranial morphology. Since greater exogamy inevitably accompanies immigration, changes cannot be interpreted solely in terms of environmental plasticity resulting from different environments.

Despite research which extends Boas's work in a number of respects, critics of cranial morphology return again and again to Boas to support the idea that environment dominates cranial morphology. Thomas (2002) observes that "Boas showed that a broad-headed population could become long headed in a single generation"(p. 105), while Armelegos and Van Gerven (2003) attribute to Boas the idea that cephalic index "…changed by the magnitude of a race in one generation…" (p. 55). Exaggerations of the difference between immigrants and their American born children probably trace back to Boas's own characterization his findings:

> In most of the European types that have been investigated the head form, which has always been considered one of the most stable and permanent characteristics of human races, undergoes **far-reaching changes** coincident with the transfer of the people from European to American soil. For instance, the east European Hebrew, who has a very round head, becomes more long-headed; the south Italian, who in Italy has an exceedingly long head, becomes more short-headed; so that in this country both approach a uniform type, as far as the roundness of the head is concerned. (Boas, 1910, p. 5) (Emphasis mine)

Boas's reference to the differences as a change in type has undoubtedly contributed to the wide spread perception that immigration produces profound changes in one generation. Neither Boas's own study, nor those of his successors, has demonstrated changes of such magnitude in first generation American born.

What recent analyses of Boas's immigrant data actually show is that the immigration effect is small compared to the variation among ethnic groups (Sparks and Jantz 2002). Using the recent re-analysis by Gravlee et al. (2003), we can observe in Figure 2 that the maximum difference in cranial index due to immigration (in Hebrews) is much smaller than the maximum ethnic difference, between Sicilians and Bohemians. It shows that long headed parents produce long headed offspring and vice versa. To make the argument that children of immigrants converge onto an "American type" required Boas to use the two groups that changed the most. Other groups change little, in the American environment as is clearly evident in Figure 2.

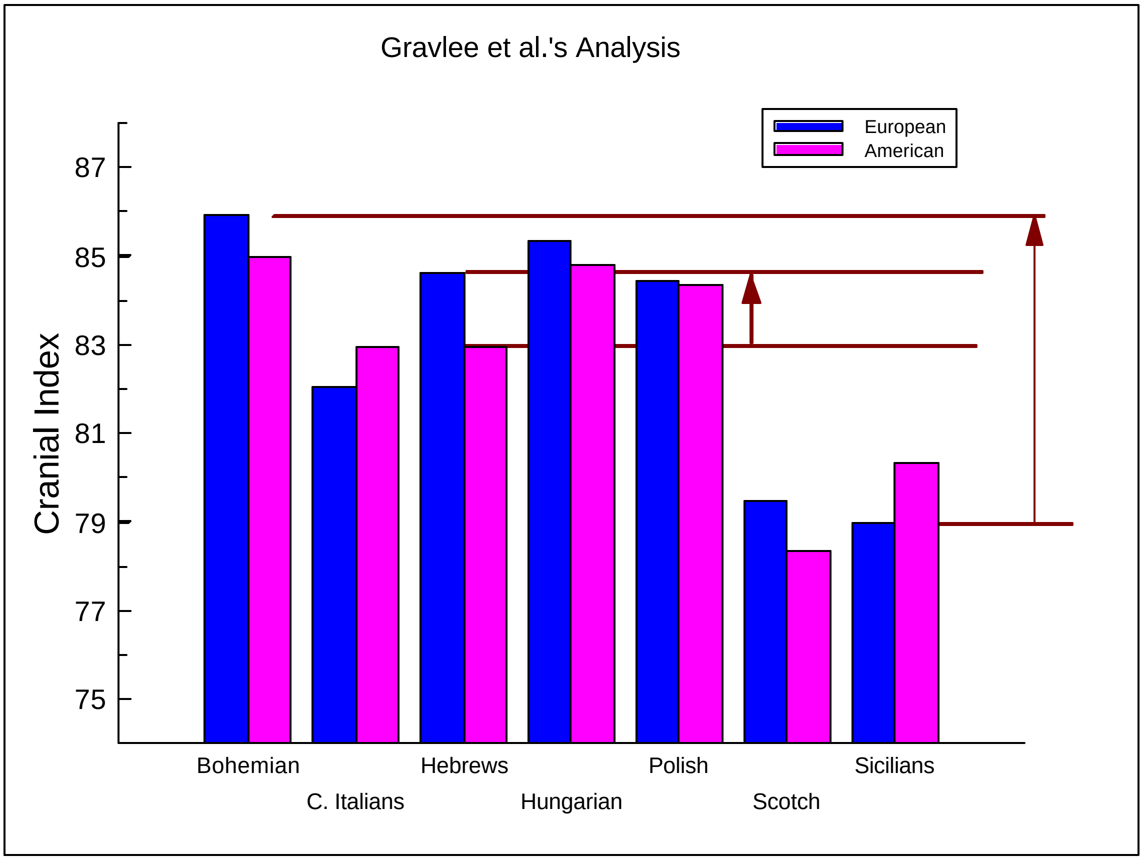

Figure 2. Graphical presentation of data from Gravelee et al. (2003) illustrating maximum differences attributable to immigration and ethnic variation.

Re-analyses of Boas's data have also not fully considered complicating issues, some of which Boas himself raised. As noted, much of Boas's argument about cranial response to environmental change rests on two groups, the Hebrews and Sicilians, the former becoming longer headed, the latter shorter headed. Boas (1940) pointed out that the Jewish practice of bedding and swathing infants, which could have impacted cranial form, was discontinued in America. Boas eventually rejected this possibility because the Sicilian cranial morphology also changed in the absence of changes in how infants were treated. However, it clearly troubled him, to the point that he conducted a study of cranial change in Armenians, who also changed child rearing practices in America and, like the Hebrews, experienced a decrease in the cranial index in America (Boas 1924). Boas's Armenian results seem to bear out his concern that Jewish head form was likewise influenced by changes in child rearing practices, but he never quite acknowledged that.

Boas also observed that break up of isolates would occur in America and could be responsible for a change in "type", anticipating Hulse's work on the subject.

Boas's data present a number of challenges because samples from different ethnic groups differ in a number of ways. The Hebrew sample contains very young children, as young as two months in American born and 1.5 years in European born. Figure 3 shows cranial index fitted to age in American and European born Hebrews. It shows that the two groups are already markedly different by ages 1-2, after which they converge and then assume a more or less parallel course. Such a pattern might make sense in terms of timing of cranial growth, most intense in the early years of life. It would also be compatible with relaxation of head binding and there seems no way choose between these two alternatives, at least without further evidence.

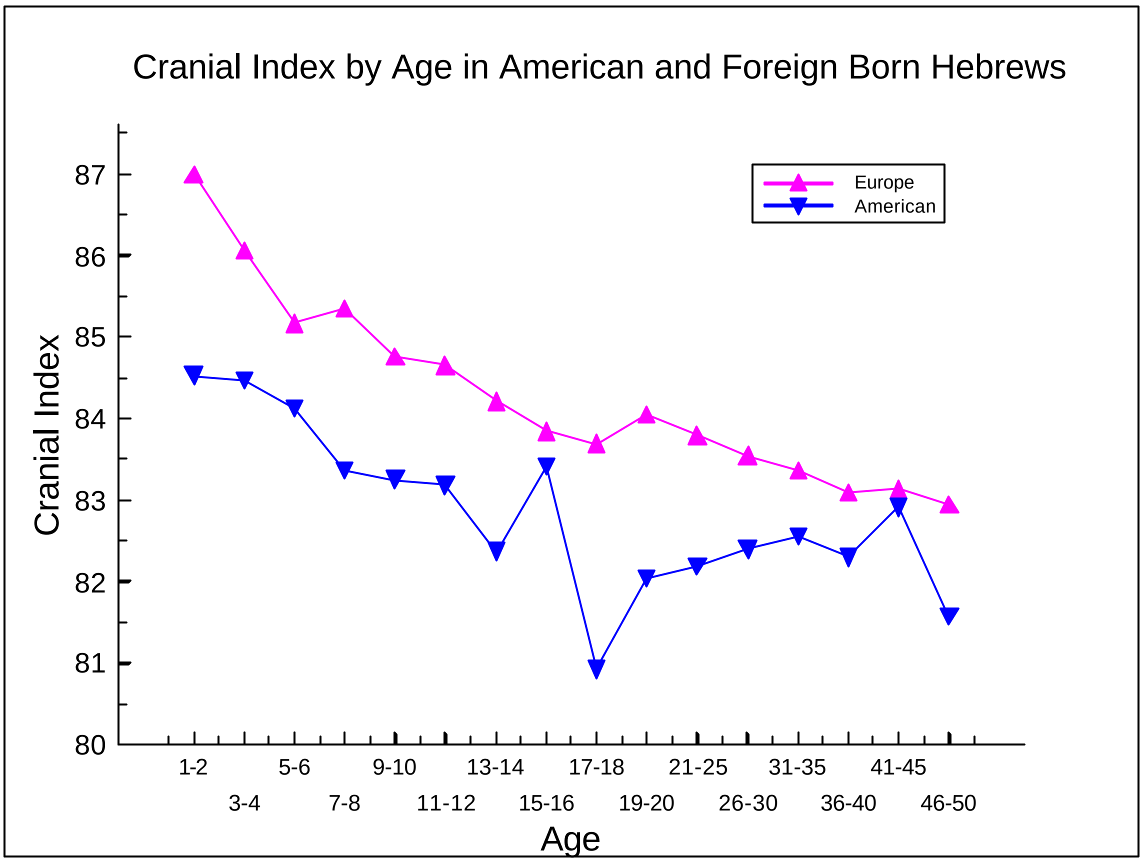

Figure 3. Plot of cranial index means on age from Boas's American and Foreign born Hebrew sample.

Sicilians, on the other hand, were sampled differently; the minimum age is 4. We cannot therefore, know how the younger cohorts differed. But clearly the pattern of cranial index in relation to age is different in Sicilians, as can be seen in Figure 4. At ages 5-6, American born and European born are nearly identical, suggesting that American and European born did not experience dissimilar patterns of cranial growth. After age six, divergence increases, suggesting different cranial growth in older cohorts. What is interesting is that it is the European born who are changing. The American born exhibit a relatively stable cranial index, while European born experience a decline with increasing age; younger individuals are more brachycephalic than older. These young immigrants will have spent their early years in Sicily. Therefore, Sicilians seem to be expressing a secular trend taking place in Europe, but not in America.

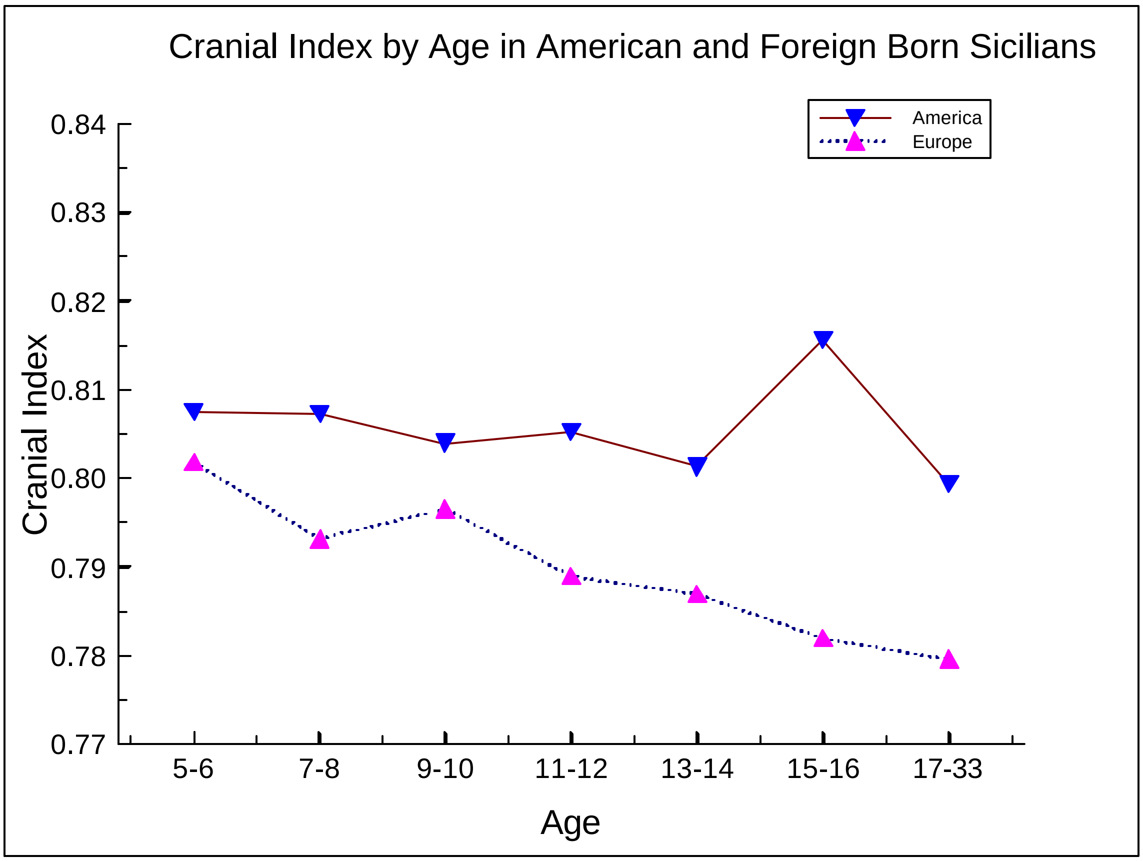

Figure 4. Plot of cranial index means on age from Boas's American and Foreign born Sicilian sample.

It is also important to note that Hebrews and Sicilians experience very different changes, which are obscured by cranial index. Table 1 shows Mahalanobis distances between migrant and American born children, computed from age and sex centered data for Hebrews and Sicilians using cranial length and breadth. It shows that Hebrews exhibit a greater difference and cranial length and breadth contribute roughly equal amounts to the change. In Sicilians, cranial length accounts for nearly all the difference between immigrants and American born. In Hebrews, American born have longer and narrower crania, while in Sicilians, the cranium is simply shorter in American born; breadth does not change.

Table 1. Mahalanobis D^2 between American and Foreign born Hebrews and Sicilians, showing the contribution of length and breadth.

Group	D^2	Head Length	Head Breadth
Sicilians	0.1331	97.22%	2.78%
Hebrews	0.2203	43.94%	56.06%

Boas produced a plot of cranial index on age very similar to these, using it to argue that Hebrews and Sicilians approach a uniform type in America. In fact the Sicilian pattern requires an interpretation opposite that of Boas's. If an environmental explanation is to be adopted, then the pattern argues that it is the European environment that changed, resulting in secular change in Europe.

At this point it is useful to briefly examine Boas's basic assumption, namely that people from different European environments entered a common American environment, which acted to homogenous them. This assumption is open to considerable question. The esteem in which different groups were held by native-born Americans, their skill levels, their ability to assimilate, all differed considerably. Table 2 shows the difference in earning power of Sicilians and Hebrews, compared to Native born whites. It shows that Sicilians earn considerably less than Hebrews, presumably because they are less likely to speak English and be literate. Hebrews are more literate, more likely to speak English and consequently earn only slightly less than Native born Whites. After a few years in the United States, Jewish immigrants earn more than Native born Whites, achieving a high degree of economic success (Chiswick 1992). The American environment therefore seems more favorable to Hebrews than to Sicilians.

Table 2. Weekly salaries of Hebrews and South Italians, 1909. *

Group	Weekly wages($)	% English speaking	% Literate
Native White	14.37	100	98.2
Hebrew	13.15	76.0	93.2
S. Italian	9.61	48.7	69.3

* From Higgs, 1971.

How would we expect cranial morphology to respond to variation in health and nutrition? Hulse (1964) showed that better health and nutrition among Swiss immigrants led to greater stature, and consequently to greater head length because head length is correlated with stature. Hence the reduced head length in American born Sicilians is consistent with their poor environment. The Hebrew increase in cranial length would also be consist with their superior environment, although the change in breadth is puzzling.

I believe at the moment any conclusion about what Boas's immigrant study showed, other than that small changes occur, is premature. His data are readily available (Boas 1928) and much more analysis will be required to fully test all of the hypotheses that can be tested using them. In order to examine changes relating to environment much more information about it is required. In America there must have been considerable variation in health and nutritional conditions among different immigrant communities, and the environment in Europe may also have changed. The irony of Boas's principal finding, that cranial index of Hebrews and Sicilians becomes more similar, may result from their different environments rather than a homogeneous American environment.

The Agriculture/Functional Model

In many parts of the world there has been a change toward shorter, broader crania in the past several thousand years. This change, referred to as brachycephalization, has been observed in Europe, Asia and America. A common explanation for this widespread trend is that it reflects functional responses to reduced masticatory stresses. The model has been formulated by Carlson and Van Gerven, (1977) based on their Nubian epipaleolithic-Neolithic series. The argument is that reduced masticatory stresses will result in crania that are shorter and higher in food producers than in hunters and gatherers. (See also Larsen 1997)

Carlson and Van Gerven's paper like Boas's before, has been cited repeatedly by those arguing that cranial morphology has little to say about genetic variation among groups. There are several reasons to question whether what Carlson and Van Gerven observed is related to subsistence change. There are about 10,000 years between the epipaleolithic and Neolithic series. It is necessary to assume genetic continuity over this lengthy time interval, for which little evidence exists. It has been argued by Turner and Markowitz, (1990) from the dental evidence that replacement is to be preferred to continuity.

Furthermore in Europe, where the data base is much richer, the period of most intensive brachycephalization occurs not with the Neolithic, but several thousand years later during the mediaeval period. Rather than being driven by agriculture, it has recently been argued that brachycephalization is driven by changes in the selection regime occasioned by a demographic transition (Boldsen 2000).

CRANIAL MORPHOLOGY, GENETIC VARIATION, AND POPULATION STRUCTURE

Evidence that genetic variation plays a major role in cranial variation has always been assumed simply because it does not track environment in any intelligible way, something that would surely have been noticed in the over 100 years of research into cranial morphology. Cranial traits exhibit moderate heritability. It is obvious that sufficient genetic variation exists in our close companion, the domestic dog, to allow selection for markedly different cranial forms (Figure 5). Some cranial traits, such as nasal index and face height, have strong climate correlations, suggesting that they have responded to climate selection.

Craniofacial variation in *Canis familiaris*

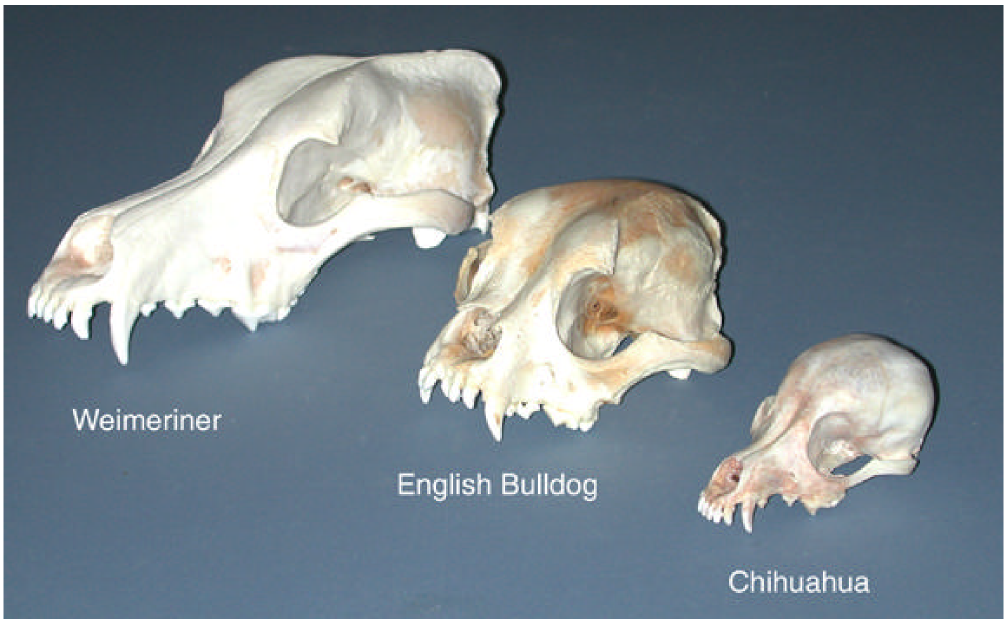

Figure 5. Three breeds of domestic dogs showing extreme craniofacial variation.

In general, where there is genetic variation, there is cranial variation, and the cranial variation is, in general, more consistent with either population structure or selection hypotheses. A few examples will suffice. Kobyliansky and Livshits, (1985) have shown that Jewish populations cluster together on anthropometric variables, despite having lived in a wide array of environments. Harding (1990) has shown that cranial morphometric variation in Europe exhibits spatial patterning very similar to blood polymorphisms and can presumably be accounted for by similar population processes. Recent explicit tests of cranial morphology have concluded that it behaves in concert with neutral markers and that selection or developmental plasticity do not erase or even obscure underlying population structure and history (Roseman 2004; Relethford 2004).

AMERICA REVISITED

If America provided a fruitful research design for Boas and others in the form of foreign born parents and their American born offspring, it continues to provide opportunities for examination of morphological change in the form of unique environments never before experienced by our species. Environmental changes relevant to human biology over just the past century can be summarized as follows:

1). Major reduction in infant mortality, from over 200/1000 births in the mid 19th century to less than 10 now.
2). Changes in diet and nutrition, to the point where over nutrition and obesity are a bigger problem than under nutrition, the problem faced by many of our ancestors.
3). Breakdown in breeding isolation, not only at level of community, but of ethnic group.
4). Major reduction in activity and hence structural loading of the skeleton.

The American environment is unparalleled in the entire evolutionary history of our species. As such it is a laboratory for the study of phenotypic response to a new, extreme, environment. Confronted with changes of this magnitude, it would be odd if a population did not respond in a number of ways. Over the past decade we have been examining changes in cranial and postcranial morphology of Americans from the mid 19th century to the present. Skeletal remains from 19th century individuals have been obtained from anatomical collections, while 20th century individuals are available via forensic cases and donated collections. We have documented changes of such magnitude that would astonish Boas. (Jantz and Meadows Jantz 2000) Much of this change is centered on the cranial base, which can be quantified as cranial vault height and cranial base breadth, as illustrated in Figure 6.

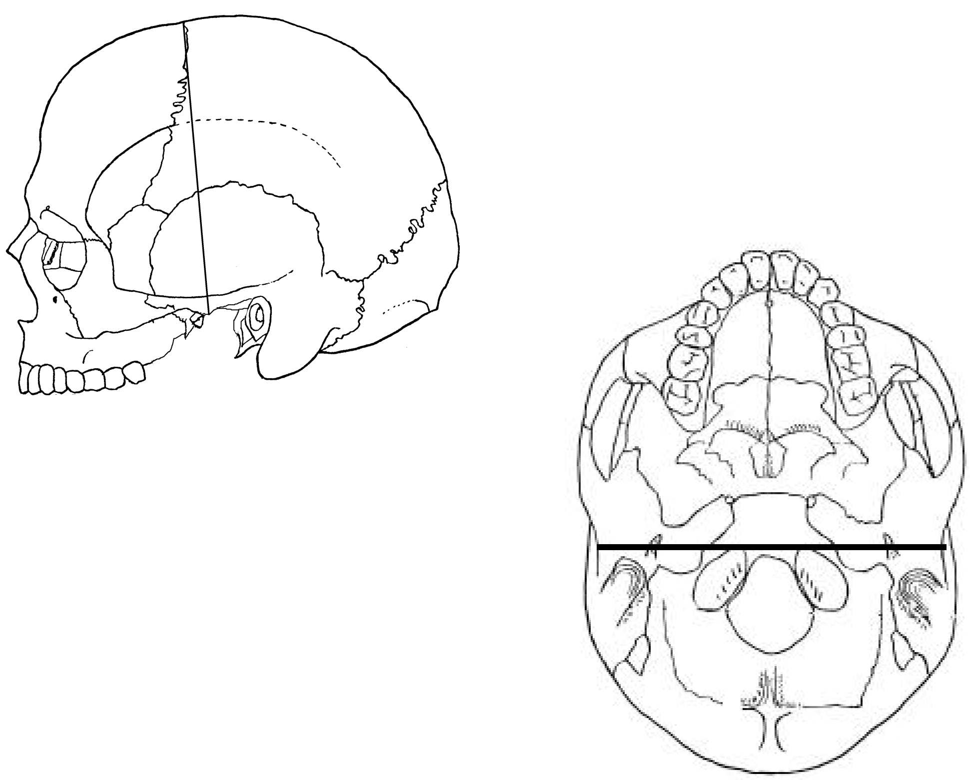

Figure 6. Illustration of measurements of cranial vault height (upper) and cranial base width (lower).

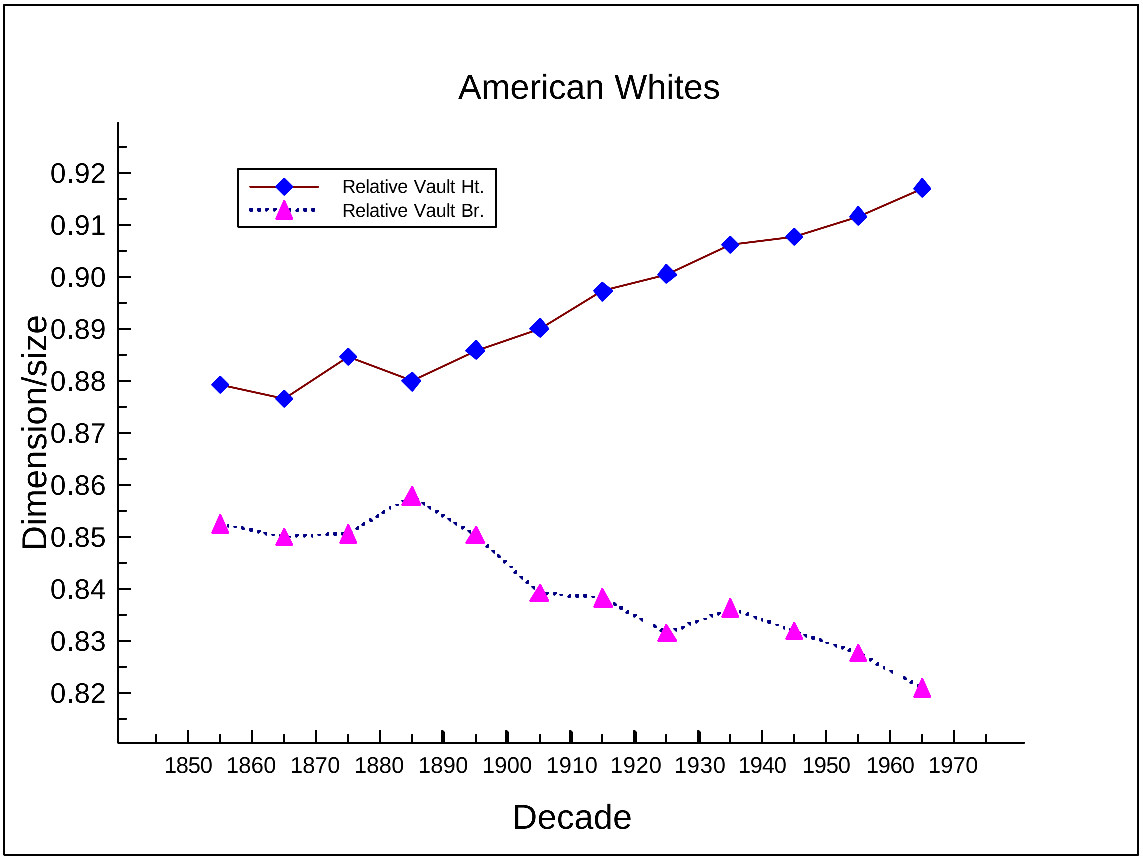

Figure 7. Relative vault height and cranial base breadth in American Whites from 1850 to 1970. Vault dimensions are expressed relative to vault size, defined as the geometric mean of vault (length x breadth x height)$^{1/3}$.

Figure 7 shows the secular changes occurring in American Whites born between 1850 and 1970. Measurements were converted to Darroch and Mosimann (1985) shape variables by dividing each by cranial vault size, defined as vault (length x breadth x height)$^{1/3}$. Each point is the mean for a decade long cohort. The sample consists of 611 individuals with known birth years from anatomical collections and modern forensic cases. Figure 7 illustrates the increase in vault height and a parallel decrease in cranial base breadth in American Whites. There is little change before 1880, but thereafter the change is astonishingly regular. Cranial vault height increases in relation to size, while vault breadth decreases. Vault height is initially about 88 % of size, and ends up at 92 % of size. Vault base breadth begins at about 85 % of size, and ends up at 82 %. These two variables reflect a major restructuring of the cranial vault, yielding a higher, narrower vault in modern people. Figure 8 show a similar change in American Blacks, based on 422 individuals of known birth year. In Blacks the change is slightly less regular and begins later, after 1900, but yields a higher, narrower vault in modern people.

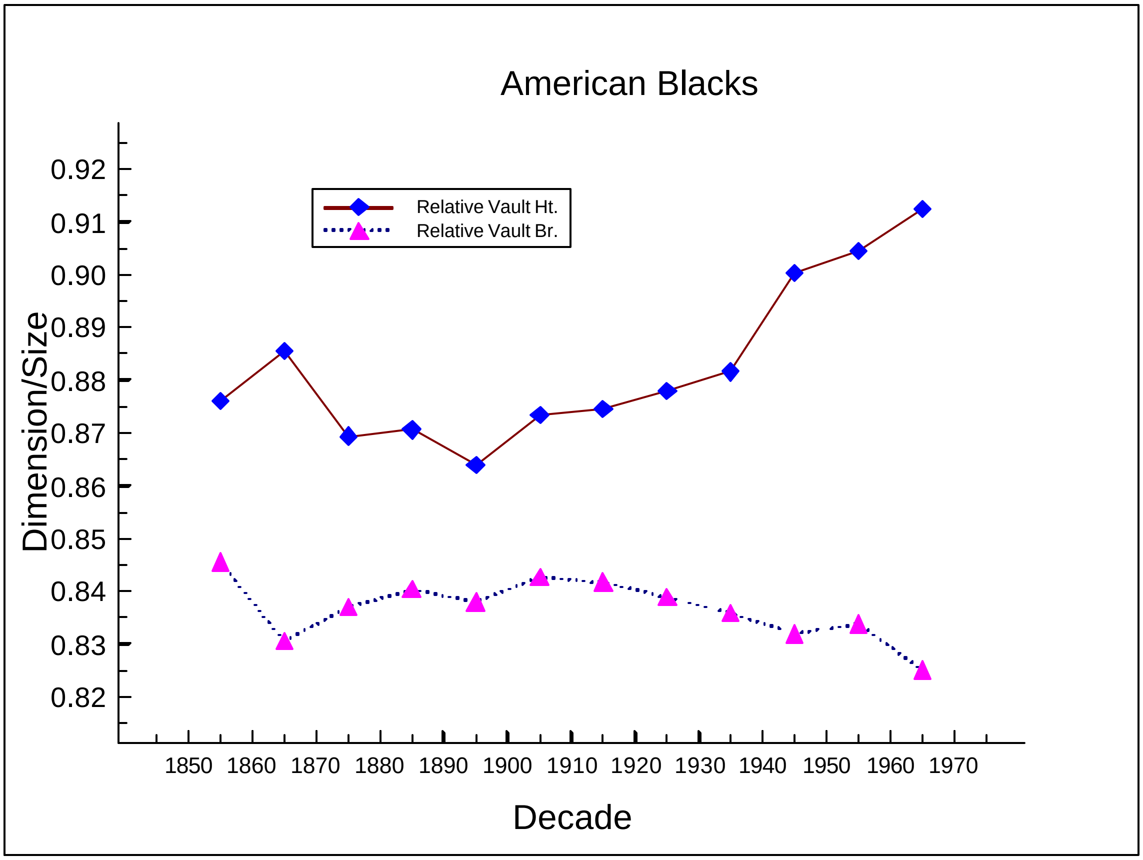

Figure 8. Relative vault height and cranial base breadth in American Blacks from 1850 to 1970. Vault dimensions are expressed relative to vault size, defined as the geometric mean of vault (length x breadth x height)$^{1/3}$.

Since the cranial base grows, it is reasonable to suppose that it, like stature, would respond to components of the environment that promote or retard growth. Cranial base growth is complicated with several independent components (Lieberman et al. 2000) Fusion of some elements, the basi-occipital synchondrosis for example, is related to significant maturational events, such as skeletal age (Scheuer and Black 2000), which are known to have experienced secular change (Himes 1984). It is therefore reasonable to hypothesize that modification of cranial vault shape is a consequence of changes in cranial base growth, and as such is an expression of the secular changes in growth we have seen in many other systems. Angel (1982) put forth a similar hypothesis some years ago relating to the value of cranial base height in assessing growth stress.

TESTING OF HYPOTHESES USING AMERICAN POPULATIONS

It is clear that environmental changes have resulted in changes in cranial morphology, affecting the vault as a result of changes in cranial base growth. It is also clear that there is genetic variation among America's various socially defined races; that has been demonstrated using genetic DNA markers, classical markers, and is evident in cranial morphology. The genetic variation originates from different continental origins and is maintained by social barriers to interracial marriage. Even though racial endogamy is breaking down the vast majority of marriages continue to be within race. Social race then, structures marriages and hence genetic variation. Boas's assumption of a common American environment is more closely approximated now than it was at the turn of the century. Therefore, one can ask whether populations converge onto a common form, as Boas predicted, by examining cranial evolution over the past 130 years. This hypothesis was tested by breaking our sample into 20-year cohorts and examining how cohorts relate to one another for Blacks and Whites. The comparison involved 15 measurements. Figure 9 shows a principal coordinates plot of distances among the cohorts. The first axis basically separates Whites from Blacks, while the second axis separates early from late. However, secular change occurs along both axes. Later cohorts have lower scores on both the first and second axes, resulting in a secular change that is oblique to the two axes. Moreover, the two groups change along a more or less parallel course, with little convergence. These results suggest that both genetic variation (because race differences are maintained) and phenotypic response to environment (because both groups undergo change) are important.

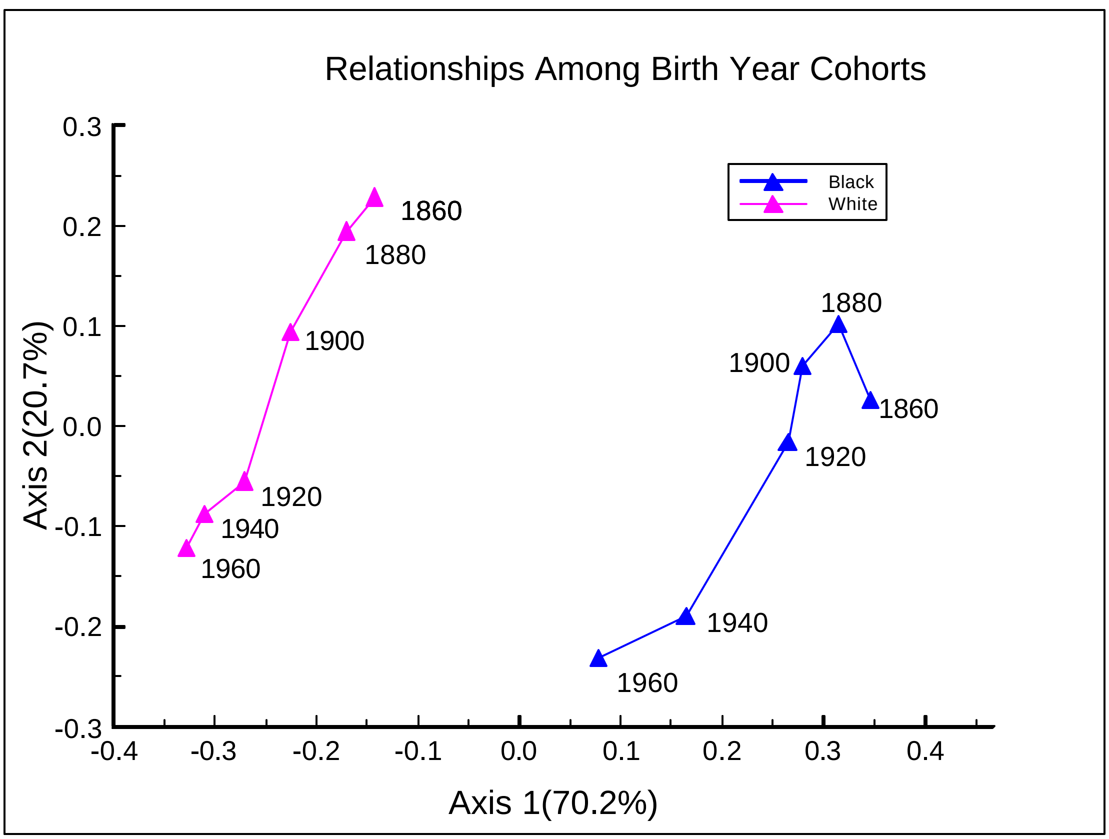

Figure 9. Principal coordinates of distances among 20-year cohorts of American Whites and Blacks, based on 15 measurements.

Lest we leave the impression that dramatic change is inevitable, we should also point to remarkable instances of stasis. The Archaic site of Indian Knoll served as a burial site for hunter-gatherer populations along the Green River in Kentucky for approximately 1000 years, from 4500 to 3500 BP (Herrmann 2002). Table 3 shows that cranial morphometric variation in the long series does not exceed that found in samples of tribal groups of modern Native Americans with time depth measured in decades.

Table 3. Mean within group distances from historic tribes compared to lineage from Indian Knoll approximately 1000 years in duration.

Source	Mean	s.d
Within tribe distance*	**5.20**	**1.00**
Indian Knoll males**	**5.17**	**1.20**
Indian Knoll females**	**4.79**	**1.02**

* Arikara, Blackfeet, Peru, Santa Cruz, Zuni
**Herrmann, unpublished

CONCLUSIONS

Several conclusions are warranted from the forgoing analysis and discussion:

1). Cranial morphology, especially cranial vault morphology, responds to environmental conditions that promote or retard growth, primarily through growth of the cranial base, to the point where cranial base growth may serve as a marker for poor environment.
2). In America, changes have been substantial, but the situation is probably atypical because of the unparalleled environmental change.
3). Environmental changes do not erase genetic variation, at least when groups inhabit similar environments.
4). It is not now possible to apportion changes between genetic and environmental causes. As noted, environmental change is confounded with isolate break down. Moreover, America has just gone through a major demographic transition. Infant and maternal survival has increased dramatically in the past 150 years, so many genotypes now survive that would not have during the 19th century.

ACKNOWLEDGEMENTS

This paper benefited from the efforts of several individuals. Dr. Nick Herrmann kindly provided information regarding Indian Knoll cranial variation. Andrea Rombauer conducted historical research on the condition of immigrants in New York. Walter Klippel provided the image of cranial variation of domestic dogs. Lee M. Jantz assisted with illustrations and read earlier drafts of the paper. I thank them all.

REFERENCES

Angel, J. L.
1982 A new measure of growth efficiency: skull base height. American Journal of Physical Anthropology 58:297-305.

Armelagos, G. J., and D. P. Van Gerven
2003 A century of skeletal biology and paleopathology: contrasts, contradictions, and conflicts. American Anthropologist 105:53-64.

Boas, F.
1910 Changes in bodily form of descendants of immigrants (final report) [Serial set no. 5663, Senate document 208, session 61-2, session-date: 1909, 1910]. Washington, DC: Government Printing Office. http://www.ebrary.com/stanford/Dillingham1.html

Boas, F.
1924 Bemerkungen ueber die Anthropometrie der Armenier. Zeitschrift feur Ethnologie 56:74-82.

Boas, F.
1928 Materials for the Study of Inheritance in Man, Contributions to Anthropology No. 6. New York: Columbia University Press.

Boas, F.
1940 Changes in bodily form of descendants of immigrants. *In* Race, Language and Culture. F. Boas, ed. pp. 60-75. New York: The Free Press.

Boldsen, J. L.
2000 Is it Possible to forget about Darwin-Human Demographic Evolution?, Research Report. No. 14. Danish Center for Demographic Research, Odense University.

Carlson, D. S., and D. P. Van Gerven
1977 Masticatory function and post-Pleistocene evolution in Nubia. American Journal of Physical Anthropology 46:495-506.

Chiswick, B. R.
1992 Jewish immigrant wages in America in 1909-An analysis of the Dillingham Commission data. Explorations in Economic History 29:274-289.

Darroch, J. N., and J. E. Mosimann
1985 Canonical and principal components of shape. Biometrika 72:241-252.

Goldstein, M. S.
1943 Demographic and Bodily Changes in Descendents of Mexican Immigrants. Austin: Institute of Latin American Studies, The University of Texas.

Gravlee, C. C., H. R. Bernard, and W. R. Leonard
2003 Heredity, environment, and cranial form: A re-analysis of Boas's immigrant data. American Anthropologist 105:125-138.

Harding, R. M.
1990 Modern European cranial variables and blood polymorphisms show comparable spatial patterns. Human Biology 62:733-745.

Herrmann, N. P.
2002 Biological affinities of archaic period populations from west-central Kentucky and Tennessee. Unpublished Ph.D. Dissertation, University of Tennessee, Knoxville.

Higgs, R.
1971 Race, skills and earnings in American immigrants in 1909. Journal of Economic History 31:420-428.

Himes, J. H.
1984 An early hand-wrist atlas and its implications for secular change in bone age. Annals of Human Biology 11:71-75.

Hulse, F. S.
1964 Exogomy and heterosis. Yearbook of Physical Anthropology 9:241-257.

Jantz, R. L., and L. Meadows Jantz
2000 Secular change in craniofacial morphology. American Journal of Human Biology 12:327-338.

Kobyliansky, E., and G. Livshits
1985 A morphological approach to the problem of the biological similarity of Jewish and non-Jewish populations. Annals of Human Biology 12:203-212.

Larsen, C. S.
1997 Bioarchaeology: Interpreting Behavior from the human skeleton. New York: Cambridge University Press.

Lasker, G. W.
1946 Migration and physical differentiation. American Journal of Physical Anthropology 4:273-300.

Lieberman, D. E., C. F. Ross, and M. J. Ravosa
2000 The primate cranial base: Ontogeny, function and integration. Yearbook of Physical Anthropology 43:117-169.

Relethford, J. H.
2004 Boas and beyond: Migration and craniometric variation. American Journal of Human Biology 16:379-386.

Roseman, C. C.
2004 Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. Proceedings of the National Academy of Sciences 101:12824-12829.

Scheuer, L., and S. Black
2000 Developmental Juvenile Osteology. San Diego: Academic Press.

Shapiro, H. L.
1939 Migration and Environment: a Study of the Physical Characteristics of Japanese Immigrants to Hawaii and the Effects of Environment on their Descendents. New York: Oxford University Press.

Sparks, C. S., and R. L. Jantz
2002 A reassessment of human cranial plasticity: Boas revisited. Proceedings of the National Academy of Sciences 99:14636-14639.

Thomas, D. H.
2000 Skull Wars: Kennewick Man, Archeology, and the Battle for Native American Identity. New York: Basic Books.

Turner, C. G., and M. A. Markowitz
1990 Dental discontinuity between late Pleistocene and recent Nubians. Peopling of the Eurafrican-South Asian triangle I. Homo 41:32-41.