

THESIS

NO CHIN LEFT BEHIND: THE MORPHOLOGICAL INTEGRATION AND VARIATION OF
THE MODERN HUMAN MENTUM OSSEUM

Submitted by

Anna Kathleen Trainer

Department of Anthropology

In partial fulfillment of the requirements

For the Degree of Master of Arts

Colorado State University

Fort Collins, Colorado

Summer 2013

Master's Committee:

Advisor: Mica Glantz

Ann Magennis
Michael Lacy

Copyright by Anna Kathleen Trainer 2013
All Rights Reserved

ABSTRACT

NO CHIN LEFT BEHIND: THE MORPHOLOGICAL INTEGRATION AND VARIATION OF THE MODERN HUMAN MENTUM OSSEUM

The chin, or mentum osseum, is regarded as one of the most unique traits that differentiate modern humans from our earlier hominin ancestors and has received intense scrutiny by scholars for well over a century. Several hypotheses are currently being investigated by researchers in attempts to elucidate the nature of the origin and function of the chin, but none of these have been satisfactorily upheld. Additionally, there are debates about what defines the chin and whether it is variable amongst extant modern humans. In an attempt to study this problem in a novel way, the current study examines whether the chin is part of a morphologically integrated set of facial and cranial characteristics, as well as whether it is variable in a diverse sample of modern human skeletal remains.

The morphological integration of the mandible with the cranium has been scrutinized in recent investigations, and results have indicated that some morphological aspects of the mandible covary with the cranium. However, these studies do not evaluate the mentum osseum itself. The chin may be independent of integration with the rest of the skull, indicating that it is a feature that evolved in response to other pressures, such as sexual selection or biomechanical constraints. Conversely, if the mentum osseum is correlated to other measurements of the skull, the appearance of the chin in modern humans may have been a pleiotropic effect of selective forces acting to reduce facial prognathism.

A diverse modern human sample was analyzed in order to test the degree of correlation and variation found in the mentum osseum. Results indicate that the mentum osseum is not statistically correlated with the majority of measurements from the mandible and cranium and may be independent of any morphological integration. Additionally, the results further demonstrate that the mentum osseum is highly variable in modern human populations.

ACKNOWLEDGEMENTS

I would like to thank everyone who made this thesis possible, from my advisors and professors to my friends and family. Without all of you, I would never have earned this degree. In particular, I'd like to thank the awesome crew of fellow Anthropology grad students I had during my time at CSU; Mica and Ann for always being there to help me out when I needed it; my far-off but ever-present group of friends back home; Charlie for putting up with me for our entire lives; and Michael for being a part of my life, even when I was very far away.

TABLE OF CONTENTS

Abstract	ii
Acknowledgements	iv
Table of Contents	v
Chapter 1: Introduction	1
Chapter 2: Background	6
Chapter 3: Materials & Methods	18
Chapter 4: Results	28
Chapter 5: Discussion	39
Chapter 6: Conclusions	54
Bibliography	60

Chapter One: Introduction

The development of the chin, or the mentum osseum, is identified as an autapomorphic feature of modern humans. Additionally, modern humans have distinct orthognathic faces, a trait that is also said to be derived (Trinkaus 2003). Conversely, Neanderthals are characterized by a receding mandibular symphysis, a retromolar gap, and distinctive mid-facial prognathism (Cartmill and Smith 2009; Rak, et al. 2002). In addition, all other archaic humans, such as *Homo heidelbergensis* and the australopithecines, also lack any chin development. In an attempt to explain these different morphologies, many hypotheses have been suggested, but none have been successfully falsified.

Currently, there are four main hypotheses in regards to the evolution of the chin. Although research on the origin of the mentum osseum has been ongoing for over a century (Blumenbach 1865; Schwartz and Tattersall 2000), recent publications show that the debate is alive and well. The explanatory models associated with the evolution of the modern human chin are:

1. The chin is a result of sexual selection (Thayer and Dobson 2010)
2. The chin is a biomechanical response to masticatory pressures (Daegling 1993; Dobson and Trinkaus 2002; Ichim 2006)
3. The chin evolved with language in modern humans as a result of the functional anatomy related to speech production (Daegling 2012; Ichim, et al. 2007; Schepartz 1993)
4. The chin has no adaptive function; it is “left behind” (Gould and Lewontin 1979; Polanski 2011; Weidenreich 1936)

The last of these hypotheses is the focus of the current study. If the mentum osseum is a part of an overall morphologically integrated system that includes portions of both the cranium and

mandible, then its emergence could have been a secondary consequence of selective pressures acting to reduce prognathism and increase basicranial flexion and the globular shape of the neurocranium, which will be detailed more thoroughly in the following chapter. Integration can be characterized as coordinated variation between biological units; the pattern and the degree to which units are integrated is related to the amount of functional and developmental relatedness between the units (Harvati, et al. 2011). Evolutionary change in one unit of an integrated set of features will impact the morphology of the other units in the integrated package (Bastir 2008).

While integration has been observed in various cranial structures (Rosas, et al. 2006), the integration of the mandible with the rest of the skull has not been examined until recently (Bastir, et al. 2005; Harvati, et al. 2011; Polanski 2011). The integration of the form of the mandibular corpus and ramus appears to be a reflection of the “catch-up” growth and morphology of the mandible in relation to the form and function of the surrounding areas of the cranium (Polanski 2011). Aspects of the mandible such as the ramus provides areas of muscle attachment for all of the major muscles of mastication, which originate on the cranium (Lieberman 2011). Therefore, the integration of these areas of the mandible and cranium is a logical conclusion, as they form an interconnected system for the purposes of mastication. However, the chin does not serve as an area of muscle attachment for any muscles related to mastication that originate on the cranium and may be free of the overall cranial integration package. Consequently, the chin may vary independently. Although the integration of the mandible with the cranium and face has been previously evaluated, the mentum osseum has not been given close scrutiny. The integration of the chin with the rest of the cranium forms the basis for the current research.

Integration can be measured through observation of statistical correlations between different skeletal areas. These correlations will reflect the variation of both size and shape in the

characteristics. For example, in the modern human skull, it has been observed that as the width of the cranium increases, so must the width of the mandibular condyles, as these two areas are integrated and articulate with one another (Antón 1994). Therefore, when studying morphological integration, it is important to examine the variation in the traits which are being considered. Some scholars have posited that the modern human chin is dimorphic; that is, it is either present or absent (Schwartz and Tattersall 2000). Others have concluded that it is a trait of scale and is variable both within extant modern humans and our earlier hominin predecessors (Dobson and Trinkaus 2002).

The usefulness of the mandible in taxonomic studies has been questioned due to its extreme variation (Fabbri 2006). Despite this, the mandible has served as the type specimen for multiple hominin species, including *A. anamensis* (Leakey, et al. 1995), *A. afarensis* (Leakey and Hay 1979), *H. ergaster* (Groves and Mazák 1975), and *H. heidelbergensis* (Schoetensack 1908). While the expression of the chin has conventionally been reserved as a fully modern human, and thus derived, condition, it is widely variable both within living human populations and can also be seen to some extent in earlier human groups, especially more recent Neandertal individuals (Franciscus and Trinkaus 1995). The degree to which these “protrusions” can be defined as true chins is widely debated (Dobson and Trinkaus 2002; Wolpoff 1980), with some researchers even questioning the validity of the term for anatomical and phylogenetic classification purposes (Schwartz and Tattersall 2000).

Nevertheless, it appears that this feature is highly variable in modern human populations. Often, this variability is expressed in a geographic or climatic gradient (Nicholson and Harvati 2006), which is possibly caused by evolutionary mechanisms such as genetic drift as well as admixture with more archaic human groups. Indeed, modern *Homo sapiens* are not the only ones

to express this geographic mandibular variability, as differences can be seen in Neandertals from different times and locations (Dobson and Trinkaus 2002; Wolpoff 1975). However, other researchers dispute that the expression of the chin is geographically distributed, either because their results indicate there is no variation by population (Humphrey, et al. 1999) or because there is no variation in the chin at all (Dobson and Trinkaus 2002). Therefore, this study additionally examines whether there is variation of the chin within populations of modern humans. The amount of variation found in the chin will have an important impact on its morphological integration, since a lack of variation in this feature would indicate that the chin is not influenced by changes in cranial shape or size.

Hypotheses

This project has a twofold purpose: to determine whether there is variability in the expression of the modern human mentum osseum, and if so, to further examine the degree of morphological integration of the mentum osseum with other cranial and mandibular measurements. To do so, the following questions will be examined: Does the mentum osseum, a supposed autapomorphic feature in modern humans, display variation in the expression of chin traits? Or is it fully expressed in all individuals? Additionally, if variation is seen, can this variation be explained as part of an overall craniofacial integration package that also affects the mandible? Or is the chin, while correlated with the emergence of other autapomorphic cranial features of modern humans, a concurrent but independent development in human evolution?

If variation and integration is found in the sample, then certain causal scenarios, such as biomechanics, behavior, or evolutionary by-products, will be examined in order to explain the evolution of this feature.

In order to test these questions, a set of hypotheses has been formulated.

1. The chin lacks variation; all five trait characteristics required to possess a chin are present in all individuals examined because all individuals are fully modern human.
2. There is no relationship between the expression of the mentum osseum and other measures of craniofacial morphology. To overturn the null, it must be statistically demonstrated that there is a relationship between changes in the mentum osseum and other areas of the cranium.

If the null of this hypothesis is upheld, then it follows that the chin may be an independent feature, and alternative hypotheses must be developed as to what caused the formation of the chin. Additionally, if the mentum osseum is found to be variable, then the human chin is not dichotomous, in terms of “presence/absence”, making it difficult to use as an autapomorphy of modern humans.

Synopsis of chapters

Chapter Two is a background of the history of the research that has been done in relation to the topic explored *herein*. Additionally, the pertinent anatomy of the skull is reviewed, and the study of morphological integration is outlined as well. Chapter Three, the Materials and Methods section, will detail the sample that was collected for the current research. Additionally, exclusionary criteria and linear measurements are outlined. The statistical procedures selected for analysis will be detailed. Chapter Four will present the results of the statistical analysis, and Chapter Five will be focused on a discussion of the results from the statistical tests and an appraisal of the validity of the hypotheses tested. Chapter Six will summarize the study and provide both implications of the results as well as propose avenues of future possible research in this area.

Chapter Two: Background

This chapter will provide background information on the morphology, integration, and evolutionary significance of the mandible. It will begin by outlining the pertinent anatomy of the mandible and its primary anatomical interactions with other skeletal and muscular systems. The problems with defining the chin, in evolutionary and technical terms, are addressed. The model developed for this study, including the morphological traits used to define the chin are then explained. Next, morphological integration is described, as well as the integration of the cranium, face, and mandible. Finally, the earliest emergence of the chin, from a geographic perspective, is detailed.

Anatomy of the mandible

The mandible is a complicated structure because the bony anatomy must maintain proper articulation with other skeletal areas, as well as provide areas for origin and insertion points for the muscles of mastication. Additionally, it must maintain strict occlusal relationships with the dentition. Although the temporomandibular joint is subject to damage and injury due to its complex structure, it is advantageous in that it allows for the mandible to move antero-posteriorly, vertically, and laterally, as well as permitting both bilateral (usually incision with the front teeth, which happens on both sides of the mouth) and unilateral (mastication of the food happening on one side of the mouth) mastication (Aiello and Dean 1990; Lieberman 2011). These movements are possible through the evolution of muscles that are able to exert both fine and powerful movements of the region through the integration of the muscles of mastication (Aiello and Dean 1990).

The mandible's main articulation is with the temporal bone at the temporomandibular joint (TMJ). This joint, along with the muscles of mastication, allows mandibular movement and force production. The interaction between these muscles and the joint are important to review because the use of these muscles and the stresses of masticatory loads have been demonstrated to heavily influence the bony morphology of the mandible, particularly the ramus (Daegling and Hylander 2000).

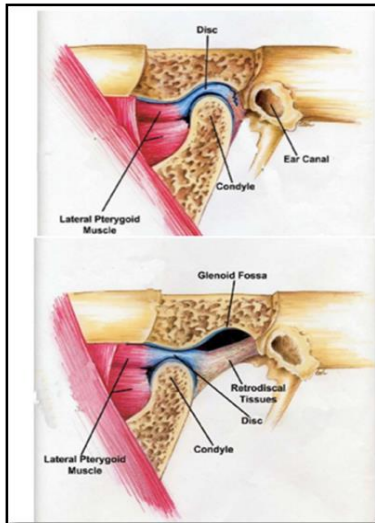


Figure 1: The TMJ joint during rest and movement. Adapted from A.D.A.M. Interactive Anatomy (2012)

other use of the jaw, the disc moves forward and down along with the condyles, and returns to its “resting” position upon closing, or adduction, of the jaw. Due to the high level of mobility of this joint, there are several ligaments and tendons that also help secure the articulation of the condyles within the TMJ.

In terms of musculature, there are four primary muscles that control the movement of the mandible (Figure

2). The largest of these is the temporalis muscle, a large fan-shaped muscle that articulates on

The TMJ is created from the articulation of the mandibular condyle with the glenoid fossa of the temporal bone, although the two bones are separated by the articular disc, or meniscus (Figure 1) (Aiello and Dean 1990). When the mandible is at rest, the teeth are not quite in occlusion, and the condyles lie below the glenoid fossa. The articular disc consists of two parts, with one portion attached to the temporal bone and the other to the condyles. During mastication, speech, or

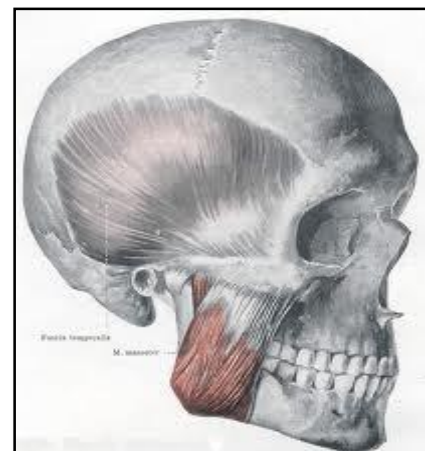


Figure 2: Muscles of mastication, lateral view. Adapted from Bock (1890)

the squamos portion of the temporal bone. It then runs through the space between the zygomatic arches and inserts on the coronoid process of the mandible (Aiello and Dean 1990; Lieberman 2011). The primary function of the temporalis is to both elevate and retract the mandible. Removal of the temporalis muscle has been demonstrated to greatly reduce, or even entirely eliminate, the coronoid process in guinea pigs (Boyd, et al. 1967), rats (Bouvier and Hylander 1984; Washburn 1947), cats (Avis 1959), and macaques (Bouvier and Hylander 1982). These studies demonstrate that mechanical stresses and loads can have a large impact on the morphology of the mandible, and Aiello & Dean (1990) state that the coronoid processes of both very young and very old modern humans can also be highly variable due to the differences between normal human strain and the strains created in mastication by individuals who are missing teeth.

The masseter muscle, which has both deep and superficial sections, originates on the zygomatic arch and inserts on the exterior surface of the mandibular ramus. The superficial section inserts on the angle of the ramus and the deep portion, which is more transverse, inserts on the lateral section of the ramus. The function of both masseteric sections is to elevate the mandible, although the deep section can also assist in moving the mandible laterally and the superficial area can make the jaw protrude slightly (Aiello and Dean 1990; Lieberman 2011).

The pterygoid muscles, specifically the medial pterygoid, have a similar location to the masseter but attach on the internal surface of the ramus and originate on the lateral pterygoid plate (Figure 3). The

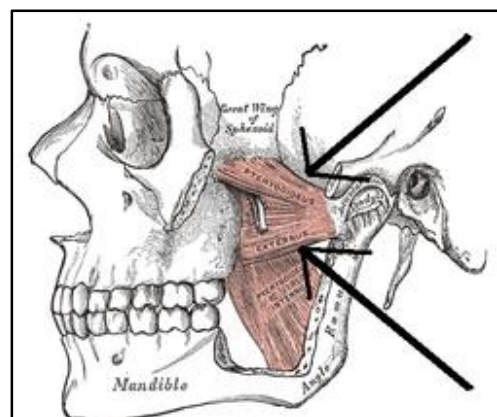


Figure 3: Medial and Lateral Pterygoids in lateral view. Adapted from Gray (2011)

lateral pterygoid also originates here, but attaches on the maxilla, near the maxillary tuberosity, and helps to secure the condyle within the TMJ (Lieberman 2011). The masseter and medial pterygoid muscles form a sort of sling around the ramus.

Additionally, there is a fifth muscle attached to the mandible, the digastric (Figure 4).

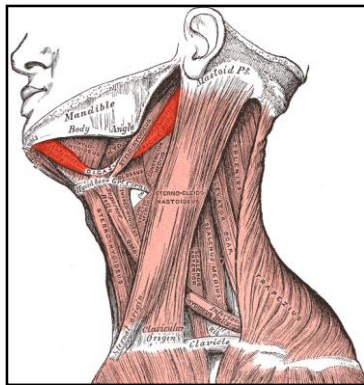


Figure 4: The digastric muscle in inferior view. Adapted from Gray (2011)

This muscle depresses the mandible as well as elevates the hyoid when the mandible is in a “fixed” position. It originates on the internal surface of the mandible, near the mandibular symphysis, and attaches near the mastoid process (Aiello and Dean 1990; Lieberman 2011). It is not a primary muscle of mastication, but is important in this study because it originates on the internal surface of the mental symphysis, and some researchers have

discussed its importance in the ability for modern humans to have normal speech capabilities, especially orthodontists (Schepartz 1993). There has been a long history of this viewpoint, which is echoed in recent studies focused on the role of speech in the evolution of the chin and the role of the digastric muscle (Daegling 2012; Haskell 1979). This hypothesis will be reviewed in more detail later in the study.

The evolution and historical context of the chin

The chin has long been maintained to be one of the most unique aspects of human morphology (Blumenbach 1865; Lieberman 2011; Schwartz and Tattersall 2000). But what exactly defines the chin, and who among our hominin ancestors possesses it? The primitive condition of the hominin mandible harkens back to an ape-like jaw (Figure 5), with a receding symphyseal surface and teeth that

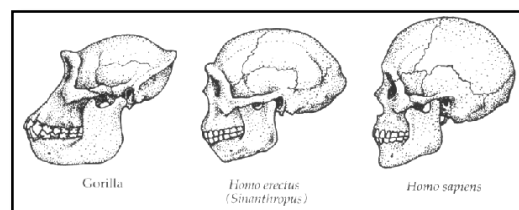


Figure 5: *H. sapiens*, *H. erectus*, and *G. gorilla* skulls in lateral view. Boule & Vallois (1957)

protruded forward to maintain occlusion with the prognathic face and maxillary teeth (Cartmill and Smith 2009; Schwartz and Tattersall 2000). Additionally, the mandible is a robust bone in apes and earlier hominins, with a dense amount of cortical bone. In humans, the robusticity of the skeleton has largely been reduced from that of earlier hominins, but the area of the chin itself is still unusually dense, more so than would be expected for its size (Daegling 2012). The modern human chin is a derived feature, seemingly unique to our species, and is formed during ontogeny from the resorption of the alveolar portion of the symphysis, which leads to the protrusion of the basal section. Although the developmental basis for the growth of the chin is straightforward, its adaptive significance has been difficult to explain (Daegling 1993; Lieberman 2011)

Weidenreich (1936) was the first to define the characteristics of the modern human mental symphysis (Figure 6), which include:

- A **mental trigone**: a variable triangle-shaped central elevation;
- **Mental fossa**: distinct depressions on both sides of the trigone;
- **Lateral tubercles**: Laterally border the mental trigone
- **Anterior marginal tubercles**: Laterally border both the mental trigone and the lateral tubercles
- **Mandibular incurvature**: When viewed from the side, a basal projection of the trigone is demarcated from the alveolar processes by a concavity

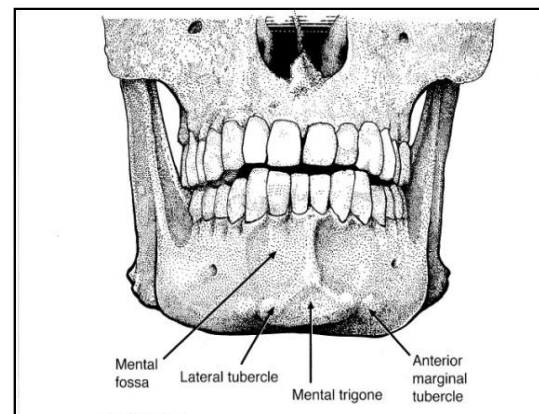


Figure 6: Characteristics of the modern human mandible
Adapted from Cartmill & Smith (2009)

According to Schwartz and Tattersall (2000), it is only those individuals who possess all of these features that can be attributed to the anatomically modern human species, and that this suite of characteristics does not appear in any earlier hominin fossils (Cartmill and Smith 2009). However, some archaic hominins, particularly Neandertals, do display projections at the inferior

border of the central mandibular corpus; therefore, the evolution of the mental eminence can be assessed as a trait of scale (Dobson and Trinkaus 2002) although Schwartz and Tattersall (2000) would deny that these projections are true chins. These five features of the mentum osseum create the basis for the response variable of the current study.

Additionally, the anatomical term “chin” has come under scrutiny, as which hominins possess it could be variable depending on the definition used by the researcher. If the chin is regarded to be merely a basal projection of the mental symphysis, then it is possible that some Neandertals possess this feature. However, if the term “chin” is used as synonymous with the term “mentum osseum” as defined above by Weidenreich (1936) as well as Schwartz and Tattersall (2000), then only modern humans possess it, although even in present day humans the amount of variation in these features is high.

Evolution of the face and cranium

When studying the evolution of the modern human mandible, it is important to investigate craniofacial evolution as well in order to garner a more holistic understanding of how these anatomical areas are integrated. Three major processes occurred during modern human cranial evolution: 1. the vertical enlargement of the braincase, producing the “forehead” and the globular shape of the human cranium; 2. an orthognathic face in which the majority of the face is now positioned under the braincase; and 3. a basicranium that exhibits an increased amount of flexure throughout the evolution of the hominin lineage (Bastir 2008). However, despite extensive research into these developmental phenomena, evolutionary explanations for these patterns have remained elusive. Models have been created that evaluate the influence of ontogenetic and evolutionary causes that conclude that a variety of factors may have been the

drivers of this change, including local evolutionary drivers as well as more generalized, organism level phenomena, such as genetic substitutions (Bastir, et al. 2005).

Morphological integration

Morphological integration can be defined as coordinated variation between skeletal elements within an individual (Olson and Miller 1999). It is measured by the quantification of skeletal measurements that can then be statistically evaluated to analyze the degree of co-variation among differing areas. There are two patterns that can be examined when looking at morphological variation: one pattern of structure and form and another of function (Cheverud 1982). These patterns can be seen in the integration of the mandibular corpus and ramus with the cranium, and can also be discerned from one another (Bastir, et al. 2005). A form of functional integration is the way in which the cranium and mandible integrate to allow for masticatory processes, while ontogenetic processes also influence the integration of the mandible and cranium during growth. Several studies have examined the way in which the mandible is integrated with the cranium, but these have focused on the corpus and ramus of the mandible and not the mentum osseum.

The position of the face in modern humans, in respect to the position of the basicranium and neurocranium, appear to be independent of causation either by ontogeny or phylogeny (Bastir, et. al 2005). This independence could account for the apparent pattern of relative variation in the position of the face. In modern humans, the increased vertical orientation of the face requires different morphological changes than does the more low and broad faces of Neandertals. With an orthognathic face, the mandible must re-orient in a superior-inferior direction, leading to a mandible that is more flexed downwards (Bastir, et. al 2005).

Morphological interactions of the mandible and cranium

The interactions of the mandible with the rest of the crania are important, and examining studies of growth and change in other cranial regions can lead to a better understanding of reasons for mandibular modification through time. Although it is known that the face, neurocranium, and basicranium form from embryologically distinct areas, basicranial shape influences facial shape, especially in terms of width (Lieberman, et al. 2000). Because it is the first area of the head to reach adult size, as well as being the area through which the head is connected to the rest of the body, the basicranium is an evolutionarily conservative area, in terms of its resistance to adaptive change, especially compared to other regions of the skull such as the neurocranium (Hughes 2003).

Cultural modification of the neurocranium has been shown to alter mandibular form, specifically in terms of widening the intercondylar breadth (Antón 1994). In the homininae, the degree of basicranial flexion has increased throughout time, with modern *Homo sapiens* exhibiting the greatest degree of flexion in any extant or extinct mammal. As encephalization increases, the size and shape of the cranial vault must alter to accommodate the increase in brain size. It has been argued that the most anatomically efficient way to accommodate this increase in brain size is not by the continued anterior, posterior, and/or superior expansion of the cranial vault, but rather by flexing the base of the cranium ventrally to accommodate the changed shape of the brain within the skull (Hughes 2003). However, the flexion of the basicranium is known to be influenced by several different genetic and ontogenetic factors, and the adaptive importance of flexion is still debated (Hughes 2003).

Earliest emergence of the mentum osseum

While the chin is considered to be an autapomorphic feature of modern humans, it is important to examine the fossil record to see when and where the emergence of this feature occurred. The current fossil evidence shows that the earliest humans possessing chins were not clustered in one specific area, but were instead widespread over a large span of time and geographic area (Figure 7).



Figure 7: Geographic distribution of the earliest "chins"

The oldest specimen with a visible mentum osseum is Omo II which is dated at 195kya (Gunz, et al. 2009). After this, the most reliable specimens all date to around 100kya, but appear in disparate areas. If the molecular and genetic data are correct, then modern humans evolved from a small population in Africa that was the result of a population bottleneck (Ambrose 1998). Whether or not this population would have been genetically isolated and thus prevented from reproducing with more archaic humans is difficult to ascertain, but the presence of both archaic

and derived features at sites such as Klasies River Mouth in South Africa (Rightmire and Deacon 1991), Qafzeh and Skhul in Israel (Schwartz and Tattersall 2000), and Zhiren Cave in China (Liu, et al. 2010) seem to indicate that interbreeding was a possibility in all of these places.

Despite large degrees of sexual dimorphism and the presence of some archaic features, the Klasies sample is considered to be early modern human and the five specimens at this site express varying degrees of mentum osseum formation (Lam, et al. 1996; Rightmire and Deacon 1991; Singer 1982). The specimen that is considered to display the strongest degree of chin development, KRM 41815, dates to somewhere between 120-100kya. Another specimen that morphologically appears to be modern and dates to around 100kya are the fossils from Zhiren Cave, China. The fossils at this site consist of the anterior portion of the mandible, preserving a clearly developed chin, as well as molar teeth. While the symphysis displays enough autapomorphic features of the chin to satisfy even the most stringent observers, there are some components of the mandible that make it seem more archaic, such as the overall robusticity (Liu, et al. 2010). The find from Zhiren Cave is important because it not only pushes back the appearance of modern humans in Asia by 60ky (Shang, et al. 2007), but possibly pushes back the origin of modern humans as well, since theoretically a long stretch of time would be needed for a migration out of Africa and expansion into the various parts of the Old World. Additionally, the remains from Skhul and Qafzeh, specifically Skhul 5 and Qafzeh 9, also date to approximately 100kya, and also display fully-fledged chins (Schwartz and Tattersall 2000). However, Skhul 5 in particular still exhibits some archaic features, such as mid-facial prognathism, supraorbital tori, and a retromolar gap (Cartmill and Smith 2009).

Despite the evidence for an early occurrence of modern features in several disparate geographic areas, this does not mean that they successfully remained in these areas and

established permanent populations at that early period. There is a dearth of evidence for modern humans in Europe or anywhere in Asia *after* the specimens examined here until around 40kya in China (Shang, et al. 2007) and 30kya in Europe (Svoboda, et al. 2002). It is possible that these early groups of modern humans may have died out or been assimilated into more archaic groups that were already established in these areas.

Variation in modern human skull shape

In modern humans, it has been noted that there are differences between the crania and mandibles of brachycephalic and dolichocephalic individuals (Antón 1994; Bastir, et al. 2005; Hughes 2003). An increase in basicranial flexure is correlated with a vertically long face and dolichocephalic individuals, while a less-flexed basicranium is associated with more brachycephalic persons. In addition, the basicrania of dolichocephalic individuals tend to be ventrally concave whereas brachycephalic individuals have dorsally concave basicrania (Bastir, et al. 2005). Furthermore, previous studies have indicated that there may be a craniofacial-mandibular integration pattern in modern humans, which is related to the degree to which the cranium is dolichocephalic or brachycephalic (Bastir, et al. 2005). Persons with dolichocephalic crania, in addition to the increased basicranial flexion and vertically elongated faces may have more retrusive mandibles, while conversely brachycephalic individuals have shorter, wider crania with vertically shorter faces and more protrusive mandibles (Bastir, et al. 2005). However, studies of these patterns do not incorporate the shape and structure of the chin into these assessments, and it is unclear if they vary in similar fashion to the rest of the craniofacial-mandibular suite.

The chin is said by some scholars to differ in the degree of its expression in modern humans (Dobson and Trinkaus 2002), but it is not clear if this variation is due to its relation with

the shape of the face or if it is an independent feature. Cheverud (1982) found that there is support for genetic integration among traits that are both developmentally and functionally related through cluster analysis of rhesus macaque crania. Conversely, it appears that some highly correlated traits have no functional or developmental significance, perhaps signifying other factors are at play, including effects of pleiotropy or genetic drift. This indicates that the not all traits are correlated due to adaptation, but could be the result of more stochastic processes. The more tightly integrated traits are, the more genetically correlated they will be, and this will influence their evolutionary possibilities. Genetic correlation can be a result of either developmental/functional causation or more stochastic processes such as drift and/or founder effect (Cheverud 1982). This study will also examine the variation in the mentum osseum between the sample populations of modern humans.

In this chapter, background information pertinent to studying the evolution of the form and function of the mandible, specifically the mentum osseum, was reviewed. Significant anatomy, including both the skeletal and musculature areas involved in mastication, was detailed so that a thorough understanding of why the mandible and cranium are integrated could be accomplished. Additionally, the importance of the mandible as a key skeletal element in human fossil history was assessed, and the history of the study done on the “chin” as an anatomical feature was examined. Some background information on morphological integration and how it has been utilized in the past was given, specifically in studying the interrelatedness of the human cranium. Finally, the evolutionary appearance of the chin was examined from a geographical and temporal perspective. In the next chapter, the methods that were developed to examine the variation and integration of the mentum osseum will be detailed.

Chapter Three: Materials and Methods

This chapter discusses the materials and methods used to assess the hypotheses explored in the present study. The composition of the skeletal sample and the exclusionary criteria are also evaluated.

Skeletal Samples

Efforts were made to collect a large and varied sample for use in this study. To that end, multiple university collections were studied in an attempt to both increase the size of the sample examined as well as to evaluate individuals with diverse ancestry. Collections from the University of Wyoming, the University of New Mexico, and Colorado State University were analyzed, as they represent sample populations from a variety of time periods and ancestral backgrounds. The total sample size from these three universities is 104 individuals.

Table 1: Sample Summary

	<i>N</i>	<i>Male</i>	<i>Female</i>
University of New Mexico	35	28	7
Colorado State University	29	18	11
University of Wyoming	40	28	12
<i>Total</i>	104	74	30

The University of New Mexico:

The sample set from the University of New Mexico comes from the University's Maxwell Museum of Anthropology. The Museum houses multiple skeletal collections, and the sample used here comes from their Documented Skeletal Collection. This collection encompasses over 250 individuals of known sex, age, and ancestry, and was collected through

donation within the past 30 years. Because of the high degree of documentation, it can be stated with certainty that the individuals used in this study ranged between the ages of 16-63 and are a fully modern population. Nearly all of the individuals were identified as “White” Caucasians, with one Hispanic individual and two individuals without ancestry information. Many potential specimens were eliminated from the study sample due to the edentulous condition of the individuals and the subsequent remodeling of the mandible and face. In total, 35 individuals from the University of New Mexico were included in the sample.

Colorado State University:

The collection from Colorado State University was obtained through excavation of a 19th century insane asylum in Colorado, and consists almost entirely of Caucasian Americans of European descent. Many of these specimens are fragmentary or in fragile/poor condition. Because of this, and due to the edentulous condition of many of the elderly specimens, only 29 of the individuals from this collection were included in the current study

The University of Wyoming

The research collection from the University of Wyoming is housed in the Human Remains Repository and has been amassed over the past several decades, through excavations by the University, nearby museums, and the State Coroner’s office. The collection is almost entirely comprised of Native Americans from Wyoming and the surrounding areas and date from the Late Archaic (and possibly earlier) through Historic time periods. Additionally, the collection also includes a few specimens of East Asian descent that lived in a nearby mining town during the late 19th/early 20th centuries. 40 individuals from this collection were evaluated for the current study.

Exclusionary criteria

Exclusionary criteria were employed during data collection due to varying degrees of skeletal preservation amongst the study sample. This was done in order to avoid biases that could be introduced when estimating measurements caused by poor preservation or lost skeletal elements. Additionally, the exclusionary criteria employed enabled individuals outside of the age criterion to be eliminated. The details of the criteria are outlined below.

Age- Juveniles and some elderly individuals were excluded from analysis. Juveniles were classified based on the eruption status of the M3, as this feature is traditionally associated with the completion of growth and the attainment of adulthood (Buikstra and Ubelaker 1994). Juveniles were excluded as their incomplete growth may result in inaccurate measurements of both the cranium and mandible. Additionally, elderly individuals were eliminated if they had extensive pre-mortem tooth loss and subsequent remodeling of the alveolar areas. This was a necessary precaution, as a heavily remodeled mandible would have a large impact on mandibular measurements due to the altered shape of the mandible (Buikstra and Ubelaker 1994).

Preservation- The sample included only those skeletons with a state of preservation that allowed a majority of the measurements to be taken accurately. Therefore, those individuals for which it was not possible to take more than five of the measurements were eliminated from the study. Various areas of the cranium and mandible were evaluated for inclusion in the data set, and the criteria were as follows: The basicranium needed to be complete only around the area of the foramen magnum, and some damage could be tolerated in this area as long as basion was undamaged. The cranial vault needed to be mostly intact, although some damage was accepted if all of the areas necessary for measurements were complete. The measurements of the face, which included nasion, prosthion, and the zygomatics (zygion), encompassed the entire area, meaning

that the face could not be broken or damaged. The mandible was the most essential skeletal element, and any damage that impacted measurements to the mandible could result in the exclusion of that individual. However, slight damage to the condyles or corpus was deemed acceptable as long as measurements were not impacted.

Measurements

A series of linear measurements were taken, utilizing spreading calipers, digital sliding calipers, and a mandibulometer, in order to ascertain a clear picture of the degree to which the mandible and cranium impact one another's development. These measurements have been adapted from various sources (Table 2). The measurements were selected from the face, basicranium, neurocranium, and mandible (Figure 8), in an attempt to get an overall depiction of skull size and shape. Linear measurements are shown in Table 2.

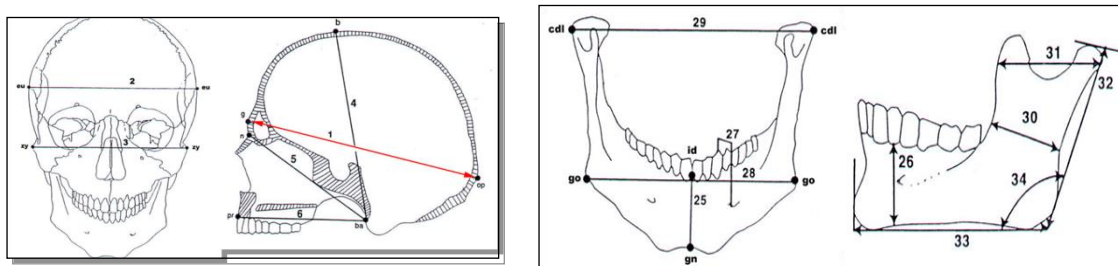


Figure 8: Cranial (left) and mandibular (right) measurements taken. Adapted from Buikstra and Ubelaker (1994)

Table 2: Measurements Taken

<i>Mandibular Measurements</i>	<i>Osteometric Points</i>	<i>Reference</i>
Chin Height	id-gn	Buikstra & Ubelaker (1994); Howells (1973)
Height of the Mandibular Body	Taken under M1	Buikstra & Ubelaker (1994); Howells (1973)
Bigonial Width	go-go	Buikstra & Ubelaker (1994); Howells (1973)
Bicondylar Breadth	cdl-cdl	Buikstra & Ubelaker (1994); Howells (1973)
Maximum Ramus Height	cdl-go	Buikstra & Ubelaker (1994); Howells (1973)
Mandibular Length	cdl-gn	Polanski (2011) Buikstra & Ubelaker (1994)
Mandibular Angle		Buikstra & Ubelaker (1994); Howells (1973)
Bucco-lingual distance	M1	Buikstra & Ubelaker (1994); Howells (1973)
Torus Breadth	mo/st-gn	Nicholson & Harvati (2006)
Retromolar gap	Present/Absent	Fransiscus & Trinkaus (1995)
Mentum Osseum Score	1-5	Dobson & Trinkaus (2002)
<i>Cranial & Facial Measurements</i>	<i>Osteometric Points</i>	<i>Reference</i>
Maximum Cranial Length	g-op	Buikstra & Ubelaker (1994); Howells (1973)
Maximum Cranial Breadth	eu-eu	Buikstra & Ubelaker (1994); Howells (1973)
Bizygomatic Breadth	zy-zy	Buikstra & Ubelaker (1994); Howells (1973)
Basion-Bregma Height	ba-b	Buikstra & Ubelaker (1994); Howells (1973)
Cranial Base Length	ba-n	Buikstra & Ubelaker (1994); Howells (1973)
Nasion Angle	ba-pr	Buikstra & Ubelaker (1994); Howells (1973)
Maxillo-Alveolar Breadth	ecm-ecm	Buikstra & Ubelaker (1994); Howells (1973)
Upper Facial Height	n-ids	Hughes (2003)
Total Facial Height	n-pr	Hughes (2003)

The Mentum Osseum Score

The chin is a difficult anatomical aspect to measure, as it encompasses a topographically diverse landscape and cannot be appropriately evaluated with linear measurements. Previous studies developed qualitative methods of observing the chin traits and characteristics (Dobson and Trinkaus 2002) and the present study has done the same. A non-continuous, ordinal assessment was developed to evaluate the degree to which the chin is expressed per the descriptive guidelines laid out by Schwartz and Tattersall (2000), Weidenreich (1936) and Dobson and Trinkaus (2002). It is called here the Mentum Osseum Score (MOS) (Dobson and Trinkaus 2002). Per these researchers, modern humans, but not earlier hominins, possess the following five derived characteristics (see Chapter 2, Figure 6 for figure):

- **A mental trigone:** a variable triangle-shaped central elevation;
- **Mental fossa:** distinct depressions on both sides of the trigone;
- **Lateral tubercles:** Laterally border the mental trigone
- **Anterior marginal tubercles:** Laterally border both the mental trigone and the lateral tubercles
- **Mandibular incurvature:** When viewed from the side, a basal projection of the trigone is demarcated from the alveolar processes by a concavity

These five traits combine to form an inverted “T” shape with mental fossae that Schwartz and Tattersall state is characteristic of extant modern humans (Schwartz and Tattersall 2000). However, Dobson and Trinkaus (2002) state that the mentum osseum, as in many skeletal features, is a trait of scale and is variable in which traits are expressed amongst modern human populations. To test these theories, the current study scored each individual from 1-5 based on how many of the above discrete traits they possessed. Traits were individually scored as either “present” or “absent”.

This method of scoring allows for a statistical assessment of the degree of chin development in each individual (Dobson and Trinkaus 2002; Franciscus and Trinkaus 1995). Each of the five qualities listed above were scored individually and then added together to create the Mentum Osseum Score (MOS). Discrete categories for ranking the development of the mentum osseum have been used in previous studies, and no known metric quantification of the chin is known; therefore, developing an assessment along these lines is most appropriate when trying to evaluate the expression of the mentum osseum (Franciscus and Trinkaus 1995).

Discrete traits

Most measurements were metric and were thus assessed using one of the calipers. However, several of the traits examined were discrete functions. For sex assessment, males and females were scored as “0” and “1” respectively for the statistical analysis. This enabled comparisons between sexes in order to determine whether sexual selection could have played a role in the development of the chin. Each individual was examined for a retromolar gap, which is a clear spatial delineation between the distal surface of the third mandibular molars and the anterior margin of the mandibular ramus (Franciscus and Trinkaus 1995). This feature is said to be an autapomorphic characteristic of Neandertals that is absent in modern humans. As such, this feature was scored as either “Present” (1) or “Absent” (0) for the individuals in this sample. Many individuals in the modern population were absent this feature due to the removal or absence of the third molars, and were therefore automatically assigned the “Absent” designation. Additionally, ancestry was evaluated using the data present in the collection in order to examine whether different populations from different times and geographical areas were distinctive in their expression of the mandibular features.

Statistics

The focus of the current study is to examine whether the chin is variable as well as to determine the ways in which the chin is integrated with other areas of the cranium. Does the chin's expression alter as other areas of the cranium change in size and shape, or is it expressed the same in all individuals? In order to evaluate this, statistical procedures must be used that examine how chin shape varies and whether it is dependent upon, or correlated with, other cranial measurements. The statistics program Stata 12 is used in this study (StataCorp 2011). Variation in the MOS can be determined by examining the distribution of the five chin traits amongst the sample. If the chin is not variable, then the five descriptive chin traits will be stable, or fixed, within the study population.

There are several methods of measuring association between variables. A correlation matrix allows for multiple variables to be investigated simultaneously, and thus will be used here. Additionally, an Ordered Logistic Regression was performed as it is the most appropriate regression equation for the current data set. This is because logistic regressions are more robust to violations of basic assumptions of equality of correlation matrices and multivariable normality than other tests, specifically linear regressions and discriminate function analysis (Franciscus and Trinkaus 1995). Furthermore, logistic regressions are appropriate when the response variable is not continuous but is instead dichotomous or ordinal. A correlation matrix was also conducted despite the data set violating some of the basic assumptions of linear regressions. This was done in order to gauge whether there was any basic correlation between any of the metric variables as well as the ordinal response variable.

Regression analyses use equations to yield predictive models for a response variable in order to evaluate the associations between the variables (Snodgrass, et al. 2011). In the current

study, the non-continuous response variable violated the assumptions of a linear regression and so an Ordered Logistic Regression was conducted. An Ordered Logistic Regression (OLR) is a variant of a normal logistic regression, except that in OLR the response variable is ordinal (here, categories from 1-5) instead of dichotomous. In OLR, the deviance, or lack of fit, is calculated, and this regression examines how far the data departs from a theoretically perfect fit (Hamilton 2009). Smaller values indicate a better fit of the data because they exhibit a smaller departure from the theoretical model than do larger values.

OLR is a means for describing how strongly the response variable is related to the explanatory variables, which are represented in odds-ratios. This means that the model is fitted in a way to describe how the explanatory variables are related to the odds that an individual fits into a particular category (Snodgrass et al. 2011), and how every unit change (whether an increase or decrease) in the response variable predicts the odds of being in a different category. Odds ratios greater than one indicate a positive relationship between the response variable and the explanatory variables, while those less than one indicate a negative relationship.

Like any regression test, an OLR is most accurate when a very small number of variables are used. Too many explanatory variables can make the results invalid or unstable. To determine which of the 18 linear variables were the most correlated with the response variable, a goodness of fit test was used for the variables shown to be most strongly correlated in the correlation matrix. Then, those variables were inserted into the OLR to get the most accurate results.

The focus of this chapter was to discuss the methods that were developed and the statistical analyses used to assess the hypotheses posed by this study. Linear and qualitative measurements were taken in an attempt to get an overall depiction of both the size and shape of the cranium and mandible. The sample was gathered from ethnically diverse university

collections composed of European Americans, Native Americans, and a small number of Chinese individuals. Statistical procedures chosen for the analysis include correlation matrices and an Ordered Logistic Regression. These procedures were chosen in order to ascertain how much variability was present in the sample as well as to test the amount of association, if any, between the Mentum Osseum Score and the remainder of the variables. The results of these tests will be explored in the next chapter.

Chapter Four: Results

The null hypothesis of the current study is that there is no relationship between variation in the mentum osseum and other measures of craniofacial morphology. To reject the null, it must be statistically demonstrated that there is a relationship between the morphology of the mentum osseum and other areas of the cranium. Additionally, the variation of the mentum osseum within modern human populations is examined. If high levels of variation are found, then the chin may not be a dichotomous feature of modern humans, and if this is the case, it calls into question its use as an autapomorphic feature of the species. Several statistical analyses were performed to determine both the amount of variation present in the sample as well as the significance of any correlations, because the degree of morphological integration between two systems can be measured by the intensity of the statistical relationships (Cheverud 1982).

Descriptive statistics

A set of initial descriptive statistics were examined to get an overall sense of the sample and its variation (Table 3). From summary statistics, it is possible to assess the variability of the sample by examining the range and standard deviation of each variable as well as the differences among individuals with regard to the discrete traits examined in this study.

Table 3: Summary Statistics

<i>Variable</i>	<i>Freq</i>	<i>Mean</i>	<i>Sd</i>	<i>Min</i>	<i>Max</i>
Mentum Osseum Score	104	4.1	0.8	2.0	5.0
Mental Trigone	102	1.0	—	0.0	1.0
Mental Fossa	95	0.9	—	0.0	1.0
Lateral Tubercle	77	0.7	—	0.0	1.0
Anterior Marginal Tubercle	72	0.7	—	0.0	1.0
Mandibular Incurvature	84	0.8	—	0.0	1.0
Chin Height	104	31.5	3.4	24.0	40.0
Height of the Mandibular Body	88	27.5	3.1	22.0	37.0
Bigonial Width	101	97.1	7.4	76.5	121.0
Bicondylar Breadth	98	114.6	6.8	98.5	131.0
Maximum Ramus Height	102	64.8	5.7	53.0	79.0
Mandibular Length	102	78.5	5.6	67.0	93.0
Mandibular Angle	102	35.2	8.5	18.0	73.0
Bucco-Lingual Distance	75	10.5	0.7	9.0	12.3
Torus Breadth	104	15.0	1.9	11.0	22.0
Retromolar Gap	5	0.0	—	0.0	1.0
Maximum Cranial Length	102	180.6	8.7	165.0	205.0
Maximum Cranial Breadth	103	135.5	6.7	120.0	150.0
Bizygomatic Breadth	99	112.1	7.8	90.0	130.0
Basion Bregma Height	93	129.9	10.0	85.0	155.0
Cranial Basion Length	100	100.0	11.4	85.0	195.0
Nasion Angle	100	95.8	6.2	75.0	110.0
Maxillo-Alveolar Breadth	73	62.4	4.6	50.0	72.0
Upper Facial Height	104	52.2	4.2	40.5	64.0
Total Facial Height	104	70.4	5.0	58.0	82.0

The first six variables shown in Table 3 are the Mentum Osseum Score (MOS) and the traits that it is comprised of. The MOS has an average of 4.1, demonstrating clearly that there is some variation within the individual traits that make up the MOS. If it were dichotomous, and fully present in all humans, then it would have a score of five for all individuals. By looking at the next five traits, it is apparent that the tubercles in particular vary in presence and absence

among individuals. An example of this is the lateral tubercles, as only 72 individuals possess this feature. However, other features, such as the mental trigone and mental fossae, are possessed by almost every individual in the sample. These two features appear fixed in the study sample, and may be fixed among modern humans as a species.

Variation between sexes

One of the four main hypotheses explaining the evolution of the chin is that of sexual selection and whether there was difference between the sexes in the distribution and possession of the mentum osseum traits. Because the study sample was heavily overrepresented by males, with 78 males versus 26 females, it was necessary to avoid sample bias in order to investigate the variation within the sample. A simple percentage was used to compare how much of the sample of males versus the sample of females had each of the mentum osseum traits. These indicate that there the distribution of traits of the MOS between males and females differ, with males being much more likely to have certain chin traits, especially the tubercles. For example, females possessed the anterior marginal tubercles only around fifty percent of the time (Table 4). However, certain traits, such as the mental trigone and mental fossae, are nearly equal in their distribution in both samples, further indicating that these traits are stable within the study sample.

Table 4: Frequency of Trait Expression by Sex

	<i>Male</i>	<i>Female</i>
Mentum Osseum Score		
Mental Trigone	0.97	1.00
Mental Fossa	0.91	0.92
Lateral Tubercle	0.77	0.65
Anterior Marginal Tubercle	0.74	0.54
Mandibular Incurvature	0.79	0.85
<i>Number of individuals</i>	74	30

Population Distribution

Ancestry was also examined, as the sample was both ethnically and temporally diverse (Table 5). Previous studies of the effect of ancestry on the morphology of the mandible have shown only weak population level separation, with more variation seen within human populations than between them (Humphrey, et al. 1999). Therefore, ancestry was not expected to have a discernible impact on the variation of the mandible, as all of the individuals in the sample were recent modern humans. Examination of the sample showed that this was the case.

Table 5: Ancestry Distribution

<i>Ancestry</i>	<i>N</i>
19th Century Caucasian Americans	29
20th Century Caucasian Americans	34
Native Americans	35
East Asians	5
Hispanic	1
<i>Number of Individuals</i>	104

The “chin” as a measurable feature

A non-metric evaluation was developed in order to quantify the chin as a variable. Per Schwartz and Tattersall (2000), any fully modern human should have the five traits as described in the methods section, which include:

- A mental trigone
- Mental fossae
- Lateral tubercles
- Anterior marginal tubercles
- Mandibular incurvature

Each of these five features were evaluated separately for each individual and were marked as either “present” (Score=1) or “absent” (Score=0). The figure below (Figure 9) shows the distributional frequency of each of the five mentum osseum traits.

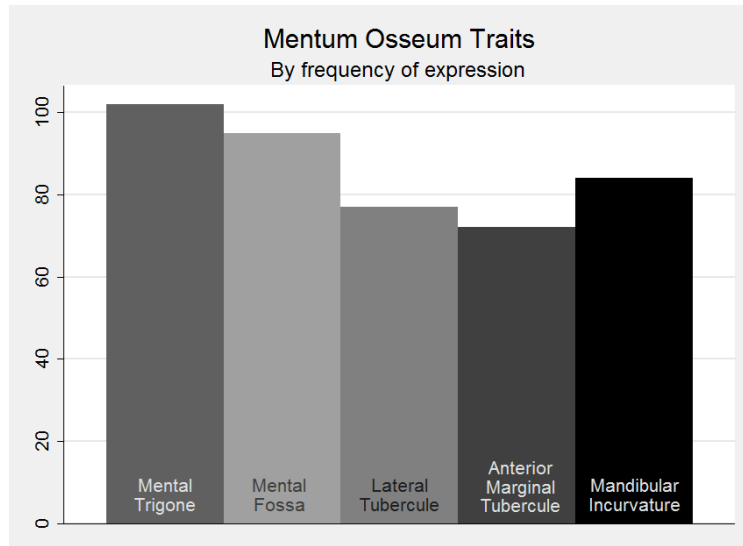


Figure 9: Frequency of the Mentum Osseum Traits

It is immediately apparent from Figure 9 that the separate components of the chin do vary in their prevalence, and that the chin does not appear to be a dichotomous, i.e. present or absent, anatomical feature. The mental trigone was the trait most frequently present, with nearly all of the individuals in the sample possessing it. Closely following the trigone is the mental fossae. These two features would seemingly go together, as the presence of a mental trigone protruding from the anterior portion of the mandibular corpus would create the depressions on each side of the symphysis that are regarded as the mental fossa. Additionally, the appearance of the mandibular incurvature is dependent upon the protrusion of the mental trigone. The features that were absent most frequently were the tubercles, especially the anterior marginal tubercles. As was discussed previously, this was particularly the case in the female sample versus the males.

The individual traits shown above were added to create the Mentum Osseum Score as described in the Methods chapter. Scores range from 0, meaning that the individual possessed none of the modern human chin characteristics, through 5, meaning the individual possessed all of the above described traits. Although the chin is variable, none of the individuals in the present

sample had fewer than two of the traits, and only one individual possessed fewer than three. Furthermore, most of the individuals did in fact have fewer than all of the traits, showing that the chin is present even without all of the prescribed necessary features. While some degree of mentum osseum development is universal amongst this sample, it appears that all five characteristics are not a requirement to possess a chin.

Statistical analysis

The statistical analyses utilized in this study allow for both the variation of the sample as well as any correlation to be examined. If there is any correlation between the variables, this will elucidate whether there may be some level of morphological integration effecting the expression of the chin.

Pairwise correlation

First, a pairwise correlation matrix of each of the 18 linear measurements with the Mentum Osseum Score (MOS) was conducted (Table 6).

Table 6: Correlation Matrix

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Mentum Osseum Score	1.00																			
2	Chin Height	-0.04	1.00																		
3	Height of the Mandibular Body	0.05	0.63	1.00																	
4	Bigonial Width	0.04	0.36	0.36	1.00																
5	Bicondylar Breadth	0.06	0.40	0.46	0.59	1.00															
6	Maximum Ramus Height	0.28	0.24	0.38	0.36	0.28	1.00														
7	Mandibular Length	0.09	0.34	0.48	0.34	0.20	0.41	1.00													
8	Mandibular Angle	-0.08	0.25	-0.11	0.16	0.10	-0.04	-0.24	1.00												
9	Bucco-Lingual Distance	0.00	0.34	0.23	0.27	0.25	0.01	0.23	0.04	1.00											
10	Torus Breadth	0.35	0.27	0.40	0.50	0.40	0.52	0.46	-0.01	0.14	1.00										
11	Retro molar Gap	0.02	0.03	0.21	0.08	0.04	-0.04	0.08	-0.02	0.01	0.03	1.00									
12	Maximum Cranial Length	0.34	0.16	0.06	0.22	0.15	0.48	0.33	0.08	0.00	0.44	-0.03	1.00								
13	Maximum Cranial Breadth	0.18	0.10	0.05	0.24	0.19	0.33	0.00	0.11	-0.09	0.22	0.08	0.21	1.00							
14	Bizygomatic Breadth	-0.06	0.38	0.53	0.57	0.56	0.30	0.36	-0.18	0.37	0.27	0.06	0.02	0.15	1.00						
15	Basion Bregma Height	0.22	0.31	0.24	0.39	0.26	0.44	0.18	0.36	0.16	0.39	-0.08	0.47	0.33	0.22	1.00					
16	Cranial Basion Length	-0.01	0.07	0.07	0.35	0.05	0.51	0.29	0.11	-0.07	0.22	0.00	0.53	0.12	0.26	0.23	1.00				
17	Nasion Angle	0.14	0.35	0.29	0.20	0.10	0.20	0.36	0.06	0.36	0.26	0.16	0.28	-0.19	0.21	0.31	0.27	1.00			
18	Maxillo-Alveolar Breadth	-0.03	0.32	0.44	0.38	0.48	0.37	0.30	0.00	0.34	0.35	0.02	0.13	0.05	0.57	0.27	0.25	0.40	1.00		
19	Upper Facial Height	0.00	0.35	0.29	0.31	0.34	0.34	0.28	0.03	0.04	0.23	0.07	0.33	0.21	0.29	0.30	0.26	0.10	0.24	1.00	
20	Total Facial Height	0.00	0.57	0.54	0.42	0.40	0.39	0.30	0.12	0.14	0.25	0.10	0.33	0.29	0.38	0.34	0.24	0.21	0.36	0.78	1.00

Variables in bold are significant at the 10 percent level

The correlation matrix measures how well the response variable, here the MOS, is predicted by the set of explanatory variables, which are represented by the linear measurements. The correlation coefficient demonstrates how well each explanatory variable is correlated with the response variable, with scores closer to one being the most correlated. A coefficient value of zero indicates there is no linear correlation between the two variables. A significance level can also be calculated, which indicates whether the amount of correlation seen between the two variables is statistically significant.

Results of this test indicate that there is little to no relationship between the MOS and the majority of the independent variables (Table 6). However, a small subset of variables appears to be correlated at the .10 level. Surprisingly, these variables are not isolated to the mandibular measurements; instead, they are equally distributed among the cranial variables as well. Torus breadth is one of the more highly correlated variables, although as it is a part of what makes up the basal projection of the mentum osseum, this result is not surprising.

However, association between variables in and of itself does not demonstrate that the variations in measurements are caused by differences in the correlated variables. The correlations, while significant at the 10% level, are not high, and may reflect a weak relationship with the MOS at best, especially since the sample size of this study was overall small (Table 7). Also, since the response variable is non-linear, further analyses were needed in order to determine if there was a true correlation between these variables.

Table 7: Significant Correlation Variables

Mentum Osseum Score	1.00
Maximum Ramus Height	0.28 '(0.00)
Torus Breadth	0.35 '(0.00)
Maximum Cranial Length	0.34 '(0.00)
Maximum Cranial Breadth	0.18 '(0.07)
Basion Bregma Height	0.22 '(0.04)

Variables are significant at the 10 percent level

Ordered Logistic Regression

The regression that was used in this analysis was an Ordered Logistic Regression (OLR). OLR differs from linear regression and is used to describe how strongly the response variables are related to the explanatory variables included in the regression. The OLR tests the probability that there is some relationship between the variables greater than zero, however small. The log coefficients demonstrate how a one unit increase in the coefficient predicts the likelihood that it is related to the outcome (Snodgrass, et al. 2011). This means that the log of the odds of the response variable is a function of the explanatory variables (Franciscus and Trinkaus 1995). The odds ratio reflects the amount of association, or non-independence, between the two variables, and is a way of testing the significance between the variables (Table 8).

Table 8: Ordered Logistic Regression

	<i>Odds Ratio (SE)</i>
Torus Breadth	1.353** (0.1604)
Maximum Cranial Length	1.066** (0.0265)
Number of Observations	102
McKelvey & Zavoina's R^2	0.176
Model X^2	17.88

*** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$

As with all regressions, results become less credible as the number of variables increases, and Ordered Logistic Regression limits the number of variables that can be included in the regression equation. Three explanatory variables are the limit past which the results may not be accurate. In order to determine which variables would be the best fit for the OLR model, a goodness of fit test was conducted which examined the contribution towards the overall model fit of individual predictors. This allows the researcher to determine which explanatory variables to keep in the final regression. Although there are many goodness of fit tests available, for the current research it was determined that McKelvey & Zavoina's R^2 was the most appropriate, as it treats the ordinal coefficients like continuous variables. It is an attempt to measure the fit of a model in terms of the proportion of the variance that is accounted for in the model.

The result of the McKelvey & Zavoina's R^2 test demonstrated that only two variables, Torus Breadth and Maximum Cranial Length, were a significant fit for the OLR model. Initially, only the variables that were found to be correlated from the correlation matrix were tested; then, the remainder of the variables was examined in order to not exclude any significant relationships. The inclusion of any additional variables was non-significant, meaning that they were not a better fit for the model than were the most significant variables.

The OLR indicates that the length of the cranium is the only significant influence on the expression of the chin; and this relationship is small, with every unit change in the MOS indicating a two millimeter increase in maximum cranial length. Torus Breadth, the other significant variable, may serve to demonstrate that as the thickness of the basal projection of the mental symphysis increases, so does the likelihood that the mentum osseum will possess more of the chin traits. For every 2mm change in Torus Breadth, the individual has 1.7 times the likelihood of having a higher Mentum Osseum Score.

Taken together, the correlation matrix and OLR indicate that the length of the head significantly impacts the shape and expression of the mentum osseum, however small this relationship may be. The variation among the majority of the linear measurements, particularly the facial measurements, does not seem to influence the chin in any way. This may not be surprising, because previous studies of morphological integration have shown the face to vary somewhat independently of the other areas of the cranium in terms of size and shape (Bastir, et al. 2005). Additionally, no mandibular variables outside of Torus Breadth (the only variable directly a part of the mentum osseum itself) have any significant relationship with the mentum osseum, indicating that the chin may in fact be independent of the biomechanical forces that alter the shape of the remainder of the mandible.

Summary

In this chapter, the results of the statistical tests were outlined, and their impact on the hypotheses was examined. The hypotheses of this study were:

1. The chin lacks variation; all five trait characteristics required to possess a chin are present in all individuals examined because all individuals are fully modern human.

2. There is no relationship between the expression of the mentum osseum and other measures of craniofacial morphology. To overturn the null, it must be statistically demonstrated that there is a relationship between changes in the mentum osseum and other areas of the cranium.

The results of this study indicate that the first null hypothesis should be rejected; the mentum osseum does display notable variation. More than half of the individuals in the study had fewer than all five of the mentum osseum characteristics, although they were all recent modern humans. This suggests that previous research denying the variability of the chin was incorrect in its conclusions. Furthermore, the chin is also notably variable between sexes, with males and females differentiating in which mentum osseum traits they displayed. This may have implications as to the reasons for the initial evolution of the mentum osseum in modern humans.

The second hypothesis is more difficult to assess. Although there is weak correlation between the mentum osseum and two of the variables, one of those variables, Torus Breadth, is a part of what makes up the chin and may not explain any morphological integration in and of itself. While cranial length was demonstrated through multiple statistical procedures to be significantly correlated to the mentum osseum, this relationship is not strong. Overall, the vast majority of the variables are not correlated to the mentum osseum score in any way, indicating that the chin is mostly independent of any morphological integration that may influence the majority of the skull.

Chapter 5: Discussion

The results of the statistical analysis demonstrate the independent nature of the mentum osseum by failing to find a statistically significant relationship between the Mentum Osseum Score (MOS) and the majority of the 18 linear variables measured. This implies that, with the exception of the length of the cranium, the size and shape of the cranium does not influence the degree of the expression of the chin. The length of the cranium is positively correlated with an increase in the number of mentum osseum traits an individual possesses; for every small increase in cranial length, the number of chin traits that the individual expresses is more likely to increase. However, while the correlation is significant, it is not strong. In a general sense, the current study fails to find support for the hypothesis that the chin is a part of the morphologically integrated craniofacial suite. Because morphological integration cannot explain the appearance and function of the chin, other explanations must be considered.

Additionally, the second hypothesis, that the “chin” is not variable in modern humans (i.e., it is either “present” or “absent”) has been overturned. Results indicate that the mentum osseum is highly variable in its expression. This is true from individual to individual and also between the sexes, with over half of the current sample possessing fewer than five of the mentum osseum traits. Males were also more likely to possess all of the chin traits than females, particularly the tubercles. This demonstrated variability leads to the conclusion that either the authors that claim the chin is not variable are incorrect, or that the definition of the chin itself needs to be reconsidered.

Hypotheses for the emergence of the chin

Research on the origin of the mental symphysis has been ongoing for over a century (Blumenbach 1865; Schwartz and Tattersall 2000), with recent publications on the subject

showing that debate concerning the etiology of the chin and its utility as an autapomorphic feature is alive and well. Four explanatory hypotheses related to the chin are relevant to the present study; the chin is 1. a biomechanical response to masticatory stress (Daegling 1993; Fukase 2007; Gröning, et al. 2011), 2. a biomechanical response to the evolution of speech (Daegling 2012; Haskell 1979; Ichim, et al. 2007; Schepartz 1993), 3. has no adaptive function, (Gould and Lewontin 1979; Polanski 2011; Weidenreich 1936), and 4. a result of sexual selection (Thayer and Dobson 2010). These hypotheses are each evaluated with respect to the results of the current research.

Hypothesis 1: The chin as a biomechanical response to masticatory stress

Several authors have proposed that the emergence of the chin in early anatomically modern humans may be explained in biomechanical terms related to masticatory stress and strain influencing the evolving cranium and mandible (Bouvier 1986; Daegling 1993; Daegling and Hylander 2000; Demes 1987; van Eijden 2000). The human mandible has biomechanical forces applied to it via multiple sources, including the muscles of mastication, the teeth, and reactionary forces from the TMJ (Ashman and Van Buskirk 1987; van Eijden 2000). The human mandible experienced lower amounts of biomechanical strains as food processing capabilities advanced, and the mandible's increased gracility through time is an adaptive response to this (Nicholson and Harvati 2006). However, biomechanical stresses are still present, if decreased, in the mandible, so the musculatures and bony anatomy must still buffer against these forces.

When a bone is loaded, e.g. when force is applied, then the bone deforms, perpendicular to the direction from which the load occurs. Tension results from this deformation, and is quantified as “stress”. Stress will result in the bone remodeling to counter the forces. There are several types of biomechanical stress: compressive (bone becomes shorter), tensile (bone is

stretched), or shear (bone is pulled parallel relative to an adjoining area of bone) stresses (van Eijden 2000). Torsion is a type of shear stress that occurs when the stress takes place in a bone that is circular in cross-section. Additionally, bone can also be loaded with bending stress, which results in both compressive and tensile forces in different parts of the bone subject to the loading strain. This is often called “wishboning” in the mandible because it is pulled apart like a wishbone under this type of stress. Bone is strongest in compression, and weaker under tensile and shear stresses (Figure 10).

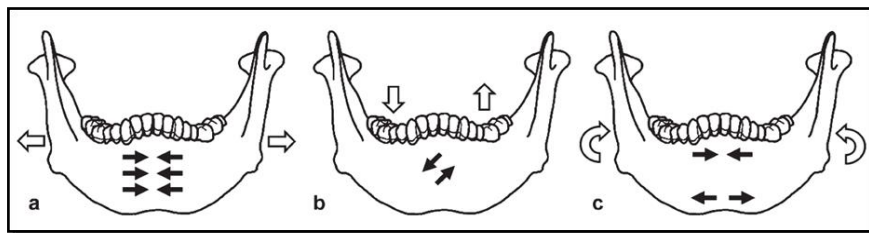


Figure 10: Biomechanical stress in the mandible. Arrows indicate the directions of masticatory stress. a) represents wishboning, b) dorsoventral shear, and c) vertical bending in the coronal plane. Adapted from Gröning et al. (2011)

The chin has been hypothesized to serve as a buttress for load resistance during mastication. Three separate hypotheses have been formulated to explain why this buttressing was necessary: 1. Lateral bending in the transverse plane, also known as wishboning, which results in lingual tension and labial compression at the symphysis; 2. Dorsoventral shear; and 3. Vertical bending in the coronal plane as the symphysis experiences twisting of the corpus around the anterior axis, which puts the basal area of the symphysis under tension stress (Dobson and Trinkaus 2002; Gröning, et al. 2011). Of these, wishboning creates the greatest magnitude of stress for the mental symphysis, and one way of alleviating this could be the remodeling of the thickness of the symphyseal area.

Because of the complexity of mandibular anatomy, the biomechanical forces the mandible is subject to are also complicated. This is primarily a consequence of the interaction between the mandible, the musculature, and the articulation of the mandible with other areas of the skull. The major biomechanical stresses on the mandible are related to its most important function, the chewing and processing of food. However, what impact these masticatory forces have on the chin itself are more difficult to determine. Similar types of biomechanical stresses are present in all mammals, although mandibular morphology differs extensively. Despite similar masticatory pressures, no other mammal has evolved a chin. Other hominins, particularly Neandertals, were more similar to modern humans in terms of skeletal form and dietary processing techniques, but did not evolve the complete complex of mentum osseum characteristics found in anatomically modern humans (Dobson and Trinkaus 2002).

While many researchers have investigated various forms of biomechanical forces as the reasoning behind the evolution of the chin, no explanation has withstood scrutiny. Several studies have focused on functional explanations for the differences found in modern and archaic human mandibular anatomy, and have concluded that although the morphology of the mandible differed between modern humans and Neandertals, they were equally resistant to masticatory stress, specifically, vertical bending and wishboning (Dobson and Trinkaus 2002). Furthermore, although Harvati and colleagues (2011) were not specifically testing biomechanical hypotheses, their results demonstrate that Neandertal and modern human mandibular morphology were not a result of mechanical requirements. That two lineages of humans had similar levels of stress resistance, despite differing mandibular anatomy, indicates that the form of the mentum osseum itself is plastic and not a remodeling response to mechanical demands. Indeed, late Pleistocene hominins, including Neandertals, show varying degrees of trait expression in the chin, as will be

outlined later in this chapter; and all have similar mandibular resistance in spite of these differences (Dobson and Trinkaus 2002).

Additionally, Ichim and colleagues (2006) “removed” the chin from a modern human mandible with computer modeling and then subjected it to normal and high levels of strain. Their conclusions indicate that functional demands had no influence on the shape of the mandible, and therefore the development of the human chin is in fact unrelated to the demands placed upon it by mastication (Ichim 2006). Furthermore, their conclusions do not indicate any mechanical advantage of the “chinned” individual of the “non-chinned” one.

In addition to the conflicting opinions on the legitimacy of the biomechanical hypothesis, one important issue with this theory is that the chin first evolved during a time of decreased dental stress through cultural adaptations which led to better food processing techniques (Lieberman 2011). Decreased dental loads would eventually result in smaller muscles of mastication and lowered biomechanical stresses. Therefore, the more gracile mandible of modern humans could have been a result of relaxed selection, leading to a craniofacial and mandibular masticatory suite that was less capable of producing large bite forces than it had been previously. The only part of the mandible that is robust in modern humans is the area of the mentum osseum itself, which has a much higher density of bone than would be expected for the size of the mandible (Fukase 2007). However, this did not appear to have any cost in terms of evolutionary fitness (Daegling 2012). A decrease in overall mandibular strength and lowered biomechanical stress, coupled with an increase in bone density in the chin suggests a more complex scenario than straightforward mechanical reasons.

While there have been have many biomechanical studies on mentum osseum, none of the testing of this model has withstood scrutiny from other scholars, and it has been concluded on

several occasions that the chin is at least partially independent of biomechanical strains related to mastication (Daegling 2012; Dobson and Trinkaus 2002; Ichim 2006). The results of the current study further indicate that this is the case. Previous studies investigating the integration of the mandible and cranium in relation to masticatory strains have found them to be highly correlated, especially the ascending ramus of the mandible with areas of the temporal bone and the zygomatics (Bouvier and Hylander 1984; Polanski 2011). The results of this study fail to find any integration between the chin and traits of the mandibular ramus, temporals, or zygomatic areas. Additionally, no correlation was found between the chin and the facial measurements, including the width of the maxillary alveolar area, implying that the chin is not a part of the formation of the dental arcade and remodeling of the mandible necessary to keep the mandibular teeth in proper occlusion with the maxillary teeth. This decoupling indicates that the chin is not a functional response to masticatory stress.

Hypothesis 2: The chin as a biomechanical response to the development of language

There is currently no agreement as to whether there are any diagnostic features of the human anatomy that indicate the development of language. However, the hypothesis that the chin evolved as a response to the biomechanical strains of speech placed on both the tongue and orofacial muscles has gained traction in recent years (Daegling 2012; Ichim, et al. 2007). Historically, two of the most unique aspects of modern humans were said to include both the evolution of the chin as well as the origin of language (Haskell 1979; Ichim, et al. 2007). Although the uniqueness of speech as being relegated solely to modern humans is questionable, it is possible that the increased biomechanical strains related to speech production may have led to bone remodeling at the mental symphysis, resulting in the chin.

Speech results in strain that is low in magnitude but high in frequency, and such strains have been demonstrated to result in cortical bone hypertrophy, such as what is seen in the mentum osseum (Daegling 2012). This type of biomechanical loading is different from what is expected from mastication forces in terms of both the magnitude and frequency seen, as well as in which muscles are involved in these activities. Specifically, mastication involves strains that are high in magnitude but low in frequency, the opposite of that seen in speech. The requirements of language would create novel demands and movements for the tongue and lips, which in turn would change the biomechanical strain patterns in the musculature connected to the mental symphysis (Ichim, et al. 2007).

Both the genioglossus muscle and the anterior belly of the digastric muscles attach on the interior surface of the mandibular symphysis, and both of these muscles are directly involved in speech production. Additionally, the rapid contraction of the tongue during speech would generate repetitive forces at the interior surface of the mental symphysis, possibly instigating heavy bone remodeling. While many muscles involved in speech production have attachment/insertion points on the mandible, the strains caused by language production would be heaviest at the anterior portion of the mandible, specifically, the chin (Daegling 2012).

There are many unresolved issues with the speech hypothesis. One of the most fundamental of these is the claim that speech and the chin evolved around the same time (Ichim, et al. 2007), yet the timing for the origin of speech is unresolved. Whether or not this event coincides with the development of the chin is, at best, speculation. Furthermore, modern humans with developmental speech disorders (specifically, Angelman's syndrome) have severely limited speech but still have normally developed chins (Daegling 2012). Although computer projections predict that a flat symphysis will remodel under the repetitive strains of speech, there is no

anatomical evidence that the chin is connected to speech production or that biomechanical strains produced by speech would have any effect on the skeletal anatomy (Daegling 2012).

Present evidence from this study cannot falsify this theory, e.g., that bone remodeling in the mentum osseum could be a response to increased loads or biomechanical strains related to speech production. However, there is currently no support that this is why the chin first evolved. The only support that is offered is that the thickness of the mandibular torus may indicate remodeling of the attachment areas of the geniglossus and digastric muscles due to biomechanical pressures. In the current study, torus breadth is the most highly correlated variable to the Mentum Osseum Score. Because torus breadth is in part a measurement of the protrusion of the basal section of the mental symphysis itself this may be a measure of the correlation between the chin traits. However, it could also indicate an area with a high likelihood of cortical bone remodeling due to muscle attachments and strain gradients. Interestingly, torus breadth was not only correlated with the Mentum Osseum Score, but was also highly correlated with all of the cranial measurements. This could indicate that torus breadth is morphologically integrated with a craniofacial suite of characteristics connected by the stresses caused the speech strains, instead of masticatory forces. Measurements other than the ones currently assessed, such as those related to the muscles of the throat and cranium, may add further support to this hypothesis, but are beyond the range of the current research.

Hypothesis 3: The chin is “left behind”

In evolutionary biology, traits are generally regarded as being the outcome of adaptive purposes; they are selected for because they perform some developmental or mechanical function more advantageously than other variants of that trait. However, it is possible that traits may evolve through integration of different morphological areas and serve no functional purpose. In

terms of the chin, this could mean that, as the shape of the cranium evolved, the overall size and shape of the mandible was reduced; but the mentum osseum itself was a secondary consequence of selection acting on the other areas of the cranium; therefore, the chin would have no adaptive function of its own (Daegling 2012). In this hypothesis, it is important to remember that the chin is a part of an integrated organism, and is not a discrete area a part from the rest of the individual. Although the results of this study show that the chin is independent from the majority of cranial, mandibular and facial measurements, it is still a part of the mandible and there are limits to its growth and projection (Gould and Lewontin 1979). Additionally, Weidenreich (1936) argued that the mentum osseum was the result of reduced alveolar support due to the reduction of the incisor roots in modern humans and has no purpose of its own, although his theory did not explain the protrusion of the chin, just the resorption of the surrounding areas. Genetic drift is an additional possible causation for the appearance of the chin, as it could have appeared in a small population of modern humans and eventually became fixed in the population. This is not a hypothesis that can be tested with the current data, but it remains a possibility.

The difficulties with the non-functional hypothesis are that there are few, if any, morphological features that cannot be classified as having some sort of function (Daegling 2012). The persistence of the chin considering its dense amount of cortical bone without some function is questionable, as this heavy concentration of bone would be energetically costly (Daegling 2012; Fukase 2007). Additionally, this theory is difficult to test, as the integration of the chin may indicate either pleiotropy or some degree of biomechanical interaction, dependent upon the areas which were integrated. The results of the current study indicate that there is little, if any, integration of the mentum osseum.

Other than torus breadth, which would seem to be correlated with the overall expression of chin shape, the only variable that was significantly correlated with the mentum osseum was cranial length. Although this relationship is weak, it is surprising in that modern humans have *shorter* heads in comparison to earlier hominins, particularly the Neandertals, who are often characterized as having long, low crania. If the expression of the chin is increased by having a longer cranium, then it would seem likely that earlier hominins would have possessed chins as well.

This research attempted to determine whether the chin is morphologically integrated with other cranial and mandibular measurements. The results suggest that it is generally not correlated with the rest of the bony skull anatomy, which would indicate that the evolution of the chin was a consequence of factors other than pleiotropy. These results were unexpected, because so many areas of the skull are integrated with one another, including the mandible. The chin, however, seems to be independent of these interactions. The lack of covariation in the mentum osseum is even more surprising when other mandibular variables are examined for correlation. For example, chin height is correlated with all of the mandibular variables, but is *not* significant with the “chin” score (MOS) itself, which further indicates that the chin is independent of any integration.

Hypothesis 4: The chin as a result of sexual selection

While most hypotheses have focused on function driving the evolution of the chin, another scenario with adaptive significance is that the chin is an outcome of sexual selection. Sexual selection can result in the retention of a trait which increases mating success, either through the attraction of mates or the intimidation of rivals (Barber 1995). Thayer and Dobson (2010) discuss psychological studies of facial attractiveness which demonstrate that a “broad

chin” is associated with social dominance in males, as well as being an indicator of masculinity to receptive females and subsequent health and genetic virility. Robust chins in males are a product of secondary sex development that begins at puberty and are linked to the growth and development of males because they indicate higher levels of testosterone. These studies also indicate that males prefer females with more narrow chins, which are said to be correlated to high amounts of estrogen and high fecundity (Thayer and Dobson 2010). It is possible that males with higher levels of testosterone (and thus more distinctive chins) may have been selected over time, leading to the establishment of this trait in modern humans today.

Sexual dimorphism in chin shape is one of the more well-established indicators of sex in human cranial remains (Figure 11), and is cited as such in the most prominent osteological texts (Bass 1971; Buikstra and Ubelaker 1994; White, et al. 2011) as well as recent studies attempting to characterize dimorphic features using 3D morphometric techniques (Garvin and Ruff 2012).

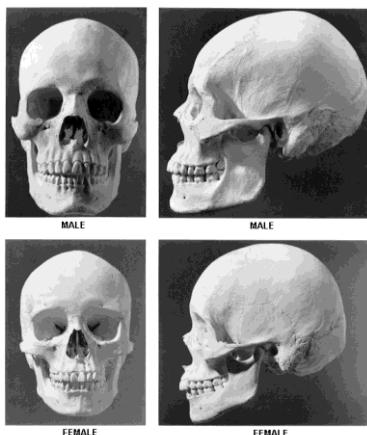


Figure 11: Sexual dimorphism of the human skull (adapted from White 2011)

While males are described as having broad, square chins, and females with more angular, narrow chins, one of the major differences cited as dimorphic is the greater prominence of the lateral and anterior marginal tubercles in males. Analysis of the data from the current research shows that only 65% of females expressed the lateral tubercles, while 79% of males did, and only 54% of females possessed the anterior marginal tubercles as opposed to 74% of males. Thayer and Dobson conclude that if the chin is demonstrated to be sexually dimorphic, any functional hypotheses, such as biomechanical pressures caused by either masticatory or speech factors, are likely incorrect (Thayer and Dobson 2010).

Some scholars have raised issues with the sexual dimorphism hypothesis. The appearance of sexual dimorphism in human chin shape implies that function may not impact the mandible's development. However, while sexual selection may have been key in the maintenance of dimorphism in chin shape, it may first have evolved as a response to other selection pressures (Thayer and Dobson 2010). Additionally, there is no evidence that males and females differ in their biomechanical response to stress and strain, despite having different growth patterns in post adolescence (Daegling 2012). If the shape of the chin does not impact the mandible's ability to buffer biomechanical stresses, then function may not be needed in order to explain the evolution of the mentum osseum.

Additionally, there is the contention of limited variation in the mentum osseum which has been falsified by the results of this study (Schwartz and Tattersall 2000). These results have indicated that the chin is highly variable in modern humans, and there are large differences in the possession of certain chin traits between males and females as well. Females in the study sample were particularly unlikely to possess both the lateral and anterior marginal tubercles, with only half of the females expressing the anterior marginal tubercles. Natural selection could have led to males with higher levels of testosterone, and thus more pronounced chins, to be selected more often than their weaker-chinned contemporaries, and the same could be true for females with higher levels of estrogen and more narrow chins. If this were the case, the chin would have been a secondary consequence of sexual selection, as the chin itself would not have been selected for, but the underlying behavioral advantages those who possessed them would have been. At the present time, the evidence that sexual selection was the driving force behind the evolution of the chin remains scarce, but further study could help elucidate these relationships. The results of this study indicate that it is a possibility.

Variation of the mentum osseum in modern and archaic humans: what is a chin?

The results of the current research demonstrate the variability of the modern human chin, specifically of the five traits that are encompassed by the Mentum Osseum Score. The traits were variable across the sample, and there were no significant differences between the different ethnic populations that made up the sample. Nearly all of the individuals possessed the mental trigone, mental fossae, and mandibular incurvature, but both the anterior marginal and lateral tubercles were highly variable in their presence and absence. More than half of the individuals in the current study did not possess all five characteristics.

Previous studies have concluded that the human chin was a trait of presence or absence, stating that true recent modern humans will have all of the characteristics of the chin described in this study (Schwartz and Tattersall 2000). This claim was a response to research which attempted to characterize some Neandertals as possessing chins in order to demonstrate the range and variability of Late Pleistocene hominins (Wolpoff 1975). Schwartz and Tattersall (2000) claim that these Neandertal individuals merely had basal projections of the mental symphysis, and that these “swellings” were not true chins. However, other scholars emphasized that while Middle and Late Pleistocene hominins did not possess fully developed chins displaying all of the typical modern characteristics, it was still a highly variable anatomical area that many archaic members of *Homo* possessed to some degree. In Figure 12, this can be seen in five different specimens.



Figure 12: Anterior view of Late Pleistocene mandibular symphyses illustrating the variation of the mentum osseum. Adapted from Dobson and Trinkaus (2002)

The top two specimens represent Middle Pleistocene humans from Atapuerca and Tighenif, the third is Amud I, a Neandertal, and the bottom two are early anatomically modern humans from Skhul and Ohalo (Dobson and Trinkaus 2002).

While Neandertals and Middle Pleistocene *Homo* did not display the fully developed chin recognized in modern humans today, the disagreements between various scholars as to the evolutionary significance of this anatomical trait may belie the true issue at hand, which is that there is no definition of what actually constitutes a chin. While this may seem to be a flippant detail, it is relevant because without a true definition of the trait, arguments about who possesses one cannot be resolved. If a chin is considered to be merely a projection at the basal section of the mental symphysis, then many earlier hominins displayed one. However, if the chin is made up of specific characteristics, such as the traits used in the Mentum Osseum Score, then it may be confined to only modern humans, despite the fact that not all modern humans possess all of the features.

Additionally, the validity of the term “chin” to describe this anatomical feature has been debated by various authors, since the feature is so variable as well as inadequately defined (Lieberman 2011; Schwartz and Tattersall 2000). Therefore, the term “mentum osseum” was used in this study in conjunction with term “chin”, as was previously done in several studies (Dobson and Trinkaus 2002; Schwartz and Tattersall 2000; Thayer and Dobson 2010; Weidenreich 1936). The “mentum osseum”, as defined by Weidenreich (1936), includes the mental trigone, which is the triangular prominence of the anterior and inferior portions of the mental symphysis as well as the tubercles, and the mandibular incurvature, which includes the mental fossae (Thayer and Dobson 2010). It may be more appropriate to dispense with the term “chin” altogether, as it is so contentious a feature and has yet to be given a definitive description

in the anthropological literature. Regardless of the definition, however, it is clear from this study as well as previous research that the chin is a highly variable trait in modern humans and possibly in earlier hominins as well.

The hypotheses of the current study were to investigate the variation within the mentum osseum. Additionally, it was intended to determine whether the chin was a pleiotropic consequence of morphological integration, which characterizes the interactions and variation of much of the rest of the skull. The results demonstrated that the mentum osseum does vary in modern humans, and that it does so independently of changes in other measurements. These results reject the null of both hypotheses; the chin appears independent of either pleiotropy or functional causation. However, the chin was found to be sexually dimorphic, with large numbers of females lacking the tubercles that are a part of the mentum osseum measurement. This indicates that the chin may be a result of natural selection by which males with more prominent chin formation were selected for reproduction over those that lacked them, and this process eventually led to the establishment of this feature. As the shape of the face and cranium evolved, the robusticity found in the mentum osseum may have remained, not for functional purposes, but as a response to sexual selection. The results of this study indicate that there is dimorphism in the chin but provide no support for the remainder of the explanations that have been formulated to explain the evolution of the chin.

Chapter 6: Conclusion

This study examined the variation and possible integration of the mentum osseum, or chin, in modern humans. The development and function of the human chin have long been a source of contention in the Paleoanthropological community because it is such a unique feature and because its function and origin have remained elusive despite years of research.

Additionally, it is important because the chin is used as an autapomorphy of modern humans and is used to differentiate a modern human from an archaic one. Although many hypotheses have been investigated over the course of the last 100 years, they are difficult to evaluate and hard to falsify. The current research is an attempt to evaluate the modern human mentum osseum, or chin, in a way that has previously attracted little attention. Recent studies of the interactions between various aspects of the human cranium and mandibular anatomy have demonstrated the importance of morphological integration in the form and function of skeletal “suites” of characteristics (Cheverud 1982; Polanski 2011). However, the chin has not previously been included in these studies of mandibular integration. Therefore, the goals of the current research were to study both the variation and potential integration of the mentum osseum with the rest of the craniofacial and mandibular suite.

Morphological integration can be defined as coordinated variation between separate units; changes in one area will impact and drive change in other areas in the integrated suite (Olson and Miller 1999). Integration is important to consider when analyzing skeletal traits because organisms must be considered as a sum of correlated parts, and not as individual units each operating under their own genetic and functional controls (Gould and Lewontin 1979). Various areas of the cranium and mandible have been shown to be highly integrated, particularly the ascending ramus of the mandible with the temporal and zygomatic areas of the cranium, as

well as the overall breadth of the cranium and mandible. As these are areas of bone articulation as well as attachment/insertion areas for the muscles of mastication, this integration makes sense in terms of biomechanical and evolutionary size constraints. However, the chin itself was not included in these earlier investigations, and as it does not serve as an attachment or articulation point for these other cranial areas, its variation was theorized to be independent (Lieberman 1995; Polanski 2011).

The hypotheses for the current research focused on the variation and possible morphological integration of the mentum osseum. Specifically, the hypotheses tested whether the chin is independent of the morphological integration that characterizes much of the rest of the skull. If so, this would have implications for the evolution and function of the chin. Additionally, the hypothesis that the chin is a dichotomous feature of either “presence” or “absence”, which was previously stated to be the case by some scholars (Schwartz and Tattersall 2000), was evaluated.

In order to test these hypotheses, a method for quantifying the chin was developed. The chin is a difficult feature to assess because it is topographically diverse and cannot be appropriately measured using linear means. Therefore, an ordinal scoring system was adapted from previous research which described the five chin “traits” that were utilized here (Dobson and Trinkaus 2002; Schwartz and Tattersall 2000). Each trait was determined to be either “present” or “absent” and then these scores were tallied to get a total expression for the mentum osseum of each individual. These scores ranged from 0-5, with “0” possessing none of the chin traits and “5” possessing all of them. A sample of 104 individuals from varied ancestral backgrounds was measured in order to get a diverse sample. Eighteen linear measurements were taken from the cranium, face, and mandible in order to try and capture any integration the chin might have with

the entire skull. An ordered logistic regression was used to evaluate correlations between the ordinal dependent variable of the mentum osseum score and the linear independent variables. This form of regression analysis was most appropriate for the current research because it allows comparison between non-continuous and continuous variables.

Results of the analysis surprisingly indicate that there is a distinct lack of coordination between the mentum osseum and the majority of the linear variables. Only two variables, torus breadth and maximum cranial length, were determined to covary with the chin. Of these two, torus breadth seems likely to be correlated with the chin because it is a measurement of the basal projection itself. Cranial length was positively correlated to the Mentum Osseum Score, meaning that as the length of the cranium increased, so did the expression of the chin. This was unexpected because modern humans are characterized by a *shortening* of the cranium, so a lengthier cranium being a predictor of a well-expressed chin was the opposite of what was expected. However, this correlation, while significant, was weak, and so the relationship itself may not explain the variation between these areas of the skull in its entirety.

The results show that the chin is both independent of morphological integration with the rest of the skull as well as that it is highly variable. The Mentum Osseum Scores for the sample ranged from 2 through 5, with over half of the individuals in the sample possessing fewer than all 5 of the traits. This demonstrates that the chin is highly variable in modern humans and that it is not a feature that is either present or absent. Furthermore, there was sexual dimorphism in the sample, especially in the tubercles of the chin, with females possessing these features less often than the males.

If the chin is independent, as the results of this study indicates, then it is important to determine what factors may have caused this feature to evolve and be maintained. Most

hypotheses have, in the past, looked to function, in the form of selection acting on the chin to help buffer biomechanical stresses, either of the masticatory or speech variety. Additionally, there is the possibility that the chin is non-adaptive and has no function, or that its presence is related to genetic drift. The original hypothesis of the investigation was that the chin was integrated with the rest of the skull, but selection acted on the other areas of the skull and not directly on the chin itself. Therefore, it would have been “left behind” as a pleiotropic side effect of selection. Finally, sexual selection has been a hypothesis of recent investigations.

Of these four hypotheses, the one that has the best support at the conclusion of this study is that of sexual selection. As the chin is independent of nearly all of the cranial and mandibular variables, biomechanical stresses do not seem to be a likely driving force behind the evolution of this feature. Additionally, the independence of the mentum osseum rejects the hypothesis that the chin is a pleiotropic consequence of cranial shape differences, as there is little indication that changes in the shape and size of the cranium impact the expression of the mentum osseum in any way. Sexual selection is supported as it is not a hypothesis of function, so the independence of this feature is not unexpected. This trait could have been selected for, as it is a supposed indicator of higher levels of fertility, since broad chins are characteristic of males with high levels of testosterone for males and narrow chins indicate high levels of estrogen for females. More virile mates would have been selected for more frequently, leading to the establishment of this trait. The arguments against the sexual selection hypothesis, specifically that there would be biomechanical differences between the sexes if males and females differed in their mentum osseum morphology, can be disregarded as the chin is indicated by the results of this study to be independent of biomechanical constraints. While some scholars may suggest that dimorphism in the chin is a secondary consequence of selection acting on different evolutionary pressures, it

may be that sexual selection was the trait which determined the expression of this unique human characteristic (Thayer and Dobson 2010).

It is possible that the method developed for evaluating the expression of the chin, called here the Mentum Osseum Score, may not be the best method for measuring this feature. The chin is difficult to quantify, and more advanced methods, such as 3D imaging, finite element analysis, or even GIS methods, which would better capture the varied topography of this feature, may be an improvement. However, the technique developed for this study focused on all of the unique aspects of the chin in an attempt to capture the variation in its entirety, and more sophisticated techniques may not change the results seen here.

This work is considered a preliminary study whose initial goals were to test whether the chin is variable and whether it is a part of the morphologically integrated suite of facial and cranial characteristics. These hypotheses were overturned, with the chin being both variable and independent of morphological integration. The results further indicate that the chin may be a consequence of sexual selection and subsequent dimorphism. Future investigation could examine this hypothesis in more detail by examining the chin traits present in a wider sample to see if the pattern of dimorphism, particularly the lack of tubercles in many of the females, was universal across individuals from a range of time and geography.

Investigations into the origin of the chin continue unabated as they have for the last one hundred plus years. The goal of this study was to create a method which would ascertain whether there was variation and integration in the mentum osseum with other areas of the skull. The results demonstrated that the chin is independent of any morphological interaction, which indicates that some hypotheses are more likely than others. While the results seem to signify that sexual dimorphism may be the dominant force in the development of the mentum osseum, more

data and further research is required in order to substantiate these claims. Furthermore, the variability of the human chin, among both archaic and extant humans, suggests that caution is necessary when the human chin is used as an autapomorphy to identify modern humans from their ancestors. The chin is one of our most unique features; but it is also one of the more inexplicable. Researchers must be willing to consider all possibilities when attempting to discern the underlying causation of the evolution of the chin, including sexual selection. Until that time, the development and function of the chin will remain elusive.

Bibliography

Aiello, L. C. and M. C. Dean

1990 *An introduction to human evolutionary anatomy.*

Ambrose, S. H.

1998 Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans. *Journal of Human Evolution* 34(6):623-651.

Antón, S.

1994 Mechanical and other perspectives on Neandertal craniofacial morphology. In *Integrative paths to the past: palaeoanthropological advances in honor of F. Clark Howell*. Englewood Cliffs, NJ: Prentice Hall., pp. 677-695.

Ashman, R. and W. Van Buskirk

1987 The elastic properties of a human mandible. *Advances in Dental Research* 1(1):64.

Avis, V.

1959 The relation of the temporal muscle to the form of the coronoid process. *American Journal of Physical Anthropology* 17(2):99-104.

Barber, N.

1995 The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology* 16(5):395-424.

Bass, W. M.

1971 *Human osteology: a laboratory and field manual of the human skeleton*. Missouri Archaeological Society Springfield, MO.

Bastir, M.A.

2008 A systems-model for the morphological analysis of integration and modularity in human craniofacial evolution. *Journal of Anthropological Sciences* 86:37-58.

Bastir, M., A. Rosas and H. Sheets

2005 The morphological integration of the hominoid skull: a partial least squares and PC analysis with implications for European Middle Pleistocene mandibular variation. In *Modern morphometrics in physical anthropology*, pp. 265-284.

Blumenbach, J.

1865 *On the Natural Variety of Mankind* (1775). London, Longman Green.

Bock, C. E.

1890 *Hand-Atlas der Anatomie des menschen*. Rengersche Buchhandlung.

- Boule, M. and H. V. Vallois
1957 *Fossil men*. Dryden Press.
- Bouvier, M.
1986 A biomechanical analysis of mandibular scaling in Old World monkeys. *American Journal of Physical Anthropology* 69(4):473-482.
- Bouvier, M. and W. Hylander
1982 The effect of dietary consistency on morphology of the mandibular condylar cartilage in young macaques (*Macaca mulatta*). *Progress in Clinical and Biological Research* 101:569.
- Bouvier, M. and W. L. Hylander
1984 The effect of dietary consistency on gross and histologic morphology in the craniofacial region of young rats. *American Journal of Anatomy* 170(1):117-126.
- Boyd, T., W. Castelli and D. Huelke
1967 Removal of the temporalis muscle from its origin: effects on the size and shape of the coronoid process. *Journal of Dental Research* 46(5):997.
- Buikstra, J. E. and D. H. Ubelaker
1994 Standards for data collection from human skeletal remains.
- Cartmill, M. and F. H. Smith
2009 *The human lineage*. Blackwell Publishing.
- Cheverud, J. M.
1982 Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution*:499-516.
- Daegling, D. J.
1993 Functional morphology of the human chin. *Evolutionary Anthropology: Issues, News, and Reviews* 1(5):170-177.

2012 The Human Mandible and the Origins of Speech. *Journal of Anthropology* 2012.
- Daegling, D. J. and W. L. Hylander
2000 Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *American Journal of Physical Anthropology* 112(4):541-551.
- Demes, B.
1987 Another look at an old face: biomechanics of the Neandertal facial skeleton reconsidered. *Journal of Human Evolution* 16(3):297-303.

- Dobson, S. D. and E. Trinkaus
2002 Cross-sectional geometry and morphology of the mandibular symphysis in Middle and Late Pleistocene Homo. *Journal of Human Evolution* 43(1):67-87.
- Fabbri, P.
2006 Mandible and Taxonomy of the Earliest European Homo. *Human Evolution* 21(3):289-300.
- Franciscus, R. G. and E. Trinkaus
1995 Determinants of Retromolar Space Presence in Pleistocene Homo Mandibles. *Journal of Human Evolution* 28:577-595.
- Fukase, H.
2007 Functional significance of bone distribution in the human mandibular symphysis. *Anthropological Science* 115(1):55-62.
- Garvin, H. M. and C. B. Ruff
2012 Sexual dimorphism in skeletal browridge and chin morphologies determined using a new quantitative method. *American Journal of Physical Anthropology*.
- Gould, S. J. and R. C. Lewontin
1979 The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205(1161):581-598.
- Gray, H.
2011 *Gray's Anatomy*. Random House.
- Gröning, F., J. Liu, M. J. Fagan and P. O'Higgins
2011 Why do humans have chins? Testing the mechanical significance of modern human symphyseal morphology with finite element analysis. *American Journal of Physical Anthropology* 144(4):593-606.
- Groves, C. P. and V. Mazák
1975 An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Casopis pro mineralogii a geologii* 20(3):225-247.
- Gunz, P., F. L. Bookstein, P. Mitteroecker, A. Stadlmayr, H. Seidler and G. W. Weber
2009 Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proceedings of the National Academy of Sciences* 106(15):6094-6098.
- Hamilton, L. C.
2009 *Statistics with Stata: updated for version 10*. Duxbury Press.

- Harvati, K., N. Singh and E. N. López
2011 A Three-Dimensional Look at the Neanderthal Mandible. *Continuity and Discontinuity in the Peopling of Europe*:179-192.
- Haskell, B. S.
1979 The human chin and its relationship to mandibular morphology. *The Angle Orthodontist* 49(3):153-166.
- Howells, W.
1973 *Cranial variation in man: A study by multivariate analysis of patterns of difference among recent human populations*. Papers of the Peabody Museum of Archaeology and Ethnology.
- Hughes, P. Z.
2003 Basicranial flexion and cranial vault architecture: variation and structural relationships, Department of Anthropology, Colorado State University, Colorado State University.
- Humphrey, L., M. Dean and C. Stringer
1999 Morphological variation in great ape and modern human mandibles. *Journal of Anatomy* 195(4):491-513.
- Ichim, I., J. Kieser and M. Swain
2007 Tongue contractions during speech may have led to the development of the bony geometry of the chin following the evolution of human language: a mechanobiological hypothesis for the development of the human chin. *Medical Hypotheses* 69(1):20-24.
- Ichim, I., Swain, M., & Kieser, J.A.
2006 Mandibular Biomechanics and Development of the Human Chin. *Biomaterials & Bioengineering*.
- Lam, Y., O. Pearson and C. M. Smith
1996 Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth. *American Journal of Physical Anthropology* 100(4):545-557.
- Leakey, M. D. and R. L. Hay
1979 Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature* 278(5702):317-323.
- Leakey, M. G., C. S. Feibel, I. McDougall and A. Walker
1995 New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376(6541):565-571.
- Lieberman, D. E.
1995 Testing Hypotheses About Recent Human Evolution From Skulls: Integrating Morphology, Function, Development, and Phylogeny. *Current Anthropology* 36:159-197.

- 2011 *The evolution of the human head*. Belknap Press of Harvard University Press, Cambridge, Mass.
- Lieberman, D. E., O. M. Pearson and K. M. Mowbray
2000 Basicranial influence on overall cranial shape. *Journal of Human Evolution* 38(2):291-315.
- Liu, W., C. Z. Jin, Y. Q. Zhang, Y. J. Cai, S. Xing, X. J. Wu, H. Cheng, R. L. Edwards, W. S. Pan and D. G. Qin
2010 Human remains from Zhirendong, South China, and modern human emergence in East Asia. *Proceedings of the National Academy of Sciences* 107(45):19201-19206.
- Nicholson, E. and K. Harvati
2006 Quantitative analysis of human mandibular shape using three-dimensional geometric morphometrics. *American Journal of Physical Anthropology* 131(3):368-383.
- Olson, E. C. and R. L. Miller
1999 *Morphological integration*. University of Chicago Press.
- Polanski, J. M.
2011 Morphological integration of the modern human mandible during ontogeny. *International Journal of Evolutionary Biology* 2011.
- Rak, Y., A. Ginzburg and E. Geffen
2002 Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. *American Journal of Physical Anthropology* 119(3):199-204.
- Rightmire, G. P. and H. J. Deacon
1991 Comparative studies of Late Pleistocene human remains from Klasies River Mouth, South Africa. *Journal of Human Evolution* 20(2):131-156.
- Rosas, A., M. Bastir, C. Martinez-Maza, A. Garcia-Tabernero and C. Lalueza-Fox
2006 Inquiries into Neanderthal craniofacial development and evolution: "accretion" versus "organismic" models. In *Neanderthals revisited: New approaches and perspectives*, pp. 37-69.
- Schepartz, L. A.
1993 Language and modern human origins. *American Journal of Physical Anthropology* 36(S17):91-126.
- Schoetensack, O.
1908 *Der unterkiefer des homo heidelbergensis: Aus den sanden von mauer bei Heidelberg*. W. Engelmann.

- Schwartz, J. H. and I. Tattersall
2000 The human chin revisited: what is it and who has it? *Journal of Human Evolution* 38(3):367-409.
- Shang, H., H. Tong, S. Zhang, F. Chen and E. Trinkaus
2007 An early modern human from Tianyuan Cave, Zhoukoudian, China. *Proceedings of the National Academy of Sciences* 104(16):6573-6578.
- Singer, R.
1982 *The Middle Stone Age at Klasies River mouth in South Africa*. University of Chicago Press, Chicago.
- Snodgrass, J. G., M. G. Lacy, H. F. Dengah II, J. Fagan and D. E. Most
2011 Magical flight and monstrous stress: Technologies of absorption and mental wellness in Azeroth. *Culture, Medicine, and Psychiatry* 35(1):26-62.
- StataCorp
2011 Stata Statistical Software: Release 12. , College Station, TX: StataCorp LP.
- Svoboda, J. A., J. van der Plicht and V. Kuzelka
2002 Upper Palaeolithic and Mesolithic human fossils from Moravia and Bohemia (Czech Republic): some new 14C dates. *Antiquity* 76(294):957-962.
- Thayer, Z. M. and S. D. Dobson
2010 Sexual dimorphism in chin shape: implications for adaptive hypotheses. *American Journal of Physical Anthropology* 143(3):417-425.
- Trinkaus, E.
2003 Neandertal faces were not long; modern human faces are short. *Proceedings of the National Academy of Sciences* 100(14):8142.
- van Eijden, T. M.
2000 Biomechanics of the Mandible. *Critical Reviews in Oral Biology & Medicine* 11(1):123-136.
- Washburn, S.
1947 The relation of the temporal muscle to the form of the skull. *The Anatomical Record* 99(3):239-248.
- Weidenreich, F.
1936 *The mandibles of Sinanthropus pekinensis: a comparative study*.
- White, T. D., M. T. Black and P. A. Folkens
2011 *Human Osteology*. Academic press.

Wolpoff, M. H.

1975 Some aspects of human mandibular evolution. *Determinants of Mandibular Form and Growth* 61.

1980 Cranial remains of middle Pleistocene European hominids. *Journal of Human Evolution* 9(5):339-358.