

MODERN VARIATION AND EVOLUTIONARY CHANGE IN
THE HOMININ EYE ORBIT

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree of Doctor of
Philosophy in the Graduate School of The Ohio State University

By

Michael P. Masters, M.A.

* * * * *

The Ohio State University
2008

Dissertation Committee:

Dr. Jeffrey K. McKee, Advisor

Dr. Scott McGraw

Dr. Paul Sculli

Approved by

Advisor
Graduate Program in Anthropology

ABSTRACT

The principal aim of this research is to investigate variation and change in orbital morphology among past and modern human groups. This involves a comparison of individuals from Western Europe (68), China (57), and South Africa (54); an investigation of how the orbit varies amid the neurocranium and lower face in *Pan*, *Australopithecus africanus*, *Homo erectus*, Archaic *Homo sapiens*, and anatomically modern *Homo sapiens* representing different grades of cranial expansion and reduced facial prognathism; an analysis of more recent change in orbital morphology among Western European groups dating to the Upper Paleolithic; as well as an examination of how temporal and spatial variation in orbital and overall craniofacial form may relate to a recent global trend of reduced visual acuity in humans.

Univariate and multivariate statistical tools are used to test hypotheses relating to these aspects of variation and evolutionary change. Analysis of Variance (ANOVA) reveals many differences in orbital form among modern human groups, with the greatest degree of inter-group variation observed for orbital volume, orbital depth, and shape of the orbital margins, while no difference was found for interorbital breadth, and biorbital breadth. Mahalanobis distance and canonical discriminant function analyses indicate that

despite these differences, the orbits are less variable compared to broader traits of the skull, and that groups with a similar overall craniofacial form can differ markedly in orbital morphology.

The orbits are found to vary in association with a grade shift in cranial size and facial prognathism, becoming more retracted relative to basion, more rectangular, and more frontated in association with increased cranial size and decreased lower facial projection. During the last 30,000 years in Western Europe, the orbits have shifted posteriorly relative to basion, while internal orbital depth has also been reduced. Shape of the orbital margins have changed most throughout this period, becoming taller and narrower, while orbital volume, orbital frontation, and interorbital breadth show no relationship to time.

An examination of eyeball size, orbit size, and spherical equivalent refractive error (SER) reveals a strong relationship between relative size of the eye within the orbit and the incidence/severity of myopia. This widespread neutral human trait is examined in the context of variation in orbital and overall craniofacial form between the sexes, among modern human populations, and throughout hominin evolution. These results indicate that future research into the etiology of juvenile-onset myopia should consider how the eyeball interacts with the matrix of structural and functional components of the skull during ontogenetic and evolutionary morphogenesis.

ACKNOWLEDGMENTS

I would like to extend the utmost thanks to Philippe Menecier for access to the multitude of collections at the Musée de l'Homme in Paris, France, and Véronique Laborde for many facets of accommodation provided while working with these materials. I would also like to acknowledge the generous support of Professor Emma Rabino Massa, Dr. Marilena Girotti and Dr. Rosa Boano at the Museo di Antropologia in Torino, Italy, Professor Edoardo Pardini at the Museo di Storia Naturale dell'Università degli Studi in Firenze, Italy, Dr. Ronald Clark and Nalini Pather at the University of the Witwatersrand in Johannesburg, South Africa, Dr. Francis Thackeray at the Transvaal museum in Pretoria, South Africa, M. Patrick Simon at the Musée d'Anthropologie in Monte Carlo, Monaco, as well as Lyman Jelleman and Dr. Yohannes Haile-Selassie from the Department of Physical Anthropology at the Cleveland Museum of Natural History in Cleveland, Ohio.

I would like to acknowledge The National Academy of Sciences, Sigma Xi, and the Department of Anthropology at The Ohio State University for providing funding to carry out a principal part of this research in Europe and South Africa, and thank Kevin Kuykendall and Stephany Potze for proffering help with transportation, theoretical, methodological, and friendly advice while working in Pretoria and Johannesburg, South Africa.

I am extremely indebted to my family and friends for providing support in numerous forms, and above all to my mother Linda Grimes, and life partner Keira Arps, for offering a tremendous amount of patients, kindness, love, and nouriture while working on this thesis project. I am also grateful for the help of my committee members Dr. Paul Sculli and Dr. Scott McGraw for providing insight, feedback, and guidance throughout this process, and most of all for the help of my advisor Dr. Jeff McKee who has been instrumental in directing my course of study, providing opportunities for fieldwork and research, putting out fires and lighting others where they should be, and for always providing motivation, encouragement, and a smile. Thank you all!

VITA

January 2, 1978.....Born – Orrville, Ohio

1996-2000.....B.A. Anthropology, French
Ohio University, Athens, Ohio

2001-2003.....M.A. Anthropology
The Ohio State University, Columbus, Ohio

2004-present.....Ph.D. Candidate, Anthropology
The Ohio State University, Columbus, Ohio

2000-2001.....Research Assistant
Department of Anthropology,
Ohio University, Athens, Ohio

2002-2003.....Graduate Teaching Assistant
School of Journalism and Communications,
The Ohio State University, Columbus, Ohio

2002-2008.....Graduate Teaching Associate
Department of Anthropology,
The Ohio State University, Columbus, Ohio

2004-2005.....Research Assistant
School of Journalism and Communications,
The Ohio State University, Columbus, Ohio

2005-2006.....Instructor
Department of Sociology and Anthropology,
Ohio Dominican University, Columbus, Ohio

2005-present.....Instructor
School of Social and Behavioral Sciences,
Columbus State Community College,
Columbus, Ohio

PUBLICATIONS

Masters, M.P. (2008) Morphological variation in the eye orbit among modern human populations. *American Journal of Physical Anthropology*. 135(46), 151.

Stewart, J., Tatarek, N., Masters, M.P. (2002) From behind bars: new anthropometric history data from Ohio Penitentiary records. *American Journal of Physical Anthropology*. 117(34), 148.

FIELDS OF STUDY

Major Field: Anthropology

Specializations: Paleoanthropology
Modern Human Craniofacial Variation

TABLE OF CONTENTS

	Page
Abstract	ii
Acknowledgments.....	iv
Vita.....	vi
List of Tables.....	xi
List of Figures.....	xiii
 Chapters:	
1 Introduction.....	1
1.1 Background.....	1
1.2 Evolution of the hominin brain, neurocranium, and face.....	3
1.3 Structural and functional components of the skull.....	4
1.4 Growth of the brain, basicranium, and face.....	6
1.5 Growth of the eye and orbit.....	9
1.6 Modern variation in human orbital morphology.....	14
1.7 Evolution of cranial globularity & facial orthognathism in <i>Homo sapiens</i>	16
1.8 Post-Pleistocene craniofacial change in <i>Homo sapiens</i>	19
1.9 Evolution of the eye, orbit, and reduced visual acuity in humans.....	22
2 Materials and Methods.....	29
2.1 Variables.....	29
2.2 Measurement error.....	34
3 Modern Human Variation in Orbital Morphology.....	38
3.1 Samples.....	38
3.2 Statistical analysis.....	40
3.3 Results of univariate comparisons of orbital variables among groups.....	42
3.3.1 Interorbital breadth and biorbital breadth.....	44
3.3.2 Index of orbital breadth to orbital height.....	44
3.3.3 Orbital height and orbital breadth.....	46
3.3.4 Basion-superior orbit and basion-orbitale.....	47

3.3.5	Orbital depth.....	48
3.3.6	Orbital frontation.....	49
3.3.7	Orbital volume.....	50
3.4	Results of multivariate analyses of orbital morphology among groups.....	52
3.4.1	Canonical discriminant function analysis.....	52
3.4.2	Mahalanobis' distance analysis.....	59
3.5	Population variation in the orbit and broader craniofacial anatomy.....	61
3.5.1	Canonical discriminant function analysis.....	61
3.5.2	Mahalanobis' distance analysis.....	66
3.6	Summary.....	67
4.	Evolutionary Change in The Hominin Orbit.....	70
4.1	Samples.....	70
4.2	Statistical analysis.....	72
4.3	Evolutionary change in the hominin face and cranium.....	74
4.4	Predicted changes in anatomical features of the orbit.....	77
4.4.1	Summary of predictions and null hypotheses.....	79
4.5	Results of regression analyses: orbital variables vs. craniofacial index.....	79
4.6	Summary.....	84
5.	Evolutionary Change in the Hominin Orbit: Upper Paleolithic to Present.....	86
5.1	Samples.....	86
5.2	Variables.....	87
5.3	Statistical analysis.....	88
5.4	Results of regression analyses: orbital variables vs. time (years B.P.).....	89
5.5	Craniofacial shape change in Western Europe: Upper Paleolithic to present.....	97
5.6	Results of regression analyses: orbital variables vs. craniofacial shape.....	102
6.	The Orbit, Eyeball, and Reduced Visual Acuity in Humans.....	107
6.1	Samples and statistical analysis.....	107
6.2	Results of test of no relationship between orbit/eye volume and SER.....	111
6.3	Sex differences in orbit/eye size in relation to SER.....	112
6.4	Sex differences in orbital volume, eyeball volume, and SER.....	115
6.4.1	Orbital volume.....	115
6.4.2	Eyeball volume.....	118
6.4.3	Incidence and severity of myopia.....	121
6.5	Growth of the eye and orbit.....	123

7.	Summary and Conclusion.....	128
	7.1 Modern human variation in orbital morphology.....	129
	7.1.1 Orbital variation in relation to overall craniofacial variability.....	131
	7.2 Long-term evolutionary change in the hominin orbit.....	133
	7.3 Evolutionary change in the hominin orbit: Upper Paleolithic-present.....	136
	7.4 An evolutionary perspective on the etiology of juvenile-onset myopia.....	141
	Bibliography.....	150

LIST OF TABLES

Table	Page
Table 2.1: Cranial and facial measurements used in this study.....	30
Table 2.2: Orbital measurements used in this study.....	30
Table 2.3: Indexes and size variables derived from linear measurements.....	31
Table 2.4: Measurement error for craniofacial variables.....	36
Table 2.5: Measurement error for orbital variables	36
Table 3.1: Samples used in analysis of orbital variation among modern humans.....	40
Table 3.2: Results of one-way ANOVA among African, Asian and European Groups...	43
Table 3.3: Pooled within-groups correlation matrix.....	54
Table 3.4: Eigenvalues and percent of variance explained by each function.....	54
Table 3.5: Wilks' lambda and Chi-square tests for each discriminant function.....	55
Table 3.6: Standardized canonical discriminant function coefficients.....	56
Table 3.7: Structure matrix.....	57
Table 3.8: Functions at group centroids.....	57
Table 3.9: Mahalanobis' distance between-groups comparisons.....	59
Table 3.10: D ² between-groups comparisons (orbital volume excluded)....	60
Table 3.11: Tests of equality of group means.....	62
Table 3.12: Eigenvalues and percent of variance explained by each function.....	63

Table 3.13: Wilks' lambda and Chi-square tests for each discriminant function.....	63
Table 3.14: Standardized canonical discriminant function coefficients.....	64
Table 3.15: Structure matrix.....	65
Table 3.16: Functions at group centroids.....	65
Table 3.17: D ² between-groups comparisons (orbital and other craniofacial traits).....	65
Table 3.18: D ² between-groups comparisons (orbital traits only).....	65
Table 4.1: Samples used in investigation of cranial, lower facial, and orbital change....	72
Table 4.2: Descriptive statistics: relative cranial size and facial length among grades...77	77
Table 4.3: Results of regression analyses, eye orbit variables vs. craniofacial index.....	80
Table 4.4: Regression analysis of orbital variables vs. cranial size & facial projection...80	80
Table 5.1: Samples of human groups from Western Europe: Upper Paleolithic–Present.87	87
Table 5.2: Test of no change in orbital morphology among European temporal groups..89	89
Table 5.3. Regression analyses: orbital variables vs. cranial index, upper facial index..102	102
Table 6.1: Modern human groups used to investigate sex differences in orbit size.....	110
Table 6.2: Intra-group sex differences in size-adjusted orbital volume.....	118
Table 6.3: Sex difference in orbit/eyeball index & percent of orbit filled by the eye....	121

LIST OF FIGURES

Figure	Page
Figure 3.1: Map of regional groups comprising the African, European, and Asian samples.....	39
Figure 3.2: Comparison of interorbital breadth and biorbital breadth (in millimeters)....	44
Figure 3.3: Among-group comparison of orbital index.. ..	45
Figure 3.4: Among-group comparison of orbital height, orbital breadth (mm).....	46
Figure 3.5: Among-group comparison of basion-superior orbit, basion-orbitale (mm)...	48
Figure 3.6: Among-group comparison of orbital depth (mm).....	49
Figure 3.7: Among-group comparison of orbital frontation (angle in degrees).....	50
Figure 3.8: Among-group comparison of orbital volume (in milliliters).....	51
Figure 3.9: Plot of individuals and group centroids along each discriminant axis	58
Figure 3.10: Plot of individuals and group centroids along each discriminant axis.....	66
Figure 4.1: Grade shift in relative cranial size in the hominin lineage.....	76
Figure 4.2: Grade shift in relative facial prognathism in the hominin lineage (mm).....	76
Figure 4.3: Comparison of orbital shape: <i>Australopithecus africanus</i> vs. <i>Homo sapiens</i> .	83
Figure 4.4: Image of Shandingdong (Upper Cave) - From Brown (1998-2005).....	84
Figure 5.1: Comparison of interorbital breadth among European groups.....	90
Figure 5.2: Comparison of orbital frontation among European groups.....	91
Figure 5.3: Comparison of orbital depth among chimpanzees and European groups.....	93

Figure 5.4: Change in orbital breadth through the Upper Paleolithic.....	94
Figure 5.5: Change in orbital height through the Upper Paleolithic.....	95
Figure 5.6: Variation in the orbital index among all temporal groups.....	96
Figure 5.7: Temporal change in facial projection since the Upper Paleolithic.....	98
Figure 5.8: Temporal change in cranial size since the Upper Paleolithic.....	99
Figure 5.9: Change in cranial shape among Western European groups.....	100
Figure 5.10: Change in facial shape among Western European groups.....	100
Figure 5.11: Comparison of long-term and recent variation in facial shape.....	101
Figure 6.1: Plot of spherical equivalent refraction (SER) vs. $(\log_{10})\text{orbit/eyeball}$	111
Figure 6.2: Plot of SER vs. index of $(\log_{10})\text{orbit/eyeball}$ volume for males.....	113
Figure 6.3: Plot of SER vs. index of $(\log_{10})\text{orbit/eyeball}$ volume for females.....	113
Figure 6.4: Comparison of sex differences in absolute orbital volume in Chinese adults	116
Figure 6.5: Intra-group sex differences in size-adjusted orbital volume.....	117
Figure 6.6: Comparison of absolute eyeball volume between male and female Chinese adults.....	119
Figure 6.7: Comparison of relative eyeball volume between male & female Chinese adults.....	120
Figure 6.8: Comparison of orbit/eyeball volume between male and female Chinese adults.....	121
Figure 6.9: Comparison of standard error of refraction between male and female Chinese adults.....	122
Figure 6.10: Comparison of eye orbit and cranial growth in African and Japanese samples	124

CHAPTER 1

INTRODUCTION

1.1 Background

Through years of travel and research, Charles Darwin was able to provide a broad account of how species adapt and change over time. Despite this invaluable contribution, the technology of his time could not provide the tools necessary to answer questions relating to the mechanisms of inheritance or the way in which complex structures could arise through the process of evolution. “To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree” (Darwin, 1859 pg. 227).

In the 150 years since this assertion, it has become much clearer how incremental changes result in highly complex systems such as the eye. This instrument for gathering visual information from the natural environment is so useful in fact that it is estimated to have arisen independently 65 times throughout the long history of life (Salvini-Plawen & Mayr, 1961; Weiss, 2002). Even with the many stages of evolutionary development and multitude of environments to which it has adapted, the general form of the eye across different organisms is remarkably similar.

Although there is a great deal of commonality in the structure of the eye among members of the animal kingdom, research has shown that the appearance of the eye in humans is relatively unique in comparison with even closely related non-human primates. This uniqueness is indicated by an exposed sclera that lacks any pigmentation, the most exposed sclera relative to eye outline of any species, and an extraordinarily elongated eye outline in the horizontal direction (Kobayashi & Koshima, 2001).

Kobayashi and Koshima (2001) suggest that the distinctiveness of the human eye is the result of social factors, such as the need to recognize the direction of an individual's gaze. While this is important in humans and some non-human primates with sophisticated social systems, and particularly in the context of group hunting, other factors such as ecological and morphological constraints have been proposed to explain the evolution of gaze perception and the unique eye of humans (Emery, 2000).

Morphological changes primarily center around reduced facial projection and an overall flattening of the face in hominoids, which has acted to reduce the cues available from the snout and head as a whole, resulting in more reliance on the eyes to indicate gaze direction (Emery, 2000). Among the hominoids, humans are characterized by a greater degree of facial reduction that has occurred in association with marked encephalization during hominin evolution. Increased cranial size in conjunction with reduced facial prognathism are important to consider in investigating the unique form of the human eye as a result of changing reliance on certain features to indicate gaze, but also due to the position of the eye and orbit amid these coalescing neurocranial and lower facial features.

1.2 Evolution of the hominin brain, neurocranium, and face

Increased brain size in hominins has contributed to a number of changes in other features of the neurocranium and face, and is thought to have modified the size and location of various traits while also impacting the functional efficiency of mastication and olfaction (Lieberman, Ross, Ravosa, 2000; Ravosa *et al.* 2000; Ross, 1995). The brain is immense in humans and has expanded considerably during the last 2 million years, though enlargement of the various structures that make up the brain have not increased isometrically during hominin evolution (Rilling, 2006).

The neocortex is greatly expanded in primates relative to most other mammals, so much in fact that it accounts for 80% of total brain mass in anthropoids (Aiello & Dean, 1990; Kornack & Rakic, 2001). During human evolution the neocortex has grown to occupy an even larger share of the brain, with a disproportionate enlargement of the temporal and prefrontal association cortices, an increase in connectivity within and among cerebral cortical association areas involved in cognition, as well as an increased gyrification of the cortical surface (Rilling, 2006). This gyrification has primarily occurred in the prefrontal cortex and is the result of bending and folding of this outermost layer as it scales with positive allometry on brain volume within the confines of a spherically shaped skull (Rilling, 2006).

The frontal lobes of the neocortex have expanded considerably during human evolution and have been widely studied as a result of their assumed role in language development and higher cognition (Wu *et al.* 2007). In early hominins the frontal lobes are relatively flat and narrow, but have become taller, wider, and more rounded over the course of human evolution (Bruner, 2003). This area of the brain has expanded to the

extent that in modern humans it sits directly over the eyes and has filled in the space previously occupied by the brow ridge in ancestors of modern humans (Moss & Young, 1960). This cerebral expansion, and in particular a more anterior position of the frontal lobes, has repositioned the brain atop the eyes and created a situation in which two different functional systems (the eyes and brain) both make use of the frontal bone. Marked encephalization throughout hominin evolution is therefore expected to influence the relative size and position of these two features, possibly resulting in decreased function of the visual system.

In chapter 4 of this thesis, relationships among the cranium, orbits, and lower face are investigated in the context of hominin evolutionary trends of increased cranial size and decreased facial prognathism. It is proposed that orbital morphology varies in predictable ways in relation to these long-term craniofacial changes, which have resulted in a number of unique characteristics of the skull in modern humans. The results of this analysis and those from chapter 5, which investigates more recent evolutionary changes in orbital morphology since the Upper Paleolithic in Western Europe, will be assessed in the context of how the eye and surrounding soft tissue may be impacted by temporal modification to the bony orbit that circumscribes this functional system.

1.3 Structural and functional components of the skull

Most changes in craniofacial form during ontogeny and throughout hominin evolution are best explained in the context of functional craniology, which is an approach to understanding the skull as a matrix of hard and soft tissues arranged in a physical network, in which the final form is a product of forces and constraints among these

structural and functional components interacting during morphogenesis (Moss & Young, 1960). These cranial constituents are interrelated by way of tensions and pressures between connective tissues, muscles, sutures, the remodeling and displacement of bone, and perhaps most importantly, expansion of organs such as the brain (Bruner, 2007).

Encephalization within the hominin lineage has resulted in a number of changes in the cranial vault, cranial base, and face, which comprise the major structural components of the skull. Relative increase in brain size during human evolution has resulted in changes to underlying structures, and can be understood in the framework of heterochrony (changes in the timing or rate of growth and development), modularity (relationship among structural units in which variation in each component is dependent upon variation in others), and allometry (shape change in relation to size) (*ibid.*).

It is also important to consider that adaptive features do not always result from these processes, but rather “during evolution, a selective pressure determining changes in one of these components (size or shape) involves secondary changes in the other. Such secondary changes are not necessarily adaptive but may be merely consequences of the adjustment within the structural system.” (Bruner, 2007 p. 1360). Selection favoring individuals with greater cognitive ability resulting from the expansion of underlying cerebral components could result in a consequent diminishment of the structurally integrated visual matrix.

Change in neighboring features that are part of the functional and structural matrix of the skull interact during ontogeny and are viewed in association with the counterpart principle of craniofacial growth, which states that “the growth of any given facial or cranial part relates specifically to other structural and geometric “counterparts”

in the face and cranium” (Enlow & Hans, 1996 p. 40). This principle has been supported by recent research showing that craniofacial levels of skull development among the neurobasicranial complex, ethmomaxillary complex, and mandible follow a superoinferior growth gradient in which the first structure to attain adult size is the neurocranium, followed by the midline cranial base, the lateral cranial floor, and lastly the ethmomaxillary complex and mandible, which reach adult size near the age of 16 years (Bastir, Rosas, O’Higgins, 2006). Early growth of the frontal and temporal lobes along with the anterior and middle cranial fossae in which they sit, are important in determining later growth of the face (Bastir & Rosas, 2006; Enlow & Hans, 1996; Kohn *et al.* 1993; Lieberman, 1998; Lieberman, Ross, Ravosa, 2000; Ross, 1995; Lieberman, Pearson, Mowbray, 2000; Martone *et al.* 1992; Zollikofer & Ponce de León, 2002).

1.4 Growth of the brain, basicranium, and face

Enlargement of the brain during ontogeny causes the basicranium to expand anteriorly and laterally, while initiating inferior movement of the cranial floor by exocranial deposition and endocranial resorption (Enlow & Hans, 1996; Lieberman, Ross, Ravosa 2000). Inferior drift in the posterior cranial fossa also helps move the cranial floor more below the middle cranial fossa, thus flexing the basicranium as a whole (Lieberman, Ross, Ravosa 2000).

The cranial base plays a vital role in creating the shape of an individual’s face and cranium throughout growth and development and contributes to differences in craniofacial form among modern human populations (Enlow & Hans, 1996; Kuroe, Rosas, Molleson, 2004; Lieberman, Ross, Ravosa, 2000; Lieberman, Pearson, Mowbray,

2000). The basicranium provides a platform on which the brain can sit and from which the face can grow, and in one way or another connects the cranium with the rest of the body. For example, this feature articulates with the mandible and vertebral column, provides a channel through which the neural and circulatory connections of the face, neck, and brain can pass, forms the roof of the nasopharynx, while housing and connecting all of the sense organs in the brain (Kuroe, Rosas, Molleson, 2004; Lieberman, Ross, Ravosa, 2000).

In humans, the cranial base appears as a cartilaginous platform called the chondrocranium at about 2 months of embryonic development. At seven weeks it is separated by the mid-sphenoid synchondrosis into the prechordal (anterior) and postchordal (posterior) portions, which grow relatively independently of each other, possibly as a result of their different embryonic origins and/or different spatial and functional roles (Lieberman, Ross, Ravosa, 2000).

The center of the basicranium near the sphenoid body reaches adult size and shape earlier than the surrounding regions, while the anterior, middle, and posterior cranial fossae grow slightly longer and more or less independently of each other (Bastir & Rosas, 2005; Lieberman, Pearson, Mowbray, 2000; Lieberman, Ross, Ravosa, 2000), with each involved in a complex series of growth events that mainly involve displacement and drift (Lieberman, Ross, Ravosa, 2000).

Despite the relative independence among dimensions of the cranial base, its size, shape, and degree of flexion play an important role in neurocranial and facial growth (Enlow & Hans, 1996; Kohn *et al.* 1993; Lieberman, 1998; Lieberman, Ross, Ravosa, 2000; Ross, 1995; Ross & Ravosa, 1993), and because the cranial base acts as a bridge

between the neurocranium and face, upon which the latter is constructed, variation in this feature also corresponds to variation in facial form among modern human groups (Enlow & Hans, 1996; Kuroe, Rosas, Molleson, 2004).

For example, an open angled basicranium results in a face that protrudes anteriorly, is vertically elongated, and is associated with a dolichocephalic headform (Enlow & Hans, 1996). In contrast, a smaller basicranial angle denotes a shorter anteroposterior midface and a wider nasomaxillary complex, which are characteristic of the brachycephalic headform. The basicranium also plays a major role in determining the shape and position of the eye orbits, which become more frontated, convergent, and ventrally flexed as the cranial base angle decreases (Cartmill, 1970; Ross, 1995; Ross & Ravosa, 1993), in association with an increase in relative brain size (Lieberman, Ross, Ravosa, 2000; Strait & Ross, 1999).

Because the brain and cranium are the first to grow, serving as a template on which the rest of the face develops (Enlow & Hans, 1996), continual selection for a larger brain throughout hominin evolution has shifted the timing and shortened the duration of growth in the mid and lower face. This has resulted in a worldwide and accelerating trend toward orthognathism, which has coincided with a shift toward cranial globularity in recent human evolution (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Hanihara, 1994, 2000; Henneberg & Steyn, 1993; Lahr & Wright, 1996; Wu *et al.* 2007). As part of this research, samples of chimpanzee and past hominin fossil species with different grades of encephalization and facial prognathism are used to investigate how eye orbit morphology varies in association with these trends of cranial expansion and facial retraction during human evolution.

1.5 Growth of the eye and orbit

In humans, the frontal lobes of the cerebrum expand forward and downward through childhood, during which time the orbital roof remodels inferiorly and anteriorly by resorption of bone on the endocranial surface and deposition on the exocranial surface directly above the eyeball and extraocular tissues (Enlow & Hans, 1996). After a majority of brain growth is complete, the nasomaxillary complex begins to move by way of primary displacement anteriorly and inferiorly away from the neurocranium, while bone is concomitantly deposited on its superior surface (*ibid.*).

This is an important time during ontogeny, and an important region of the skull concerning relationships among the brain, orbit, eye, and extraocular tissues, as changes in the timing or rate of growth in these regions may have implications for the proper development and functioning of the eye. This is of particular concern given that endocranial resorption and exocranial deposition of bone on the superior surface of the eye orbit may conflict with growth of the eye and extraocular tissue within it, particularly given that the eye grows independently of the orbit.

Although the eyeball lies predominantly within the orbit, it is not considered to directly influence its size. “In considering all the evidence produced it appears that the size of the orbit is dependent upon the size of the eyeball in only the most general way and that the two structures can vary in size independently to a surprising extent” (Schultz, 1940 pg. 408). Schultz’s early analysis is one of few examining how the eyeball varies in association with the eye orbit, and includes an investigation of this relationship in small samples of extant non-human primates, and in male and female adult and subadult humans.

Schultz (1940) observes a negative allometric relationship between the eyeball and orbit with respect to body weight, in which orbital volume increases more rapidly than eyeball volume as body weight increases. This shows that larger bodied primates possess a relatively small eyeball in a large orbit, while smaller primates have eyes that occupy a larger percentage of the orbit. This relationship is also found to exist in humans with different body sizes, as larger bodied males possess larger orbits relative to eye size, and females with smaller bodies have eyes that occupy a larger proportion of the orbit (Schultz, 1940). In fact, among all primates eyeball size relative to both body size and orbit size is always greater in females than in males of the same species (*ibid.*).

Growth of the eye occurs more slowly in comparison to that of the orbit during postnatal ontogeny in humans, resulting in a larger relative size of the eye orbit in individuals with larger bodies, though during prenatal growth and until about the 6th month in utero the eyes and orbits grow isometrically (Dixon, Hoyte, Ronning, 1997). Following this initial period of associated growth during the first 6 months in utero, eyeball growth actually outpaces orbital growth to the extent that half of the globe protrudes out of the orbit. This pattern then reverses and for the next five years the eye orbit grows at a faster rate than the eyeball (Dixon, Hoyte, Ronning, 1997).

Studies of interspecific allometry show that this reversal in the pattern of eyeball and orbital growth is similar in the chimpanzee, wherein the eyeball fills 92% of the orbit in the late fetal stage, but only 24% in adulthood. In humans by contrast, the eyeball occupies 75% of the orbit during the same late fetal stage, and approximately 32% in adulthood (Dixon, Hoyte, Ronning, 1997, Schultz, 1940). The larger percentage of the orbit that the eyeball occupies in adult humans compared to chimpanzees and primates as

a whole, is due in part to the larger absolute volume of the human eyeball, as orbital volume is approximately the same in both chimpanzees and humans (Schultz, 1940).

Because the eyeball does not dictate growth of the orbit, it is important to understand how each develops independently throughout life, and particularly in the context of neighboring structural and functional features of the skull. The eyeball has been shown to grow most rapidly during the first years of life, with a majority of this growth occurring in the anterior segment (Todd *et al.* 1940; Weale, 1982). It then expands more slowly through later life with the exception of a short spurt between 10-12, and another increased rate of growth from the age of fourteen until the early twenties (Salzmann, 1912; Weiss, 1897). In contrast to the early growth phase that takes place primarily in the anterior segment of the eye, during this later stage of development a majority of enlargement occurs in the posterior segment of the eyeball (Salzmann, 1912; Weiss, 1897; Weale, 1982).

The orbits also complete most of their total growth relatively early in life, reaching 80% of adult size at age 3, and 94% of adult size at age 7 in humans (Scott, 1953). The remaining 6 percent of growth occurs during childhood and is primarily restricted to the transverse plane, or in an equatorial orientation relative to the eyeball (Waitzman *et al.* 1992). Later growth of this region demonstrates the importance of investigating each orbital area separately, as different segments develop somewhat independently of each other during ontogeny.

The lateral margin of the orbit is primarily made up of the greater wing of the sphenoid and part of the zygomatic bone, which together increase in area during growth spurts around age two and then again during separate spurts between ages 8 and 11 in the

sphenoid, and between 5 and 6 in the zygomatic region (Dixon, Hoyte, Ronning, 1997). The lateral wall of the orbital margins, which is one of few areas that continues growth throughout childhood (Waitzman *et al.* 1992) also grows by remodeling, with deposition on the lateral surface and resorption on the medial (Enlow & Hans, 1996). Because the interorbital region changes relatively little after birth (Waitzman *et al.* 1992), this deposition acts to widen the eye orbits while moving the lateral walls away from the nasal region between them.

Growth of the medial orbit is one of the most complex portions of this feature, as it is made up of the greatest number of bones with marked variation in their articulations. The medial wall as a whole increases relatively little during two growth spurts, with one during the first year of life, and the second between 6 and 8 years (Dixon, Hoyte, Ronning, 1997). Most growth that does occur in the medial wall of the orbit is anterior in direction. In young adults the medial orbital rim lies slightly in front of the lateral rim, but during ontogeny the nasal wall moves the medial rim anteriorly while remodeling of the cheekbones moves the lateral wall posteriorly, so that at maturity the two are separated by a greater distance with the medial orbit positioned more anteriorly relative to the lateral orbital margins (Enlow & Hans, 1996).

The roof of the orbit grows most rapidly for the first three months after birth, and maintains this pace until the end of the first year. As with the lateral orbit, this superior orbital region also grows again during later life, as a second spurt occurs sometime between age nine and eleven (Lang, 1983). As described above, the pattern of growth in this region is predominantly the result of forward and downward expansion of the frontal lobes, during which time the orbital roof moves by growth remodeling anteriorly and

inferiorly through deposition on the exocranial side, or the internal orbital roof, and resorption on the endocranial surface just below the frontal lobes (Enlow & Hans, 1996).

During this period the malar region is relocating posteriorly through deposition on the anterior surface and resorption on the posterior, which together with forward and downward movement of the orbital roof, creates a more obtuse facial angle relative to the Frankfurt Horizontal Plane. This angle is a unique human characteristic to the exclusion of all other mammals (Enlow & Hans, 1996), and is primarily the result of encephalization and reduced facial prognathism throughout human evolution that occur by way of changes to the pattern of growth and development in the brain, cranial vault, basicranium, and face during this time (Cobb, 2008; Lieberman, McBratney, Krovitz, 2002; Bastir *et al.* 2008).

The floor of the orbit is primarily formed by the zygomatic bones that make up the anterior and lateral portion of the base of this feature, and the maxilla, which is also the roof of the maxillary sinus. During ontogeny there is a threefold increase in the area occupied by these bones, which primarily occurs in association with the forward and downward displacement of the nasomaxillary complex by way of maxillary sutural growth (Enlow & Hans, 1996). During this anterior and inferior migration of the nasomaxillary complex however, the orbital floor and nasal floor grow away from each other, which acts to increase facial height while also limiting the amount of net inferior movement in the floor of the eye orbit.

During early childhood the nasal floor is nearly in line with the floor of the eye orbits, but moves downward during displacement of the nasomaxillary complex until it becomes substantially separated from the orbital floor in adulthood. In order to maintain

its relative position during forward and downward displacement of the entire unit, the floor of the eye orbit remodels upward by depositing bone on the superior surface (orbital side) and resorbing bone on the inferior surface (maxillary sinus side) (Enlow & Hans, 1996).

It would be expected that the size of the eye orbits would decrease during growth and development, as both the roof and floor are depositional surfaces. Depositing bone on the superior and inferior surfaces of the orbit could be particularly problematic given the large amount of soft tissue that lies within it, including the nerves, blood supply, muscles, fat, and an eyeball that continues expanding later in life, and with a bulk of this growth occurring in the posterior globe that lies within the orbit.

Enlow and Hans (1996) argue that the internal size of the orbits do not decrease during these periods of roof and floor remodeling as a result of the V-principle, which states that despite deposition on the interior surfaces of V-shaped bone configurations, its overall dimensions increase as a result of the entire complex moving toward the larger end during growth. These authors go on to mention that displacement associated with sutural bone growth in and around the orbit also help to enlarge it during ontogeny, however they add that these processes change the orbit relatively little during later childhood.

1.6 Modern variation in human orbital morphology

It is important to consider that application of the V-principle may not be equally appropriate for all human populations, and particularly among East Asians who possess very flat faces compared to Europeans, Sub-Saharan Africans, and Australians (Badawi-

Fayad & Cabanis, 2007; Hanihara, 2000; Hennessy & Stringer, 2002). Individuals and groups with anteroposteriorly shorter skulls and flatter faces are characterized by less forward growth of the nasomaxillary complex out from the basicranium, which diminishes the degree to which the V-shaped orbit can move toward the open end and become enlarged. Posterior remodeling of the malar region during growth and an upward movement of the orbital floor relative to the nasal floor also work in the opposite direction of this anterior migration of the orbit, further limiting forward displacement and expansion.

Many studies have investigated variation in cranial and facial form among modern human populations, and have shown that a number of differences exist among them (Bruner & Manzi, 2004; Enlow, 1982; Hanihara, 1996, 2000; Hennessy & Stringer, 2002; Howells, 1973, 1989; Lahr, 1996; Roseman & Weaver, 2004). However, humans as a whole actually show lower levels of interpopulation differentiation in craniofacial anatomy when compared to other terrestrial mammals of similar body size (Roseman & Weaver, 2004). In general, the degree of craniometric variability among modern human populations is relatively limited, and in agreement with past studies of genetic variation (Relethford, 1994). Additionally, variation among groups is relatively continuous and changes gradually across space, with some degree of overlap in the genotype and phenotype of various features (Bruner & Manzi, 2004; Lahr, 1996; Hanihara, 1996; Howells, 1973; Relethford, 1994).

Despite these common aspects of craniofacial form, and a relative uniformity in cranial size across modern human groups (Badawi-Fayad & Cabanis, 2007; Bruner & Manzi, 2004; Howells, 1973) some level of variation does exist between them; and in

fact more variation exist between regional group pairings than between males and females within each group (Hennessy & Stringer, 2002). These differences in craniofacial form among modern human groups are well documented, though little is known about how the orbits vary among them, particularly concerning the degree of variation that exists in the internal anatomy of this feature. This thesis will contribute to studies of craniofacial diversity among modern human groups by investigating a number of characteristics of the orbit and contiguous midfacial anatomy among samples of individuals drawn from Western European, Far East Asian, and Sub-Saharan African populations.

1.7 Evolution of cranial globularity and facial orthognathism in *Homo sapiens*

Anatomically modern humans are generally characterized by a small face that is short, high, and pushed back under the vault, a high vertical forehead, enlargement of the parietal region of the upper cranium, a flexed cranial base, a rounded occiput, an occipital protuberance on the occipital bone, a canine fossa, and a mental eminence (Lahr & Wright, 1995). These traits are primarily the result of facial retraction and neurocranial globularity that result from changes in cranial development and particularly a relative size increase in the temporal and frontal lobes of the brain (Bastir *et al.* 2007; Lieberman, McBratney, Krovitz, 2002).

The effect of these variables on cranial shape, which results in structural autapomorphies useful for separating anatomically modern humans from earlier archaic *Homo sapiens* forms, can also be understood by comparing patterns of growth between humans and chimpanzees. During the early stages of postnatal ontogeny in *Pan*, relative

length of the anterior and middle cranial fossae decreases in association with an increase in relative length and height of the face. These cranial fossae continue to shorten after neural growth is complete, and facial height and length continue to increase in association with facial projection (Lieberman, McBratney, Krovitz, 2002). By contrast, the face stays retracted beneath the anterior cranial base and the neurocranium remains highly globular during ontogeny in *Homo sapiens*.

Cranial globularity is a unique feature of modern human skulls and is largely the result of increased cranial base flexion and changes in relative size of certain brain structures. Expansion of the frontal and temporal lobes of the brain are an important component of this flexion, as they act to lengthen the anterior cranial base and influence the size of the anterior and middle cranial fossae, respectively (Lieberman, McBratney, Krovitz, 2002).

In addition to an increase in relative size of these basicranial components, anatomically modern *Homo sapiens* are characterized by a distinct forward and lateral expansion of the anterior portion of the middle cranial fossa relative to the optic and maxillary nerve foraminae compared to archaic *Homo sapiens* and *Homo erectus* (Bastir, *et al.* 2008). As a result of this anterior movement of the middle cranial fossa relative to these nerve foraminae, the maxillary tuberosities and the orbits are also shifted anteriorly in relation to basicranial and neurocranial structures (Bastir *et al.* 2008).

Forward movement of the middle cranial fossa also correlates with forward projection of the greater sphenoid wings, which shift the posterior maxillary plane anteriorly, rotating it clockwise when viewed laterally from the right side (Bastir *et al.* 2008; McCarthy & Lieberman, 2001). The vertical boundary of the posterior maxillary

plane is highly related to factors influencing the basic design of the face, and is considered one of the most important structural and developmental planes of the entire craniofacial complex (Enlow & Hans, 1996). This plane is tightly constrained at 90° relative to the anterior cranial base in humans and non-human primates (Bastir *et al.* 2008; Enlow, 1990; Lieberman, Ross, Ravosa, 2000; Lieberman, McBratney, Krovitz, 2002; McCarthy & Lieberman, 2001), and is also constrained at 90° relative to the neutral horizontal axis throughout growth and development in all mammals (Bromage, 1992; Enlow & Hans, 1996).

An increase in relative size of the frontal and temporal lobes of the brain, expansion and forward movement of the anterior and middle cranial fossae, forward projection of the greater sphenoid wings, and rotation of the posterior maxillary plane thus act to create the uniquely globular cranium and ventrally rotated face that lies under the anterior cranial fossa in anatomically modern humans (Bastir *et al.* 2008; McCarthy & Lieberman, 2001; Lieberman, McBratney, Krovitz, 2002).

Throughout hominin evolution a marked increase in neocortical volume has occurred in which the frontal, temporal, occipital, and parietal lobes have expanded in association with increased intellectual capacity (Bastir *et al.* 2008; Rilling, 2006; Wu *et al.* 2007). As described above, these changes are associated with modification to underlying basicranial and facial structures, and have resulted in a more anteroposteriorly shorter face through time. However, the extent to which the entire skull has rotated, and the face and orbits have become tucked up under the brain, is a unique derived feature of anatomically modern humans (Cobb, 2008; Bastir *et al.* 2008; Lieberman, McBratney, Krovitz, 2002).

1.8 Post-Pleistocene craniofacial change in *Homo sapiens*

Modern human populations are characterized by disparate craniofacial features (Bastir *et al.* 2008; Bruner & Manzi, 2004; Hanihara, 1996, 2000; Hennessy & Stringer, 2002; Howells, 1973, 1989; Kuroe, Rosas, Molleson, 2004), however a general shift toward brachycephaly and facial orthognathism has occurred ubiquitously among nearly all human groups (Brown, 1989, 1992; Carlson, 1976; Carlson & Van Gerven, 1977; Wu *et al.* 2007). Although the pattern of craniofacial change is similar across human populations, few studies have focused on orbital and midfacial change and to what degree this feature varies in association with a shift toward brachycephaly and facial orthognathism.

Two recent investigations have examined diachronic change in the orbits and their association with neighboring craniofacial traits among Chinese groups dating to the Holocene (Brown & Maeda, 2004; Wu *et al.* 2007). These and other studies echo a reduction in overall cranial and facial size in which brain volume, the cranial vault, the oro-facial skeleton, and general skeletal robusticity are reduced following the Pleistocene period (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Lahr & Wright, 1996; Smith *et al.* 1985, 1986; Wu *et al.* 2007). This reduction likely began slightly earlier than the Holocene however, as it is estimated that since the Upper Paleolithic in Europe, cranial and facial dimensions have been reduced by 10-30% (Kidder *et al.* 1992).

While these changes occur in Europe and China, reduction during this period was not accompanied by brachycephalization in Sub-Saharan African groups (Henneberg & Steyn, 1993). In the Nubian region of northern Africa however, an overall increase in

cranial and facial height occurs in association with a decrease in the anteroposterior length of both the calvarium and face, resulting in brachycephalization and facial orthognathism during the last 5,000 years in this region (Carlson, 1976). In a subsequent study these same changes were also found to occur in this region over a longer period of time dating back to the Mesolithic age (Carlson & Van Gerven, 1977).

In China, Wu *et al.* (2007) show that certain aspects of the orbits change considerably since the Neolithic, and vary to a greater extent than most other features of the face and cranium. Shape of the orbital margins show the greatest degree of variation throughout this time period, which is primarily the result of a reduction in orbital breadth from the Neolithic to the Bronze Age, and then a continuation of this decrease in orbital breadth accompanied by a rapid increase in orbital height from the Bronze Age to the present. Change in these orbital dimensions are also accompanied by a decrease in cranial and facial size, a decrease in facial prognathism, an increase in cranial globularity, a taller and narrower nasal aperture, and a narrowing of mediolateral facial dimensions as a whole (Wu *et al.* 2007).

Brown and Maeda (2004) observe many of the same changes in craniofacial form among Chinese adults over analogous time periods, and in addition to investigating height, breadth, and shape of the orbital margins, these authors examine how volume of the orbit has changed since the Neolithic, and how it varies in association with other traits of the face and cranium.

While diachronic change in most aspects of the orbit were investigated using skulls dating to between 7,000 years BP and the present, due to the fragile nature of the bones that make up the orbital cavity, Brown and Maeda (2004) were not able to directly

investigate change in orbital volume among these groups. However, by comparing the crania of Japanese and Australian Aborigine samples that represent more “modern” and “ancestral” temporal groups from East Asia, respectively, they are able to deduce how orbital volume varies in association with adjacent craniofacial features during the last 10,000 years in this region.

Brown & Maeda (2004) show that since the Chinese Neolithic cranial robusticity and endocranial volume are reduced, along with a reduction in posterior tooth size, loss of alveolar bone, and a subsequent reduction in facial prognathism. These trends corroborate the results of the above studies of craniofacial change in size across Africa, Europe, and Asia over a similar time period. In relation to change in orbital morphology throughout the Chinese Neolithic, a pattern of relative and absolute increase in orbital height emerges, which in association with decreasing orbital breadth, results in taller, narrower, and more circular shaped orbital margins (Brown & Maeda, 2004); a strong trend also observed by Wu *et al.* (2007). This increase in orbital height and decrease in orbital breadth occurs in association with a reduction in supraorbital breadth, a decrease in facial height, and a reduction in facial prognathism throughout the last 7,000 years in this region.

As part of this dissertation research, orbital morphology is investigated among Western European groups from different time periods dating to the Upper Paleolithic in order to understand diachronic change in this feature and within this region. These same orbital characteristics are examined in relation to changes in cranial and facial form, which undergo a considerable degree of modification throughout this time period in Europe, and many other regions of the world. The results of this analysis are also

assessed in relation to patterns of change in orbital morphology among Chinese groups dating to the Neolithic, investigated by Brown & Maeda (2004) and Wu *et al.* (2007).

1.9 Evolution of the eye, orbit, and reduced visual acuity in humans

Many studies have shown that a decrease in craniofacial size and robusticity, as well as a shift toward brachycephalization, occur relatively ubiquitously across different regions during the last 7,000 – 10,000 years (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Lahr & Wright, 1996; Wu *et al.* 2007). However, change in orbital morphology has not been investigated to the same extent in each of these regions. An aim of this thesis research is to contribute to a global understanding of change in orbital morphology by investigating multiple aspects of this feature and how it varies in association with other cranial and facial features among Western European groups over the last 30,000 years.

This type of investigation is of particular importance considering that orbital volume and other aspects of this feature have been found to vary in association with changes in contiguous features of the face and cranium through time (Brown & Maeda, 2004; Wu *et al.* 2007). Additionally, change in size, shape, or orientation of the orbits in association with temporal modification to the broader craniofacial anatomy, may have implications for proper functioning of the visual system.

One prominent feature that shows a marked degree of modification in Asia is shape of the orbital margins, which have become taller, narrower and generally more rounded in the last 7,000 years (Brown & Maeda, 2004; Wu *et al.* 2007). It has also been shown that a large orbital height relative to orbital breadth is inversely related to orbital

volume ($r = -0.568$), which means that high and narrow orbits are smaller in size than lower more rectangular ones (Brown & Maeda, 2004). These authors also show that a strong positive relationship exists between supraorbital breadth and orbital volume ($r = 0.88$), and between facial prognathism and orbital volume ($r = 0.83$), which indicates that as faces become narrower and more orthognathic, respectively, the amount of space within the orbit decreases. Reduction in the size of these features and in association with the orbital margins becoming taller and more rounded throughout the Chinese Neolithic indicates that the orbits also diminish in size during this period (Brown & Maeda, 2004).

Change in orbital morphology throughout the East Asian Holocene, and particularly in relation to shape and volumetric modification associated with other craniofacial trends, may impact visual acuity in groups that undergo such changes through time. Although Brown and Maeda (2004) observe temporal size and shape change in the orbits of this East Asian sample, they do not address the issue of vision in the functional sense, but do point out that “If it is the total volume occupied by the eyeball, extraocular muscles, nerves and blood supply which are important, rather than just the size of the eyeball, then there would need to be some functional compensation for any significant reduction in orbit length and volume” (Brown & Maeda, 2004 pg. 38).

This raises an important question concerning the role of the orbit in maintaining keen eyesight, and how changes in this feature may impact vision, particularly due to its location between a retracting lower face and expanding neurocranium throughout hominin evolution. The orbits circumscribe a number of different soft tissue components and the relationship among them changes throughout life. Modification to the timing or rate of growth in these various cranial, lower facial, and orbital features during ontogeny

or throughout hominin evolution could impact the relationship among them and possibly alter the shape of the eyeball, impinging on its ability to accurately focus light on the posterior retinal wall.

Myopia is the primary source of reduced vision throughout the world, and has become so common in some populations that it has recently been labeled an epidemic (Mak *et al.* 2005; Park & Congdon, 2004). Most myopia is juvenile-onset, which typically begins during adolescence and progresses steadily until the late teens or early twenties (Goss & Grosvenor, 1990). Refractive error associated with this condition occurs with an axial elongation of the eye, which increases the vitreous depth and subsequently increases the focusing power of the cornea, resulting in an image that is erroneously focused in front of the retina (Lam *et al.* 1999, Mak *et al.* 2005).

Myopia has become unusually common in the modern world, to the extent that it affects 80-90% of individuals in some East Asian populations (Goldschmidt, Lam, Opper, 2001; Lam, *et al.* 1999; Park & Congdon, 2004). It is also found to occur earlier in life and at a higher frequency among Chinese schoolchildren compared to younger individuals of African or European descent (Ip *et al.* 2008; Lam *et al.* 1999). Additionally, women have a higher rate of myopia than men, develop the condition earlier in life, and have greater degree of spherical equivalent refractive error when growth ceases (Angle & Wissman, 1980; Grosvenor & Goss, 1999; Lam *et al.* 1999; Ip *et al.* 2008; Parssinen & Lyyra, 1993; WGMPP, 1989).

Despite the widespread occurrence and severe impact of juvenile-onset myopia in certain regions, the pathogenesis of this condition is still poorly understood (Cordain *et al.* 2002; Goldschmidt, 1999; Grosvenor & Goss, 1999; Quinn *et al.* 1999), and current

models fall short of explaining why myopia is so common, and consistently found to correlate with variables like ancestry, sex, intelligence, and socioeconomic status. Two commonly cited explanations for this type of refractive error are the biological theory and the use-abuse or near-work model (Angle & Wissman, 1980; Cordain *et al.* 2002; Miller, 2000; Quinn *et al.* 1999; Saw *et al.* 2002).

The near-work hypothesis ascribes myopia progression to the permanent malformation of the eyeball caused by muscles tensing during regular use throughout an individual's lifetime. Evidence to support this hypothesis generally comes from the higher rate of myopia among more intelligent people and those in higher socioeconomic classes. In this model it is presumed that intelligence is the result of reading throughout life, and that this act causes the muscles to tighten and distort the eyeball, however it has yet to be shown how convergence and eye strain can permanently alter the shape of a human eyeball (Angle & Wissmann, 1980).

Another problem with this model relates to the ambiguous relationship between correlation and causality in observational studies, and with reference to the near-work hypothesis it cannot be known whether reading produces myopia over time as assumed by the near-work camp, or rather if myopes read more because of an overall greater thirst for knowledge associated with a pre-existing higher level of intelligence (Mak *et al.* 2005; Miller, 2000; Saw *et al.* 2004; WGMPP, 1989).

A final objection to the use-abuse/near-work model is that it doesn't account for why some individuals, who do as much or more reading as other members of the same group, do not develop myopia. If near-work were a primary contributor to the development of near-sightedness, then any highly literate population should be affected

in roughly the same proportions (Angle & Wissmann, 1980; Cordain, *et al.* 2002). Many studies indicate that college students, people of higher socioeconomic status, and generally the more educated have higher rates of myopia, but even within these brainy groups a majority of individuals (who presumably do equal amounts of reading) don't develop near-sightedness.

The biological model attributes myopia progression to genetic errors associated with growth of the eye tissue, and is supported by myopia prevalence studies among family members, and concordance rates of myopia among twins (Angle & Wissmann, 1980). For example, a higher concordance rate was found between monozygotic (92.2%) compared to dizygotic twins (79.3%) in a study of myopia prevalence in Taiwan (Chen, Cohen, Diamond, 1985), which suggests that at least some of the pathogenesis of myopia may be attributable to genes; but exactly what genes are responsible for myopia development and how genetics can explain the ubiquitous pattern of eyeball malformation, as well as the ethnic, economic, sex, and social correlates is still not understood.

Juvenile-onset myopia is the result of an axial elongation of the eye, an increase in vitreous depth, and an increased focusing power of the cornea; the result of which is an image that is focused in front of the retina (Lam *et al.* 1999; WGMPP, 1989). Because these are the main contributors to the development of myopia in every population around the world, some other mechanism besides genetic mutation controlling eyeball growth must be responsible. It is improbable that a mutation affecting eye growth would cause the same distortion of the eyeball throughout the world, or that it could have originated in

one group and spread to all other areas within only a few thousand years, particularly because near-sightedness is selectively neutral.

A genetic mutation that diminishes eyesight could only persist in a population that does not rely extensively on acute vision for survival, or is capable of developing some means to physically correct the focal error; as a result it can only be in recent human history that genes affecting visual acuity would be permitted to persist (Cordain *et. al.* 2002; Miller, 1992). If there is a heritable genetic component to the pathogenesis of myopia a relaxation of selection pressure favoring individuals with keen eyesight would make it possible for such a gene or genes to endure. However, even though visual deterioration would be permitted in recent human history, a mutation affecting eye growth cannot be the only cause of juvenile-onset myopia, as this condition develops in highly patterned ways and occurs at a very high rate in some populations but not others. The common pattern of myopia development and the many biological and social correlates would not occur if myopia were a purely genetic abnormality.

Most research investigating the etiology of juvenile-onset myopia has focused on the eyeball as a relatively isolated unit, overlooking its close proximity to and spatial relationship with surrounding extraocular tissues, the orbit, facial framework, neurocranium, and brain. As a result, the final section of this thesis examines the relationship between the eyeball and orbit, and how relative size of the globe within the bony orbit relates to the frequency and severity of myopic refractive error. This research also aims to provide a model for investigating reduced visual acuity in humans, and contribute to an understanding of the degree to which modern variation and evolutionary change in orbital and overall craniofacial morphology may explain the common eye form

association with juvenile-onset myopia, why this selectively neutral condition occurs in such high frequency in modern humans, and why it is consistently found to correlate with ancestry, sex, intelligence, and age.

The principal objective of this dissertation research is to provide a comprehensive description of modern variation and evolutionary change in the hominin orbit. In chapter 3 of this thesis, variation in orbital morphology is investigated among modern human ancestral groups from Western Europe, China, and South Africa in order to understand the pattern and degree of variation among them for this feature, and how its variability relates to general differences in craniofacial form. In chapter 4, the orbit is examined in relation to hominin trends of cranial expansion and reduced facial prognathism to investigate how relative size and orientation of the orbits vary in association with these morphological changes during human evolution.

Chapter 5 examines more recent evolutionary change in orbital morphology, focusing on Western European groups dating to the Upper Paleolithic, and involves a separate analysis of how the orbits vary in relation to changes in shape of the face and cranium in this region throughout the last 30,000 years. Finally, in chapter 6 of this thesis relative size of the eye within the orbit is investigated in the context of spherical equivalent refractive error to investigate whether a larger eye within a smaller orbit is associated with the incidence and severity of juvenile-onset myopia in Chinese adults. The results of this analysis are then examined in the context of different patterns of growth and development between the sexes, across modern human group, and in relation to the results of these separate investigations of hominin evolutionary change and modern variation in orbital morphology.

CHAPTER 2

MATERIALS AND METHODS

2.1 Variables

In this study, continuous traits of the orbits, lower face, and cranium are used to investigate variation among modern human and past hominin groups. These data were collected using standard landmarks following the methods of Howells (1973) and White (2000) for characteristics of the face and cranium (Table 2.1), and Schultz (1940) and Moore-Jansen et al. (1994) for measures of the orbits (Table 2.2). Indices and size estimates are also derived from these linear measures in order to better understand variation and change in size and shape of the skull (Table 2.3). Because few studies have focused principally on the orbit, additional measures have been included in order to better understand modern variation, evolutionary change, and how this feature varies in relation to neighboring craniofacial traits.

Craniofacial Variables	Label	Landmarks
Maximum Cranial Length	gol	(g – op)
Basion – Prosthion Length	bpl	(ba – pr)
Maximum Cranial Breadth	xbc	(eu – eu)
Minimum Frontal Breadth	wfb	(ft – ft)
Bizygomatic Diameter	zyb	(zy – zy)
Upper Facial Height	nph	(n – pr)
Basion – Bregma Height	bbh	(ba – b)
Nasal Height	nlh	(n – ns)
Basion – Nasion Length	bnl	(ba – n)
Upper Facial Breadth	ufb	(fmt – fmt)

Table 2.1: Cranial and facial measurements used in this study

Orbital Variable	Label	Landmarks
Orbital Breadth	obb	Dacryon (d) – Ectoconchion (ec)
Orbital Height	obh	Distance between the superior and inferior orbital margins taken at the midline and at a right angle to orbital breadth
Orbital Frontation	obf	Angle formed between the Frankfurt Horizontal and vertical plane of the orbital margins
Orbital Volume	obv	Orbit filled with mustard seed and transferred to graduated cylinder. Measured in milliliters (mL) 1 milliliter (mL) = 1 Cubic Centimeter (cc)
Orbital Depth	obd	Distance from ectoconchion to the most posterior point of the anterior opening on the optic canal
Basion-Sup. Orbit	bsc	Chord from Basion to the most superior midpoint on the orbital margins
Basion-Inf. Orbit	bio	Chord from Basion to the most inferior midpoint of the orbital margins
Biorbital Breadth	ekb	Ectoconchion (ec) - Ectoconchion (ec)
Interorbital Breadth	dkb	Dacryon (d) - Dacryon (d)

Table 2.2: Orbital measurements used in this study

Indices & Size Estimates	Label	Landmarks
Cranial Index	cri	$xcb * 100 / gol$
Orbital Index	obi	$obb * 100 / obh$
Upper Facial Index	ufi	$nph * 100 / zyb$
Cranial SizeGM	crg	$(gol * xcb * bbh)^{.33333}$
Orbital SizeGM	obg	$(obb * obh * obd)^{.33333}$

Table 2.3: Indexes and size variables derived from linear measurements

Size of the orbit is investigated using measurements of orbital volume (obv), orbital depth (obd), distance from basion to the superior and inferior orbital margins (bso, bio), orbital breadth (obb), orbital height (obh) as well as bi-orbital and interorbital breadth (ekb, dkb). A ratio of orbital width/height was created to test for differences in shape of the exterior margins (obi), and vertical orientation of the orbit relative to the Frankfurt Horizontal Plane facilitates an examination of population differences, and evolutionary change in orbital frontation (obf).

Orbital frontation was determined by measuring the angle formed between a straight vertical line across the upper and lower orbit and the Frankfurt Horizontal Plane (porion to orbitale). This was determined in 1877 by the International Congress of Anthropologists to be a standard plane for normal skull orientation (Byrnes, 2007), and represents a flat line that runs parallel to the floor in most individuals. However, the biological rationale of the Frankfurt Horizontal Plane (FH) as a way of orienting skulls in reference to normal head position has recently come into question (Barash, Marom, 2008; Strait & Ross, 1999).

In this investigation the FH is not used to determine “normal” skull position, but rather as a basic standard reference point for determining orbital frontation due to its passage through orbitale on the inferior orbital margins. Orbitale is used as the vertex between the FH and a ray running across the upper and lower margins of the orbit, and the angle formed between them is measured to determine the degree of vertical rotation of the orbits relative to this standard plane.

An important element of understanding orbital variation and change involves an estimation of orbital volume, however because the posterior orbit is composed of thin fragile bone, it is often impossible to obtain accurate volumetric measurements in past human groups dating to before the Neolithic. In modern humans and non-human primates the orbit is typically in good condition and rigid enough to allow a direct measure of its capacity. In these samples, careful volumetric measurements are recorded by lining the orbit with a thin piece of plastic wrap, filling it to the orbital margins with mustard seed, and then transferring the seed to a graduated cylinder to determine the actual metric volume in milliliters.

A similar technique was used in a recent study of modern humans from Tohoku Japan (Brown & Maeda, 2004), and along with 64 other craniofacial variables from this Japanese sample, were made available to researchers on the author’s website (Brown P., 1998–2003). Sex differences in orbital capacity across different samples of modern humans are investigated in chapter 6 of this thesis using orbital volume data collected by Brown and Maeda, (2004).

A comparison of the technique described by these authors and that used as part of this research indicates that both yield nearly identical results. This ensures that minor

differences in measurement technique will not confound the investigation of population affinities. Though these two techniques yield consistent results, because a different researcher collected these orbital volume data as part of a separate study, the degree of interobserver error cannot be known.

In addition to this orbital volume measurement recorded in milliliters, a separate indicator of orbital size is used in the analysis of evolutionary change in orbital morphology since the Upper Paleolithic investigated in chapter 4. This provides an additional estimate that enables the inclusion of more individuals that would otherwise be excluded due to poor preservation of the thin bones that make up the interior orbit.

This orbital size variable is derived from the geometric mean of orbital height, orbital breadth, and orbital depth (Height * Width * Depth)^{.33333} following the methods of González-José *et al.* (2005). The geometric mean of these three variables provides an estimate of volume, which is the same as that of a rectangular prism with side lengths equal to each measure of orbital depth, width, and height. Though the orbit is more pear-shaped than cuboid, this provides an estimate of its volume when damage to the fragile bone of its internal structure prohibits accurate measure in milliliters.

In addition to these continuous traits of the face and cranium, other quantitative and categorical variables such as *age*, *sex*, *ancestry*, *species*, and *time* are used for addressing questions and testing hypotheses relating to orbital development, interspecific variation, sex differences, and how much change is characteristic of this feature through time. In most cases sex was listed in the museum database or written on individual skulls, though when not available it was estimated using different skeletal indicators after Burns (1999), and was marked indeterminate if a clear distinction could not be made. In

this study most research questions involve an investigation of population variation and evolutionary change among broader ancestral and temporal groupings; as a result sex determination was primarily done to ensure an equal number of male and female adults within each sample.

Age of the individual was also most often in the registry of each museum where data were collected, though if not listed, full eruption of the third molar was used to determine if the individual was an adult and could therefore be included in the sample. The only anthropological collection in which measurements were taken on individuals from different stages of growth was in the Dart Collection at the University of the Witwatersrand in Johannesburg, South Africa, and chronological age was available for each skull in the collection. This sample consists of 50 individuals (age range 0-17 years) from primarily the Sotho and Zulu tribes of South Africa.

The geologic age of ancient hominin fossils was taken from estimates provided by multiple authors and summarized in Schwartz & Tattersall (2002). Dates for more recent skulls from different time periods since the Upper Paleolithic were taken from the museum registry. In many cases the general period from which they came was given in lieu of a specific date for each skull, in which case the middle date for this age range was recorded.

2.2 Measurement error

Measurements were repeated multiple times on individual skulls throughout the data collection phase of research in order to investigate the repeatability of each measurement used in the analysis. Measurements were repeated on the same crania

upward of 5 times for 23 different skulls at different museums over the course of 4 years of data collection. In each case dimensions were recorded from a randomly selected skull, which was then set aside until later in the day or for the following day to ensure that repeated measures wouldn't be biased by consecutive quantification. Measurement error was assessed following the method described in White (2000), page 307.

Variables of the cranium and face were found to be slightly more consistent, deviating only 0.56% from the average of each measurement. By comparison, variables of the orbit were found to diverge by 1.07% on average. Though most orbital variables are as accurate or in some cases more accurate than those taken from other features of the cranium and face, interorbital breadth, orbital volume, and the distance from basion to orbitale have measurement errors above 1%, which acts to increase the average error for these orbital variables (Tables 2.4 & 2.5).

Seeds used to estimate volume of the orbit were sifted to ensure that each was roughly the same size, and the same seeds were used at each museum where data were collected. Additional precautions were taken to ensure that the measurement technique was consistent throughout, as it was recognized prior to beginning data collection that some error is inherent in volumetric estimations of the orbit using seed, partially due to the less well defined border in the upper corner of the medial orbital margin (Schultz, 1940). Even with these precautions and the meticulousness with which orbital volume was taken, measurement of this trait is found to be the least repeatable of all variables, with an average difference from the mean measurement of 2.97%.

Craniofacial Variables	Label	Error
Cranial Length	gol	.68%
Cranial Breadth	xcb	.83%
Basion-Bregma Height	bbh	.44%
Basion-Nasion Length	bnl	.82%
Basion-Prosthion Length	bpl	.51%
Nasion-Prosthion Length	nph	.64%
Nasal Height	nlh	.51%
Zygomatic Breadth	zyb	.07%
Average Measurement Error		.56%

Table 2.4: Measurement error for craniofacial variables

Orbital Variables	Label	Error
Orbital Breadth	obb	.46%
Orbital Height	obh	.54%
Interorbital Breadth	dkb	1.36%
Biorbital Breadth	ekb	.52%
Basion-Superior Orbit	bso	.89%
Basion-Orbitale	bio	1.21%
Orbital Depth	obd	.74%
Orbital Frontation	obf	.98%
Orbital Volume	obv	2.97%
Average Measurement Error		1.07%

Table 2.5: Measurement error for orbital variables

Each chapter of this thesis examines different aspects of the orbit, focusing on modern human variation, the relationship between orbital morphology and neighboring craniofacial traits throughout hominin evolution, orbital variation in European samples dating to the Upper Paleolithic, and the relationship among the eyeball, orbit and spherical equivalent refractive error. Because each subdivision uses different samples

and different methods of analysis to test hypotheses and address anthropological questions, the materials and methods section specific to each investigation is presented at the beginning of each chapter.

CHAPTER 3

MODERN HUMAN VARIATION IN ORBITAL MORPHOLOGY

3.1 Samples

Craniofacial data were collected from skulls of individuals representing different modern human ancestral groups, and analyzed to investigate differences in orbital morphology using analysis of variance (ANOVA), Mahalanobis' distance D^2 , and canonical discriminant function analysis. As a result of variation in overall craniofacial anatomy among populations from Sub-Saharan Africa, Western Europe, and East Asia, it is expected that significant differences in the orbit also exist among the three samples used in this investigation. A null hypothesis of no difference is tested using ANOVA, while Mahalanobis' distance and discriminant function analysis are used to examine how these samples differ in orbital morphology, and to understand to what degree the orbits vary among groups in relation to broader craniofacial form. These samples consist of individuals from the Sotho and Zulu tribes from South Africa; the cities of Macau, Guangzhou, Hong-Kong, Xiamen, and Shangi, which lie south of the Yangtze River in the Guangdong and Fujian provinces of China; and from France, Germany, Switzerland, and Italy in Western Europe (Figure 3.1).

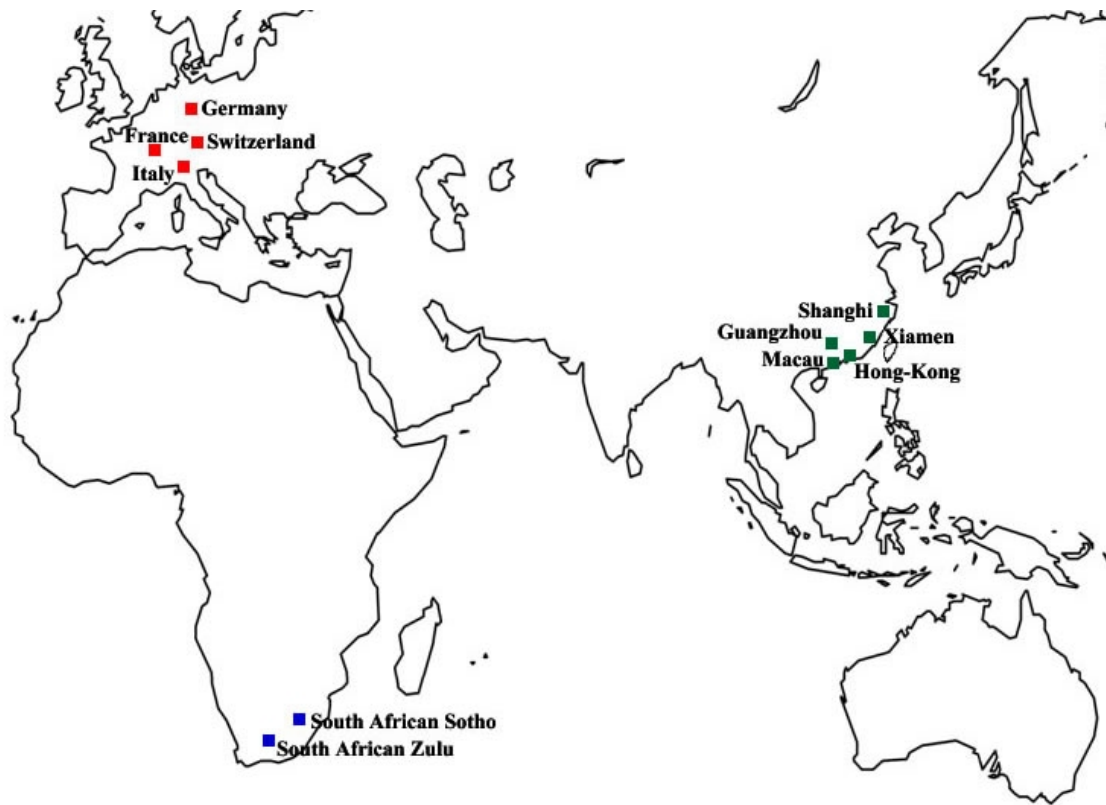


Figure 3.1: Map of regional groups comprising the African, European, and Asian samples

Each sample contains nearly equal numbers of male and female adults, and was selected to reflect a wider range of variation within these regions in order to minimize error that can result from focusing on only one group from a specific locality. For simplicity, these samples will be referred to as African, Asian, and European throughout the remainder of the thesis. These data were collected at the University of the Witwatersrand in Johannesburg, South Africa, and from Le Laboratoire d'Anthropologie Biologique at the Musée de l'Homme in Paris, France (Table 3.1).

Sample	Sample Size	Repository
African	54	UW
Asian	57	MNHN
European	68	MNHN
UW - Dart collection, University of the Witswatersrand, Johannesburg, South Africa		
MNHN- Laboratoire d'Anthropologie Biologique, Musée de l'Homme, Paris, France		

Table 3.1: Samples used in analysis of orbital variation among modern humans

3.2 Statistical analysis

Mahalanobis' distance (D^2), discriminant function analysis, and analysis of variance (ANOVA) are used to investigate variation in orbital morphology among the three samples listed above. Analysis of variance is used to test the null hypothesis of no difference among groups for each individual orbital trait, and provides an accurate picture of how these features differ among Africans, Asians, and Europeans. However, this method is limited in its ability to explain overall differences among them. Discriminant function analysis and Mahalanobis' D^2 are able to provide a more comprehensive depiction of differences in skeletal morphology by focusing on a number of traits simultaneously, and because of this advantage are commonly employed in comparative analyses of modern human populations (Aftandilian *et al.* 1994; Manly, 2004).

Assumptions of the Mahalanobis' Generalized Distance procedure (Mahalanobis, 1936) are equal covariance within each subdivision, and that traits in each subpopulation are normally distributed (Lalouel, 1980). It is often difficult to accurately estimate the covariance in order to check the equality assumption, and due to the nature of anthropological samples the normality assumption is also occasionally not met (Manly, 1994; Penrose, 1954; Pietrusewsky, 1999). Large sample sizes help increase the

robusticity of the method against violation of these assumptions, though even very large samples can still be affected by non-normality, unequal spreads, and inaccurate covariance estimates.

In general, multivariate analyses are not as robust against violations of the equal variance and normality assumptions compared to regression analysis and ANOVA (Manly, 2004), and should therefore be validated in practice by testing for substantial skewness and kurtosis (Lalouel, 1980). As a result, these data were checked for multivariate normality using PRELIS 2.80 (Jöreskog & Sörbom, 1981-2007) and did not show statistically significant levels of skewness or kurtosis for the analysis using only orbital variables (Chi-Square = 3.178, $p = 0.204$) or for that using orbital and other craniofacial traits (Chi-Square = 0.920, $p = 0.631$). Additionally, the pooled within-class covariance matrix is used in the Mahalanobis' D^2 analysis to reduce the chance of violating the equal covariance within subdivisions assumption associated with this method.

An important benefit of these multivariate procedures is that unlike others, such as the Penrose size and shape test, the mean measure of divergence (MMD), and multiple regression analysis, Mahalanobis' D^2 and discriminant function analysis are able to account for the intercorrelation of traits. This is important because if covariance among measures are not identified and accounted for it can lead to an unequal representation of variables.

Many functional systems are housed within the limited area of the human skull, and consequently the orbits covary with other traits of the face and cranium. In fact, the exploration of these relationships is an important part of understanding evolutionary

change in orbital anatomy and will be examined in chapters 4 and 5 of this thesis. In multiple regression analysis it is necessary to throw out one of the correlated variables, but the use of these multivariate statistical methods ensures that potentially valuable data will not be lost as a result of multicollinearity.

Discriminant function analysis also has the added benefit of providing information relating to which traits contribute most to inter-group differences in craniofacial variation. The relative size of the first eigenvalue (λ_1) can be used to determine the amount of sample disparity described by the first discriminant function (Z_1), and therefore which variables are most important for delineating groups (Manly, 2004). Because the first few canonical variates account for a large percentage of population variation, these functions can be plotted with the groups used in the analysis to provide a partial graphical depiction of the relationships among them. However, plots of these functions are only meant to provide a partial representation of the results obtained from the distance analysis (Pietrusewsky, 1999), and will not be viewed to the exclusion of the other statistical results.

3.3 Results of univariate comparisons of orbital variables among groups

The results of individual univariate comparisons of morphological features of the orbit among Africans, Asians, and Europeans reveal that the null hypothesis of no difference is rejected for most orbital characteristics, with the exception of biorbital ($p = 0.102$) and interorbital breadth ($p = 0.585$). The null hypothesis can also not be rejected for the measure of basion-orbitale ($p = 0.055$) at $\alpha = 0.05$, though some degree of variation is recognizable among these three samples. The remaining seven characteristics

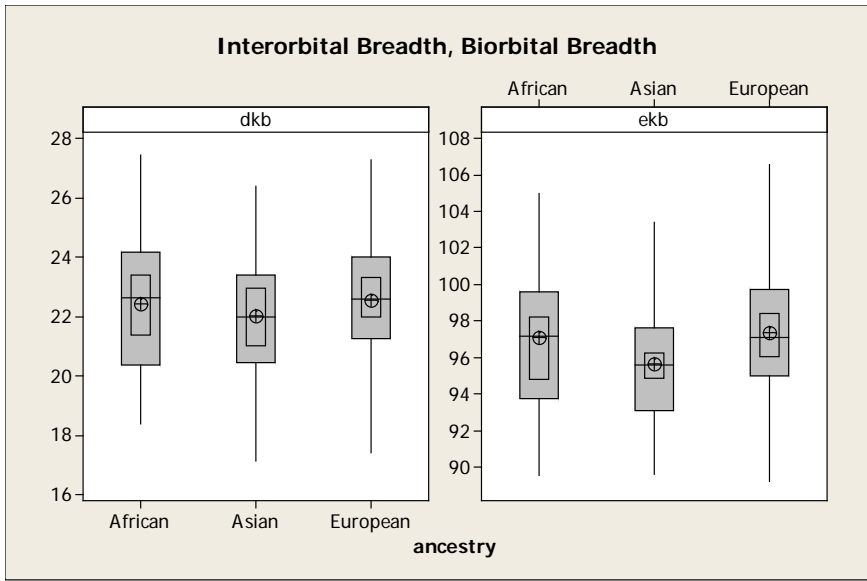
of the orbit are found to be statistically different among groups, with the greatest degree of difference seen in orbital depth, orbital breadth, and orbital volume (Table 3.2). How the African, Asian, and European samples differ with regard to each orbital trait is examined below.

Orbital Dimension	Samples	N	Mean	s.d.	F	p
Interorbital Breadth	African	53	22.341	2.34	0.54	.585
	Asian	57	22.047	1.96		
	European	68	22.535	2.17		
Biorbital Breadth	African	53	97.019	3.99	2.32	.102
	Asian	57	95.804	3.34		
	European	68	97.367	3.89		
Orbital Breadth	African	53	40.134	2.10	8.06	.000
	Asian	57	38.789	1.51		
	European	68	39.755	1.74		
Orbital Height	African	53	33.408	1.90	3.79	.025
	Asian	57	34.272	2.11		
	European	68	33.353	1.83		
Basion-Superior Orbit	African	53	100.36	4.39	6.38	.002
	Asian	57	101.34	3.67		
	European	68	98.910	4.30		
Basion-Orbitale	African	53	86.500	4.24	2.95	.055
	Asian	57	87.750	3.88		
	European	68	85.948	4.90		
Orbital Depth	African	53	47.466	2.34	9.79	.000
	Asian	57	48.770	2.46		
	European	68	46.815	2.53		
Orbital Volume	African	53	25.608	2.09	9.32	.000
	Asian	57	26.854	1.82		
	European	68	27.730	2.97		
Orbital Frontation	African	53	88.596	3.39	3.67	.028
	Asian	57	89.807	2.69		
	European	68	90.142	2.91		

Table 3.2: Results of one-way ANOVA among African, Asian, and European Groups

3.3.1 Interorbital breadth and biorbital breadth

Though differences among these three samples for interorbital breadth (dkb) and biorbital breadth (ekb) are not statistically significant, the pattern of variation in the relative location of group means is consistent for both measures. It can be seen that the European and Asian samples show the greatest degree of divergence, while the mean value for the African sample falls between these two, and shows slightly more affinity to the European group (Figure 3.2).



⊕ - Mean symbol, inside box – median confidence interval, outside box – interquartile range

Figure 3.2: Comparison of interorbital breadth and biorbital breadth (in millimeters)

3.3.2 Index of orbital breadth to orbital height

Though not included in the above univariate tests of no difference among groups due to a violation of the normality assumption for the Asian sample, a ratio of orbital breadth to orbital height ($obb * 100 / obh$) provides an indication of the relative

proportions of the orbital margins, and whether the orbit is more circular or rectangular in shape. With this index a large value reflects a horizontally elongated and vertically shorter orbit (or a more rectangular shape), and a smaller value indicates that the orbit is relatively tall and narrow (a more rounded shape).

This investigation reveals that the African and European samples possess similar orbital shapes, but that the Asian group is characterized by a much taller and narrower orbital outline. Though it is not practical to perform a significance test for this variable due to skewness in the Asian sample, this pattern of inter-group variation in the orbital margins is well known and is commonly used to determine ancestry in skeletal samples as a result of common population differences in the relative size of orbital breadth and orbital height (White, 2000).

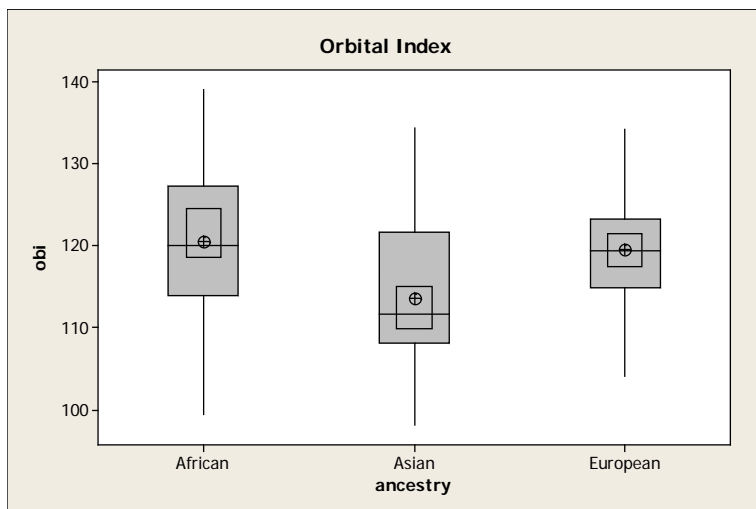


Figure 3.3: Among-group comparison of orbital index

3.3.2 Orbital height and orbital breadth

A closer look at the variables that make up this index reveals that the unique orbital shape in the Asian sample is the result of both a larger orbital height and smaller orbital breadth compared to Africans and Europeans (Figure 3.3). It can also be seen from Figures 3.2, 3.3, and Table 3.2 that Africans are characterized by the opposite orbital shape of that of the Asian group, in which the former possesses a wider more rectangular orbital margin by comparison. This characteristic is primarily the result of a larger average orbital breadth in the African sample, as average orbital height is nearly identical between this and the European group. The European orbital shape is intermediate between Africans and Asians, but shows much more affinity to the African sample.

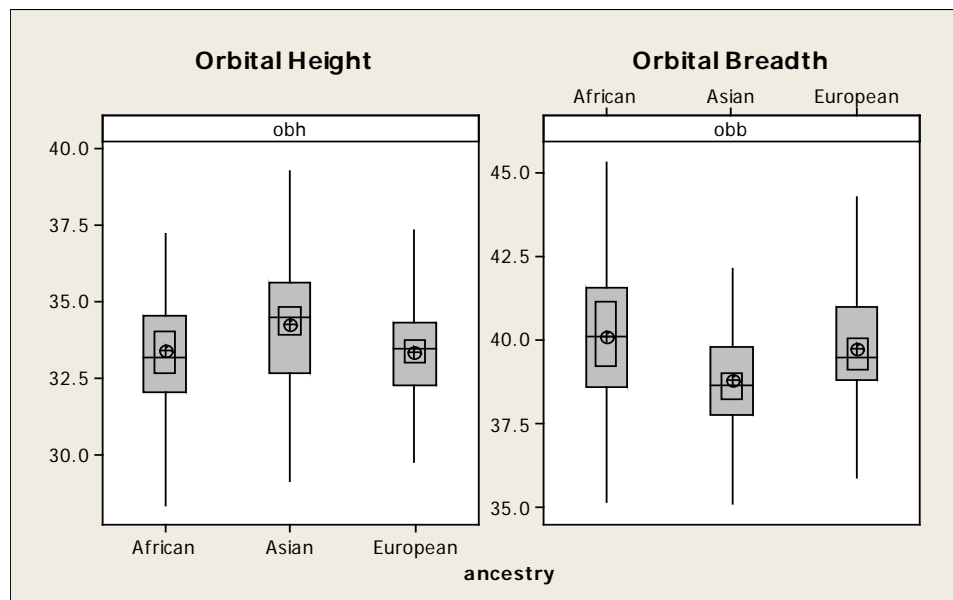


Figure 3.4: Among-group comparison of orbital height, orbital breadth (mm)

3.3.4 Basion-superior orbit and basion-orbitale

The two measurements taken from basion to the superior (bso) and inferior (bio) margins of the orbit yield slightly different results in relation to the null hypothesis of no difference among groups, though the relative location of the mean for Africans, Asians, and Europeans is consistent in both. A one-way analysis of variance shows that the null hypothesis of no difference among groups is rejected for basion-superior orbit ($p = 0.002$) as a result of the greater distance between basion and the superior orbital margins in the Asian group, and relatively small length between these points in Europeans.

Though not significantly different, these samples show the same pattern of inter-group variation in basion-orbitale (bio) as that observed for basion-superior orbit (bso), in which the greatest disparity exists between the Asian and European samples, with the African group mean located between these two extremes. The above pattern indicates that the Asian sample is characterized by a greater degree of orbital projection out away from this mid-cranial point on the base of the skull, and that the orbits are more posteriorly located in the European sample.

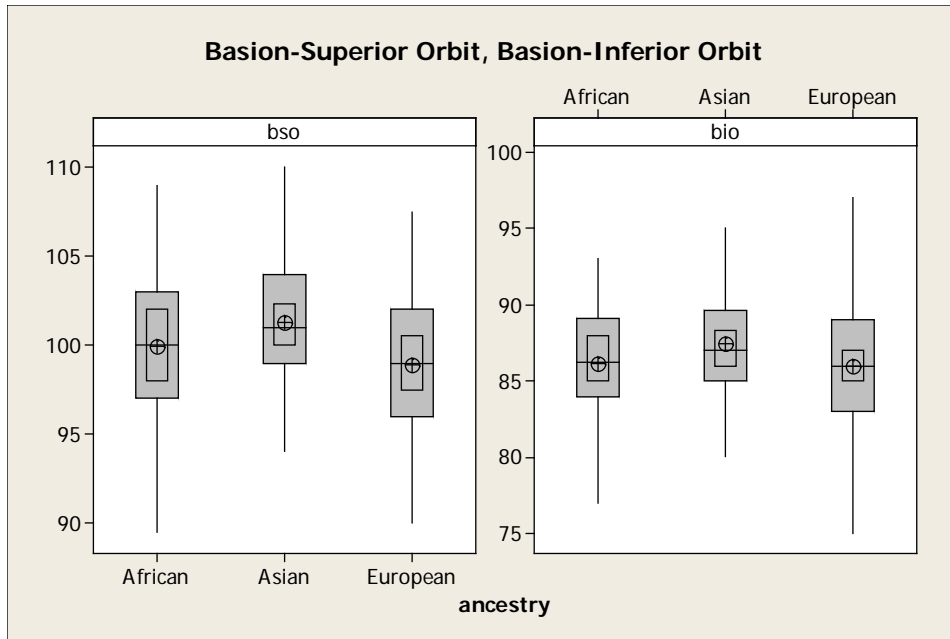


Figure 3.5: Among-group comparison of basion-superior orbit, basion-orbitale (mm)

3.3.5 Orbital depth

Depth of the orbit was obtained by measuring the distance from ectoconchion on the lateral edge of the orbital margins to the most posterior point on the anterior surface of the optic canal. The null hypothesis of no difference among groups for this orbital depth variable is rejected ($p < 0.000$), and it can be seen that a relatively large amount of variation exists among the three samples investigated (Figure 3.5). As with many of the other inter-group comparisons of orbital morphology, the greatest difference in orbital depth is between the Asian and European samples, and again Africans show more affinity to the European form.

The larger orbital depth in this Asian sample corresponds with the above measures of basion-superior orbit and basion-orbitale, which were also found to be larger

in this group. Greater projection of the upper and lower orbital margins out from the base of the skull would be expected to correlate with an anteroposterior elongation of the orbits. The consistently higher values for each trait in the Asian sample, and lower values in the European sample are an indication of this relationship.

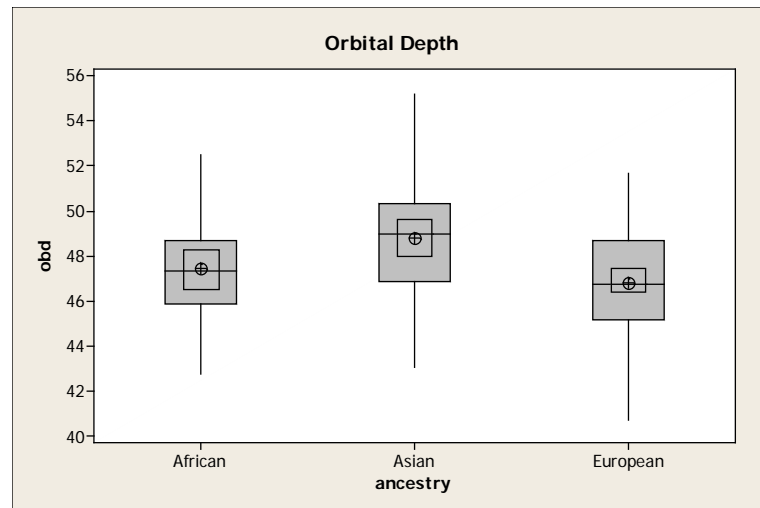


Figure 3.6: Among-group comparison of orbital depth (mm)

3.3.6 Orbital frontation

A test of no difference among groups in the vertical orientation of the orbital margins using one-way analysis of variance shows that at least two of the samples are statistically different ($p = 0.028$). It is easily observable that the African group has the smallest angle formed between the orbital margins and the Frankfurt Horizontal Plane (Figure 3.6), and in fact individual two-sample t-tests show that this angle is statistically different from both Asians ($p = 0.043$), and Europeans ($p = 0.017$). Among them, the orbits are oriented more rostrally in the European sample.

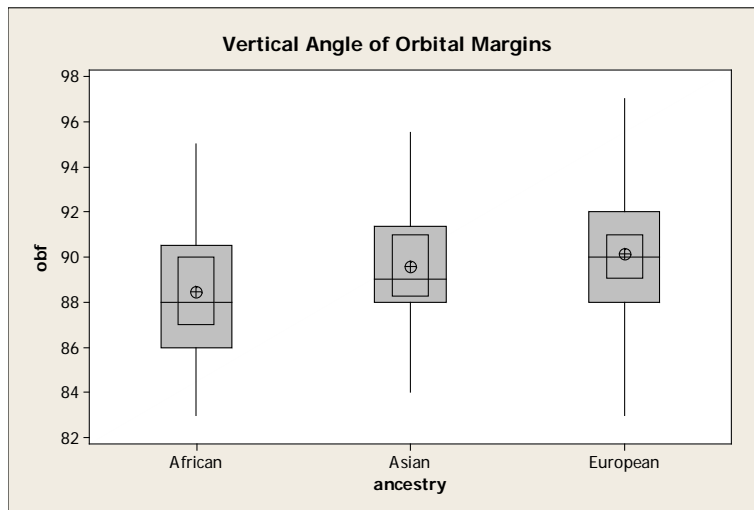


Figure 3.7: Among-group comparison of orbital frontation (angle in degrees)

3.3.7 Orbital volume

In this comparison of orbital size, Europeans are found to possess the largest volume as well as the highest level of intra-group variation (Figure, 3.7). This sample can be seen to differ most in relation to the African group, however a two-sample t-test shows that orbital volume is statistically different between the European and Asian samples as well ($p = 0.003$). This pattern of variation among group means, in which Europeans and Asians share a more similar morphology to the exclusion of Africans, is one of few orbital features shared between these two groups, as most traits have been found to differ most between the European and African samples.

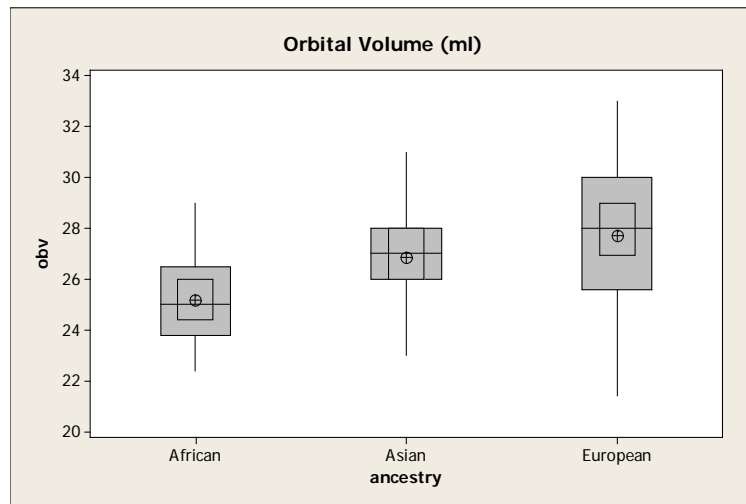


Figure 3.8: Among-group comparison of orbital volume (in milliliters)

Of the nine orbital characteristics examined in this univariate analysis, 67% follow a pattern in which the greatest mean difference is between the Asian and European samples with Africans falling between the two. In orbital features with this pattern of inter-group variation, Africans are more similar to Europeans 83% of the time, and only draw nearer to the Asian sample in 17% of comparisons. This general pattern indicates that with the exception of orbital frontation and orbital volume, Africans and Europeans share a more similar morphology to the exclusion of the Asian sample.

This univariate analysis is valuable for testing null hypotheses of no difference among groups in size, shape, and orientation of the orbits, and to observe patterns of variation among them with regard to each orbital feature. However, understanding the relative contribution of each trait to correct-group classification, interpreting population affinities, and visualizing orbital variation is made easier with the use of multivariate

statistical tools. In the next section the above nine traits are combined to investigate orbital morphology among these African, Asian, and European samples using Mahalanobis' distance and canonical discriminant function analysis. Additionally, variation in orbital characteristics among these groups is assessed in the context of broader differences in craniofacial anatomy.

3.4 Results of multivariate analyses of orbital morphology among groups

3.4.1 Canonical discriminant function analysis

A multiple discriminant function analysis was carried out using nine measurements of the orbit to investigate how well these traits distinguish among the African, Asian, and European samples used in this analysis. The standardized canonical discriminant function coefficients are used to investigate which traits contribute most to group separation, and Mahalanobis' distance matrices to examine overall differences among groups when all orbital characteristics are considered collectively. A discriminant function analysis is also performed using these nine orbital variables as well as nine additional measurements of the neurocranium, mid, and lower face, to investigate the contribution of the orbit to group separation with regard to other aspects of human craniofacial anatomy.

Prior to the investigation, checks of normality, skewness, kurtosis, and the presence of outliers were carried out for each independent variable used in this analysis, both within groups and with all groups combined. A few outliers were identified, though when checked against the original datasheet most were found to be recording errors. The few that were not recording errors were determined to be a natural part of the variation

and were kept in the dataset, however they were not found to have considerable influence on the distribution and mean for those variables. Additionally, as stated in the materials and methods section at the beginning of this chapter, a check of multivariate normality was carried out using the PRELIS 2.80 statistical software package (Jöreskog & Sörbom, 1981-2007), which did not show statistically significant levels of skewness or kurtosis for these orbital variables (Chi-Square = 3.178, $p = 0.204$).

The correlation matrix is used in place of the variance-covariance matrix in this analysis as a result of different units for orbital frontation (in degrees) and orbital volume (in milliliters), while all other variables were measured in millimeters. Because the canonical discriminant function coefficients will not reliably assess the relative contribution of the predictor variables if the independents are highly correlated, multicollinearity in the pooled within-groups correlation matrix of the independent variables was assessed.

As a general rule of thumb multicollinearity is not a problem as long as there are no variables in the correlation matrix with $r > 0.90$ and not several with $r > 0.80$ (Garson, 2008). That criterion is met for this analysis, and it can be seen in the correlation matrix (Table 3.3), that there are no variables with $r > 0.90$, only one with $r > .80$ (bso/bio), and one with a correlation greater than 0.70 (ekb/dkb). Differences between the structure matrix and discriminant function coefficients will also be evaluated as a safeguard against multicollinearity.

	obb	obh	obd	obv	obf	ekb	dkb	bs0	bio
Correlator obb	1.000	.183	.216	.399	.088	.734	.006	.313	.199
obh	.183	1.000	-.098	.133	-.067	.166	.017	.029	-.179
obd	.216	-.098	1.000	.603	.052	.456	.228	.508	.477
obv	.399	.133	.603	1.000	.175	.586	.295	.510	.373
obf	.088	-.067	.052	.175	1.000	.031	-.058	.143	-.177
ekb	.734	.166	.456	.586	.031	1.000	.570	.520	.444
dkb	.006	.017	.228	.295	-.058	.570	1.000	.322	.346
bs0	.313	.029	.508	.510	.143	.520	.322	1.000	.835
bio	.199	-.179	.477	.373	-.177	.444	.346	.835	1.000

Table 3.3: Pooled within-groups correlation matrix

The eigenvalue and Wilks' lambda tables provide information about the efficacy of each discriminant function, or how well they separate cases into their respective groups. The characteristic roots of the discriminant functions indicate that the first accounts for 60% and the second for 40% of the total variance (Table 3.4). The low Wilks' lambda significance value resulting from the chi-square statistic tests shows that the canonical roots do far better than chance at separating groups, and that the model as a whole is effective (Table 3.5).

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.674	59.8	59.8	.635
2	.452	40.2	100.0	.558

Table 3.4: Eigenvalues and percent of variance explained by each function

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	.411	119.051	18	.000
2	.689	50.001	8	.000

Table 3.5: Wilks' lambda and Chi-square tests for each discriminant function

The standardized canonical discriminant function coefficients are used to determine the relative importance of each independent variable to group classification. Coefficients with large absolute values correspond to traits with a greater discriminating ability, and because they are standardized it is possible to compare the relative weight of variables measured on different scales.

This analysis reveals that orbital volume (obv), distance from basion to the superior (bso) and inferior margin of orbit (bio), as well as orbital depth (obd) are most important for their unique contribution to the first discriminant function (Table 3.6). Along the second vector orbital breadth (obb) has the greatest discriminating ability, as do biorbital breadth (ekb), interorbital breadth (dkb), orbital frontation (obf), orbital height (obh), and again the distance from basion to the superior and inferior orbital margins, though in the second discriminant function the relative contribution of these variables is reversed.

	Function	
	1	2
obb	.425	-1.219
obh	.166	.666
obd	.802	.278
obv	-1.082	.026
obf	-.361	.656
ekb	-.583	.719
dkb	.254	-.678
bso	1.273	-.715
bio	-.791	.997

Table 3.6: Standardized canonical discriminant function coefficients

The structure coefficients represent simple correlations between the independent variables and the discriminant functions and do not measure the unique, controlled association of the discriminating variables, as do the standardized discriminant coefficients. Because the structure coefficients show the order of importance of discriminating variables by total correlation in multiple discriminant function analysis, they can also be used to assess the relative importance of each independent variable on each dimension, and along with the functions at group centroids table, are helpful in assigning meaningful labels to these functions.

This analysis indicates that orbital volume, and distance from basion to the superior and inferior orbital margins are most strongly correlated with the first discriminant function (Table 3.7). However, it should be noted that the contribution of basion-orbitale (bio) may be due in part to collinearity with the measure of basion-superior orbit (bso), as it was found that basion-orbitale had a high Wild's lambda value, was not statistically different among groups in the above univariate analysis ($p = 0.055$),

and therefore is not expected to contribute appreciably to the model. The largest correlates with the second discriminant function are orbital breadth, orbital frontation, orbital height, and biorbital breadth. Orbital depth is found to correlate rather strongly with both discriminant functions in the structure matrix.

	Function	
	1	2
obv	-.381	.139
bso	.332	.160
bio	.200	.149
obb	-.020	-.469
obf	-.192	.304
obd	.268	.286
obh	.131	.283
ekb	-.066	-.219
dkb	-.052	-.117

Table 3.7: Structure matrix

ancestry_1	Function	
	1	2
1.000	.641	-.781
2.000	.488	.836
3.000	-1.164	-.074

Table 3.8: Functions at group centroids

Plotting individual cases on the axes formed by the two discriminant functions, in association with the structure matrix and group centroids tables, gives a graphical representation of which traits contribute most to group separation along each dimension of the canonical roots (Figure 3.9). Along the axis of the first discriminant function it is clear that the African and Asian samples are more similar to the exclusion of Europeans, which is predominantly a product of the large negative value for orbital volume (obv) in the first function (Table 3.7).

The distance between basion and the superior (bso) and inferior (bio) margins of the orbit also account for much of the difference between Europeans relative to the other two groups. This is indicated by the high positive value of these two independent

variables in the first discriminant function of the structure matrix, and the location of the European group centroids more toward the negative end of Function 1 (Figure 3.9). Other contributors to the separation of Europeans along the first dimension are a smaller orbital depth and a more obtuse angle formed by the vertical plane of the orbit relative to the Frankfort Horizontal.

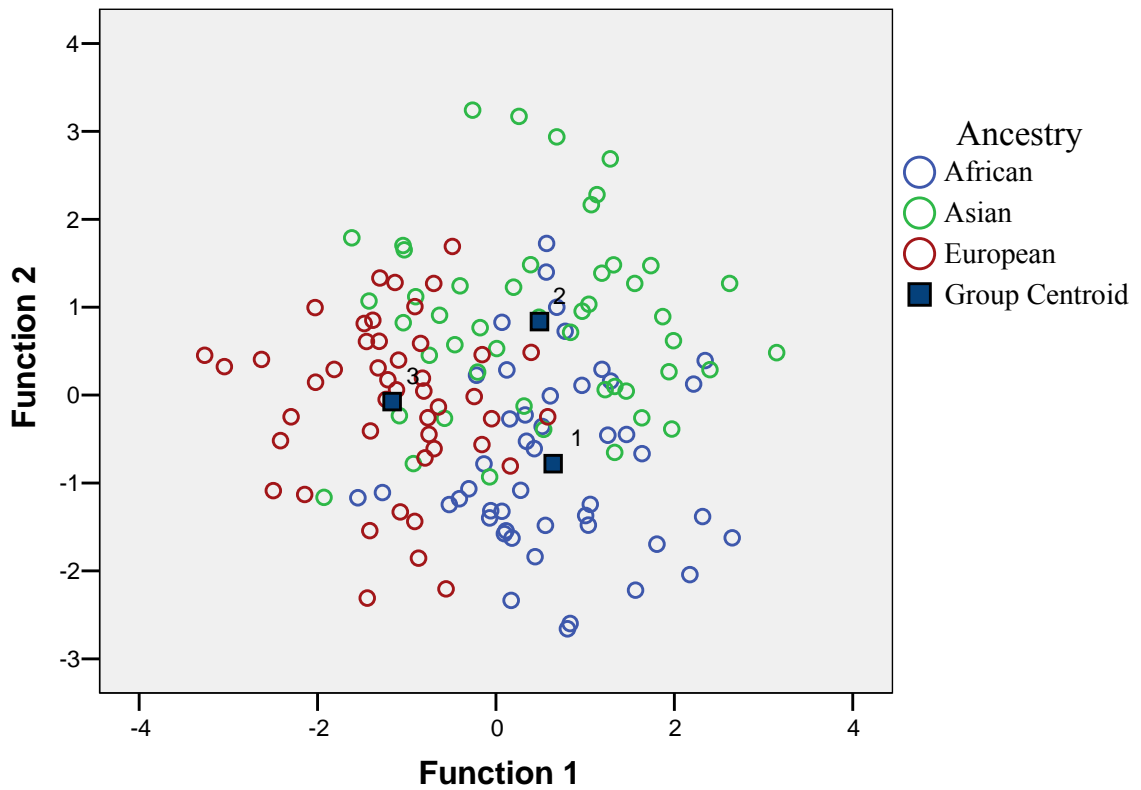


Figure 3.9: Plot of individuals and group centroids along each discriminant axis

Along the second dimension, orbital breadth contributes considerably to group separation and shows that Africans and Asians are most divergent along this axis, indicating between them a wider and narrow orbital breadth, respectively. Interorbital

and biorbital breadth also follow this same pattern in which both traits are wider in Africans and narrower in Asians. The position of the Asian group centroid toward the positive end of the second dimension also indicates that this sample has a more frontated orbital plane, a deeper orbital depth, and a larger orbital height with respect to the other groups, and particularly in comparison with the African sample. These relationships corroborate the differences observed among groups in the previous section using one-way analysis of variance.

3.4.2 Mahalanobis' distance analysis

A Mahalanobis' distance analysis also highlights the pattern of between-group affinities described in the previous univariate comparison of these orbital variables. For example, in the last section Asians and Europeans displayed the most dissimilarity in 67% of comparisons. This pattern is reiterated in this multivariate analysis, which shows that the Asian and European samples have the highest distance value, indicating the greatest overall disparity between groups (Table 3.9).

Samples	Asian	European
African	1.80745	3.19353
Asian		3.70921

Table 3.9: Mahalanobis' distance between-groups comparisons

In the previous section it was determined that Africans are more similar to Europeans in 83% of comparisons, which is not indicated in the above Mahalanobis'

distance matrix, which shows the African and Asian samples to be most similar in orbital morphology. However, this is primarily the result of the large disparity in orbital volume between the African and European samples. When orbital volume is not included in the analysis and distance is determined by the other 8 variables, it is found that overall orbital morphology is most similar between the African and European groups (Table 3.10).

Samples	Asian	European
African	1.98795	0.88047
Asian		2.31137

Table 3.10: D^2 between-groups comparisons (orbital volume excluded)

These univariate and multivariate analyses indicate that several modern human populations exhibit differences in size, shape, and orientation of the orbit. However, the plot of canonical discriminant functions does not fully separate them into clearly distinguishable groups, indicating that these samples possess some level of shared orbital morphology. In the next section, additional cranial and facial variables are added to the discriminant analysis to examine the relative importance of the orbits to group separation, and to assess whether the same pattern of inter-group differentiation exists when comparing these samples using more traits that reflect broader differences in craniofacial anatomy.

3.5 Populations variation in the orbit and broader craniofacial anatomy

3.5.1 Canonical discriminant function analysis

Additional cranial and facial variables were added to this discriminant function analysis to investigate how well orbital characteristics delineate groups in the context of broader craniofacial anatomy. Interorbital and biorbital breadth were not included in this expanded study because they were found to be highly correlated with zygomatic breadth, orbital breadth, upper facial breadth, and to some extent each other. Additionally, a preliminary investigation that included these two variables with the other 14 craniofacial traits showed that they do not substantially contribute to group separation. Basion-nasion length and basion-orbitale were also removed because of multicollinearity and their lack of contribution to the model.

It is clear from the low Wilks' lambda and associated significance values in the tests of equality of group means table that craniofacial traits as a whole are much more variable in relation to most orbital characteristics among these three samples (Table 3.11). For example, with the exception of maximum cranial length (gol), mean differences are considerably larger for all other cranial and facial traits with regard to those of the orbit. Variables with the most potential for discriminating between groups are maximum cranial breadth (xcb), upper facial breadth (ufb), nasal height (nlh), and cranial height (bbh).

	Wilks' Lambda	F	df1	df2	Sig.
gol	.943	4.083	2	135	.019
xcb	.412	96.189	2	135	.000
zyb	.692	29.979	2	135	.000
bbh	.672	32.943	2	135	.000
bpl	.851	11.850	2	135	.000
ufb	.565	52.023	2	135	.000
nph	.803	16.567	2	135	.000
nlh	.611	42.918	2	135	.000
obb	.906	6.999	2	135	.001
obh	.958	2.950	2	135	.056
obd	.901	7.444	2	135	.001
obv	.926	5.364	2	135	.006
obf	.941	4.199	2	135	.017
bso	.909	6.773	2	135	.002

Table 3.11: Tests of equality of group means

The eigenvalues and Wilks' lambda tables produced by this extended discriminant analysis show that the first canonical root alone is highly effective at classifying cases into their respective ancestral group (Tables 3.12 & 3.13). This is indicated by the large eigenvalue and percentage of variance explained by the first dimension. The second function, which is orthogonal to the first, explains less of the variation but is also statistically significant ($p < 0.000$), and the large canonical correlation coefficients show that each is highly correlated with ancestral groups, and accounts for much of the variability in discriminant scores.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3.253	65.3	65.3	.875
2	1.726	34.7	100.0	.796

Table 3.12: Eigenvalues and percent of variance explained by each function

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	.086	314.920	28	.000
2	.367	128.887	13	.000

Table 3.13: Wilks' lambda and Chi-square tests for each discriminant function

Traits with the greatest discriminating ability for the first canonical root in the standardized canonical discriminant function coefficients table are upper facial breadth (ufb), nasal height (nlh), maximum cranial length (gol), and orbital breadth (Table 3.14). For the second discriminant function, maximum cranial breadth (xcb), zygomatic breadth (zyb), and cranial height (bbh) are non-orbital craniofacial traits that contribute most to group separation, while orbital volume (obv) and orbital depth (obd) are also important variables in this dimension.

Orbital frontation (obf) and basion-superior orbit (bso) also add to the discrimination of groups along the first and second functions, respectively. This indicates that despite the greater degree of variation among modern human populations in

non-orbital cranial and facial traits, as indicated by the test of equality of means table (Table 3.11), characteristics of the orbit also vary and are useful for assigning cases to their appropriate group.

	Function	
	1	2
gol	-.499	.083
xcb	.296	-.981
zyb	.079	.551
bbh	.277	.516
bpl	.029	.171
ufb	.745	.136
nph	-.261	.081
nlh	.651	.243
obb	-.486	-.331
obh	-.059	.262
obd	-.062	.494
obv	-.128	-.545
obf	.300	.232
bs0	-.216	-.387

Table 3.14: Standardized canonical discriminant function coefficients

The structure matrix, functions at group centroids table, and plot of individuals along the discriminant dimensions help to visualize and assign meaningful labels to these canonical roots (Tables 3.15, 3.16, and Figure 3.10). One can see a clear trend along the first dimension in which Asians and Europeans are characterized by a much broader and taller cranium, as well as a taller and more orthognathic face in relation to the African sample. Orbital characteristics that contribute to separation along the first discriminant axis are orbital breadth (obb), orbital frontation (obf), and orbital volume (obv), although their contribution relative to other craniofacial traits is limited.

	Function	
	1	2
xcb	.550	-.505
ufb	.486	-.043
nlh	.398	.265
zyb	.359	.119
bbh	.319	.302
bpl	-.206	.147
obb	-.148	-.136
obf	.138	-.002
obv	.133	-.112
gol	-.127	.068
obd	.014	.252
bso	-.032	.237
nph	.219	.228
obh	.056	.139

Table 3.15: Structure matrix

Ancestry	Function	
	1	2
African	-2.442	-.058
Asian	1.234	1.536
European	1.380	-1.688

Table 3.16: Functions at group centroids

In contrast to the first discriminant function, which separates the African group from the other two, the second divides the European from the Asian sample. Along this dimension, the primary difference between individuals from Asia and Europe relates to variation in height and width of the cranium and length of the face. However, outside of these few disparate features, characteristics of the orbits contribute more to separation along the second discriminant axis than the first, and show that Europeans possess larger and wider orbits in contrast to the relatively tall, narrow, and deep orbits of the Asian sample.

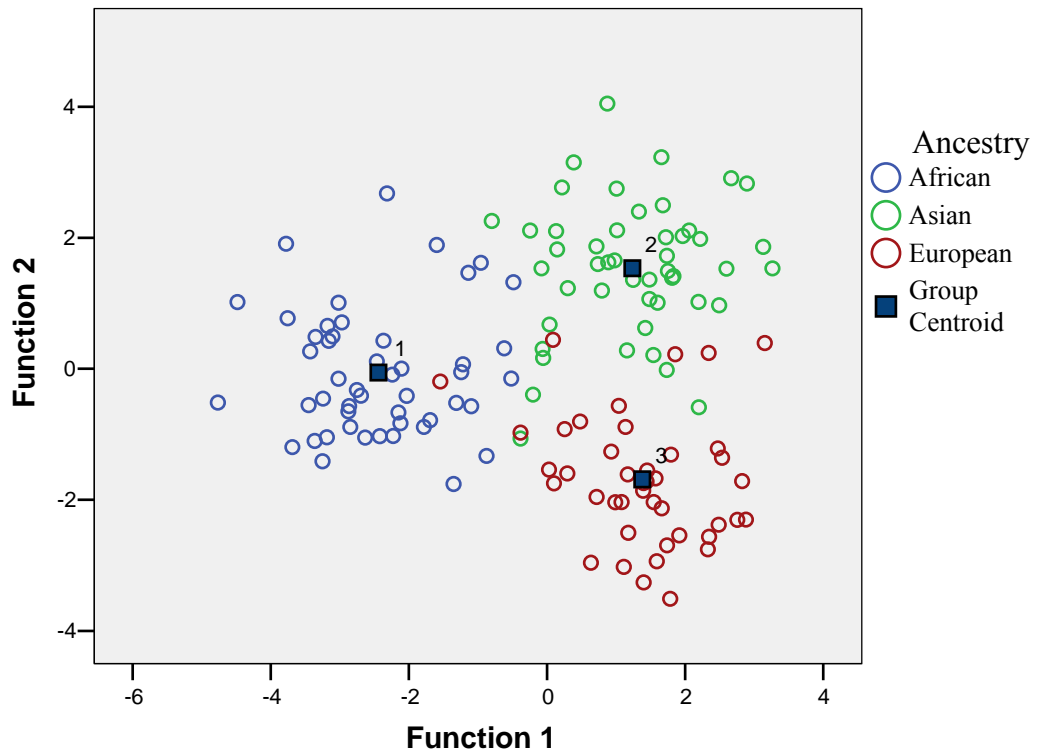


Figure 3.10: Plot of individuals and group centroids along each discriminant axis

The first discriminant function primarily separates groups based on features of the face and cranium, while separation along the second dimension is largely the result of differences in orbital morphology. This pattern shows that the second discriminant function captures much of the same pattern of population variation in orbital morphology described in both the univariate analysis of variance, and discriminant function analysis when only orbital traits were used.

3.5.2 Mahalanobis' distance analysis

When orbital along with other craniofacial traits were included in the above discriminant function analysis, Asians and Europeans were most similar to the exclusion

of the African sample, however once these common features of the face and cranium were accounted for by the first canonical root, the European and Asian groups became the most divergent. Along this second dimension the African sample was located between Asians and Europeans, and showed slightly more affinity to the European sample. This reversal in inter-group affinity is also indicated by a comparison of the Mahalanobis' D^2 matrices when all variables are considered (Table 3.17), and when only traits of the orbit are included in the analysis (Table 3.18).

Samples	Asian	European
African	20.9960	31.2139
Asian		15.4776

Table 3.17: D^2 between-groups comparisons (orbital and other craniofacial traits)

Samples	Asian	European
African	1.80745	3.19353
Asian		3.70921

Table 3.18: D^2 between-groups comparisons (orbital traits only)

3.6 Summary

Morphological characteristics of the orbit that are most variable among the African, Asian, and European samples include orbital volume (obv), orbital depth (obd), basion-superior orbit (bso), and orbital breadth (obb), and are also those that contribute most to group separation in the multivariate analyses. Interorbital breadth (dkb), biorbital

breadth (ekb), and basion-orbitale (bio) were not found to be statistically different among these samples, however the low significance value for basion-orbitale in a one-way analysis of variance ($p = 0.055$) indicates that some degree of divergence exists among them. Additionally, while a significance test was not carried out for “shape” of the orbital margins, it is clear that general differences exist among groups. The most notable difference is between the Asian and African samples, in which the former possesses high and narrow orbits (a more rounded shape), and the latter is characterized by lower and wider orbital margins (a more rectangular shape).

The above univariate and multivariate analyses indicate that orbital morphology is variable among Asian, African, and European populations, however fewer differences exist among them in relation to overall craniofacial form. The higher Wilks' lambda and lower significance values of non-orbital traits (Table 3.11), as well as the greater degree of separation among groups in the discriminant functions plot (Figure 3.10), and Mahalanobis' distance matrix (table 3.17), indicate that less variation exists among African, Asian, and European populations in orbital morphology relative to other traits of the face and cranium.

Although both sets of features are useful for ascribing individuals to their appropriate ancestral group, the different patterns of affinity among them when craniofacial traits are used, and when only orbital traits are used in the analysis, indicates that these features do not vary in strict association with adjacent anatomical units in modern humans. If size and shape of the orbits were determined solely by contiguous craniofacial characteristics, it is expected that the same relationship would exist among each sample regardless of which suite of traits are included in the analysis. This indicates

that the orbit is not tightly integrated with the skull as a whole, but suggests instead that this feature interacts multifariously with different structural and functional components of the face and cranium.

Though the orbits vary somewhat independently of adjacent traits across modern human groups, this feature would be expected to vary in association with neighboring cranial and facial features throughout hominin evolution as a result of marked changes in craniofacial form that occur during this 5-7 million year time period. In the next chapter, the relationship between orbital and contiguous craniofacial characteristics will be examined in the context of long-term trends of encephalization and reduced facial prognathism during human evolution.

CHAPTER 4

EVOLUTIONARY CHANGE IN THE HOMININ ORBIT

4.1 Samples

Data were obtained from past hominin groups and a sample of *Pan troglodytes* to investigate temporal change in the orbits and their relationship to neighboring features in the context of long-term trends of cranial expansion and facial reduction. Measurements were taken on skulls of wild-shot chimpanzees from Abong Mbong, Ebolwa, and Djaposten, Cameroon, kept at the Cleveland Museum of Natural History. This sample, characterized by a more ancestral cranial and facial form, is used as an outgroup in order to understand orbital morphology in an earlier phase of hominin evolution.

Though chimpanzees have certainly undergone evolutionary changes since the bifurcation of these two lineages, they possess many ancestral features characteristic of early hominins. During human evolution, a marked increase in brain size has occurred in association with a reduction in tooth size and the degree of facial prognathism. The small brain and highly prognathic face of modern chimpanzees represents an earlier level of morphological complexity. Including this species as an early representative of this grade shift in hominin craniofacial form allows for a better understanding of how the orbit varies in association with these long-term evolutionary trends.

Craniofacial measurements were taken on the original fossils of *Australopithecus africanus* (STS 5, STS 71, STW 505) at the University of the Witwatersrand in Johannesburg, South Africa, to represent an early hominin grade in this analysis. To capture variation in craniofacial form in hominins with a greater degree of encephalization and reduced lower facial projection, craniometric data were obtained from the original fossil of *Homo erectus* (SK 847) at the University of the Witwatersrand, from a cast of *Homo erectus* at the Cleveland Museum of Natural History, and from published measurements taken from the original fossils of KNM-ER 3733 and KNM-ER 3883 (Wood, 1991).

Recent studies have found that despite many differences between anatomically modern humans and Neanderthals, the latter has retained a number of archaic traits in midsagittal shape of the face and cranium (Bruner, Manzi, Arsuga, 2003; Bruner *et al.* 2004). Because of the greater projection of the midface and more ancestral cranium in this species, casts of three Neanderthal skulls were measured at the University of the Witwatersrand to represent an archaic *Homo* grade.

Four skulls of individuals representing anatomically modern humans from the European Upper Paleolithic were measured at the Musée de l'Homme in Paris, and at the Musée d'Anthropologie Préhistorique in Monte Carlo, Monaco. These include Grotte des Enfants 4 & 5, Cro-Magnon 1, and the exceptionally well-preserved Abri Pataud 1. Individuals in this sample possess large crania and retracted faces that sit below the anterior cranial fossa, considered autapomorphies of anatomically modern *Homo sapiens* (Bastir *et al.* 2008; Lieberman, 2002).

This sample represents the most morphologically complex form in this analysis of correlations between the orbit, cranium, and lower face, and was chosen in lieu of a recent modern human sample because a major anthropological question concerns how the orbit changes in association with increased cranial size and reduced facial length throughout hominin evolution. Since the Upper Paleolithic, and particularly through the Holocene, cranial capacities have decreased by 95 –165 mL for males and 74 – 106 mL for females (Henneberg, 1988). Because of this more recent decrease in cranial size, the Upper Paleolithic group represents more accurately the last grade in this series, and is used to represent more modern skulls characterized by a greater degree of encephalization and reduced facial prognathism (Table 4.1).

Species	Sample Size	Actual/Cast	Repository
<i>Pan troglodytes</i>	30	Actual	CMNH
<i>Australopithecus africanus</i>	3	Actual	UW/TM
<i>Homo erectus</i>	4	Actual/Cast	UW/CMNH*
Archaic <i>Homo</i>	3	Casts	UW
Anatomically modern <i>Homo sapiens</i>	4	Actual/Casts	MNHN/MAMC

UW - University of the Witswatersrand, Johannesburg, South Africa

MNHN - Muséum national d'Histoire naturelle, Musée de l'Homme Paris, France

MAMC- Musée d'Anthropologie Préhistorique, Monte Carlo, Monaco

TM - Transvaal Museum, Pretoria, South Africa

CMNH – Cleveland Museum of Natural History, Cleveland, Ohio, USA

* Measurements for KNM-ER 3733 and KNM-ER 3883 from Wood (1991)

Table 4.1: Samples used in investigation of cranial, lower facial, and orbital change

4.2 Statistical analysis

In this chapter, the above samples are used to investigate how orbital morphology varies in association with long-term trends of encephalization and reduced facial

prognathism, characteristic of hominin craniofacial evolution. It is predicted that the orbits vary in conjunction with these converging features of the skull, and that specific changes result from the posterior movement of the face, and expansion of the cranium out over the orbits during this long period of evolutionary change. Cranial size in this temporal series is estimated from the geometric mean of cranial length, cranial breadth, and cranial height (length * breadth * height)^{.33333}, and lower facial projection as the distance from basion to prosthion.

Four changes in orbital morphology are predicted to occur in association with encephalization and reduced facial prognathism. A null hypothesis of no relationship is tested with separate regression analyses for each orbital variable against measures of cranial size and facial prognathism, and is rejected if the relationship is significant at $\alpha = 0.05$, and if the direction of this covariation is in agreement with the a priori predictions.

Because cranial size increases while facial prognathism decreases throughout human evolution, and because these two variables are highly correlated in this dataset (Pearson correlation = -0.948, $p < 0.0000$), a ratio of Cranial Size to Facial Projection, or a Craniofacial Index (CFI), is used to investigate how the orbits vary with these features in each regression analysis. This index captures long-term trends of encephalization and reduced facial prognathism in the sample, and represents individuals with large crania and retracted faces (a more modern craniofacial form) with a high CFI, and individuals with small crania and large projecting faces (characteristic of earlier hominin evolution) with a low CFI.

Because each species, and even temporal groups within the same species, are not of equal morphological size, all linear measurements were size-adjusted prior to the

analysis. This was done to remove any confounding effects of size difference among species and to allow the comparison of orbital traits, which would otherwise simply reflect overall size differences among groups. This adjustment was carried out by dividing each individual by the geometric mean of 11 variables of the skull, following the methods of Jungers *et al.* (1995). This technique is part of the Mosimann framework (Darroch & Mosimann, 1985), which has been effectively applied in a number of different studies (exp. Ackerman, 2005; González-José *et al.* 2005; Lieberman *et al.* 2000) and is superior to other methods of size-adjustment including C-scores, residual adjustments, and discarding the first principal component (PC1) of the logged variance-covariance matrix (Jungers *et al.* 1995).

4.3 Evolutionary change in the hominin face and cranium

In this chapter the orbit is examined among samples representing different grades of variation in relative size of the cranium and face to investigate how this feature varies in relation to long-term changes in craniofacial anatomy in the hominin lineage. It is presumed that the orbits vary in patterned ways in association with trends of encephalization and reduced facial prognathism as a result of morphological integration among these structural and functional cranial components during evolutionary morphogenesis (Bruner, 2007; Lieberman, McBratney, Krovitz, 2002; Lieberman, Krovitz, McBratney, 2004; Moss & Young, 1960). More specifically, it is predicted that the orbital margins move posteriorly, the vertical angle of the orbit becomes more frontated, and that the orbit becomes vertically shortened and horizontally elongated as the face retreats and the brain expands and grows out over the eyes.

A decrease in orbital depth and orbital volume is also predicted in association with these craniofacial trends, though due to poor preservation of the internal orbit of most hominin fossils it is not currently possible to test these predictions. However, more recent evolutionary change in the internal anatomy of the orbit including depth and volume will be investigated in the next chapter. Change in these and other features of the orbit are investigated among Western European groups dating to the Upper Paleolithic, which are characterized by better preservation of the orbital anatomy and are made up of larger samples within each temporal group.

Encephalization and reduced facial prognathism are two trends that best characterize craniofacial change during hominin evolution. These large-scale shifts in skeletal anatomy involve an absolute and relative increase in brain size, and a reduction in the face, both in terms of its size relative to the brain, and its anterior-posterior position relative to the cranial base (Lieberman, Krovitz, McBratney, 2004). These trends of relative size increase in the crania, and decrease in relative size of the lower face are easily observable across *Pan*, *Australopithecus*, and *Homo* (Figures 4.1 and 4.2).

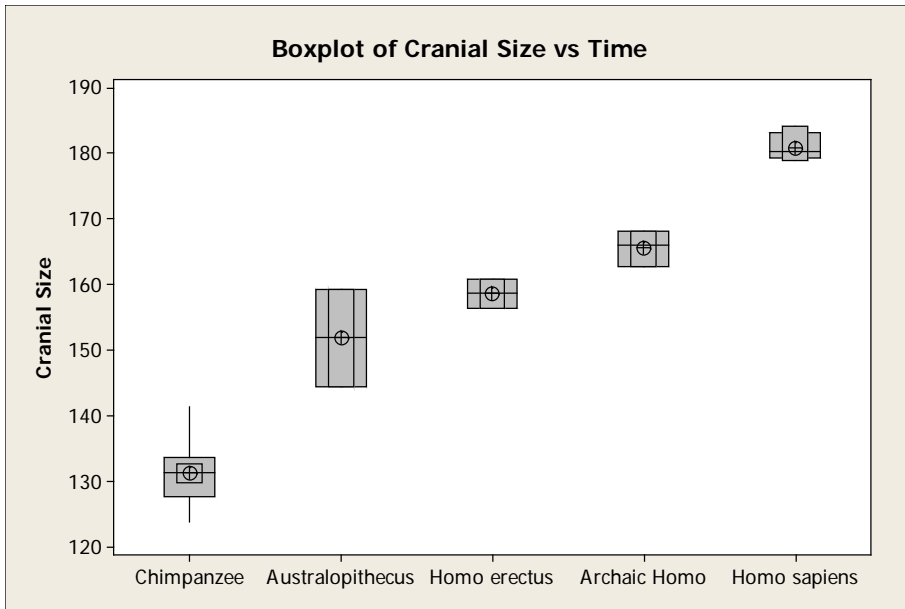


Figure 4.1: Grade shift in relative cranial size in the hominin lineage

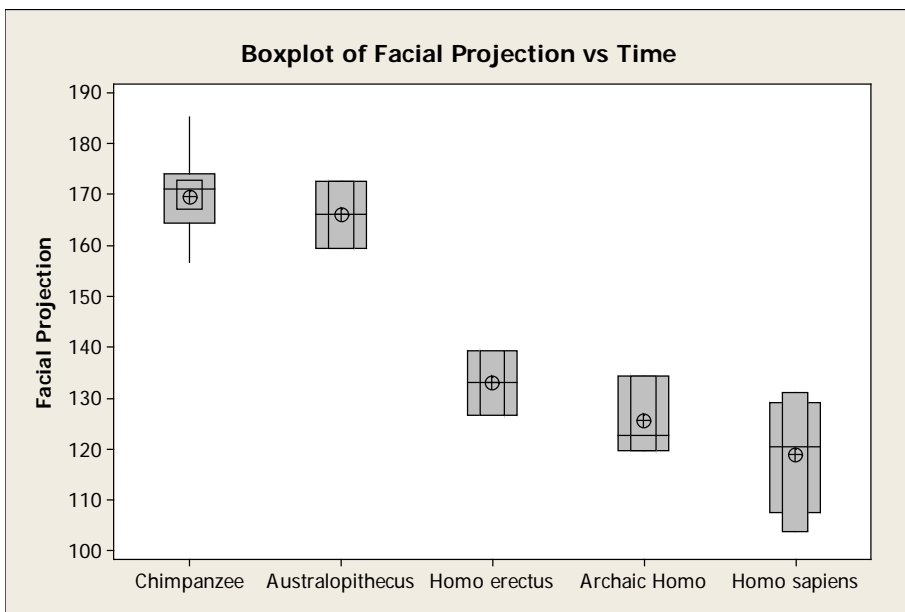


Figure 4.2: Grade shift in relative facial prognathism in the hominin lineage (mm)

Size Adjusted Feature	Species	N	Mean	s.d.
Cranial Size	<i>Pan troglodytes</i>	30	131.29	4.27
	<i>Australopithecus</i>	2	151.83	10.55
	<i>Homo erectus</i>	2	158.60	3.15
	<i>Archaic Homo</i>	3	165.58	2.68
	<i>Homo sapiens</i>	4	180.89	2.23
Facial Prognathism	<i>Pan troglodytes</i>	30	169.60	6.34
	<i>Australopithecus</i>	2	165.99	9.31
	<i>Homo erectus</i>	2	133.00	9.05
	<i>Archaic Homo</i>	3	125.54	7.66
	<i>Homo sapiens</i>	4	119.00	11.40

Table 4.2: Descriptive statistics: relative cranial size and facial prognathism

Predictions relating to how orbital anatomy is expected to vary in association with these long-term craniofacial trends in hominin evolution are evaluated by testing a null hypothesis of no relationship between orbital features and contiguous craniofacial characteristics among chimpanzees and hominin species with varying degrees of encephalization and facial prognathism. The null hypothesis of no relationship between features of the orbit and adjacent craniofacial traits was tested using separate regression analyses with each orbital trait as the dependent variable, and an index of cranial size to facial prognathism as the independent variable.

4.4 Predicted changes in anatomical features of the orbit

Most mammalian species including non-human primates, are characterized by long faces and low sloping foreheads that protect a brain positioned behind the orbits (Enlow & Hans, 1996). However, throughout hominin evolution the cranial base has

flexed in association with neurocranial expansions while the alveolar process and nasomaxillary complex have shifted posteriorly toward them, to the extent that in anatomically modern humans the orbits and lower face are tucked up under the anterior cranial base (Lieberman, McBratney, Krovitz, 2002; Lieberman, Ross, Ravosa, 2000; Bastir et al. 2008). These changes raise questions concerning how size, shape, and orientation of the orbits change in association with the coalescence of these craniofacial characteristics during human evolution.

Three specific changes are predicted in the external anatomy of the orbits in association with encephalization and reduced facial prognathism throughout the evolution of the hominin lineage. These, along with a summary of null hypotheses tested, are listed below.

- 1) It is predicted that facial reduction contributes to a posterior migration of the orbital margins relative to basion, with most of this backward movement occurring in the inferior segment as a result of its shared anatomy with the nasomaxillary complex. The superior orbital margins are also projected to move posteriorly as the entire face retreats, however they are assumed to vary less in association with CFI as a result of cranial expansion above the orbits, which would act to restrict posterior movement of the upper orbital region.
- 2) The expected result of differential movement in the relative position of the superior and inferior orbital margins is a more obtuse angle of the orbit relative to the Frankfurt Horizontal Plane. Frontation of the orbital margins is predicted to occur as the brain fills the space above the orbits, while at the same time lower facial retraction moves the inferior orbital margins posteriorly. Increased orbital

frontation as a response to an increase in relative brain size and/or a reduction in palatal length and maxillary recession has been suggested by Cartmill (1970), and Ross (1995).

- 3) Lastly, it is predicted that the orbital margins become shorter and wider in response to the posterior migration of the face and forward movement of the cranium out over the orbits, resulting in their becoming horizontally elongated and vertically compressed, or more rectangular in shape.

4.4.1 Summary of predictions and null hypotheses

- 1) Predicted Result – Negative relationship between basion-superior orbit, basion-orbitale and the craniofacial index (CFI)
Ho: No relationship between basion-superior orbit vs. CFI
Ho: No relationship between basion-orbitale vs. CFI
- 2) Predicted Result – Positive relationship between orbital frontation and CFI
Ho: No relationship between orbital frontation vs. CFI
- 3) Predicted Result – Positive relationship between orbital breadth and CFI
– Negative relationship between orbital height and CFI
– Positive relationship between Orbital Index and CFI
Ho: No relationship between orbital size/shape and CFI

4.5 Results of regression analyses: orbital variables vs. craniofacial index

The result of these regression analyses indicate that the orbits vary in relation to cranial expansion and reduced facial prognathism, and that predicted changes in orbital morphology as a result of their position between these converging traits, are supported by the direction and strength of these relationships (Table 4.3).

Variables	N	Coefficient	t	p	R ²
1) Basion-Superior Orbit	43	-0.10072	-2.35	0.023	11.90%
Basion-Orbitale	43	-0.22840	-6.97	0.000	54.20%
2) Orbital Frontation	41	0.11823	4.04	0.000	29.50%
3) Orbital Breadth	44	0.08667	6.83	0.000	51.40%
Orbital Height	44	-0.05741	-4.48	0.000	31.30%
Orbital Index	44	0.40793	8.92	0.000	64.40%

Table 4.3: Results of regression analyses, orbital variables vs. craniofacial Index (CFI)

The null hypothesis of no change in position of the orbital margins is rejected for both basion-superior orbit ($p = 0.023$) and basion-orbitale ($p < 0.000$), and it can be seen from the lower level of significance and smaller R² value that the superior orbital margins vary less in association with changes in the face and cranium. This dichotomy between the superior and inferior orbital margins is also apparent when these traits are regressed separately against cranial size and facial length (Table 4.4).

Orbital Variables	Cranial Size			Facial Prognathism		
	t	p	R ²	t	p	R ²
Basion-Sup. Orbit	-0.86	0.395	1.8%	3.22	0.002	19.8%
Basion-Orbitale	-4.68	0.000	34.8%	10.66	0.000	73.0%
Orbital Frontation	4.78	0.000	37.0%	-4.19	0.000	30.5%
Orbital Breadth	6.24	0.000	46.4%	-7.45	0.000	55.2%
Orbital Height	-4.80	0.000	33.9%	2.88	0.006	15.5%
Orbital Index	8.63	0.000	62.4%	-7.68	0.000	56.7%

Table 4.4: Regression analysis of orbital variables vs. cranial size & facial projection

Both the superior and inferior orbital components are positively correlated with facial prognathism, to the extent that reduction in this feature explains 73% of the variance in basion-orbitale, though only about 20% in basion-superior orbit. Basion-orbitale is also reduced in association with an increase in cranial size, but this relationship is not found to be significant in regard to the superior orbital margins ($p = 0.395$). This incongruity is likely the result of cranial expansion offsetting the posterior retraction of the upper orbital area.

The null hypothesis of no change in vertical orientation of the orbit is also rejected ($p < 0.000$), as the orbit becomes more frontated in association with increased cranial size and decreased facial prognathism. The relationship between the orbital angle and these craniofacial features is also found to be approximately equal, indicating that orbital frontation may be equally influenced by expansion of the frontal lobes above, and retraction of the maxilla below these features.

In addition to the role of cranial expansion and reduced lower facial protrusion in increasing the orbital angle among members of this gradistic scheme, basicranial flexure (Ross & Ravosa, 1993) and a more orthograde posture (Daebelow, 1929), which increase during hominin evolution, have also been proposed as factors influencing orbital orientation (Lieberman *et al.* 2000). For example, significant negative correlations have been found between the cranial base angle and degree of orbital frontation among haplorhines ($r = -0.43$) and anthropoids ($r = -0.52$), meaning that the orbits become more frontated in species with a greater degree of cranial base flexure (Ross, 1995).

Ross (1995) also finds a relationship between orthogrady and orbital frontation in strepsirhines and platyrrhines, though a causal relationship between these variables was not supported. Rather, orbital frontation is considered to be more the result of increased cranial base flexure and enlargement of the temporal lobes, which help explain the extreme frontation of the orbits in anthropoids. The current research also corroborates these findings, as it is the species with larger crania, and more developed frontal lobes (Bruner, 2003; Wu *et al.* 2007) that also possess the highest orbital angle. However, these data also suggest that reduced facial prognathism is an important contributor to the degree of orbital frontation, at least among hominins, though certainly the effects of orthogrady, cranial base flexure, expansion of the frontal lobes, and posterior movement of the maxilla are not mutually exclusive.

It was predicted that orbital height would decrease and orbital breadth increase in association with the cranium expanding out over the orbits and the lower face migrating posteriorly toward them over the course of human evolution. This is supported by a significant positive relationship between the CFI and orbital breadth ($p < 0.000$), and a negative relationship between CFI and orbital height ($p < 0.000$). The result of this shift in relative size between orbital height and orbital breadth is a more rectangular shape of the orbital margins.

Comparing skulls of *Australopithecus africanus* and anatomically modern humans from the European Upper Paleolithic, which display orbital features characteristic of earlier and later hominins, respectively, it can be seen that the orbits become more rectangular and appear to slope inferolaterally away from nasion (Figure 4.3). Change in

the orbital angle in the coronal plane was not investigated as part of this research, though viewed anteriorly members of this later grade appear to possess an orbital shape and orientation that differs from those of earlier forms.



Frontal view of Sts 5



Frontal View of Cro-Magnon 1

Figure 4.3: Comparison of orbital shape: *Australopithecus africanus* vs. *Homo sapiens*

This midfacial configuration characterized by short and elongated orbits that slope moderately downward away from nasion, is also observable in anatomically modern humans from Far East Asia dating to the Mesolithic period (Figure 4.4).

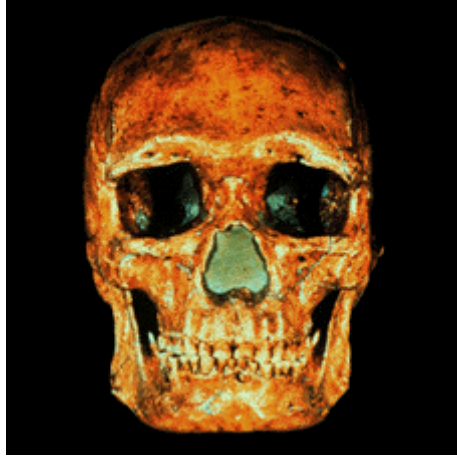


Figure 4.4: Image of Shandingdong (Upper Cave) - From Brown (1998-2005)

The similar shape and orientation of the orbits in skulls of individuals from the Upper Paleolithic and Mesolithic in both Europe and the Far East indicate that a common pattern of temporal change in craniofacial anatomy that occurs following this general time period in Europe, Asia, Africa, and Australia (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Henneberg & Steyn, 1993; Lahr & Wright, 1996; Smith *et al.* 1985, 1986; Wu *et al.* 2007), may have originated earlier, and in response to cranial expansion and posterior movement of prosthion and the entire nasomaxillary complex during hominin evolution.

4.6 Summary

Throughout hominin evolution a considerable increase in cranial size has occurred in association with a reduction in facial size and prognathism. Variation in orbital morphology has not previously been investigated in the context of these morphological shifts, but is important to understand as a result of the orbits position amid the expanding

neurocranium and retracting lower face. This current investigation reveals that the orbital margins vary in association with these long-term evolutionary changes, becoming vertically shorter, horizontally elongated, more frontated, and retracted relative to basion, with a greater degree of reduction in the inferior orbital margins.

This analysis provides knowledge of how the orbits change in association with long-term evolutionary trends in the hominin lineage, but are limited in the extent to which change in the internal anatomy of the orbits can be understood, due to a limited hominin fossil record and poor preservation of the fragile bone comprising the orbital walls. In the next chapter, orbital variation is examined in the context of temporal change in craniofacial anatomy across Western European groups dating to the Upper Paleolithic. These samples comprise a larger number of individuals with more complete internal orbital cavities, which facilitates a greater understanding of recent evolutionary change in orbital morphology and how this feature varies in association with neighboring craniofacial characteristics throughout the last 30,000 years in this region.

CHAPTER 5

EVOLUTIONARY CHANGE IN THE HOMININ ORBIT: UPPER PALEOLITHIC TO PRESENT

5.1 Samples

This chapter expands on the previous analysis of orbital form in relation to evolutionary changes in the face and cranium, but focuses on a more condensed time period using well-preserved individuals from more groups within this sequence, with the aim of understanding recent evolutionary change in the orbit of our own species. This analysis is carried out using samples of European *Homo sapiens sapiens* from 6 different time periods dating back to the Upper Paleolithic (Table 5.1), and tests a null hypothesis of no change in orbital morphology within this temporal series. Additionally, orbital variation is examined in the context of cranial and facial shape changes that characterize the last 30,000 years of evolution in this region.

Time Period	Years Before Present	Sample Size	Repository
Upper Paleolithic	35,000 – 12,000 b.p.	4	MAMC/MNHN
Epipaleo-Mesolithic	12,000 – 7,000 b.p.	4	MSN/ MNHM
Neolithic	7,000 – 4,500 b.p.	39	MSN/MNHN
Copper Age	4,500 – 4,100 b.p.	17	MSN/MAE
Bronze/Iron Age	4,100 – 2,700 b.p.	20	MSN/MNHN
Modern	< 500 b.p	58	MNHN

MNHN - Musée National d'Histoire Naturelle, Musée de l'Homme Paris, France
MAE - Museo di Antropologia ed Etnografia, Torino, Italy
MAMC - Musée d'Anthropologie à Monte Carlo, Monaco
MSN - Museo di Storia Naturale dell'Università degli Studi di Firenze, Italy

Table 5.1: Samples of human groups from Western Europe: Upper Paleolithic–Present

Although these data were collected from individuals recovered from archaeological sites in different parts of Western Europe, due to migration in and out of the region throughout this 30,000-year period it is possible that later groups are not directly descended from those that preceded them. However, in similar studies using samples from different time periods within a particular region, time is a reliable indicator of group affiliation (Brown & Maeda, 2004; Carlson & Van Gerven, 1977; Hanihara, 1994), and when individuals representing each group are drawn from slightly different areas within the broader region, as is the case with these samples, the effects of migration and admixture are less pronounced (Wu *et al.* 2007).

5.2 Variables

Eleven orbital characteristics are examined among these six groups, and as in the previous chapter, linear dimensions were size-adjusted for each individual prior to the analysis (Table 5.2). This was done to remove the confounding effect of overall size differences among groups, which are less pronounced in this temporal series, though

because of a general reduction in cranial and post-cranial size and robusticity since the Upper Paleolithic in Europe and around the world (Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Henneberg & Steyn 1993; Kidder *et al.* 1992; Lahr & Wright, 1996), not adjusting for size would simply show a decrease in each variable in association with this general trend.

5.3 Statistical analysis

In this chapter a null hypothesis of no change in orbital anatomy is evaluated among groups from different time periods since the Upper Paleolithic in Western Europe. To test whether orbital morphology changes linearly through time, a regression analysis with each orbital trait as the dependent variable, and time as the independent variable is carried out separately for each characteristic. In contrast to the previous chapter in which hypotheses concerning relationships between the orbits and surrounding craniofacial traits were tested, in this analysis no predictions were made regarding how these features change over time, or covary with other craniofacial features.

Trends of encephalization and facial reduction that characterize most of human evolution are reversed, and minimal, respectively, and rather it is predominantly change in shape of the skull that occurs throughout this 30,000-year period (Brown, 1992; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Kidder *et al.* 1992; Lahr & Wright, 1996; Wu *et al.* 2007). As a result, orbital morphology is investigated in the context of these more recent evolutionary changes in craniofacial shape since the Upper Paleolithic in Europe, however no a priori predictions were made concerning relationships among them.

5.4 Results of regression analyses: orbital variables vs. time (years B.P.)

The results of this analysis indicate that the null hypothesis of no change in orbital morphology since the European Upper Paleolithic is rejected for all variables except interorbital breadth, orbital size, and orbital frontation (Table 5.2). The null hypothesis is rejected for the remaining orbital variables that change linearly with time, though the direction and strength of these relationships vary among them.

Variable	# Sample	Coefficient	t	p	R²
Orbital Breadth	142	0.000071	2.39	0.018	3.9%
Orbital Height,	142	-0.000194	-5.00	0.000	15.2%
Orbital Index	142	0.000847	6.02	0.000	20.50%
Orbital Frontation	136	0.000007	0.16	0.874	0.00%
Orbital Volume	84	-0.000025	-0.24	0.814	0.10%
Orbital SizeGM	120	-0.000012	-0.41	0.679	0.10%
Orbital Depth	120	0.000226	3.65	.0000	10.10%
Basion-Sup. Orbit	109	0.000298	3.49	0.001	10.20%
Basion-Orbitale	109	0.000251	2.7	0.008	6.40%
Biorbital Breadth	142	0.000013	2.34	0.021	3.80%
Interorbital Breadth	142	0.000021	0.5	0.620	0.20%

Time: Present (0) to Upper Paleolithic (~ 30,000 years B.P.)

Table 5.2: Test of no change in orbital morphology among European temporal groups

Relative stasis of the 3 remaining orbital variables also provides some insight into recent evolution of this anatomical region. A limited degree of temporal change in interorbital breadth, orbital size, and orbital frontation likely relates to functional constraints associated with proper functioning of the nasal cavity and nasopharynx,

adequate space within the orbits for the eye and extraocular tissues, and an orbital orientation that is perpendicular to the visual plane. Interorbital breadth was not part of the predictive model of how the orbit is expected to vary in relation to long-term craniofacial trends in the previous chapter. However, a post-hoc analysis of this feature shows no consistent pattern of change among hominin groups, and no statistically significant relationship with encephalization and reduced facial prognathism ($t = 1.15$, $p = 0.253$). A lack of change in interorbital breadth also characterizes the last 30,000 years of evolution in Western Europe, and while some variation is observable among groups, the linear change that characterizes most other orbital traits is not evident in this feature (Figure 5.1).

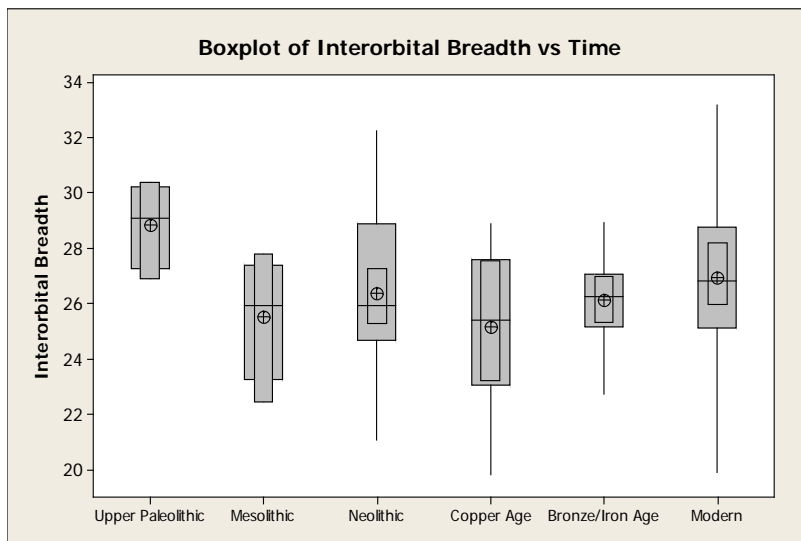


Figure 5.1: Comparison of interorbital breadth among European groups

Orbital frontation also shows no linear relationship to time since the European Upper Paleolithic, but was found to vary in association with the CFI in chapter 4. In this

previous chapter it was determined that cranial expansion and facial reduction explain 30% of the variance in orbital frontation, with a trend toward more frontated orbits in more modern forms. However, there is little deviation from an approximately 90° angle among temporal groups investigated here (Figure 5.2), which likely relates to the relative cessation of craniofacial trends investigated in the previous chapter, and preservation of the horizontal visual plane in fully orthograde anatomically modern humans.

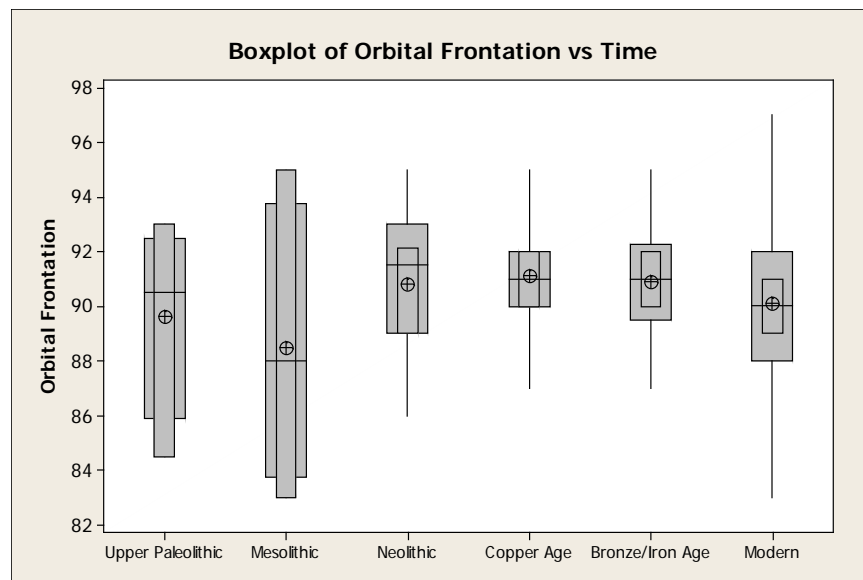


Figure 5.2: Comparison of orbital frontation among European groups

Temporal homogeneity in orbital volume and orbital sizeGM may also relate to structural or functional constraints in this anatomical region. Schultz (1940) reports absolute orbital volume measurement among “fossil man” that are the largest among all primate groups including gorillas (Kabwe - 42.0 cc, La Chapelle aux Saints – 39.5 cc, Gibraltar – 34.5 cc). These values are far larger than orbital volume measurements in

Western European temporal groups sampled for this research, and in comparison with other studies of orbital size in extant humans. If *Homo heidelbergensis* is the ancestor of anatomically modern *Homo sapiens*, this indicates a marked reduction in orbital volume within the past 150,000 to 300,000 years.

Because the orbit of these Neanderthal and Archaic *Homo* forms is far larger than the eye would have been in these species, adequate space would have existed for the soft tissue components of the eye, and a reduction in orbital capacity since 200,000 years b.p. until 30,000 years b.p. likely would not have impinged on the functionality of the optic system. A lack of change in orbital volume since the Upper Paleolithic suggests that further reduction in the size of this feature may have been limited by the functional constraint of ocular soft tissue anatomy, particularly given that overall size of the skull was reduced throughout this period, and that it was only in recent human history that we have been able to correct aberrant vision.

With the exception of the above variables, most orbital traits do show a linear relationship with time, and some continue the pattern of change observed in the previous chapter. For example, basion-superior orbit and basion-orbitale showed an inverse relationship to the craniofacial index, meaning that these distances were reduced as cranial size increased and the lower face shifted posteriorly. And despite a slowed rate of facial retraction and a reversal of cranial expansion since the Upper Paleolithic, posterior movement of the midfacial region continues throughout the last 30,000 years, as indicated by a decrease in measures of basion-superior orbit and basion-orbitale.

Due to limited preservation of the posterior orbit in fossil hominins it was not possible to investigate orbital depth in relation to encephalization and facial reduction in

the previous chapter. However, it is clear that a reduction in orbital depth has occurred since the Upper Paleolithic in Western Europe ($p < 0.000$). Plotting the chimpanzee sample from chapter 3 (which represented the most primitive grade in that analysis) among groups in this temporal series indicates that the reduction in orbital depth that has occurred over the last 30,000 years may be the continuation of a broader trend. However, without data from past hominin species representing intermediate grades, it cannot be known if orbital depth is reduced in association with cranial expansion and reduced facial prognathism during human evolution.

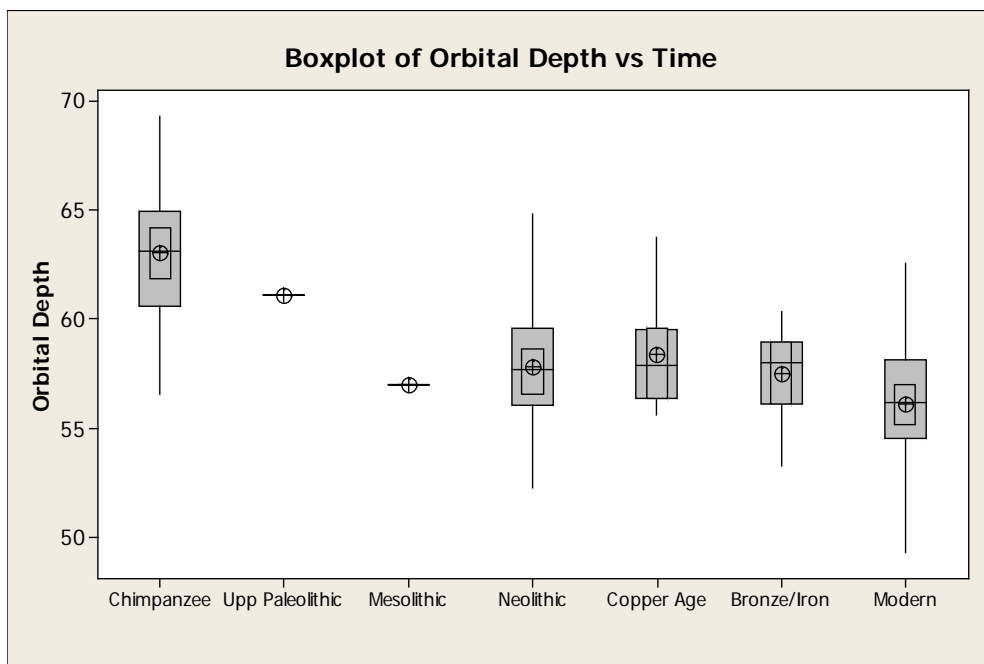


Figure 5.3: Comparison of orbital depth among chimpanzees and European groups

In addition to depth of the internal orbit and position of the orbital margins relative to basion, orbital height is characterized by a marked degree of change since the

Upper Paleolithic (Figure 5.4). The rapid increase in orbital height that occurs over this time period is also accompanied by a statistically significant decrease in orbital breadth (Figure 5.5). The combined effect of change in these orbital measures is a pronounced decrease in the orbital index, or a shift toward higher and more rounded orbits.

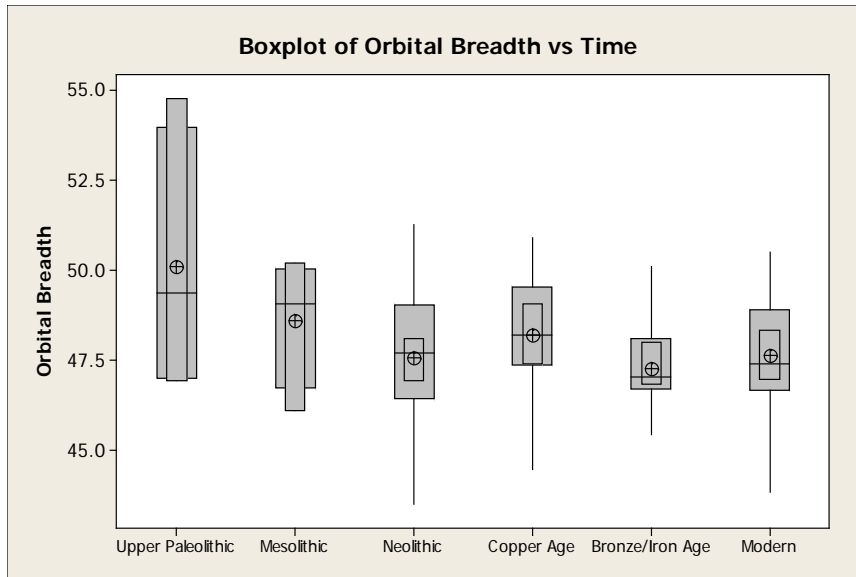


Figure 5.4: Change in orbital breadth through the Upper Paleolithic

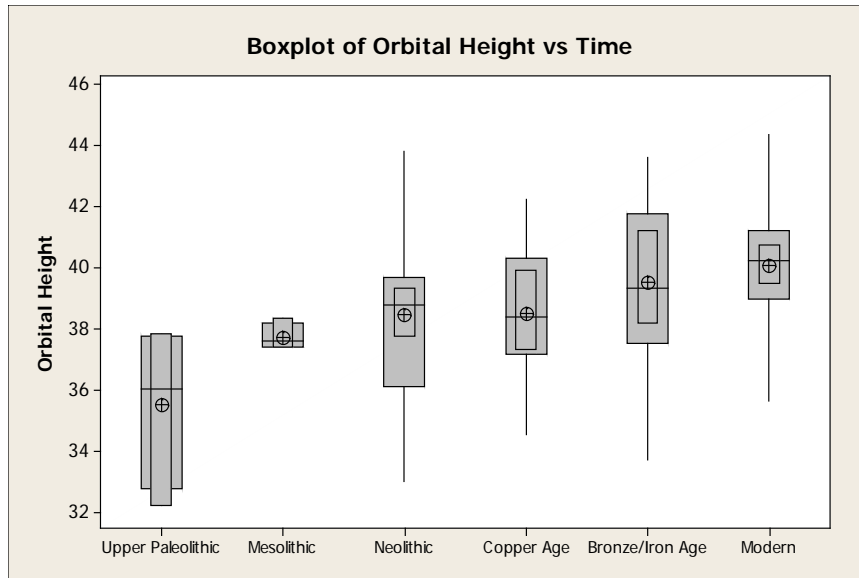


Figure 5.5: Change in orbital height through the Upper Paleolithic

Temporal change in orbital shape among Western European groups in which the orbital margins become taller, narrower and generally more rounded has also been observed in studies of diachronic change in East Asian orbital morphology, though within a slightly narrower time span (Brown 1987; Brown & Maeda, 2004; Wu *et al.* 2007). The greater contribution of orbital height to the observed shape change in this investigation of Western European groups corroborates the findings of Brown & Maeda, (2004), who show that orbital height increases substantially and most rapidly in the last 3500 years, while orbital breadth is found to decrease only slightly between the Neolithic and recent periods. In contrast to these results, Wu *et al.* (2007) show that from the Neolithic to present orbital breadth decreases by 3.6% and orbital height increases by only 3.2%.

Regardless of the relative contribution of orbital height or orbital breadth in generating taller and narrower orbits through time, this orbital feature is found to change more since the Upper Paleolithic than any other trait in this study, and is also among the most variable craniofacial characteristics in East Asian temporal groups dating to the Neolithic period (Brown & Maeda, 2004; Wu *et al.* 2007). This recent shift toward taller and narrower orbits in Europe and the Far East stands in stark contrast to the pattern of change in orbital margin shape associated with long-term trends of cranial expansion and reduced facial prognathism observed in chapter 4. In the preceding chapter it was shown that the eye orbits become vertically shortened and horizontally elongated in association with a grade shift in craniofacial form. However, following the Upper Paleolithic this trend reverses and the orbits become mediolaterally narrower and vertically elongated, with much of this shape change resulting from an increase in orbital height (Figure 5.6).

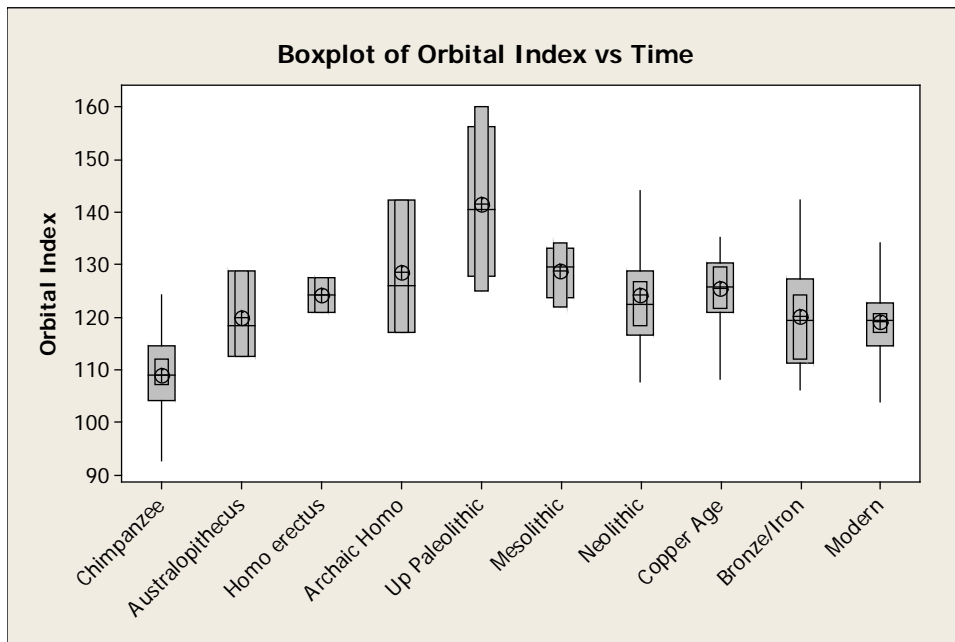


Figure 5.6: Variation in the orbital index among all temporal groups

This shift in the direction of orbital shape change since the onset of the Upper Paleolithic in Europe is likely the result of cranial and facial shape changes that have occurred across most regions of the globe during equivalent time spans. These craniofacial shape changes primarily involve an increase in brachycephalization and facial height, and a continued decrease in facial prognathism, which occur in association with a global decrease in cranial size and robusticity (Brown, 1992; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Kidder *et al.* 1992; Lahr & Wright, 1996; Wu *et al.* 2007), however brachycephalization is not found to occur with decreased cranial size among Sub-Saharan African groups during this time period (Henneberg & Steyn, 1993).

As a result of these more recent global changes in craniofacial form, this investigation examines how the orbits vary in relation to the cranial index and upper facial index among Western European temporal groups. These indexes capture much of the variation in craniofacial shape change throughout this period and are used to examine to what degree observed patterns of variation in size, shape, and orientation of the orbit described in the above section are associated with craniofacial shape changes in Western Europe within the last 30,000 years.

5.5 Craniofacial shape change in Western Europe: Upper Paleolithic to present

Prominent trends of cranial expansion and facial reduction that occur during hominin evolution are minimal in relation to shape changes in the skull since the European Upper Paleolithic. Though not statistically significant at $\alpha = 0.05$, a regression

of facial projection vs. time indicates that a slight reduction in facial prognathism ($t = 1.92$, $p = 0.058$) does continue throughout this time period in Western Europe (Figure 5.7). However, expansion of the cranium does not continue, but rather shows a slight *decrease* in size since the Upper Paleolithic ($t = 2.39$, $p = 0.018$), with the actual peak around the Mesolithic (Figure 5.8). This corroborates the findings of Henneberg (1988) who found that peak cranial size for males (1593 CC) and females (1502 CC) from the Northwest quadrant of the Old World were also obtained during the Mesolithic period.

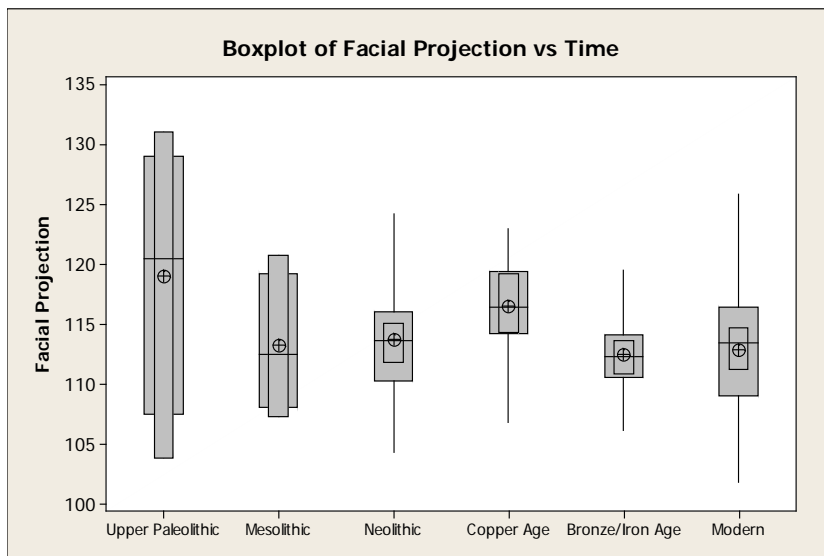


Figure 5.7: Temporal change in facial projection since the Upper Paleolithic

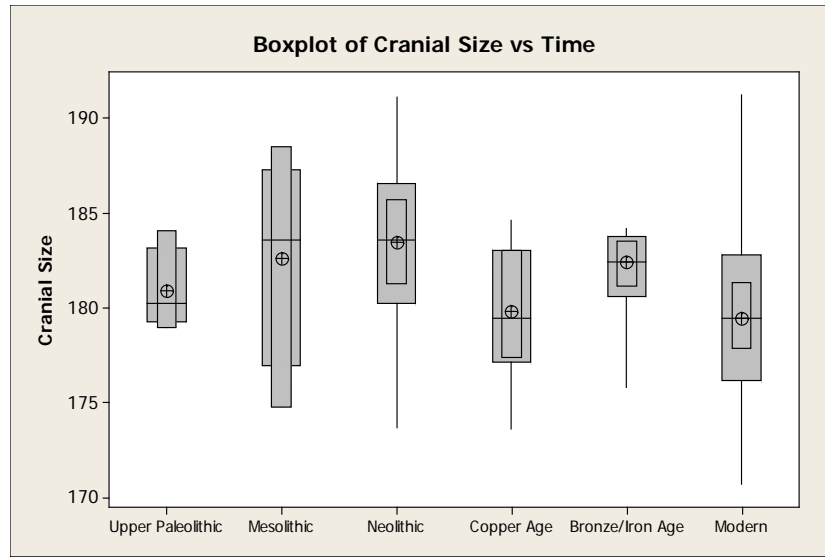


Figure 5.8: Temporal change in cranial size since the Upper Paleolithic

Rather than a continuation of long-term trends of facial reduction and cranial expansion, evolutionary change in Western Europe is better characterized by shape change in which the cranium becomes wider and anteroposteriorly shorter, or more brachycephalic ($t = -5.78$, $p < 0.000$), while the face becomes narrower and vertically elongated ($t = -2.95$, $p = 0.004$) throughout this 30,000 year time period (Figures 5.9, 5.10). With the exception of Sub-Saharan Africa (Henneberg & Steyn, 1993), these same cranial and facial shape changes have been documented in many different populations throughout the Old and New World (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Lahr & Wright, 1996; Nakahashi, 1993; Rothhammer *et al.* 1982), and recent data indicates that these features are still evolving in similar ways (Wu *et al.* 2007).

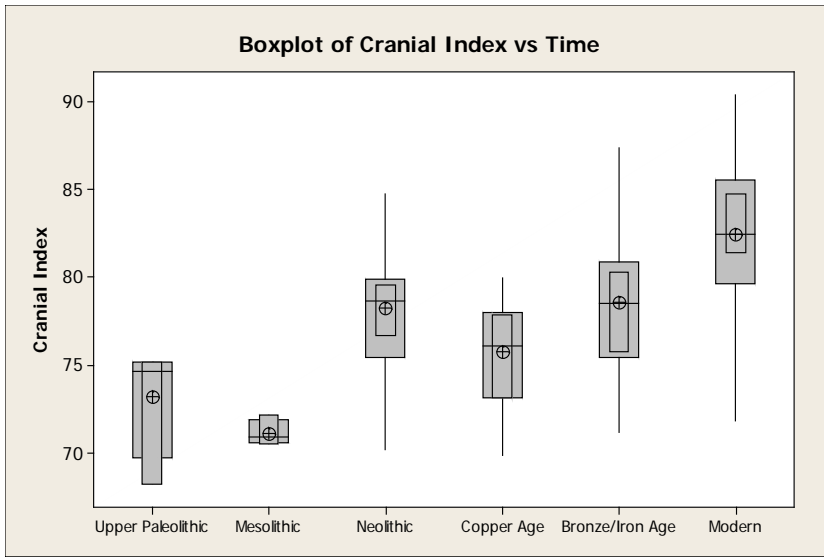


Figure 5.9: Change in cranial shape among Western European groups

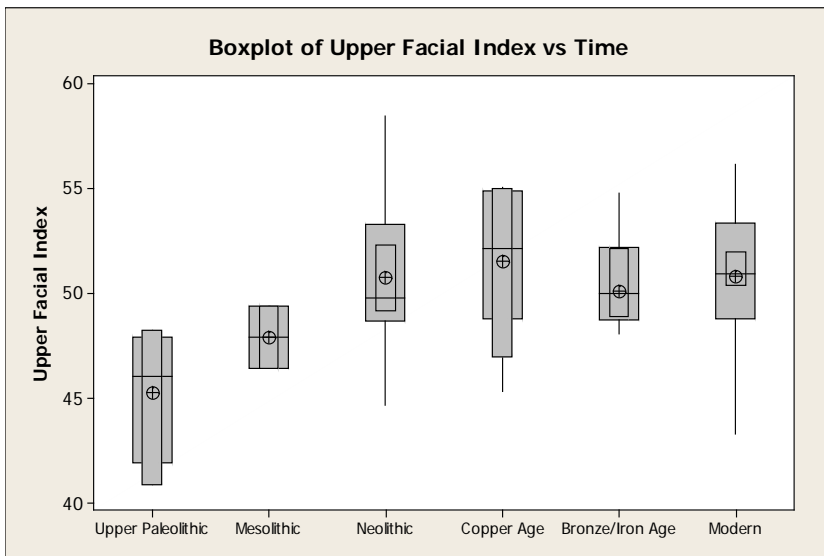


Figure 5.10: Change in facial shape among Western European groups

Facial shape change since the Upper Paleolithic is a product of an increase in facial height ($T = -2.90$, $p = 0.004$), which again is a reversal from the pattern that

characterizes much of human evolution. A reduction in facial height occurs in association with a long-term trend of reduced facial prognathism in the hominin lineage, but as facial projection continues to decrease slightly through the Upper Paleolithic, facial height begins to increase, though this change is not completely linear and appears to increase most between the Upper Paleolithic and Mesolithic periods, and again following the Copper age (Figure 5.11). This increase in facial height also occurs in association with a reduction in facial width ($T = 5.51, p < 0.000$) following the Upper Paleolithic, resulting in a shift toward longer and narrower faces in Western European groups during this 30,000-year period.

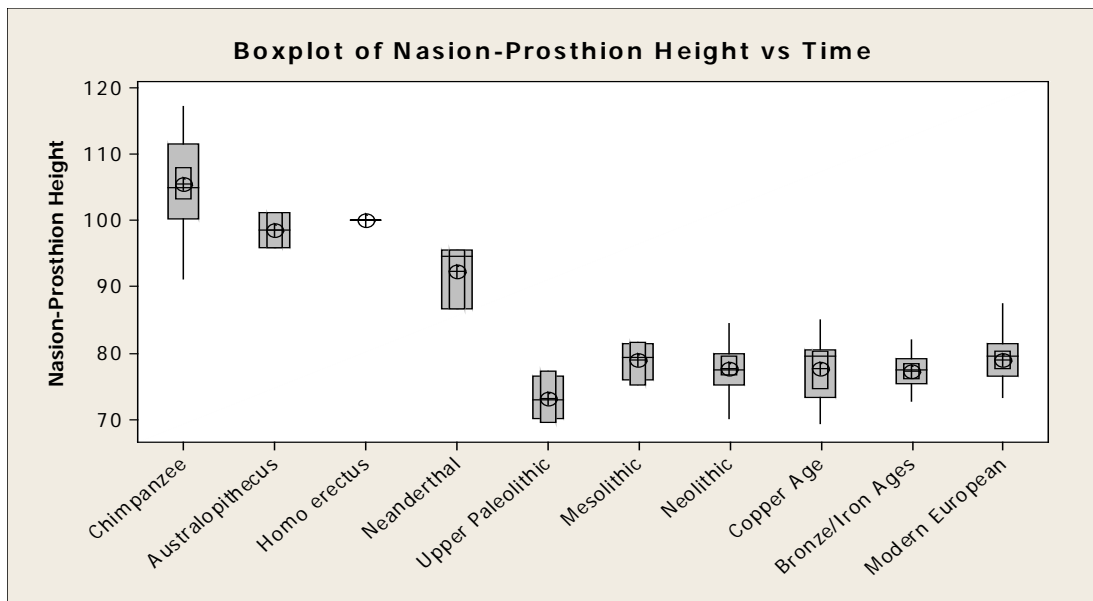


Figure 5.11: Comparison of long-term and recent variation in facial shape

5.6 Results of regression analyses: orbital variables vs. craniofacial shape

An investigation of how the eye orbit varies in relation to the cranial and upper facial indexes indicates that many of the changes in orbital morphology observable since the Upper Paleolithic in Western Europe can be understood at least in part by these craniofacial shape changes (Table 5.3).

Orbital Variables	Cranial Index			Upper Facial Index			CumR ²
	Coefficient	t	p	Coefficient	t	p	
Orbital Breadth	0.014806	0.47	0.636	-0.17339	-3.48	0.001	10.5%
Orbital Height	0.147524	3.64	0.000	0.19608	3.04	0.003	14.5%
Orbital Index	-0.43712	-2.88	0.005	-1.0820	-4.47	0.000	17.8%
Orbital Frontation	-0.05440	-1.03	0.307	-0.09336	-1.12	0.267	1.8%
Orbital Volume	-0.06742	-0.89	0.376	-0.2348	-2.03	0.046	5.8%
Orbital SizeGM	0.03749	1.82	0.071	-0.08931	-2.51	0.014	8.8%
Orbital Depth	-0.07678	-1.42	0.158	-0.33446	-3.89	0.000	13.1%
Basion-Sup. Orbit	-0.42667	-6.66	0.000	-0.6540	-6.26	0.000	41.7%
Basion-Orbitale	-0.42194	-5.27	0.000	-0.6927	-5.31	0.000	32.4%
Biorbital Breadth	-0.01704	-0.33	0.744	-0.55571	-6.71	0.000	28.8%
Interorbital Breadth	-0.05302	-1.16	0.249	-0.21250	-2.92	0.004	7.3%

Table 5.3. Regression analysis of orbital variables vs. cranial index, upper facial index

Each orbital characteristic that varies significantly in relation to the cranial index and upper facial index are correlated in a way that is consistent with evolutionary changes in orbital morphology that have occurred in this region during the last 30,000 years. Although these craniofacial changes do not explain all of the variation in the orbit through time, they indicate that a narrowing and elongation of the face and a shift toward

brachycephalization in Western Europe since the Upper Paleolithic are important for understanding recent evolutionary change in this feature.

In looking at size and shape of the orbital margins it can be seen that orbital breadth does not vary in relation to cranial shape, but does decrease as the upper facial index increases, with the same being true of biorbital breadth. In contrast, orbital height is positively correlated with both shape features, which one might expect particularly in relation to the upper facial index, in which a vertical increase in facial height and decrease in facial width would be assumed to affect in a similar way these same dimensions of the orbit. However, Brown & Maeda (2004) found that throughout the Neolithic in China, orbital height increases substantially even while facial height is reduced in that region.

In nearly every case, orbital variables are more highly correlated with shape of the face than with shape of the head, which is understandable given their inclusion in the facial framework. However, the relationship between basion-orbitale and basion-superior orbit is negatively correlated with both cranial and facial shape variables and to approximately the same degree. This is of particular interest given that the upper facial index comprises two variables that indicate the relationship between height and width of the face in the coronal plane, though measures of basion-orbitale and basion-superior orbit lie in the parasagittal plane. Orbital depth also decreases in association with increased facial height and decreased facial breadth, but is not statistically related to change in cranial shape. This too is surprising given that orbital depth might be expected to decrease more as a result of anterior-posterior shortening of the skull rather than in relation to a narrowing and elongation of the face.

Although the direction and magnitude of the relationship between orbital morphology and craniofacial shape largely mimics observed changes in orbital features during the last 30,000 years in Western Europe (section 5.4 above), orbital size deviates slightly from this pattern. Both orbital volume and the geometric mean of orbital height, breadth, and depth remained relatively unchanged since the Upper Paleolithic, however both show a statistically significant negative relationship to the upper facial index, meaning that as the face becomes taller and narrower, space within the orbits is diminished.

Brown and Maeda (2004) show that among skulls of Australian Aborigines and Tohoku Japanese, which represent changing craniofacial form since the end of the Pleistocene, orbital volume is highly correlated with supraorbital breadth, lower facial prognathism, and shape of the orbital margins. Among these crania a broader supraorbital region, more projecting facial skeleton and lower orbital index (more rectangular shape) are associated with a larger orbital volume. Change in these features, including a strong trend toward higher and narrower orbits, is considered to reflect a decrease in orbital volume that occurred throughout the Holocene in China (Brown & Maeda, 2004).

A test of these relationships among European crania spanning a slightly longer time period shows no relationship between orbital volume and measures of supraorbital breadth ($p = 0.144$), facial prognathism ($p = 0.287$), or shape of the orbital margins ($p = 0.804$). A test of these relationships using raw data obtained from these skulls (non-size-adjusted variables) also shows no relationship between orbital volume and facial prognathism ($p = 0.399$), or orbital volume and shape of the orbital margins ($p = 0.441$).

A statistically significant relationship between orbital volume and supraorbital breadth was discovered using the raw data ($t = 6.46$, $p < 0.000$), and while absolute size of the supraorbital region does decrease slightly in Western Europe during the last 30,000 years ($p = 0.045$), this is largely the product of an overall decrease in skull dimensions, as relative size does not show the same relationship to time ($p = 0.946$). Additionally, as described above there is no apparent decrease in orbital size in Western Europe during the last 30,000 years in this region, despite a statistically significant relationship between the upper facial index and both orbital volume ($p = 0.046$), and the geometric mean of orbital length, width, and height ($p = 0.014$).

This discrepancy in patterns of change in orbital volume between European and Chinese groups over similar time periods may help explain why visual acuity has diminished faster, and why myopia occurs at a higher frequency among many East Asian groups relative to Western Europeans and Sub-Saharan Africans (Goldschmidt, Lam, Opper, 2001; Lam *et al.* 1999; Park & Congdon, 2004). A decrease in orbital volume in association with supraorbital narrowing, facial retraction, and changing shape of the orbital margins throughout the Holocene in China could affect the amount of space available for the eye and extraocular tissues. These changes are particularly important to consider given that eyeball size does not directly influence size of the orbit in humans (Chau *et al.* 2004; Schultz, 1940).

If the volume of the orbits is reduced and the contents within them are not able to counter this reduction, the eyeball may be forced into a more anterior position (Brown & Maeda, 2004), or become compressed within the orbit as a result of brain growth above, and a superoposterior relocation of the maxilla and zygomatic bones below the eyeball.

Additionally, because the eyeball scales with negative allometry to the bony orbit with respect to body size (Schultz, 1940), a reduction in cranial and post-cranial size throughout this period (Brown, 1992; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Kidder *et al.* 1992; Lahr & Wright, 1996; Wu *et al.* 2007), could further contribute to compression of the eye and extraocular tissues within the bony orbit.

In the following chapter, an analysis of the incidence and severity of myopic refractive error is examined in the context of size of the eye within the orbit, to investigate whether visual acuity is reduced in individuals and groups with large eyes in relatively small orbits. The relationship between size of the eye, orbit, and spherical equivalent refractive error is then assessed in the context of results from the preceding chapters investigating craniofacial change and modern variation in the hominin orbit.

CHAPTER 6

THE ORBIT, EYEBALL, AND REDUCED VISUAL ACUITY IN HUMANS

6.1 Samples and Statistical Analysis

In a recent study, high-resolution magnetic resonance scans were used to investigate whether eyeball volume and eye orbit volume are interrelated, and how each correlates with refractive errors in Chinese adults (Chau *et al.* 2004). The spherical equivalent refraction error (SER) was recorded to assess an individual's quality of vision, and skull height, length, and breadth were measured to explore possible relationships between myopia and cranial dimensions, as well as to identify which correlates most with orbital volume (Chau *et al.* 2004).

The authors point to an investigation of eyeball and orbital volumes in juvenile chickens that showed a positive correlation between these variables (Wilson *et al.* 1997), and which is thought to be the result of the globe exerting pressure on the bony orbit during growth, causing it to expand. This chick study also revealed that induced myopic and hyperopic eyes were found to result in larger and smaller orbits respectively, which was considered further evidence that eyeball size influences the size of the orbit in chickens (Wilson *et al.* 1997).

In humans however, the eyeball and orbit are not correlated in this way (Chau *et al.* 2004), and only a weak relationship exists between them ($r = 0.13$, $p = 0.005$), which

corroborates the findings of other researchers investigating the association of these hard and soft tissues of the eye (Kay & Kirk, 2000; Schultz, 1940). Additionally, it was found that inducing myopia or hyperopia did not correlate with larger or smaller orbits in humans as it did in chicks, but rather it was discovered that the opposite relationship exists among them (Chau *et al.* 2004). For example, the most hyperopic individuals had an orbital volume 2.37 cm^3 larger than the most myopic subjects, and that the eyeball of the most myopic subjects was 1.07 cm^3 larger than the most hyperopic individuals in the study (Chau *et al.* 2004, emphasis added).

Reading this statement suggested that looking at the eyeball and the orbit separately may not show the true relationship between these features and how they relate to refractive error in humans, and suggested that the relative size of the eyeball *within* the orbit may better explain the incidence and severity of this condition. Because Chau *et al.* (2004) published their raw data in the article, it is possible to address this question by constructing a hypothesis predicting that individuals with a larger orbit/eyeball index will be less myopic (as a result of more space within the orbit for the eyeball and extraocular structures, which fill a large portion of the orbit in humans), and individuals with a lower orbit/eye index will have a higher spherical equivalent refractive error due to inadequate space within the orbit for these optical components. This index was derived from measurements taken by Chau *et al.* (2004) with a high-resolution MR scanner on 33 Chinese adults aged 19-42, determined to be free of eye and orbital pathologies prior to the analysis.

Regression analysis is used to test the null hypothesis of no relationship between the orbit/eyeball index and spherical equivalent refractive error (SER) measured in

dioptries (in which a lower value indicates greater spherical error and more severe myopia). Alternatively it is predicted that a positive relationship exists between these measures, and that individuals with smaller orbits and larger eyes are limited by available space within this bony enclosure for the eyeball and extraocular tissue, resulting in deformation of the globe and improper refraction of light upon the retina.

The current investigation also involves an analysis of sex differences in SER and the orbit/eyeball index, and predicts that the ubiquitously higher frequency of myopia in females can be understood in the context of their generally larger eye in a smaller orbit. This sex disparity has been shown to exist in humans, where on average the female eye fills 5.7% more of the orbit compared to men, with similar proportions reported between the sexes across the primate order (Schultz, 1940). This part of the investigation is carried out using two-sample t-tests to evaluate a null hypothesis of no difference between the sexes in volume of the eyeball, orbit, orbit/eyeball index, and SER.

An assessment of sex differences in orbital volume within and across seven samples of modern humans is also carried out in conjunction with the above analysis of SER and orbit/eye volume. Data used in this comparison include measures of orbital volume from 6 samples representing African, Asian, and European ancestral groups. These include the above sample of Chinese adults (Chau *et al.* 2004), orbital volume measurement from a Tohoku Japanese sample (Brown & Maeda, 2004) made available on the author's website (Brown P., 1998–2003), and volumetric measurements taken in association with this dissertation research (Table 6.1).

Sample	Sample Sizes			Method	Data
	Female	Male	Total		
South African	22	26	48	MS	UW
African American	29	29	58	MS	CMNH
European	17	16	33	MS	MNHN
European American	19	31	50	MS	CMNH
Japanese	22	22	44	MS	BROWN
Chinese	16	17	33	MRI	CHAU

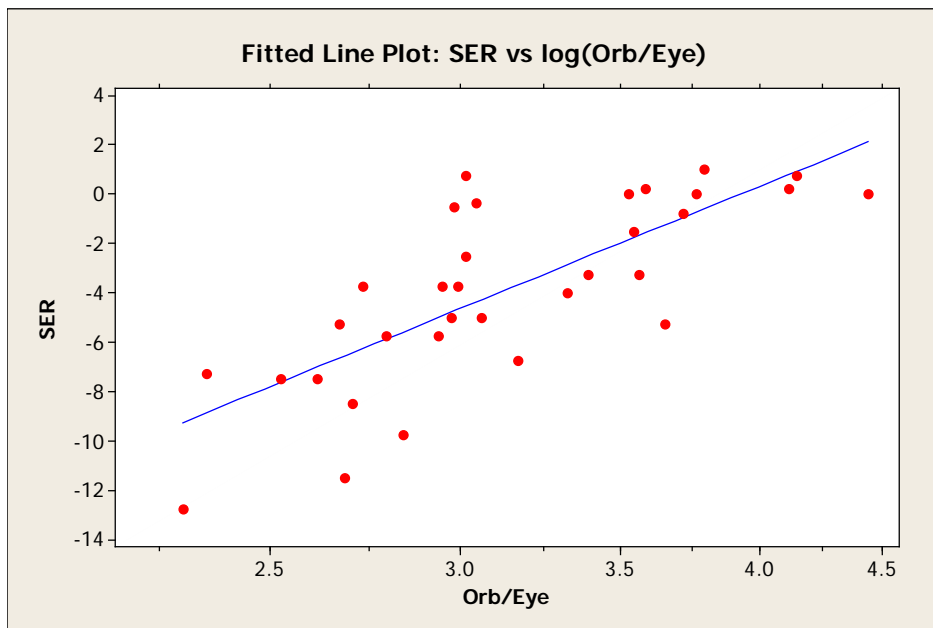
UW - The Dart collection, University of the Witswatersrand, Johannesburg, South Africa
CMNH – Hamman-Todd collection, Cleveland Museum of Natural History, Cleveland, OH
MNHN - Musée National d'Histoire Naturelle, Musée de l'Homme Paris, France
BROWN – Published data collected by Peter Brown (Brown P., 1998–2003).
CHAU – Published data from (Chau, *et al.* 2004).
MS – Volume estimated from filling orbit with mustard seed
MRI – Volume estimated from Magnetic Resonance Imaging

Table 6.1: Modern human groups used to investigate sex differences in orbit size

Though it is not possible to investigate differences in the relationship between size of the eye and orbit among modern human populations based on these data, relative growth of the orbit is compared between South African and Tohoku Japanese samples to examine patterns of orbital growth and development between two groups with distinctly different craniofacial features. The African sample comprises 64 individuals with approximately 3 from each year since birth between 0 and 25 years of age, while the Tohoku Japanese sample (Brown P., 1998–2003), is made up of 30 individuals with slightly fewer numbers from each age group between 5 and 25 years. Though these samples differ slightly in age structure, this comparison facilitates a better understanding of population-specific changes in orbital volume throughout growth and development, and how these differences may relate to the etiology of juvenile-onset myopia.

6.2 Results of test of no relationship between orbit/eye volume and SER

The results of this analysis demonstrate that a highly significant positive relationship exists between SER and relative size of the eyeball within the orbit ($p < 0.0001$), to the extent that the orbit to eyeball index explains 58.3% of the variance in SER. Also, as predicted individuals with the lowest orbit/eyeball index, meaning those with a larger eye in a smaller orbit, show the highest degree of refractive error and resultantly the most severe myopia, while individuals with higher values, or smaller eyeballs in a larger orbit, are less myopic (Figure 6.1).



$$[\text{SER} = -23.62 + 39.77 \log_{10}(\text{Orb}/\text{Eye}), R^2 = 58.3\%, p < 0.0001]$$

Figure 6.1: Plot of spherical equivalent refraction (SER) vs. (log₁₀)orbit/eyeball

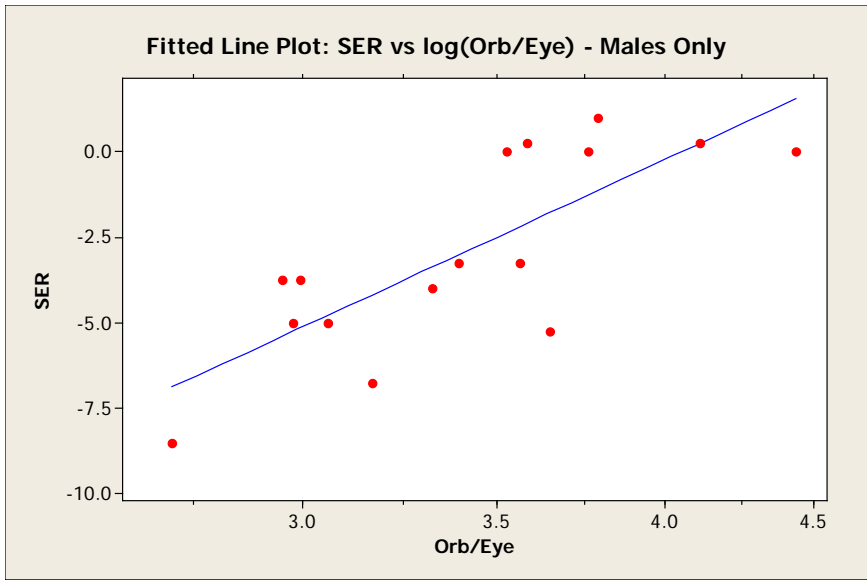
These results indicate that a strong association exists between the degree of refractive error and the amount of space the eyeball occupies within the orbit, though of perhaps even greater interest is that individuals with orbit/eye indices greater than

approximately 3.5 show little to no sign of myopia at all (right side of Figure 6.1). This corresponds to an eye that occupies approximately 29% of the orbit, and appears from the above graph to be an important point at which the eyeball and extraocular tissues begin to vie for space within the orbit.

It can also be seen in Figure 6.1 that all individuals with an orbit/eye index of less than approximately 3.0 show some indication of myopia, and that the severity of refractive error continues to increase below this point. This represents another important threshold in the relationship between the eye and orbit within this sample, and indicates that within the Chinese population individuals with an eyeball that occupies more than 33% of the orbit develop myopia, and that the severity of the refractive error increases as this percentage grows.

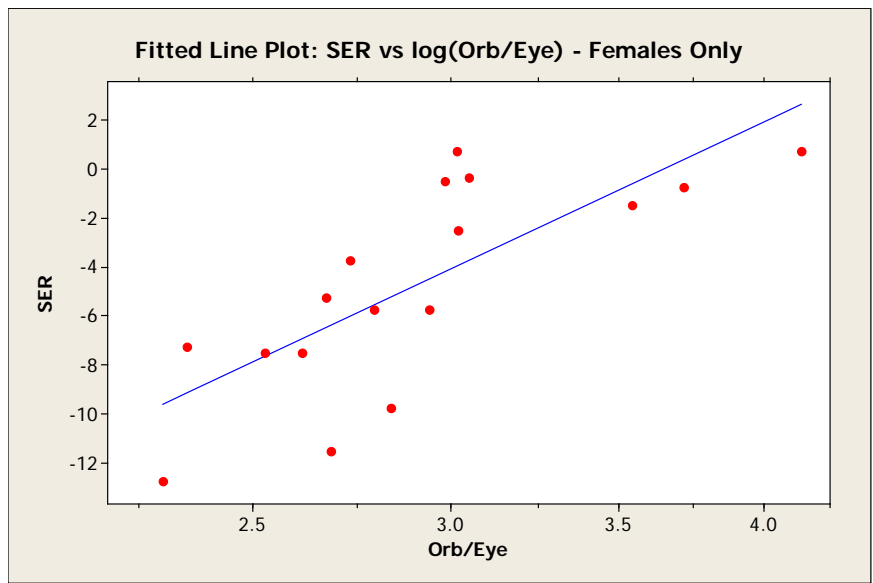
6.3 Sex differences in orbit/eye size in relation to SER

Orbit to eyeball indices below 3.0 and above 3.5 appear to be important thresholds for either the development of myopia or the retention of emmetropia. However, in looking at separate graphs of SER plotted against the index of orbital to eyeball volume in males (Figure 6.2) and females (Figure 6.3), it can be seen that these points actually represent the same threshold between emmetropic and myopic eyes, but show up as two separate points when males and females are combined in the same graph (Figure 6.1). These sex-separate graphs indicate that myopia begins to develop in females with an orbit/eyeball index below 3.0, and in males with an index below 3.5, and that in both sexes visual acuity continues to decrease below these respective points.



[SER = - 23.83 + 39.22 logten(Orb/Eye), R² = 61.8%, p < 0.0001]

Figure 6.2: Plot of SER vs. index of (log₁₀)orbit/eyeball volume for males



[SER = - 26.91 + 47.87 logten(Orb/Eye), R² = 57.1% p < 0.0001]

Figure 6.3: Plot of SER vs. index of (log₁₀)orbit/eyeball volume for females

In females there is a clear difference in the incidence of myopia between individuals with an orbit/eye value above and below 3.0, which corresponds to an eye that occupies approximately 33.3% of the orbit. This shows that females with eyeballs that fill more than a third of the orbit are more likely to be myopic, and that as the percentage grows the severity of this condition worsens. This same point at which myopia develops also exists in males, however it is shifted toward the right on this graph and corresponds to an eyeball that fills only about 28.6% of the orbital cavity.

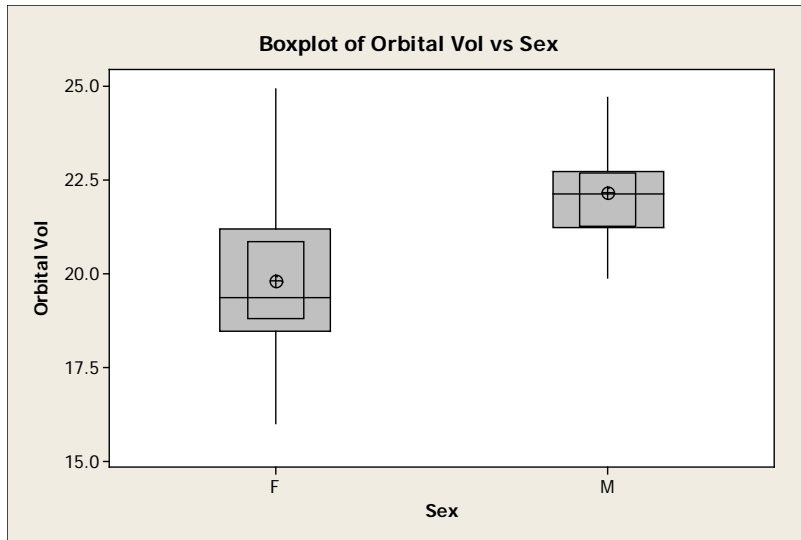
This sex disparity makes it appear as though males are more likely to develop myopia due to the lower percentage of orbital occupancy at which it begins to occur. However, it can be seen from Figure 6.2 that 43% of males have refraction errors approximating 0 dioptres (indicating relative emmetropia), while only about 27% of females in this sample have acute vision. This is likely the result of observed relationships among the eyeball, orbit, and body size, in which eyeball volume scales with negative allometry to orbital volume as body size increases (Kay & Kirk, 2000; Schultz, 1940). Therefore, the larger body size of males naturally correlates with an eyeball that occupies a smaller percentage of the orbit. Additionally, males possess larger extraocular muscles and fat volumes (Forbes *et al.* 1985), which acts to compensate for the greater size of the orbit to some extent, lowering the percentage of orbital occupancy at which myopia begins to develop. To better understand these differences in absolute and relative size of the eye and orbit, sex differences for each variable are examined independently.

6.4 Sex differences in orbital volume, eyeball volume, and SER

6.4.1 Orbital volume

In studies of juvenile-onset myopia women are universally found to have a higher frequency and more severe refractive error compared to men (Angle & Wissman, 1980; Grosvenor & Goss, 1999; Ip *et al.* 2008; Lam *et al.* 1999; Parssinen & Lyyra, 1993; Saw *et al.* 2008). Size of the eye is also a predictor of the occurrence and severity of myopia, in which a larger eyeball is correlated with its axial elongation, an increase in vitreous depth, increased focusing power of the cornea, and an image that is erroneously focused in front of the retina (Lam *et al.* 1999; WGMPP, 1989). This relationship is commonly reported, but there is perpetual vacillation concerning the mechanism of this ocular distortion, and why it occurs more frequently in women than in men.

A comparison of orbital volumes from data published by Chau *et al.* (2004) reveals that males have significantly larger orbits compared to females ($p = 0.001$), with an average difference of approximately 2.33 cm^3 . The male orbit is also found to be far less variable by comparison, to the extent that the variance for females ($\sigma^2 = 5.30$) is more than three times that for males ($\sigma^2 = 1.59$) (Figure 6.4).



[♀ \bar{x} = 19.81 σ = 2.30 / ♂ \bar{x} = 22.14 σ = 1.26, p = 0.001]

Figure 6.4: Comparison of sex differences in absolute orbital volume in Chinese adults

A larger absolute size of the orbit in males is not especially surprising given that orbit size is related to body size and men are generally larger than women. However, even after adjusting for size differences between the sexes it can be seen that females possess a much smaller relative orbit size compared to men in each sample (Figure 6.5).

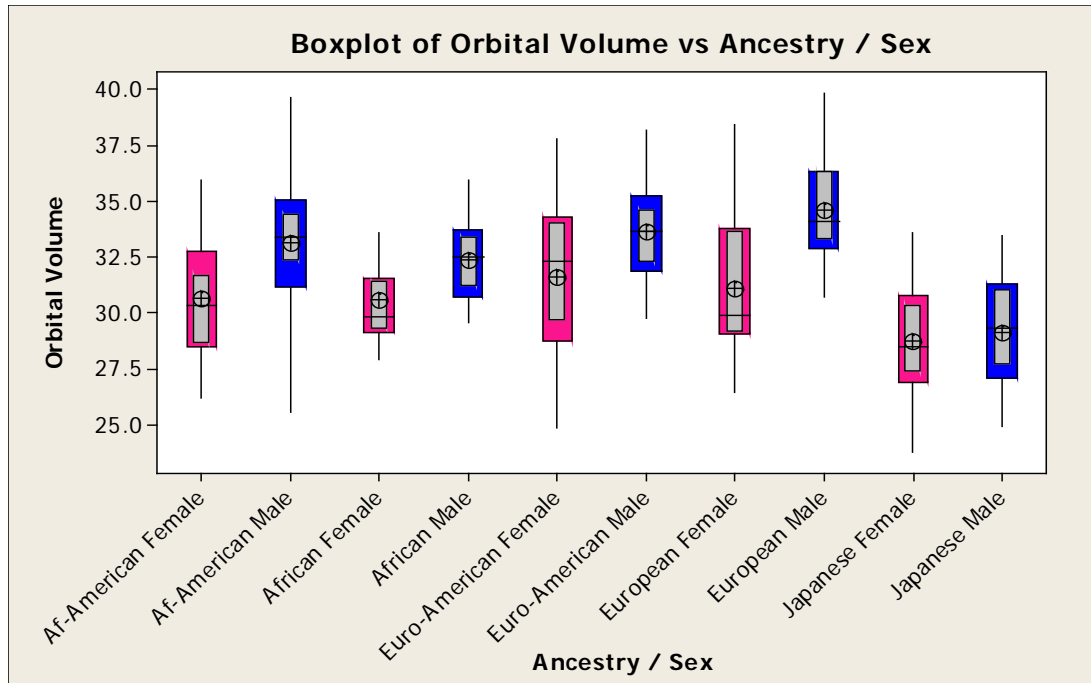


Figure 6.5: Intra-group sex differences in size-adjusted orbital volume

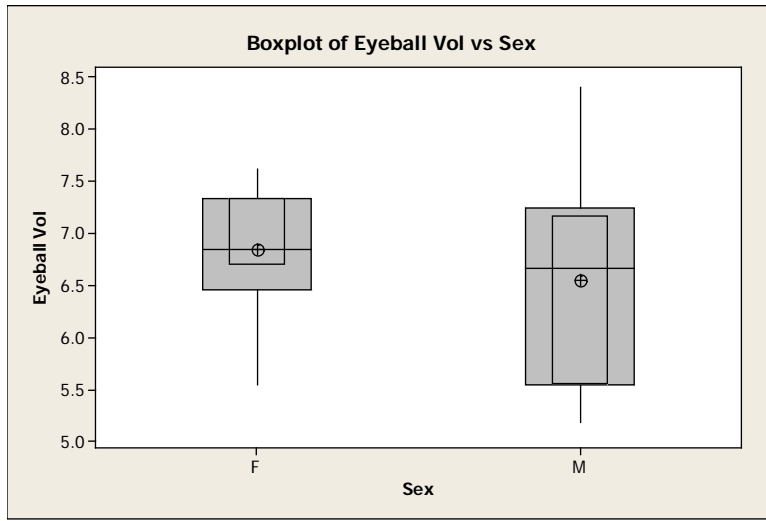
With the exception of the Tohoku Japanese sample, size-adjusted orbital volume values are statistically different between males and females within each sample (Table 6.2). The lack of significance between the sexes in this Japanese sample may relate to the comparatively small absolute and relative size of the orbit among all individuals in this group. In fact, the average orbital volume value of males in this sample even falls substantially below the average of every female group in the analysis. The comparatively low relative orbital volume in the Japanese sample may limit the degree of variation that can exist between the sexes, as both already have limited space available for the eyeball, muscles, blood supply, nerves, and fat that lie within the confines of the orbit.

Ancestral Group	N	mean	s.d.	t	p
African-American Female	29	30.63	2.61	-3.37	0.001
African-American Male	29	33.11	3.00		
African Female	22	30.58	2.00	-3.25	0.002
African Male	26	32.38	1.81		
European-American Female	29	31.65	3.34	-2.45	0.017
European-American Male	31	33.65	2.97		
European Female	17	31.13	3.37	-3.41	0.002
European Male	16	34.61	2.44		
Japanese Female	22	28.77	2.80	-0.45	0.654
Japanese Male	22	29.14	2.58		

Table 6.2: Intra-group sex differences in size-adjusted orbital volume

6.4.2 Eyeball volume

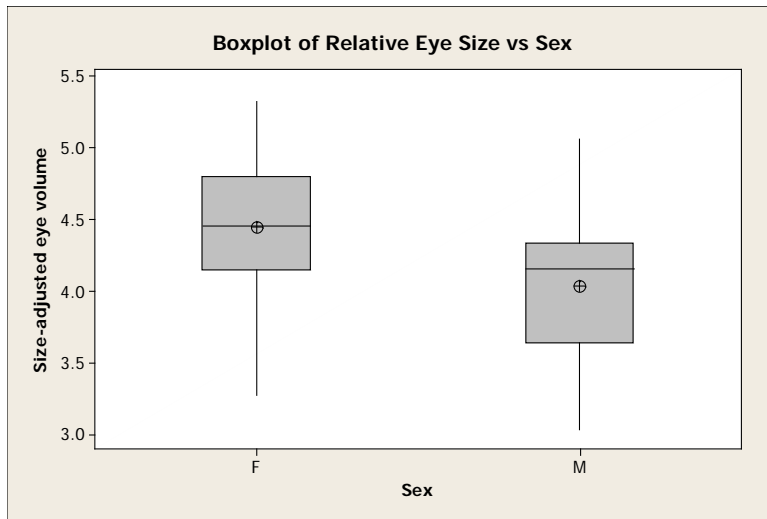
A comparison of eyeball volume between male and female Chinese adults using data collected by Chau *et al.* (2004) reveals that no statistically significant difference ($p = 0.368$) exists in the size of the eyeball between the sexes (Figure 6.6). It is interesting to note however that females possess a slightly larger absolute eyeball volume compared to males in this sample, which is counter to the above pattern of larger absolute and relative size of the orbit in males.



[♀ $\bar{x} = 6.836$, $\sigma = 0.882$ / ♂ $\bar{x} = 6.546$, $\sigma = 0.940$, $p = 0.368$]

Figure 6.6: Comparison of absolute eyeball volume between male and female Chinese adults

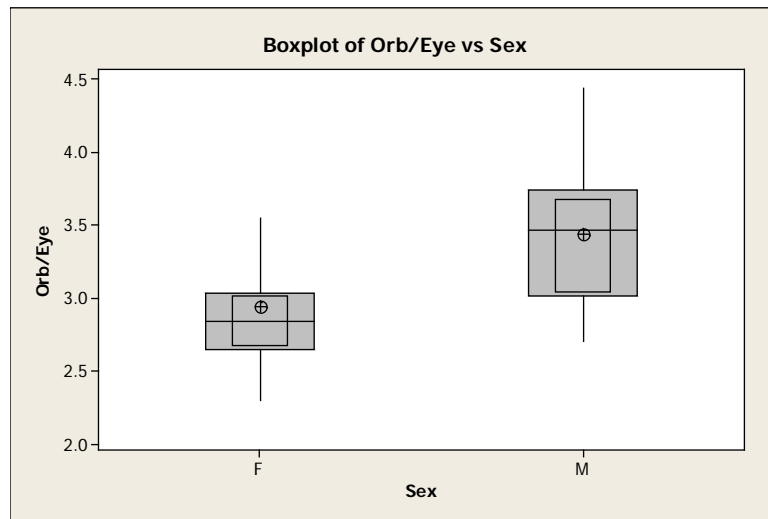
Schultz (1940) observed that within humans and among all primates with the exception of the marmoset, females possess a larger relative eyeball size compared to male conspecifics. Though body size was not collected by Chau *et al.* (2004), dividing eyeball volume by the geometric mean of cranial length, width, and height for each individual in this sample provides an estimate of relative eye size in proportion to overall size of the neurocranium. A comparison of size-adjusted eyeball volume between the sexes in this sample of Chinese adults shows that relative size of the eyeball is larger in females than in males (Figure 6.7), corroborating the results of Schultz (1940).



[♀ \bar{x} = 4.446, σ = 0.573 / ♂ \bar{x} = 4.038, σ = 0.491, p = 0.030]

Figure 6.7: Comparison of relative eyeball volume between male & female Chinese adults

The above analysis shows that absolute and relative size of the orbit is larger in males than females in this sample of Chinese adults, but that females possess a larger relative eyeball size, despite comparable values of absolute eyeball volume between the sexes. A comparison of sex differences in eyeball volume relative to that of the orbit shows that females have a significantly lower average orbit/eye value compared to men ($p = 0.005$), which corresponds to an eyeball that occupies 34% of the orbit in females, and 29.1% in males (Figure 6.8, Table 6.1).



[♀ \bar{x} = 2.936 (34.0%) σ = 0.480 / ♂ \bar{x} = 3.438 (29.1%) σ = 0.461, p = 0.005]

Figure 6.8: Comparison of orbit/eyeball volume between male and female Chinese adults

Sex	Index			Percent		
	[Average]	[Min – Max]	[Range]	[Average]	[Min – Max]	[Range]
Female	2.94	2.3 – 3.7	1.4	34%	27% - 43.5%	16.5%
Male	3.44	2.7 - 4.5	1.8	29.1%	22% - 37%	15%
Combined	3.19	2.3 – 4.5	2.2	31.35%	22%-43.5%	21.5%

Table 6.3: Sex difference in orbit/eyeball index / Percent of orbit filled by the eye

6.4.3 Incidence and severity of myopia

It was shown in the above section that a strong positive relationship exists between spherical equivalent refractive error (SER) and the index of orbital volume to eyeball volume in both males and females. It was also found that there is a clear shift

away from emmetropia in individuals with eyeballs larger than 33.3% of orbital volume in women, and larger than 28.6% of orbital volume in men.

In both sexes the average orbit/eye index is below the threshold at which point individuals begin to develop myopia (Table 6.3), which corresponds to an average SER of -4.76 dioptres in females, and -2.94 dioptres in males. Despite an average refractive error that is nearly -2 dioptres lower in females, the difference in this sample is not significant at $\alpha = 0.05$ (Figure 6.9). However, it can be seen that a greater number of females are myopic by comparison, and that all of the most severe cases of refractive error are found in this sex group; including the worst case in which this individual has both the lowest orbit/eyeball index (2.29), corresponding to an eyeball that occupies 44% of the orbit, and the most severe case of myopia in the sample (-12.75).

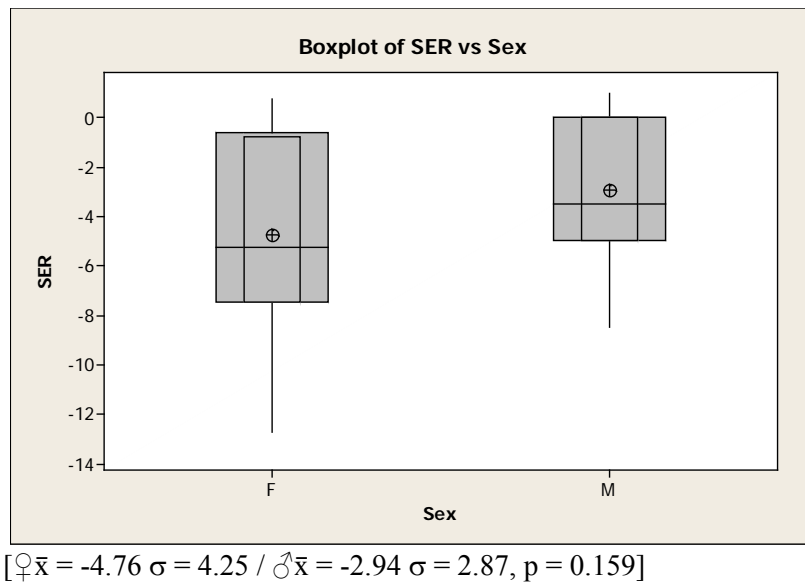


Figure 6.9: Comparison of refraction error between male and female Chinese adults

6.5 Growth of the eye and orbit

Chau *et al.* (2004) point out in their analysis that in some individuals with severe myopia the enlarged eyeball, characteristic of myopes in general, was compressed against extraocular tissues. However, they do not address the question of why the eyeball would be compressed against surrounding soft tissue structures if there were room enough for each within the confines of the orbit. The rectus muscles, blood supply, nerves, and particularly fat that occupy the area around the eyeball would be expected to exert pressure on the globe and cause deviations from its natural spherical state in individuals and groups with orbits that are small in relation to size of the globe and extraocular tissues that fill it. The above analysis of relative size of the eyeball within the bony orbit and how this index varies in association with the occurrence and severity of juvenile-onset myopia lends evidence to this proposal.

Because it does not take much pressure to bring an image out of focus, even minor force resulting from compression against extraocular tissue could impact vision, but not be apparent in MR scans until a significant degree of penetration occurs. Though more importantly, because the degree of myopia does not change significantly after growth ceases in adult individuals (Goss *et al.* 1990), and actually begins to improve after about age 50 (Fledelius & Stubgaard, 1986; Mutti & Zadnik, 2000), disparities in growth of the eyeball and orbit during ontogeny, which are shown to follow separate trajectories (Schultz, 1940; Kay and Kirk, 2000; Chau *et al.* 2004), could result in a permanent malformation of the eyeball.

Different growth trajectories of the orbit and eyeball are likely contributors to the onset of myopia early in life and the continued deterioration of vision until growth

ceases. Additionally, different patterns of growth and development in groups with variable cranial and facial forms may contribute to an understanding of population differences in the frequency and severity of juvenile-onset myopia. This is partially exhibited through a comparison of orbital growth and development between individuals of South African and Japanese ancestry, which shows that the orbit reaches adult size much earlier in the African group by comparison (Figure 6.10). Growth of the cranium is relatively consistent between the two, though the Japanese reach peak size slightly later, which also correlates with the later achievement of adult orbital size around the age of 20 years.

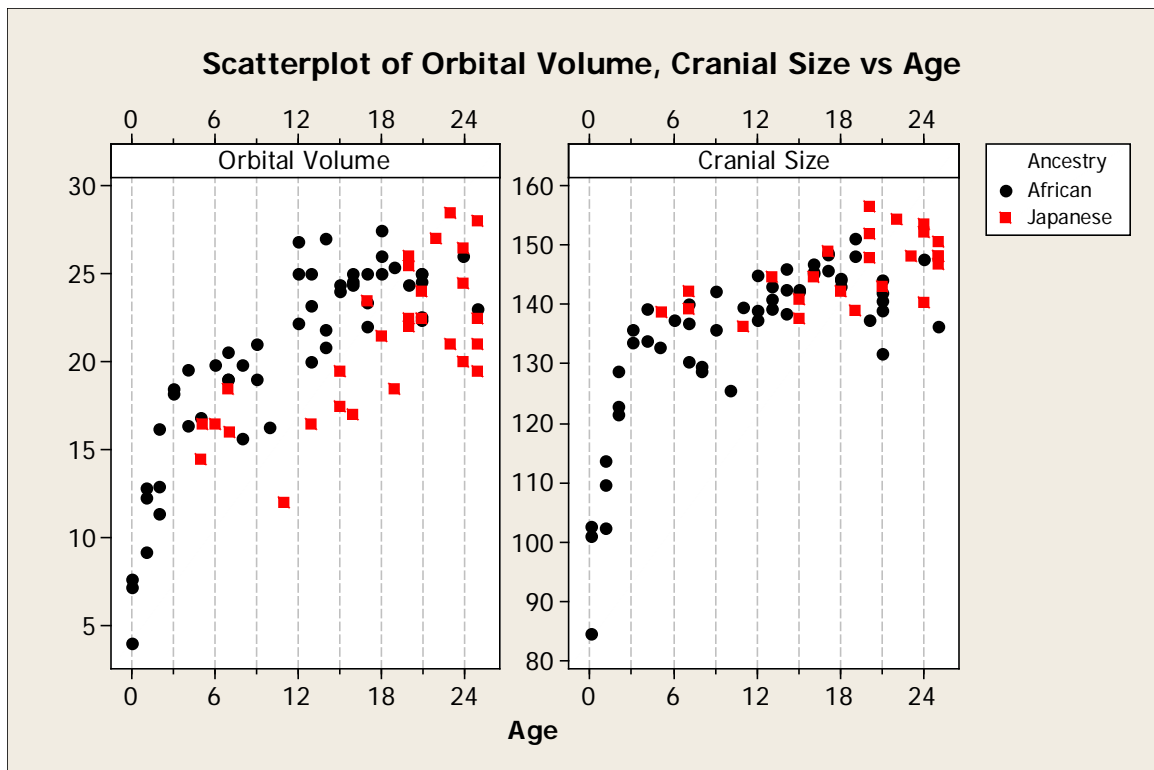


Figure 6.10: Comparison of orbital and cranial growth in African and Japanese samples

The above comparison indicates that in the African group the orbit grows rapidly in early life and continues a slower growth between 3 and 9 years, followed by a rapid increase in size around puberty. By comparison the Japanese sample shows little growth through adolescents, and doesn't exhibit an increase in orbital volume until about 6 years after the African group, with growth in this feature occurring primarily between ages 18 and 24 years. Other studies based on skeletal, hormonal, and other indicators of growth and development have also shown that a general delay in growth is characteristic of Asian populations compared to African and European groups (Ashcroft & Lovell, 1964; Ashcroft *et al.* 1966; Bogin, 1999; Herman-Giddens *et al.* 1997).

Investigating differences in patterns of growth and development in the neurocranium and face of males and females may also contribute to an understanding of why women develop myopia earlier in life, have a higher frequency of the condition, and have a more severe degree of spherical error when growth ceases. For example, in a recent longitudinal growth study of individuals of European descent, sexual dimorphism in the neurocranium of human males and females is found to be present during early life, and remain relatively constant throughout ontogeny; however marked differences exist between the sexes in regard to their facial growth trajectories (Bulygina, Mitteroecker, Aiello, 2006).

These authors show that sexual dimorphism in facial size develops postnatally and increases throughout growth and development, which is primarily due to male hypermorphosis. By contrast females experience a considerable decline in the rate of facial growth around age 13, and stop growing altogether at about age 15 (Bulygina, Mitteroecker, Aiello, 2006). These differences are important given the high percentage

of the orbit that the eyeball fills in females, and the continued growth of the eyeball within the orbit even after facial growth is complete.

By comparison, the eyeball has been shown to grow most rapidly during the first years of life, and then more slowly during later life but with a short spurt between 10-12, and another increased rate of growth from the age of 14 until the early 20s (Salzmann, 1912; Weiss, 1897; Weale, 1982). The rapid period of enlargement early on is primarily in the anterior segment of the eye, which attains much of its complete size during the first year of postnatal life. However, the last increase in size following the fourteenth year primarily involves an enlargement of the posterior segment of the eyeball (Salzmann, 1912; Weiss, 1897), which if out of step with orbital growth could result in its compression against internal soft tissues, with most distortion occurring in the more supple globe.

The late development of this posterior segment would likely contribute to the occurrence and progression of juvenile-onset myopia in individuals and groups that are characterized by less overall skeletal growth, and particularly growth of the face. This is especially important to consider given that early growth of the brain and neurocranium largely influence when and how the face develops (Enlow & Hans, 1996). Forward and downward growth of the brain and basicranium, resulting in less facial growth away from these supraorbital features, may well vertically compress the soft tissue within the orbit and result in an axial elongation of the lissome globe.

Compression of the eyeball in the parasagittal plane is also understandable in the context of differential growth among various components of the orbit during ontogeny, in which later development occurs only in the lateral portion of this feature. Orbital

expansion throughout childhood is primarily restricted to the transverse plane, or in an equatorial orientation with respect to the eyeball (Waitzman *et al.* 1992), while the roof of the orbit is remodeling anteriorly and inferiorly by resorption on the endocranial surface and deposition on the exocranial surface of the frontal bone within the orbit, which is primarily driven by forward and downward expansion of the frontal lobes (Enlow & Hans, 1996). Additionally, a second growth spurt occurs around the age of nine to eleven years in the superior portion of the orbit (Lang, 1983), further contributing to this downward movement of the orbital roof above the eyes and extraocular tissues.

Further research is needed to investigate how different patterns of growth between the eye and orbit among modern human populations and between the sexes relate to the onset and progression of juvenile-onset myopia. Investigating variation in the timing and rate of development among the brain, neurocranium, lower face, orbits, eyeballs, and extraocular tissues may help explain the increased incidence of juvenile-onset myopia in recent human history, and why it occurs with greater frequency and severity among different human groups and between the sexes. Additionally, future research should employ high resolution MRI or CAT scan technology, comprise multiple ancestral groups with equal numbers of males and females, and utilize a longitudinal approach, as cross-sectional data are not capable of detecting slight aberrations in the eyeball and to what degree they relate to compression against contiguous hard and soft tissues within the orbit during growth and development.

CHAPTER 7

SUMMARY AND CONCLUSION

7.1 Modern human variation in orbital morphology

As part of this thesis research, variation in orbital anatomy is compared among three diverse modern human samples using univariate and multivariate statistical tools. The results of this analysis indicate that several differences exist among them in relation to size, shape, and orientation of the orbits. Of the 11 orbital traits investigated only 3 showed no statistically significant degree of divergence among groups, and included the distance between the most lateral margins of the orbits (biorbital breadth), width of the nasal area between the orbits (interorbital breadth), and projection of the inferior orbital margins relative to basion (basion-orbitale).

Traits that are most variable among the modern human groups investigated in this analysis include orbital depth, orbital volume, and shape of the exterior orbital margins. Orbital depth is largest in the Asian sample and differs most from the European group in this regard. The deep orbits in this sample are likely related to the greater degree of orbital convergence, fronto-orbital, and midfacial flatness of East Asian groups (Hanihara, 2000). This facial form draws ectoconchion more anteriorly, thus lengthening the distance between the lateral orbital margins and the most posterior point of the interior orbit from which this measurement was taken.

Although Europeans possess the shortest internal orbital depth, overall volume of the orbital cavity is much larger in this sample, particularly in comparison with the African group. Despite this disparity in orbital size however, Africans and Europeans share a more similar orbital morphology to the exclusion of the Asian sample in 83% of univariate comparisons. Relative size of orbital breadth and orbital height (orbital index) is the most variable of all traits in this among-group univariate comparison. The Asian sample is characterized by the largest orbital height and smallest orbital breadth, which together results in a tall, narrow and more rounded orbital opening. The orbit in the African sample is at the opposite extreme, and is much shorter, wider, and more rectangular in shape. Though a significance test could not be carried out due to a violation of the normality assumption in the Asian sample, this pattern of variability in orbital shape is well documented among modern human populations, and as a result is commonly used in the classification of ancestry in osteological analyses (White, 2000).

In the current study, orbital shape in the European sample fell between Africans and Asians and showed slightly more affinity to the African group. This is particularly interesting given the degree to which orbital height has increased and orbital breadth decreased since the Upper Paleolithic in Western Europe (chapter 5), and indicates that this same trend has occurred even more rapidly, or over a longer time period in China (Brown & Maeda, 2004; Wu *et al.* 2007).

Variation in shape of the orbital margins among these modern human groups is also interesting because both biorbital and interorbital breadth are not statistically different among them. Orbital breadth is much smaller in the Asian sample however, and is more important than orbital height in creating the distinctive form of the orbital

margins in this group. The slightly smaller biorbital breadth and generally narrower face of individuals in the Asian sample also contributes to their distinctively high and narrow orbital margins.

A multivariate comparison of the African, Asian, and European samples using only orbital traits, separates groups most along the first discriminant function based on differences in orbital volume, orbital depth, and the distance from basion to the superior and inferior orbital margins. Along this dimension, the European sample is most different from the other two, which is primarily the result of a much larger orbital volume, and relatively small values for orbital depth, basion-superior orbit, and basion-orbitale.

The pattern of variation among modern human groups for these four traits, which most separate Europeans from the Asian and African samples, is consistent with results obtained from the examination of temporal change in Western Europe in chapter 5. This part of the investigation revealed that during the last 30,000 years in Europe, orbital volume remained relatively large, while all three measures of orbital depth were significantly reduced (obd, bso, bio).

After accounting for the variance explained by the first discriminant function (which primarily separates Europeans from the other two samples), it is the Asian group that differs most from the other two along the second discriminant axis. This departure is primarily the result of a narrower biorbital and orbital breadth, and taller, deeper, and more frontated orbits in the Asian sample. The product of this discriminant function analysis corroborates the results in the previous section using one-way analysis of

variance, but offers more information about the relative contribution of each variable to group separation, and provide a much more holistic picture of population differences in orbital morphology.

7.1.1 Orbital variation in relation to overall craniofacial variability

Although the orbits do show a considerable degree of variation among modern human groups, they are far less variable in comparison with other craniofacial traits. With the exception of maximum cranial length, mean differences are noticeably larger for all other cranial and facial measures in comparison with those of the orbits. Variables that discriminate most among the three samples considered in this analysis primarily involve height and width of the face and cranium.

A discriminant function analysis using all cranial, facial, and orbital variables shows that the Asian and European groups share a more similar overall craniofacial form, despite possessing the greatest number of differences in orbital anatomy revealed in the univariate and multivariate analyses with only orbital variables. Considering all traits of the face and cranium, the European and Asian samples are most separate from the African sample along the first discriminant function as a result of their broader and taller crania, and narrower, taller, and more orthognathic faces.

The African group by comparison is characterized by a longer and narrower skull with a shorter, wider, and more prognathic face. Other comparative morphology studies have also pointed out the similarity between Europeans and Asians, and their divergence from the craniofacial form of Africans and Austro-melanesians (Hanihara, 1996, 2000; Hennessy & Stringer, 2002; Howells, 1989). These dichotomous features also help in the

classification of dry skulls and assigning them to a particular ancestral group in forensic investigations (Burns, 2007; White, 2000).

Orbital characteristics that contribute most to group separation along the first discriminant axis include breadth, volume, and frontation, with each following the same pattern of group differences observed in the previous analyses using only orbital variables. After accounting for the variance explained by the first discriminant function, (which mainly separates Africans out from the European and Asian samples), most cranial, facial, and orbital differences exist between the European and Asian groups. Additionally, because these samples are more similar in cranial and facial form, much of the separation between them along this dimension is the result of a disparity in orbital morphology, in which Europeans possess a wider and larger orbit, while Asians are again distinguished by their relatively tall, narrow and deep orbits.

The first discriminant function primarily divides groups based on features of the face and cranium, while separation along the second dimension is largely the result of differences in orbital morphology. This indicates that despite a greater degree of variation that exists among modern humans in cranial and facial form, orbital characteristics also vary and are useful for assigning cases to their appropriate ancestral group. This also indicates that orbital traits are relatively independent of surrounding cranial and facial features in modern humans, as these characteristics of the skull demarcate along different canonical roots, and show different patterns of group affinity depending on whether orbital variables are included in the analysis.

For example, despite the disparate orbital attributes of Asians and Europeans, these groups share a similar overall craniofacial form, and when cranial and facial

characteristics dominate the discriminant analysis, Asians and Europeans are most similar to the exclusion of the African sample. However, once these are accounted for by the first discriminant function and orbital differences contribute more to the model, the greatest disparity exists between Asians and Europeans. Consequently, the second discriminant function, which considers all orbital, lower facial, and neurocranial traits, captures much of the same pattern of inter-group variation in orbital morphology described in both the analysis of variance, and discriminant function analysis when only orbital traits were used. This indicates that the orbit is not tightly integrated with other craniofacial traits that distinguish between these ancestral groups, but rather that orbital form is somewhat independent of these other features in modern humans.

7.2 Long-term evolutionary change in the hominin orbit

The hominin lineage is unique among mammals in the extent to which the brain has enlarged relative to other anatomical regions, particularly considering that most of this growth has taken place only within the last 2 million years of human evolution. A considerable degree of modification has also taken place in the facial form of past hominin groups in association with this cranial expansion. Though these changes are well documented in the hominin lineage, little is known about how the orbits vary in association with the convergence of the face and neurocranium around this midfacial region. As a result, this study investigates the relationship among these features in *Pan*, *Australopithecus*, and *Homo*, which are characterized by different grades of encephalization and facial prognathism, and tests predictions regarding the direction and strength of these relationships.

Six orbital variables were used to investigate three general regions of the external orbit predicted to covary with cranial size and facial prognathism. As the lower face retracts toward an expanding and forward projecting neurocranium, the inferior orbital region was predicted to drift posteriorly, and to a greater extent than the superior orbital margins, which together would result in a more frontated eye orbit relative to the Frankfurt Horizontal Plane. Shape of the orbital margins was also expected to change and become vertically shortened and horizontally elongated in association with convergence of the face and cranium above and below the orbital region.

A test of no relationship between six orbital variables and the craniofacial index (CFI), which captures this grade shift in craniofacial form, reveals that the null hypothesis is rejected for each orbital trait, and that predicted patterns of covariation among these features are supported by the direction and strength of these relationships. For example, in this analysis it was shown that as cranial size increases and facial prognathism decreases, which is indicated by an increase in the craniofacial index, orbital projection relative to basion is reduced. Though both basion-superior orbit (bso) and basion-orbitale (bio) are inversely related to the craniofacial index, the position of the inferior orbital margins relative to basion is more highly correlated with CFI. This means that as the neurocranium expands out over the orbits, the superior orbital margins move posteriorly to a lesser extent than the inferior orbital margins that migrate posteriorly in association with lower facial retrognathism.

This discrepancy between the upper and lower aspects of the orbits is also related to an increase in orbital frontation. As the craniofacial index increases and the inferior orbital margins shift posteriorly to a greater extent than the superior margins, the entire

orbit becomes more frontated, or more vertically oriented relative to the Frankfurt Horizontal Plane. This analysis indicates that a strong relationship exists between orbital orientation and changes in the cranium and face during human evolution. This finding also corroborates Cartmill's (1970) proposal that increased orbital frontation would occur in response to an increase in relative brain size and/or a reduction in palatal length and maxillary recession. However, though strong relationships exist between orbital frontation and these cranial and facial features, frontation of the orbit must also be understood in the context of a shift toward more orthograde posture (Daebelow, 1929, Weidenreich, 1941), increased basicranial flexure (Ross, 1995; Ross & Ravosa, 1993), and increased relative brain size (Lieberman, Ross, Ravosa, 2000; Strait & Ross, 1999) that occur in association with these craniofacial trends during hominin evolution.

A more orthograde posture has been suggested as a contributor to frontation of the orbits, which occurs in association with increased relative brain size and flexure of the cranial base, each acting to rotate the mid and lower face inferiorly and contributing to klinorhynchy in species with these postural, brain, and basicranial characteristics (Bastir *et al.* 2008; Bookstein *et al.* 2003; Enlow & Hans, 1996; Lieberman & McCarthy, 2000; Lieberman, Ross, Ravosa, 2000; Lieberman, McBratney, Krovitz, 2002; Ross, 1995; Strait & Ross, 1999). During this craniofacial transformation in hominin evolution, the brow ridge essentially acts as a hinge between the expanding braincase and posteriorly relocating face, to the extent that the orbits and ethmomaxillary complex swing below the anterior cranial base and under the frontal lobes of the brain in anatomically modern *Homo sapiens* (Bruner, 2007; Lieberman, 2000; Lieberman, Ross, Ravosa, 2000; Lieberman, McBratney, Krovitz, 2002).

A final prediction relating to how the orbital opening varies in association with increased cranial size and decreased facial prognathism is also supported in this analysis. Orbital height is found to decrease as orbital breadth increases in association with an expanding cranium that grows out over the orbits, and an ethmomaxillary complex that relocates posteriorly toward them. The result of this craniofacial coalescence is an overall shape change in which the orbits become mediolaterally elongated and superoinferiorly shortened.

The wide rectangular shape of the orbital margins resulting from a shift in relative size of orbital height and orbital breadth is highly characteristic of anatomically modern humans from the Upper Paleolithic in Europe and Asia (chapter 5), and extant groups from Sub-Saharan Africa (chapter 3). Following the Upper Paleolithic however, the trend toward superoinferiorly shorter and more elongated orbits associated with a grade shift in craniofacial form began to reverse, and the orbital margins become taller and narrower, taking on a more rounded shape. This more recent trend has also been documented among East Asian groups dating to the Holocene (Brown & Maeda, 2004; Wu *et al.* 2007), and is investigated as part of a larger examination of orbital change through the European Upper Paleolithic in chapter 5 of this thesis.

7.3 Evolutionary change in the hominin orbit: Upper Paleolithic to present

Numerous changes in orbit morphology are observable within the last 30,000 years in Western Europe. Most notable among them is a relatively rapid increase in orbital height, which in association with a decrease in orbital breadth and biorbital breadth results in a high, narrow, and more rounded shape of the external orbital margins.

As previously mentioned, this decrease in orbital index (obi) since the Upper Paleolithic mimics a trend that occurs in Asia (Brown & Maeda, 2004; Hanihara, 1994; Wu *et al.* 2007), but stands in contrast to that which characterizes most of our evolutionary history. This divergent pattern of change in shape of the orbital margins is likely associated with a slowing, cessation, and/or reversal of certain long-term trends in the evolution of hominin craniofacial anatomy.

Throughout much of our evolutionary history the neurocranium has expanded upward, forward, and outward while the lower facial region retreats posteriorly toward it. However, during the last 30,000 years in Western Europe and in other regions of the world, absolute and relative cranial size have decreased in association with a minimal degree of facial retraction. Most changes in skull morphology throughout this time period involve shape modification, and more specifically a shift toward brachycephalization and an increase in the facial index (a narrower vertically elongated facial form) (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Hanihara, 1994; Henneberg, 1988; Lahr & Wright, 1996; Wu *et al.* 2007).

Though no predictions were made concerning how the orbits vary in relation to neighboring features in this analysis of orbital change since the Upper Paleolithic, an extemporized investigation of these features shows that the orbital index and many other orbital variables are correlated with these cranial and facial shape changes. It should be pointed out that although the orbits vary in association with brachycephalization and an increase in the facial index throughout this time period, they are not viewed as the only source of influence, as other contiguous features certainly covary with the orbits as well.

Nevertheless, orbital traits that change most during this time are also those that are most highly correlated with the cranial and facial indexes, and the pattern of covariation among them follows that which would be expected in association with trends of brachycephalization and a narrowing and elongation of the face. For example, the orbital margins and three measures of orbital depth are most strongly associated with the time variable, indicating that they have changed significantly since the Upper Paleolithic. These features are also highly correlated with the cranial index and upper facial index, and covary with them in a way that is consistent with craniofacial shape changes that have occurred in this region over the last 30,000 years.

Although long-term trends of increased cranial capacity and decreased facial prognathism do not persist, some orbital traits found to vary in association with these craniofacial changes, which are characteristic of a majority of human evolution (chapter 4), continue through the European Upper Paleolithic. For example, both the upper and lower orbital margins moved posteriorly relative to basion in association with increased cranial size and decreased facial prognathism, and each measure continues to decrease through the Upper Paleolithic. While both the upper and lower orbital margins continue to move posteriorly, there is a shift in which of these regions change most during this time period.

In chapter 4 it was found that basion-orbitale decreases far more than the measure of basion to the superior orbital margins in association with an increase in the craniofacial index CFI, which is likely a result of the brain moving forward and maintaining the relative position of the upper orbit, while the zygomatic and maxilla that together make up the lower orbital region move posteriorly in association with the retracting face.

Following the Upper Paleolithic however, the superior orbital margins are shown to retreat slightly more compared to the inferior orbital region, which is likely the result of a greater reduction in size of the supraorbital tori, as well as a slowed rate of reduction in facial prognathism during recent human evolution.

The relative position of the upper and lower orbital margins, in association with these other craniofacial trends, also influences the vertical angle of the orbits. Orbital frontation occurs in association with cranial expansion and facial reduction during hominin evolution, and is equally correlated with change in both features above and below the orbits. As the upper orbital margins move posteriorly to a lesser extent than the inferior margins in association with cranial expansion above and facial retraction below the orbital opening, the angle becomes more obtuse and approaches 90 degrees in more modern groups with a higher craniofacial index.

Compared to the vast majority of human evolution, orbital frontation does not change considerably during the last 30,000 years in Western Europe, but rather maintains an approximately 90 degree orientation throughout this period, and actually appears to decrease slightly following the Neolithic and particularly after the Copper Age. Although the superior and inferior orbital margins both continue to move posteriorly, because the lower region no longer retreats to a greater extent than the upper, this long-term trend of orbital frontation is largely arrested. Orbital frontation is also not found to correlate with either the cranial index or upper facial index, which capture general changes in cranial and facial shape within this region over the last 30,000 years.

As a result of poor preservation in the fragile bony orbit of fossil hominins, change in the internal anatomy of this feature relative to cranial expansion and facial

retraction could not be evaluated. However, many skulls of anatomically modern humans dating back to the Upper Paleolithic have retained much of the internal orbital structure, which facilitates an analysis of more recent evolutionary changes in orbital depth and volume, as well as an assessment of how they covary with craniofacial shape changes that have taken place during this time.

Both measures of volume are among only four orbital characteristics, including orbital frontation and interorbital breadth, which show no statistically significant relationship to time in this investigation of orbital change since the European Upper Paleolithic. In fact a later investigation of interorbital breadth showed that this feature does not vary in relation to cranial expansion or reduced facial prognathism throughout broader hominin evolution, nor did it vary among the three modern human samples in this study, indicating that it is a highly conserved region of the skull across time and space.

Although orbital volume does not show a relationship to time in this investigation of morphological change in Western Europe, both measures of orbital volume are inversely related to the upper facial index, which increases since the Upper Paleolithic in this region. This indicates that an increase in facial height and decrease in facial breadth is accompanied by a reduction in orbital size. However, because orbital volume remains constant throughout this time period, these facial shape changes do not influence relative orbital size in any appreciable way. Additionally, a decrease in orbital volume that occurs in association with decreased supraorbital breadth, lower facial prognathism, and the orbital index in East Asia since the Neolithic (Brown & Maeda, 2004), is not

consistent with morphological changes in the orbit and broader craniofacial complex of temporal groups in Europe.

While orbital volume remains relatively constant since the Upper Paleolithic in Western Europe, a statistically significant decrease in orbital depth is found to occur. This decrease in the anteroposterior length of the orbit would be expected in association with a decrease in cranial length and a posterior movement of the upper and lower orbital margins, which also take place throughout this period. Reduction in basion-superior orbit (bso), basion-orbitale (bio), and orbital depth (obd) within Western Europe over the last 30,000 years, also helps explain the statistically lower value for each of these variables in modern Europeans when compared with African and Asian samples in the analysis of modern human variation carried out in chapter 3.

7.4 An evolutionary perspective on the etiology of juvenile-onset myopia

A decrease in anterior projection of the upper and lower orbital margins, which occurs in association with increased cranial size and decreased facial prognathism (chapter 4), and continues in association with a reduction in orbital depth throughout the last 30,000 years in Western Europe (chapter 5), may be important to consider in investigating the etiology of myopia in European/Caucasian groups. A more forward projecting (exophthalmic/proptotic) eye resulting from a decrease in orbital depth, becomes anterior to the concave segment of the orbital roof and floor in which it is meant to rest. Because the inferior and superior aspects of the orbital opening curve toward each other, a more forward eye and extraocular tissues may become compressed against these hard tissue components of the orbit.

A statistically significant negative correlation between proptosis and spherical equivalent refractive error has led some researchers to suggest that degree of refractive error be considered in studies of exophthalmia, as it is assumed that the increased axial length of the eyeball in myopes causes it to protrude out from the orbit (Migliori *et al.* 1984; Quant & Woo, 1992). However, it is also highly likely that more proptotic eyeballs become compressed within the orbit, which would cause them to become axially elongated and subsequently increase myopic refractive error as a response to this superoinferior pressure being applied to the eye and extraocular tissues as they shift forward toward the smaller part of the orbit. This suggests that increased axial length of the myopic eye is not a contributing factor to exophthalmia, but rather a possible result of its protrusion.

A rapid increase in orbital height that occurs throughout the Upper Paleolithic in Europe and Asia would diminish the amount of pressure applied to the eye and ocular tissue if it were to shift anteriorly in association with a decrease in both orbital depth and orbital projection through time. However, Brown and Maeda (2004) show that this shape change, in which the orbits become taller and rounder, is associated with an overall *decrease* in orbital volume in their East Asia temporal analysis. This relationship between orbital shape and orbital volume was not found to exist among groups from Western Europe dating to the Upper Paleolithic in the current study, and in fact no decrease in absolute or relative size of the orbit was detected in this region (chapter 5).

At the end of their article, Brown and Maeda (2004) state that “if it is the total volume occupied by the eyeball, extraocular muscles, nerves and blood supply which are important, rather than just the size of the eyeball, then there would need to be some

functional compensation for any significant reduction in orbit length and volume” (pg. 38). A reduction in orbital volume and orbital depth would require some form of functional compensation to allow adequate space for proper growth and development of the eye, particularly given that the eyeball and orbit follow separate growth trajectories. However, as a result of long-term evolutionary trends in hominin evolution in which increased relative brain size initiates flexing of the basicranium and the deposition of bone on the exocranial surface of the anterior cranial base, while also limiting the amount of available time and space for outward and downward growth of the nasomaxillary complex, it is not likely that any form of functional compensation could occur which would free up space for the mass of soft tissues within the orbit.

During much of our evolutionary history, the relationship between the brain, eye, orbit, and lower face would be regulated by the necessity of keen vision associated with a hunter/gatherer subsistence strategy. Selective pressure favoring individuals with better eyesight would be relaxed following the advent of corrective lenses, but may have begun in association with social stratification and a division of labor in human society long before this technology was available. Social stratification allows individuals with skills that only require one to work within arms-length of the face (making clothing, tallying commercial activities, etc.) to continue to survive and reproduce even without highly acute vision.

A broad division of labor with high levels of social stratification began during the Neolithic, at which time individuals could remove themselves from the burdens of subsistence and engage in other crafts, trading goods and services for food produced by others. However, while the development of agriculture allowed some members of society

to engage in non-subsistence activities without an imposed opportunity cost, relaxation of selective pressure favoring those with keen eyesight may have begun even earlier, as tool-making, which has been an exceptionally valued skill for far longer, allows individuals to produce highly coveted items that can be traded for parts of animals they were used to kill by others. With relaxation of this selective pressure in the human past, changes among structural and functional units of the skull in association with brain peramorphosis and facial paedomorphosis may have begun to impinge on the space previously reserved for the visual system, particularly given that the brain and eye share multiple bones that house their respective soft tissue components.

The orbits, along with the eyeballs and extraocular tissues circumscribed by them, are separated from the frontal lobes of the brain by a very thin sliver of bone that protrudes slightly into the anterior braincase. This bone is so thin in fact, that in many individual dry skulls investigated as part of this dissertation research it was translucent enough to see into the orbit looking down on the anterior cranial base with the calvarium removed. The close configuration of the brain, anterior cranial fossa, orbit, and eye, is a result of an absolute and relative increase in brain size, in which the frontal lobes have expanded and moved forward to the point that they have come to rest atop the eyes, and have all but erased the supraorbital tori in modern humans (Bruner, 2007; Moss & Young, 1960).

This craniofacial form is considered a unique feature of humans to the exclusion of all other mammalian groups (Enlow & Hans, 1996), and is a likely contributor to the high incidence of juvenile-onset myopia in our species, as a result of competition among important functional units within the limited space of the human

skull. Although the eyeball lies predominantly within the orbit, it does not directly influence orbital size (Chau *et al.* 2004; Schultz, 1940), but rather eye growth keeps pace with growth of the brain (Salzmann, 1912; Todd *et al.* 1940; Weale, 1982; Weiss, 1897), and both are thought to be the product of pleiotropic gene control (Mak, *et al.* 2005). In contrast, the orbits grow in association with the rest of the cranium (Waitzmann *et al.* 1992) and have been shown to vary in association with overall body size, to the extent that body mass and area of the orbital opening are correlated at $r = 0.987$ (Kappelman, 1996).

If growth of the eye and brain are a product of pleiotropy, prolonged brain growth throughout hominin evolution would also act to increase size of the eyeball, while at the same time limiting available space for the eye and extraocular tissues within the orbit, due to brain growth above this region in recent human evolution. Change in the timing and rate of growth in the neurocranium and face in association with increased encephalization throughout hominin evolution, would eventually reach a point in which continued expansion of both the eyes and brain would result in their competing for space in this anatomical region. And while the brain can bend and fold within the confines of the cranium, the eye cannot.

Additional expansion of either of these features due to genetic or epigenetic factors during growth would further contribute to superoinferior pressure being applied to the eye, and result in myopic refractive error from an increase in its axial length and corneal curvature. The correlation between myopia and intelligence for example, is likely the result of epigenetic changes in which the frontal lobes develop more during early life as a result of increased cognitive stimulation. The benefit of higher intelligence

comes at a cost to visual acuity however, as the size/shape of the upper orbital region may be affected by this extended neural development.

The link between diabetes and myopia (Fledelius, 1983) may also be understood in this context. A shift toward a more Westernized diet consisting of foods high in sugar and saturated fat often leads to myopia, in association with diabetes and general weight gain (Cordain *et al.* 2002). Additional deposition of fat around the eye (which comprises a large part of the total orbital volume) would again impinge on the globe, as long-term evolutionary changes in craniofacial form have left little room to compensate for these additional tissues within the already limited space of the orbit.

Lastly, because relative size of the eye within the orbit increases as body size decreases (Schultz, 1940; Kay & Kirk, 2000), a global reduction in cranial and postcranial size and robusticity following the Pleistocene (Brown 1987; Brown & Maeda, 2004; Carlson, 1976; Carlson & Van Gerven, 1977; Henneberg, 1988; Lahr & Wright, 1996; Wu *et al.* 2007) would also be expected to further increase the percentage of orbital volume filled by the eye and extraocular tissues.

In chapter 6 of this thesis, an analysis of eyeball volume, orbital volume, and refractive error in Chinese adults indicated that the relative size of the eye within the orbit is an important predictor of myopia. Individuals with large eyes and small orbits tend to be more myopic and have a greater degree of refractive error, while those with large orbits and relatively small eyes boast keener vision. Because orbit size and body mass are highly correlated (Kappelman, 1996), and a negative allometric relationship exists between the eyeball and orbit with respect to body size (Schultz, 1940), a reduction in overall size and robusticity since the Mesolithic would act to increase the percentage of

the orbit occupied by the eye, and bring humans as a whole closer to the point at which these tissues vie for space. An added decrease in orbital volume in East Asia (Brown & Maeda, 2004) would act to exacerbate an existing trend toward increased relative eye size, and may help explain the unusually high frequency of myopia in this region. The higher incidence rate among certain Asian groups may also be understood in the context of different patterns of growth and development among modern human populations.

The eyeball has been shown to grow fastest early in life and with another spurt between 10-12 years of age (Wheale, 1982), though many East Asian groups are characterized by delayed growth and development, as indicated by a number of dental, skeletal, and sexual indicators. For example, in a study of European, African, Afro-European, and Chinese descendent populations, it was found that no significant difference in height or weight existed among the first three groups; but at every age the Chinese group was significantly lighter and shorter than the other three, even after nutritional, socioeconomic, and environmental effects were accounted for (Ashcroft & Lovell, 1964; Ashcroft *et al.* 1966; cited in Bogin, 1999). Other studies also support these findings, showing differences in the timing of tooth eruption (Gillett, 1998; Smith, Gannon, Smith, 1995), and sexual maturity indicators (breast development, pubic hair, menses) in groups with different ethnic origins (Herman-Giddens *et al.* 1997).

In chapter 6 of this thesis it was shown that orbital growth is delayed by approximately 6 years in a sample of Japanese sub-adults in comparison with individuals from two tribes in South Africa, corroborating the results of these prior studies. Delayed development of the orbit and other facial components among groups characterized by neurocranial peramorphosis and facial hypomorphosis, may result in divergent growth

trajectories between the eye and orbit, and consequently compression of the more lithesome globe within the bony structure of the orbital cavity.

Differences in patterns of growth and development in the neurocranium and face of males and females have also been shown to exist, and may contribute to an understanding of why women have a higher frequency of juvenile-onset myopia than men, develop the condition earlier in life, and have a more severe degree of refractive error when growth ceases (Angle & Wissman, 1980; Grosvenor & Goss, 1999; Lam *et al.* 1999; Ip *et al.* 2008; Parssinen & Lyyra, 1993; WGMPP, 1989).

In a recent sex-based longitudinal growth study, sexual dimorphism in the neurocranium of human males and females was found to be present during early life, and remain relatively constant throughout ontogeny, however facial growth trajectories between the sexes were found to differ noticeably (Bulygina, Mitteroecker, Aiello, 2006). For example, sexual dimorphism in facial size develops postnatally and increases throughout growth and development, which is primarily the result of hypermorphosis in males. Females on the other hand experience a considerable decline in the rate of facial growth around age 13, and stop growing altogether at about age 15 (Bulygina, Mitteroecker, Aiello, 2006). This growth pattern is particularly important in the context of later expansion of the posterior segment of the eyeball, and the larger relative size of the eye in females.

The model proposed in this thesis attributes the high frequency of juvenile-onset myopia in humans to changes in the relationship among different hard and soft tissue components of the skull during growth and development, and throughout hominin evolution. Most studies investigating the pathogenesis of this condition have primarily

considered the eye as an isolated entity, with little attention paid to its association with the neurocranium, basicranium, viscerocranium, and above all its relative interment within circumscribing extraocular tissues and an orbit that consists of seven bones with heterogeneous relationships to neighboring craniofacial units. The results of this anthropological investigation indicate that future research into the etiology of juvenile-onset myopia should consider how the eyeball interacts with the orbit and broader matrix of structural and functional components of the skull, in the context of both ontogenetic and evolutionary morphogenesis.

BIBLIOGRAPHY

Aiello, L., Dean, C. (1990) *An Introduction to Human Evolutionary Anatomy*. Academic Press Limited. San Diego, CA

Ackermann, R. R., & Krovitz, G. E. (2002) Common patterns of facial ontogeny in the hominid lineage. *Anat Rec*, 269(3), 142-147.

Aftandilian D, Buikstra J, Finnegan M, Hass J, Kice D, Nichol C, Owsley D, Rose J, Schoeninger M, Scott G, Turner C. II, Ubelaker D, Walker P, Weidl E (1994) Standards, for data collection from human skeletal remains. Eds. Jane E. Buikstra and Douglas H. Ubelaker. *Proceedings of a Seminar at The Field Museum of Natural History*

Angle, J., Wissmann, D., (1980) The Epidemiology of Myopia. *American Journal of Epidemiology* 11(2), 220-228

Ashcroft MT, Lovell HG (1964) Heights and weights of Jamaican children of various racial origin. *Tropical and Geographical Medicine* 16:346-353

Ashcroft MT, Heneage P, Lovell HG (1966) Heights and weights of Jamaican schoolchildren of various ethnic groups. *Am J Phys Anthropol* 24(1), 35-44

Badawi-Fayad, J., Cabanis, E. (2007) Three-dimensional procrustes analysis of modern human craniofacial form. *Anatomical record-advances in integrative anatomy and evolutionary biology*. 290(3), 268-276

Bastir M, Rosas A. (2004) Facial heights: Evolutionary relevance of postnatal ontogeny for facial orientation and skull morphology in humans and chimpanzees. *J Hum Evol* 47(5), 359-381.

Bastir M, Rosas A. (2004) Comparative ontogeny in humans and chimpanzees: Similarities, differences and paradoxes in postnatal growth and development of the skull. *Annals of Anatomy-Anatomischer Anzeiger* 186(5-6), 503-509.

Bastir M, Rosas A. (2005) Hierarchical nature of morphological integration and modularity in the human posterior face. *Am J Phys Anthropol* 128(1), 26-34.

- Bastir, M., Rosas, A., O'Higgins, P. (2006) Craniofacial levels and the morphological maturation of the human skull. *Journal of Anatomy*, 209(5), 637-654
- Bastir, M., O'Higgins, P., & Rosas, A. (2007). Facial ontogeny in Neanderthals and modern humans. *Proc Biol Sci*, 274(1614), 1125-1132.
- Bastir M, Rosas A, O'Higgins P (2007). 3D architecture of the middle cranial fossa and modern human origins. *Am J Phys Anthropol* 44, 69-69 Suppl.
- Bastir, M., Sobral, P. G., Kuroe, K., & Rosas, A. (2008). Human craniofacial sphericity: a simultaneous analysis of frontal and lateral cephalograms of a Japanese population using geometric morphometrics and partial least squares analysis. *Arch Oral Biol*, 53(4), 295-303.
- Bastir, M., Rosas, A., Lieberman, D., O'Higgins, P. (2008) Middle Cranial Fossa Anatomy and the Origin of Modern Humans. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, 291(2), 130-140
- Bogin, B. (1999) *Patterns of Human Growth*. Cambridge University Press
- Bookstein F., Gunz P., Mitteroecker P., Prossinger H., Schaefer K., Seidler H. (2003) Cranial integration in Homo: singular warps analysis of the midsagittal plane in ontogeny and evolution. *J Hum Evol* 44:167–87
- Bromage TG. (1992) The ontogeny of pan-troglodytes craniofacial architectural relationships and implications for early hominids. *J Hum Evol* 23(3), 235-251.
- Brown P. (1998–2003) Australian and Asian Palaeoanthropology. <http://metz.une.edu.au/~pbrown3/palaeo.html>
- Brown. P. (1987) Pleistocene homogeneity and Holocene size reduction: the Australian human skeletal evidence. *Archaeology in Oceania* 22: 41-67.
- Brown, P. (1989) Coobool Creek. *Terra Australis* 13, Department of Prehistory, Research School of Pacific Studies, Australian National University: Canberra;
- Brown, P. (1992) Recent human evolution in East Asia and Australasia. *Philosophical Transactions of the Royal Society London, Series B* 337:235-242.
- Brown, P. and Maeda, T. (2004) Post-Pleistocene diachronic change in East Asian facial skeletons: the size, shape and volume of the orbits. *Anthropological Science*. 112:29-40
- Bruner E, Manzi G, Arsuaga J-L (2003) Ecephalization and allometric trajectories in the genus Homo: evidence from the Neandertal and modern lineages. *Proc Natl Acad Sci USA* 100:15335–15340.

- Bruner, E., Saracino, B., Passarello, P., Ricci, F., Tafuri, M., Manzi, G., (2004) Midsagittal cranial shape variation in the genus *Homo* by geometric morphometrics. *Coll. Antropol.* 28, 99-112.
- Bruner, E., Manzi G. (2005) CT-based description and phyletic evaluation of the archaic human calvarium from Ceprano, Italy. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, 285A,(1), 643-657
- Bruner, E. (2007) Cranial shape and size variation in human evolution: structural and functional perspectives. *Childs Nervous System* 23(12) 1357-1365
- Bulygina, E, Mitteroecker, P., Aiello L. (2006) Ontogeny of facial dimorphism and patterns of individual development within one human population. *American Journal of Physical Anthropology* 131(3) 432-443
- Burns K. (1999) *Forensic anthropology training manual*. New Jersey: Prentice-Hall
- Carlson DS., Van Gerven DP. (1977) Masticatory function and post-Pleistocene evolution in Nubia. *Am J Phys Anthropol* 46(3), 495-506
- Carlson DS. (1976) Temporal variation in prehistoric Nubian crania. *Am J Phys Anthropol* 45(3), 467-84
- Cartmill, M. (1970) *The orbits of arboreal mammals: a reassessment of the arboreal theory of primate evolution*. Ph.D. Dissertation, University of Chicago.
- Chau, A., Fung, K., Pak, K., Yap, M (2004) Is eye size related to orbit size in human subjects? *Ophthalmic and Physiological Optics*, 24(1) 35-40
- Chen, C., Cohen, B., Diamond E. (1985) Genetic and environmental effects on the development of myopia in Chinese twin children. *Ophthalmic Pediatrics and Genetics*, 6 ½:113-119
- Cobb, S. N. (2008). The facial skeleton of the chimpanzee-human last common ancestor. *J Anat*, 212(4), 469-485.
- Cordain, L., Eaton, B., Miller, J., Lindeberg, S., Jensen, C. (2002) An evolutionary analysis of the aetiology and pathogenesis of juvenile-onset myopia. *Acta Ophthalmologica Scandinavica* 80: 125-135
- Darroch JN, Mosimann JE (1985) *Biometrika* 72:241–252.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*, 6th ed. John Murray, London

Dixon, A., Hoyte, D., Ronning, O. editors (1997) *Fundamentals of craniofacial growth*. CRC Press, Boca Raton, Florida

Dabelow, A. (1929) *Über Korrelationen in der phylogenetischen Entwicklung der Schädelform I. Die Beziehungen Zwischen Rumpf und Schädelform*. *Gegenb. Morpholog. Jahrb.* 63, 1-49

Emery N.J. (2000) *The eyes have it: neuroethology, function and evolution of social gaze*. *Neuroscience and biobehavioral reviews*. 24(6), 581-604

Enlow, D., Pfister, C., Richardson, E., Kuroda, T. (1982) *An analysis of black and caucasian craniofacial patterns*. *The Angle Orthodontist*. 52(4), 279-287

Enlow, D. H. (1990). *Facial Growth*, 3rd ed. Philadelphia: Saunders.

Enlow D., Hans, M. (1996) *Essentials of Facial Growth*. W.B. Saunders Company. Philadelphia, Pennsylvania

Fledelius, H. C. (1983) *Is myopia getting more frequent? A cross-sectional study of 1416 Danes aged 16 years +*. *Acta Ophthalmologica*. 61: 545-559

Fledelius, H. C., & Stubgaard, M. (1986). *Changes in eye position during growth and adult life as based on exophthalmometry, interpupillary distance, and orbital distance measurements*. *Acta Ophthalmol (Copenh)*, 64(5), 481-486.

Fledelius, H. C., & Stubgaard, M. (1986). *Changes in refraction and corneal curvature during growth and adult life. A cross-sectional study*. *Acta Ophthalmol (Copenh)*, 64(5), 487-491.

Forbes G, Gehring DG, Gorman CA, Brennan MD, Jackson IT. (1985) *Volume measurements of normal orbital structures by computed tomographic analysis*. *AJR Am J Roentgenol* 145:149–154

Garson, GD. (2008) *Discriminant function analysis*. *Statnotes: Topics in Multivariate Analysis*. Retrieved 01/02/2008 from <http://www2.chass.ncsu.edu/garson/pa765/statnote.htm>

Goldschmidt, E. (1999) *Myopia in humans: can progression be arrested?* In *Myopia and the Control of Eye Growth*, Ciba Foundation Symposium 155. John Wiley & Sons, New York, N.Y.

- Goldschmidt, E., Lam, C., Opper, S. (2001) The development of myopia in Hong Kong children. *Acta Ophthalmologica Scandinavica*. 79:228-232
- Gonzalez-Jose, R., Neves, W., Lahr, M. M., Gonzalez, S., Pucciarelli, H., Hernandez Martinez, M., et al. (2005). Late Pleistocene/Holocene craniofacial morphology in Mesoamerican Paleoindians: implications for the peopling of the New World. *Am J Phys Anthropol*, 128(4), 772-780.
- Gonzalez-Jose, R., Ramirez-Rozzi, F., Sardi, M., Martinez-Abadias, N., Hernandez, M., & Pucciarelli, H. M. (2005). Functional-cranial approach to the influence of economic strategy on skull morphology. *Am J Phys Anthropol*, 128(4), 757-771.
- Goss, D. A., & Grosvenor, T. (1990). Rates of childhood myopia progression with bifocals as a function of nearpoint phoria: consistency of three studies. *Optom Vis Sci*, 67(8), 637-640.
- Grosvenor TP, Goss DA. (1990) *Clinical Management of Myopia*. Boston: Butterworth-Heinemann
- Hanihara T. (1994) Craniofacial continuity and discontinuity of Far Easterners in the late Pleistocene and Holocene. *J Hum Evol* 27(5), 417-441.
- Hanihara T. (1996) Comparison of craniofacial features of major human groups. *Am J Phys Anthropol* 99(3), 389-412.
- Hanihara T. (2000) Frontal and facial flatness of major human populations. *Am J Phys Anthropol* 111(1), 105-134.
- Henneberg, M. (1988). Decrease of human skull size in the Holocene. *Hum Biol*, 60(3), 395-405.
- M. Henneberg, M. Steyn. (1993) Trends in cranial capacity and cranial index in Sub-Saharan Africa during the Holocene. *Am. J of Human Biology* 5(4), 473-479
- Hennessy RJ, Stringer CB. (2002) Geometric morphometric study of the regional variation of modern human craniofacial form. *Am J Phys Anthropol* 117(1), 37-48.
- Herman-Giddens, Marcia E., Slora, Eric J., Wasserman, Richard C., Bourdony, Carlos J., Bhopkar, Manju V., Koch, Gary G., Hasemeier, Cynthia M. (1997) Secondary Sexual Characteristics and Menses in Young Girls Seen in Office Practice: A Study from the Pediatric Research in Office Settings Network *Pediatrics*. 99: 505-512
- Howells, W. (1973) *Cranial Variation in Man: A Study by Multivariate Analysis of Pattern of Differences Among Recent Human Populations*. Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University 67: 1-259.

Howells W. (1989) Skull shapes and the map. Pap Peabody Mus. 79: whole volume. Cambridge, MA: Harvard. p 1–189.

Ip, J., Huynh, S., Rogaei, D. Kifley, A., Rose, K., Morgan, I., Wang J. Mitchell, P. (2008) Ethnic differences in refraction and ocular biometry in a population-based sample of 11-15 year-old Australian children. *Eye*. 22: 649-656

Jöreskog, K.G. & Sörbom, D. (1981-2007) LISREL 8.7 Computer Software
Lincolnwood, IL: Scientific Software International, Inc.

Kappelman, J. (1996) The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution*. 30: 243-276

Kay, RF., Kirk EC. (2000) Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am J Phys Anthropol* 113: 235–262

Kidder, J. H., Jantz, R. L. & Smith, F. H. (1992). Defining modern humans: A multivariate approach. In (G. Bräuer & F. H. Smith, Eds) *Continuity or Replacement*, pp. 157–177. Rotterdam: Balkema.

Kobayashi, H., Koshima, S., (2001) Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *Journal of Human Evolution*. 40: 419-435

Kohn LAP, Leigh SR, Jacobs SC, Cheverud JM. (1993) Effects of annular cranial vault modification on the cranial base and face. *Am J Phys Anthropol* 90(2), 147-168.

Kornack D. R., Rakic P. (2001) Cell Proliferation Without Neurogenesis in Adult Primate Neocortex. *Science*. 294: 2127

Kuroe, K., Rosas, A., & Molleson, T. (2004). Variation in the cranial base orientation and facial skeleton in dry skulls sampled from three major populations. *Eur J Orthod*, 26(2), 201-207.

Lahr M. (1996) *The evolution of modern human diversity*. Cambridge: Cambridge University Press.

Lahr M., Wright R. (1996) The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *J Hum Evol* 31(2):157-191.

Lalouel, J. (1980) Distance Analysis and Multi-determinate Scaling. In: J.H. Mielke and M. H. Crawford (eds.) *Current Developments in Anthropological Genetics*. 209-250. Plenum Press, N.Y.

- Lam, C., Edwards, M., Millodot, M., Goh, W. (1999) A 2-year Longitudinal Study of Myopia Progression and Optical Component Changes among Hong Kong Schoolchildren. *Optometry and Vision Science* 76(6), 370-379
- Lang, J. (1983) *Clinical Anatomy of the Head: Neurocranium, Orbit, & Craniocervical Regions.* (Klinische Anatomie des Kopfes) Springer-Verlag, Berlin
- Lieberman, D. (1998) Sphenoid shortening and the evolution of modern human cranial shape. *Nature*. 393:158-162
- Lieberman, D. (2000) Ontogeny, homology, and phylogeny in the hominid craniofacial skeleton: the problem of the browridge. In: O'Higgins P, Cohn M (eds) *Development, growth and evolution.* Academic, London, 85-122
- Lieberman D. (2002) Human evolution through developmental change. *American Anthropologist* 104(4), 1245-1246.
- Lieberman, D., McCarthy, R. (2000) The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions. *Journal of Human Evolution*. 36(5), 487-517
- Lieberman, D., Pearson, O., Mowbray, K. (2000) Basicranial influence on overall cranial shape. *Journal of Human Evolution*. 38:291-315
- Lieberman, D., Ross, C., Ravosa, M. (2000) The Primate Cranial Base: Ontogeny, Function, and Integration. *Yearbook of Physical Anthropology*. 43:117-169
- Lieberman D., McBratney BM, Krovitz G. (2002) The evolution and development of cranial form in *Homo sapiens*. *Proc Natl Acad Sci U S A* 99(3), 1134-1139.
- Lieberman, D., Krovitz, G. E., & McBratney-Owen, B. (2004). Testing hypotheses about tinkering in the fossil record: the case of the human skull. *J Exp Zool B Mol Dev Evol*, 302(3), 284-301.
- Mahalanobis, P. (1936) On the generalized distance in statistics. *Proceedings of the National Institute of Sciences Ccutta* 2: 49-55
- Mak MWM, Kwan TS, Cheng KH, Chan RTF, Ho SL. (2006) Myopia as a latent phenotype of a pleiotropic gene positively selected for facilitating neurocognitive development, and the effects of environmental factors in its expression. 66: 1209–1215
- Martone, V., Enlow, D., Hans, M., Broadbent, H., Oyen, O. (1992) Class I and Class III malocclusion sub-groupings related to headform type. *Angle Orthodontist*. 62(1), 35-42

- McBratney BM, McCarthy RC, Lieberman DE. (2000) Facial projection and the origin of modern humans. *Am J Phys Anthropol*:223-223.
- McCarthy RC, Lieberman DE. (2001) Posterior maxillary (PM) plane and anterior cranial architecture in primates. *Anat Rec* 264(3), 247-260.
- Migliori, M., Geoffrey, J., Gladstone. (1984) Determination of the normal range of exophthalmometric values for black and white adults. *American Journal of Ophthalmology*. 98,438-442
- Miller EM. (1992) On the correlation of myopia and intelligence. *Genet Soc Gen Psychol Monogr*. 118: 361–383.
- Moore-Jansen, P. , Ousley, S., Jantz, R. (1994) Data Collection Procedures for Forensic Skeletal Material. Report of Investigation no. 48. Knoxville, TN: University of Tennessee.
- Moss M., Young R. (1960) A functional approach to craniology. *Am J Phys Anthropol* 18: 281–292.
- Mutti DO, Zadnik K. (2000) Age-related decreases in the prevalence of myopia: longitudinal change or cohort effect? *Invest Ophthalmol Vis Sci*. 41(8):2103-2107.
- Park DJ, Congdon NG. (2004) Evidence for an “epidemic” of myopia. *Ann Acad Med Singapore*. 33: 21–6
- Nakahashi, T. (1993) Temporal craniometric changes from the Jomon to the modern period in western Japan. *Am. J. Phys. Anthropol*. 90: 409-425
- Parssinen, O., Lyyra, A. (1993) Myopia and myopic progression among schoolchildren: a three-year follow-up study. *Investigative Ophthalmology & Visual Science*. 34: 2794-2802
- Park DJ, Congdon NG. (2004) Evidence for an “epidemic” of myopia. *Ann Acad Med Singapore*. 33: 21–6.
- Penrose, L. (1954) Distance, size, and shape. *Annals of Eugenics* 18: 337-343
- Pietrusewsky, M. (1999) Multivariate Craniometric Investigations of Japanese, Asians, and Pacific Islanders. In: *Interdisciplinary perspectives on the origins of the Japanese: International Symposium, September 25-28, 1996 / edited by Omoto Keiichi*. : International Research Center for Japanese Studies
- Quinn, G., Shin, C., Maguire, M., Stone, R. (1999) Myopia and ambient lighting at night. *Nature*, 399: 113-114

- Quant, J., Woo, G. (1992) Normal values of eye position and head size in Chinese children from Hong-Kong. *Optometry and Vision Science*. 70(8), 668-671
- Ravosa, Noble, Hylander, Johnson, Kolwalski, (2000) Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *Journal of Human Evolution*. 38: 667-693
- Relethford, J. H. (1994). Craniometric variation among modern human populations. *Am J Phys Anthropol*, 95(1), 53-62.
- Rilling, JK (2006) Human and nonhuman primate brains: Are they allometrically scaled versions of the same design? *Evolutionary Anthropology: Issues, News, and Reviews*. 15(2), 65-77
- Roseman CC., Weaver TD. (2004) Multivariate apportionment of global human craniometric diversity. *Am J Phys Anthropol* 125: 257-263
- Ross, C. F. (1995) Allometric and functional influences on primate orbit orientation and the origins of the Anthropoids. *Journal of Human Evolution*. 29: 201-227
- Ross, C., Ravosa, M. (1993) Basicranial flexion, relative brain size and facial kyphosis in nonhuman primates. *Am. J. Phys. Anthropol*. 91: 305-324
- Rothhammer, F., Cocilovo JA., Quevedo S., et al. (1982) Microevolution in prehistoric Andean populations: Chronologic craniometric variation. *Am. J. Phys. Anthropol*. 58: 391-396
- Salvini-Plawen, L. and Mayr, E. (1961) in *Evolutionary Biology*, (Vol. 10) (Hecht, M.K., Steere, W.C. and Wallace, B., eds), pp. 207–263, Plenum Press
- Salzmann, M. (1912) *The anatomy and histology of the Human Eyeball in the normal state, its development and senescence*. Translated by Brown, E.V.L. University of Chicago Press
- Saw SM, Katz J, Schein OD, Chew SJ, Chan TK. (1996) Epidemiology of myopia. *Epidemiol Rev*. 18: 175–187.
- Saw SM, Hong CY, Chia KS, Stone RA, Tan D. (2001) Nearwork and myopia in young children. *Lancet*. 357:390.
- Saw SM, Chua WH, Hong CY, et al. (2002) Nearwork in early onset myopia. *Invest Ophthalmol Vis Sci*. 43: 332–339.

- Saw, MS., Tan, S., Fung, D., Chia, K., Koh, D., Tan, D., Stone, R. (2004) IQ and the Association with Myopia in Children Investigative Ophthalmology and Visual Science. 45: 2943-2948
- Schultz, AH. 1940. The size of the orbit and of the eye in primates. *Am J Phys Anthropol* 26: 389-408
- Schwartz, J., Tattersall, I. (2002) *The Human Fossil Record, Volume One, terminology and Craniodental Morphology of Genus Homo (Europe)*. Wiley-Liss, N.Y.
- Schwartz, J., Tattersall, I. (2002) *The Human Fossil Record, Volume Two, Craniodental Morphology of Genus Homo (Africa and Asia)* Wiley-Liss, N.Y.
- Schwartz, J., Tattersall, I. (2002) *The Human Fossil Record, Volume Four, Craniodental Morphology of Early Hominids (Genera Australopithecus, Paranthropus, Orrorin), and Overview*. Wiley-Liss, N.Y.
- Scott, JH. (1953) The cartilage of the nasal septum: a contribution to the study of facial growth. *Br Dental J.* 95: 37
- Smith P., Wax Y., Becher A., and Einy S. (1985) Diachronic variation in cranial thickness. *American Journal of Physical Anthropology*, 67: 127-133.
- Smith P., Wax Y., Adler F, Silberman D., and Heinic G. (1986) Post-Pleistocene changes in tooth root and jaw relationships. *Am J of Phys Anthropol* 70: 339-348.
- Strait D., Ross C. (1999) Kinematic data on primate head and neck posture: implications for the evolution of basicranial flexion and an evaluation of registration planes used in paleoanthropology. *Am J Phys Anthropol* 108:205–222.
- Todd, T., Beecher, H., Williams, G., Todd, A. (1940) The weight and growth of the human eyeball. *Human Biology*. 12(1), 1-20
- Waitzman, A. A., Posnick, J. C., Armstrong, D. C., & Pron, G. E. (1992). Craniofacial skeletal measurements based on computed tomography: Part II. Normal values and growth trends. *Cleft Palate Craniofac J*, 29(2), 118-128.
- Weale, R. (1982) *A Biography of the Eye: Development, Growth, Age*. H.K. Lewis & Co.
- Weiss, L. (1897) *Über das Wachstum des menschlichen Auges*. *Anatom. Hefte*, Bd. 8
- Weidenreich F. (1941) The brain and its role in the phylogenetic transformation of the human skull. *Trans Am Phil Soc.* 31: 321–442.

- Weiss, K. (2002) How the Eye Got its Brain. *Evolutionary Anthropology*. 11: 215-219
- White, T.D. (2000) *Human Osteology*, second ed. Academic Press, New York.
- Wilson, K. T., Sivak, J. G. and Callender, M. G. (1997) Induced refractive anomalies affect chick orbital bone structure. *Exp. Eye Res.* 64: 675–682.
- Wood, B.A., (1991) *Koobi Fora Research Project, Vol. 4: Hominid Cranial Remains*. Oxford University Press, New York.
- Working Group on Myopia Prevalence and Progression (1989). *Myopia: prevalence and progression*. Washington, D.C: National Academy Press.
- Wu, X., Wu L., Zhang Q., Zhu, H., Norton C. (2007) Craniofacial morphological microevolution of Holocene populations in northern China. *Chinese Science Bulletin*. 52(12), 1661-1668