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Plasticity and Population Structure: Exploring Secular Trends in the Three- Dimensional Cranial Morphology of the Modern Portuguese

Katherine Elizabeth Weisensee
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Katherine Elizabeth Weisensee entitled "Plasticity and Population Structure: Exploring Secular Trends in the Three- Dimensional Cranial Morphology of the Modern Portuguese." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Anthropology.

Richard Jantz, Major Professor

We have read this dissertation and recommend its acceptance:

Lyle W. Konigsberg, Murray K. Marks, Karla J. Matteson

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Katherine Elizabeth Weisensee
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Abstract

Significant secular changes have been documented in several worldwide populations over the past 200 years; these changes include increased stature and weight, increased cranial vault height, and a narrowing of the cranial vault width (Angel 1976; Boas 1912; Jantz 2001; Jonke et al. 2007; Little et al. 2006). A variety of hypotheses have been proposed as to the origins of the observed changes. This dissertation uses a documented collection of skeletons from the 19th and 20th centuries to describe the precise nature of the changes using three-dimensional methods and explores possible causes underlying the changes including individual environmental effects, demographic parameters, and spatial effects.

Three-dimensional cranial landmarks from 500 identified individuals from the New Lisbon Skeletal collection in Lisbon, Portugal were collected along with available demographic data. The birth years represented in the sample range from 1805-1960. The Portuguese sample provides the opportunity for understanding the genetic and environmental components of the observed changes. The highly circumscribed nature of the skeletal collection, which contains only individuals from the relatively homogenous Portuguese population, enables a comparison of the observed changes with information about individual environmental effects, such as socioeconomic status and health status. The impact of the demographic transition that characterizes modern populations is also examined; the modern demographic transition is characterized by a decrease in mortality followed by a decrease in fertility. Also, information regarding the place of birth and place of death for

individuals in the sample is used to model the spatial effects on cranial morphology and to demonstrate the maintenance of genetic structure in spite of significant secular changes.

In addition to providing a unique sample for testing theories related to the causes of secular trends, this research also provides a new way of documenting secular trends. In previous research, secular changes have primarily used traditional linear craniometric data, anthropometric data, or conscript records to document change. The use of three-dimensional data enables a more exact description of changes in the cranial form and provides the opportunity for a more precise understanding of the basis for change.

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Chapter 1: Introduction

This research examines secular change in the craniofacial morphology of the Portuguese from 1800 to 1950. The goal is to identify changes in environmental factors during the study period and to associate these factors with changes in the craniofacial morphology of a modern population. The period under study represents a time when major transformations were occurring in the demographic structure of the Portuguese population as a result of intensified urbanization, changing mortality patterns, and improved medical care. The intensity of these environmental changes was typical of those experienced by populations around the world over the past 200 years and have resulted in significant changes in the craniofacial morphology of both the Portuguese and other modern populations.

Over the first 100,000 years of human existence the world's population reached nearly 1 billion people in 1800, within the next two hundred years the population increased to more than 6 billion people living on earth. This 6-fold increase in the population over 200 years resulted from significant changes in the way people shaped their environment and in turn altered the ways in which the new modern environment shaped people. During the same period the urban population increased from 25 million people living in urban areas in 1800 to 3.2 billion in 2000, which represents a 128-fold increase (Rogers and Williamson 1982). Not only are more people living in urban areas today than ever before, but the demographic structure of the population has also changed significantly. Life expectancy of a person born in 1800 was about 30 years and more than half died before they reached adulthood. In 2000, life expectancy worldwide was 64 years and there is an expectation in developed countries that nearly all individuals will survive infancy and childhood. This has been characterized as "…the crowning achievement of the modern era, surpassing wealth, military power, and political stability in import," (Riley 2001, 1). The impact of these dramatic changes on human biology is the focus of the current research.

This dissertation involves analyzing osteometric data on a sample of identified skeletons from the New Lisbon skeletal collection held at the Bocage Museum in Lisbon, Portugal. This research fits into a broader agenda of examining underlying causes behind secular changes that have been observed in several modern populations. Significant secular changes over the past 200 years have been previously documented in several American and European samples. These secular trends include an increase in stature and weight, increased cranial vault height, and a narrowing of the cranial vault width (Angel 1976; Cameron et al. 1990; Jantz and Jantz 2000; Jantz 2001; Komlos 1994; Spradley 2006). These changes have been observed in White and Black populations and in males and females. A pattern of change in the craniofacial morphology has begun to emerge from across these diverse groups. However, the American sample is complicated by a variety of factors which makes it difficult to determine the precise environmental or genetic factors which may be driving the secular changes.

While the evidence of secular change in America is compelling, the samples used are not ideal for understanding the exact causes behind the observed changes. The

American samples, while broadly representative of the general population, are taken from a wide range of geographical areas that are sampled at different times. For example, turn of the 19th century individuals were living in Cleveland or St. Louis, while the individuals with later birth years come from all over the country. Moreover, many of the samples are taken from anatomical or forensic collections. These types of collections may or may not be representative of the population at large, as they tend to be of lower economic status. The American samples are additionally complicated by the fact that America experienced many waves of immigrants that came into the country at different times and settled in different areas. The Lisbon collection addresses many of the complicating factors seen in the American sample. The Lisbon collection is taken solely from the city's three main cemeteries; therefore all of the individuals contained in the collection were experiencing similar environmental conditions as Lisbon became a modern, urban center. Additionally, because the skeletons come from Lisbon's cemeteries the sample represents a relatively random sample of the population at large. Finally, during the study period Portugal experienced very little foreign immigration, so the sample contains little variation due to immigrant populations.

The availability of the New Lisbon collection allows for the causes behind the observed changes to be explored more specifically than in previous studies. Researchers have postulated numerous possibilities for the causes behind the changes in the craniofacial morphology of modern people. The secular trends have alternately been attributed to changes in diet and masticatory stress, improved health and living conditions, the breakdown of traditional marital patterns and increased heterozygosity, or resulting from the modern demographic transition. None of these explanations is necessarily exclusive of the others, but due to the unique nature of the Lisbon collection each of these causes may be explored with greater precision.

The New Lisbon skeletal collection contains over 1700 identified individuals recovered from Lisbon's three main cemeteries with birthdates ranging from 1805-1975. This collection is unique in that it contains so many identified skeletons with a long time span represented. This sample provides the opportunity for understanding both the genetic and environmental components of the observed secular changes. The highly circumscribed nature of the skeletal collection, which contains only individuals from the Portuguese population, enables documenting the observed changes, without conflating the changes with influxes of large migrant populations, as is the case with American samples from a similar time period. The availability of additional demographic data enables a more in-depth understanding of the changing environmental conditions. Information about an individual's early life and socioeconomic status will be used to contextualize the observed secular changes. This unique collection provides an excellent opportunity for testing hypotheses related to the causes of secular changes in modern populations.

In addition to providing a unique sample for testing theories related to the possible causes of secular trends, this research also provides a new method for documenting secular trends. In previous research, secular changes have primarily been documented using traditional linear craniometrics, anthropometric data, or conscript records. The use of three-dimensional landmark data enables a more exact description of changes in the cranial form and provides the opportunity for a more precise understanding of the basis for change.

The goals of this research are: 1) to document changes that have occurred in the sample population over the past 150 years and to compare the Portuguese with samples from a similar time period in other countries, 2) to relate the changes to improvements in individual environmental factors, such as immigrant status, socioeconomic status, and health status, 3) to relate the changes to mortality and fertility parameters that define the modern demographic transition and 4) to examine the question of whether the secular changes erase the underlying genetic structure of the population.

The first part of this dissertation provides the theoretical framework for this work and a review of the relevant literature. Developmental phenotypic plasticity provides a body of theory for placing short-term secular changes within an evolutionary framework. In previous research there has been some tension in placing these short-term changes within an evolutionary context. Recent theories related to phenotypic plasticity provide a means for understanding how the variation produced during growth and development can ultimately result in genetic accommodation and evolutionary change in a population. By understanding the short-term changes in the population within this evolutionary framework, a more complete understanding of how and why populations change over both the short and long-term may begin to emerge. Studies of short-term secular changes have been undertaken by researchers from a variety of disciplines, from economic history to demography and anthropology. The multidisciplinary scope of these studies will be reviewed in the second chapter of this dissertation.

The next chapter provides the background about the nature and make-up of the New Lisbon collection. A brief description of the modern history of Lisbon and Portugal are discussed. This will provide a historical context for understanding the nature and tempo of the changes that took place both in the city of Lisbon and more broadly in Portugal and Europe. As discussed earlier, the past 200 years have been a time of exceptional changes in human populations and Portugal is typical of many of the changes seen in Western capitals from this time period. By providing a background regarding the changing environmental conditions, the differential stress experienced during growth and development and ultimately changes in the craniofacial morphology may be better understood. Chapter 4 provides a review of geometric morphometrics methods and the other methods of analysis used for this research.

In the next chapter the results from the analysis will be presented. Chapter 5 provides a description of the changes observed in the craniofacial form of the Portuguese. Statistical tests demonstrate that the Portuguese have experienced significant changes over time in their craniofacial morphology and using geometric morphometrics methods, these changes are visualized and isolated by specific cranial region. The changes in morphology are compared with similar studies from the U.S., in order to determine if the pattern of change is similar among different populations from the same time period. Next, available demographic data are used to document the ways that different environmental factors are associated with changes in the craniofacial morphology. The variables available are related to an individual's immigrant status, socioeconomic status, health status, and the Lisbon's population juvenile mortality and fertility rates. These environmental conditions will be used in place of year of birth to model secular changes.

Finally, a spatial analysis of individuals' places of birth is used to demonstrate that the underlying genetic structure of the population is preserved in spite of significant secular changes in the population.

The final chapter discusses the results within an historical and theoretic context, defining the pattern of change observed over time and across different environmental conditions. These results demonstrate the significant impact of the modern environment on craniofacial morphology. The magnitude of these changing environmental conditions is unprecedented within human history and the extreme nature of these changes provides a good testing ground for examining the evolutionary significance of phenotypic plasticity in humans.

Chapter 2: Literature Review

This chapter provides a review of the relevant literature. It begins by discussing the evolutionary significance of short-term changes within populations and the potential impact of developmental phenotypic plasticity on long-term evolutionary change. The questions of why studying short-term changes is important and how short-term changes are studied is addressed. Next, the impact of the modern environmental changes is discussed in terms of changing demographic patterns and urbanization. Finally, a discussion of research into short-term secular changes in human populations during the Holocene is provided. The literature reviewed focuses on the variety of explanations that have been given for understanding the causes behind the changes and provides a discussion of the explanations within the framework of developmental phenotypic plasticity.

Developmental Phenotypic Plasticity

Over the past two decades, developmental phenotypic plasticity has become a topic of intensified research in evolutionary theory (de Jong 1995; DeWitt and Scheiner 2004; Scheiner and Lyman 1991; Via 1993; West-Eberhard 2003b). However, the relationship between phenotypic plasticity and evolutionary theory is only beginning to be understood. It was previously thought that the variation produced by differential growth and development in response to the environment was simply noise and not part of evolutionary processes. Mayr (1961) divided the levels of explanation for changes in biological processes into proximate and ultimate causes. The proximate causes of change relate to understanding the immediate sources of change. Plasticity or aspects of growth and development are generally grouped under this heading. Ultimate causes, in contrast, provide a level of explanation in terms of natural selection and adaptation; providing longer-term evolutionary explanations for population change. This division into short-term causes of population change versus long-term causes of population change has often been interpreted as meaning that proximate causes have little to do with evolution. Whereas only by examining ultimate causes, such as mutation and genetic drift, are evolutionary processes in populations understood, for example Brace's (1963) Probable Mutation Effect. However, West-Eberhard (2003a) points out,

> There is no one-to-one relation between phenotypes and genes, yet a gene mutation is often visualized as the originator of a new phenotypic trait. Development is seen as a homeostatic, canalizing, constraining force, yet it is the originator of all adaptive change. Proximate mechanisms are excluded from ultimate (evolutionary) explanations, yet a proximate mechanism (development) produces the variation that is screened by selection…Theoretical incorporation of developmental plasticity calls for changes in thinking about virtually every major question of evolutionary biology, and resolves some of its most persistent controversies, (pg. 3).

The reluctance of evolutionary biologists to place developmental plasticity on equal footing with more long-term changes comes from the historical tradition of evolutionary theory. Evolution is classically defined as the change in an allele frequency from one generation to the next. The definition of evolution focuses entirely on the genotype and was codified as the structure and function of DNA was being uncovered (Sarkar 2004). Early on the overwhelming paradigm in evolutionary theory was that there was a one-to-one correspondence between genes and phenotypic expression. However, it is clear that there is not a one-to-one correspondence between genes and individual traits, rather there is a complex interaction of genes with the environment to produce the phenotype. The idea that genes evolve, or that there is a genotype that can have a maximum fitness and be well-adapted to the environment cannot be supported. It is only through the interaction of genes with environmental factors that a well-adapted phenotype may respond to evolutionary forces. Figure 1 provides a diagram of how developmental phenotypic plasticity may be incorporated into genetic changes (West-Eberhard 2003a). Research questions that focus on adaptive selection through natural selection must work on the level of the phenotype. Natural selection acts to maximize the fitness of the phenotype and developmental plasticity plays a critical role in the outcome of the phenotype. Therefore, evolutionary explanations must involve an understanding of developmental plasticity.

Evolution must involve changes at the genetic level in order to be passed to subsequent generations; there can be no debate about this statement. However, the role of

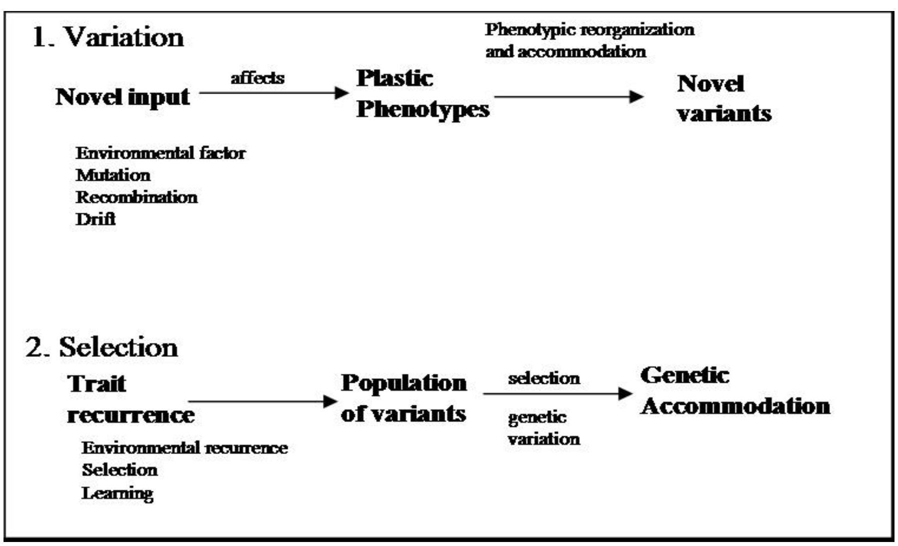

Figure 1. Model of genetic accommodation from phenotypic plasticity West-Eberhard (2003a, 140).

genes in driving evolutionary change rather than following or responding to the phenotype is now under consideration. One explanation is provided by the Baldwin Effect (Baldwin 1902).

> The Baldwin effect is a process by which organic selection leads to evolutionary (genetic) change. Baldwin's Organic selection, the underlying mechanism of the Baldwin effect, is differential survival (selection) in which phenotypic accommodation to extreme conditions during individual ontogeny allow enhanced survival of appropriately responding individuals. Generations of organic selection can lead to genetic (congenital or phylogenetic) change that makes the accommodation the norm." (West-Eberhard 2003a, 24).

The Baldwin effect provides one example of how variation produced during growth and development can have long-term consequences in a population that drive evolutionary change. The short-term changes observed in human populations over the past two hundred years may provide evidence of these types of accommodation.

The Fetal Origins Hypothesis provides another possible means of exploring the ways in which short-term changes can impact longer-term evolutionary changes within populations. The Fetal Origins Hypothesis was first proposed by Barker and colleagues (Barker 1990) based on a series of studies, which examined the association between infant mortality rates and the causes of death in adults within the same generation. In a series of studies, they determined that differing rates of infant mortality significantly affect the rates of adult mortality within a single generation (Barker 1998; Barker et al. 2002; Barker and Osmond 1986). The most significant associations uncovered were between birth weight and coronary heart disease (Joseph and Kramer 1996). Barker sums up the research this way, "People who are small at birth remain biologically different through life because of the persisting constraints and adaptations that accompany slow early growth. Their different morphology and physiology leads them to respond differently to the biological and social environments in later life," (Barker 2002, 310).

The Fetal Origins Hypothesis proposes that there is a critical period early in life during which exposure to negative factors affects adult health regardless of the intervening experiences later in life. The affects of under-nutrition include altered gene expression, reduced cell numbers, imbalance between cell types, altered organ structure, and changes in the pattern of hormonal release and of tissue sensitivity to hormones. Moreover, fetal under-nutrition leads to a reduced growth rate and a reduced gene expression for mechanisms of somatic repair (Fogel 2004, 21). These types of studies have repeatedly demonstrated a significant relationship between early health and its impact on adult outcome. Furthermore, these studies have demonstrated that this relationship exists not only within a single individual's lifetime, but across generations.

This intergenerational effect has been documented in several studies. For example, a study of women whose mother's experienced the Dutch Winter famine of 1944-45 while pregnant, found that birth size was related to the trimester in the pregnancy when the famine was experienced and that the effects on birth weight also influence the size of women's offspring. Martin (2004) found in a British sample that a woman's size at age 7 was a better predictor of her offspring's birth weight than was her adult height, indicating that the environment experienced during the early development of the parent impacts the early development of that individual's offspring. Scrimshaw and Behar (1965) found that the component of childhood height that best predicted offspring birth weight was leg length, which is a sensitive marker of early life nutrition. This affect has been termed, intergenerational phenotypic inertia and can be summarized as "the fetal nutritional signal reflects the mother's chronic nutrition tracing back to her own uterine environment, and thereby to prior generations of the matriline, this may allow the fetus to "see" an average nutritional environment as sampled over decades and even generations" (Barker 1998, 12).

This type of fetal response differs from traditional views of both heritability and phenotypic plasticity. The heritability of traits passed from parent to offspring is normally defined solely in terms of genetic material, while phenotypic plasticity is generally defined in terms of the impact of the environment on an individual's growth and development. Intergenerational phenotypic inertia implies that an individual's growth and development is tempered by their immediate environment, but with a window into past environmental conditions. The ability of a fetus to react not only to its immediate conditions, but also to previous environmental conditions would be adaptive in long-lived organisms, such as humans. This type of response falls intermediary between plastic changes that occur during growth and development and longer-term effects of natural selection in a population.

> Developmentally plastic traits that change only gradually across generations are good candidates for predictive cures, because they potentially filter the noise of short-term fluctuations, thereby allowing the fetus to see the signal of any underlying pattern of sustained and thus more adaptively relevant change…It will force the phenotype to lag when changes are rapid and sustained, maintaining growth of offspring at a less-optimal level…[this] Provides significant advantages over the more protracted phenotypic lag resulting from natural selection, (Fogel 2004).

Evolutionary theory dictates that the forces of evolution will operate on the population in order to produce individuals with the greatest fitness. According to the Fetal Origins

Hypothesis, fitness is maximized not only within the current generation, but across two or three generations (Fogel 2004).

The fact that there have been significant changes in the phenotype of humans experiencing extreme environmental change over the past 200 years has been well-documented. However, the explanations for these changes have been hotly debated. Some view the changes as having purely mechanistic causes, such as changes in diet, because real genetic change could not have accumulated in the genotype over such a short period of time (Carlson and Van Gerven 1977). Others use the evidence of short-term changes to make a case that the phenotype, reflected specifically in cranial morphology, does not reflect the genetics of a population; for the same reason, the genetic differences that would be necessary to cause these changes could not have accumulated over such a brief period. However, the Baldwin effect and intergenerational phenotypic inertia provide alternative ways of understanding the changes observed in humans. The focus on the evolutionary significance of developmental plasticity provides an important framework for placing the secular changes observed in humans within an evolutionary context.

The Impact of Demographic Transitions on Morphology

Over the past 10,000 years, humans have been impacted by three major demographic transitions that have had profound consequences on their morphology (Boldsen 2000). The first transition resulted in an overall gracilization of the skeleton and occurred as a consequence of the shift in subsistence strategies from hunting-gathering to agriculture. The second major morphologic shift resulted in a broadening of the crania, although the impetus for this shift remains under debate. The third major transition has occurred over the past two hundred years and has resulted in an increase in overall stature and changes in the crania that have not yet been well-defined.

Many cross-disciplinary studies have examined the consequences of the third transition on the morphology of modern people. The significant secular changes over the past two hundred years were first identified by the Nobel-prize winning economic historian, Robert Fogel. While attempting to link individual experiences with economic principles, he observed that stature records could be used as a proxy for the economic status of a population (Fogel 2004). Historical stature data taken from conscript records, voting records, and slave records have demonstrated that over the past 200 years human populations have experienced unprecedented change both in stature and other morphological indicators (Komlos and Baten 2004).

The third transition is a unique and radical event in human history. Over the past two hundred years the human population has undergone changes that are off the scale of earlier periods. The tempo and scale of change in modern populations is huge in comparison to earlier events in human history. These changes have radically altered many of the evolutionary forces which we might have expected to be acting in populations in earlier time periods. Over the first 100,000 years of human existence the population increased to nearly 1 billion people; during the past 200 years the human population has grown to more than 6 billion. In 1800 the average life expectancy was about 30 years and more than half of all individuals born died before they reached adulthood (Riley 2001). Today, life expectancy around the world is about 64 years and in developed countries infant and childhood mortality make up a small fraction of all deaths (Mercer 1990). As a consequence of these changes individuals that would never have contributed to the gene pool are now surviving and reproducing; although at the same time fertility is declining (Livi Bacci 1971). Changes in growth and development have also been significant as infants and children are no longer stressed by disease and malnutrition (Mercer 1990). This leads to changes in expectation about the size of adults both in terms of overall stature and with regard to allometric changes.

Sterns and Koella (1986) examined the relationship between growth rates and age-at-maturity across various taxa of organisms from fish to humans. “Growth rate thus acts as a cue for upcoming environmental events that cause changes in adult or juvenile mortality and have done so dependably through evolutionary time,” (Sterns and Koella 1986, 895). The authors develop a reaction norm model for the association between earlier maturation, juvenile mortality, and overall size. They demonstrate that the shift to faster maturation from the 19th to the 20th century in Europeans is associated with an increase in overall size and is related to the dramatic reduction in juvenile mortality around the turn of the century. They state that a move towards earlier maturation probably occurred two other times in human history; once during the shift from scavenging to hunting and gathering and again during the adoption of agricultural practices.

> Environmental variation produces variation in growth rates and age- and size-specific mortality rates. These changes operate over evolutionary time to mold the genetically determined shape and position of the maturation trajectory. They also work within a single generation to produce a purely phenotypic response that determines the point on the trajectory where a single organism matures, (Sterns and Koella 1986, 909).

According to their model, high juvenile mortality results in a delay in maturation when age and size of the parent and the parents’ fecundity rate is accounted for in the model, see also (Dressino and Pucciarelli 1997). The risk of the parent in delaying maturity may be offset by the decreased juvenile mortality rate in the offspring generation which results in a delay in maturation when juvenile mortality is high, see also (Osmani and Sen 2003). In humans, faster maturation is generally associated with an overall increase in size. In examining archaeological samples, Kemkes-Grottenthaler (2005) found that taller individuals were more likely to live longer.

Hamilton et al. (2007b) examine the evolutionary significance of variation in body size in human populations. Conventionally variability in body size is thought to originate from differential access to nutrition resulting in changing levels of growth and development. The authors examined a variety of traditional human populations, both hunter-gatherers and agriculturalists, and found that in populations with higher population density body size was reduced. They argue that this decrease in size was due to increased disease load and malnutrition and selection for individuals that develop faster and earlier. The authors state that the variation in body size is caused by an evolved reaction norm leading to earlier reproductive maturity and smaller body size in populations with high density (Hamilton et al. 2007a). By incorporating life history theory, the authors demonstrate that when the probability of survivorship is low it is more costly to delay the age at first reproduction through pathways seen in Figure 2. While the study looks at traditional human populations, expectations about the impact of population density on human morphology may carry over to populations experiencing early urbanization when juvenile mortality was exceptionally high.

Walker et al. (2006) surveyed world-wide hunter-gatherer and agriculturist populations and examined the relationship between growth trajectory, mortality, and

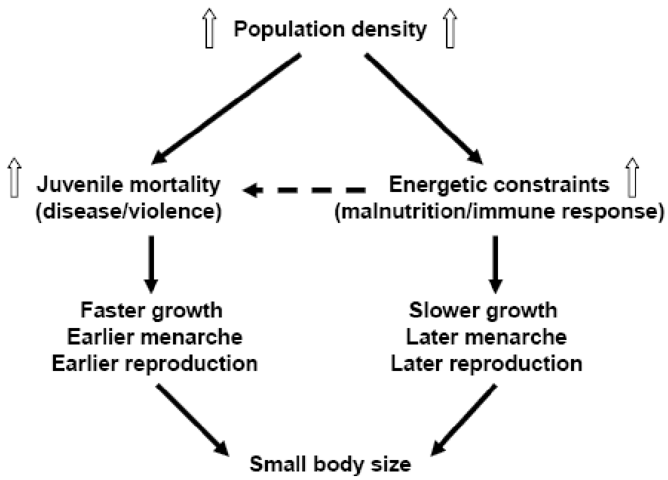

Figure 2. Figure 5 in (Hamilton et al. 2007a).

menarche. The authors report that in groups with better environmental conditions, growth tends to occur faster and puberty occurs earlier; concurrently in populations with high mortality growth in females tends to be faster and earlier. They argue that in situations where there is a high risk of mortality from disease or accidents the earlier and faster growth pattern would be favored more than where high mortality was the result of malnutrition.

Boldsen (2000) contends that differential survival is the main cause for changes in the morphology of humans over the past 10,000 years. He found that just preceding the three major morphological shifts in humans there was a corresponding shift in mortality patterns. For example, the brachycephalization observed in human populations at the end of the Middle Ages occurred at the same time that there was a major shift in mortality patterns. This shift in mortality patterns resulted in a substantial increase in the mortality parameter associated with juvenile mortality, as the incidence of death from major epidemics, such as the plague, became more common.

Gage and Zansky (1995) examined the relationship between anthropometrics and mortality across age groups and sexes. They found a significant correlation between mortality and anthropometrics. The variable most significantly associated with mortality was height, while height-for weight showed the weakest correlation. Interestingly, 6-year-olds showed the strongest correlations between anthropometrics and mortality, while adults and newborns showed the weakest correlations.

In the past 200 years there have been dramatic changes in the demographic structure of the population, beginning with a decrease in juvenile mortality. However, the decrease in juvenile mortality was not a linear decline across time (Riley 2001). Across Europe and American, prior to large-scale urbanization, there was an overall decline in mortality, but as urban centers became more populated mortality levels increased (Mercer 1990). As more people began to move into cities following the industrialization in the end of the 18th century and first half of the 19th century, diseases and epidemics became more common. The epidemics associated with high population density, such as cholera and yellow fever, resulted in increased mortality rates especially among the young. It was not until public health initiatives and vaccination programs were successfully initiated in the second half of the 19th century that survivorship was forced up and mortality down. The first group affected by the decline in mortality was children, while infant mortality tended to be more resistant to mortality declines. Over time this group also experienced a decline in mortality. Finally, adult mortality slowly decreased from the beginning of the 20th century though the invention of more advanced medical procedures. This pattern of increased mortality followed by plummeting mortality levels has been observed in populations around the world that experienced intense urbanization (Fogel 2004).

Research into the third transition began in England and many of the models for how the modern health transition took place come from these initial studies. There is, however, a great deal of variation in the rate and pattern of mortality change both between and within countries. The variation within one country may be extreme, in Spain in 1860 life expectancy ranged from 25 years to over 40 years depending on the region examined (Schofield and Reher 1991, 4). However, some generalizations may be made across modernizing countries which led to increased longevity. In general, the first group to experience a decline in mortality was children aged 1-14 years; these declines were often large. Following the decline in childhood mortality, infant mortality went down although it was generally somewhat more resistant to change. Finally, adult survivorship increased slowly. These general trends suggest that decreased mortality of children and infants is the single largest initial contributor to increased survivorship of any group (Schofield and Reher 1991, 6). The controversy about the causes underlying the rise in survivorship, "pit nutrition against public health, living standards against social organization, and levels of income against scientific advance" (Schofield et al. 1991, 7). Researchers tend to place lesser or greater weight on both public health and standard of living practices versus improved medical care for forcing survivorship up in modern populations.

Economic historians working with stature data from a number of different published sources have identified recurrent patterns in the socio-economic history of a country as related to its effect on the stature of the population. One such pattern is the association between decreased stature and urbanization,

> The first recorded downturn took place in Europe during the second half of the eighteenth century and another occurred in America during the Antebellum decades. Both were accompanied by rapid population growth, by urbanization, and by the expansion of the industrial sector. In both instances the relatively slow growth of the agricultural labor force and the absence of technological breakthroughs in food production, coupled with the increased urban demand for food, meant that the price of nutrients increased both absolutely and relatively to industrial products (Komlos 1998, 354).

This paradox of increased economic growth associated with a decline in stature and the overall well-being of the population has been used to demonstrate that there is not necessarily a linear relationship between morphological and economic indicators, see also (Tatarek 2006).

Woitek (2003) looked at the relationship between economic cycles and changes in height among a variety of 19th century populations from the U.S. and Europe. The author found a tight correlation between changing economic conditions and stature. He further reports that downturns in economic conditions most severely impact infants and that the repercussions of these poor conditions during infancy continue to affect the individual throughout life. Alderman et al. (2006) demonstrated that growth stunting in the pre-school years had long-term consequences, including fewer years of completed schooling and shorter adult stature.

Komlos (1998) discusses the relationship between population growth and industrialization that has been identified using historic records. He found that the most recent population expansion started in Europe in the 1730s and predated the beginning of the Industrial Revolution. Population expansions had previously occurred in Europe in

1300s and 1600s. The previous population expansions were unsustainable and ended with large-scale epidemics, like the Black Plague. However, the progress made during the Industrial Revolution allowed the most recent population expansion to continue. Advances in public health and sanitation kept the spread of epidemics under control in urban centers and allowed for ever greater population expansion. (Komlos 1998, 355). However, across Europe during the second half of the eighteenth century height declined as a result of inadequate access to nutritional resources. The lack of resources was brought about by a variety of factors beginning with the increase in population size coupled with severe weather changes resulting in poor agricultural returns. This decrease in height has been documented in several populations in Europe, including England, Sweden, Austria, Italy, and Bavaria (Komlos and Baten 2004).

Migration is one of the fundamental evolutionary forces that has shaped human populations. The past 200 years of human history have seen unprecedented movements, both internationally and into urban centers. The mass movement of people from rural to urban centers began in Europe and America 200 years ago and continues to be a major force in developing nations today. Rural-to-urban migration is one of the most common types of movement in human populations today. The impact of urbanization on human populations has been studied from a number of different perspectives.

Bogin (1988) points out four reasons why the study of rural-to-urban migration is important for understanding human populations. First, the urban environment represents a unique environmental niche into which humans have been introduced and the adaptation of organisms to new environments is of interest to biology. Also, rural-to-urban movements have been the most common type of migration to occur throughout human history and continue to occur with increasing intensity around the world. Finally, the long-term impact of rural-to-urban migration on the human phenotype is not well understood.

The urban penalty has been documented in several populations, whereby rural inhabitants are generally taller than their urban counterparts in the early periods of industrialization. This pattern is reversed over time and urban inhabitants are taller from the beginning of the 20th century. Craig and Watson (1998) found that before the mid-19th century individuals that lived closer to food sources had an advantage over those that had to pay the transportation costs, this advantage has been documented in Maryland, Japan, Ireland and Scotland. This advantage disappears after the 1850s as a result of the reduction in transportation costs with the availability of railroads and the use of refrigeration. Large height advantages have also been reported in comparing upper and lower-class individuals, especially in the early part of the Industrial Revolution (Alter et al. 2004; Komlos 1994). In the U.S., the secular increase in height over the past few centuries has ended with the birth cohorts from the middle of the 20th century (Sunder 2005).

Several studies have examined the detrimental effects of urbanization on human populations in the 19th and 20th centuries. Budnik and Liczbinska (2006) used historic records to compare mortality patterns in urban and rural areas of Poland from the late 19th century to the early 20th century. They found a large difference in mean age-at-death between urban and rural areas with the life expectancy of a newborn in an urban area of

31.6 years compared to 42.12 years in rural areas. The authors attribute this difference to access to clean water and sanitation systems and the high prevalence of diseases, such as tuberculosis in urban areas. In the Polish sample, neonatal mortality rates were higher in rural areas; however, post-neonatal mortality rates were higher in urban areas. In examining the impact of industrialization and urbanization on children's health in England, Lewis (2002) found that while there were differences between medieval urban and rural populations, the effect of industrialization had a much more detrimental impact on the health of the populations. In urban Japan, the same pattern of an initial increase in mortality and morbidity, followed by an improvement in environmental conditions from better sanitation systems and food supplies was documented (Nagaoka and Hirata 2007).

Steckel (2002) found that urbanization had a detrimental effect on stature in worldwide populations. Periods associated with intense urbanization are generally associated with a decrease in stature. This is likely the result of increased exposure to pathogens as a result of inadequate public health standards. Urbanization and industrialization are also associated with the spread of disease because of increased availability of major transportation systems, like roads and railways. These transportation systems facilitated the movement of disease between urban centers. The increase in the number of students attending public school may also be associated with increased spread of disease.

Floud and Harris (1997) found that in Britain, urban-born men were shorter than rural-born men from 1800-1870, the period associated with intensified urbanization in Britain. In general, countries that industrialized later were somewhat buffered by the detrimental effects of urbanization because knowledge of public health measures were already known. Given the previously mentioned findings, Steckel questions,

> If low urbanization and low population density were good for health, it is a fair question to ask why so many of the preindustrial populations were so short, compared with their industrial counterparts. After all, the adverse factors of urbanization and population density tended to increase with industrialization. With the exception of the US and Britain in the late industrial phase, there must have been something good for health about industrialization that more than offset the features that were bad, (Steckel 2000, 16).

Steckel observed that stature in the early Middle Ages was at its maximum in Europe; this was followed by a steady decline that only began to increase around 1750. In 1500 there was only one city in Europe with more than 100,000 people and over the next two hundred years urbanization increased dramatically. This was also a period when international trade routes were established and with these came increased exposure to many different types of disease. Stature improvements began following the declines of the 16th and 17th centuries, even so it is generally assumed that urbanization is bad for health. Steckel argues that it was the improvement in nutrition that drove the changes. Specifically, the agricultural outputs increases that followed this period and were the result of improved climate and agricultural tools.

Blanco et al. (1992) examined differential growth and stature in urban versus rural individuals in Venezuela. They found that urban-born children were taller and heavier than rural-born children. Additionally, the growth differences continued into adulthood in boys, while among girls the growth differences disappeared in adulthood. Dufour and Piperata (2004) examined the consequences of rural to urban migration in Latin America over the past 50 years. This type of migration has intensified in this region of the world in the past half century. The authors point out a number of trends that occur throughout

Latin American as a result of rural to urban migration. One common trend seen across the region is that fertility in migrants is generally intermediate between their rural and urban counterparts, with rural individuals experiencing the highest fertility and urban individuals experiencing the lowest fertility. Also, in comparing recent urban immigrants to long-term urban residents, it appears that recent immigrants tend to experience higher rates of mortality and morbidity. This may be the result of exposure to the urban environment or due to the fact that recent immigrants tend to live in the more impoverished parts of the city. The authors point out that it is difficult to discuss an "urban" environment because cities tend to be very diverse places.

In examining the stunting effect of small pox in 19^{th} century Britain, Oxley (2006) found that among a sample of Irish there was no stunting effect for those individuals that remained in Ireland during their adolescence, but among individuals that migrated to London there was a significant stunting effect on their growth. The author argues that small pox provides a good proxy for urban density in the sample. The sample demonstrates that significant detrimental impact on stature in urban London throughout the 19^{th} century, but especially in the early part of the century and especially with regards to newly arriving immigrants.

Padez (2002) examined the secular trends in Portuguese males using military records from 1904-1998. The author reports a significant increase in height over the study period of nearly 9 cm. The study also uncovered significant differences in height among different regions of Portugal, with the tallest individuals coming from Lisbon in the 1998 sample and among the tallest in the 1904 sample. Gordon and Grier (1992) looked into secular changes from the anthropometric data from the U.S. army. They found significant linear trends across the samples from 1911-1970. They also found that the place of birth had a significant relationship in some of the racial groups examined and hypothesized that the difference in the increase in U.S.-born versus foreign-born individuals may have an impact on the results of the secular trend analysis. In another study, it was observed that height has increased 10-15 cm. in the past century in America and Europe and the body mass index (BMI) increased from around 23 in 1894 to 26.5 in 1991, for 45 year olds (Fogel 2004).

Developmental Plasticity and Secular Changes

Discussions of secular changes first enter anthropological research with Boas' influential study on the plasticity of the cranial form in immigrants to the U.S. (Boas 1912). Boas observed a significant difference in the average cranial form between American-born and foreign-born offspring of immigrants to the U.S., most significantly in Hebrew and Sicilian populations. Boas found that the foreign-born offspring of Hebrews generally exhibited a rounder head, while their American-born offspring tended to have longer heads. He found the opposite trend in the Sicilian population, which went from longer to shorter heads within a single generation. Boas posits a few hypotheses for the biological causes for the observed differences in cranial morphology from one generation to the next. These include heterosis, improved environmental conditions, and changes in cradle boarding practices.

Angel (1982) was among the first to identify the secular trend of an increase in cranial vault height in modern Americans. Angel suggests that flattening of the cranial base results from a stressful environmental or from poor nutrition. Under inhibited bone growth the cranial base cannot resist gravitational forces and the forces of the brain weight ultimately result in a flattening of the cranial base. Angel's sample consisted of 166 individuals from the Terry collection and forensic cases, with birth years ranging from 1860-1960. Angel attempted to account for heterozygosity in the sample by examining surnames. He calculated the frequency of different types of surnames (i.e. British, East European, German, etc) and concluded that the earlier groups do not differ significantly from the later groups. Angel pointed out that the earliest group did not have access to as wide variety of food and that they were highly affected by infant mortality and childhood diseases, such as rickets. The secular trends observed in the sample include an increase in stature of 4.5 cm. Moreover, Angel documented an association between changes in stature with skeletal indicators of childhood stress, including nutritional and illness related stress. Angel reported that cranial base height was larger in the later sample, both in overall size and with size removed. The results demonstrated that base size and stature do not increase as dramatically as the base height. The width of the cranial base also increased significantly and outpaced increases in the vault width. Angel pointed to a corresponding increase in the pelvic depth and hypothesized that the cranial base and pelvic depth were responding to the same changes in environmental factors, mainly decreased nutritional stress during growth and development. The growth period affecting the cranial base and the pelvis are different, the cranial base growth period begins and finishes earlier while the pelvic growth lasts through puberty. Once again Angel used index measurements to account for size variability in the sample. The advantage of using geometric morphometrics is that it allows for size to be examined without conflating size with shape changes. Angel states that a better investigation of secular trends would take into account class, nutritional data, and better control of genetic continuity.

Jantz and Meadows Jantz (2000) reported on dramatic changes in the cranial form of American populations during the past 135 years. The sample was divided into White and Black males and females. Secular trends were documented using five cranial measurements. The sample was broken down in decade birth-year cohorts. The authors found a significant secular change in the cranial vault height for all four groups. In addition, there was a stronger relationship between shape changes than size changes. There is a clear relationship between stature and cranial vault height and a similar pattern was reported in stature of Americans from the same time period. The samples used in the study represent a wide geographical dispersion. The samples come from anatomical collections and the forensic databank. These samples may be representative of the entire American population, broadly speaking, but because the samples do not represent a real breeding population nor do they represent a random sample of Americans over time, they therefore have limited usefulness in testing hypotheses related to the specific causes behind the observed secular changes.

In a follow-up to the 2000 study, Wescott and Jantz (2005) reconstructed 13 two-dimensional landmark coordinates from a sample of Americans with birth years ranging from the 1830s to the 1970s. The sample was divided into five twenty-five year birth cohorts. This study also demonstrated significant changes in cranial morphology with an increase in cranial vault height representing the largest component of secular change. This study demonstrated that change in the cranial vault was restricted mainly to the inferior movement of the cranial base at basion. Wescott and Jantz (2005) suggest that growth allometry changes documented in the postcranial skeleton probably carry over to the crania, because the vault shape changes more than the vault size.

Jonke et al. (2007) examined secular trends in Austrian soldiers from the 19th and 20th centuries. The study used lateral cephalograms of living soldiers in the Austrian army and cephalograms from documented 19th century soldiers. The use of cephalograms limits the data available for study and only changes in the facial skeleton are explored. The authors use the cephalometric data to examine the allometric and non-allometric components of group differences between the 19th and 20th century samples. The results of the analysis demonstrate that the 19th and 20th century individuals are different in both shape and size, but the trend between size and shape is opposite. By utilizing methods from geometric morphometrics the authors detected trends related to changes in size and separately to detect changes in shape. The analysis uncovered a surprising discordance between the two components and one that had not been previously documented. There is no analysis of the environmental factors that may have influenced the differences between the two groups, but it is conceivable that such analysis could more explicitly identify environmental changes driving the secular trend. The authors suggest that the study could be improved by using 3D data in order to incorporate variation due to changes in width.

Stynder et al. (2007) examined craniofacial changes in South Africans during the Holocene. The authors report a decrease in cranial size from 4,000 to 3,000 B.P. followed by a period of recovery. There were two major shifts in the environment during the study period, the first occurred at about 4,000 B.P with a period of increased population growth and reduced mobility, the second shift occurred at 2,000 B.P. when domesticated animals and pottery vessels were introduced. The only significant morphological changes to occur in the population were during the period of population growth at 4,000 B.P., while no changes were associated with the dietary shifts or introduction of agriculture. Stynder et al. (2007) hypothesize that the cranial size decrease and associated shape changes came about due to increased nutritional stress as a result of the larger population. The authors dismiss the often cited cause of the craniofacial changes as resulting from a change in diet and the introduction of agriculture, and point out that the changes pre-date any major dietary shifts. Moreover, the study argues for an environmental cause as opposed to a genetic cause associated with immigration driving the observed changes. The lowest variation was seen in the period of reduced cranial size and the changes seem to reverse following 3,000 B.P., both of which indicate that cause of the observed changes is environmental.

In a recent study on secular changes in modern populations, Little et al. (2006) compared anthropometric measurement from three cohorts of children from rural Mexico from 1968-2000. Four craniofacial measurements were examined over the study period. The earliest two cohorts showed stunted growth resulting from undernutrition, while the latest cohort showed a significant change in craniofacial morphology. The latest cohort displayed a decrease in cranial vault length and a narrowing of bizygomatic width. The authors use a number of environmental parameters from the community to determine the causes of the observed secular changes over time. The first factor that they investigated was the change in masticatory stress. The researchers compared a 24-hr. dietary recall among the cohorts to look for differences in masticatory stress. They reported no differences between the cohorts in the dietary recall. However, from the earliest two cohorts to the latest cohort, maize processing changed from exclusively stone-ground to exclusively machine-ground. The authors suggested that this change represents a change from harder to softer food and accounts for a major component of the observed changes in cranial morphology. The authors looked at additional changes in the environment that may be related to changes in craniofacial morphology. A low rate of migration into the community throughout the study period is known from public records. However, in the segments of the sample that experienced the largest heterozygosity to due immigration, there was a corresponding increase in bizygomatic breadth and a decrease in cephalic index. The researchers also investigated the role of changes in natural selection on the population. From the middle cohort (1978) to the latest cohort (2000), childhood mortality declined from 65% to 16%. Across the three cohorts, height did not increase between 1968 and 1978, however from 1978 to 2000 height significantly increased by 6 cm. The authors suggest that the changes in craniofacial morphology preceded the changes in height, which they argue lends support to the significant affect of the change in maize production on the secular trend.

The research is interesting for a number of different reasons. First, the authors are able to correlate the changes in the environment within a well-defined community to changes in the craniofacial morphology. The changes experienced in this community parallel changes that occurred across developed nations, although the changes are somewhat delayed in time and occur with increased intensity. The documented changes that occurred over 32 years in this population help to explain changes observed in other populations, although there are a number of limitations to the study. First, the use of anthropometric data limits the number of measurements available for study. Second, it is difficult to assess cranial vault height using anthropometrics and the authors do not report this measure. The change in cranial vault height has been shown to be a major component of the secular changes observed in other modern populations (Wescott and Jantz 2005). Thirdly, the investigation examines changes in a rural community. While the community has been impacted by modern developments, the majority of the families continue to work in agriculture. A significant change affecting a large part of the human population over the past two hundred years is the impact of urbanization. Moreover, Little et al. (2006) state, “the relationship between size, morphological complexity, and size/form remains unclear” (2006, 134). Methods, such as geometric morphometrics, are uniquely capable of examining secular trends related to shape changes, size changes, and the interaction between the two.

Lewin et al. (1973) reported that secular changes that resulted in increased stature in Finnish Lapps also impacted craniofacial morphology. Increases in stature were associated with increased head length and decreased head breadth. An increase in stature was also associated with increased facial height while facial breadth was unchanged. Facial height was found to be the most significant factor impacting secular changes. The pattern of change is somewhat different among the sexes. These changes were not the result of greater genetic admixture, as the population remained highly isolated across the study period; childhood mortality was also high across the study period, however secular changes were more pronounced in high status families. The study suggests that the changes in the crania are the result of different growth patterns between parents and children. The authors also found an overall reduction in head circumference which has previously been associated with malnutrition (Bielicki and Welon 1964; Ghai and Sandhu 1968; Neyzi et al. 1966; Robinow and Jelliffee 1966).

In Japan, a different pattern of craniofacial change has been observed. The secular trend seen since the beginning of the 20th century is that the cranial vault has increased in breadth. This increased breadth follows a similar pattern of increased stature also observed in the population (Kouchi 2000). According to the author, the secular change towards increased cranial width has stopped occurring in the birth cohort in Japan. The author argues that improvements in environmental conditions best explain the pattern of change observed. Their findings suggest that a single pattern of cranial change may not be symptomatic of improved environmental conditions and that genetic or social influences may dictate the types of changes observed. In other words, individuals living in similar environmental conditions will still reflect the underlying genetic differentiation in their cranial morphology. Lieberman et al. (2000) found that the component of the cranial base that contributed most to the overall cranial shape was cranial base width and that cranial base width is impacted by brain volume.

Secular changes in human craniofacial morphology are often attributed to changes in diet and masticatory stress. Brace et al. (1987) showed that over the past 100,000 years tooth size in humans has been reduced mainly associated with the introduction of cooking methods 10,000 years ago which reduced the amount of force necessary for processing food. Brace argues that this is an example of relaxed selection whereby mutations occurred resulting in a reduction in overall dental size. Lieberman et al. (2004) also found that facial size was reduced in hyraxes that were fed on diets of raw versus cooked foods.

Carlson and van Gerven (1977) examined changes in cranial morphology in ancient Nubian populations. The sample consists of 3 groups separated by a 10,000 year period. The earliest group is from hunter-gatherers, the middle group is mixed hunter-gatherer and agriculturalists and the latest group is from dedicated agriculturalists. The earliest group consists of craniometrics from 12 individuals and is separated from the later two groups by at least 5,000 years. The earliest group appears much differentiated from the later two groups. The later groups were found to have higher, shorter cranial vaults with less facial prognathism. There is no discussion of sex differences in the sample; it seems possible that the craniometrics were not corrected for sex differences. This appears quite problematic in light of the very small sample size in the earliest group. The authors argue that the difference is due to changes in subsistence strategies and the adoption of agriculture. Carlson and van Gerven state that the differences are unlikely the result of population movements, however recent research has shed some doubt on those conclusions and suggests that Neolithic populations were very migratory (Diamond and Bellwood 2003). The authors suggest that move towards a more brachycephalic cranial morphology reflects the shift towards agriculture in wide range of populations. Others have found that the shift towards a shorter cranial vault postdates the agricultural revolution and may be associated with changes in selection and mortality patterns during the early to mid Middle Ages (Boldsen 2000; Kondova and Cholakov 1994; Necrasov and Cristesc 1974).

Sardi et al. (2006) also examined the effect of different subsistence strategies on cranial morphology using samples from Argentina. The authors found that largest differences related to size where hunter-gatherers were generally larger compared to agriculturalists. They further found that there was a large difference in the amount of variation in difference functional components, with the masticatory and posteroneural components showing the largest differences. They attribute the changes to a shift in lower nutritional quality in the diets of agriculturalists, a reduction in amount of growth hormone in sedentary populations, and changes in functional demands due to differences in masticatory stress. However, the first two causes presented as minimal with greater emphasis placed on the functional response model.

Many of the secular changes documented in previous studies are centered on the cranial base (Wescott and Jantz 2005). The cranial base is a difficult region of the skull to study because many of the features and landmarks are located on the endocranial surface. The growth and development of this region are particularly important for a better understanding of the morphological changes. The cranial base shows a unique growth trajectory in comparison with other regions of the skulls. The majority of growth in the cranial base occurs before 5 years of age. Sgouros et al. (1999) reported that even during this early period of growth there are differences between males and females. Sgouros et al. (1999) used CT scans of children in order to document growth changes; therefore they were able to demonstrate the 3d changes occurring in the cranial base. The largest difference between males and females was in the growth pattern in the anterior fossa, whereby males show a more rapid growth resulting in decreased angulation and a more forward projection. Females showed little change in the anterior fossa throughout the growth period, while the posterior fossa in females was the site of more intense growth before 5 years. Measures of width in both the middle and posterior cranial fossa experienced the largest increase before age 5 years in both sexes.

Lieberman (1998) contends that many of the cranial features that define anatomically modern humans are related to the cranial base. He found that the largest differences among *Homo* groups come from a rapid reduction in the size of the sphenoid bone early in development. The author suggests that it was changes in the sphenoid that led to the rapid development of morphology that defined anatomically modern humans.

Ingervall and Lewin (1974) found that facial prognathism is negatively correlated with the curvature of the cranial base. They also report that secular changes from 1952 to 1972 in 20-year-old Swedish males resulted in crania becoming shorter and broader. The sample shows little evidence that the changes were the result of genetic differentiation in the population and were likely driven by changes in environmental conditions. The authors argue that the cranial base remains relatively unchanged across the study period and further that the cranial base is under greater genetic influence compared to the cranial vault or face. Additionally, there is evidence that the cranial base has a strong influence on the cranial vault and face; although the vault and face are more influenced by epigenetic and environmental factors.

Bookstein et al. (2003) found that the cranial length and height influence the shape of the cranial base, whereby a more angular cranial base results in a shorter cranial vault. In examining an ontogenetic series the authors found that throughout growth the anterior cranial base did not change, while the cranial vault and face altered their shapes. The authors report a larger correlation between the cranial vault and face, then between either and the cranial base. The correlation suggests that individuals with taller cranial vaults have more retrognathic faces.

In a study on the growth of Old World Monkeys, Dressino and Pucciarelli (1997) found that malnutrition generally affects size components with less of an effect on shape changes, although different functional components are more significantly affected. For instance, the masticatory and middle neural components exhibit the largest changes, followed by the respiratory and optic components, and the least affected regions are the anterior and posterior neural components. The face was generally more affected by malnutrition compared to the neurocranium. Also, those components that finished growth earlier and faster tended to be less effected by malnutrition compared to later developing components. The middle cranial fossa would be similar to the cranial height in humans. This is also the component that changes the most during the 19th and 20th centuries.

Implications for Craniometric Research

Reletheford (2004) discusses the relative contribution of plasticity and genetics for understanding craniofacial morphology. He points out the Boas' data suggests that a small component of the observed variation in the sample is explained by developmental plasticity, however these differences do not obscure differences among the ethnic groups and that genetic differences explain a large component of the variation. Researchers' specific questions must dictate the level of exploration, whether developmental plasticity or genetic differentiation. Genetic variation may be controlled in order to look at developmental plasticity or developmental plasticity may be controlled for in order to examine genetic questions. Larson (1994) argues that most craniofacial variation can be explained in terms of functional adaptation, conversely he states that in some cases population history may be reconstructed. The fact that Carlson and Van Gerven (1977) explain the changes that they observe over a 10,000 year period purely as a response to a change in mechanical forces acting on the crania demonstrates as little understanding of biological processes as those early anthropologists that interpreted variation among populations as reflecting differences in fixed racial types. The cranial morphology of the Nubians was undoubtedly influenced by a shift in diet, but over such a long time period many other factors also affected the population. The changes in cranial morphology must be understood from the many different influences on the phenotype, both environmental and genetic. The finding that either of those contributes to the variation does not change the fact that the other is also a significant component. Carlson and van Gerven were reacting against an earlier tradition that cranial morphology was solely and most importantly a reflection of genetics, and were following Boas' example. This was an important point to make at a time when the plastic nature of the skull was under recognized. However, it is now important to move beyond the dichotomy that cranial morphology is either influenced by the environment or genetics, in order to integrate a coherent organizing principal where each facet is understood and the phenotype is understood as a response to both. The only way that a unifying theory is possible is to have better samples. Models should be derived from samples of known origin where the processes acting on the system are well understood. There are too many unknown factors influencing the Nubian sample and yet it remains a commonly cited study to discuss the significance of secular changes in cranial morphology.

The numerous examples of inferring population history from craniometrics demonstrate that those relationships can be determined even when other processes are acting on the system. Relethford and Blangero's (1990) model-bound methods for examining cranial variation enable researchers to frame questions of population differentiation within the context of quantitative genetics. Both Sparks and Jantz (2003) and Gravlee et al. (2003) demonstrated that population history was maintained even when plasticity was significant. Relethford and Blangero's (1990) models have been shown to be robust to the effects of only moderate heritability of traits. The only caveat that these researchers and others have pointed out is that the additive genetic matrices and phenotypic matrices must be proportional in order for genetic relationships to be recoverable. Their research has demonstrated the relatively small effect of cranial plasticity and that these models are robust at recovering population history, even with only moderately heritable traits. Most importantly, researchers have shown that the variation present in craniometrics is closely matched to the variation seen in other genetic markers. Relethford (1994) compared worldwide samples of craniometrics with genetic markers taken from similar populations and found that in both types of data the level of worldwide variation is about 10%. Roseman and Weaver (2004) also found that population history had a significant effect on the pattern of regional variation observed in a worldwide sample comparing craniometric and genetic markers.

The current research focuses on the evolutionary significance of short-term secular changes in the modern Portuguese population. The Portuguese sample addresses many of the short-comings in other samples. The Portuguese sample is not greatly influenced by immigration as is the case in the modern samples from the U.S. The sample may be considered as more representative of a real breeding population than anatomical or forensic collections. Due to the availability of historical documents changing environmental conditions are more precisely documented than in archaeological samples.

From the previous literature several patterns of secular change in modern populations begin to emerge. It is clear that the third demographic transition has had a significant biological impact on human populations. Moreover, there appears to be a significant impact on human populations exposed to urban environments. Initially the urban conditions are much poorer compared to rural conditions; this is seen in the reduced stature of urban-dwelling people in the initial period of industrialization. Following improvements in sanitation and vaccination programs, juvenile and infant mortality declined and stature in urban populations surpassed rural populations. The cranial morphology of modern populations appears to be towards taller cranial vaults and faces. In the U.S. population the cranial vault get shorter, while in the Japanese the cranial vault gets longer. There is also a tendency toward a more reduced facial breadth over time. Several studies have found that those areas of the skeleton that are most affected by environmental insults early in development tend to change most significantly over time, such as the cranial base. The ways in which the changes in the craniofacial morphology of the Portuguese sample compares to other modern populations will be explored and the changing environmental conditions more precisely characterized in relation to changes in cranial morphology of the population. Chapter 3 discusses the historical changes that occurred in Portugal and in Europe during the study period in order to characterize the changing environmental components.

Chapter 3. Historical Background and Materials

Portuguese History

The borders of Portugal have remained unchanged since the 13th century when the Moors were driven from the Southern part of the country (Birmingham 1993). Over the next three centuries the Portuguese led the world in explorations, colonizing islands in the Atlantic Ocean and discovering sea trade routes to Asia and the New World. The golden age of modern Portugal began in the first part of the 18th century. The natural resources extracted from the Portuguese colony, Brazil, especially gold were used to finance the expansion of the economy until the late 18th century. The proceeds from Brazilian gold enabled monumental public works projects. Lisbon has always been the largest city in Portugal. In 1755 Lisbon was struck by an earthquake that was felt in every major European capital and completely decimated the city. The entire city was destroyed by the initial quake and the fires and tidal waves that followed. Large shanty towns sprung up all around the central city. In 1807 Napoleon's armies invaded and devastated large regions of the country and Portugal's economy did not recover for decades. The early signs of industrialization were stagnated throughout the early part of the 19th century as a result of these upheavals. Agriculture suffered, and large parts of the rural population were afflicted by famine and disease. Further adding to economic difficulties, Portugal gave up the sole trading rights of Brazil to England in 1810 (Wheeler 1978).

Urbanization began in Europe at the end of the Middle Ages, although there was a large degree of variability from North to South. It is not until the 1500s that large cities began to emerge in Northern Europe, while in Southern Europe urban centers were somewhat more common (Steckel 2002). The estimated population of Lisbon in 1415 was already 55,000 and Lisbon remained one of Europe's largest cities throughout the next 400 years (Baptista and Rodrigues 1996, 50). At the beginning of the 1800s, Lisbon was one of the ten largest cities in Europe. Throughout its history, the rural areas of Portugal lagged behind much of Europe, but the urban centers of Lisbon and Oporto, closely followed developments that were occurring in the rest of Europe (Birmingham 1993). During the Victorian Age, Lisbon was connected to Paris by railway and architectural achievements from the botanical gardens to the Maria II Opera House rivaled any architectural achievements seen elsewhere in Europe. In 1908 the monarchy was overthrown and a period of political disorder set in with 45 governments established from 1910-1926. This period lasted until an authoritarian government headed by Salazar was installed in 1932 (Pereira and Mata 1996). Salazar's government isolated Portugal and impeded economic growth and modernization and Portugal did not re-join the European community until the 1970s.

The population growth of Lisbon fluctuated throughout the 19th and 20th centuries, from 1800 to 1857 population growth was fairly flat and even experienced declines following periods of economic hardship. The last of the large-scale epidemics to sweep through the city in 1857 and subsequently began a period of intense growth which lasted until about 1950 (Birmingham 1993). The population growth was fueled by the mass movements of people from rural areas. During this same period many people that were emigrating from the rural countryside were not only going to Portugal's urban centers, but were leaving the country for Brazil and the United States. Between 1850 and 1930, 2 million people left the country, with 2 million more leaving between 1930 and 1970 (Veiga et al. 2007). By the end of the 19^{th} century 7.1% of the entire Portuguese population lived in Lisbon, this figure rose to nearly 10% by 1950.

In 1851 a French-style revolution had been completed in Portugal and a period of modern developments began (Pereira and Mata 1996). From the middle of the 19^{th} century telegraph lines came into use, 200 km of all-weather roads were built every year, and an extensive railway system was built. In 1868 there were urban protests as a result of an economic recession which demonstrated the growing importance of urban workers in the Portuguese economy. A period of intense industrialization began in 1871 with imports of machinery rising 10-fold in six years.

North-South regional differences exist in Portugal. The North was traditionally more religious, with higher population density, higher fertility, and higher emigration rates. The North has mainly small family farms, while in the South land is held by few individuals with landless peasants making up the majority of the population. Portugal also had a strong duality between urban centers and rural areas. The urban centers of Lisbon and Porto were experiencing slow modernization throughout the 19^{th} and 20^{th} centuries; the rural areas however maintained very traditional lifestyles. The fertility transition documented in most modernizing countries occurred in Portugal in the 1920s and is marked by a sharp decline in fertility levels throughout the country. In Lisbon, the fertility decline preceded other regions in Portugal. The decline in fertility was preceded by a decline in mortality and improved socioeconomic conditions (Oliveira 2006).

In the 1950s it was estimated that 53% of a middle class family's income was spent on food, 68% for poorer industrial workers, and 80% for rural workers (Instituto

Nacional de Estatistica, 1953). The waves of immigrants arriving in Lisbon created large housing shortages and the living conditions were generally poor. In 1950 only 54% of houses in Lisbon had a toilet (Abecasis 1950). Throughout the first half of the 20th century Lisbon had higher infant mortality rates and higher mortality rates from infectious and communicable diseases compared to rural areas of the country and this pattern reversed only after about 1960 (Reis 1960). The infant mortality rate for Portugal in 1920 was 123.2 per 1000 births, in 1930 it was 83.8 per 1000 births, and in 1950 it reached 51.9 deaths per 1000 births. While these declines do not match those seen in other Western European countries, they are nonetheless large (Mausy-Strobant 1997). The age at menarche in Portugal decreased steadily from 15 years in 1880-1890 to 12.4 years in 1980 (Padez and Rocha 2003), indicating continual improvements in environmental conditions.

Post-neonatal mortality rate is a sensitive indicator of infant health (Kessel 1990). Between 1930 and 1960 the post-neonatal mortality rate in Portugal declined by nearly 50%, from 95.5 per 1,000 live births in 1930 to 47 per 1,000 in 1960. Also, from 1950 to 1960 the maternal mortality rate went from 355 to 115.5 deaths per 100,000 women, this corresponds to the more common use of Caesarian sections, the availability of antibiotics, and an understanding of blood types and blood transfusions. The average life expectancy was also much improved, wherein males in 1900 could be expected to live 43 years and females 47 years, in 1960 the life expectancy for males was 63 years and for females 69 years.

Pereira et al. (2000) examined the mtDNA diversity in the modern Portuguese population. They divided their sample into Northern, Central, and Southern Portugal. A higher level of diversity in the country was found compared to earlier studies. They did not detect a statistically significant difference among the three regions, although they did find differences in two haplotypes which showed a North to South gradient. The unique haplotypes are from North and sub-Saharan Africa and are likely the result of the Muslim occupation of Portugal in the 8th century and later the slave trade, which Portugal participated in during the 15th and 16th centuries. A study using Y-chromosome data revealed similar results, with no statistically significant differences found among the three regions (Beleza et al. 2006). Mantel tests comparing genetic and geographic distances were insignificant. The Y-chromosome is especially susceptible to genetic drift and this study shows little evidence of this process in the Portuguese sample. The homogeneous nature of both males and females in the Portuguese population is demonstrated in both of these studies; although both studies also demonstrate that certain haplotypes occurred with differing frequencies from North to South. Surname analysis has also confirmed that the Portuguese population is highly homogeneous (Pato et al. 1997).

Collection demography

The New Lisbon skeletal collection is held at the Bocage Museum in Lisbon, Portugal. The collection contains over 1700 documented skeletons. Dr. Louis Lopez began collecting skeletons from three local cemeteries in the 1980s. The collection was started to replace an earlier collection that was held at the museum. The earlier collection was destroyed in a fire that damaged the Bocage Museum in the 1978.

The skeletons come to the collection from one of three cemeteries in Lisbon. The protocol for burial is that an individual is buried for approximately five years during which time skeletonization occurs. Following burial, the remains are exhumed by cemetery workers, washed with a high pressure washer, and placed in small, cement mausoleums. The mausoleums are rented by family members and if the payments lapse the families are notified that the remains will be removed. After a period of some years without payment the skeletons are removed from the mausoleums. When the skeletal remains are removed from the mausoleums, the remains are either buried in communal graves, cremated, or curated at the museum. When remains are removed from the mausoleums, the skeleton may come from any time period, remains from earlier periods may be removed at the same time as skeletal remains from later periods. Therefore, as the collection expands individuals are added to the collection that represent not just the most recent deaths, but also earlier burials. The skeletons are generally complete and well-preserved. The identities of the individuals are known and biographic information is available for many individuals. This information includes: name, place of birth, year of birth, date of death, occupation, address at death, marital status, and cause of death. In 1959 death records were moved from the cemetery to government offices; therefore individuals that died after 1959 have more limited biographical information. The year of birth, for example, is not known for people that died after 1959. The collection contains over 1700 skeletons from people that died from 1801 to 1975. The individuals in the collection represent mainly the middle socioeconomic segment of the population. The wealthiest individuals were generally buried in perpetual graves, while the poorest individuals were buried directly in communal graves. For families unable to pay for the secondary interment in the mausoleums, the remains were placed directly in the communal graves following burial (Cardoso 2005). The expenses associated with these burial practices indicate that individuals represented in the skeletal collection are mostly those of the middle income people and represents a higher socioeconomic status compared to most other modern, reference collections.

Chapter 4: Methods

Table 1 shows the sample sizes by birth-year cohort. Landmark coordinates were collected from 451 individuals, with approximately equal numbers of males and females represented. Age-at-death was known for all individuals that died before 1959; however for individuals that died after 1959 age was estimated using standard procedures (Buikstra and Ubelaker 1994). Table 2 provides a list of the landmark coordinates and definitions that were collected and used for subsequent analysis. A total of 67 bilateral and mid-sagittal points were collected from each individual, Figures 3-5 show the locations of the landmarks. The three-dimensional cranial landmarks were collected using a Microscribe 3DX digitizer and 3Skull software (Ousley 2004). Crania were placed on a metal ring stand in order to stabilize the skull while digitizing. The ring stand allowed all landmarks to be accessed without moving the crania.

Table 1. Sample size by birth cohort and sex.

	Males	**Females**	**Total**
1810-1839	5	8	13
1840-1859	23	20	43
1860-1879	41	51	92
1880-1899	42	48	90
1900-1919	45	42	87
1920-1939	44	46	90
1940-1959	20	16	36
Total	220	231	451

Table 2. Cranial landmarks and definitions.

Landmark (abbreviation)	Definition
Facial Landmarks	
Alare (alar)	The most lateral point on the nasal aperature (Bass 1971)
Dacryon (dac)	The point on the medial border of the orbit where the frontal, lacrimal, and maxilla intersect (Martin 1956)
Ectoconchion (ect)	The intersection of the most anterior of the lateral border of the orbit and a line bisecting the orbit along its long axis (Howells 1973)
Frontomalare Anterior (fma)	Intersection of orbit with fronto-malar suture
Frontomalare temporale (fmt)	The most laterally positioned point on the fronto-malar suture
Jugale (jug)	The point on the lateral zygomatic of deepest curvature
Mlspt	The maximum malar projection point
Mpl	The most laterally projecting point on the marginal process of the zygomatic bone
Nasion (nas)	The point of intersection of the naso-frontal suture and the mid-sagital plane
Nasale inferius (nasi)	The most inferior point of intersection of the nasomaxillary suture
Nasale superius (nass)	The point of intersection of the frontonasal, frontomaxillary, and nasomaxillary sutures
(ndspt)	The deepest point on the nasal bone profile
(nlhi)	The most inferior point on the nasal aperature
Prosthion (pro)	The most anterior point on the alveolar border of the maxilla between the central incisors in the mid-sagittal plane
(sispt)	The most projecting point on the nasal bones in the mid-sagittal plane
Staurion (4corn)	Intersection of median and transverse palatine sutures
Subspinale (ssp)	The point of deepest curvature between prosthion and the anterior nasal spine
(wnb)	The point of minimum distance between the left and right nasomaxillary sutures

Table 2, continued.

Landmark (abbreviation)	Definition
Zygomaxillare (zygom)	The most inferior point on the zygomaticomaxillary suture
Zygoorbitale (zygoo)	Zygomaticomaxillary suture at the orbital margin
Zygotemporale inferior (zyti)	The most inferior point on the zygomaticotemporal suture
Zygotemporale superior (zyts)	The most superior point on the zygomaticotemporal suture
Cranial Vault Landmarks	
Asterion (ast)	The junction of the lambdoid, parietomastiod, and occipitomastoid sutures
Auriculare (aub)	Point on the lateral aspect of the root of the zygomatic process at the deepest incurvature (Moore-Jansen et al. 1994)
Bregma (brg)	The point where the sagittal and coronal sutures intersect
Euryon (eur)	The most laterally positioned point on the cranial vault (Martin 1956)
Glabella (glb)	The most forwardly projecting point in the mid-sagittal plane at the lower margin of the frontal bone
Lambda (lam)	The point where the two branches of the lambdoidal sutures meet with the sagittal suture (Martin 1956)
Mastoideale (mast)	The most inferior point on the mastoid process
Metopion (met)	The most projecting point on the frontal bone
Opisthocranion (opg)	The most posteriorly projecting point on cranial vault
Porion (por)	The point superior to the external auditory meatus
(paspt)	The point of maximum projection in the midline of the parietal bones
Supraglabellare (spglb)	The point between glabella and the frontal eminence in the mid-sagittal plane of the frontal bone
Sphenion (sph)	The intersection of the sphenofrontal and coronal sutures
Stephanion (stp)	The point of intersection of the inferior temporal line with the coronal suture
Cranial Base Landmarks	
Basion (bas)	Point where anterior margin of the foramen magnum is intersected by the mid-sagital plane (Martin 1956)

Table 2, continued.

Landmark (abbreviation)	**Definition**
(flac)	Medial border of foramen lacerum on cranial base
(fob)	Point of maximum breadth of the foraman magnum
Hormion (hor)	The intersection of the ala of the vomer and sphenoid
Opisthion (ops)	Point where posterior margin of the foramen magnum is intersected by the mid-sagital plane (Martin 1956)
Staphylion (sta)	The most posterior point on the posterior nasal spine
Stenion (ste)	Point on the cranial base at the intersection of the sphenoid and temporal bones near the spine of the sphenoid bone

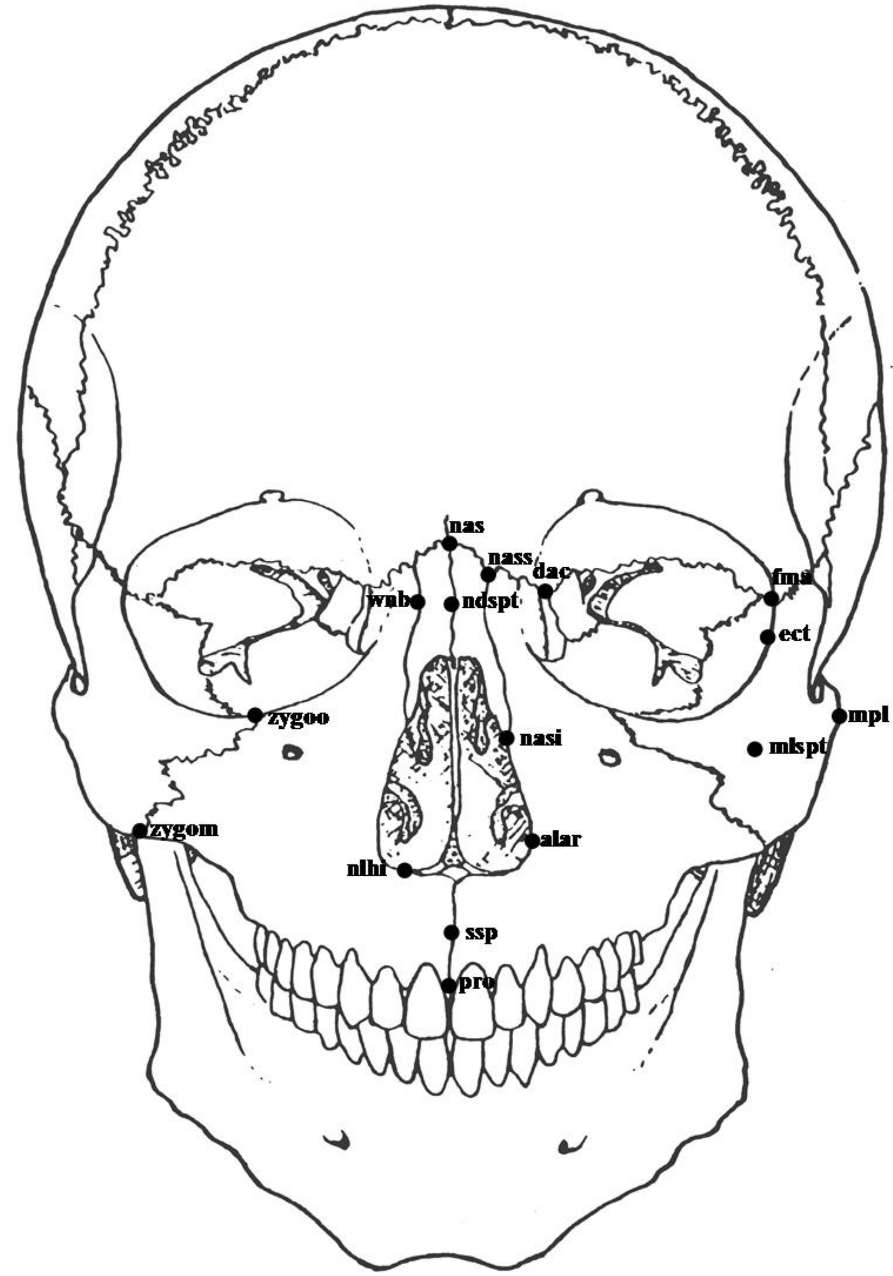

Figure 3. Landmarks from frontal view of skull.

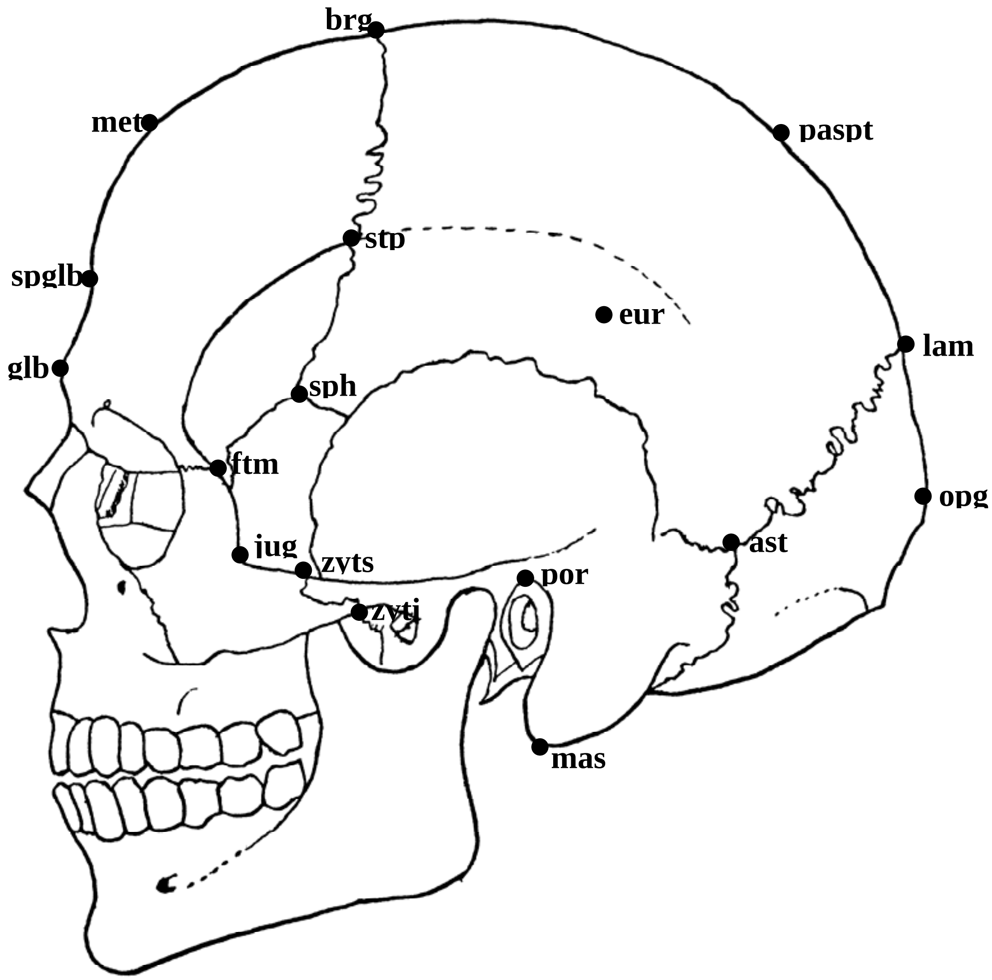

Figure 4. Landmarks from lateral view of skull.

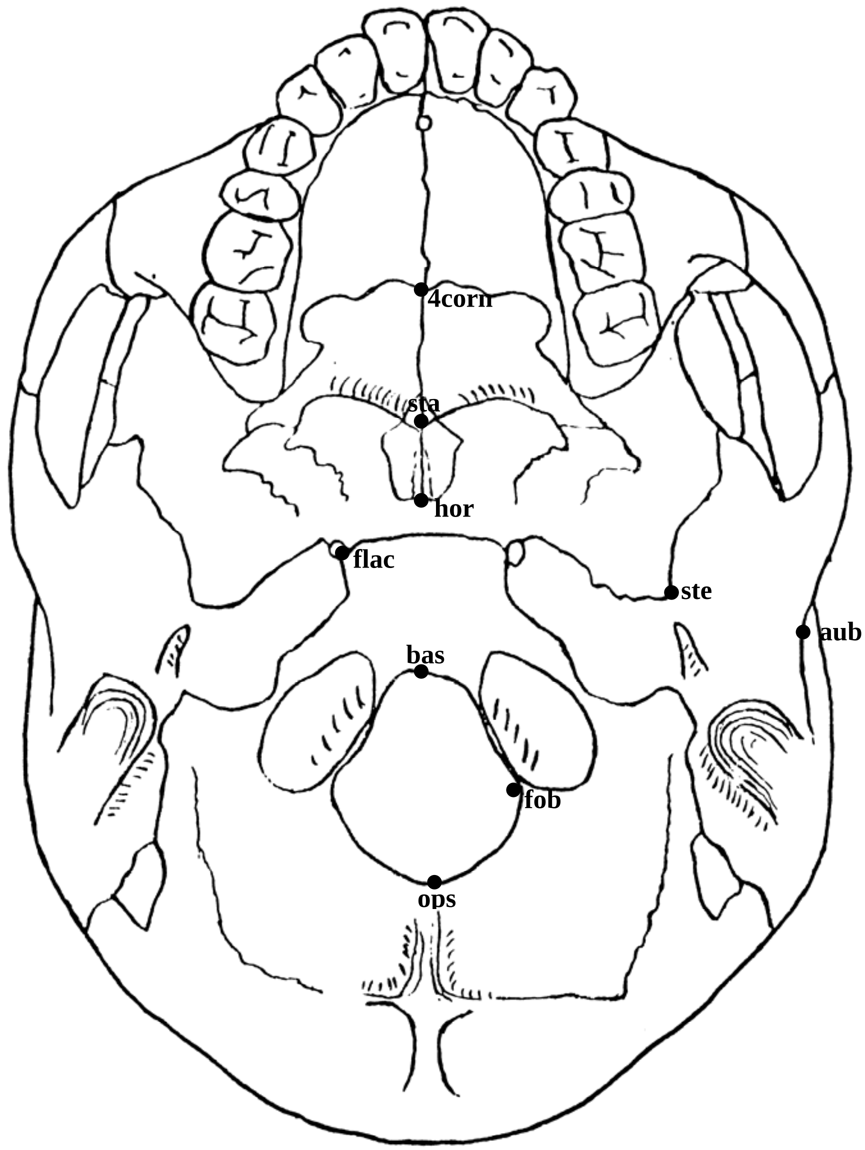

Figure 5. Landmarks from inferior view of skull.

Continuous midsagittal points are also collected by running the digitizer over the surface of the crania. The continuous data points are used to calculate the subtenses of the frontal, parietal, and occipital points. Only crania without missing landmarks were used in the analysis. All of the data was collected by the author between May and August 2006 at the National Museum of Natural History in Lisbon, Portugal.

Geometric Morphometrics

The first step in analysis of coordinate data is to align all of the specimens into a common coordinate system. This is accomplished using Generalized Procrustes least-squares superimposition. Figure 6 shows the landmarks coordinates before and after the Procrustes superimposition. Procrustes superimposition eliminates non-shape related variation produced due to specimen's orientation, size, and rotation (Rohlf and Slice 1990). In order to accomplish this all of the specimens are translated to a common point, scaled to a common size, and rotated to a common orientation. In the case of least-squared Procrustes superimposition the differences between individual specimens and a reference specimen is used as the optimization parameter; with more than two specimens the mean shape is used as the reference configuration. The results of the Procrustes superimposition are residual coordinate values. These values cannot be represented in tradition Euclidean space and instead may be represented in a hemispheric modification of Kendall's spherical shape space (Kendall and Kendall 1980). In the process of performing the Procrustes superimposition degrees of freedom are lost as the variation from translation, scale, and rotation are removed.

Figure 6. Landmark coordinates before and after GLS Procrustes fit.

For 3-dimensional data, the number of landmarks (*p*) will be reduced to 3*p*-7 (Rohlf 1996). The distance between the specimens and the reference shape can be defined as the Procrustes distance. The Procrustes distance is a distance in radians which is calculated as the arcsine of the minimum chord distance between any two shapes in Kendall's space (Adams 1999). The centroid size can also be calculated from the landmark coordinates. Centroid size is the size measure used in geometric morphometrics and is defined as the square root of the summed squared distances of each landmark from the centroid of the landmark configuration (Zelditch et al. 2004).

Due to the fact that GLS-landmarks are located in a non-Euclidean space, it is common to project the landmarks onto a linear tangent space and to use the coordinates of the tangent space to create a new set of shape variables that will have the properties of linear variables. It is not convenient to perform standard multivariate statistical methods in a curved space; therefore the projection of the variables onto the tangent space is necessary. By performing a principal component analysis (PCA) of the Procrustes coordinates the shape variables are projected onto a tangent plane and the principal component scores can be used for further statistical analysis. Moreover, it is possible to determine the types of shape changes associated with each principal component. The calculation of the principal component scores was performed in morphologika[2] 2.5 (O'Higgins and Jones 2006). A table of the principal components, eigenvalues, and the percent of variation explained is seen in Table 3. The first 50 principal component scores explain 86.5% of the variation. When sample sizes are large enough the first 50 principal components are used for further multivariate statistical analyses. For analyses with smaller sample sizes, the first 25 principal components are used, which account for 70% of the variation in the sample. The principal components are mean centered on sex in order to eliminate differences among sexes.

Another way of projecting shapes onto a tangent plane is to use a thin-plate spline transformation. Thin-plate splines transform the coordinates of one specimen onto the coordinates of a second specimen within a linear space and are analogous to deforming a thin metal sheet across two specimens (Bookstein 1991; Thompson 1942). Thin-plate spline deformations can be decomposed into uniform and non-uniform components. For 3-dimensional data there are $3p$-7 non-uniform shape variables and 5 uniform components. The geometrically orthogonal elements of the non-uniform components are referred to as partial warps. The partial warps scores plus the uniform components are a set of shape variables that may be used in standard multivariate analysis. The tps series of programs uses the partial warp scores for statistical analysis (Rohlf 2003).

Table 3. Eigenvalues and percent variation explained for PC1-PC50.

PC	Eigenvalue	% of Total Variance Explained	Cumulative Variance Explained	PC	Eigenvalue	% of Total Variance Explained	Cumulative Variance Explained
PC 1	0.000405	10.3	10.3	PC 26	3.93E-05	1.0	71.3
PC 2	0.00032	8.1	18.4	PC 27	3.75E-05	1.0	72.3
PC 3	0.000233	5.9	24.4	PC 28	3.52E-05	0.9	73.2
PC 4	0.000175	4.5	28.8	PC 29	3.43E-05	0.9	74.1
PC 5	0.000164	4.2	33.0	PC 30	3.41E-05	0.9	74.9
PC 6	0.00014	3.5	36.5	PC 31	3.27E-05	0.8	75.8
PC 7	0.000134	3.4	39.9	PC 32	3.13E-05	0.8	76.6
PC 8	0.000129	3.3	43.2	PC 33	2.99E-05	0.8	77.3
PC 9	9.7E-05	2.5	45.7	PC 34	2.85E-05	0.7	78.0
PC 10	9.61E-05	2.4	48.1	PC 35	2.84E-05	0.7	78.8
PC 11	8.01E-05	2.0	50.1	PC 36	2.57E-05	0.7	79.4
PC 12	7.91E-05	2.0	52.2	PC 37	2.5E-05	0.6	80.1
PC 13	7.26E-05	1.8	54.0	PC 38	2.39E-05	0.6	80.7
PC 14	7.06E-05	1.8	55.8	PC 39	2.34E-05	0.6	81.3
PC 15	6.47E-05	1.6	57.4	PC 40	2.22E-05	0.6	81.8
PC 16	6.4E-05	1.6	59.1	PC 41	2.15E-05	0.5	82.4
PC 17	6.16E-05	1.6	60.6	PC 42	2.08E-05	0.5	82.9
PC 18	5.55E-05	1.4	62.0	PC 43	2E-05	0.5	83.4
PC 19	5.33E-05	1.4	63.4	PC 44	1.87E-05	0.5	83.9
PC 20	5.09E-05	1.3	64.7	PC 45	1.83E-05	0.5	84.3
PC 21	4.92E-05	1.3	65.9	PC 46	1.79E-05	0.5	84.8
PC 22	4.6E-05	1.2	67.1	PC 47	1.74E-05	0.4	85.2
PC 23	4.46E-05	1.1	68.2	PC 48	1.63E-05	0.4	85.6
PC 24	4.22E-05	1.1	69.3	PC 49	1.59E-05	0.4	86.1
PC 25	4.07E-05	1.0	70.3	PC 50	1.57E-05	0.4	86.5

In a recent online forum Slice (2007, personal communication) points out, “You should be aware, or will soon find out, that 3D TPS are not nearly as satisfying as their 2D counterparts. The deformation represented is an interpolation of volumetric changes that cannot be displayed very well as 2D projections.” Therefore, shape changes are also explored using 2-dimensional data. Two-dimensional coordinates were calculated using Morpheus (Slice 2002), by aligning the specimens along the XY plane and then dropping the z-coordinate from the data. tpsReg (Rohlf 2003) performs a multivariate test for a generalized linear model which predicts shape variation from independent variables for 2-dimensional data. The tpsReg program generates plots of the deformation in shape from the reference that corresponds to independent variables. In order to examine the shape changes in 3-dimensions, the Morpheus software was used (Slice 2002). Morpheus calculates the mean shape of different groups and provides a spline plot comparing the shape changes across groups.

Year of Birth

In order to investigate the significance of cranial shape change over time, the sample was divided into 20-year birth cohorts. The first 50 principal components were used to examine the secular changes in the crania. A canonical discriminant function was performed with the birth-year cohorts in order to investigate the relationship between the cohorts and to determine whether a temporal trend exists in the data. A canonical discriminant function seeks to maximize among-group differences by creating linear combinations of quantitative variables. The PROC CANDISC procedure was used in SAS 9.1 (SAS 2002-2004) to perform the analysis. The DISTANCE option in the PROC

CANDISC procedure also provides the Mahalanobis distances among the cohorts. Two separate analyses were performed, one in which the sexes were grouped together and a second in which males and females were grouped separately by cohort.

Cranial shape changes over time are also evaluated using multivariate regression. Year of birth is known for the individuals in the sample, therefore the artificial distinction in grouping the data into birth cohorts is not necessary and year of birth can be used in a multivariate regression. The year of birth is used as the independent variable and the first 50 principal components as the dependent variables. The relationship between centroid size and year of birth is also evaluated using linear regression. The multivariate and linear regressions are performed using PROC REG in SAS 9.1 (SAS 2002-2004).

In order to visualize the differences in cranial shape over time, both 2-dimensional and 3-dimensional shape changes were explored. 2-dimensional thin-plate spline plots show the deformation of the reference shape to early and late shapes calculated using tpsReg (Rohlf 2003) and 3-dimensional spline plots of shape differences were generated using Morpheus (Slice 2002).

Individual Environmental Characteristics

The fact that cranial shape changes over time does not indicate that the function of time is somehow driving morphological changes. Rather, time is used as a proxy for changing environmental or genetic components across the sample. In order to explore the effects of different environmental conditions on the sample, cranial shape changes are evaluated using a variety of variables, including immigrant status, socioeconomic status, and health status.

Migrant Status

In order to examine the effect of immigration status on the cranial shape changes, information of individuals' place of birth was used to examine differences. Place of birth was known for 322 individuals in the sample. The place of birth was classified either as urban resident or rural immigrant. A number of studies have demonstrated the detrimental effects of recent immigration into urban centers in several worldwide populations. Individuals born in Lisbon were classified as urban residents and individuals born outside of Lisbon were classified as rural immigrants. There were a total of 194 rural births and 128 urban births in the sample. No information on the age at immigration is available for the sample. A MANOVA test was used to test for differences between the two groups using PROC REG in SAS 9.1 (SAS 2002-2004). A permutation test using also used to verify the significance of the results using PAST (Hammer et al. 2006). The relationship between centroid size and migrant status is also evaluated using linear regression in SAS 9.1.

Socioeconomic Status

The impact of socioeconomic status on cranial morphology is addressed by using information about individuals' occupations. This data is known for 164 males in the sample. Cardoso (2005) divided the jobs from the sample into manual and non-manual, with manual jobs indicting a lower socioeconomic status and non-manual indicating a higher socioeconomic status. A list of the jobs and their classification is seen in Table 4. Cardoso found a weak association between growth rates in children and their father's occupation. The first 25 principal components were used in this analysis because of smaller sample sizes. A MANOVA test was used to test for differences between the two groups using PROC REG in SAS 9.1 (SAS 2002-2004). A permutation test using also used to verify the significance of the results using PAST (Hammer et al. 2006).The relationship between centroid size and socioeconomic status is also evaluated using linear regression in SAS 9.1.

Health Status

The cause of death is known for 223 individuals from the Lisbon collection. The causes of death were arranged into two categories, deaths caused by infectious disease and deaths caused by cardiovascular disease. Eighty-eight individuals died from infectious diseases, such as tuberculosis, typhus, and cholera and 135 individuals died

Table 4. Classifications of jobs as either non-manual or manual following Cardosa (2005).

Non-manual (n=99)	**Manual (n=65)**
Accountant	Blacksmith
Bank clerk	Cork worker
Civil servant	Factory worker
Pharmacist	Locksmith
Tax collector	Sailor
Professor	Farmer
Engineer	Tailor
Shop owner	Worker
Land owner	Bricklayer

from cardiovascular diseases and diseases of old age, such as heart attacks, arterioscleroses, and senility. The distribution of these types of deaths by year of birth is seen in Figure 7. The figure shows the shift from a high rate of death from infectious diseases before the turn of the 20th century to a high rate of death from cardiovascular diseases and diseases of old age after the turn of the century. A MANOVA test was performed to test for differences between the two groups using the first 30 principal components. The relationship between centroid size and health status is also evaluated using linear regression in SAS 9.1 (SAS 2002-2004).

Demographic Transition Parameters

Mortality

The demographic transition associated with the modern period is defined by two events, the first is a decline in mortality, especially juvenile mortality and the second is a decline in fertility. These two demographic parameters are known from historical records in Portugal. The relationship between mortality and cranial morphology was explored using a number of different parameters. First, census data is available from 1888-1940 for Lisbon. The mortality by age group for Lisbon is given in census records. Using these data, hazard parameters from a 5-parameter Siler model were calculated in R. The hazard rates were determined for three groups: 0-1 years, 1-5 years, and 5-20 years. The number of census years available is somewhat variable; therefore the mean hazard rate was calculated for 10-year periods. The results of the hazard rate analysis are seen in Figure 8. The three hazard rates were used to examine the relationship with changes in cranial

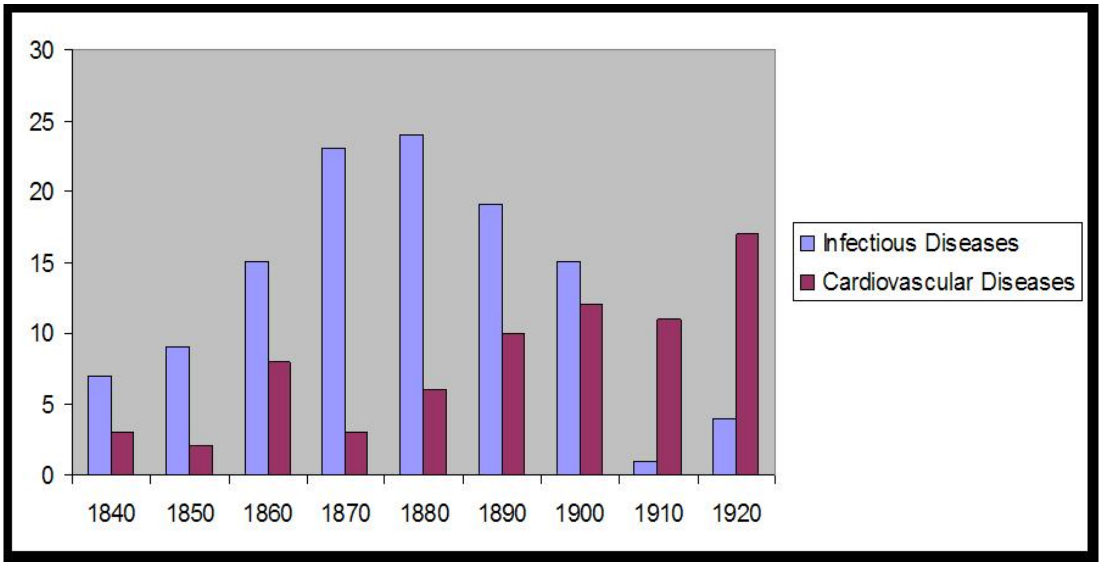

Figure 7. Distribution of cause of death by year of birth for 225 individuals in the Lisbon sample.

morphology. The crude death rate for Portugal was also available from 1800 to 1950 and this variable was also used to examine the relationship between mortality and cranialmorphology changes. A multivariate regression analysis of the four mortality rates with PC1-PC50 and centroid size was performed using PROC REG in SAS 9.1 (2002-2004).

Fertility

Fertility is also known from historical records and was calculated by Livi Bacci (1971). As with most countries experiencing the demographic shift associated with the third transition, fertility declined dramatically during the late 19th and 20th centuries. This fertility decline was most extreme in urban centers and this pattern continues to be observed in Latin American and Southeast Asia, which entered the third transition later than Europe and North America. Fertility has been extensively studied using census

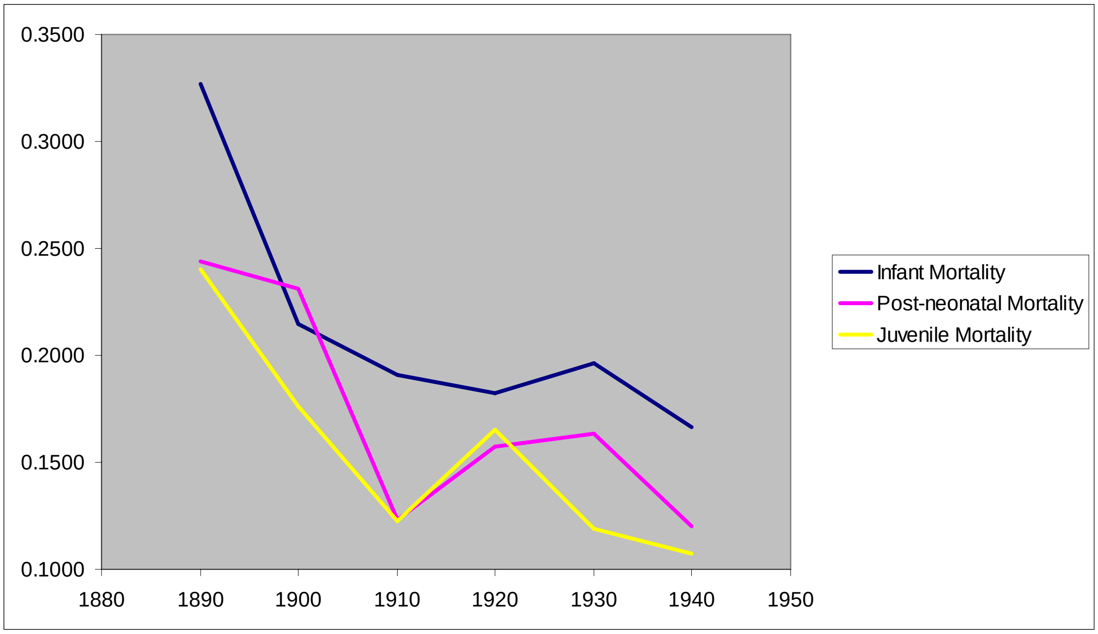

Figure 8. Results from hazard analysis of three age groups: 0-1 years, 1-5 years, and 5-20 years calculated from census records from Lisbon.

records dating back to the 1864 census in Portugal. An index of general fertility is used to examining the relationship between morphological changes and this demographic parameter (Livi Bacci 1971). From 1864-1888 the index of general fertility is calculated on a national basis, subsequently the general fertility index is known for Lisbon. From 1911 to 1940 the general fertility index in Lisbon is reduced by more than half, although the indices from 1890 and 1900 are similar to the general national trends. Therefore, using the national statistics for the earlier cohorts should be a similar approximation to the Lisbon trends. Figure 9 shows a plot of the general fertility index across the sample period. A multivariate regression analysis of fertility with PC1-PC50 and centroid size was performed using PROC REG in SAS 9.1 (2002-2004).

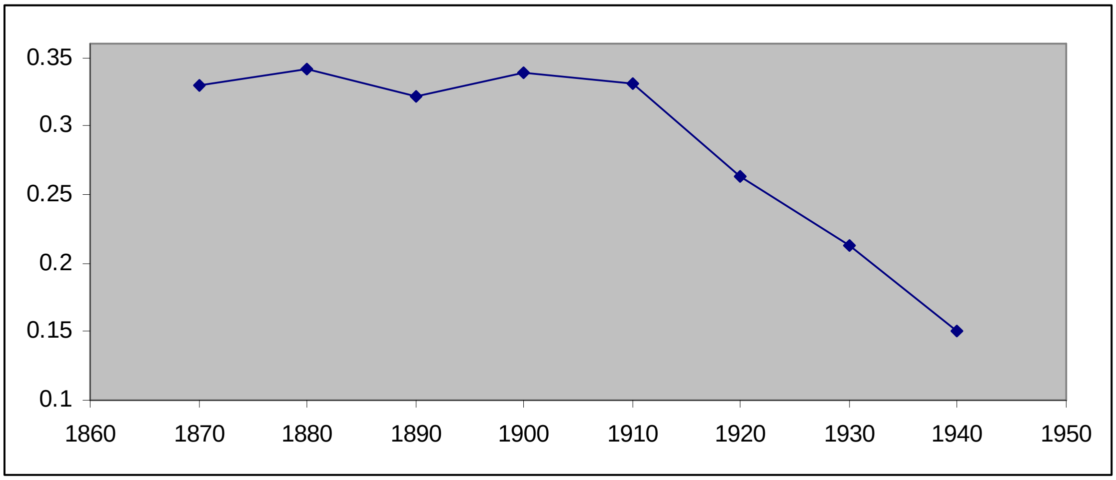

Figure 9. General fertility index by year for Lisbon calculated using census records.

Spatial Structure

The role that spatial patterns has on the morphological variation observed in the sample was investigated. Spatial patterns are likely the result of genetic variation within the country. Although previous genetic studies on the Portuguese have indicated a low rate of heterogeneity, they have also found variability along the North-South axis. Individuals were grouped into the administrative district of birth. The map of the 18 administrative districts within Portugal is seen in Figure 10. Sixteen of the 18 districts were represented in the sample. A canonical discriminant analysis was performed using the PROC CANDISC procedure was used in SAS 9.1 (SAS, 2002-2004) using the first 30 principal components. The Procrustes distance matrix calculated in morphologika was used to compare geographic distance to phenotypic distance. A geographic distance matrix among the districts was constructed using Google maps. A Mantel test was performed to compare the Procrustes and geographic distance matrices using Mantel 3.1

Figure 10. Map of Portugal's 18 administrative districts.

(Relethford 2000).The data were divided into North, Central, and South areas, with the North and Central areas divided by the Douro river and the Central and South areas divided by the Tagus river, this type of regional division has been used in several other genetic studies (Beleza et al. 2006). The latitude and longitude values for the district capitals were used as a continuous location variable. A multivariate regression analysis of location with PC1-PC50 was performed using PROC REG in SAS 9.1 (2002-2004). The relationship between centroid size and latitude and longitude is also evaluated using linear regression. Also, to control for temporal effects partial tests of both location and year of birth were examined. Shape variation among the regions is explored by comparing the mean shape of the Northern Districts with the mean shape from the Southern Districts using Morpheus (Slice 2002).

Regression Models

In order to examine the variables that best explain the variation in the sample, a McHenry's variable selection algorithm was used. The McHenry's algorithm (McHenry 1978) is one of the few methods available for performing variable selection in multiple multivariate regression in NCSS (Hintze 2006). The variables selected are usually the same as when using all possible variable selection; however it is possible to use for multivariate regressions. The first 50 principal components were used in the variable selection routine along with migration status, cause of death, and fertility, year of birth, age, latitude and longitude of birth place. If the environmental and genetic variables are selected first and year of birth adds little explanatory value to the model, then that would indicate that the variation inherent within the year of birth variable is being accounted for using the other variables. The regression model was validated using a holdout sample. The total sample was randomly split into one sample of 301 individuals and one sample of 150 individuals. The large sample was used to construct the regression model and the smaller sample was used to validate the model in order to determine if the regression results are sample specific.

Chapter 5: Results

Year of Birth

A canonical discriminant analysis was performed with the sample divided into 20-year birth cohorts. The first and second canonical correlations are .524 and .476. The first canonical variate represents 38% of the variation and the second canonical variate represents 29% of the variation, therefore the first two canonical variates represent 67% of the among-group variation. The eigenvalues associated with the first two canonical variates are both significant. A plot of the first two canonical variates is seen in Figure 11. This plot demonstrates a temporal trend associated with the first axis, whereby the 19^{th} century cohorts are grouped together on the positive end of the plot and the 20^{th} century cohorts are grouped on the negative end. The multivariate test of group mean differences indicates that the groups are significantly different, with the Wilks' Lambda of 0.323 (p=<0.0001). Table 5 shows the distances between birth cohorts.

With the sexes separated, the first and second canonical correlations are .746 and .550. Figure 12 shows a plot of the first and second canonical values, the first canonical axis explains 35% of the variation and the second canonical axis explains 12% of the variation in the sample. The first axis separates the sexes, while the second axis shows a temporal trend, with the earliest cohorts at the bottom of the plot and the later cohorts at the top of the plot. The temporal trend is clear for the females with the birth cohort increasing in sequential order. The temporal pattern in males is

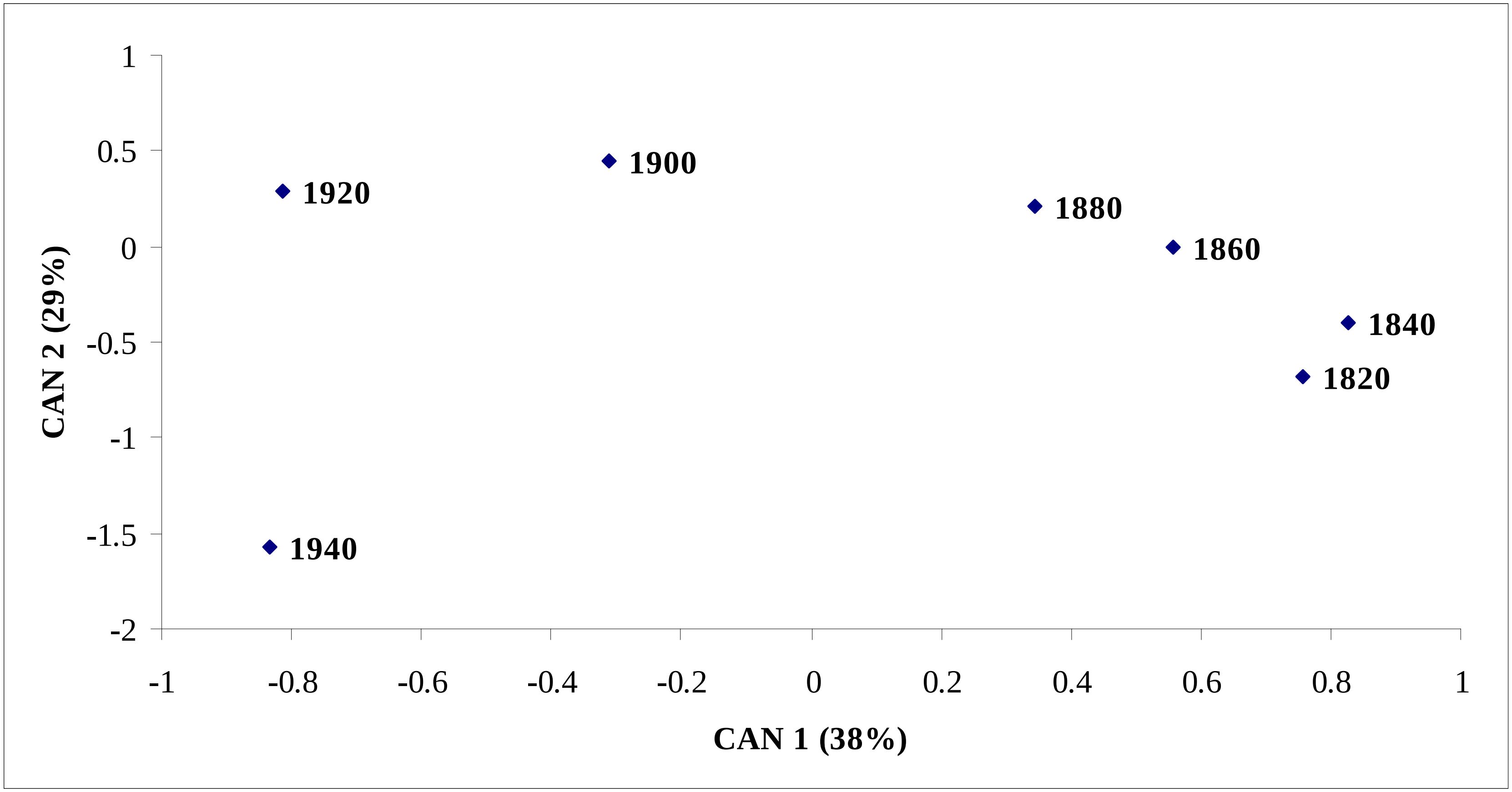

Figure 11. Canonical plot of birth year cohorts.

Table 5. Distance matrix for birth cohorts, significant distances are shown in bold italics.

Cohort	1820	1840	1860	1880	1900	1920	1940
1820	0						
1840	4.99	0					
1860	5.52	***3.51***	0				
1880	5.32	2.24	1.60	0			
1900	6.06	***3.89***	***2.19***	1.33	0		
1920	6.89	***4.15***	***3.01***	***2.18***	1.62	0	
1940	7.92	***6.22***	***5.02***	***4.89***	***4.69***	***4.38***	0

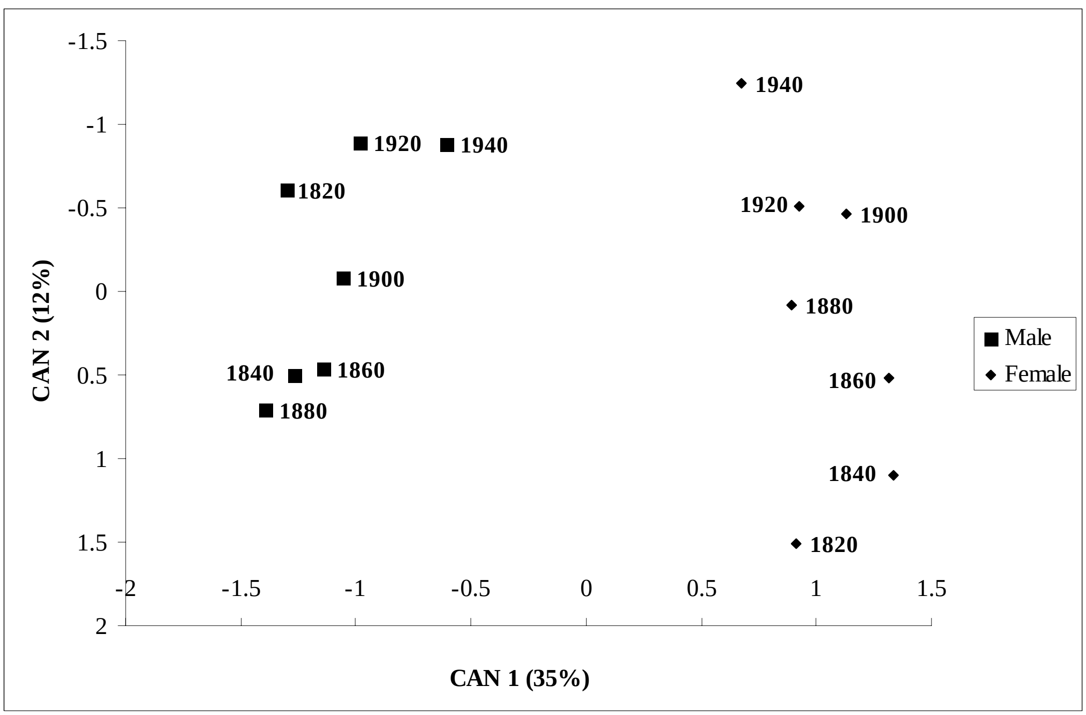

Figure 12. Canonical plot of birth-year cohorts by sex.

not as clear, with the earliest cohort grouping with 20th century groups. Aside from the earliest cohort however the remaining birth cohorts display the temporal trend.

The results of the multivariate regression are given in Table 6. The model of year of birth with the first 60 principal components demonstrates that there is a significant change in cranial morphology over time. A plot of the residuals with year of birth shown in Figure 13 demonstrates that the variability is homoscedastic or distributed randomly across all the years.

The results of the regression analysis examining the relationship between centroid size and year of birth are given in Table 6. There is not a significant change in the centroid size over time in the sample in males or females. Figure 14 shows a plot of centroid size with year of birth for males and females and it is clear that size does not change over time.

Year of birth is significantly associated with PC 4, 7, and 13. The variation along PC 4 is associated with a change in cranial vault and facial height, with cranial vault height increasing with decreasing PC scores. PC 7 is associated with a change in facial prognathism and flexion in the cranial base. PC 13 is associated with changes in the cranial vault width.

The 2-dimensional spline plot shown in Figures 15 and 16 allows the shape differences between the earliest and latest birth cohorts to be compared. The lines in the figures show the magnitude and direction of shape change from the reference shape. The plot of the earliest cohort shows that the face is more retrognathic. In addition, the cranial base is located more superiorly and posteriorly. Lambda moves inferiorly and slightly posteriorly. The plot of the latest cohort in Figure 16 shows

Table 6. Results of regression analysis of PC1-PC50 and centroid size on year of birth.

Multivariate test of significance:					
n=450	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.8154	1.80	50	397	0.0012
Centroid size Females	0.9987	0.29	1	227	0.5883
Centroid size Males	0.9999	0.00	1	217	0.9966

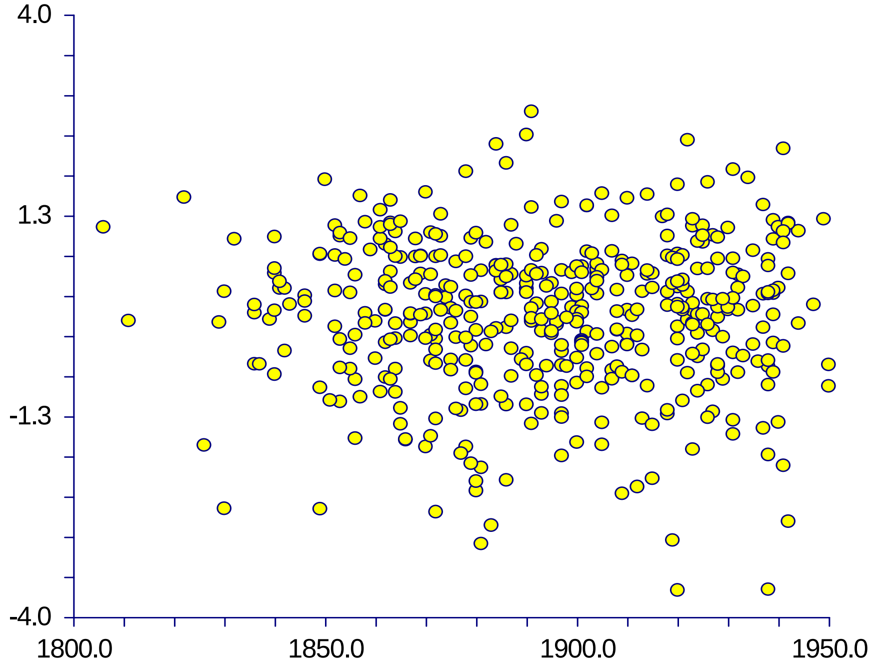

Figure 13. Plot of residuals versus year of birth.

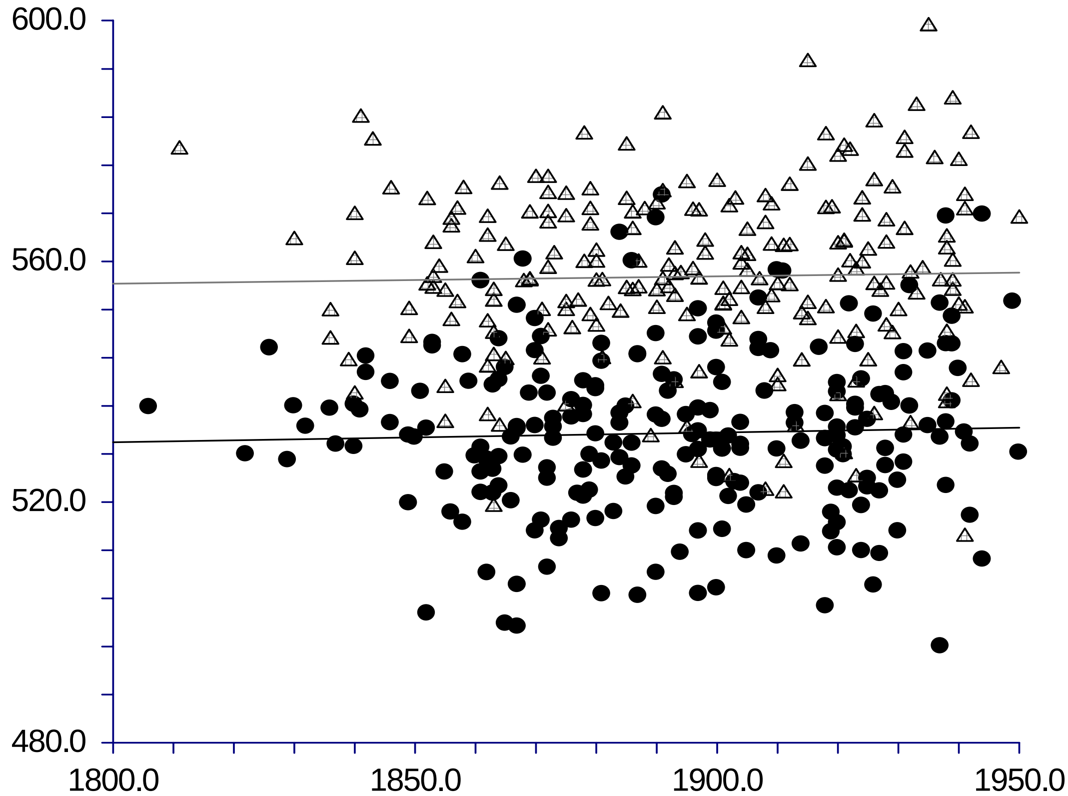

Figure 14. Plot of Centroid Size versus Year of Birth. Males are represented by triangles and females are represented by circles.

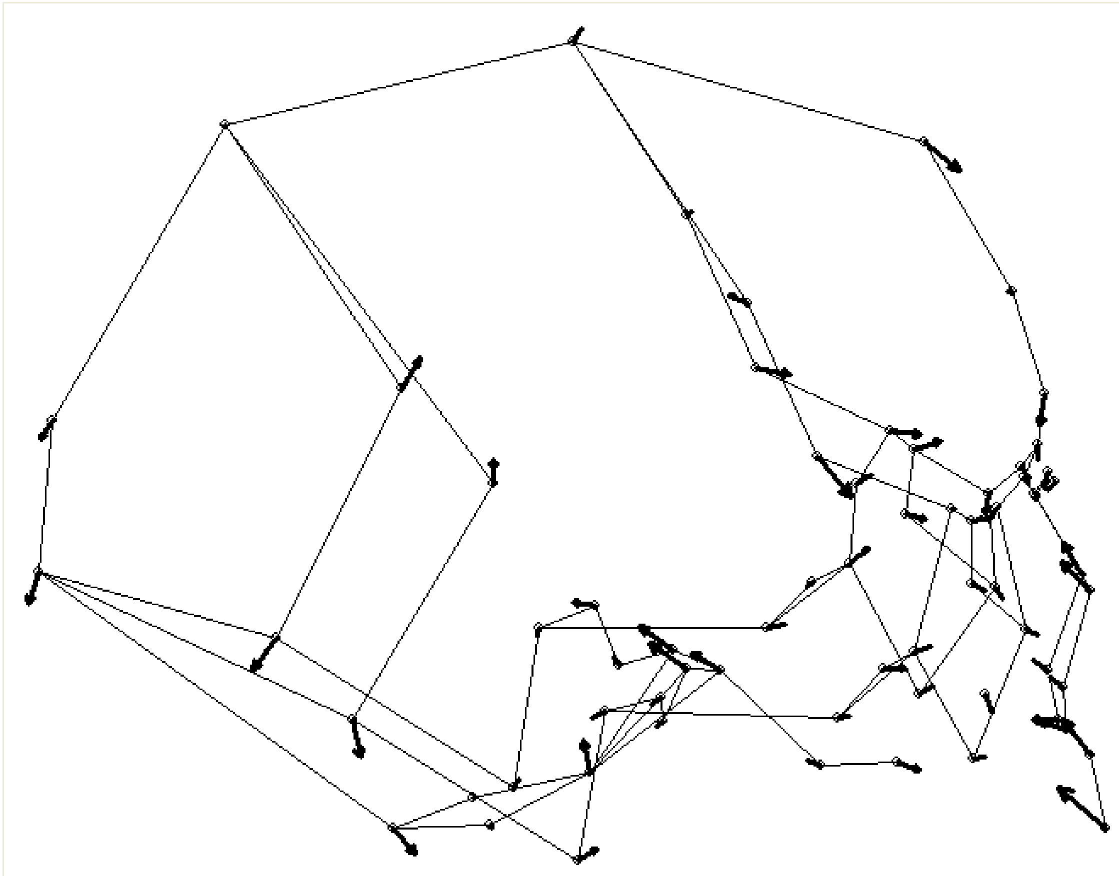

Figure 15. Spline plot of the consensus shape with the vectors showing the direction and magnitude of change towards the earliest birth cohort. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

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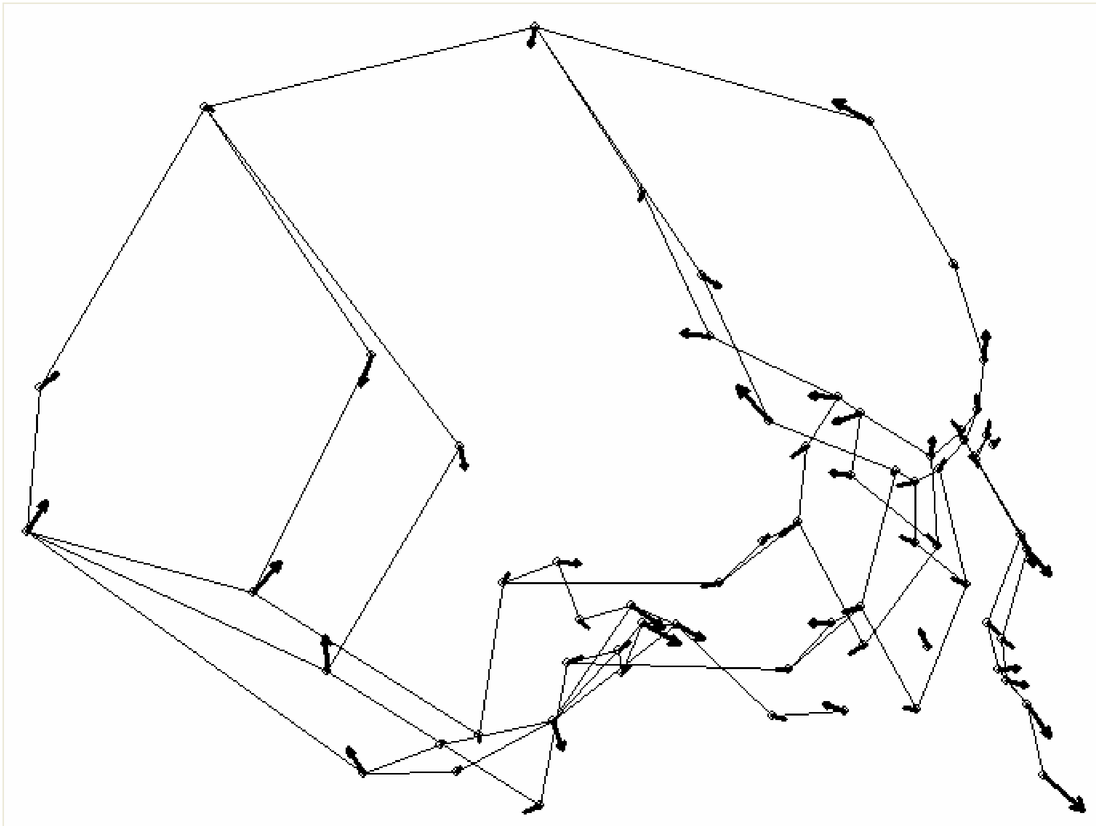

Figure 16. Spline plot of the consensus shape with the vectors showing the direction and magnitude of change towards the latest birth cohort. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

that over time the face becomes more prognathic while the cranial base moves inferiorly and anteriorly.

The shape changes are also visualized using the 3-dimensional coordinates in Figures 17 and 18. The 3-dimensional plots show the mean shape of the earliest cohort with the vectors showing the magnitude and direction of change for the latest cohort. The lines have been exaggerated by a factor of 5 so that the changes are more obvious. A frontal view of the mean shapes seen in Figure 17 shows an increase in the facial height and an overall narrowing of the face and cranial vault. A lateral view shown in Figure 18 shows that there is an increase in facial height over time. The cranial vault height also increases resulting from an inferior movement of basion while bregma remains relatively unchanged.

Individual Environmental Characteristics

Migrant Status

A MANOVA test of the first 50 principal components demonstrates a significant difference between the urban residents and rural immigrants as seen in Table 7. A two group permutation test based on 2000 permutations of the rural and urban groups of the first 5 principal components confirmed the previous results with a p-value of 0.0105. The linear regression of ln(Centroid size) also shows that there is a significant difference in size among the two groups for females, but not for males. Figures 19-22 show the shape changes associated with the immigrant status.

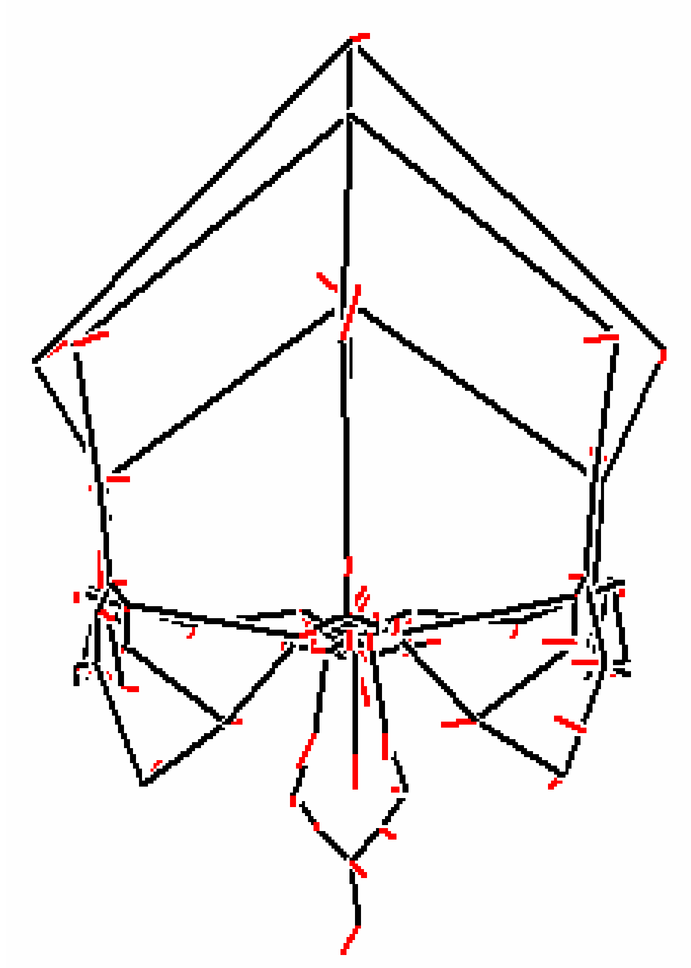

Figure 17. Frontal view of the shape change over time, wireframe of mean shape of the earliest birth cohort with the lines showing the magnitude and direction of change to latest birth cohort mean shape. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

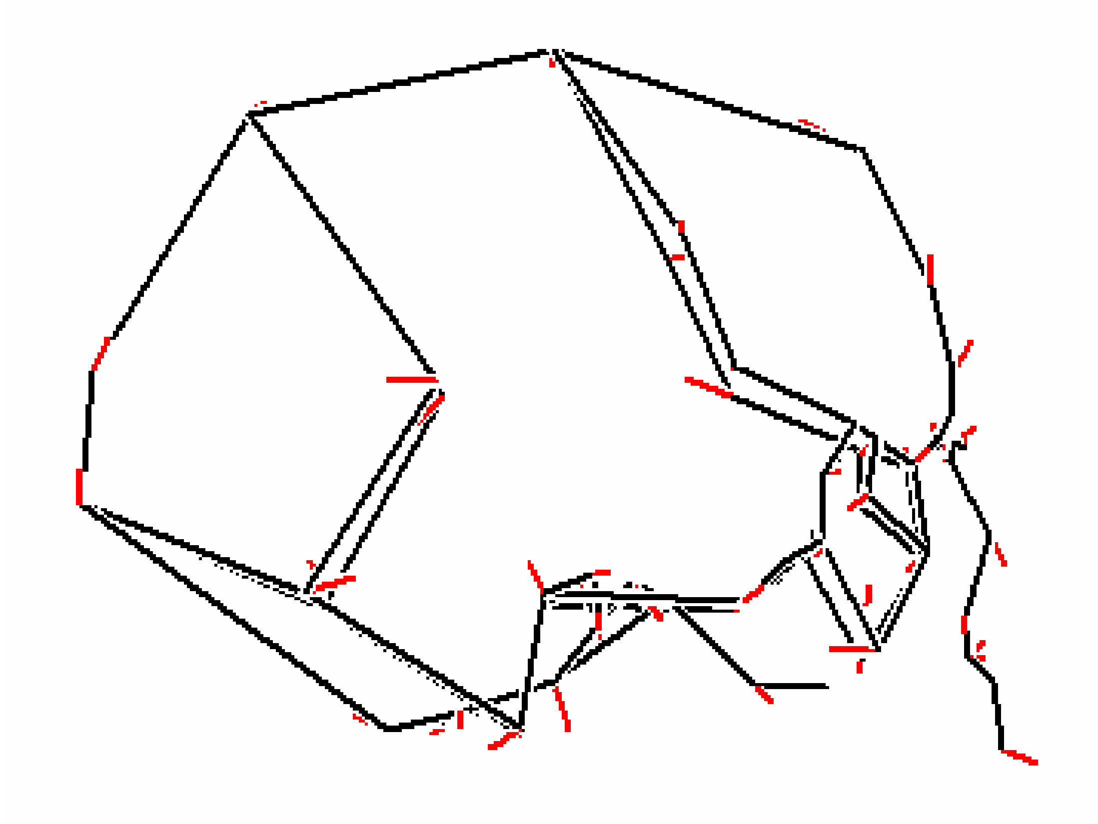

Figure 18. The lateral view of the shape change over time, wireframe shows the mean shape of the earliest birth cohort with the lines showing the magnitude and direction of change to latest birth cohort mean shape. The vectors are exaggerated by a factor of 6 for greater legibility (Bookestein 2000).

Table 7. Results of MANOVA test for migrant status with PC1-PC50 and centroid size

Multivariate test of significance:					
n=314	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.6516	2.81	50	263	<0.0001
Centroid Size Females	0.9734	4.40	1	161	0.0376
Centroid Size Males	0.9959	0.61	1	149	0.4350

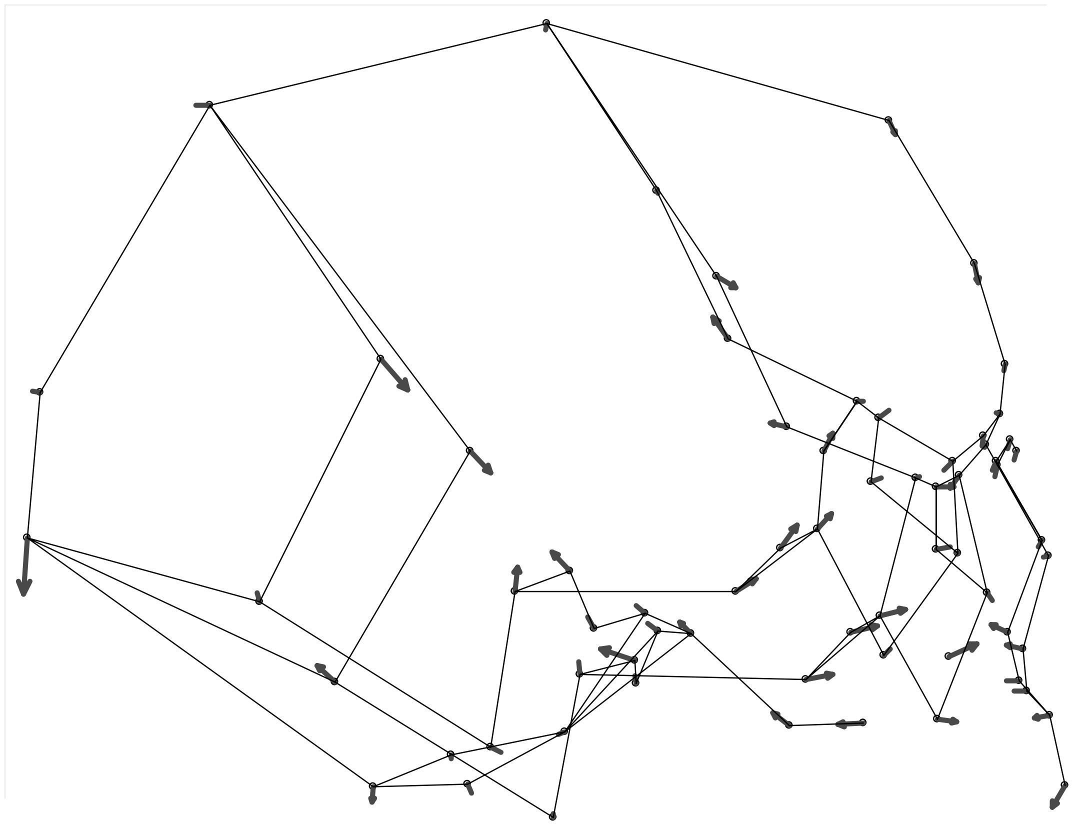

Figure 19. Mean shape across all individuals with the vectors showing direction and magnitude of change for rural births. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

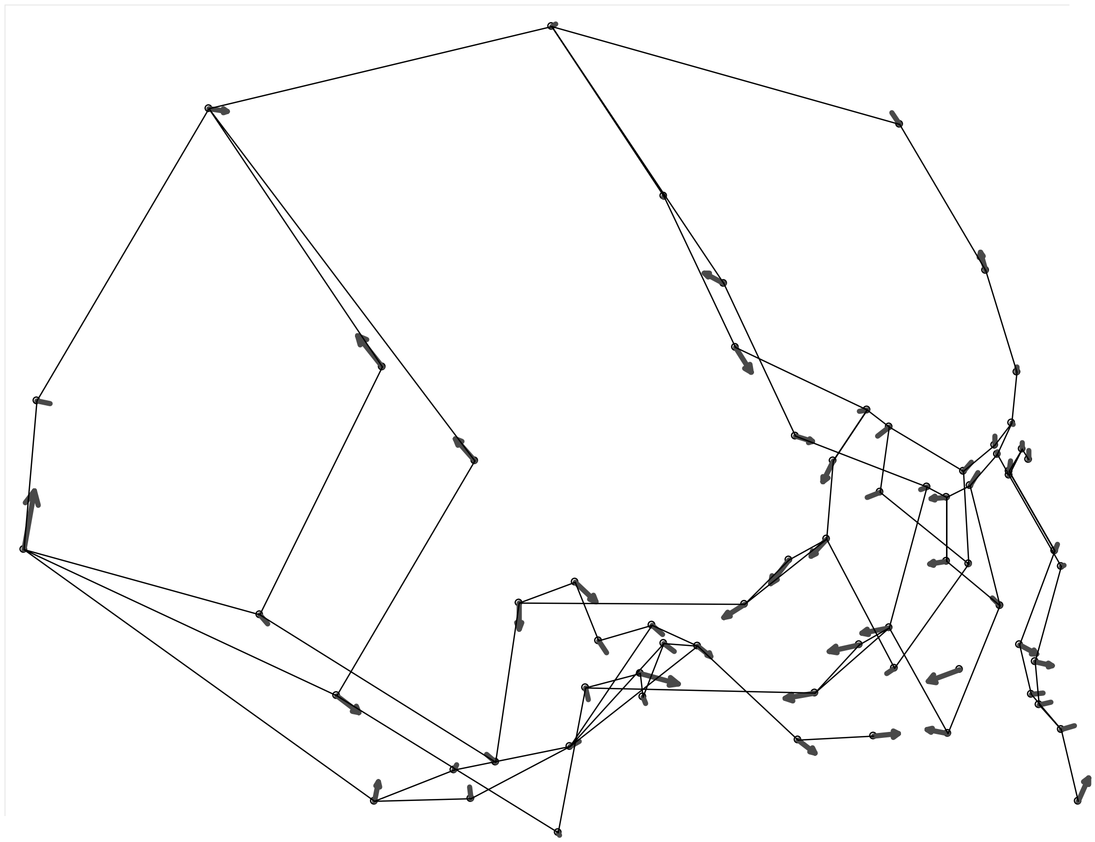

Figure 20. Mean shape across all individuals with the vectors showing direction and magnitude of change for urban births. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

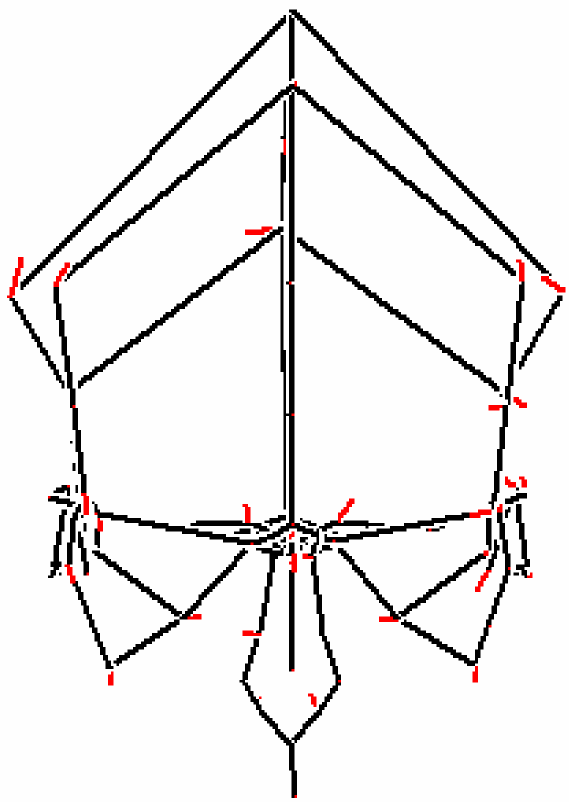

Figure 21. Frontal view with wireframe showing the mean shape of urban births with lines showing the magnitude and direction of change for rural births. The vectors are exaggerated by a factor of 8 for greater legibility (Bookstein 2000).

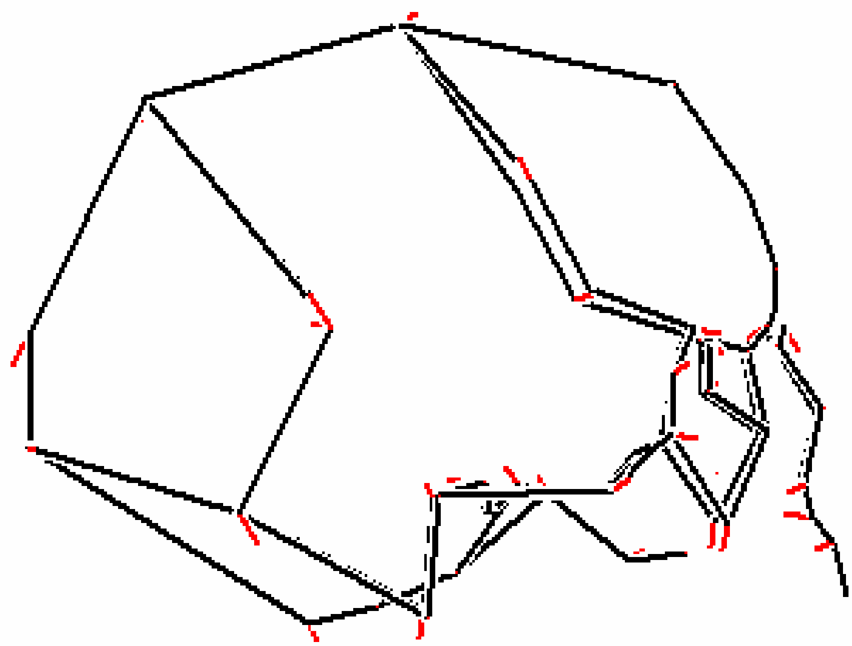

Figure 22. Lateral view with wireframe showing the mean shape of urban births with lines showing the magnitude and direction of change for rural births. The vectors are exaggerated by a factor of 8 for greater legibility (Bookstein 2000).

For rural immigrants the cranial shape becomes more retrognathic with the cranial base more superiorly located and a narrower cranial vault. The pattern of change is similar to that seen in the secular change with urban-born individuals having similar shape changes as later born individuals and rural-born individuals being more similar to individuals born earlier in time, with the exception of cranial vault width which shows an opposite trend. Over time the cranial vault becomes narrower, however the rural group shows a narrower cranial vault in comparison to the urban group.

Socioeconomic Status

Based on the first 25 principal components, there is a significant difference between manual and non-manual workers as seen in Table 8. The Wilks' Lambda value is 0.76 with a p-value of 0.0371. A permutation test of 2000 permutations confirms the significance of the differences (p-value=0.02). Figures 23 and 24 show the shape differences between manual and non-manual workers. Figure 23 shows the change from the mean shape of all individuals to the mean shape of manual workers. There is a general increase in the size of cranial vault, especially in the anterior cranial vault. The cranial base also appears to move superiorly. Figure 24 demonstrates the shape change associated with non-manual workers, where the cranial base moves inferiorly and the anterior cranial vault moves posteriorly.

Table 8. Results of MANOVA test for PC1-PC25 and centroid size with manual versus non-manual jobs.

Multivariate test of significance:					
n=161	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC25	0.7658	1.65	25	135	0.0371
Centroid Size Males	0.9922	1.24	1	159	0.2665

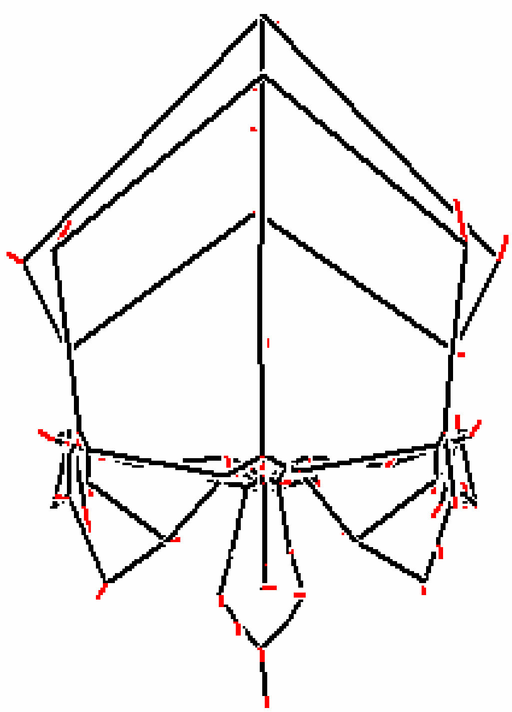

Figure 23 Frontal view of spline plot with wireframe showing mean shape of manual worker and lines showing magnitude and direction of shape change for non-manual workers. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

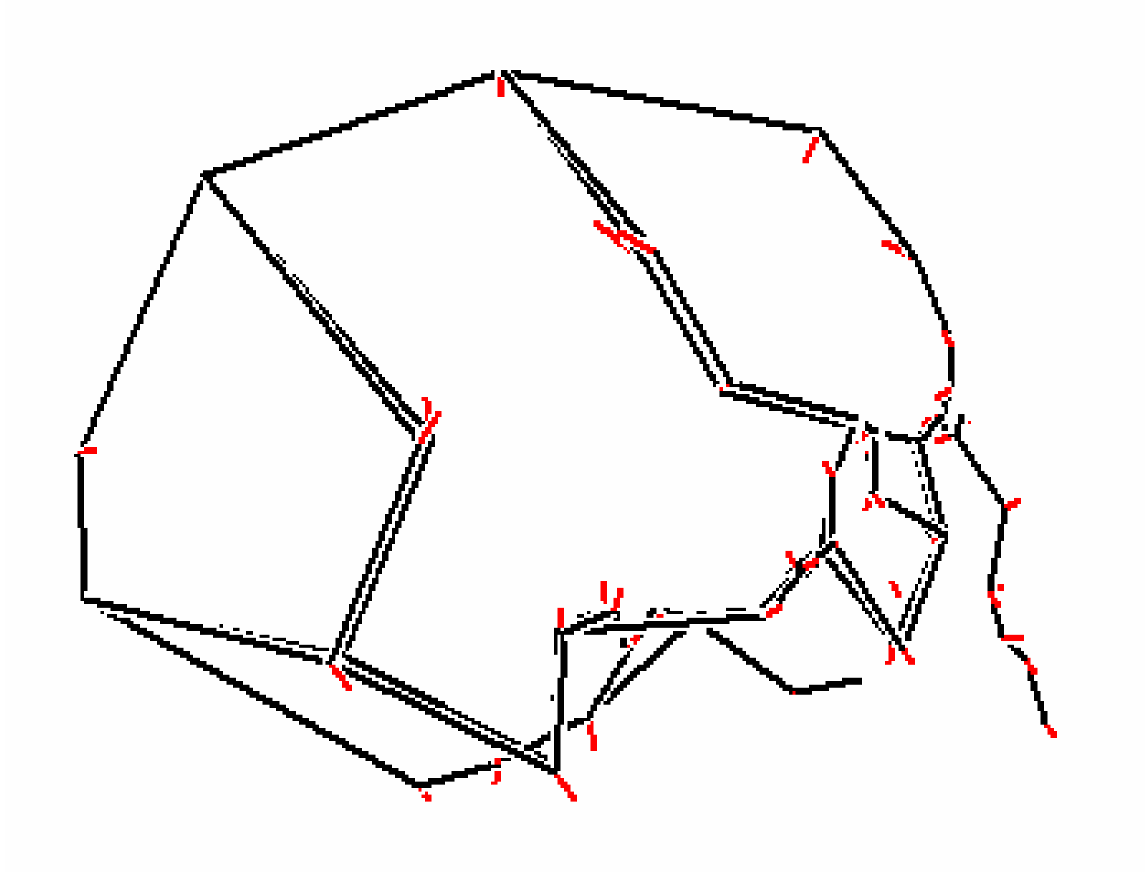

Figure 24. Lateral view of spline plot with wireframe showing mean shape of manual worker and lines showing magnitude and direction of shape change for non-manual workers. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

Cause of Death

The results from the MANOVA test are given in Table 9. There is a significant difference between the two groups and the p-value associated with the test is 0.0021. ln (Centroid) size was significant for females, but not significant for males. The shape changes associated with cause of death are seen in Figures 25-28. The cranial vault is wider in individuals that died from a cardiovascular disease and narrower in individuals that died from an infectious disease. Individuals that died from cardiovascular diseases were more retrognathic, while individuals that died from infectious diseases were more prognathic. This may be the result of the different ages represented in the two groups, with a greater number of older individuals in the cardiovascular groups and more young individuals in the infectious disease group. In addition, lambda is located more anteriorly in individuals that died from cardiovascular disease compared to individuals that died from infectious diseases.

Table 9. Results of multivariate test of significance of cause of death with PC1-PC50 and centroid size.

Multivariate test of significance:					
n=165	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.5652	1.91	50	124	0.0021
Centroid Size Females	0.9542	4.12	1	86	0.0455
Centroid Size Males	0.9998	0.01	1	85	0.9107

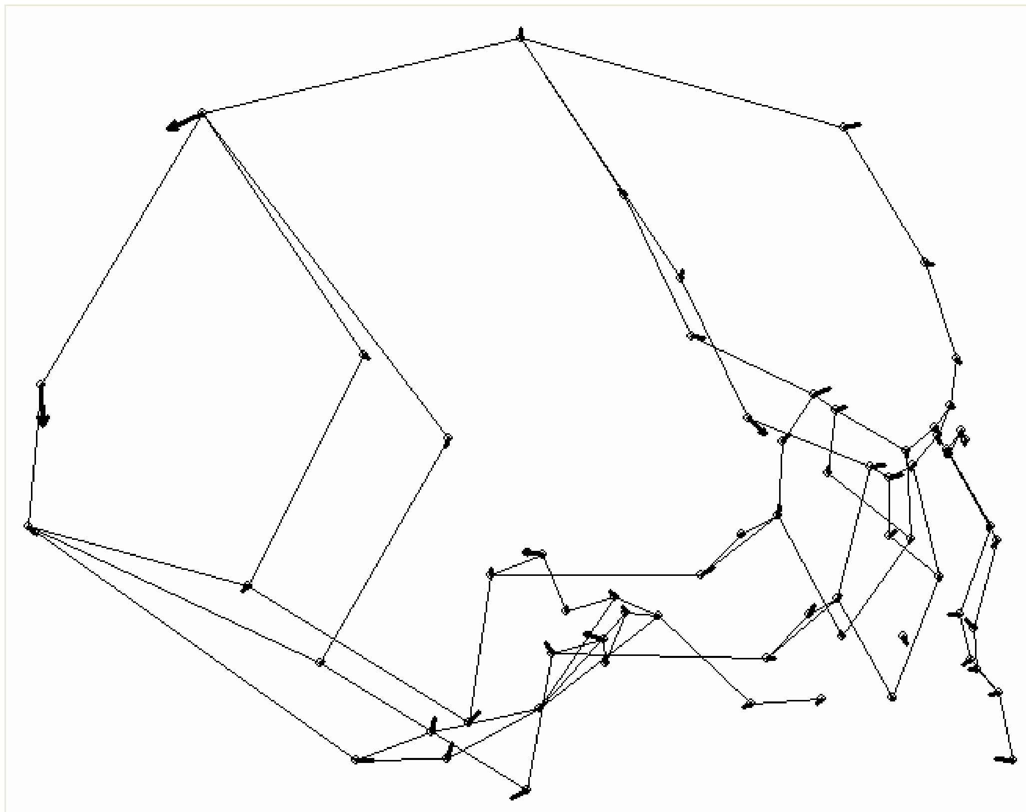

Figure 25. Mean shape with arrows showing the magnitude and direction of change to mean shape for individuals that died from cardiovascular diseases. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

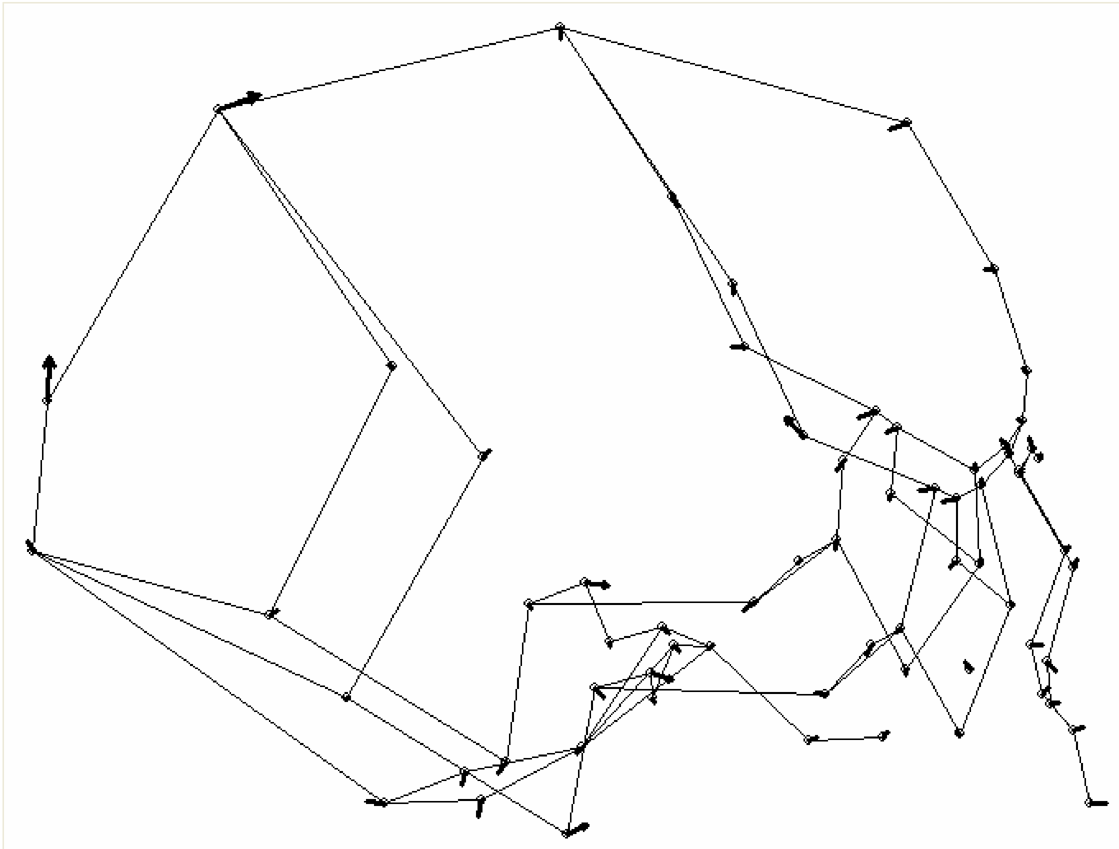

Figure 26. Mean shape with arrows showing the magnitude and direction of change to mean shape for individuals that died from infectious diseases. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

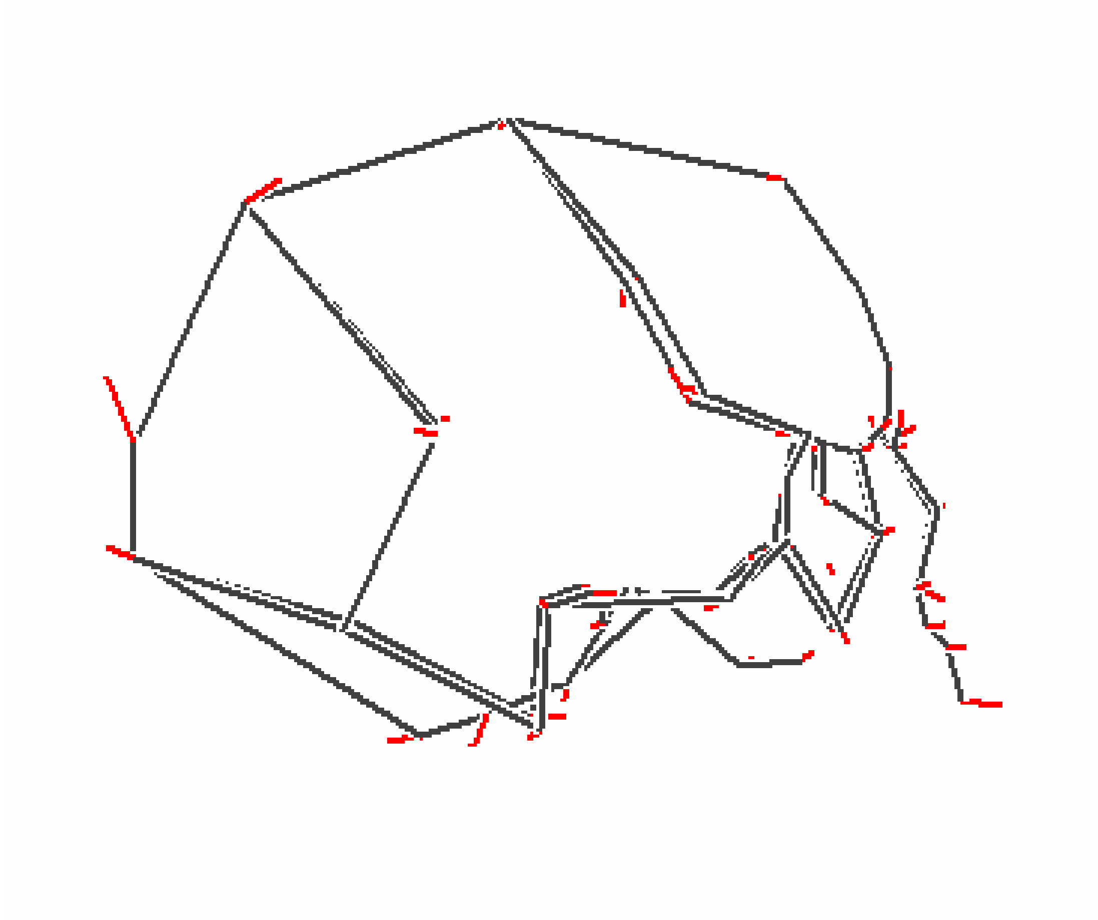

Figure 27. Lateral view of mean shape of individuals that died from cardiovascular disease with red lines showing the direction and magnitude of change to the mean shape of individuals that died from infectious disease. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

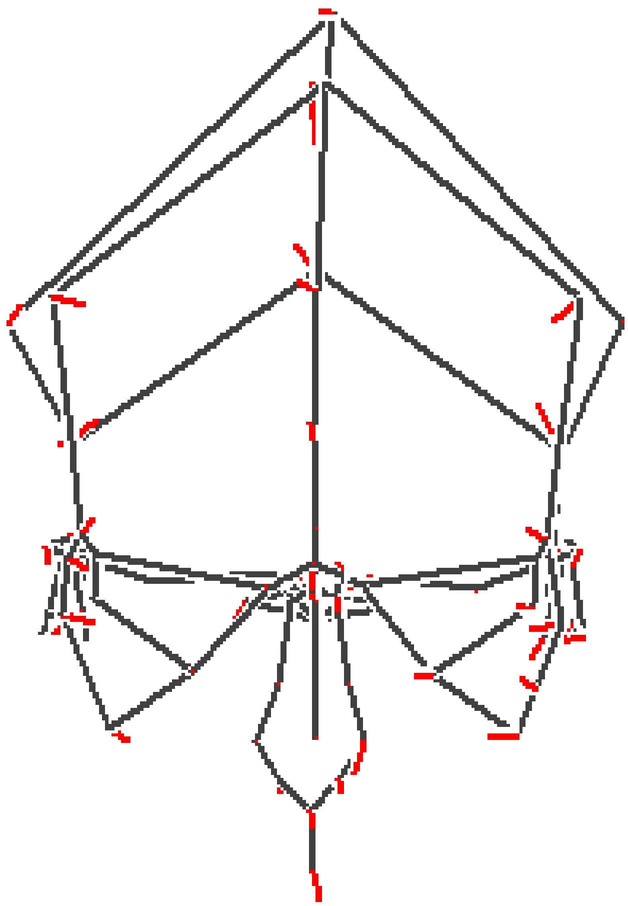

Figure 28 Frontal view of mean shape of individuals that died from cardiovascular disease with red lines showing the direction and magnitude of change to the mean shape of individuals that died from infectious disease. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

Demographic Parameters

Mortality

The relationship between cranial morphology and mortality is explored using a number of different mortality parameters. The results of the regression analysis for all of the mortality parameters are given in Table 10. The only mortality parameter that is significantly associated with changes in cranial morphology is the juvenile hazard rate, after the variation associated with age-at-death is removed. The Wilks lambda for this regression equation is 0.7428, with a corresponding p-value of 0.0431. Interestingly, juvenile mortality has been shown to be the first mortality component to decline during the modern demographic transition. Juvenile hazards are only known from individuals with birth years after 1890, a total of 259 individuals were included in the analysis. The results of the regression analysis for juvenile mortality controlling for age and the relationship between ln(Centroid size) and juvenile mortality are seen in Table 11. ln(Centroid Size) is not significantly associated with the juvenile hazard in either males or females. Figures 29 and 30 show the shape changes associated with a low and high juvenile hazard. The low juvenile hazard rate is associated with a more inferiorly place cranial base, shorter facial height, and lambda is located more anteriorly and superiorly. The high juvenile hazard rate is associated with the cranial base being located more superiorly, a taller facial height, and a longer cranial vault resulting from a posterior movement of lambda.

Table 10. Results of multivariate regression of PC1-PC50 on mortality parameters.

Multivariate test of significance:					
n=259	Wilks' Lambda	Fs	df1	df2	p-value
Infant Hazard Rate	0.7937	1.08	50	208	0.3451
Infant Hazard Rate with age controlled	0.8201	0.91	50	207	0.6495
Postneonatal Hazard Rate	0.8126	0.96	50	208	0.5555
Postneonatal Hazard Rate with age controlled	0.7811	1.16	50	207	0.2356
Juvenile Hazard Rate	0.7652	1.28	50	208	0.1221
Juvenile Hazard Rate with age controlled	0.7428	1.43	50	207	***0.0431***
Crude Death Rate	0.8757	1.13	50	397	0.2669
Crude Death Rate with age controlled	0.8799	1.08	50	396	0.3363

Table 11. Results of multivariate regression of PC1-PC50 and centroid size on juvenile hazard rate controlling for age effects.

Multivariate test of significance:					
n=259	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.7428	1.43	50	207	0.0431
Centroid Size Females	0.9846	0.96	2	123	0.3870
Centroid Size Males	0.9957	0.28	2	130	0.7566

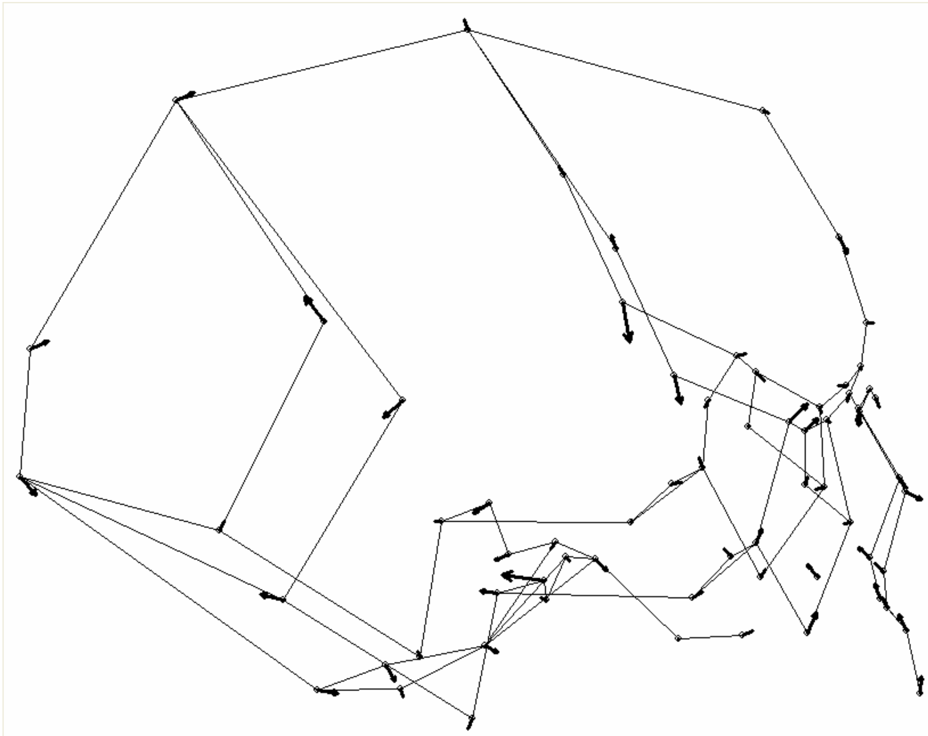

Figure 29. Mean form of sample with arrows showing magnitude and direction of low juvenile hazard rate. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

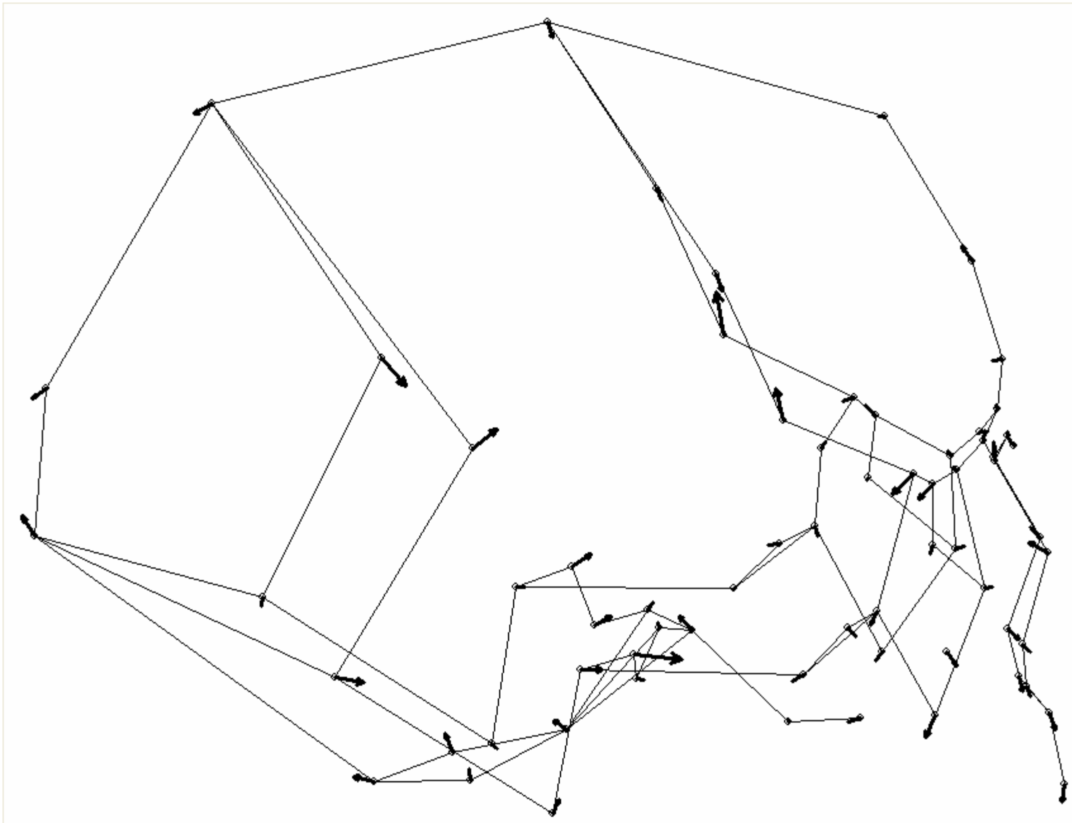

Figure 30. Mean form of sample with arrows showing magnitude and direction of high juvenile hazard rate. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

Fertility

The results from the regression analysis are seen in Table 12. These results demonstrate significant changes associated with changing level of fertility. There is not a significant change in ln(Centroid size) in either males or females associated with different levels of fertility. The cranial shape changes associated with fertility are seen in Figures 31-34. Figure 32 shows changes associated with low fertility. The changes include a more forward projecting face, posterior movement of the cranial base, and anterior movement in the cranial vault. The high fertility group shows a more posteriorly projecting face, the cranial base is positioned more superiorly, and there is some lengthening of the cranial vault at lambda.

Spatial Structure

The effect of latitude and longitude of the individuals' district of birth are examined. The results of the regression analysis are seen in Tables 13 and 14. Table 13 demonstrates the significant effect of latitude on the birth district on cranial morphology; Table 14 also indicates that longitude has a significant effect. Size

Table 12. Results of multivariate regression of PC1-PC50 and centroid size on fertility rate.

Multivariate test of significance					
n=450	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.8408	1.50	50	397	0.0190
Centroid Size Females	0.9980	0.44	1	227	0.5069
Centroid Size Males	0.9953	1.01	1	227	0.3150

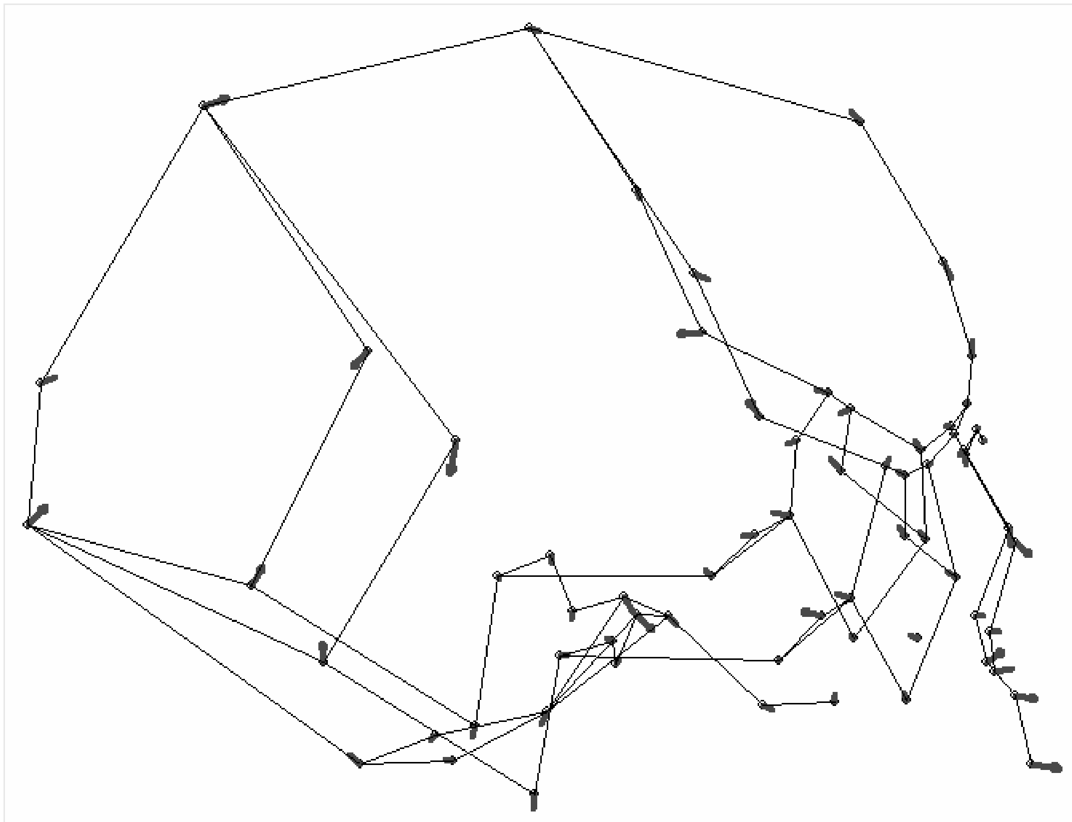

Figure 31. Mean form of sample with arrows showing magnitude and direction of low fertility populations. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

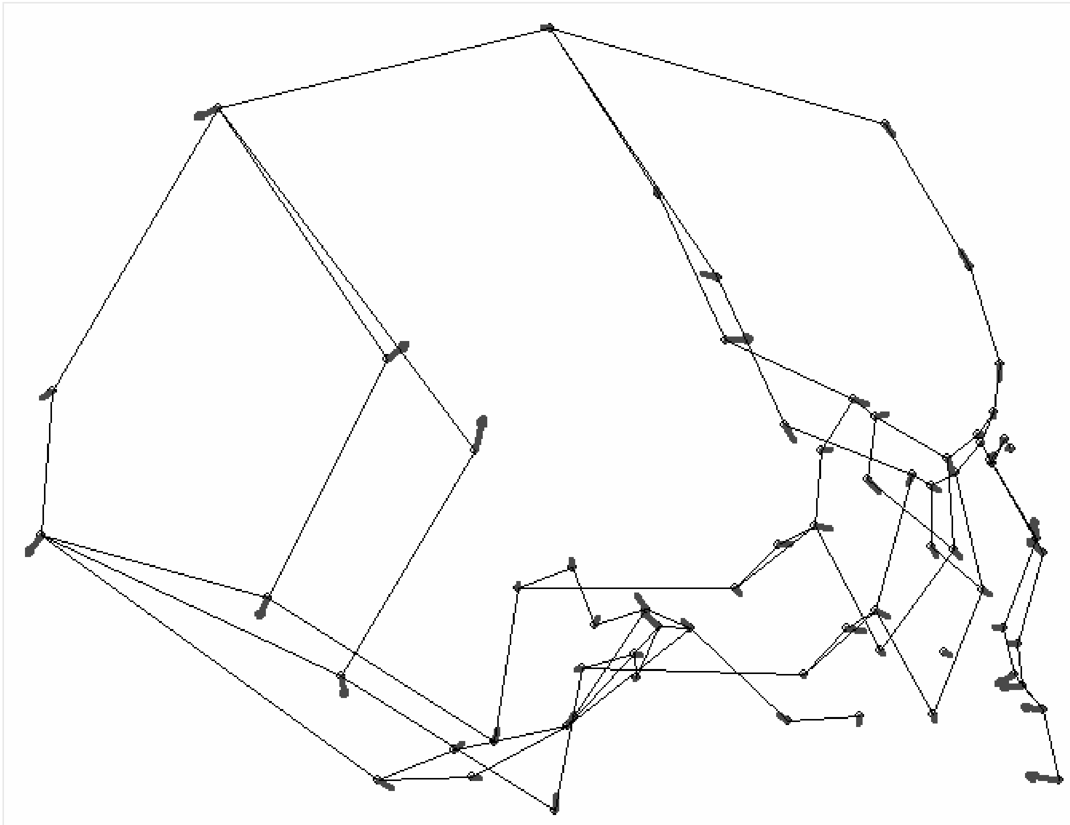

Figure 32. Mean form of sample with arrows showing magnitude and direction of high fertility populations. The vectors are exaggerated by a factor of 10 for greater legibility (Bookstein 2000).

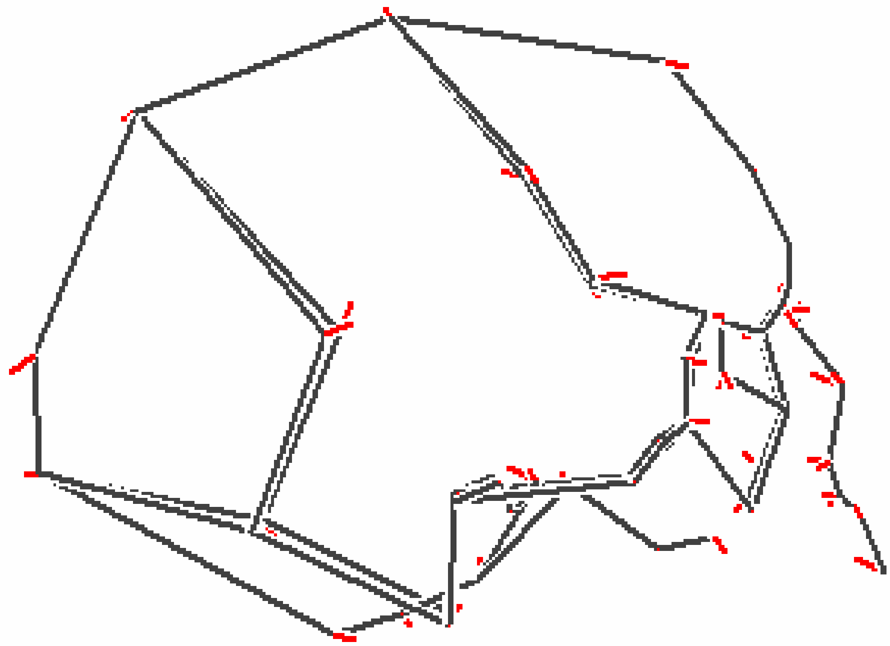

Figure 33. Mean shape of low fertility with lines showing direction and magnitude of change to high fertility group. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

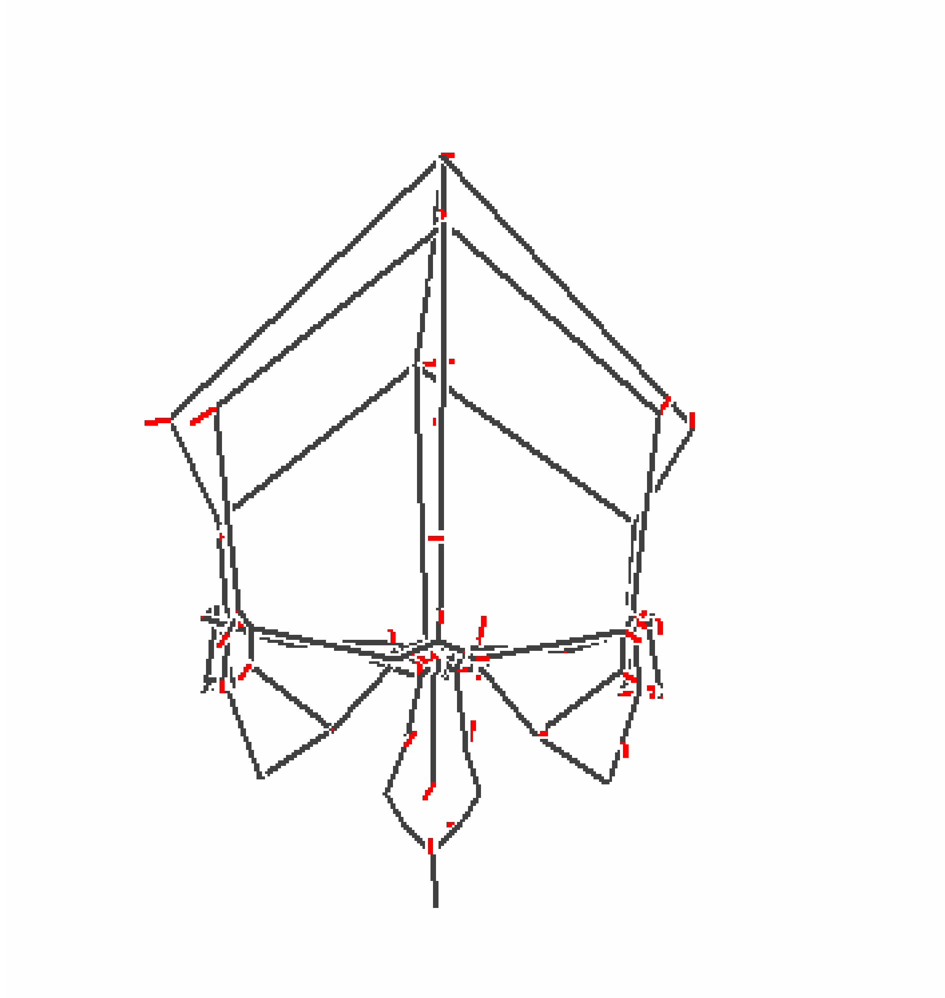

Figure 34. Mean shape of low fertility with lines showing direction and magnitude of change to high fertility group. The vectors are exaggerated by a factor of 6 for greater legibility (Bookstein 2000).

Table 13. Results of multivariate regression of PC1-PC50 and centroid size on latitude.

Multivariate test of significance:					
n=285	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.6611	2.40	50	234	<0.0001
Centroid Size Females	0.9845	2.34	1	149	0.1234
Centroid Size Males	0.9867	1.77	1	132	0.1856

Table 14. Results of multivariate regression of PC1-PC50 and centroid size on longitude.

Multivariate test of significance:					
n=285	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50	0.6407	2.62	50	234	<0.0001
Centroid Size Females	0.9892	1.62	1	149	0.2046
Centroid Size Males	0.999	0.06	1	132	0.8119

does not vary by either latitude or longitude for females or males. Partial tests of year of birth, latitude and longitude show that controlling for any of the two factors; the third factor remains significant, indicating that both temporal and genetic effects significantly affect cranial morphology independently; these results are seen in Table 15. A plot of the first two principal components from the Portuguese districts is seen in Figure 35, the two axes account for 37% of the variation in the sample. The x-axis demonstrates a North-South component with the most Southern districts clustering together on the negative extreme, and the Northern provinces clustering on the

Table 15. Results of multivariate regression of PC1-PC50 on latitude, longitude, and year of birth controlling for each of the other variables.

Multivariate test of significance:					
n=285	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50 = year of birth (yob), latitude, longitude	0.3251	2.11	150	696	<0.0001
Year of birth: Controlling for latitude and longitude	0.7120	1.88	50	232	0.0010
Latitude: Controlling for yob and longitude	0.7133	1.86	50	232	0.0011
Longitude: Controlling for yob and latitude	0.7083	1.91	50	232	0.0007

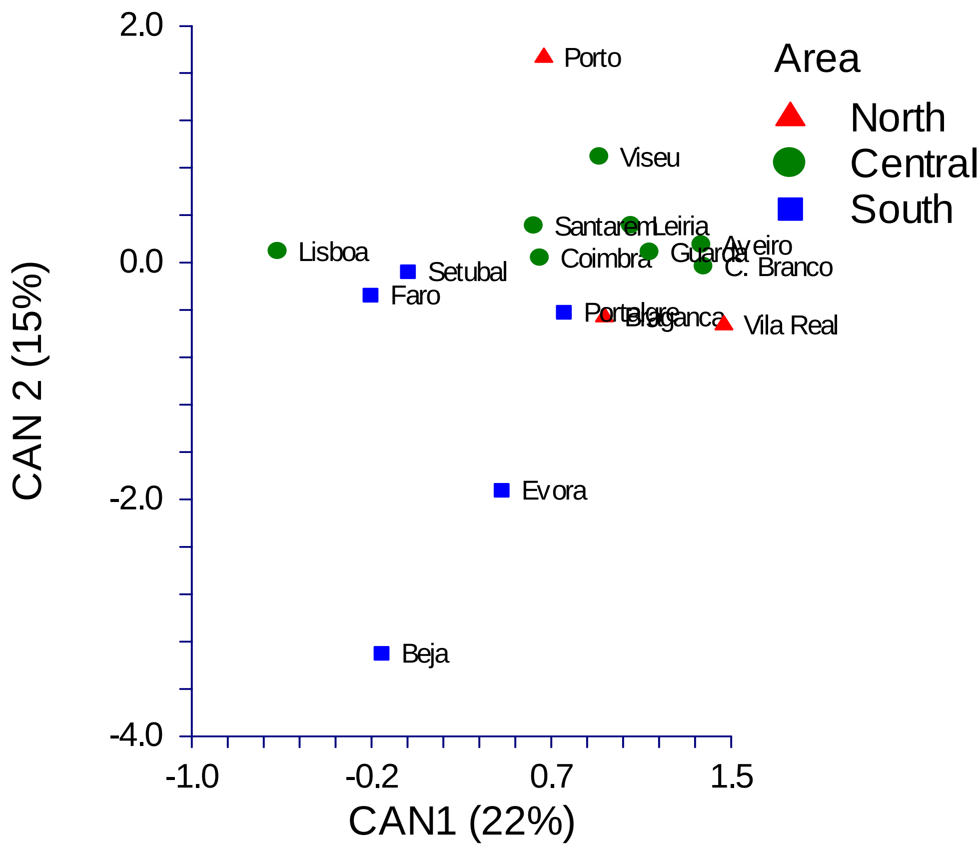

Figure 35. Plot of the first two canonical axes by Portuguese administrative districts.

positive extreme of the axis, with Lisbon grouping with the Southern districts. The second axis also separates North and South, although there is little differentiation between central and northern regions as defined by the Douro River. There does not appear to be any differentiation between coastal and interior provinces based on the first two principal components. Table 16 is a distance matrix among the districts. A second matrix of geographic distances was also constructed and a Mantel test comparing the two matrices found a significant correlation between the Procrustes distance matrix and the geographic distance matrix ($r = 0.3439$, $p = 0.0210$ from 999 randomizations). A plot of the two distance matrices seen in Figure 36 shows that as geographic distance increases, the Procrustes distances also increase. Portugal is a small country with no extreme environments represented, for example, high altitudes or extreme cold. Therefore it seems unlikely that the spatial variation is cause by environmental adaptation. Instead the spatial variation likely reflects the genetic history of the country. The North-South gradient of variation has been documented in previous genetic studies. The cranial morphology changes associated with the spatial differentiation are seen in Figures 37 and 38. The largest component of change is in the maximum frontal breadth, which is located more superiorly in the South. The breadth also appears to become narrower in the Southern districts. The Southern districts also have a slightly more inferiorly projecting cranial base, more facial prognathism, and lambda is located more superiorly. Interestingly, Boldsen (2000) uses frontal breadth as a measure of genetic differentiation in his medieval Danish samples and the region of the crania that shows the most spatial differentiation is the frontal breadth.

Table 16. Mahalanobis Distance Matrix between Administrative Districts in Portugal. Italics indicate a significant distance

	Aveiro	Beja	Braganca	CBranco	Coimbra	Evora	Faro	Guarda	Leiria	Lisboa	Portalgre	Porto	Santarem	Setubal	VilaReal	Viseu
Aveiro	0.00															
Beja	***20.40***	0.00														
Braganca	13.50	***22.89***	0.00													
CBranco	5.48	***19.95***	10.85	0.00												
Coimbra	5.78	***18.23***	7.27	3.38	0.00											
Evora	***13.44***	15.77	13.36	8.76	10.38	0.00										
Faro	9.77	***20.28***	***16.33***	5.24	6.29	6.46	0.00									
Guarda	5.68	***21.02***	12.39	4.74	7.21	9.49	7.29	0.00								
Leiria	5.84	***23.02***	11.97	3.53	4.41	9.66	4.94	5.20	0.00							
Lisboa	***7.30***	***16.75***	***10.63***	***4.88***	3.34	***8.35***	3.28	6.01	4.84	0.00						
Portalgre	13.09	18.89	8.50	8.44	5.44	12.94	13.84	11.27	8.22	7.70	0.00					
Porto	***16.75***	***32.97***	***21.37***	***17.45***	***16.95***	***27.32***	***21.26***	13.80	***19.21***	***15.21***	***22.41***	0.00				
Santarem	6.59	***21.27***	11.58	3.92	4.12	9.56	5.16	5.85	4.45	3.42	7.91	***17.87***	0.00			
Setubal	8.03	***18.00***	***17.85***	8.27	8.34	10.17	7.55	6.38	9.02	5.15	12.97	13.61	6.96	0.00		
VilaReal	12.97	***22.25***	***20.10***	6.93	11.32	13.15	11.75	11.46	12.18	***10.96***	14.77	***21.84***	10.54	14.33	0.00	
Viseu	10.16	***25.21***	13.78	5.09	5.77	***14.95***	8.22	9.70	5.06	5.93	8.31	***16.61***	5.30	10.65	10.07	0.00

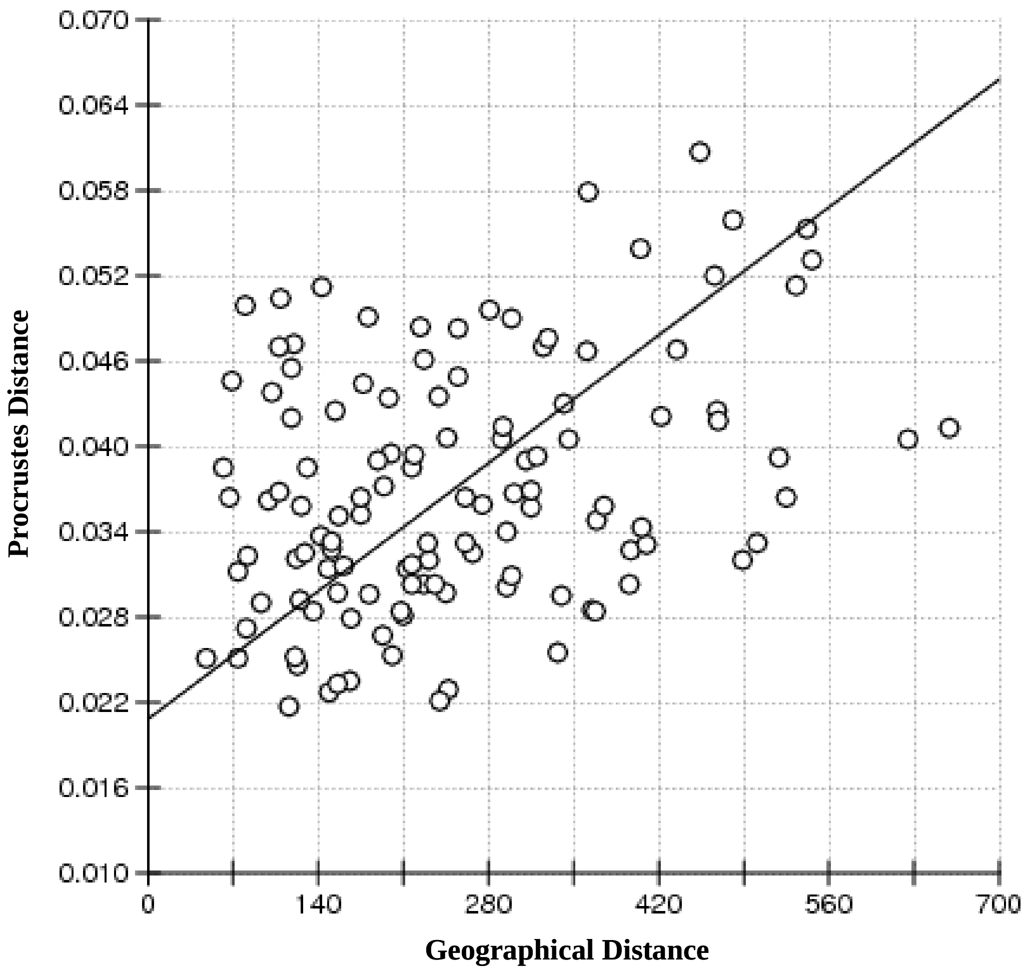

Figure 36. Plot of results of Mantel test showing the correlation between Procrustes distance and geographical distance.

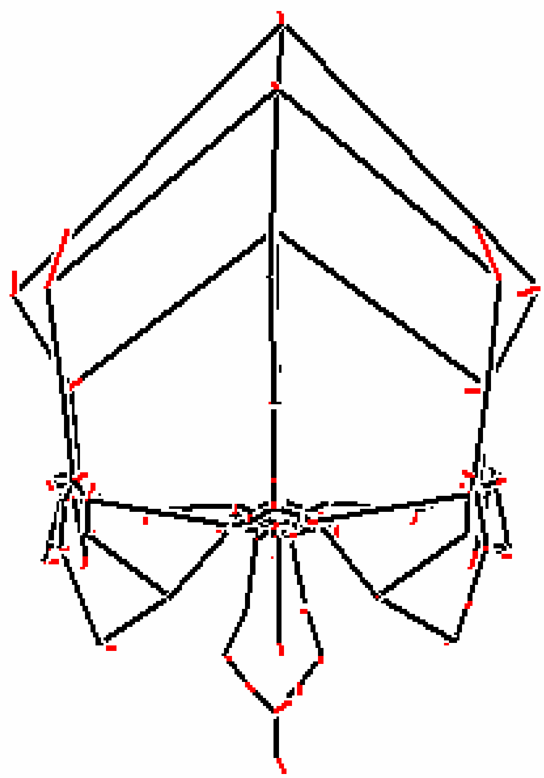

Figure 37. Frontal view of spline plot with wireframe showing mean shape of Northern districts and lines showing magnitude and direction of change of Southern districts. The vectors are exaggerated by a factor of 2 for greater legibility (Bookstein 2000).

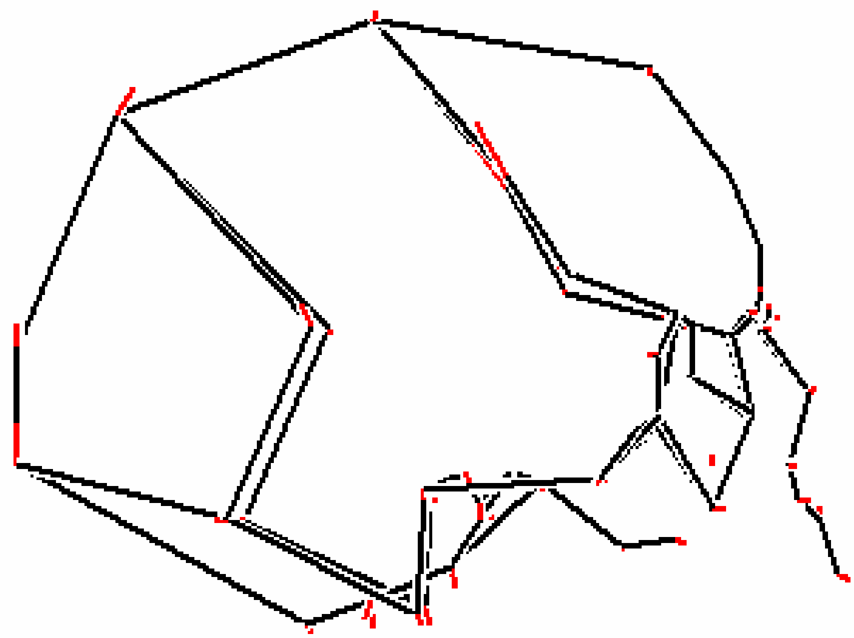

Figure 38. Lateral view of spline plot with wireframe showing mean shape of Northern districts and lines showing magnitude and direction of change of Southern districts. The vectors are exaggerated by a factor of 2 for greater legibility (Bookstein 2000).

Multivariate Test of Population Change

The results of the McHenry's variable selection routine are seen in Table 17. These results show that variables, other than year of birth, explain most of the variation in the sample. The six environmental variables, such as immigrant status, latitude and longitude, and cause of death are more informative for explaining the variation in the sample and adding year of birth does not greatly increase the amount of variation explained. The results from a seven-variable regression model are seen in Table 18. The Wilks' lambda for the model is 0.05, which is very small and suggests that the model explains most of the variation in the sample. In order to validate the model, a holdout sample was used. The total sample was divided into two groups, the larger one was used to construct the regression model and the smaller one was used to validate the model. The results from the model validation are seen in Table 18. The results demonstrate that the model is not sample specific and significance is seen in both the large sample and the holdout sample. In comparison with the year of birth regression results seen in Table 19, which has a corresponding Wilks' Lambda of 0.55, suggesting that the other variables explain more of the variation in the sample.

Table 17. Results of McHenry's variable selection routine using first 50 principal components.

Model Size	Wilks' Lambda	Variables (n=155)
1	0.485879	Age
2	0.293224	Age, Longitude
3	0.179698	Age, Cause of Death, Longitude
4	0.111061	Cause of Death, Longitude, Age, Urban/Rural
5	0.072962	Latitude, Longitude, Cause of Death, Age, Urban/Rural
6	0.049784	Fertility, Latitude, Longitude, Age, Urban/Rural, Cause of Death
7	0.035243	Year of Birth, Latitude, Longitude, Population Density, Age, Urban/Rural, Cause of Death

Table 18. Results of multiple multivariate regression analysis for principal components with environmental variables.

Multivariate test of significance					
	Wilks' Lambda	Fs	df1	df2	p-value
PC1-PC50 n=155	0.0519	1.28	300	599	0.0057
Model Validation					
PC1-PC15: Sample n=101	0.2499	1.42	90	457	0.0119
PC1-PC15: Holdout Sample n=54	0.0589	1.44	90	198	0.0187

Model: PCs = Fertility, Latitude, Longitude, Age, Urban/Rural, Cause of Death

Table 19. Results of multiple multivariate regression analysis for PC1-PC50.

Multivariate test of significance					
n=450	Wilks' Lambda	Fs	Df1	df2	p-value
PC1-PC50	0.5595	1.69	150	1185	<0.0001

Model: PC1-50=Year of Birth, Year of Birth^2, and Age

Chapter 6: Discussion

This project examines the question whether, under modern environmental conditions, a pattern of secular change occurs across populations. The pattern of secular change observed in Portugal is the result of changing environmental conditions and is similar to the changes observed in the U.S. population from a similar time period. Due to the fact that international immigration into Portugal during the study period was very limited, the pattern of change is not the result of immigrants entering the population at different times and settling in different places. The pattern of secular change is also not likely the result of a change in diet as the Portuguese did not experience substantial changes in the diet during the study period. The variation in the population was examined using four types of variables. The first was year of birth in order to compare the Portuguese experience with other populations from a similar time period and undergoing similar changes. The second were those that reflect the effects of individual environmental characteristics. The individual environmental characteristics available from the sample include information on immigrant status, socioeconomic status, and health status. The effect of the modern demographic transition was also explored. The modern demographic transition has occurred in nearly every population over the past 200 years and is characterized by declining mortality levels, followed by declining fertility levels. Finally, the variation in the sample was examined for spatial structure, which parallels the genetic structure of Portugal. The results reveal that the improvements in individuals' environmental conditions and changes in the demographic parameters of the population both have significant effects on cranial morphology. However, the significant secular changes in the population do not eliminate the underlying genetic structure in the Portuguese sample. The cranial morphology is shown to reflect both differences in environmental condition, while still maintaining the genetic relationship within the sample.

Year of Birth

The results from the analysis of the three-dimensional morphometrics with year of birth demonstrate an interesting pattern of change. There is a close parallel with the changes observed in the American population from a similar time period. In morphological analyses of both American Blacks and Whites, the crania of both groups become taller, narrow, and longer over time (Moore-Jansen 1989; Wescott and Jantz 2005). The cranial morphology of the Portuguese from a similar time period also becomes taller and narrow, with an increase in length over time. Additionally, in the Portuguese an overall increase in facial height is seen, this change has also been observed in the U.S. Black population from 1700 to 1975 (Spradley 2006).

As in previous studies, the results from the Portuguese suggest that the secular changes are seen most intensely in the cranial base. The changes in the cranial base have been previously attributed to environmental effects, especially during early growth and development. The cranial base finishes growing by about age 5; therefore, any early environmental insults may be reflected in differential growth in this region. The parallel environmental conditions affecting both the U.S.

and Portugal from this time period must be broadly equivalent. Both countries were becoming more urbanized. Both countries were experiencing changing mortality patterns as deaths during infancy and childhood became less common. Sanitation and water quality improvements reduced the risk of morbidity and mortality from diarrheal diseases which especially effect the growth and development of children. Generally, the secular changes are associated with changes in shape since size does not vary across the sample with year of birth.

One possible explanation is that as health improves the brain grows larger and the cranial vault experiences changes to accommodate this growth. The cranial vault height tends to increase as a result of the increased brain growth. The results suggest that the changes in the cranial base may be better characterized by examining the region anterior to basion. The triangular region from basion to hormion and the medial sides of the foramina lacerum appears to be an area of substantial change. Hormion moves anteriorly and inferiorly and this region is the location of sphenooccipital synchondrosis. It has been suggested that the anterior cranial base may be an important region for documenting changing growth patterns, although the anterior cranial base is defined mainly by internal landmarks. However, the changes associated with the external surface of this region suggest that this area may be important for defining the changes in cranial morphology.

Individual Environmental Characteristics

In studies of secular change, year of birth is used as a proxy for the impact of changing environmental conditions on cranial morphology. There is not some intrinsic property of time that shapes cranial morphology, rather time acts as proxy for documenting changing conditions in populations. The 19th and 20th centuries have been periods when intensive changes have occurred in both the environmental and genetic aspects of human populations. Due to the nature of the Lisbon collection, some of those variables on which time substitutes for can be examined with greater focus.

In order to characterize the changes in cranial morphology over time differences among environmental characteristics were also explored. These variables include immigrant status, socioeconomic status, and health status. In several studies of rural to urban migration, researchers have noted the disadvantage of recent immigrants to urban areas. The impact of urbanization has been a fundamentally defining component of population change in the past two centuries. As the spread of urbanization intensifies in regions outside of Europe and America, the impact of urbanization has been more closely examined. Researchers have asked the question of whether cities are universally bad for people. "Environment, as mediated by such factors as socioeconomic status, is the primary determinant of biological change in growth and development following rural-to-urban migration," (Bogin 1988, 103). Recent immigrants tend to be at an economic disadvantage and to live in the poorest parts of the city. Rural-to-urban migrants have higher rates of disease than urban natives (Baker 1984; Way 1976). Urban migrants have increased risks for the development of tuberculosis, hypertension, and coronary heart disease. Migrants to the city increase their exposure to disease by contacting new groups of people, increased physical stress from fatigue and malnutrition and increasing psychological stress. Several studies have demonstrated that due to the increased stress of migrants they consistently have more health problems than either rural or urban sedentes across geographic areas, including Zulus, Easter Islanders, Iranians, and Senegalese (Benyousseff et al. 1974; Cruz-Coke et al. 1964; Scotch 1963; Stromberg et al. 1974). The results of these studies would suggest that recent immigrants are at a disadvantage compared to urban sedentes. The difference between rural immigrants and urban sedentes was one of the most significant variables of those analyzed in this study. It appears that the urban environment had a significant effect on the cranial morphology of individuals. The most significant difference between the two groups is found in the anterior cranial base, whereby the triangular region defined by basion, hormion, and foramina lacerum is positioned more inferiorly and anteriorly in urban sedentes compared to rural immigrants. Because there is no data available for an individual's age at immigration, the effects of the urban environment cannot be precisely defined, however individual's that were born in Lisbon and died in Lisbon likely were more established in the community and had an advantage over newly arriving rural immigrants. Moreover, the conditions of rural immigrants that would cause them to migrate to an urban center indicate that their living conditions may not have been adequate in their place of birth.

A second variable that was used to characterize individual environmental conditions was socioeconomic status. Socioeconomic status was assessed by dividing male occupations into manual and non-manual jobs. Using the same Lisbon collection, Cardoso (2005) found that there was some differentiation in the growth retardation of children based on their father's occupation. The results from the current analysis indicate that the cranial morphology is significantly different based on socioeconomic status. The differences in morphology appear again to be related to the cranial base. The main differences between the two groups are an inferior movement of basion and opisthion, an increase in facial height, and a narrowing of the cranial vault in non-manual workers, while a superior movement of the anterior cranial vault is seen in manual workers. High socioeconomic status would provide individuals with better access to nutritional resources, better housing conditions, and better access to health care. Socioeconomic status tends to remain somewhat static across generations, so that an individual that is of higher socioeconomic status is more likely to have children that are share the higher status with improved access to resources. Regardless of the conditions of the city at different periods in time, high status individuals would likely have better nutrition and experience lower rates of stress that would detrimentally affect growth and development.

The last environmental variable used to characterize individual experiences is health status. There was a significant difference in the cranial morphology of individuals that died from infectious diseases versus cardiovascular diseases. Individuals that experience greater stress during growth and development may be more susceptible to death from infectious diseases compared to individuals that die from cardiovascular diseases. However, the results from the morphological analysis do not seem to confirm this hypothesis. Individuals that died from infectious diseases tended to have cranial bases that were more inferiorly placed, although the largest differences in morphology were that individuals that died from infectious diseases had longer and narrower cranial vaults and increased facial prognathism. Previous research has suggested that within generations with high infant mortality that corresponding rates of cardiovascular disease also tends to be higher (Barker 2003). Therefore, cardiovascular disease may be indicative of some long-term effect of growth disruption, while death from infectious disease may be the result of random effects. This hypothesis about the differences between infectious diseases versus cardiovascular diseases fits the current sample.

Demographic Parameters

The demographic transition that characterizes modern populations begins with a decline in mortality followed by a period of stabilization and later a period of fertility decline. The crude death rate in Portugal declines beginning in about 1800 and reaches a period of stabilization by 1850. The demographic transition in Portugal is delayed compared with many other parts of Western Europe; however by excluding rural areas of the country the outlook of Lisbon is more similar to other European countries. The first group to experience declines in mortality in the modern demographic transition is juveniles. The last major epidemic to sweep through Lisbon occurred in 1859; thereafter the prevalence of certain types of infectious diseases declined, such as yellow fever and cholera. The containment of major epidemics would have had a substantial effect on young people, although the introduction of tuberculosis in high density areas was also a factor at the turn of the century. In Lisbon beginning in 1874 there was intensified interest in improving basic sanitation networks and major public works projects like the introduction of electric tramways. These types of improved including better sanitation and declining rates of epidemic disease would have been felt most dramatically in juvenile mortality. It is notable that the only mortality parameter that is significantly associated with changes in cranial morphology is the juvenile hazard rate. Juvenile mortality is significantly associated with changes in cranial morphology when age effects are controlled; meaning that when the variation produced by differences in age at death is controlled there is a significant relationship between juvenile mortality and cranial morphology. The differences in cranial morphology between the two groups are that the cranial base is located more inferiorly, the cranial vault is shorter anterior/posteriorly and the facial height is also shorter with a lower juvenile hazard rate. The pattern seen in the cranial base is similar to that seen from the previous results, whereby improvements in environmental conditions are associated with an inferior movement of the cranial base.

The second parameter that defines the modern demographic transition is a reduction in fertility rates. The fertility transition in Portugal occurred in 1916-1920 (Bailey 2006), however in Lisbon, the fertility decline began before 1890 (Bacci 1971). There is a significant relationship between changes in cranial morphology and the general fertility index in Lisbon. The morphological changes associated with fertility are seen in increasing facial prognathism in the low fertility group and an anterior and inferior movement of the external surface of the anterior cranial base as defined by the triangular region from basion to hormion and the foramina lacerum. While basion moves slightly inferiorly the largest component of change is seen around hormion and foramina lacerum, which move inferiorly in the low fertility group. Once again the largest components of cranial change are seen in the cranial base, with the base moving inferiorly, perhaps to accommodate increased brain growth.

Boldsen (2000) found that just preceding the major morphological shifts in humans over the past 10,000 years, there were major shift in mortality patterns. The brachycephalization that occurred at the end of the Middle Ages is associated with an increase in juvenile mortality resulting from major epidemic episodes. The differential survival associated with these demographic shifts appears to be, at least partial, responsible for corresponding changes in cranial morphology. Stella and Koella (1986) found that juvenile mortality is the most important component for determining growth rates across taxa of organisms. Walker et al. (2006) also conclude that mortality rates play a critical role in determining the growth trajectory in populations. Stynder et al. (2007) found that the morphological changes in South Africans in 4,000 B.P. were likely associated with changes in population structure and there were not any significant changes associated with the dietary shifts. The results from the current research support the conclusion that changes in population structure play an important role in driving the secular changes observed in the modern Portuguese.

Spatial Structure

In examining the variation within the Lisbon sample, it is important to point out that the underlying genetic structure as reflected in the spatial structure of the sample is not obscured by the secular changes. Rather the spatial and temporal aspects of the population differentiation can both be observed in the samples. The ability to identify the underlying genetic structure is not lost with the occurrence of secular changes. As Relethford (2004) points out in his discussion of the re-analysis of the Boas data, the secular changes observed in Boas' sample explain a small part of the variation and that the genetic difference among the population are maintained. Analysis of the secular trends in the U.S. also confirm these findings, as Blacks and Whites are apparently responding to the same changes in environmental conditions, but they are not converging on a common form. The underlying genetic structure is still observable, in spite of the secular changes acting on both populations. Different levels of variation may be examined, the variation produced by secular changes may be controlled in order to look at genetic differences and the genetic differences may be controlled to look at plastic changes. "One person's noise may be another person's signal," (Relethford 2004, 381). This holds true for the Lisbon sample, whereby changes in environmental conditions and population structure are clearly shaping cranial morphology, but the underlying spatial and genetic structure of the population can still be seen.

Boas' 1912 study of secular changes has been the most influential research for interpreting short-term changes in human populations. The most important contribution of Boas' study was to demonstrate that racial types, part of the dominant scientific paradigm of his time, were in fact changeable and not fixed ideals. This study resulted in a watershed change within the scientific community where typological thinking was replaced by a modern understanding of the continuous spectrum of human variation. However, the validity of Boas' conclusions has more recently been questioned (Gravlee et al. 2003; Sparks and Jantz 2003). Sparks and

Jantz (2003) point out that the “significant” changes that Boas observed from one generation to the next were often times overstated. The misrepresentation and misinterpretation of Boas’ results has caused major difficulty in more recent studies of modern human variation.

Some researchers have used Boas’ study to claim that because Boas demonstrated that cranial morphology could experience significant change from one generation to the next, cranial morphology does not accurately reflect the genetics of a population and should not be used as a measure of population history, population change, or to look at evolutionary change within humans (Carlson and Van Gerven 1977; Larsen 1997). Aside from the fact it has been demonstrated that Boas overstated the significance of his results, the debate about the plasticity of cranial morphology and its ability to accurately reflect genetic changes in a population hint at the larger debate that has been articulated by studies of developmental phenotypic plasticity. The underlying case of those researchers that state that cranial morphology cannot be used for evolutionary studies of modern humans because it has been demonstrated that the crania is plastic and responds to environmental change, is precisely what West-Erberhard and others are arguing against. That specifically because crania are plastic and do respond to environmental changes and are influenced by differential growth and development are precisely the reasons that they should be used to study evolutionary changes in humans. The variation produced as a result of plasticity, whether plasticity in an individual’s lifetime or plasticity defined across one or two generations, is the variation that evolutionary forces act upon. The variation produced by plastic changes is not something outside of interest of those people interested in the evolutionary process, but rather understanding phenotypic plasticity is fundamental to understanding evolutionary processes. Because of the extreme environmental changes that have been experienced by humans over the past 200 years, studies from this period are especially well-suited to examining the role of phenotypic plasticity in the evolution of humans and their cranial morphology.

The hypotheses outlined by Boas, as well as other researchers explanations for the changes in cranial morphology have been highly influential in defining the ways that anthropologists understand secular changes. According to Boas, one possibility for the short-term secular changes exhibited in the American population is the increased diversity of the population as people moved out of small, isolated communities and into the diverse, urban environments of the U.S. This explanation for change is compatible with expectations that cranial morphology reflects genetic history. Whereby, a change in the mating patterns would, within a short period of time produce changes in the phenotype in response to the genetic differences. A second possibility is of a process of selection related to mortality, or a differential response as individuals moved from rural to urban settings. Differential survival or susceptibility to morbidity and mortality as a result of individuals being introduced into a new environment would theoretically fall under the phenotypic plasticity explanations of population change. Some individuals would be better able to survive and adapt to the new environmental conditions and would exhibit greater fitness, not necessarily at the genetic level, but as a result of differential ontogenetic processes. Therefore, those individuals would survive and reproduce with greater success, which would eventually lead to changes in the genetics of the population.

Alternatively, individuals with some pre-adaptive genetic advantage to the new environmental conditions would differentially be better suited for the new conditions and would be more likely to survive and reproduce. This does not answer the question about whether it is a genetic predisposition that gives certain individual an adaptive advantage to a new environment or whether the new conditions affect the differential ontogenetic processes, which ultimately leads to better adapted individuals. Most likely, it is some combination of the two; however it is clear that studies that pit genetic versus plastic change are not useful in understanding the evolutionary processes that affect humans. Rather, we need to examine the phenotype as the outcome of the complex interaction of genetics and environment, both of which have profound effects on the ways that populations change over time.

Developmental plastic changes are apparently a driving force behind the observed secular changes both in the Portuguese sample and in other modern populations. These plastic changes are best understood and interpreted when they are contextualized within an evolutionary framework. The phenotype is not just a blank genetic structure that responds to the forces from the environment. It is an important force in evolutionary processes and it is what makes the study of the changing cranial morphology interesting from an evolutionary perspective. The genotype and phenotype must be understood together because each is acting and influencing the other.

Research from the modern period and documented collections like the Lisbon collection are important for understanding the processes that drive phenotypic plasticity for several reasons. First, the ability to associate individuals with specific changes in environmental conditions and the existence of historical records on changes in population structure allows for a more thorough understanding of the processes that are affecting the system. Additionally, by using the data collected from documented collection it may be possible to create models of population change which can then be used to understand earlier populations for which extensive documentation does not exist. The many different data sources available to look at individuals from this time period enable a more in-depth level of understanding of identifiable characteristics of populations in transition. Many of the assumptions made in bioarchaeological research can be tested using the known data available from modern collections. By using these known samples a better understanding of the variation present in the archaeological record emerges.

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Vita

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