A Comparative Radiographic Investigation of Variation in Facial Projection in Anthropoid Primates

by

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ABSTRACT

Facial projection—i.e., the position of the upper face relative to the anterior cranial fossa—is an important component of craniofacial architecture in primates. Study of its variation is therefore important to understanding the bases of primate craniofacial form. Such research is relevant to studies of human evolution because the condition in *Homo sapiens*—in which facial projection is highly reduced, with the facial skeleton located primarily inferior (rather than anterior) to the braincase—is derived vis-à-vis other primates species, including others in the genus *Homo*. Previous research suggested that variation in facial projection is explained by: (1) cranial base angulation; (2) upper facial length; (3) anterior cranial base length; (4) anterior sphenoid length; and/or (5) anterior middle cranial fossa length. However, previous research was based on taxonomically narrow samples and relatively small sample sizes, and comparative data on facial projection in anthropoid primates, with which these observations could be contextualized, do not currently exist.

This dissertation fills this gap in knowledge. Specifically, data corresponding to the hypotheses listed above were collected from radiographs from a sample of anthropoid primates (N = 37 species; 756 specimens) . These data were subjected to phylogenetically-controlled multiple regression analyses. In addition, multivariate and univariate models were statistically compared, and the position of *Homo sapiens* relative to univariate and multivariate regression models was evaluated.

The results suggest that upper facial length, anterior cranial base length, and, to a lesser extent, cranial base angle are the most important predictors of facial projection. *Homo sapiens* conforms to the patterns found in anthropoid primates, suggesting that

these same factors explain the condition in this species. However, a consideration of the evidence from the fossil record in the context of these findings suggests that upper facial length is the most likely cause of the extremely low degree of facial projection in *Homo sapiens*. These results downplay the role of the brain in shaping the form of the human cranium. Instead, these results suggest that reduction in facial skeleton size—which may be due to changes in diet—may be more important than previously suggested.

DEDICATION

To the memory of my grandparents—

Norm and Toni Norris and

Howard and Jeanne Ritzman

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CHAPTER 1—INTRODUCTION

This dissertation investigates variation in the relative spatial positions of the superior portion of the facial skeleton and cranial base in anthropoid primates. This feature—termed "facial projection"—is commonly used to describe variation in primate craniofacial form (Lieberman, 1995, 1998, 2011; Lieberman et al., 2000a, Lieberman et al., 2002; McBratney-Owen and Lieberman, 2003). Thus, the results of this research provide important insights regarding the basis of primate craniofacial form. Moreover, because facial projection is highly reduced in *Homo sapiens*, this research is relevant to studies of human evolution, and, in particular, sheds light on the evolution of modern human cranial form.

In *Homo sapiens*, facial projection is reduced, with the orbits and associated structures located almost entirely beneath the anterior cranial base (Weidenreich, 1941, 1947; Moss and Young, 1960; Lieberman, 1995, 1998, 2008, 2011; May and Sheffer, 1999; Spoor et al., 1999; Lieberman et al., 2000b, 2004; McBratney-Owen and Lieberman, 2003; Lieberman and Bar-Yosef, 2005). This condition is unique among primates, as well as among mammals, in which the upper face projects to varying degrees anteriorly from the margin of the anterior cranial base (Weidenreich, 1941; Weidenreich, 1947; McBratney-Owen and Lieberman, 2003). Furthermore, this condition is derived vis-à-vis other primate species, including other hominin species (Weidenreich, 1941; Moss and Young, 1960; Lieberman, 1995, 1998, 2011; May and Sheffer, 1999; Lieberman et al., 2000a, 2002; McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003). It has also been argued that the extremely reduced facial projection in *Homo sapiens* accounts for many of the differences in cranial form between *Homo*

sapiens and other species in the genus *Homo* and is therefore critically important to understanding the evolution of modern human cranial form (Lieberman, 1995, 1998, 2000; Lieberman et al., 2000b).

Lieberman and colleagues (Lieberman, 2000, 2011; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003) presented a model for understanding variation in facial projection in anthropoid primates. This model predicts that interactions between specific aspects of the morphology of the cranial base and facial skeleton explain variation in facial projection. Particularly, this model posits that variation in facial projection is underlain by four features of the cranial base—i.e., anterior cranial base length, cranial base angle, anterior sphenoid length, and anterior middle cranial fossa length. These features, in turn, are thought to be related to the relative size of the brain and/or its component parts (Lieberman, 2011, 2008; Bastir et al., 2008; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003). Lieberman and colleagues' model also predicts that the length of the superior part of the facial skeleton—a feature that is not directly related to the anatomy of the brain—also influences variation in facial projection in anthropoids.

The Lieberman model has been tested in ontogenetic samples of *Homo sapiens* and *Pan troglodytes* (Lieberman, 1998, 2000; McBratney-Owen and Lieberman, 2003), which showed that the greater degree of facial projection in *Pan troglodytes* is primarily due to anteroposteriorly longer upper facial skeletons and shorter anterior cranial bases. They further demonstrated that differences between *Homo sapiens* and *Pan troglodytes* in anterior cranial base length are evident throughout ontogeny, whereas differences in

upper facial length only appear during later stages of ontogeny, after the cessation of brain growth.

Lieberman (1998) argued that the extreme reduction in facial projection in *Homo sapiens* relative to other species of *Homo* is due to the evolution of shorter anterior portions of the sphenoid (i.e., from sella to foramen caecum) in this species. However, these results were challenged by Spoor et al. (1999), who argued that this reduction is instead due to increased cranial base flexion, reduction in the size of the facial skeleton, and enlargement of the middle cranial fossae. Due to the discrepancy in these results, there is no consensus on the structural basis for reduction in facial projection in *Homo sapiens*.

Currently, no comparative data on facial projection and its causes exist for taxonomically broad samples of anthropoid primates. Therefore, it is difficult to contextualize the findings of previous research on extant anthropoids. That is, without these data, it is not possible to determine whether the differences in facial projection between *Homo sapiens* and *Pan troglodytes* represent generalizable patterns for how anthropoid crania are assembled, and it cannot be determined whether the factors that contribute to ontogenetic differences in facial projection in these two species also characterize differences between adults in other species of anthropoids. What is more, the explanations for variation in facial projection in hominins, particularly the extremely reduced facial projection possessed by *Homo sapiens*, cannot be understood fully without these comparative data, and it cannot be determined if *Homo sapiens* fits more general trends present in anthropoids or, by contrast, if unique explanations account for this aspect of modern human cranial form.

This dissertation aims to fill this gap in our knowledge of primate craniofacial form. Specifically, this study poses two general research questions: (1) What factors explain variation in facial projection in anthropoid primates? and (2) Does *Homo sapiens* depart from patterns identified in anthropoids? These questions are addressed using data collected from radiographs of anthropoid primates (N = 37 species; 756 specimens). Specifically, these data were used to test hypotheses derived from Lieberman's model (see above). Because these hypotheses are not mutually exclusive (i.e., more than one of the proposed explanations could act in concert to explain variation in facial projection), they were tested using both univariate and multivariate statistical techniques, and the appropriate statistical methods were used to control for phylogenetic nonindependence among the species in the sample. The position of *Homo sapiens* relative to trends that characterize other higher primates was also statistically evaluated.

This dissertation is organized into six chapters. Chapter 2 reviews the relevant literature regarding facial projection in anthropoid primates. The materials used to test these hypotheses as well as the methods for data collection and analysis are described in Chapter 3. Chapter 4 lays out the specific hypotheses that will be tested in this dissertation, and the results of the dissertation are reported in Chapter 5. Finally, Chapter 6 discusses the results, in particular, their relevance to studies of human evolution, and offers conclusions regarding the hypotheses and research questions addressed in this dissertation.

CHAPTER 2—BACKGROUND

This chapter reviews the relevant literature regarding facial projection in anthropoid primates, including its definition and its relevance to the human fossil record. After outlining some important principles of primate craniofacial architecture, this chapter also sets out the key explanations for variation in facial projection in anthropoid primates, as these will form the basis for the hypotheses tested in this dissertation (see Chapter 4).

WHAT IS FACIAL PROJECTION?

Facial projection is defined here as the anteroposterior position of the upper face[1] relative to the anterior cranial base. Following the work of Lieberman and colleagues (Lieberman, 1995, 1998, 2011; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003), the definition used here emphasizes the spatial separation (or lack thereof) between the upper face and the anterior part of the anterior cranial base and, more generally, the spatial separation of the brain case and the upper face. This modified definition harkens back to Weidenreich's (1941, 1947) seminal work, which highlighted variation in the relative positions of the braincase and upper face in *Homo sapiens*, *Pan troglodytes*, and fossil species in the genus *Homo*. This idea is epitomized in the following passage (Weidenreich, 1941: 386; see also Figs. 2.1 and 2.2):

[1]"Upper face" is defined here following Bilsborough and Wood (1988) as the "supraorbital torus and periorbital region," whereas the "middle face" is defined as "the nasal aperture and surrounding area, including the malar region," and the "lower face" is defined as "the naso-alveolar clivus and the alveolar regions of the premaxilla". The term "facial skeleton" is used here to refer to refer to the entire face, comprising the upper, middle, and lower face.

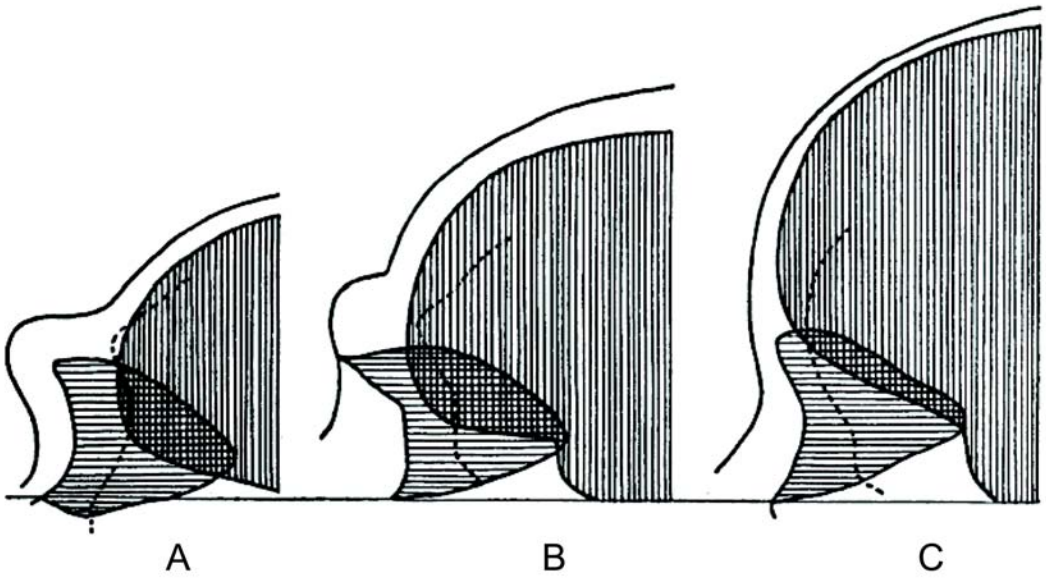

Figure 2.1. Weidenreich's illustration of the topographical relation between the orbit (horizontal hatching) and the brain case (vertical hatching) in male *Pan troglodytes* (A), a female *Homo erectus* specimen (B), and a male *Homo sapiens*. Adapted from Weidenreich (1947).

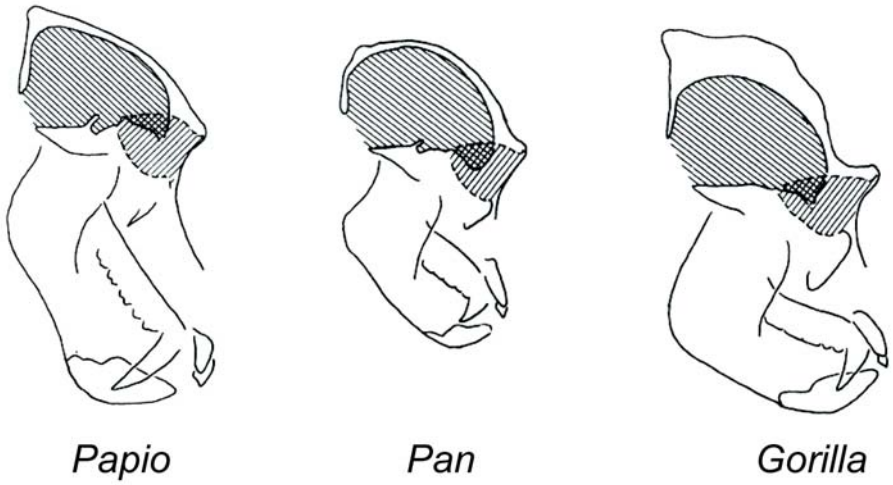

Figure 2.2. Lateral views of *Papio*, *Pan*, and *Gorilla* skulls showing the spatial interrelationships between the orbits and braincase. Vertical hatching represents the orbits and upper face; horizontal hatching represents the braincase; cross-hatching represents area of overlap of the orbits/upper face and braincase. Adapted from Shea (1986).

> The orbit in the chimpanzee is overlapped by the brain case only in its posterior portion and correspondingly the roof formed by the far-projecting supraorbitals. In man, however, the brain case is expanded to such an extent as to have caused the disappearance of the supra-orbitals and the orbit now underlies the entire brain case. *Sinanthropus* [i.e., *Homo erectus*/*ergaster*] also in this regard represents an intermediary stage. This transfiguration makes evident that the orbit as a constituent of the face retained most of its original position, while the brain case because of its enlargement in volume takes active part in the alteration of the topographical relation between the two structures.

Ravosa (1988, 1991a, b; see also Shea, 1985, 1986) also noted this phenomenon—particularly the variation among primates in the spatial relationship between the orbits and the anterior cranial base—and termed it "neural-orbital disjunction."[2]

It is important to contrast the definition of facial projection used here from other anatomical phenomena and previously employed definitions. For example, facial projection, as defined here, is distinct from facial prognathism, which describes the projection of the lower face relative to the upper face, rather than describing the position of the upper face relative to the anterior cranial fossa (Bilsborough and Wood, 1988; McBratney-Owen and Lieberman, 2003). Likewise, facial retraction, which is simply defined as the lack of facial projection, differs from facial orthognathism, which is the lack of prognathism (McBratney-Owen and Lieberman, 2003).

The definition of facial projection employed here also differs from facial kyphosis insofar as kyphosis describes the angular relationship between some aspect of facial morphology (e.g., the palate or the axis of the orbits) and some aspect of the cranial base or neurocranium (Lieberman et al., 2000b; Ross and Ravosa, 1993). In contrast, facial projection is the anteroposterior position of upper face relative to the anterior cranial base, and is quantified using linear measurements rather than angular ones. Similarly,

[2] McBratney-Owen and Lieberman (2003) incorrectly attributed this term to Weidenreich (1941).

facial projection differs from klinorhynchy, which also describes rotation of the facial skeleton (in the midsagittal plane) relative to the brain case—in this case, the condition in which the facial skeleton is rotated forwards away (ventrally) from the neurocranium (Shea, 1985; Aiello and Dean, 2002).

It is also important to make a distinction between facial projection, as defined here, and facial projection as defined elsewhere (most notably by Bilsborough and Wood [1988]). Bilsborough and Wood (1988) measured "facial projection" as the distance between porion and various other ectocranial landmarks positioned around the face; similar measurements were employed by Schultz (1955). "Facial projection," as defined here, differs from these measures insofar as it employs endocranial landmarks to quantify the anteroposterior distance of the upper face relative to the anterior cranial base.

Previous researchers have used two metric definitions of facial projection. The first of these metric definitions was proposed by Lieberman and colleagues (Lieberman, 1998; McBratney-Owen and Lieberman, 2003), who defined facial projection as the linear distance between nasion and foramen caecum, measured perpendicular to the Posterior Maxillary (PM) Plane (the plane marking the posterior limit of the facial skeleton and the anterior border of the middle cranial fossa; see below for further discussion). This measurement is similar to the definition of "upper facial projection" used by May and Sheffer (1999), although their measurement was made between nasion and the "anterior base point," defined as the anterior end of the cribriform plate. Moreover, these two measurements differ in terms of the planes to which they are registered. Whereas Lieberman and colleagues measured facial projection perpendicular to the PM Plane, May and Sheffer (1999) measured "upper facial projection" parallel to a

line drawn between tuberculum sella and the anterior base point. Although these two definitions differ in terms of the specific landmarks that were employed and the planes used to register measurements, both describe the separation between the upper face and the anterior cranial base. Data do not currently exist with which the effect of these methodological differences can be judged.

The second metric definition of facial projection was used by Ravosa (1988; 1991a, b) to test competing models of brow ridge size in primates. This variable is not termed "facial projection"; instead it was named "anterior orbital axis length." Regardless, this variable describes the anteroposterior position of the upper face relative to the anterior cranial base, as it measures the degree to which the bony orbits extend anteriorly beyond the anteriormost limit of the anterior cranial fossa (see Fig. 2.3). Specifically, an isosceles triangle (triangle ABC) represents the orbit in lateral view and in two dimensions, with the unequal vertex located at the orbital aperture of the optic canal (point A). The equal sides of this triangle have endpoints on the superior and inferior orbital borders (points B and C, respectively), and have lengths equal to the distance between orbital aperture of the optic canal and the intersection of the superior orbital border with the anterior cranial fossa (point A). The unequal side of this triangle (line segment BC) is referred to as the orbital plane, and the anterior orbital axis (AOA) is defined as a line perpendicular to, and bisecting, the orbital plane and continuing anteriorly to the point where it intersects a line orthogonal to it, drawn from the most anterior point on the inferior orbital border.

Ravosa (1988; 1991a, b) showed that AOA length is positively correlated with anteroposterior brow ridge thickness in anthropoid primates (see also Shea, 1985; Shea,

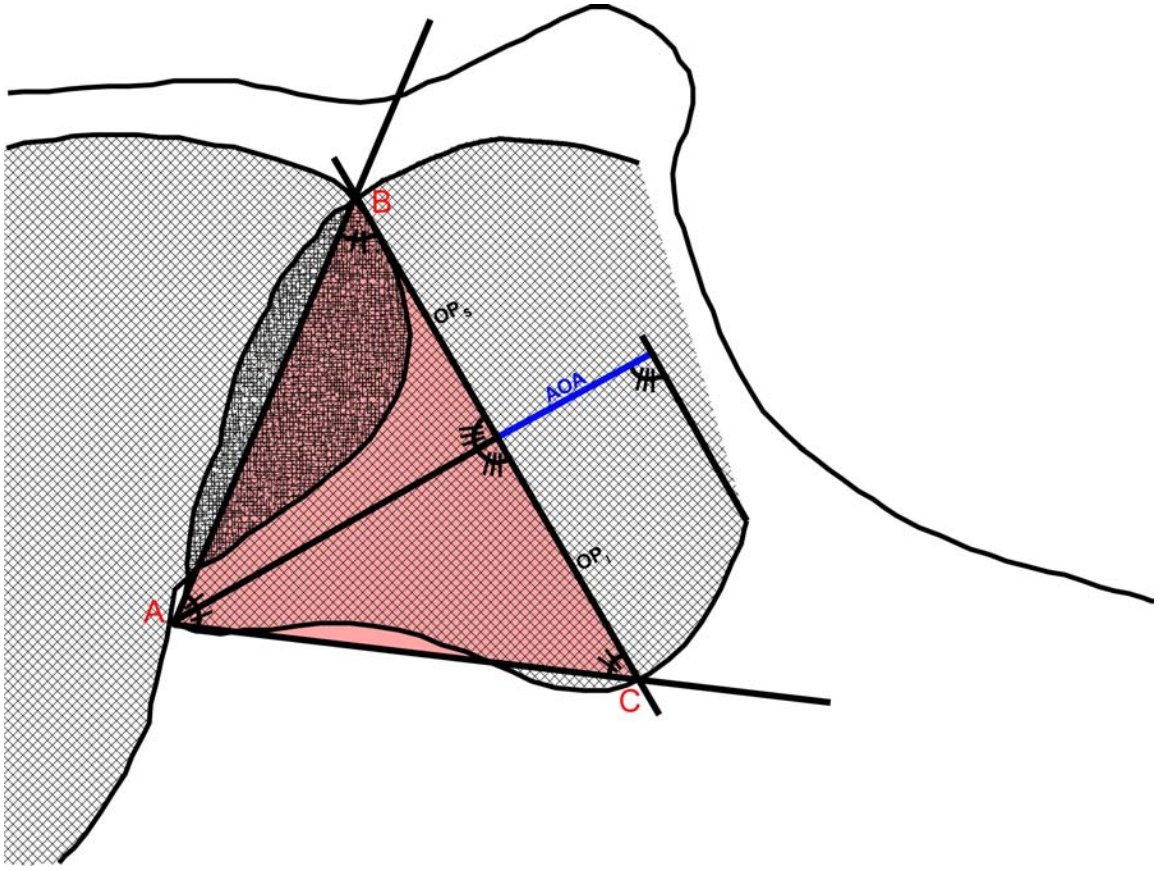

Fig. 2.3. Illustration of the anterior orbital axis (AOA) length. The isosceles triangle (triangle ABC) depicting the orbit is shown in semi-transparent red. The equal sides of this triangle (line segments AB and AC) extend to the margins inferior and superior orbits, respectively, and each has a length equal to the distance between the orbital aperture of the optic canal (point A) and the intersection of the anterior cranial fossa and the superior orbital border (point B). The unequal side of this triangle is defined as the optic plane, which can be divided into superior (OP_S) and inferior segments (OP_I). The anterior orbital axis (AOA), shown in blue, bisects the optic plane and continues anteriorly to the point at which it intersects a line orthogonal to it and drawn from the most anterior point on the inferior orbital border.

1986). These results therefore demonstrated that the degree of facial projection, as measured using AOA, is associated with brow ridge size in anthropoids. Specifically, species with greater degrees of facial projection (i.e., with a larger spatial separation between the upper face and anterior cranial base) possess anteroposteriorly longer supraorbital tori because the form of these structures stems from their roles as anatomical "bridges" between the upper face and anterior cranial base (Shea, 1985; Shea, 1986; Ravosa, 1988; Ravosa, 1991a, b).

FACIAL PROJECTION AND THE HOMININ FOSSIL RECORD

Owing to the lack of sufficiently complete fossil crania, relatively little research has been conducted investigating variation in facial projection in early hominins. However, a large amount of research on this subject has been conducted on later hominin species. This research has focused on the extremely low degree of facial projection in *Homo sapiens* (Lieberman, 1995, 1998, 2008, 2011). Specifically, in *Homo sapiens*, the upper face lies almost entirely beneath the anterior cranial fossa (Weidenreich, 1941; Weidenreich, 1947; Moss and Young, 1960; Lieberman, 1995, 1998, 2008, 2011; May and Sheffer, 1999; Spoor et al., 1999; Lieberman et al., 2000b, 2004; McBratney-Owen and Lieberman, 2003; Lieberman and Bar-Yosef, 2005). Moreover, this configuration—in which the orbits are nearly completely "tucked under" the neurocranium—is unique among primates, as well as among mammals, wherein upper faces project (to varying degrees) anteriorly from the margin of the anterior cranial fossa (Weidenreich, 1941; Weidenreich, 1947; McBratney-Owen and Lieberman, 2003).

Due to its apparent uniqueness among primates and mammals, the extreme lack of facial projection in *Homo sapiens* (often referred to as "facial retraction," see above) has

been frequently included in "trait-list" approaches to diagnosing *Homo sapiens* (e.g., Day and Stringer, 1982; Stringer et al., 1984; Groves, 1989; Tattersall, 1992; Lieberman, 1995; Lahr, 1996). In addition, Lieberman and colleagues (Lieberman, 1995, 1998, 2000; Lieberman et al., 2000b) argued that the extreme lack of facial projection, along with neurocranial globularity, are fundamental uniquely-derived features of *Homo sapiens*, arguing that variation in these two features account for many of the differences in overall cranial form between *Homo sapiens* and "archaic" *Homo* species (i.e., *Homo heidelbergensis* and *Homo neanderthalensis*). Moreover, these authors argue that these features underlie other features that have been considered autapomorphies of *Homo sapiens* (e.g., brow ridge size and frontal angle).

Lieberman and colleagues (Lieberman, 1998; Lieberman et al., 2002) tested for differences in facial projection between *Homo sapiens* and other Middle and Late Pleistocene hominin species (Table 2.1). Lieberman (1998) showed that facial projection (measured as the distance from foramen caecum to nasion, see above) in *Homo sapiens* is significantly lower than in samples of *Homo neanderthalensis*, *Homo heidelbergensis*, and *Homo erectus*.[3] Subsequently, Lieberman et al. (2002) performed a similar comparison of facial projection in hominins; however, in this case, the authors compared

[3]The sample of *Homo sapiens* included both Holocene and Pleistocene specimens; however these two groups did not differ significantly in facial projection. The sample of Pleistocene *Homo sapiens* included the following specimens: Cro Magnon I, Obercassel I, Obercassel II Skhul IV, Skhul V, and Abri Patoud. The sample of *Homo neanderthalensis* included the following specimens: La Chapelle aux Saints, La Ferrassie I, Monte Circeo, La Quina V, and Gibraltar I. The sample of *Homo heidelbergensis* included the following specimens: Broken Hill, Petralona, and Steinheim. The sample of *Homo erectus/ergaster* included the following specimens: OH 9 and KNM-ER 3733.

TABLE 2.1. Summary of results of comparisons of facial projection among fossil hominins and Homo sapiens *from Lieberman and colleagues (Lieberman, 1998; Lieberman et al., 2002*

(Lieberman, 1998)

GROUP	Mean Facial Projection (mm.)	St. Dev.
Holocene *Homo sapiens*	14.6	2.4
Pleistocene *Homo sapiens*	16.1	2.1
Homo neanderthalensis	21.4[a]	4.8
Homo heidelbergensis	24.6[a]	10.1
Homo erectus	20.0[a]	1.8

(Lieberman et al., 2002)

GROUP	Mean Size-Corrected Facial Projection	St. Dev.	Range
Holocene *Homo sapiens*	0.40	0.04	0.32 - 0.48
Pleistocene *Homo sapiens*	0.46	0.04	0.42 - 0.49
"archaic *Homo*"	0.56[a]	0.03	0.51 - 0.58

[a] Denotes samples that are significantly different from the combined *Homo sapiens* sample

size-corrected values of facial projection. Size-correction was achieved by dividing values of facial projection by a geometric mean of facial and neurocranial dimensions. The results showed a significant difference in size-corrected facial projection between *Homo sapiens* and "archaic *Homo*." Interestingly, Lieberman et al., (2002) observed no overlap in the ranges of facial projection for *Homo sapiens* and "archaic *Homo*" (see Table 2.1). Taken together, these results suggest that, whether size-corrected or raw measurements are employed, *Homo sapiens* is distinct from *Homo heidelbergensis* and *Homo erectus*/*ergaster* in possessing a very low degree of facial projection.

What is clear from this review is that relative to all other hominin species (as well as compared to other primates and mammals, see above), *Homo sapiens* is unique in possessing a very low degree of facial projection, and the condition in *Homo sapiens*—in which the upper face is positioned almost entirely beneath, rather than in front of, the anterior cranial base—is similarly unique.

As discussed in further detail below, many of the explanations for variation in facial projection in anthropoids invoke changes in the anatomy of the brain that are

reflected in the cranial base and also have effects on facial positioning. Therefore it is important to briefly discuss what is currently known about hominin brain evolution. Although a vast literature on this subject exists (e.g., Tobias, 1967; Holloway, 1975, 1981, 1988; Falk, 1985, 1987; Falk and Conroy, 1983; Falk et al., 2000), this review will focus on Middle-Late Pleistocene brain evolution, as this is the period during which the most dramatic changes in facial projection occurred.

Most discussions of brain evolution in later hominins are centered on comparisons of endocasts representing *Homo sapiens* and *Homo neanderthalensis*. Such studies suggested that, compared to *Homo neanderthalensis*, *Homo sapiens* is characterized by an enlargement of the parietal and occipital lobes (Bruner et al., 2003; Bruner, 2004; Bruner, 2008). Other species in the genus *Homo* (i.e., *Homo erectus*/*ergaster*, *Homo heidelbergensis*, and *Homo neanderthalensis*), on the other hand, possess relatively shorter and flatter—and thus smaller—parietal lobes (Bruner et al., 2003; Bruner, 2004, 2008). *Homo sapiens* also possesses temporal poles (i.e., the most anteriorly projecting aspects on the temporal lobes) that are positioned more anteriorly than in *Homo neanderthalensis* (Bastir et al., 2008, 2011). However, it should be noted that this inference is based on the morphology of the middle cranial fossae, rather than observations from endocasts.

Comparisons of brain anatomy between *Homo sapiens* and living great apes can also inform some of the noteworthy, derived features of the modern human brain. Most aspects of the human neocortex (i.e., the part of the cerebral cortex that covers the two cerebral hemispheres) are allometrically scaled versions of apes' neocortices (Semendeferi et al., 2002; Bush and Allman, 2004; Rilling, 2006; Conroy and Smith,

2007; see also Smaers and Soligo, 2013). However, there are deviations from this general pattern. The occipital lobes and cerebellum in *Homo sapiens*, for example, are relatively smaller than in apes; the decrease in size of the occipital lobe is thought to be related to the relative increase in the size of the parietal lobes (Bruner et al., 2003; Holloway et al., 2003; Rilling, 2006; Aldridge, 2011). Notably, the temporal lobe in *Homo sapiens* is as much as 25% larger than in great apes (Semendeferi et al., 2001; Rilling and Seligman, 2002; Rilling, 2006; Aldridge, 2011). If this increase in size is associated with elongation of the anterior portion of the temporal lobes, it may also accord with differences between *Homo sapiens* and *Homo neanderthalensis* in the position of the temporal poles (Bastir et al., 2008; Lieberman, 2008). It is also worth noting that the increase in relative temporal lobe size in *Homo sapiens*, compared to the great apes, is largely due to increases in the amount of white matter, which may suggest that *Homo sapiens* possesses a greater number of neuronal connections in the temporal lobe (Schenker et al., 2005; Rilling, 2006).

KEY PRINCIPLES OF ANTHROPOID CRANIOFACIAL ARCHITECTURE

This section outlines five important principles related to craniofacial architecture in anthropoid primates. It is important to note that the discussion that follows is not meant to be an exhaustive survey of all the critical principles underlying anthropoid cranial morphology. Instead, only those principles that are of direct relevance to understanding previous research on facial projection are reviewed. To that end, each principle is discussed with special attention paid to the bearing it has on previously suggested explanations for variation in facial projection in anthropoid primates. These explanations will then be presented in the succeeding section.

The Functional Matrix Hypothesis

The functional matrix hypothesis (FMH) suggests that the primary causes of skeletal form are functional matrices (FMs), which are composed of soft tissues and associated spaces (e.g., the muscles and spaces associated with the nasopharynx) (van der Klaauw, 1948-1952; Moss and Young, 1960; Moss and Salentijn, 1969a, b). The FMH proposes that, in the skull, there are a few fundamental matrices, each of which is related to a specific function (e.g., vision, olfaction, hearing, balance, digestion, swallowing, and chewing) (Moss, 1968, 1997c, d). These matrices are considered to be independent of one another, are "genetically determined and functionally maintained" (Moss, 1968: 69), and control the form and position of the associated skeletal elements (Moss, 1968, 1971, 1981, 1997c, d). The growth and development of the craniofacial skeleton, therefore, results from epigenetic responses to the growth of soft tissue and other stimuli (Moss, 1968, 1971, 1981, 1997c, d). In this way, the FMH predicts that growth and development of the bony aspects of the skull are "secondary" and "compensatory" responses to the growth and development of the associated FMs (Moss, 1997a).

The relevance of the FMH to explanations of variation in facial projection in anthropoids stems from the fact that, as mentioned above, many of these explanations invoke changes in the anatomy of the brain as ultimate causes for variation in facial projection. Specifically, the FMH proposes that the skeletal tissues surrounding the brain are thought to develop as a secondary response to the growth and development of the brain capsule, which includes the brain and associated meninges (Moss, 1968, 1971, 1981, 1997b, c, d; Moss and Salentijn, 1969a). Thus, the FMH asserts that, insofar as variation in the cranial base is related to variation in facial projection, the ultimate

explanation for variation in facial projection is variation in the anatomy of the brain and associated soft tissues.

These predictions of the FMH received some support from studies of cranial abnormalities and experimental investigations of laboratory animals whose brains had been modified to increase or decrease the sizes of certain parts of the brain. The majority of these studies (e.g., Moss, 1954; Moss and Young, 1960; Mooney and Siegel, 2002; see also Young, 1959; Richtsmeier et al., 2006) focused on the neurocranial vault, and showed that the size and shape of the neurocranium is in part a secondary consequence of the development of the brain. Research also showed that experimental changes in brain anatomy of laboratory mice and rats can affect the bony anatomy of the cranial base, which supports the idea that the FM associated with the brain exerts an influence on the morphology of the neurocranium and cranial base (see also Moss, 1975; Boughner et al., 2008).

Despite the support it has received from experimental studies and investigations of cranial anomalies, the FMH has also been criticized. Particularly, the argument that skeletal tissues are controlled solely by the FMs with which they are associated (i.e., they are not regulated by genes) is likely an overstatement, as all bones likely possess some intrinsic growth potential independent of the associated FMs (Lieberman, 2011; see also Hall, 2005; Marcucio et al., 2011). In addition, some evidence (Scott, 1956; van Limborg, 1970; but see Moss and Rankow, 1968; Moss and Salentijn, 1969b) suggests that the growth of skeletal tissues actually influences the growth of some FMs, contrary to the predictions of the FMH. Finally, research showed that most bones participate in more than one FM, which is reflected in significant correlation between bones in different

FMs (Cheverud, 1982, 1989, 1995; Zelditch, 1988; Zelditch and Carmichael, 1989; Zelditch et al., 1990; Zelditch and Fink, 1995; Zelditch et al., 1995; Hallgrimsson et al., 2007; see also Martinez-Abadias et al., 2012). These results suggested that individual FMs may not be as independent as suggested by the FMH.

The Part-Counterpart Principle

Another important principle that predicts the manner in which the soft tissues in the skull interact with bony tissues (and the way that different parts of the skull are interrelated) is the Part-Counterpart Principle (PCP). Proposed by Enlow and colleagues (Enlow et al., 1971, 1975; Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow, 1990; Enlow and Hans, 1996), the PCP suggests that the skull comprises a series of parts whose growth and development corresponds to specific counterparts. In particular, the PCP suggests that specific parts of the brain (and the surrounding sense organs) constrain the form of the nasomaxillary complex via the cranial base, which shares boundaries with both regions (Enlow et al., 1971, 1975; Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow, 1990; Enlow and Hans, 1996). For example, the frontal lobe, which is positioned superior to the anterior cranial fossa, is thought to have a strong influence on the form of the nasomaxillary complex. Moreover, because of their structural association on opposite sides of the anterior cranial fossa, the anterior nasomaxillary complex and the frontal lobes form a part-counterpart pair according to the PCP (see Fig. 2.4). Likewise, the temporal lobes are thought to influence the shape and size of the oropharyngeal airway, and the nasopharynx and mandibular ramus are considered counterparts to the temporal lobes, based on their positions on opposite sides

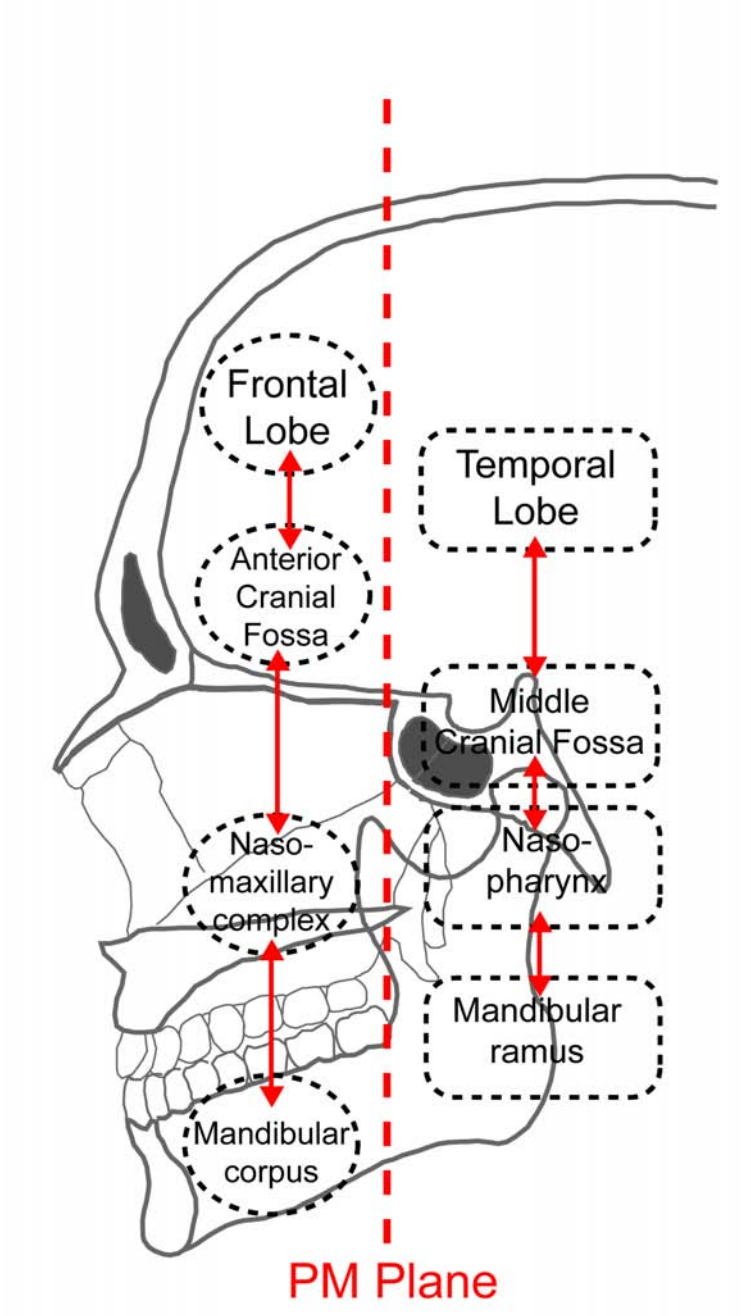

Figure 2.4. Schematic view of the part-counterpart principle. There are two sets of part-counterpart sets—i.e., one anterior to the Posterior PM Plane (the parts/counterparts in this set are depicted by ovals) and one posterior to the PM Plane (the parts/counterparts in this set are depicted by rounded rectangles). Within each set, each unit (e.g., frontal lobe, anterior cranial fossa, temporal lobe) forms a part-counterpart pair with the unit to which it is connected by a double-headed, red arrow. Either unit in each pair can be referred to as a "part" or a "counterpart"—i.e., parts and counterparts are interchangeable. Adapted from Lieberman (2011).

of the middle cranial fossa (Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow et al., 1975; see also Bastir and Rosas, 2005).

Another key part of the PCP is the PM Plane (Fig. 2.5). The PM Plane is a line[4] that describes the posterior margin of the facial skeleton in the midline (Lieberman, 2011). The PM Plane is determined on radiographs by connecting two points: (1) the midpoint of the anterior-most points of the greater wings of the sphenoid on the left and right sides (which are typically offset in lateral radiographs) and (2) the midpoint of the most postero-inferior point on the left and right maxillary tuberosities (which are also typically offset in lateral radiographs) (Enlow et al., 1971; Enlow and Moyers, 1971; Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow, 1990; McCarthy and Lieberman, 2001). Thus, this line forms the border between two compartments: the anterior compartment (which includes the anterior part of the frontal lobe, the anterior cranial fossa, the eyeballs and orbits, the nasomaxillary complex and palate, and the oral cavity and mandibular corpus) and the posterior compartment (which includes the anterior portion of the temporal lobes, middle cranial fossa, nasopharynx, oropharynx, and mandibular ramus). Therefore, the PM Plane forms the boundary between the anterior and middle cranial fossae, as well as the boundary between the middle cranial fossa and the nasomaxillary complex.

These relationships are relevant to understanding variation in facial projection in anthropoids because they dictate that changes in the orientation of the PM Plane will cause concomitant changes in the orientation of the NHA to maintain their perpendicular

[4] As pointed out by McCarthy and Lieberman (2001), the PM Plane is not technically a plane at all. Rather it is a line that connects a superior point (i.e., the anterior-most extent of the greater wings of the sphenoid) and an inferior point (i.e., the most postero-inferior point on the maxillary tuberosities).

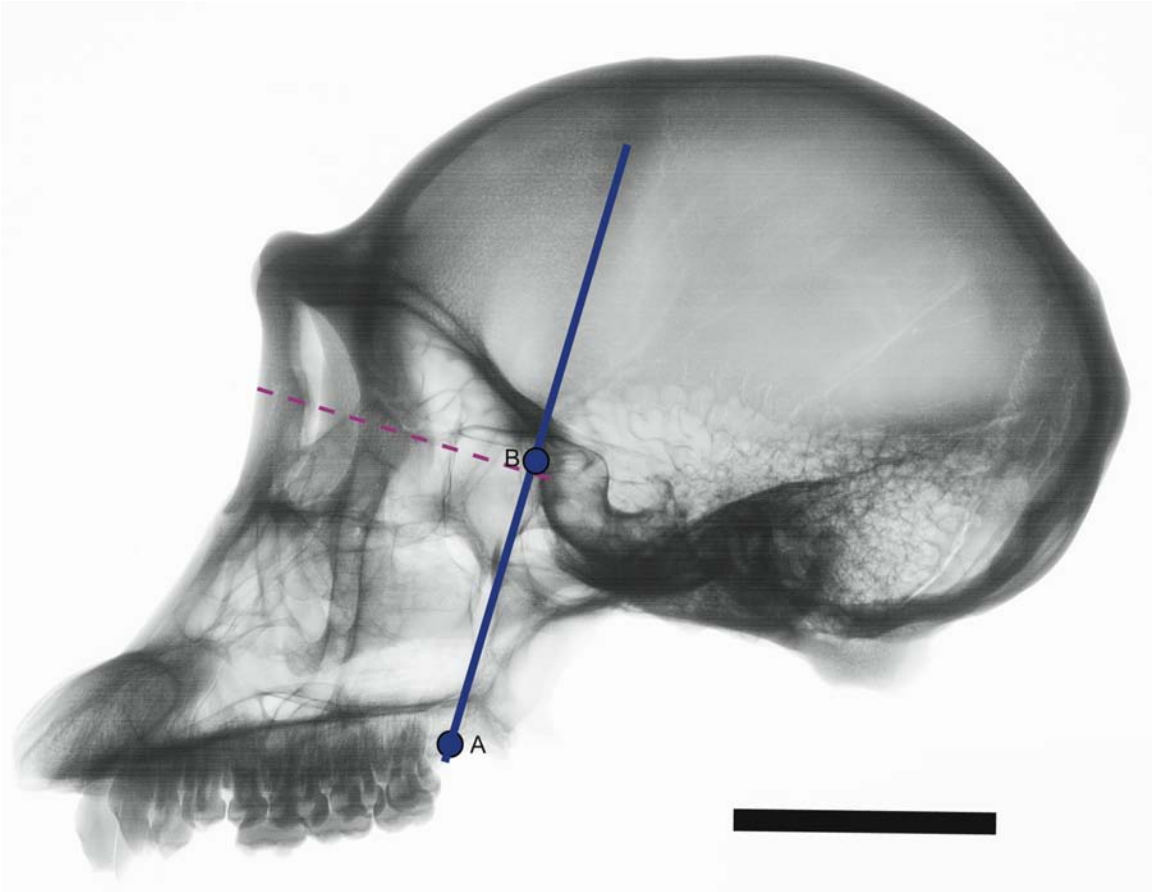

Figure 2.5. The PM Plane. The PM Pane is depicted by the solid, blue line. A: the average of the most postero-inferior point on the left and right maxillary tuberosities; B: the average of the anterior-most extent of the greater wings of the sphenoid on the left and right sides. Scale bar is 40 mm. The PM Plane reflects an important constraint to craniofacial architecture in primates in that it always lies nearly perpendicular to the Neutral Horizontal Axis (NHA; depicted by the dotted, pink line), which describes the orientation of the orbits (i.e., the center axis of the bony orbits, modeled as cones) (Enlow and Azuma, 1975; Enlow, 1990; McCarthy and Lieberman, 2001). Specifically, McCarthy and Lieberman (2001; see also Bromage, 1992) showed that in anthropoids, the mean angle between the PM Plane and the NHA is 90.0°, with a standard deviation of 0.38°. The PM Plane maintains a relatively invariant relationship with the floor of the anterior cranial fossa. In particular, the PM Plane and the floor of the anterior cranial fossa always form an angle of 5° or less (Lieberman, 2001).

relationship. In addition, changes in the orientation of the NHA will require corresponding changes in the orientation of the anterior cranial base to maintain the relationship between the NHA and the floor of the anterior cranial base. These observations led Lieberman and colleagues (Lieberman et al., 2000b; McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003; Lieberman, 2011, 2000) to propose the existence of a "facial block" (consisting of the entire facial skeleton, as defined here).[5] Specifically, these authors argued that, because the floor of the anterior cranial fossa forms the roof of the facial skeleton and the PM Plane forms the posterior margin of the facial skeleton, the whole facial skeleton forms a block (i.e., the "facial block") that, together with the anterior cranial base, rotates dorsally or ventrally as a unit (Lieberman et al., 2000b; McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003; Lieberman, 2011). The axis of rotation of the facial block, these authors argued, lies near the junction of the middle cranial fossa and the facial skeleton, approximately at the anterior-most point on the greater wings of the sphenoid.

Therefore, according to the facial block hypothesis, dorsal or ventral rotation of the NHA will cause associated rotation of the PM Plane; correspondingly, rotation of the PM Plane requires equivalent rotation of the NHA (Lieberman, 2000, 2011; Lieberman et al., 2000; McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003; see also Ravosa, 1988; Bastir et al., 2008). Additionally, rotation of the anterior cranial base (e.g., what occurs when CBA increases or decreases, see below) will cause concordant

[5] The fact that the face (as well as the neurocranium and basicranium) represent semi-independent units has been corroborated by research that showed that the patterns of covariation of these three units is partially independent (see Cheverud, 1982, 1988, 1995, 1996; Marroig and Cheverud, 2001; Strait, 2001; Gonzalez-Jose et al., 2004; Ackermann, 2005; Bastir and Rosas, 2005; Hallgrimsson et al., 2007)

rotation in the NHA (and consequently the PM Plane), and vice-versa (Fig. 2.6). The linkage of the NHA, PM Plane, and the floor of the anterior cranial fossa suggested by the facial block hypothesis is critically important to many explanations of variation in facial projection in anthropoids (see below).

Midline and Lateral Basicranial Structures

Research has shown that midline and lateral elements of the cranial base are relatively independent and each can have independent effects on the form and/or position of the facial skeleton (Seidler et al., 1997; Baba et al., 2003; Bastir and Rosas, 2005, 2006; Bastir et al., 2006, 2008, 2011; Neaux et al., 2013). Bastir and Rosas (2006), for example, showed that in *Homo sapiens*, the morphology of the lateral cranial base explains variation in the size, shape, and position of the facial skeleton better than does the midline cranial base. In addition, elements of the midline and lateral cranial base in *Homo sapiens* are only loosely integrated with one another (Bastir and Rosas, 2005), as Bastir et al. (2006) showed that these elements are not closely linked during ontogeny in *Homo sapiens*. Similar results were found in comparisons of *Homo sapiens* and *Pan troglodytes* (Neaux et al., 2013). Specifically, these results showed that, in both species, the lateral basicranium is more closely linked to variation in facial morphology and that the lateral and midline cranial base are not closely correlated. This relative dissociation between the lateral and midline cranial base and the more or less independent effect each has on the morphology of the facial skeleton is important to explanations of facial projection because it suggests that the lateral basicranium may be more important than the midline basicranium in explaining to overall variation in facial morphology in some anthropoid species. However, the relative effects of these two aspects of the cranial base

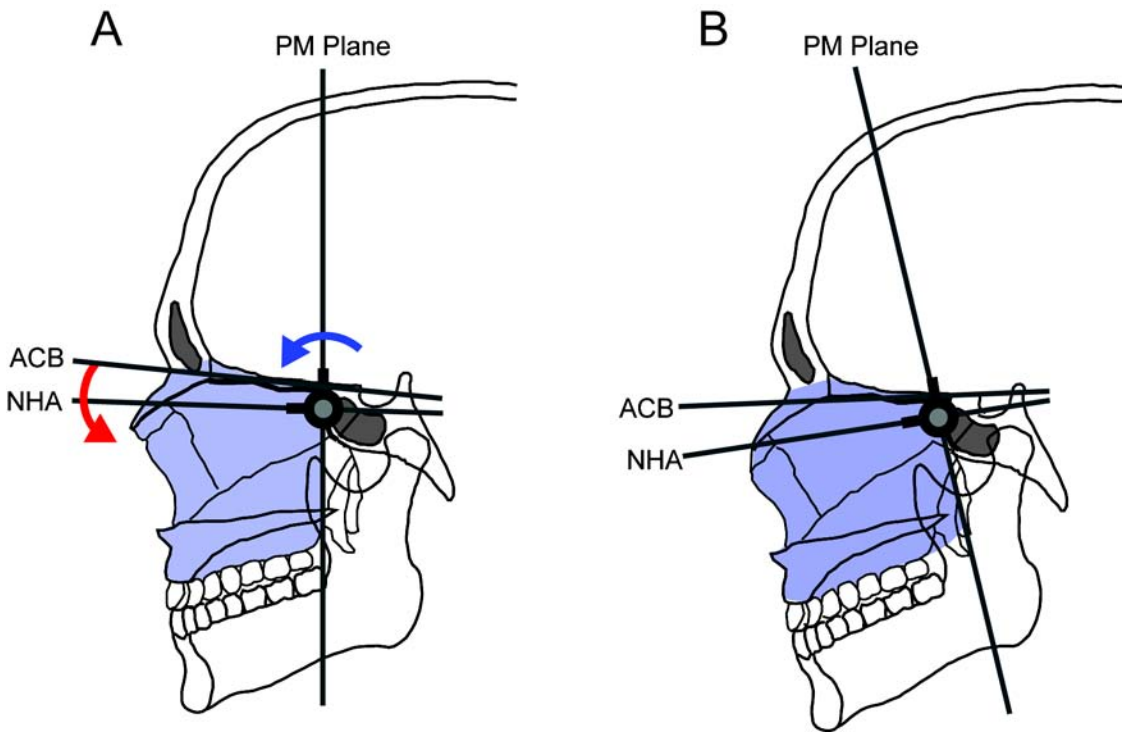

Figure 2.6. Visual depiction of the relationship between the NHA, PM Plane, and anterior cranial base predicted by the facial block hypothesis. A: The original positions of the PM Plane, anterior cranial base (ACB) and Neutral Horizontal Axis (NAH) with the directions of rotation indicated. B: The rotated positions of the PM Plane, ACB, and NHA. The blue shaded areas are the "facial blocks" in the respective drawings. Note that such rotation can be initiated by rotation of the PM Plane, ACB, or NHA (i.e., by the rotation shown in blue or the rotation shown in red); rotations in the opposite direction are also possible. The thick, grey-centered black circle with line segments extending onto the NHA and PM Plane is the axis of rotation around which the facial block is argued to rotate. Adapted from Lieberman (2011) and McCarthy and Lieberman (2001).

on facial morphology in all anthropoid primates, and, more importantly, the specific effects that each has on variation in facial projection is not currently known.

Craniofacial Growth and Development

An understanding of craniofacial growth and development—particularly the ontogeny of the facial skeleton and anterior cranial base—can provide important insights about the processes that produce variation in facial projection in anthropoid primates. The skull grows from three semi-independent units (i.e., the neurocranium, face, and basicranium) (de Beer, 1937; Moss and Young, 1960; Enlow, 1968, 1990; Cheverud, 1982; Schilling and Thorogood, 2000; Sperber, 2001), and, in the context of the present study, it is particularly important to understand the interrelationships of these three units during ontogeny. The growth of the neurocranium and cranial base, which grow via intramembranous and endochondral ossification, respectively, correspond closely with the growth of the brain, and growth of these parts of the cranium is faster than the growth of the facial skeleton (Lieberman et al., 2000a; Sperber, 2001). The facial skeleton, on the other hand, grows via intramembranous ossification, corresponding more closely with skeletal growth and continues to grow anteriorly and inferiorly from the cranial base after growth of the neurocranium and cranial base have ceased (Biegert, 1957; Enlow, 1966; Enlow, 1968; Moore and Lavelle, 1974; Richtsmeier et al., 1993; Lieberman et al., 2000b; O'Higgins et al., 2001).

The degree of facial projection exhibited in adults, then, is determined by the degree to which the facial skeleton grows forward of the anterior cranial fossa. Some of the anterior growth of the facial skeleton is due to growth in other parts of the facial skeleton (in particular, at the maxillary tuberosities). This growth causes the whole facial

skeleton to migrate anteriorly relative to the middle cranial fossa. In the upper face, growth also occurs through the process of a drift (i.e., the movement of a wall of bone relative to other parts via deposition on one surface and resorption on the opposing surface [Lieberman, 2011]). Specifically, the anterior surface of the frontal bone is a depository field, whereas the opposing surface is a resorptive field (Duterloo and Enlow, 1970), causing the anterior surface of the frontal bone (including the supraorbital portion) to drift anteriorly, independent of the opposite surface on the inner table, which remains attached to the frontal lobe.

Cranial Base Angle

Cranial base angle (CBA)—i.e., the angle that describes the orientation of the anterior, middle, and posterior cranial fossae relative to one another in the midsagittal plane (Lieberman, 2011)—is an important component of overall cranial variation in primates, and, in particular, has been argued to play an important role in modulating variation in facial projection (Lieberman, 1998, 2011; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003). The best-supported explanation for variation in CBA is that decreases in CBA increases the space available in the cranium for the brain, accommodating increases in relative brain size without increasing the overall size of the neurocranium (Cameron, 1924, 1925, 1926; Biegert, 1957, 1963; Gould, 1977).

This idea—termed the "spatial packing hypothesis"—has been supported in broad taxonomic examinations of haplorrhines (Ross and Ravosa, 1993), which demonstrated a significant positive correlation between CBA and relative brain size (i.e., the index of relative encephalization [IRE], which is calculated as the cube-root of neurocranial volume divided by cranial base length). Ross and Ravosa (1993) found that, in

haplorrhines, the degree of cranial base flexion was significantly positively correlated with the angle of orbital orientation (i.e., the angle formed between the axis of the orbits and the cranial base) and the angle of facial kyphosis (i.e., the angle formed between the floor of the nasal cavity and the cranial base). In other words, they demonstrated that species with smaller CBAs (i.e., more flexed cranial bases) also exhibit more ventrally deflected orbits and midfaces, situating the entire facial skeleton more beneath the anterior cranial base.

The spatial packing hypothesis was also evaluated in hominins (Ross and Henneberg, 1995). Results of this study showed that all hominin species that were measured (*A. africanus*, *Homo ergaster, H. heidelbergensis*, and *H. sapiens*) have more flexed cranial bases than non-hominin primates; however, none of the non-human hominin species differed significantly from *Homo sapiens* in CBA despite relatively large differences in brain size (Ross and Henneberg, 1995). This study also demonstrated that, in *Homo sapiens*, CBA was correlated with both orbital orientation and the angle of facial kyphosis. However, CBA was not correlated with IRE, and orbital orientation and the angle of facial kyphosis were also shown to be uncorrelated. Moreover, results of studies of prenatal ontogenetic series of *Homo sapiens* did not support the predictions of the spatial packing hypothesis, which posits that CBA increases during prenatal ontogeny when relative brain size increases (Jeffery, 1999, 2002, 2003; Jeffery and Spoor, 2002).

It has also been hypothesized that CBA is related to the size and/or shape of the facial skeleton (Biegert, 1957, 1963; Ross and Ravosa, 1993; Bastir et al., 2006; Rosas et al., 2006; Bastir, 2008; Lieberman et al., 2008). This hypothesis was tested by Biegert (1957), who analyzed ontogenetic and interspecific adults samples of humans and non-

human primates, finding that, in non-human primates, CBA decreased as facial size increased postnatally. These results led Biegert (1957) to formulate a "bi-directional" hypothesis regarding CBA—i.e., that an increase in facial skeleton size relative to brain size will be associated with an increase in CBA, whereas an increase in brain size relative to facial skeleton size will be associated with a decrease in CBA.

Biegert's (1957) bi-directional hypothesis has received mixed support. Ross and Ravosa (1993) found support for this hypothesis in platyrrhines only; there was no significant correlation between relative facial size and CBA in other primate groups. However, Ross and Ravosa (1993) used palate length as a proxy for facial size, ignoring other vertical and transverse dimensions that are important determinants of overall facial skeleton size *sensu* Biegert (1957). Postnatal ontogenetic data in *Homo sapiens*, however, supported the bi-directional hypothesis, demonstrating that during ontogeny, relatively larger facial skeletons are associated with increases in CBA (i.e., less flexed cranial bases). This hypothesis may also explain the results reported above by Jeffery and colleagues (Jeffery, 1999, 2002, 2003; Jeffery and Spoor, 2002), who showed significant correlations between increasing overall body size (which may be a close proxy of facial growth since the facial skeleton grows on a skeletal trajectory, see above) and CBA in fetal samples of *Homo sapiens*.

Biegert's (1957) bi-directional hypothesis was also re-tested by Bastir et al. (2010) in interspecific samples of anthropoid primates using geometric morphometric methods. Their results provided support for the bi-directional hypothesis. Specifically, they showed that CBA is significantly associated with both relative brain size and relative

facial skeleton size (i.e., CBA is negatively correlated with relative brain size and positively correlated with relative facial size).

Experimental data have also been brought to bear on the bi-directional hypothesis. Studies of mutant mice strains (selected to have larger than normal facial skeletons) showed that strains with relatively larger brains or relatively shorter cranial bases have more flexed cranial bases (i.e., lower CBAs) than control strains (Hallgrimsson et al., 2007; Lieberman et al., 2008; see also Lopez et al., 2008). In addition, studies of artificial cranial deformation demonstrated that head-binding practices are associated with significantly decreased CBAs (Anton, 1989; Cheverud et al., 1992; Kohn et al., 1993). This increased flexion is likely due to the fact that head binding restricts anteroposterior and/or mediolateral expansion of the neurocranium as the brain grows; therefore, the cranial base flexes to accommodate the growth of the brain and these artificial constraints on neurocranial growth. Studies of mouse models have corroborated the results of interspecific analyses that showed a correlation between relative facial size and increased CBA. These studies showed that mouse strains with larger facial skeletons have less flexed cranial bases than strains with smaller facial skeletons (Hallgrimsson and Lieberman, 2008; Lieberman et al., 2008).

Although the results described above support the predictions of Biegert's (1957) bi-directional hypothesis, Strait (1999) argued that basicranial length rather than brain size may be driving the correlation between CBA and relative brain size. Noting the well known negatively allometric relationship between body mass and brain size (Weidenreich, 1941; Jerison, 1973; Martin, 1981) and the negatively allometric relationship between body mass and IRE, Strait (1999) questioned why larger-bodied

taxa (which possess relatively smaller brains relative to body size) have the largest values for IRE—i.e., these taxa, although having small brains for their body size, have the most severe spatial-packing problems, based on large values for IRE. The answer, according to Strait (1999), lies in the fact that basicranial length scales with strong negative allometry with body mass. Therefore, the high values for IRE in large-bodied taxa are explained by the evolution of shorter cranial bases rather than phylogenetic increases in brain size. Furthermore, Strait (1999) demonstrated that noncortical elements of the brain (i.e., diencephalon, mesencephalon, and medulla) also scale with strong negative allometry relative to body mass, suggesting that these components of the brain are indirectly responsible for the evolution of cranial base flexion (see also McCarthy, 2001). These results, particularly the suggestion that decreased basicranial length helps to explain increased basicranial flexion in larger-bodied taxa, are germane to studies of human evolution because a relatively short cranial base is a purported synapomorphy of the hominin clade (Kimbel et al., 2004; Kimbel and Rak, 2010; see also Kimbel et al., 2014).

A major issue regarding cranial base flexion in primates is the position of *Homo sapiens* relative to the patterned variation observed in other primates. In particular, Ross and Henneberg (1995) argued that *Homo sapiens* possesses a much less flexed cranial base than expected based on the scaling relationship of CBA and IRE in haplorrhine primates. These authors argued that cranial base flexion is constrained to be greater than 90° because greater flexion than this may restrict the airway and associated structures. In contrast, Spoor (1997) found that *Homo sapiens* does not possess a less flexed cranial base than expected based on its relative brain size.

These different conclusions regarding the position of *Homo sapiens* are due in large part to differences in the methods used to quantify IRE and CBA (McCarthy, 2001). Following Ross and Ravosa (1993), Ross and Henneberg (1995) measured CBA as the angle between the endocranial surface of the basiooociput and the sphenoid plane (see Chapter 4 for a more precise definition of this measurement) and IRE as the cube root of neurocranial volume divided by a measure of cranial base length that does not include the cribriform plate. On the other hand, Spoor (1997) measured CBA as the angle between the posterior cranial base (basion-sella) and the anterior cranial floor (sella-foramen caecum) and IRE as the cube root of neurocranial volume divided by a measure of cranial base length that did include the cribriform plate.

Further investigations have not completely resolved this issue. For example, McCarthy (2001) demonstrated that variation in the methods used to quantify CBA and IRE have profound effects on the position of *Homo sapiens* relative to other anthropoids. Specifically, using Spoor's (1997) measurements of CBA and IRE, *Homo sapiens* does not differ significantly from the predicted value of CBA based on regressions of all anthropoids. Using Ross and Ravosa's (1993) measurements, however, *Homo sapiens* departs significantly from the anthropoid pattern, possessing a significantly more flexed cranial base than expected. This fact, McCarthy (2001) argued, is because compared to other anthropoids, the hominoid sphenoid plane constitutes a relatively smaller proportion of the length of the anterior cranial base, which increases IRE in these taxa. This effect is exaggerated in *Homo sapiens*, which possesses a significantly shorter cranial base than other hominoids when the length of the cribriform is included in the

measure of cranial base length.[6] Differences in how CBA is measured may also effect the position of *Homo sapiens*, despite the fact that the two measures of CBA are significantly correlated. These differences, McCarthy (2001) argued, are due to the anteroposteriorly long dorsum sellae in *Homo sapiens*, which results in more acute CBAs when Spoor's (1997) measurement is employed (see also Lieberman and McCarthy, 1999).

Using phylogenetic comparative analyses and an expanded sample including non-primate mammals, Ross et al. (2004) also failed to resolve the issue regarding *Homo sapiens'* position relative to other primates. Specifically, Ross et al. (2004) argued *Homo sapiens*' cranial base is no more flexed than expected for a descendant of the *Paranthropus-Homo* clade. However, this degree of flexion is less than expected when predicted from the basal hominoid node.

EXPLANATIONS FOR VARIATION IN FACIAL PROJECTION

The most comprehensive model to explain variation in facial projection in anthropoid primates was proposed by Lieberman and colleagues (Lieberman, 2000, 2011; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003). This model (Fig. 2.7), which is based largely on the principles of craniofacial architecture outlined above, describes interactions among five variables that are thought to affect variation in facial projection: (1) anterior cranial base length; (2) upper facial length; (3) cranial base angle; (4) anterior sphenoid length; and (5) anterior middle cranial fossa length.

[6] It should be noted that McCarthy (2001) advocated the use of Spoor's (1997) measurement of cranial base length (and, consequently, his measure of IRE, as well), which includes the cribriform plate. This argument was based on the fact that, in anthropoids, the cribriform plate is parallel or nearly parallel to the sphenoid plane and thus contributes to the overall length of the cranial base (see Baer and Nanda, 1976; Moss and Vilmann, 1978).

According to Lieberman's model, the length of the anterior cranial base (i.e., the distance between sella and foramen caecum) affects facial projection because this length defines the space inferior to which the upper face is situated. With all other variables held constant, relatively longer anterior cranial bases should be associated with decreased facial projection because a greater proportion of the anteroposterior dimension of the upper face (i.e., upper facial length) can fit below the anterior cranial fossa. Thus, when the anterior cranial base is longer, less of the upper face will project anterior to the anterior cranial base, resulting in reduced facial projection. The predicted influence of upper facial length[7] (i.e., the distance between the PM Plane and nasion) on variation in facial projection is related to the effect of anterior cranial base length (see above). In particular, all other variables being equal, the longer the anteroposterior dimension of the upper face is, the more the upper face will project anterior to the anterior cranial base. Thus, increases in the relative upper facial length are predicted to be associated with increases in facial projection.

CBA influences variation in facial projection because, as mentioned above, the base of the anterior cranial base forms the roof of the facial skeleton, and, due to this shared border, the anterior cranial base and the roof of the facial skeleton tend to rotate together as a relatively stable unit (Lieberman, 2000; McCarthy and Lieberman, 2001). Consequently, according to Lieberman's model, increased cranial base flexion (i.e., decrease in values of CBA) causes a concomitant ventral deflection of the upper facial

[7] Lieberman and colleagues (Lieberman, 1998, 2000; McBratney-Owen and Lieberman, 2003; Lieberman et al., 2004) referred to this variable as "mid-facial length." However, because this variable describes the length of the part of the facial skeleton associated with the orbits and periorbital region (i.e., the "upper face" as defined by Bilsborough and Wood [1988]), this measurement is referred to here as "upper facial length."

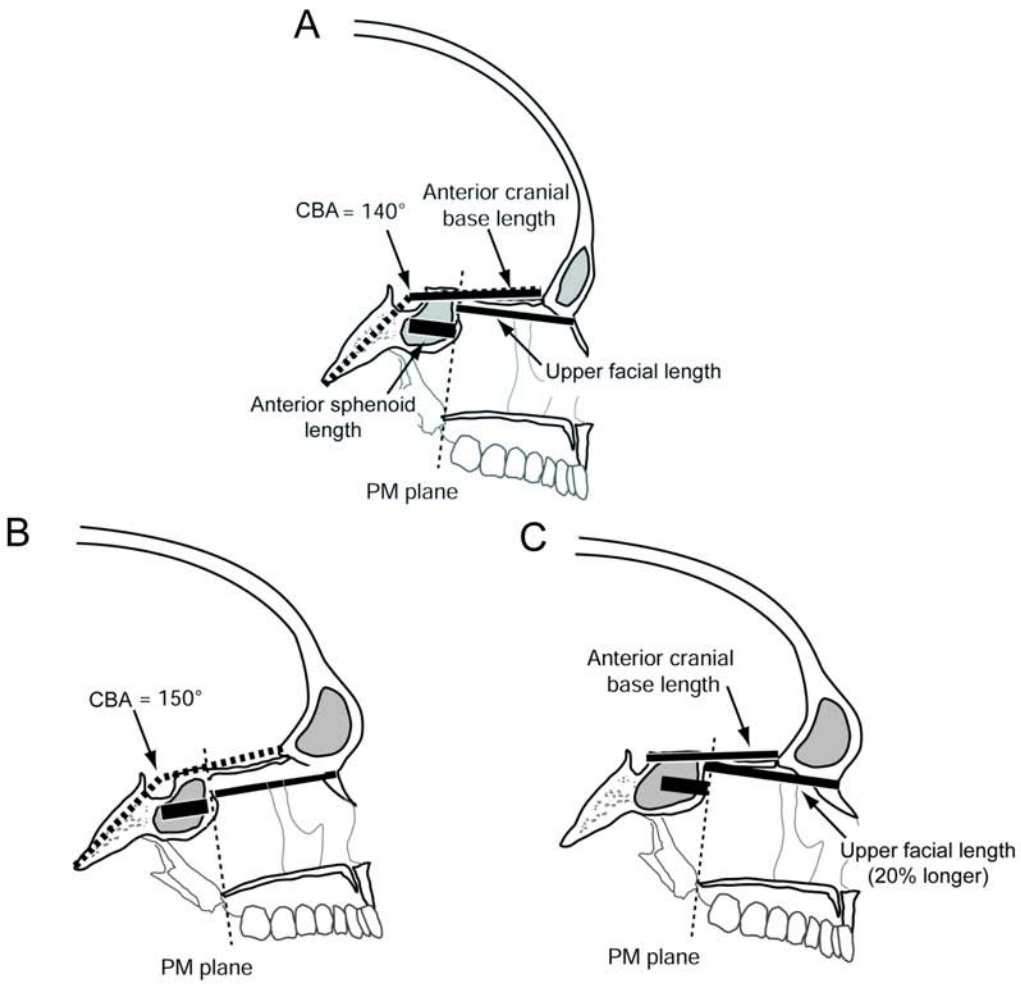

Fig. 2.7. A visual depiction of the model for facial projection proposed by Lieberman and colleagues (Lieberman, 2000, 2011; Lieberman et al., 2000b; McBratney-Owen and Lieberman, 2003). In B, CBA is increased 10° relative to A, resulting in an increase in facial projection. In C, upper facial length is 20% longer than in A, resulting in an increase in facial projection. An increase in the anterior cranial base length (not shown) is predicted to cause a decrease in facial projection. An increase in anterior sphenoid length (not shown) is predicted to cause an increase in facial projection.

facial skeleton, repositioning the upper face to a more posterior position relative to the anterior cranial base (i.e., a decrease in facial projection). Conversely, decreased cranial base flexion (i.e., increase in values of CBA) causes the upper face to be positioned more anteriorly relative to the anterior cranial base (i.e., an increase in facial projection).[8]

In Lieberman's model, anterior sphenoid length (i.e., the distance between sella and the PM Plane in lateral view) is predicted to influence facial projection because this distance determines the position of the PM Plane relative to sella—i.e., an increase in anterior sphenoid length "pushes" the PM Plane anteriorly (Lieberman, 2000). Therefore, when all other variables are held constant and anterior sphenoid length is relatively greater, the PM Plane will be more distant from sella. Because the PM Plane marks the posterior margin of the facial skeleton, facial projection is predicted to increase when anterior sphenoid length increases.

Lieberman and colleagues (Lieberman et al, 2000; McBratney-Owen and Lieberman, 2003) recognized that anterior sphenoid length (as defined above) is actually a measure of the length of the middle cranial fossa anterior to sella. This is because anterior sphenoid length is measured from sella to the PM Plane, which is defined superiorly by the anteriormost point on the greater wing of the sphenoid (see above). Moreover, because the greater wings of the sphenoid are located lateral to the midline of the cranial base, anterior sphenoid length, unlike the variables discussed above, describes the morphology of the lateral basicranium, rather than the midline basicranium.

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[8] Ross (2013) has criticized this part of Lieberman's model. Specifically, Ross (2013) argues that, if the anterior cranial base forms the roofs of the upper face, then flexion of the cranial base will not change the position of the upper face relative to the anterior cranial base. This fact, Ross (2013) argued, is due to the fact that, when cranial base flexion increases, the anterior cranial base and upper face will exhibit the same degree of flexion, and their positions relative to each other will not be affected.

The length of the anterior portion of the middle cranial fossa can also be measured from a superior view. Specifically, Ritzman et al. (2009, 2010) measured this variable on superior radiographs as the distance between sella and the anteriormost margin of the middle cranial fossa and termed this measurement, anterior middle cranial fossa length (Fig. 2.8). This alternate measurement accords more closely with the results of Bastir et al.'s (2010) geometric morphometric comparison of middle cranial fossa morphology in *Homo sapiens* and *Homo neanderthalensis*, which showed that the anteriormost point on the middle cranial fossa in *Homo sapiens* projects further anteriorly relative to sella vis-à-vis *Homo neanderthalensis* (see also, Bastir et al. 2011). Bastir et al. (2010) argued that this difference may help explain the fact that *Homo sapiens* exhibits a lower degree of facial projection than *Homo neanderthalensis*. Specifically, these authors argued that the increase in length of the anterior middle cranial fossa may cause the PM Plane to rotate ventrally (or counterclockwise when viewed from the left), which in turn, causes concomitant rotation of the NHA, resulting in decreased facial projection (see also McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003; Lieberman, 2008; Bastir et al., 2011) (see Figs. 2.6 and 2.8).

It is important to note that lengthening of the anterior portion of the middle cranial fossa can be the result of two processes (or a combination of both): (1) overall lengthening of the middle cranial fossa; (2) an anterior shift in the anterior margin of the middle cranial fossa relative to other structures in the basicranium. In other words, the length of the anterior portion of the middle cranial fossa can be caused by: (1) an overall lengthening of the middle cranial fossa, such that the portion anterior to sella becomes longer, (2) an anterior repositioning of the entire middle cranial fossa without an increase

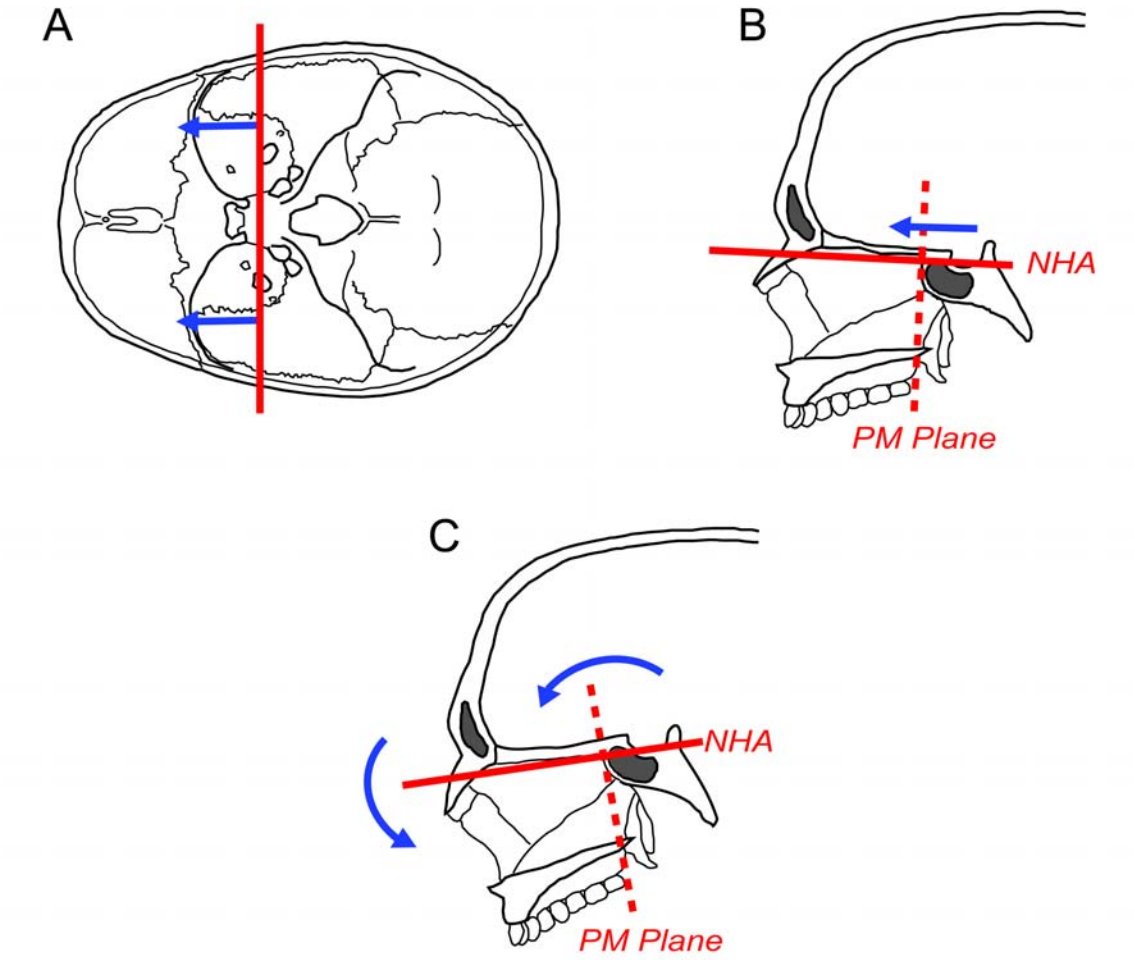


Figure 2.8. Illustration of the affect of anterior middle cranial fossa length on variation in facial projection. A: The blue arrows represent an increase in the length of the anterior portion of the middle cranial fossa. B: Increase in the length of the anterior portion of the middle cranial fossa shown in lateral view. According to this explanation, increase in the length of the anterior portion of the middle cranial fossa causes the PM Plane to rotate ventrally, which, in turn, causes a corresponding ventral rotation of the NHA (shown in C). The ventral rotation of the NHA repositions the upper face more posteriorly relative to the anterior cranial base, resulting in decreased facial projection.

in its length, or (3) a combination of these two processes.

Given the fact that anterior sphenoid length and anterior middle cranial fossa length describe the same anatomical phenomenon, it is somewhat paradoxical that increases in one (i.e., anterior sphenoid length) are predicted to cause increases in facial projection, whereas increases in the other (i.e., anterior middle cranial fossa length) are predicted to cause decreases in facial projection. This apparent paradox stems from the fact that the explanations associated with increases in these two variables vary in terms of the predicted outcome on the PM Plane. In particular, the explanation associated with anterior sphenoid length posits that such an increase will cause the PM Plane to be "pushed" anteriorly without rotation (see above). The explanation associated with anterior middle cranial fossa length, on the other hand, suggests that increases in this length will cause the PM Plane to rotate ventrally. The difference between these explanations is presented in Figure 2.9.

No *a priori* data exist to judge which of these outcomes (if either) results from changes in anterior middle cranial fossa/anterior sphenoid length, and a combination of these two outcomes is also possible. Moreover, because these two measurements are anatomically identical, it follows that changes in either (i.e., increases in anterior sphenoid length or anterior middle cranial fossa length) could result in either outcome (i.e., increased or decreased facial projection). However, as described above, previous researchers have chosen to associate the measurement that is made in lateral view (i.e., anterior sphenoid length) with increases in facial projection and the measurement that is made in superior view (i.e., anterior middle cranial fossa length) with decreases in facial projection. This convention will be followed in the present study.

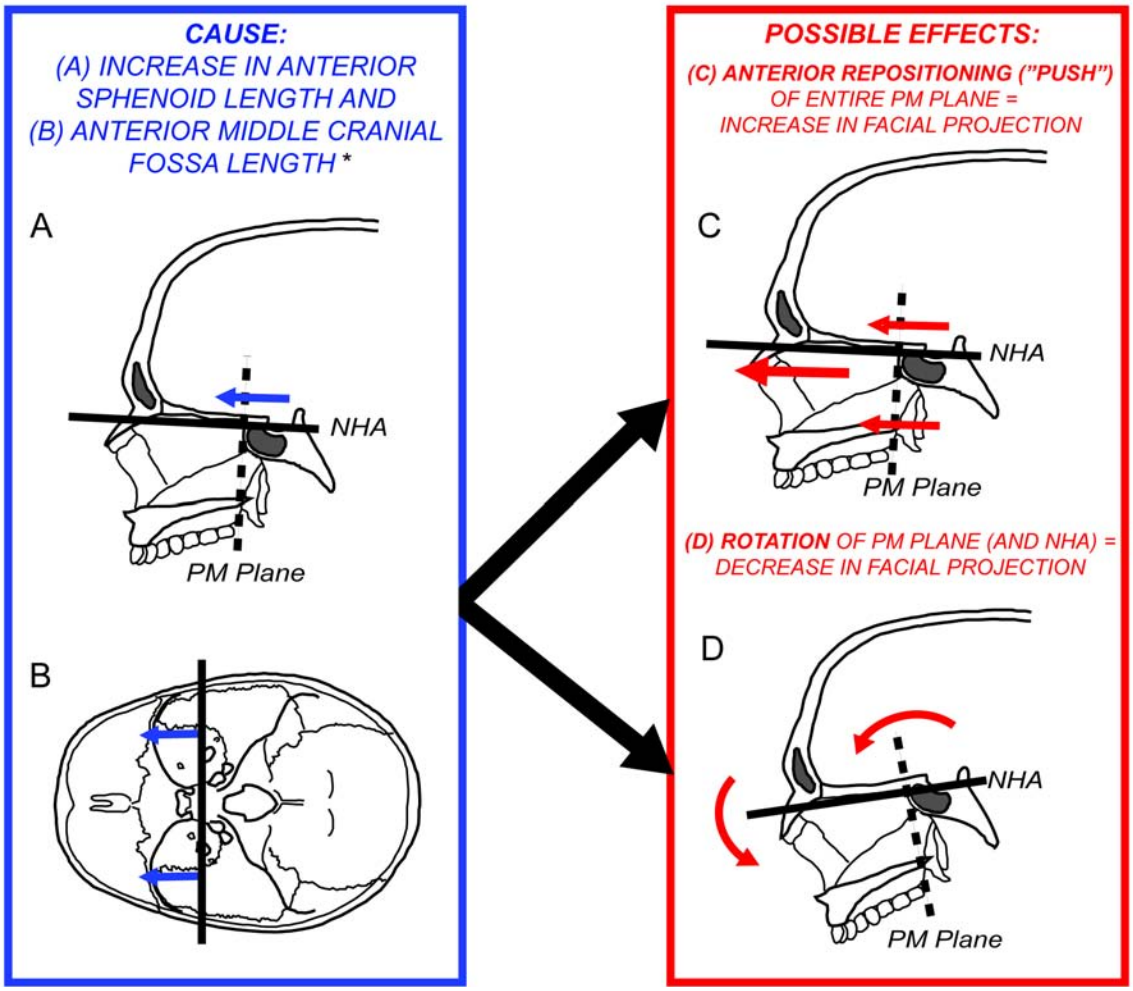


Figure 2.9. Depiction of the two possible outcomes of an increase in anterior sphenoid length/anterior portion of the middle cranial fossa. A: An increase in anterior sphenoid length. B: An increase in the length of the anterior portion of the middle cranial fossa. NOTE: The phenomena depicted in A and B describe the same anatomical phenomenon in different radiographic views (i.e., lateral view in A and superior view in B). C: Depiction of how an increase in anterior sphenoid length/anterior portion of the middle cranial fossa causes the entire PM Plane to be shifted (i.e., "pushed") anteriorly, resulting in an increase in facial projection. D: Depiction of how an increase in anterior sphenoid length/anterior portion of the middle cranial fossa causes the PM Plane to rotate ventrally, which, in turn, causes ventral rotation of the NHA, resulting in a decrease in facial projection.

In sum, Lieberman's model posits that, among the five variables hypothesized to affect variation in facial projection, three (cranial base angle, upper facial length, and anterior sphenoid length) will be positively associated with increased facial projection—i.e., increases in these variables are predicted to cause increases in facial projection. The model posits that the other two variables (anterior cranial base length and anterior middle cranial fossa length), on the other hand, will be associated with decreased facial projection—i.e., increases in these variables are hypothesized to cause decreases in facial projection. Importantly, Lieberman's model stipulates that any of the variables described above can have an influence on variation in facial projection. Moreover, the explanations associated with each of these variables are not mutually exclusive, and it is likely that combinations of these variables act in concert to influence variation in facial projection.

PREVIOUS TESTS OF LIEBERMAN'S MODEL

Lieberman's model has been tested in ontogenetic samples of extant primates as well as the hominin fossil record. Research on ontogenetic samples of *Homo sapiens* and *Pan troglodytes* were aimed at identifying the developmental underpinnings of differences in facial projection between these two species (Lieberman, 2000; McBratney-Owen and Lieberman, 2003). Lieberman (2000) showed that relatively low degrees of facial projection in *Homo sapiens* are primarily due to the fact that this species possesses relatively shorter upper facial skeletons and longer anterior cranial bases throughout ontogeny. That study, however, also showed that anterior cranial base length, upper facial length, anterior sphenoid length, and cranial base angle all have significant independent influences on variation in facial projection during ontogeny in *Homo sapiens*. In *Pan troglodytes*, variation in facial projection is significantly influenced by

the independent effects of all of these variables except anterior cranial base length.[9] McBratney-Owen and Lieberman (2003) further showed that differences between chimpanzees and humans in anterior cranial base length are apparent at all ontogenetic stages, but differences in upper facial length do not appear until the age at which facial growth has ceased (see also Lieberman, 1998).

Lieberman (1998) argued that *Homo sapiens* exhibits an extreme lack of facial because the anterior sphenoid length in this species is shorter compared to *H. erectus*/*ergaster*, *H. heidelbergensis*, and *H. neanderthalensis*. Furthermore, Lieberman (1998) discounted the influence of upper facial length and anterior cranial base length on differences in facial projection between *H. sapiens* and other species in the genus *Homo* because significant differences in these measures were not found between a sample of Pleistocene *Homo sapiens* (i.e., Cro-Magnon I, Obercassel I and II, Skhul IV and V, and Abri Pataud) and the samples of each of the other *Homo* species, respectively.

Lieberman's (1998) results, however, were challenged by Spoor et al. (1999), who found errors in Lieberman's (1998) measurements of anterior sphenoid length. Spoor et al.'s (1999) study, which also included better quality radiographs and computed tomography scans of Gibraltar I and Broken Hill (i.e., *Homo heidelbergensis*), demonstrated that there were no significant differences in anterior sphenoid length between samples of Pleistocene and modern *Homo sapiens* and *Homo heidelbergensis*. That study, therefore, cast substantial doubt on Lieberman's (1998) claim that reduction in anterior sphenoid length underlies the reduction of facial projection in *Homo sapiens*. Instead, Spoor et al. (1999) argued that this reduction likely has a multifactorial basis,

[9] Anterior middle cranial fossa length was not included in this study.

including reduction in the size of the facial skeleton, increased cranial base flexion, and enlargement of the middle cranial fossae (see also, Lieberman et al., 2000a; O'Higgins et al., 2001).

Taken together, the results summarized above suggest that, insofar as the difference between *Pan troglodytes* and *Homo sapiens* represent general trends in anthropoids, intraspecific (i.e., ontogenetic) variation in facial projection is underlain primarily by differences in upper facial length and anterior cranial base length. In addition, these factors seem to explain interspecific differences, at least those between *Homo sapiens* and *Pan troglodytes*. However, these studies do not provide taxonomically-broad data on variation in facial projection (or its proposed causes) in anthropoid primates. Without these data, it is difficult (if not impossible) to identify any general trends in facial projection or in the factors that have been proposed to explain variation in facial projection. Lieberman's (2011) characterization of the explanations for variation in facial projection in early hominins seem to suggest that these explanations are varied and that reduction/increase in facial projection may have different causes in different lineages, despite the fact that these species are closely related. However, as discussed above, it is difficult to contextualize these changes and in the absence of comparative data on variation in facial projection and its proposed causes in anthropoids. Furthermore, owing to the dearth of comparative data on facial projection and its causes, it is difficult to contextualize the extreme lack of facial projection exhibited by *Homo sapiens*. It is this gap in knowledge that this dissertation aims to fill.

A NOTE ON THE USE OF THE COMPARATIVE METHOD

The present study employs a comparative approach to understanding the evolution of extremely reduced facial projection in *Homo sapiens*. Specifically, this dissertation tests hypotheses regarding explanations for variation in facial projection using interspecific samples of adult anthropoid primate species. This approach permits the identification of any apparent patterns in the factors that underlie variation in facial projection in anthropoid primates. Moreover, the comparative approach allows evaluation of the condition in *Homo sapiens* relative to these patterns. In other words, this approach addresses the two research question outlined in Chapter 1 by recognizing potential trends in anthropoid primates and determining whether or not *Homo sapiens* fits any such trends.

Importantly, the comparative approach can also be used to more fully understand the nature of the "uniqueness" of *Homo sapiens* in regards to the extreme reduction in facial projection exhibited by this species. For example, the results of this study may demonstrate that variation in facial projection in the comparative sample of extant primates is explained well by some explanatory variable and that *Homo sapiens* possesses the same relationship between the explanatory variable and facial projection that is evident across the entire sample of anthropoids. In a statistical context, *Homo sapiens* would fall on or near the regression line for the bivariate relationship between the explanatory variable and facial projection, albeit at lower values of facial projection than in the rest of the sample. In this case, the "uniqueness" of *Homo sapiens* is really a difference in degree, rather than a difference of kind. In addition, in this case, it would be reasonable to hypothesize that fossil hominin species also fit the patterns evident in the

comparative sample, indicating that facial projection in these species is also explained by the same factors at work in extant species. On the other hand, if there is a strong pattern in extant anthropoids, but *Homo sapiens* does not fit this pattern, then it is likely that a different set of factors underlies the condition in *Homo sapiens*. In this case, extremely reduced facial projection in *Homo sapiens* can be regarded as a difference in kind rather than degree and would indicate that this condition is truly unique in *Homo sapiens*. Also, in this case, it would not be appropriate to use the patterns apparent in the comparative sample to develop hypotheses about the explanations for variation in facial projection in hominins. Thus, the comparative approach allows the detection of patterns in extant primates as well as the evaluation of the fit of *Homo sapiens* relative to these patterns. Importantly, this approach provides the crucial comparative data that can be used potentially to inform hypotheses about the human fossil record.

CHAPTER 3—MATERIALS AND METHODS

This chapter describes the samples used to test the hypotheses outlined in the previous chapter. Specifically, this chapter provides information about the origin and composition of the samples and details the methods used to collect data from these samples, including metric, radiographic, and geometric morphometric methods. This chapter also discusses the statistical methods employed in this dissertation.

SAMPLES AND TAXA

The 37 anthropoid species, which make up the sample for this dissertation, are listed in Table 3.1. The specimens representing these taxa are housed at the National Museum of Natural History (Smithsonian Institution), Washington D.C. All specimens were adult, based on the full eruption of both mandibular and maxillary third molars,[1] and no visibly pathological specimens were included. Males, females, and specimens of unknown sex were included (sex was based on museum records).

The taxonomy employed in this dissertation followed the taxonomy of Groves (2001), who elevated many taxa previously considered subspecies to full species, including: (1) *Chlorocebus pygerythrus*, which was previously recognized as a subspecies of *Chlorocebus* or *Cercopithecus aethiops*; (2) *Gorilla beringei*, formerly considered a subspecies of *Gorilla gorilla*; and (3) *Pongo abelii*, which had been recognized as a subspecies of *Pongo pygmaeus*.[2]

The composition of this sample was designed to capture as much variation as

[1] M2s were used to judge adulthood in *Saguinus geoffroyi* and *Callicebus torquatus*, which, like all callitrichines except *Callimico goeldii*, lack M3s.
[2] Note that, while *Pongo pygmaeus* is included in the sample for this dissertation, *Pongo abelii* is not, due to the limited number of specimens for *Pongo abelii*. Importantly, specimens representing *Pongo pygmaeus* and *Pongo abelii* were not pooled.

TABLE 3.1. Species included in this study with sample sizes broken down by sex.

	Radiographic Analysis				Geometric Morphometric Analysis			
	M	F	U	TOTAL	M	F	U	TOTAL
PLATYRRHINI								
Alouatta palliata	12	15	4	31	6	10	1	17
Aotus lemurinus	15	15	0	30	13	12	0	25
Ateles geoffroyi	13	14	3	30	10	13	3	26
Cacajao melanocephalus	5*	4	0	9	3	4	0	7
Callicebus torquatus	4	8	3	15	4	8	3	15
Cebus albifrons	15	15	0	30	13	15	0	28
Cebus capucinus	15	15	0	30	14	15	0	29
Chiropotes satanas	7	10	1	18	6	7	1	14
Lagothrix lagotricha	6	6	0	12	6	5	0	11
Leontopithecus rosalia	6	9	3	18	5	9	2	16
Pithecia pithecia	2	2	9	13	0	0	8	8
Saguinus geoffroyi	14	13	0	27	12	12	0	24
Saimiri sciureus	15*	15*	0	30	0	5	1	6
CATARRHINI								
CERCOPITHECOIDEA								
Cercopithecinae								
Cercocebus torquatus	6	5	0	11	6	5	0	11
Cercopithecus mona	3	0	27	30	3	0	26	29
Cercopithecus nictitans	8	3	17	28	8	3	13	24
Chlorocebus pygerythrus	15	15	0	30	15	14	0	29
Erythrocebus patas	5	4	0	9	5	4	0	9
Lophocebus albigena	4	4	0	8	4	3	7	14
Macaca cyclopis	4	7	2	13	4	7	2	13
Macaca nemestrina	8	5*	0	13	6	5	0	11
Miopithecus ogouensis	11	18	1	30	11	18	1	30
Papio anubis	6	1	0	7	6	1	0	7
Papio ursinus	11	5	2	18	10	5	2	17
Colobinae								
Colobus guereza	17	16	3	36	17	10	3	30
Nasalis larvatus	19	9	0	28	18	9	0	27
Piliocolobus badius	5*	15	0	20	4	15	0	19
Pygathrix nemaeus	6	0	0	6	6	0	0	6
Rhinopithecus roxellana	0	5	3	8	0	4	3	7
Trachypithecus cristatus	9	16	0	25	9	14	0	23
HOMINOIDEA								
Gorilla beringei	6	7	0	13*	0	0	0	0
Gorilla gorilla	11	2	0	13*	0	0	0	0
Homo sapiens	14	13	5	32	12	6	5	23
Hylobates lar	10	20	2	32	10	8	2	20
Hylobates muelleri	9	11	0	20	8	10	0	18
Pan troglodytes	6*	11	2	19	0	11	0	11
Pongo pygmaeus	8	5	1	14	0	0	0	0
TOTALS	330	338	88	756	254	267	83	604

possible in facial projection across anthropoid primates. Additionally, no data on facial projection in anthropoids exist. Therefore, no *a priori* targeted pair-wise comparisons could be designed nor could individual clades of interest be identified. Instead, the strategy employed here was to sample widely across anthropoid primates. As shown in Table 3.2, the sample included genera from all anthropoid families and from over two-thirds of all anthropoid genera.

RADIOGRAPHIC METHODS

All specimens were radiographed using the digital radiograph system in the Division of Fishes at the National Museum of Natural History (Smithsonian Institution). The components of the digital radiograph system included a Kevex CU017 x-ray control unit, a Kevex PX S5-724EA x-ray source, a Varian Medical Systems PaxScan 4030 x-ray tablet, and a Varian Medical Systems PaxScan 4030 DC power supply. A Dell Optiplex desktop computer was used to control the digital radiograph system (Fig. 3.1).

The x-ray tablet was balanced with a carpenter's level and was positioned at a distance of 69.2cm from the x-ray source (see Fig. 3.1). Leveling of the x-ray tablet was necessary to minimize errors due parallax and/or obliquity (Merow, 1982; Merow and Broadbent, 1990). To maximize the field of view, smaller specimens were raised towards the x-ray source using a ~15 cm. radio-transparent riser.

Each specimen was radiographed in two views: (1) with the left side of the cranium positioned closest to the x-ray source (hereafter referred to as "lateral" radiographs); and (2) with the superior aspect of the cranium positioned closest to the x-ray source (hereafter referred to as "superior" radiographs) (Fig. 3.2).

TABLE 3.2. Sample divided by family with genera per taxon and total genera.

TAXONOMIC GROUP	GENERA IN SAMPLE/TOTAL GENERA
Anthropoids[a]	31/45
Platyrrhines	12/16
Family Cebidae	4/6
Subfamily Callitrichinae	2/4
Subfamily Cebinae	1/1
Subfamily Saimiriinae	1/1
Family Aotidae	1/1
Family Pithecidae	4/4
Subfamily Callicebinae	1/1
Subfamily Pitheciinae	3/3
Family Atelidae	3/5
Subfamily Alouattinae	1/1
Subfamily Atelinae	2/4
Catarrhines	19/29
Superfamily Cercopithecoidea	
Family Cercopithecidae	14/21
Subfamily Cercopithecinae	8/11
Subfamily Colobinae	6/10
Superfamily Hominoidea	5/8
Family Hylobatidae	1/4
Family Hominidae	4/4

[a]Groves (2001) refers to the taxon containing platyrrhines and catarrhines as the Infraorder Simiiformes; however, the more commonly used term, used term, "anthropoids," was be used in this dissertation instead.

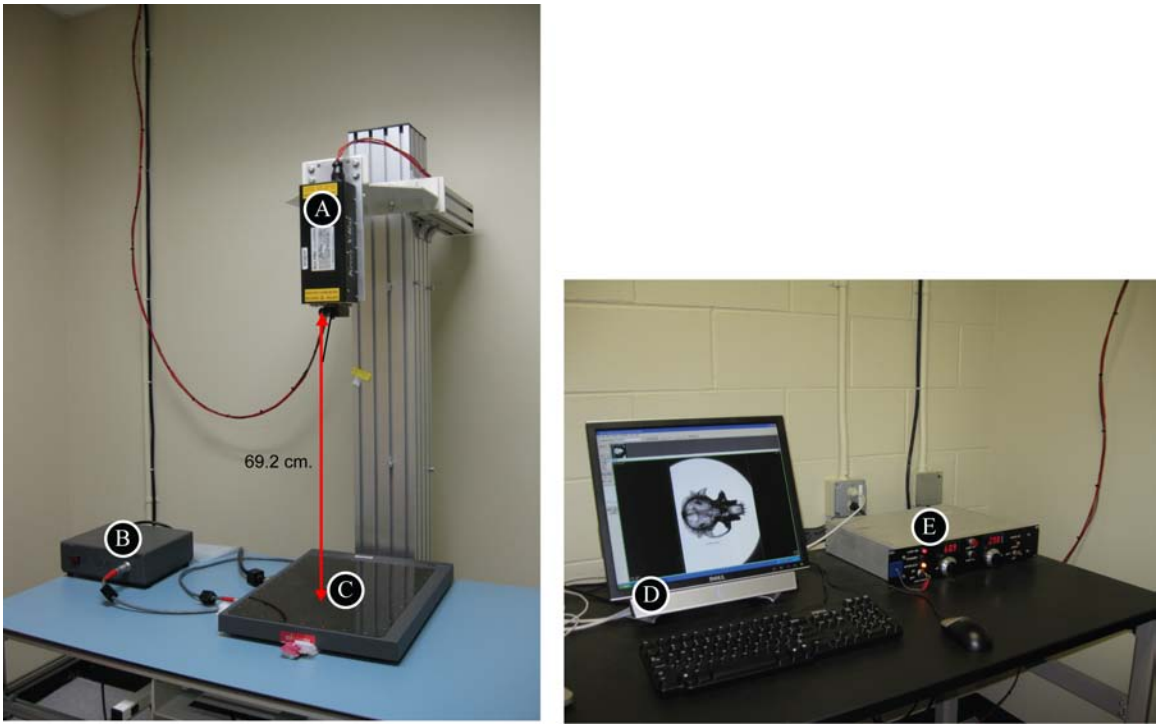


Figure 3.1. Digital radiograph system used in the present study: Kevex PX-724EA x-ray source (A), Varian Medical Systems PaxScan 4030 DC power supply (B), Varian Medical Systems PaxScan 4030 x-ray tablet (C), Dell Optiplex desktop computer (D), Kevex CU017 x-ray control unit (E). The distance between the x-ray tablet and the x-ray source (shown in red) was 69.2 cm. (see text for further details).

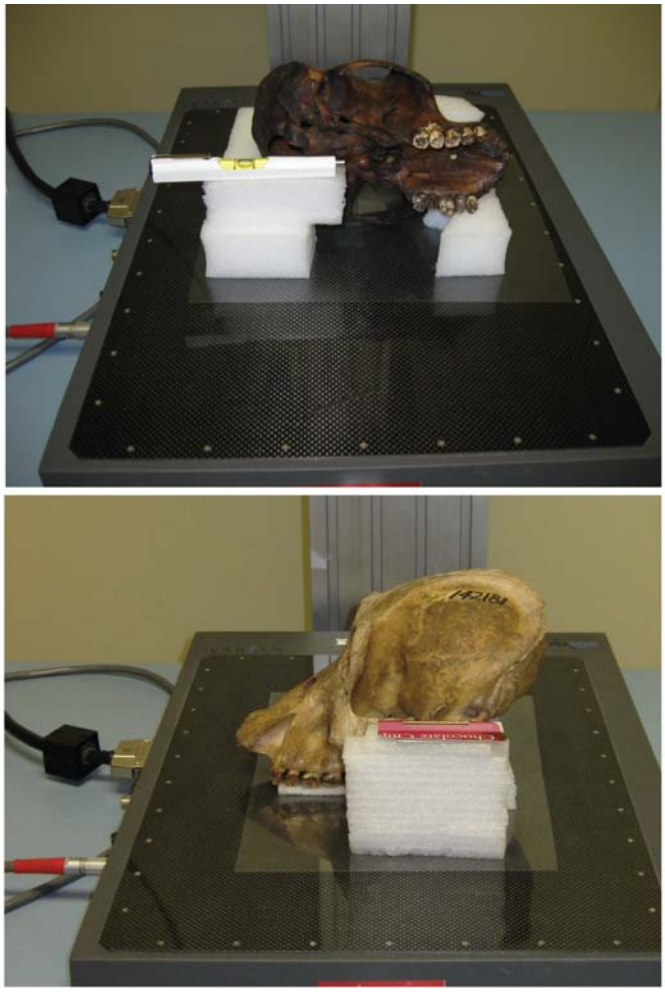


Figure 3.2. Photographs of the radiograph set up: lateral radiograph (top) and superior radiograph (bottom).

Ethafoam® blocks were used as specimen supports to position them in lateral and superior views. To ensure that the positioning for lateral radiographs was standardized, two distances were measured: (1) the distance from the surface of the x-ray tablet (or the surface of the riser for smaller specimens) and prosthion; and (2) the distance from the surface of the x-ray tablet (or the surface of the riser). The specimen's position was then was readjusted until these two distances were equal. For superior radiographs, specimens were oriented in Frankfurt Horizontal. Distances were measured between the surface of the x-ray tablet (or riser) and left and right orbitale and the distance between the x-ray tablet (or riser) and porion. Specimens were then readjusted until these distances were equal. A radio-opaque scale was placed in each radiograph. Using Ethafoam® blocks, the scale was positioned at the same distance from the x-ray source as the mid-sagittal plane in lateral radiographs and the same distance from the x-ray source as porion in superior radiographs. The scale was leveled using a bubble level. See Fig. 3.2 for photos of the setups for superior and lateral radiographs.

MEASUREMENTS

Radiographic Measurements

Data for eight variables were collected on the radiographs of each specimen (seven from lateral radiographs and one from superior radiographs). All radiographic data were collected using ImageJ (Abramoff et al., 2004) and were scaled using the scale included in each radiograph (see above).

As discussed in Chapter 2, there are two prevalent measures of facial projection that have been used in previous studies—i.e., Ravosa's (Ravosa, 1988; Ravosa, 1991a, b) "anterior orbital axis length" and Lieberman and colleague's (Lieberman, 1998;

McBratney-Owen and Lieberman, 2003) "facial projection." In this study, data for both of these measurements were collected (Ravosa's "anterior orbital axis length" is denoted as "Facial Projection 1" and Lieberman and colleague's "facial projection" is denoted as "Facial Projection 2"). As explained in more detail below, statistical tests to evaluate the correlation of these two measurements also were conducted.

The two facial projection variables were collected from lateral radiographs. These variables were as follows:

(1) Facial Projection 1 (FP1): (Ravosa, 1988; Ravosa, 1991a, b) (Fig 3.3) The distance between the orbital plane (OP) and the inferior orbital rim (IOR) measured along the orbital axis (OA) and perpendicular to OP, with OP, IOR, and OA defined as follows: (1) OP is a line segment extending from the point of overlap between the anterior cranial fossa and the superior border of the orbit (point A) and, point C, a point on the inferior orbit equidistant from point B (the orbital aperture of the optic canal) as point A; (2) OA extends from point B, bisects the orbital plane (line segment AC), and continues to point D; and (3) line segment DE connects IOR (point E) to point D and lies perpendicular to OA (line segment BD).

(2) Facial Projection 2 (FP2): (Lieberman 1998, 2011; McBratney-Owen and Lieberman, 2003; Lieberman et al., 2004) (Fig. 3.4) The distance between sellion[3] (see Table 3.3 for a list of craniometric points used in this study and their definitions) and foramen caecum point perpendicular to the PM Plane (the plane that defines the posterior margin of the facial skeleton and the

[3] Due to the difficulty in locating nasion on radiographs, sellion was used to substitute for nasion (see Kimbel et al., 1984; Rak, 1988, 1993).

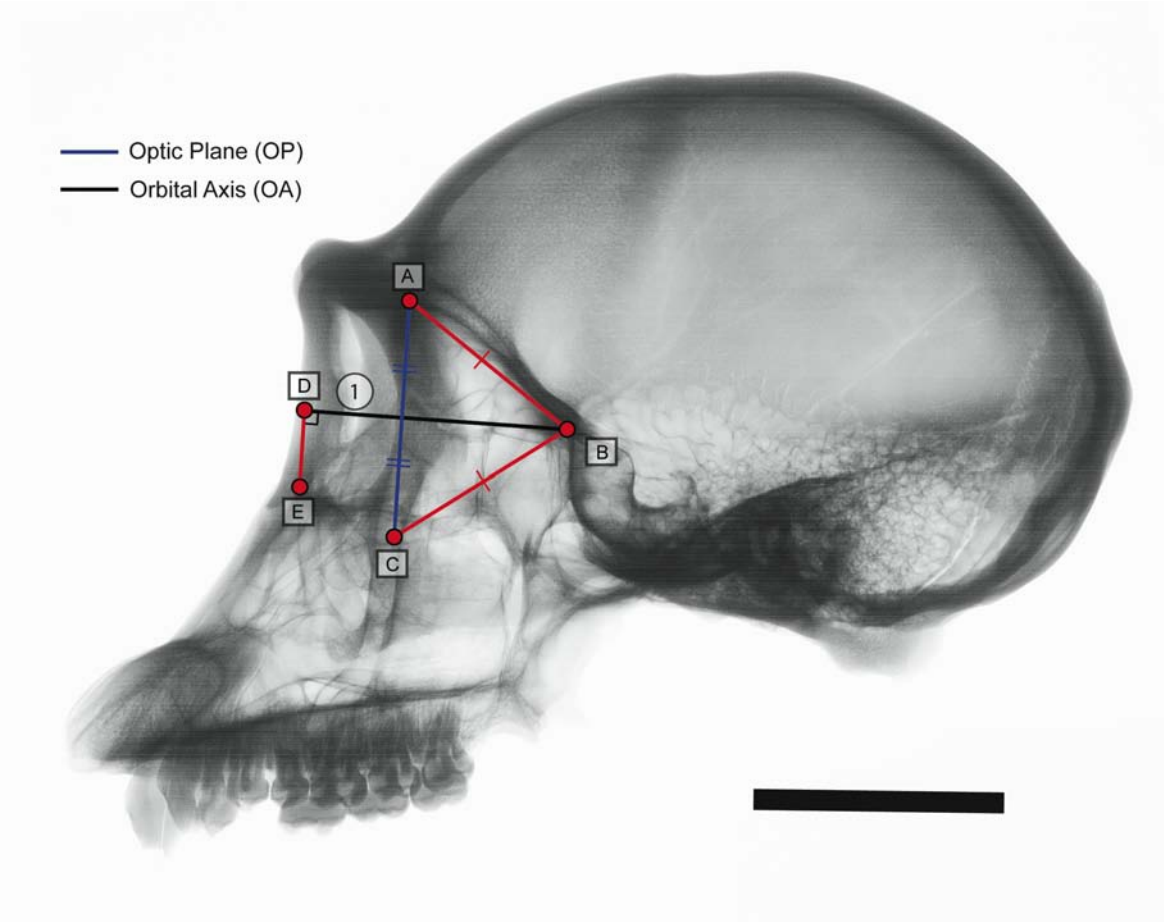


Figure 3.3. Illustration of Facial Projection 1 (FP1; labeled 1 in figure). Landmarks are as follows: Point of overlap between the anterior cranial fossa and the superior orbital border (A), orbital aperture of the optic canal (B), point on the inferior orbit equidistant from point B as A (C); intersection of line segment BD and line segment DE (which is perpendicular to line segment BD) (D); inferior orbital rim (E). Scale bar is 40 mm. See text for further details.

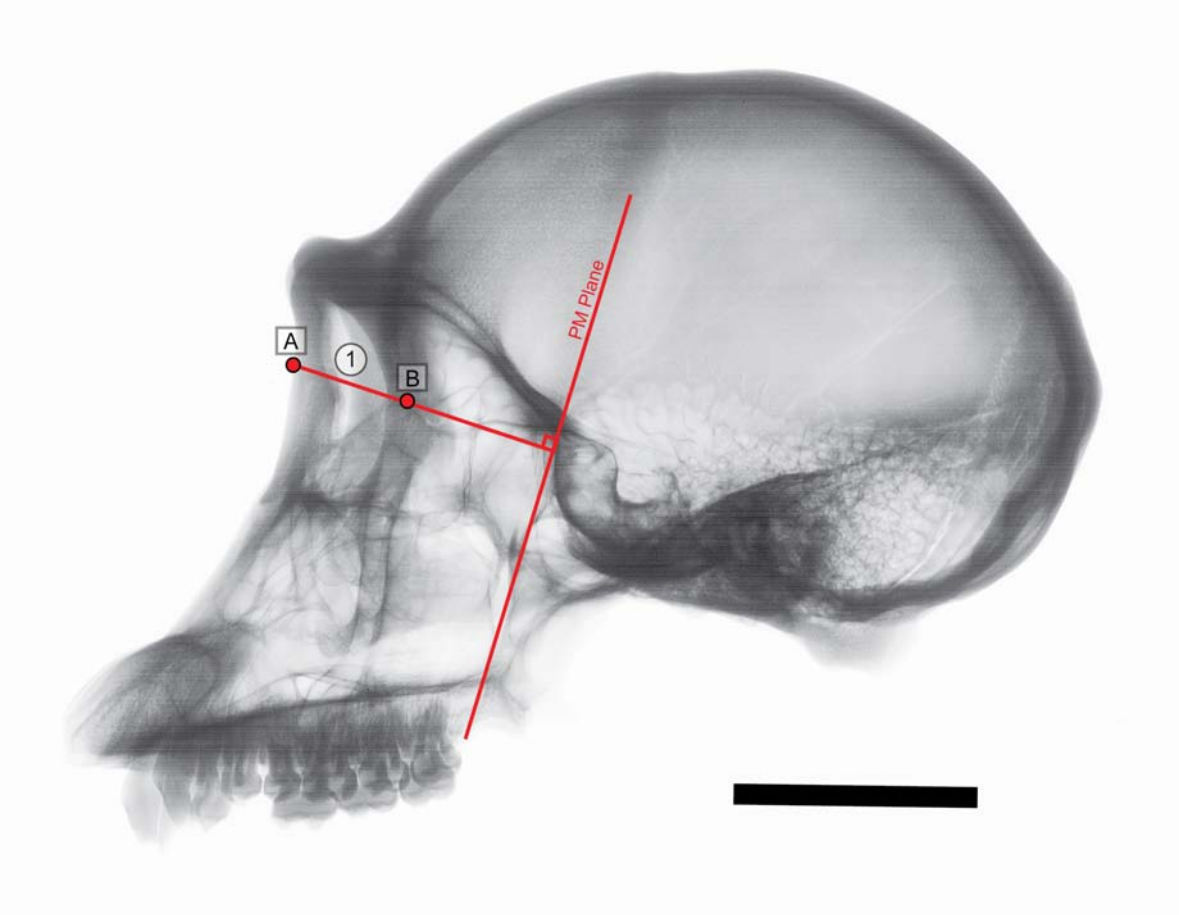


Figure 3.4. Illustration of Facial Projection 2 (FP2; labeled 1 in figure). Landmarks are as follows: sellion (A), and foramen caecum point (B). Scale bar is 40 mm. See text for further details.

TABLE 3.3. List of craniometric points and their definitions.

CRANIOMETRIC POINT	DESCRIPTION[a]
Prosthion	the midline point at the most anterior point on the alveolar process of the maxillae
Orbitale	the lowest point on the orbital margin
Porion	the uppermost point on the margin on of the external acoustic meatus
Foramen caecum point	the pit on or above the cribriform plate between the crista galli and the endocranial wall of the frontal bone (McCarthy, 2001)
Sella	the center of the sella turcica, independent of the countours of the clinoid processes (Lieberman et al., 2000)
Basion	the midline point on the anterior margin of the foramen magnum
Sellion	the deepest point in the anterior facial profile in lateral view (Kimbel et al., 1984)
Nasion	the midline point where the two nasal bones and the frontal intersect
Inion	the point on the ectocranial midline at the base of the external occipital protuberance at the point at which the superior nuchal lines merge in the external occipital protuberance
Vertex	the highest ecxtocranial point on the skull's midline when the skull is in Frankfurt Horizontal[b]
Staphylion	the point on the median palatine (intermaxillary) suture where a line drawn between the posterior ends of the alveolar ridges crosses the midline
Ectomolare	the most lateral point on the outer surface of the alveolar margins of the maxilla

[a] All descriptions come from White et al. (2012) unless otherwise indicated

[b] Frankfurt Horizontal is a plane defined by three points: right and left porion and left orbitale (White et al., 2012)

and the anterior margin of the middle cranial fossa; see Chapter 2 for further definition and discussion).

There are also two widely used measures of cranial base angle, and there is some disagreement over which measure is more appropriate for taxonomically broad comparisons, such as the current study (see Chapter 2 for further discussion). Due to the lack of consensus on the best method for measuring cranial base angle, both measures were employed in this study. The measurement of cranial base angle favored by Spoor (1997) is denoted as "Cranial Base Angle 1," whereas the cranial base angle measurement used by Ross and colleagues (Ross and Ravosa, 1993; Ross and Henneberg, 1995) is denoted as "Cranial Base Angle 2."

The two measurements of cranial base angle, both of which were measured on lateral radiographs were as follows:

(3) Cranial Base Angle 1 (CBA1): (Spoor, 1997) (Fig. 3.5) The inferior angle formed between a line segment connecting foramen caecum point and sella (line segment AB) and a line segment connecting sella and basion (line segment BC).

(4) Cranial Base Angle 2 (CBA2): (Ross and Ravosa, 1993) (Fig. 3.6) The inferior angle between the occipital clivus (OC) and sphenoid plane (SP), where OC and SP are defined as follows: (1) OC is a line segment from basion to the posterior edge of the sphenooccipital synchondrosis (or to the midsagittal portion of the cranial base posterior to dorsum sella, in specimens in which the sphenooccipital sychondrosis is not visible); and (2) SP is a line segment from the apex of the superiormost midline point on the slope of the

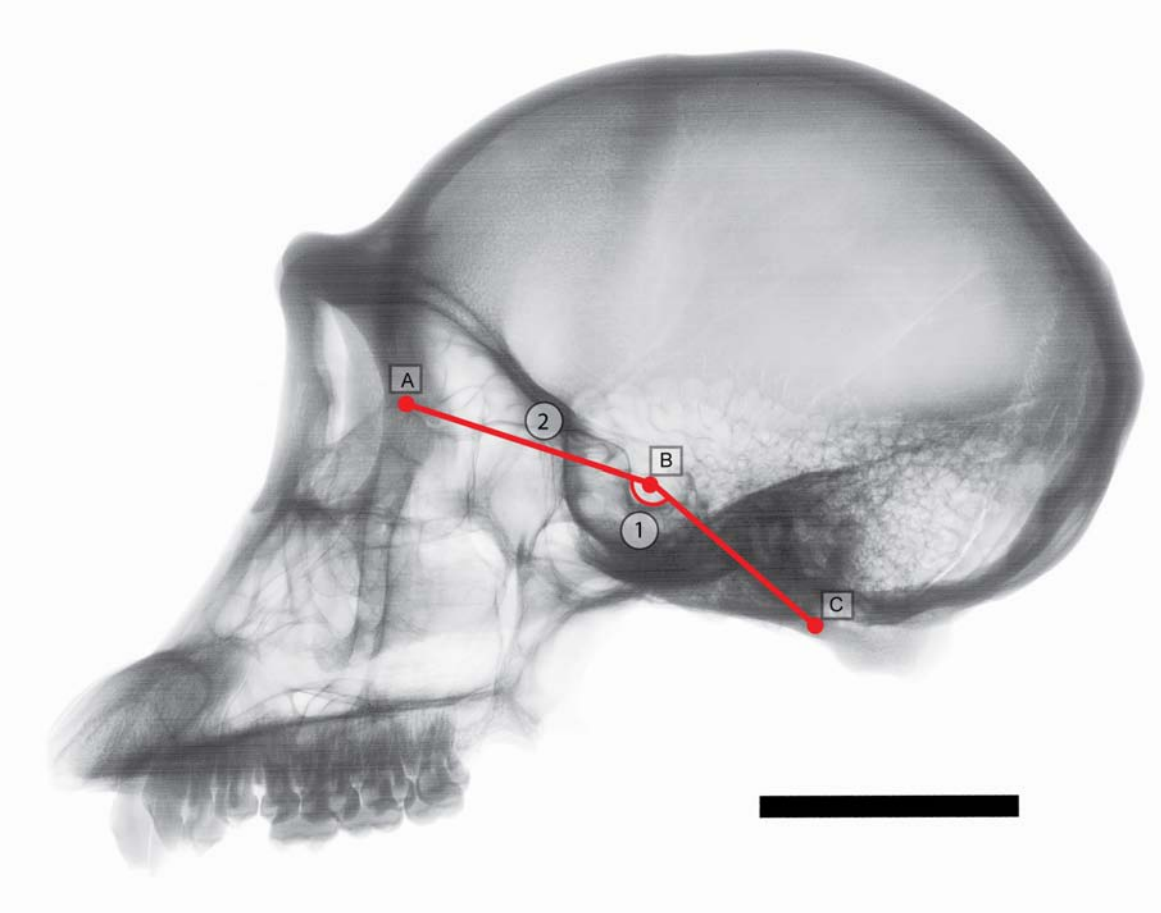


Figure 3.5. Illustration of Cranial Base Angle 1 (CBA1; 1 in figure) and Anterior Cranial Base Length (2 in figure). Landmarks are as follows: foramen caecum (A), sella (B), and basion (C). Scale bar is 40 mm. See text for further details.

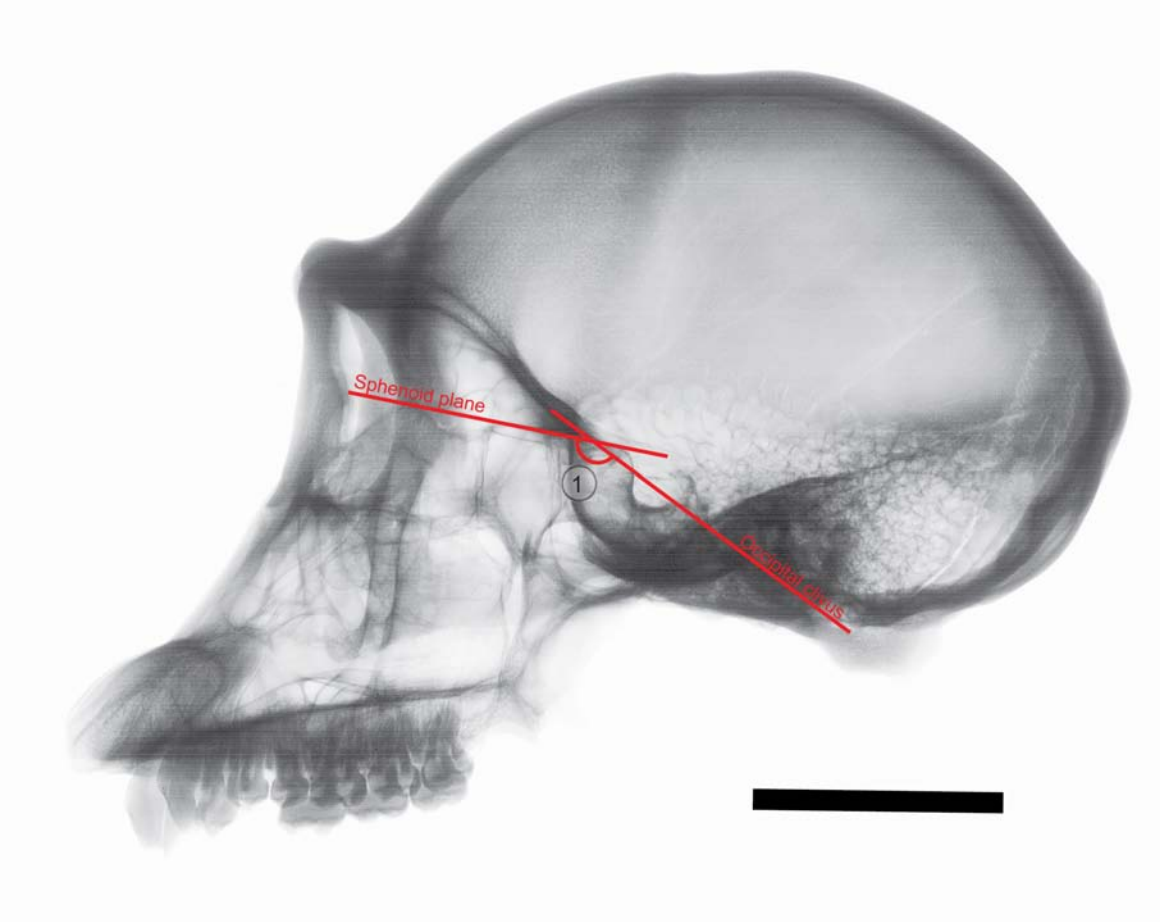


Figure 3.6. Illustration of Cranial Base Angle 2 (CBA2; 1 in figure). Scale bar is 40 mm. See text for further details.

chiasmatic sulcus to the superiormost point on the sloping posterior surface of the pit in which the cribriform plate is located.

The remaining three variables collected from lateral radiographs were as follows:

(5) Anterior Cranial Base Length (ACBL): (Lieberman, 1998, 2000, 2011; McBratney-Owen and Lieberman, 2003; Lieberman et al., 2004;) (Fig. 3.5) The distance between sella and foramen caecum point.

(6) Upper Facial Length (UFL): (Lieberman, 1998, 2000, 2011; McBratney-Owen and Lieberman, 2003) (Fig. 3.7) The distance between the PM Plane and sellion, measured perpendicular to the PM Plane.

(7) Anterior Sphenoid Length (ASL): (Lieberman, 1998, 2000, 2011; Lieberman et al., 2000a; McBratney-Owen and Lieberman, 2003) (Fig. 3.7) The distance between sella and the PM Plane, measured perpendicular to the PM Plane.

The variable collected from the superior radiographs was as follows:

(8) Anterior Middle Cranial Fossa Length (AMCFL): (Fig. 3.8) The distance between the anteroposterior center of the sella turcica (i.e., the projection of sella in the anteroposterior plane) and the most anterior point on the middle cranial fossa measured parallel to the mid-sagittal plane.

Cranial Size Measurements

Six variables were collected from all specimens to adjust for size (size adjustment procedures are described below in the 'Size adjustment' section). These measurements were collected from dry specimens using Mitutoyo 500-197-20 Digimatic digital calipers. These six measurements were as follows (see also Figure 3.9):

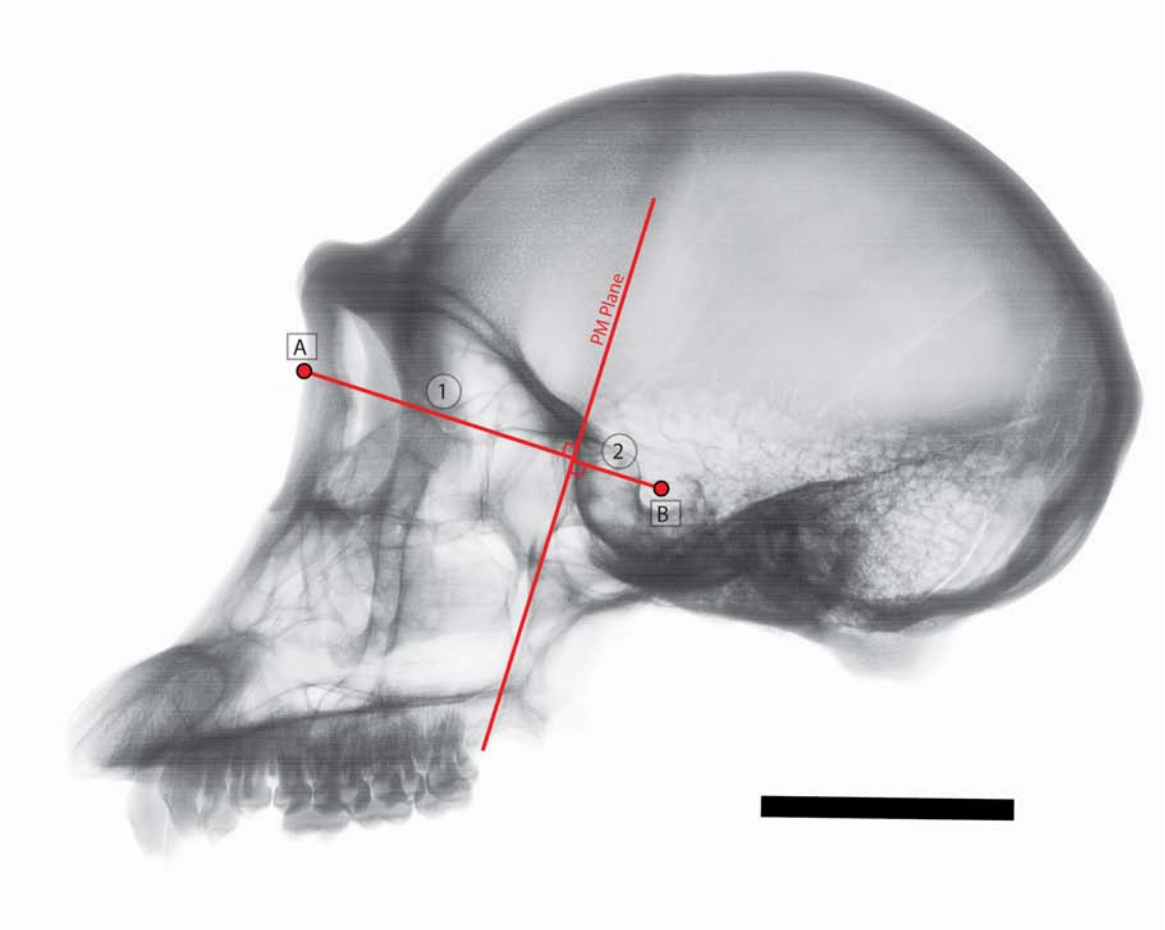


Figure 3.7. Illustration of Upper Facial Length (UFL; 1 in figure) and Anterior Sphenoid Length (ASL, 2 in figure). Landmarks are as follows: sellion (A), sella (B). Scale bar is 40 mm. See text for further details.

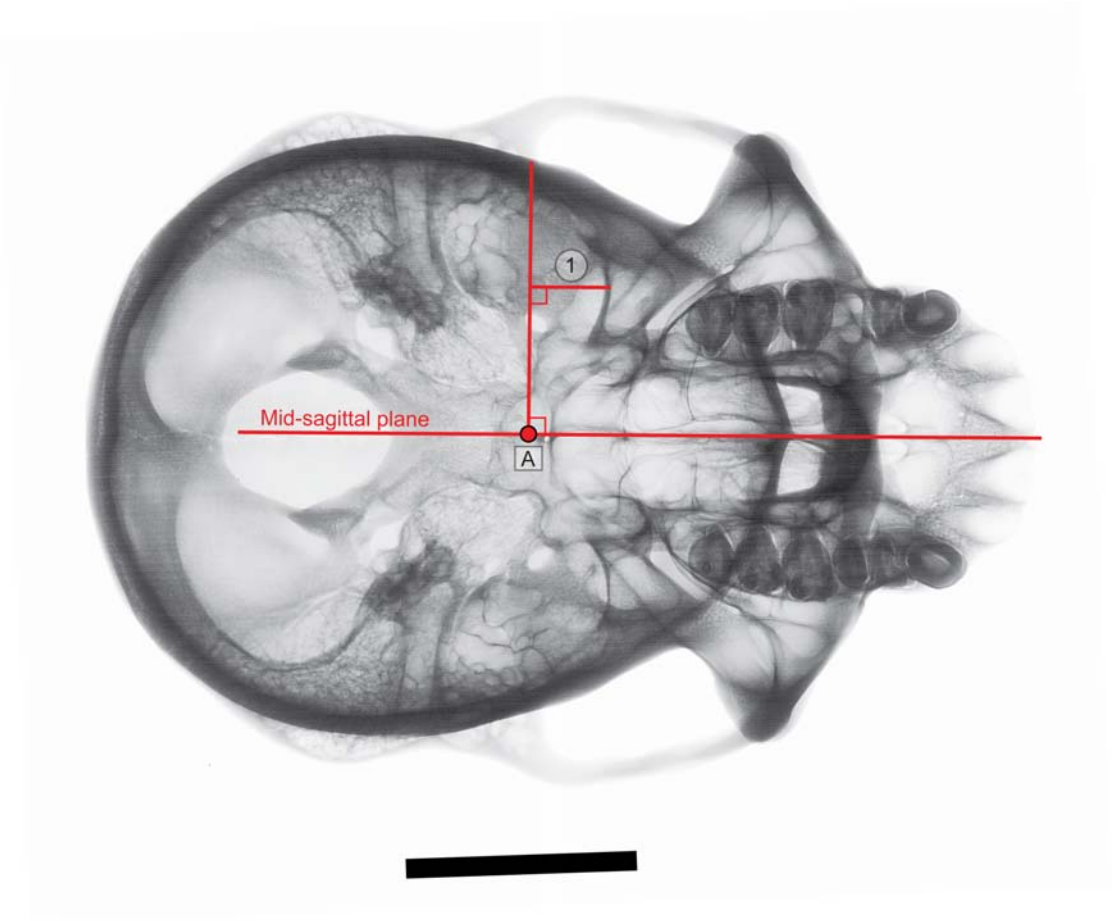


Figure 3.8. Illustration of Anterior Middle Cranial Fossa Length (AMCFL; labeled [1] in figure). Landmarks are as follows: mid-sagittal point midway between the anterior and posterior clinoid processes. Scale bar is 40 mm. See text for further details.

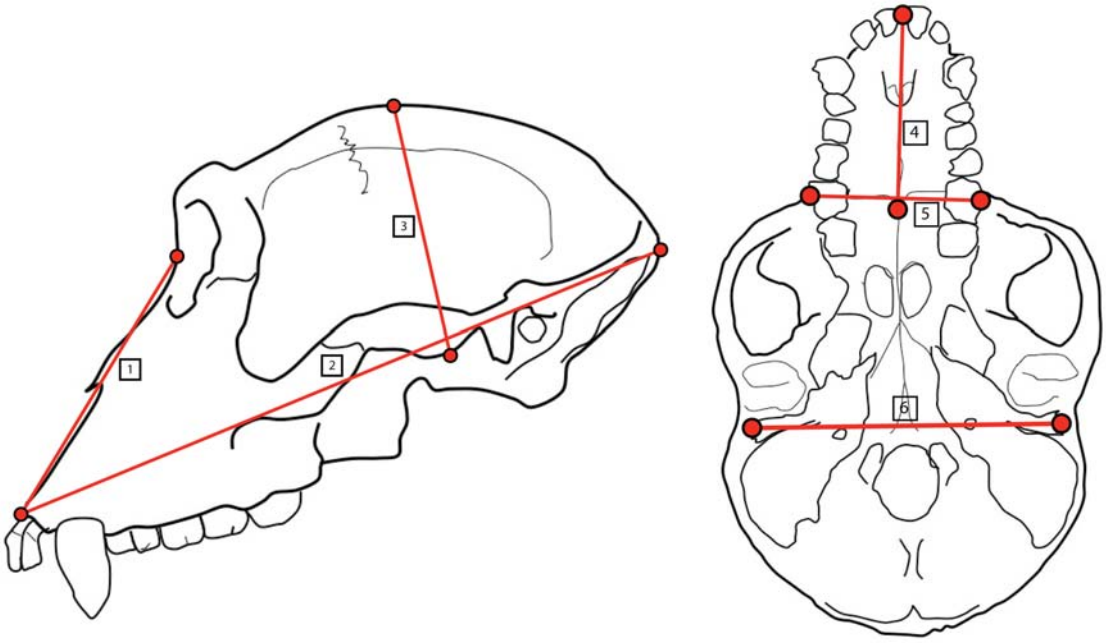


Figure 3.9. Illustration of cranial measurements used for size adjustment. Measurements are as follows: Facial Height (1), Skull Length (2), Neurocranial Height (3), Palate Length (4), Palate Width (5), and Cranial Width (6).

(1) Facial Height: the distance from prosthion to nasion;

(2) Cranial Length: the distance from prosthion to inion;

(3) Neurocranial Height: the distance from basion to vertex;

(4) Palate Length: the distance from prosthion to staphylion;

(5) Palate Width: the distance from right ectomolare to left ectomolare; and

(6) Cranial Width: the distance from right porion to left porion.

GEOMETRIC MORPHOMETRIC METHODS

A geometric morphometric analysis was performed to describe variation in middle cranial fossa shape and the position of the middle cranial fossa within the basicranium. Although this analysis could not be used to text explicitly any of the hypotheses outlined in the next chapter, the geometric morphometric methods were designed to address issues related to Hypothesis 5. Specifically, this hypothesis predicts that increased length of the anterior middle cranial fossa will be associated with decreased facial projection. However, lengthening of the anterior middle cranial fossa can be the result of two processes (or a combination of both): (1) overall lengthening of the middle cranial fossa; (2) an anterior shift in the anterior margin of the middle cranial fossa relative to other structures in the basicranium. The geometric morphometric component of this project was designed differentiate between these two phenomena.

To capture the shape of the basic configuration of the cranial base, five landmarks were digitized from scaled superior radiographs of each specimen (see Table 3.1 for sample sizes). The five landmarks are as follows:

(1) The most anterior point on the neurocranium;

(2) The point on the mid-sagittal plane located midway between the anterior and posterior clinoid processes;

(3) Basion

(4) The most posterior point on the neurocranium; and

(5) The point on the ectocranial surface of the neurocranium marking the most lateral point on the neurocranium.

Thirty sliding semi-landmarks were also digitized from the superior radiograph of each specimen. Sliding semi-landmarks (also referred to simply as "semi-landmarks" or "sliding landmarks") are points drawn along a curves that are impossible to describe with homologous landmarks because the landmark positions along the curve cannot be homologized across individuals; thus, these points must be estimated (Bookstein, 1996/7; Adams et al., 2004; Gunz et al., 2005; Reddy et al., 2005; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013). The estimation of the positions of sliding semi-landmarks was achieved by "sliding" the semi-landmarks to minimize bending energy (Gunz et al., 2005; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013;) using the program tpsRelw (Rohlf, 2010b). In other words, the positions of the semi-landmarks were shifted along the curve until they matched, as closely as possible, the corresponding points along the outline of a reference curve (in this case, the reference curve is the "consensus" or mean configuration) (Adams et al., 2004; Gunz et al., 2005; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013).

In this study, the sliding semi-landmarks were digitized by drawing curves along the outline of middle cranial fossa from the point adjacent to the posterior margin of the anterior clinoid process. These curves continued to the point at which the petrous ridge

intersects the inner table of the neurocranium or, in specimens in which the petrous ridge did not intersect with the inner table of the neurocranium, to the point at which the petrous ridge intersects with the sigmoid sulcus (see Fig 3.10). Approximately 50 landmarks were plotted; however, specimens had variable number of total points used to draw the curve (mean = 52.5; range = 40-78; standard deviation = 6.3). These points were then resampled using the program tpsDig (Rohlf, 2009) to create 30 landmarks which were placed roughly equidistantly along the curve. Once the sliding semi-landmarks were slid, they were treated as landmarks and were combined with the five landmarks to form the landmark configurations utilized in subsequent shape analyses (see Adams et al., 2004; Mitteroecker and Gunz, 2009).

Landmark configurations were superimposed using Generalized Procrustes Analysis (GPA), which removed the effects of size, rotation, and translation. All landmark configurations were then subjected to principal component analyses (PCA) so that variation in middle cranial fossa size, shape, and position could be summarized and examined visually. Separate PCAs were performed for each species and for sexes within each species wherever appropriate (see below), and consensus landmark configurations for each species were produced. The consensus landmark configurations of all species and for sexes within species wherever appropriate were submitted to an additional PCA. All landmarks and sliding semi-landmarks were digitized using the program tpsDig (Rohlf, 2010a). TpsRelw (Rohlf 2010b) was used to slide the sliding semi-landmarks and to perform the GPA and PCA.

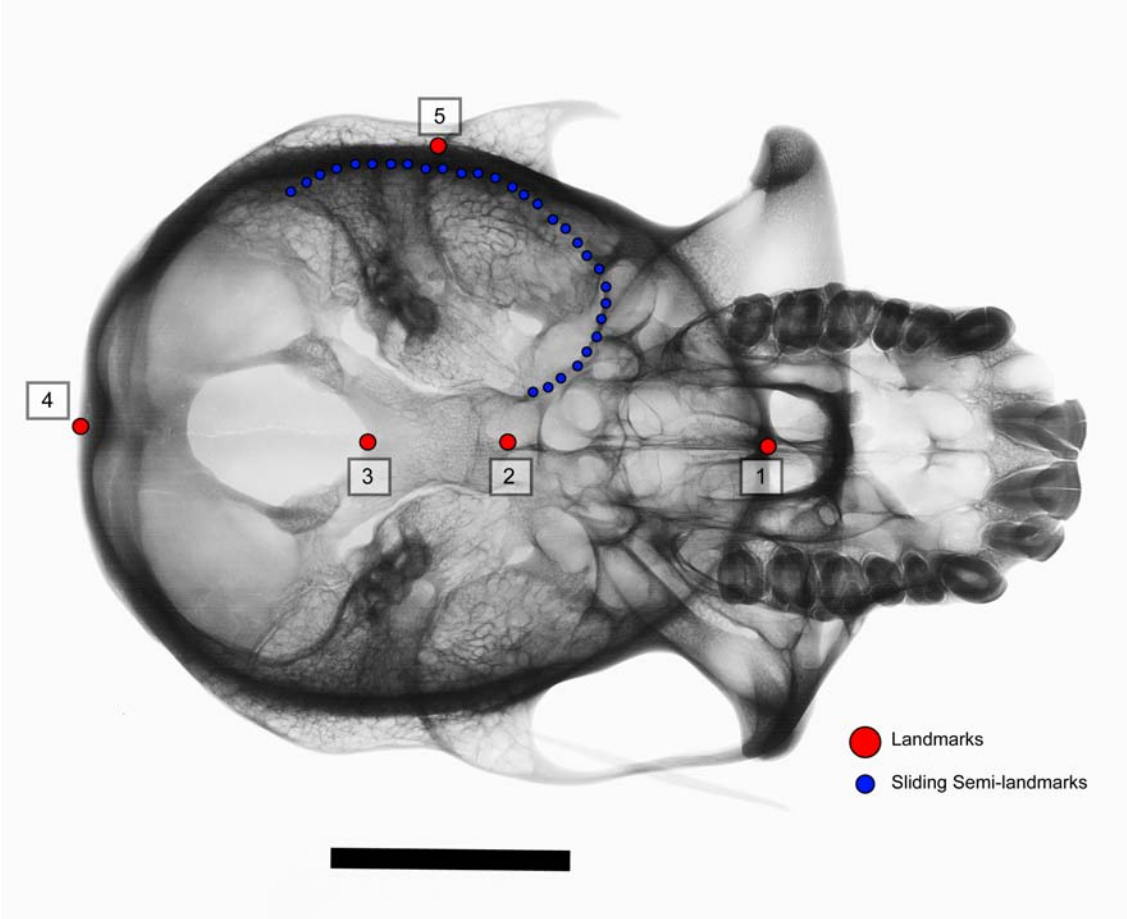


Figure 3.10. Landmarks and sliding semi-landmarks employed in the geometric morphometric analysis. Landmarks are indicated by larger, red circles; sliding semi-landmarks are indicated by smaller, blue circles. Landmarks are as follows: the anterior-most point on the neurocranium (1); the point on the mid-sagittal plane midway between the anterior and posterior clinoid processes (2); basion (3); the posterior-most point on the neurocranium (4); and the point on the ectocranial surface of the neurocranium marking the most lateral point on the neurocranium (5). Scale bar is 40 mm.

ANALYTICAL PROCEDURES

Phylogenetic Generalized Least Squares

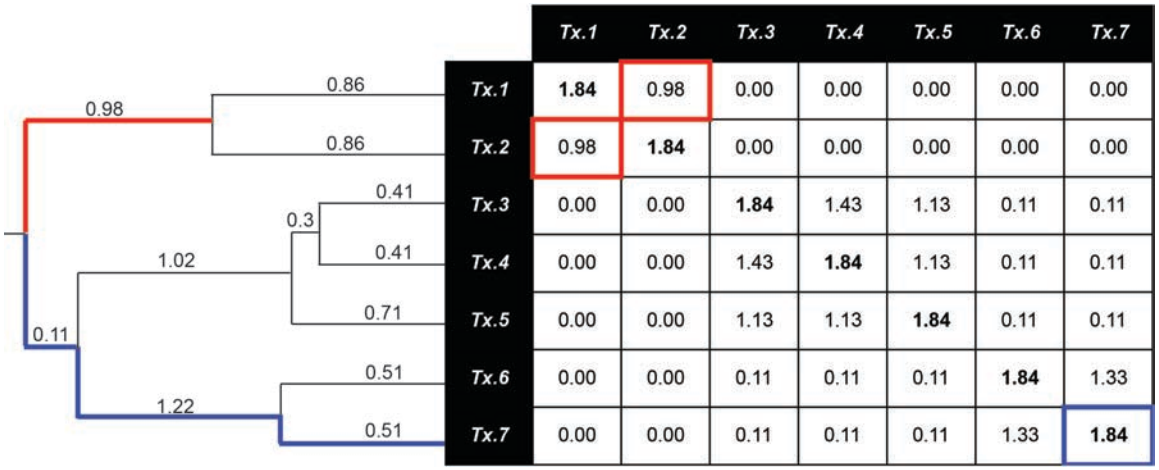
Phylogenetic Generalized Least Squares (PGLS) was used to perform all regression analyses. PGLS is an extension of an ordinary generalized least squares (GLS) analysis and is one of many techniques available for addressing the problems of phylogenetic nonindependence in comparative data (Grafen, 1989; Martins and Hansen, 1997; Pagel, 1997; 1999; Garland and Ives, 2000; Rohlf, 2001). GLS models the relationship between independent traits and a dependent variable using the following equation:

$$Y = \alpha + X_1\beta_1 + X_2\beta_2 + \ldots + X_n\beta_n + \varepsilon$$

(where $X_1, X_2, \ldots X_n$ are n independent traits, Y is the dependent trait, α is the y-intercept, $\beta_1, \beta_2, \ldots \beta_n$ are the coefficients/slopes for the n dependent variables, and ε is the residual [or error] term).

Unlike non-generalized least squares, GLS does not require the assumption that the errors are non-independent. Specifically, in PGLS, the non-independence of the errors is specified by incorporating phylogenetic relatedness into the error term using a phylogenetic variance-covariance matrix (Fig. 3.11). A phylogenetic variance-covariance matrix is constructed such that the diagonals (variances) are the lengths from the root of the tree to the last common ancestor of the two species and the off-diagonals are the distances between the root of the tree and the common ancestor of the two taxa.

The degree of phylogenetic signal in the data can be estimated and used to scale



	Tx.1	Tx.2	Tx.3	Tx.4	Tx.5	Tx.6	Tx.7
Tx.1	**1.84**	0.98	0.00	0.00	0.00	0.00	0.00
Tx.2	0.98	**1.84**	0.00	0.00	0.00	0.00	0.00
Tx.3	0.00	0.00	**1.84**	1.43	1.13	0.11	0.11
Tx.4	0.00	0.00	1.43	**1.84**	1.13	0.11	0.11
Tx.5	0.00	0.00	1.13	1.13	**1.84**	0.11	0.11
Tx.6	0.00	0.00	0.11	0.11	0.11	**1.84**	1.33
Tx.7	0.00	0.00	0.11	0.11	0.11	1.33	**1.84**

Figure 3.11. An example of how tree topologies and branch lengths are used to construct a phylogenetic variance-covariance matrix. The numbers on the branches on the phylogenetic tree (left) are the branch lengths. The diagonals in the phylogenetic variance-covariance matrix (right) are the lengths from the root of the tree to each of the tips. The off-diagonals are the distances between the root of the tree and the common ancestor of the two taxa in question. The diagonal value (variance; outlined in blue) for taxon 7 (Tx. 7) is calculated by summing the lengths of the branches from the tip to the root of the tree (shown in blue: 0.51 plus 1.22 plus 0.11 equals 1.84 units of time). The off-diagonal values (covariance; outlined in red) for taxa 1 and 2 (Tx. 1 and Tx. 2) are calculated by summing the lengths of the branches from the node representing the common ancestor of the two taxa to the root of the tree (shown in red: 0.98). Adapted from Nunn (2011) and Orme et al. (2013).

the phylogenetic variance-covariance matrix. In this study, the phylogenetic variance-covariance matrix was scaled using a maximum likelihood estimate of lambda (ML λ) (Freckleton et al., 2002; Revell, 2010). ML λ is a phylogenetic transformation that maximizes the likelihood of the observed data assuming a Brownian motion model of evolution (Freckleton et al., 2002). When ML λ equals zero there is no phylogenetic signal in the data—i.e., there is no phylogenetic covariance in the data and the data resemble a "star phylogeny" in which all species radiated simultaneously from a single ancestor (Felsenstein, 1985). When ML λ equals one, there is a strong phylogenetic signal in the data—i.e., the data are consistent with a Brownian motion model of character evolution characterized by phylogenetic variance-covariance matrix.

The phylogenetic trees for this study were consensus trees from 10K Trees Version 3, which houses 10,000 phylogenetic trees derived from an analysis of 17 genes (Arnold et al., 2010). The consensus tree for the complete dataset used in this dissertation is shown in Fig. 3.12. One alteration to the 10K Trees tree was made: *Miopithecus talapoin* (which was not included in the present study but is included in the 10K Trees data) was used to replace *Miopithecus ogouensis* (which was included in the present study but is not included in the 10K Trees data). This substitution is acceptable because the species in the genus *Miopithecus* are thought to be monophyletic (Groves, 2001), implying that substituting one species in the clade for another will not affect the topology or branch lengths of the tree, and it will not alter the phylogenetic variance-covariance matrix.

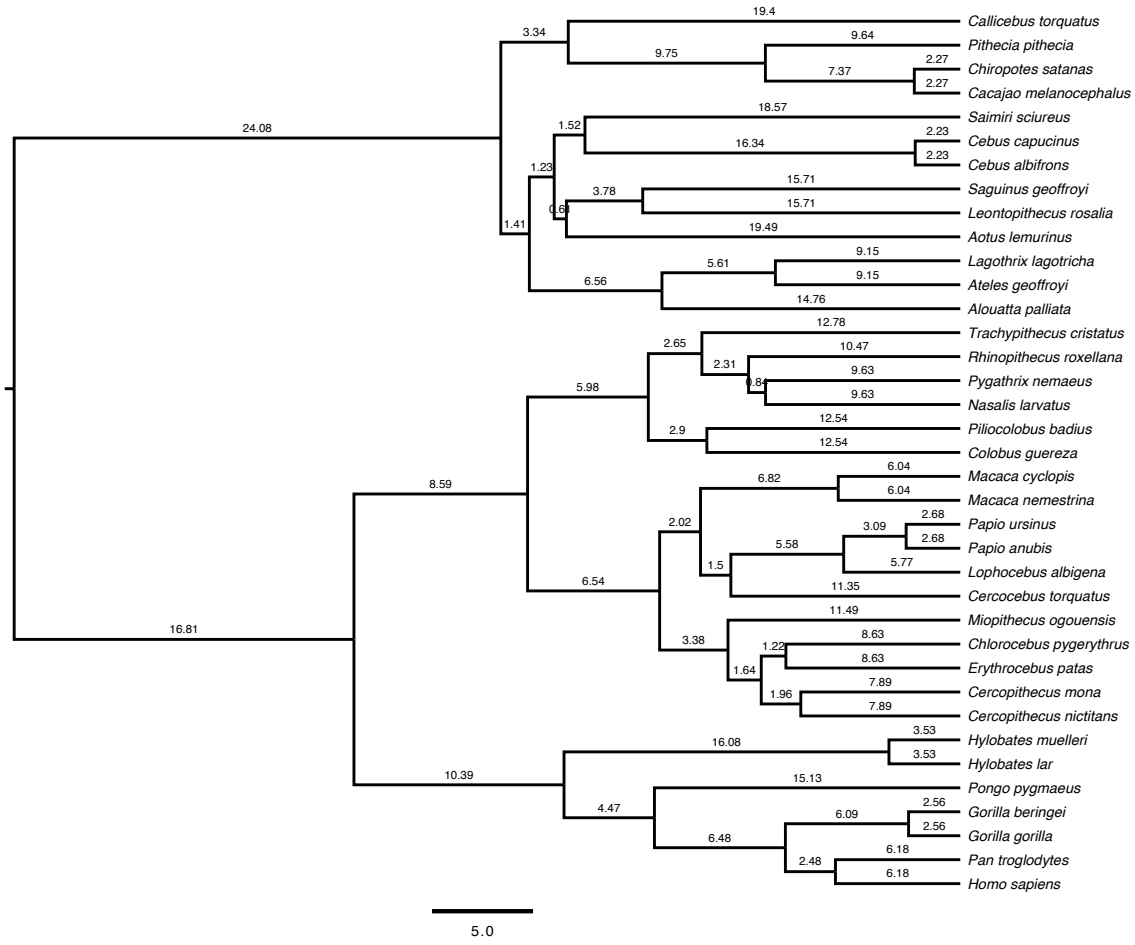


Figure 3.12. The phylogenetic tree used in this study. The numbers on the branches are branch lengths in millions of years.

Size Adjustment

Two methods for size adjustment were used in this dissertation—i.e., shape-ratios and phylogenetically-controlled residuals. Shape-ratios were computed by dividing the variable of interest by a geometric mean of the five cranial size measurements (see above). Phylogenetically-controlled residuals were produced by calculating the residuals from a PGLS regression of the variable of interest on a geometric mean of the five cranial size measurements.

It is important to highlight the differences between these two size adjustment methods and the detrimental effects each can have on interspecific analyses like those conducted here. Shape-ratios represent relative size—i.e., dividing the size of a given structure by a variable representing cranial size produces a variable representing the size of that structure relative to the size variable (Smith, 2005). Shape-ratios are not completely size-free, as size-related shape changes (i.e., allometry) may not be removed (Corruccini, 1987, 1995; Albrecht et al., 1993, 1995; Jungers et al., 1995). As the range of sizes represented by the species in the sample employed here is large, the allometric effects maintained when employing shape-ratios for size adjustment will potentially confound results of the interspecific regression analyses.

Unlike shape-ratios, using residuals for size adjustment statistically removes size and size-related shape change from a given variable (Corruccini, 1987, 1995; Jungers et al., 1995). This method is therefore referred to as "controlling for size" (Smith, 2005). By regressing a given variable on a size variable, this method considers the scaling relationship between the two variables as a criterion of subtraction, with the slope of the

regression line represents functional equivalence (Pilbeam and Gould, 1974; Gould, 1975).

Many authors (e.g., Reist, 1985; Packard and Boardman, 1987, 1988; Albrecht et al., 1993, 1995) have argued that residuals are a more appropriate method for size adjustment because shape-ratios do not control for size-related shape change. However, the fact that residuals are size-free can present problems in interspecific analyses. In particular, there is not normally a good basis for the assumption that the scaling relationship between the variables represents functional equivalence (Smith, 1980; Corruccini, 1987, 1995; Harvey and Pagel, 1991; Jungers et al., 1995). Instead, this scaling relationship often represents differences in function that are related to size, and removing size-related shape change may remove important functional information (Harvey and Pagel, 1991; Jungers et al., 1995; Oxnard, 1978; Smith, 1980).

Unlike shape-ratios or non-phylogenetic residuals, phylogenetically-controlled residuals control for the effects of phylogenetic nonindependence in the dataset when computing the residuals. This is an important advantage of using phylogenetically-controlled residuals because, as Revell (2009) demonstrated, failing to account for phylogenetic relatedness when performing size adjustment procedures (e.g., computing residuals from an ordinary least-squares regression of a given variable on a size variable) can result in significantly elevated variance and Type I error in the estimation of regression parameters. This effect exists whether or not the data are later submitted to statistical procedures to account for phylogenetic nonindependence (Revell, 2009).

Multiple regression analyses included an additional method for size adjustment—i.e., using the size variable as an independent variable in a multiple regression model. In

these analyses, variables were adjusted for size by including the size variable (i.e., the geometric mean of the five cranial size measurements) as one of the independent variables. This approach was advocated by Freckleton (2002, 2009), who warned that using residuals can bias analyses if the size variable covaries with one or more of the independent variables.

Design of Regression Analyses

Both univariate and multivariate PGLS regressions were performed. For univariate regressions, the dependent variable was one of the measures of facial projection (i.e., FP1 or FP2), whereas the independent variables represented each of the hypothesized explanations for variation in facial projection (i.e., CBA1, CBA2, ACBL, UFL, ASL, and AMCFL). Therefore, for each level of analysis (see below), 12 univariate regressions were run. In addition, each regression was run using each method for size adjustment for a total of 24 univariate regressions for each level of analysis (Table 3.4).

In the multivariate regression analysis, as in the univariate analyses, one of the measures of facial projection was treated as the dependent variable. In general, multiple regression models including all of the hypothesized explanations for variation in facial projection as independent variables were included. However, there were two exceptions to this generalization. First, as they are both measures of cranial base angle, CBA1 and CBA2 were never included in the same multiple regression model. These variables are also highly correlated (see "Correlation of Variables" subsection below), which causes

TABLE 3.4. Univariate regression analyses. The color of the shading of the boxes corresponds to the hypothesis that will be tested by each regression analysis.

SIZE-ADJUSTMENT METHOD: SHAPE RATIOS						
			Independent Variables			
Dependent Variable	**CBA1**	**CBA2**	**ACBL**	**UFL**	**ASL**	**AMCFL**
FP1	FP1 v. CBA1	FP1 v. CBA2	FP1 v. ACBL	FP1 v. UFL	FP1 v. ASL	FP1 v. AMCFL
FP2	FP2 v. CBA1	FP2 v. CBA2	FP2 v. ACBL	FP2 v. UFL	FP2 v. ASL	FP2 v. AMCFL

SIZE-ADJUSTMENT METHOD: PHYLOGENETICALLY-CONTROLLED RESIDUALS						
	CBA1	**CBA2**	**ACBL**	**UFL**	**ASL**	**AMCFL**
FP1	FP1 v. CBA1	FP1 v. CBA2	FP1 v. ACBL	FP1 v. UFL	FP1 v. ASL	FP1 v. AMCFL
FP2	FP2 v. CBA1	FP2 v. CBA2	FP2 v. ACBL	FP2 v. UFL	FP2 v. ASL	FP2 v. AMCFL

HYPOTHESIS 1
HYPOTHESIS 2
HYPOTHESIS 3
HYPOTHESIS 4
HYPOTHESIS 5

the problem of multicollinearity (see "Assumptions of Multiple Regression Analysis" subsection below). Second, because they both capture the same aspect of basicranial morphology, and are thus highly correlated (see discussion in Chapter 2), ASL and AMCFL were never used in the same regression model.

This research design resulted in four models. The independent variables included in each of these four models were as follows:

(1) Model 1: CBA1, UFL, ASL, and ACBL

(2) Model 2: CBA1, UFL, AMCFL, and ACBL

(3) Model 3: CBA2, UFL, ASL, and ACBL; and

(4) Model 4: CBA2, UFL, AMCFL, and ACBL

Each of these models was run using each of the three size adjustment techniques outlined above. Additionally, each of the models was run using both FP1 and FP2 as the dependent variable. Table 3.5 summarizes the multiple regression analyses that were conducted.

Assumptions of Multiple Regression Analysis

As an extension of ordinary least squares multiple regression, PGLS analysis makes certain assumptions regarding the data being analyzed. When these assumptions are violated, the results of the PGLS may be inaccurate (Keith, 2006; Tabachnick and Fidell, 2007). Therefore, it is important to outline these assumptions, the effect that violation of each may have on the results, and the methods that were used to test each assumption. The assumptions of multiple regression are as follows (Keith, 2006; see also, Harris, 1975; Neter et al., 1989; Montgomery et al., 2001; Gelman and Hill, 2007; Tabachnick and Fidell, 2007):

TABLE 3.5. Multivariate regression analyses. Boxes with no shading represent models that use FP1 as the dependent variable, whereas boxes shaded gray represent models that use FP2 as the dependent variable.

SIZE-ADJUSTMENT METHOD: SHAPE RATIOS					
	Dependent Variable		Independent Variables		
MODEL 1	FP1	CBA1	UFL	ASL	ACBL
MODEL 2	FP1	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP1	CBA2	UFL	ASL	ACBL
MODEL 4	FP1	CBA2	UFL	AMCFL	ACBL
MODEL 1	FP2	CBA1	UFL	ASL	ACBL
MODEL 2	FP2	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP2	CBA2	UFL	ASL	ACBL
MODEL 4	FP2	CBA2	UFL	AMCFL	ACBL
SIZE-ADJUSTMENT METHOD: PHYLOGENETICALLY-CONTROLLED RESIDUALS					
MODEL 1	FP1	CBA1	UFL	ASL	ACBL
MODEL 2	FP1	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP1	CBA2	UFL	ASL	ACBL
MODEL 4	FP1	CBA2	UFL	AMCFL	ACBL
MODEL 1	FP2	CBA1	UFL	ASL	ACBL
MODEL 2	FP2	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP2	CBA2	UFL	ASL	ACBL
MODEL 4	FP2	CBA2	UFL	AMCFL	ACBL
SIZE-ADJUSTMENT METHOD: SIZE VARIABLE AS INDEPENDENT VARIABLE					
MODEL 1	FP1	CBA1	UFL	ASL	ACBL
MODEL 2	FP1	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP1	CBA2	UFL	ASL	ACBL
MODEL 4	FP1	CBA2	UFL	AMCFL	ACBL
MODEL 1	FP2	CBA1	UFL	ASL	ACBL
MODEL 2	FP2	CBA1	UFL	AMCFL	ACBL
MODEL 3	FP2	CBA2	UFL	ASL	ACBL
MODEL 4	FP2	CBA2	UFL	AMCFL	ACBL

(1) The dependent variable is a linear function of the independent variable(s);

(2) The error associated with each observation is independent from the errors of other observations;

(3) The variance of the errors is not function of any of the independent variables;

(4) The errors are normally distributed; and

(5) The independent variables are not correlated.

There is no formal statistical test for the first assumption—i.e., there is no precise way of determining whether or not the dependent variable is a linear function of the independent variables. However, careful examination of the results and visual examination of data plots help determine if this assumption has been violated, such as when correlations are ubiquitously weak and/or when plots suggest a non-linear relationship between the dependent and independent variables. In this study, it was assumed that this assumption was not violated; however, care was taken to inspect the results for indications to contrary.

The second assumption does not apply to PGLS regression analysis. As discussed above, PGLS does not assume that the errors of observations are independent. Instead, the phylogenetic variance-covariance method and ML λ are used to specify the degree of phylogenetic relatedness among the species in the analyses.

The third assumption—i.e., that the variance of the errors is not a function of any of the independent variables (i.e., homoscedasticity)—was tested by examining plots of fitted values versus phylogenetic residuals. In these plots, a pattern in which the variance of the phylogenetic residuals increases with increases in predicted values may indicate

heteroscedasticity (i.e., that the third assumption is violated). However, no such patterns were observed in any of the analyses conducted in this study.

The fourth assumption was tested in two ways. First, this assumption was tested by examining normal probability (Q-Q) plots, which plot sample quantiles against theoretical quantiles. When the errors are approximately normally distributed, this plot will reflect a roughly linear relationship between the sample quantiles and theoretical quantiles, whereas a curvilinear relationship suggests that the data are not normally distributed (Keith, 2006). Second, this assumption was tested using a Shapiro-Wilk's test for normality on the phylogenetic residuals from the PGLS analyses (Shapiro and Wilk, 1965). A significant p-value (at $\alpha = 0.05$) from this test was taken as indication that the null hypothesis (i.e., that the sample residuals are drawn from a normally distributed population) was rejected (Shapiro and Wilk, 1965; Crawley, 2007).

In cases in which the null hypothesis from the Shapiro-Wilk's test for normality was not supported, two procedures were conducted. First, variables were $\log_{10}$ transformed, and the Shapiro-Wilk's test for normality was repeated. If the residuals were still not normally distributed, the original data were subjected to a Box-Cox transformation. The Box-Cox transformation (Box and Cox, 1964) is a procedure that estimates the best method for transforming a given data set (in this case, the phylogenetic residuals from the PGLS analysis) to normality (Sokal and Rohlf, 1995). In particular, this method provides a log-likelihood function of exponents to which the dependent variable can be raised to make the data fit a normal distribution (Sokal and Rohlf, 1995). After applying the Box-Cox transformation, the residuals were once again tested for normality using the Shapiro-Wilk's test.

It should be noted that, in some cases, neither of the steps outlined above were successful in normalizing the data. However, the assumption of normality of errors is generally the least important of the assumptions of regression, and, for the purpose of estimating regression parameters (i.e., as opposed to making predictions), this assumption is largely unimportant (Neter et al., 1989; Montgomery et al., 2001; Gelman and Hill, 2007). For this reason, analyses that violated the assumption of normality were still performed, but this violation was noted and considered when interpreting the results of the affected analyses.

The final assumption—i.e., that the independent variables are uncorrelated (also termed, "multicollinearity")—applies only to multivariate regression analyses. Specifically, when independent variables included in multiple regression models have a perfect (or nearly perfect) linear correlation, the effect on regression parameters can be dramatic (Montgomery et al., 2001; Keith, 2006). Specifically, correlated variables are statistically redundant (i.e., they have the same relationship with the dependent variable as they do with another), and their individual effects on the dependent variable cannot be accurately separated, resulting in potentially inaccurate regression parameters (including the correlation coefficient and coefficient of determination) (Montgomery et al., 2001).

In this study, the assumption that the independent variables are uncorrelated was tested by performing pairwise Pearson product-moment correlations between independent variables (see below). As discussed above, this procedure indicated that CBA1 and CBA2 and that ASL and AMCFL were highly correlated; thus, these variables were not used together in any of the multiple regression analyses. It should be noted that correlations between independent variables were encountered in other cases as well. In

these cases, the correlations were relatively weak, and these analyses were performed despite the potential confounding effect of multicollinearity. However, the degree of multicollinearity in each analysis was noted and the results were interpreted with caution when multicollinearity was more prevalent.

Outputs from PGLS Regressions

Each univariate PGLS regression yielded three important parameters. These parameters, and their importance in the context of the current study, are as follows:

(1) Maximum Likelihood Lambda (ML λ): As discussed above, this parameter provides an estimate of the degree of phylogenetic signal in the data;

(2) Correlation Coefficient (*r*):[4] The correlation coefficient permits an evaluation of the direction and strength of the correlation between the independent and dependent variable. The associated *p*-value tests the null hypothesis that the population correlation is zero (i.e., that there is no relationship between the independent and dependent variables). In the univariate analyses, a hypothesis will be rejected at any given level of analysis (see below) whenever the null hypothesis for the relationship between the dependent variable and the variable of interest is not overturned and/or when the direction of the correlation is the opposite from the respective prediction (see Chapter 4). In the multivariate PGLS regression analyses, a significant *r*-value indicated that an independent variable is

[4] This dissertation used ordinary least squares regression, a Model I regression method. Although a Model II method may be more appropriate (i.e., since both X and Y variables are measured with error and the error variance is symmetrical [Smith, 2009]), the difference between Model I and II techniques is only relevant in the context of best-fit lines (e.g., their slopes, confidence intervals, etc.); correlation coefficients and coefficients of determination produces by the two methods are mathematically identical (Smith, 2009).

significantly correlated with the dependent variable controlling for the other independent variables; and

(3) Coefficient of Determination (r^2): The coefficient of determination indicates the proportion of the variance in the dependent variable that is accounted for by variation in the independent variable. This parameter provides a more empirically interpretable measure of the strength of the relationship than does the correlation coefficient. The correlation coefficient will also be used to compare the explanatory power of different independent variables in the univariate analysis.

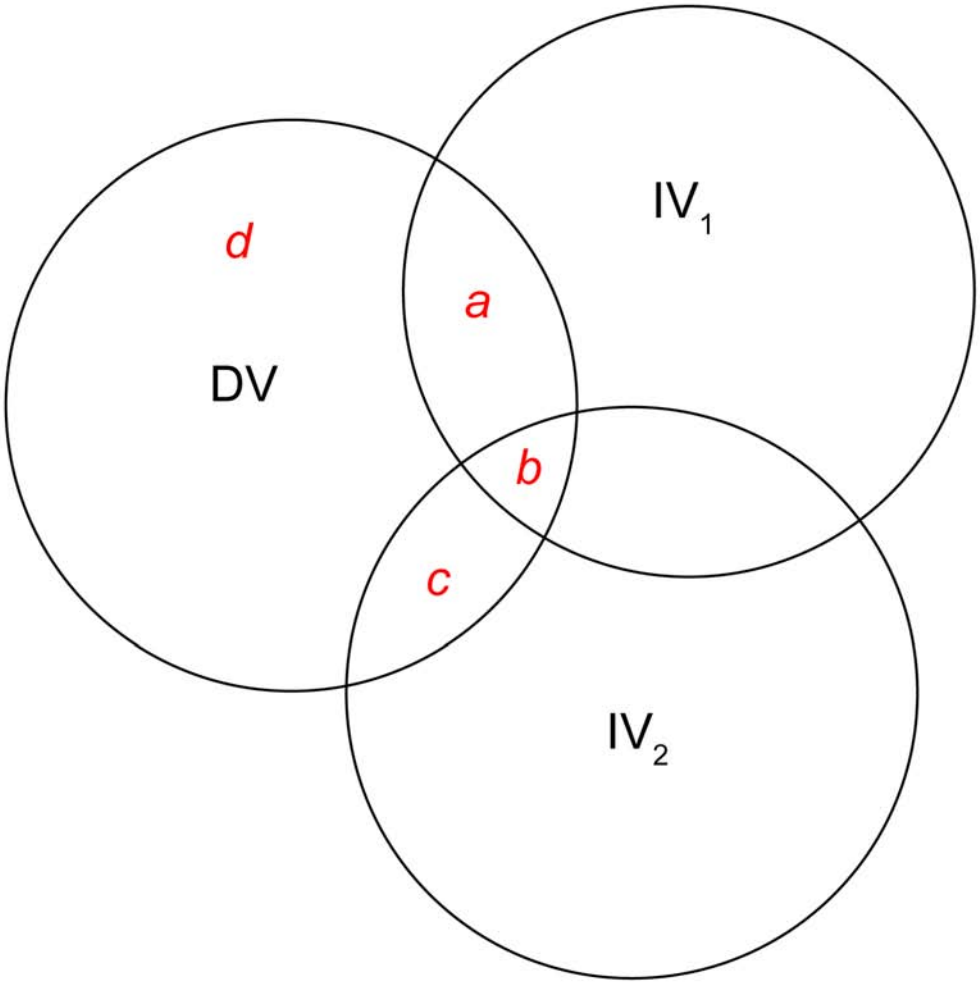
In addition to ML λ, r, and r^2, the multivariate PGLS analyses also yielded two parameters that were not produced for the univariate analyses—i.e., adjusted r^2 and semi-partial r^2 (SPR^2). Unlike the non-adjusted r^2, which increases whenever additional independent variables are added regardless of the contribution of that variable, adjusted r^2 adjusts for the number of independent variables in the model. An adjusted r^2 can become smaller (or even negative) when additional independent variables are added, and additional variables will only increase the adjusted r^2 if adding the variable improves the fit of the model more than would be expected by chance alone (Neter et al., 1989; Montgomery et al., 2001; Tabachnick and Fidell, 2007).

SPR^2 indicates the unique contributions of each independent variable in a multiple regression model (Keith 2006; Tabachnick and Fidell, 2007). Specifically, SPR^2 is the contribution of a given independent variable on the dependent variable, when the contributions of the other independent variables on the independent variable of interest held constant (Keith, 2006). This differs from the partial r^2, a widely used alternative, in which the contributions of the other independent variables on the independent variable of

interest as well as the contribution of the other independent variables on the dependent variable are controlled (Tabachnick and Fidell, 2007; see Figure 3.13). Therefore, SPR^2 indicates the contribution of a given independent variable to the total variance in the dependent variable (Tabachnick and Fidell, 2007). SPR^2 was calculated by computing r^2 for a given multiple regression model, calculating the r^2 of the same multiple regression with the independent variable of interest removed, and subtracting the first r^2 (i.e., for the entire model) from the second (i.e., from the model with the variable of interest removed). SPR^2 was only calculated for a given variable when the model being employed was significant (based on the *p*-value associated with *r* for the model was significant; $\alpha = 0.05$) and the given variable was significant (based on the *p*-value associated with the *r* for the variable was significant; $\alpha = 0.05$). In the multivariate analyses that employed the cranial size measurement (i.e., the geometric mean of the cranial size measurements, see above) for size adjustment, SPR^2 was not calculated for the cranial size variable.

Comparing Models – Akaike's Information Criterion

It is not appropriate to directly compare r^2 and adjusted r^2 because these two sample statistics describe different properties of the data—i.e., r^2 denotes the percentage of the variance in the dependent variable that is explained by the independent variable(s), whereas adjusted r^2 denotes the percentage of variance in the dependent variable explained by only those independent variables that truly affect the dependent variable, based on a *t*-test (Hurvich and Tsai, 1989). Therefore another means of comparison was needed to compare the fit of models used in the univariate analyses to the fit of models used in the multivariate analyses.



SEMI-PARTIAL R^2 (IV_1): $a / (a + b + c + d)$

PARTIAL R^2 (IV_1): $a / (a + d)$

Figure 3.13. Comparison of semi-partial and partial r^2. This figure represents a simple situation with one dependent variable (DV) and two independent variables (IV_1 and IV_2). The circles represent the total variance of each variable. The red, italicized letters represent regions of overlap in the variances of the variables (i.e., a and c represent the contributions of IV1 and IV2 to DV, respectively, d represents the shared contribution of IV1 and IV2 to DV, and d represents the variance in DV that is not explained by variance in either of the IVs.

In this study, Akaike's Information Criterion (AIC) was used for this purpose. AIC is a measure of the goodness of fit of a model with the additional inclusion of a penalty that is a function of the numbers of parameters being estimated (Keith, 2006; Crawley, 2007; Tabachnick and Fidell, 2007). In other words, calculation of AIC considers both the fit of the model and the number of independent variables in the model. If the fit of two models is the same, the model with fewer independent variables will have a lower AIC, suggesting that it is a better model, thus discouraging overfitting (i.e., adding superfluous, uninformative variables) (Keith, 2006). Particularly, the corrected AIC (or AICC) was used in the present study. AICC is identical to AIC except that it takes into account the sizes of the samples being examined (Hurvich and Tsai, 1989).

AICC was calculated for each combination of facial projection variable and size adjustment method (i.e., FP1 + shape-ratios; FP1 + phylogenetically-controlled residuals; FP2 + shape-ratios, and FP2 and phylogenetically-controlled residuals). Specifically, AICC was calculated for the best univariate model (based on r^2) and the best multivariate model (base on adjusted r^2) for each level of analysis (see below). This procedure allowed the single best model (i.e., the model with the lowest AICC) to be identified for each level of analysis.

Comparing *Homo sapiens* to Regression Models

Because one main goal of this dissertation is to determine whether or not *Homo sapiens* fits any apparent patterns regarding the explanations for variation in facial projection, it is important to outline the statistical methods that were used for this purpose. Two methods were used to determine how well *Homo sapiens* fits the patterns found in the regression analyses. First, 95% prediction intervals for all regressions were

calculated and it was determined whether or not *Homo sapiens* fit within these intervals.[5] *Homo sapiens* was omitted from these calculations to avoid it from influencing the prediction intervals and potentially biasing the results in favor of *Homo sapiens* falling within the confidence intervals. The second method was examination of studentized residuals. Studentized residuals (i.e., dividing the residuals by an estimate of their variances) are residuals that have been standardized to account for the fact that the variances of residuals from a regression may vary. This standardization permitted direct interpretation of the observations in terms of their fit to the regression relative to other observations. In this dissertation, if *Homo sapiens*' studentized residual was greater than ± 3,[6] it was considered an outlier, indicating that *Homo sapiens* did not closely fit the pattern indicated by the remainder of the data. It is important that these two methods were used in concert because, when correlations are weak, prediction intervals will be very wide, and even outlying observations may not fall outside of the prediction intervals. Examination of the studentized residuals is not affected by the strength of the correlation; thus this procedure will identify such observations even if they are within the prediction intervals. Prediction intervals and studentized residuals were calculated to determine the

[5] It should be noted that, at the present time, computer programs/functions for calculating phylogenetically controlled prediction intervals are not available. Therefore, non-phylogenetic prediction intervals were calculated and the value for *Homo sapiens* were compared to these intervals.

[6] Studentized residuals follow a *t*-distribution with *n*-*p*-1 degrees of freedom (where *n* is sample size and *p* is the number of regression parameters) (Stevens, 1984; Quinn and Keough, 2002). Therefore the confidence intervals described by $\pm$ 3 studentized residuals will vary by sample and analysis. However, $\pm$ 3 studentized residuals has been advocated as a rule of thumb for detecting outliers in regression analyses (see Jones and Purvis, 1997; Cooper and Kamilar, 2012; Lovegrove and Mowoe, 2014; Veilleux and Kirk, 2014).

position of *Homo sapiens* only in the models that were determined to be the best models for each level of analysis (see above).

Correlation of Variables

In addition to PGLS regression analyses, non-phylogenetic pairwise tests of correlations (i.e., Pearson product-moment correlations) among size-adjusted variables were conducted; these tests were conducted at all relevant levels of analysis (see below) and helped to evaluate whether or not the assumption of multicollinearity (see above) was violated and, if so, the severity of the violation. Such tests also indicated the degree of correlation between variables that are alternative methods for measuring the same anatomical phenomenon—i.e., facial projection (FP1 and FP2) and CBA (CBA1 and CBA2).

Tests of Sexual Dimorphism

The degree of sexual dimorphism in each species was assessed by comparing male and female subsamples using two-tailed t-tests. This comparison was performed in each species using size-adjusted variables (both methods of size correction were used) and for both facial projection variables (i.e., FP1 and FP2) and all dependent variables (i.e., CBA1, CBA2, ASL, UFL, ACBL, and AMCFL). These tests demonstrated that relatively little sexual dimorphism exists in any of the variables (see Appendix A). Specifically, using shape-ratios, no variable exhibited significant sexual dimorphism in more than 18% of the species (mean = 10.17%; standard deviation = 6.50%). Using phylogenetically-controlled residuals, no variable exhibited sexual dimorphism in more than 9% of the species (mean = 2.94%; standard deviation = 3.72%). Due to the low degree of sexual dimorphism, sexes were pooled in all analyses.

Statistical Analysis of Geometric Morphometric Data

Statistical analyses of the geometric data were performed to explore variation in the size and shape of the middle cranial fossa, as well as its position within the cranial base. Particularly, for each relevant level of analysis (see below), the first five principal components (PCs 1-5) from the geometric morphometric PCA were treated as independent variables in univariate PGLS regressions, where the dependent variable was one of the measures of facial projection (i.e., FP1 or FP2). In so doing, individual PCs that were significantly correlated with facial projection were identified. Although the proportion of the overall variation explained by the PCs varied by level of analysis, the first five PCs usually explained roughly 95% of the overall shape variation; this fact motivated the decision to retain the first five PCs. The shape change along each significant PC was explored using wireframe diagrams, paying particular attention to shape changes related to lengthening of the middle cranial fossa and/or changes in the position of the middle cranial fossa within the cranial base.

Units and Levels of Analysis

For each species, size-adjusted values for each variable were averaged to create species means, which were the basic unit of analysis. In order to be included in analyses, species were required to be represented by five or more specimens.

Analyses were conducted in four units of analysis representing four taxonomic groups—i.e., anthropoids, catarrhines, hominoids, and platyrrhines (see Table 3.1 for more information). The first three of these focus on the taxonomic groups containing *Homo sapiens* and permit evaluations of the hypotheses at three different taxonomic

levels (inter-infraordinal [among anthropoids], among catarrhines,[7] and inter-superfamilial [among hominoids]). This targeting of *Homo sapiens* reflects one of the goals of this dissertation—i.e., to determine what factor(s) explain facial projection in anthropoids and whether or not *Homo sapiens* fits any apparent patterns.

ERROR ANALYSES

Two forms of error analysis were conducted on the radiographic measurements and the cranial size measurements: (1) percent measurement error (calculated following White (1991); and (2) repeated measures analyses of variances (ANOVA). These analyses were performed on data obtained by repeating all measurements three times for a randomly chosen sample of 30 specimens. All repeat trials were conducted at least seven days after the previous trial.

Percent measurement error and the results of the repeated measures ANOVA for the radiographic measurements are reported in Table 3.6. Percent measurement error was higher for anterior sphenoid length and anterior cranial base length. However, all values were less than the general accepted level of 2%. For all variables, the results of the repeated measures ANOVA were not significant, indicating no significant difference between the values of the measurements taken in the three trials. Percent measurement error and the results of the repeated measures ANOVA for the cranial size measurements are reported in Table 3.7. Percent measurement error was relatively high for all variables except skull length, which had a very low percent measurement error. The percent measurement errors for all of the measurements other than palate length were below 2%. This may have resulted from difficulty in reliably locating the craniometric point,

[7] Groves (2001) does not assign a specific taxonomic rank to catarrhines (or platyrrhines).

TABLE 3.6. Percent measurement error and results of repeated measures ANOVA for the radiographic measurements used in this study.

		Repeated Meas. ANOVA	
VARIABLE	**Perc. Meas. Error**	**F**	**P**
Facial Projection 1	0.77%	0.002	0.998
Facial Projection 2	0.76%	0.000	>0.999
Cranial Base Angle 1	0.64%	0.004	0.996
Cranial Base Angle 2	0.37%	0.002	0.998
Upper Facial Length	0.34%	0.000	>0.999
Anterior Sphenoid Length	1.52%	0.028	0.972
Anterior Cranial Base Length	1.87%	0.003	0.997
Anterior Middle Cranial Fossa Length	0.86%	0.000	>0.999

TABLE 3.7. Percent measurement error and results of repeated measures ANOVA for the cranial size measurements used in this study.

		Repeated Meas. ANOVA	
Variable	**Perc. Meas. Error**	**F**	**P**
Skull Length	0.16%	<0.001	>0.999
Cranial Width	1.08%	0.025	0.975
Neurocranial Height	1.54%	0.093	0.911
Facial Height	1.24%	0.006	0.994
Palate Length	2.14%	0.063	0.939
Palate Width	1.26%	0.036	0.965

staphylion, in some specimens. Specifically, this error may be due to difficulty in reliably locating the line drawn between the posterior ends of the alveolar ridges (staphylion lies at the intersection of the with the intermaxillary suture) (see Table 3.3). Although the percent measurement error exceeded 2%, the magnitude of the measurement error was not deemed great enough to warrant omission; thus, palate length was not excluded from this study. For all cranial size variables, the results of the repeated measures ANOVA were not significant, indicating no significant difference between the values of the measurements taken in the three trials. The fact that the repeated measures ANOVA for palate length was strongly non-significant further

reinforces that the variation in this measurement due to intraobserver error is not statistically significant, further supporting the decision to retain this variable in all analyses.

CHAPTER 4—HYPOTHESES AND PREDICTIONS

This chapter lays out the hypotheses that will be tested in this dissertation. In addition, the corollary predictions and criteria of rejection for each hypothesis are presented.

HYPOTHESIS 1

Hypothesis 1 (H1): variation in facial projection (FP1 or FP2) is explained by variation in cranial base angle (CBA1 or CBA2) (Fig. 3.1).

Cranial Base Angle influences variation in facial projection because the base of the anterior cranial base forms the roof of the facial skeleton, and, due to this shared border, the anterior cranial base and the roof of the facial skeleton tend to rotate together as a relatively stable unit (Lieberman, 2000; McCarthy and Lieberman, 2001). Consequently, increased cranial base flexion (i.e., decrease in values of CBA) causes a concomitant ventral deflection of the upper facial skeleton, repositioning the upper face to a more posterior position relative to the anterior cranial base (i.e., a decrease in facial projection). Decreased cranial base flexion (i.e., increase in values of CBA), on the other hand, causes the upper face to be positioned more anteriorly relative to the anterior cranial base (i.e., an increase in facial projection).

Prediction 1 (P1): increases in cranial base angle (CBA1 or CBA2) will be associated with increases in facial projection (FP1 or FP2) (positive correlation).

Criteria for Rejection (CR1): (a) H1 will be rejected if the correlation between facial projection (FP1 or FP2) and cranial base angle (CBA 1 or CBA 2) is not significant (at $\alpha = 0.05$) or (b) if the correlation is significant and negative.

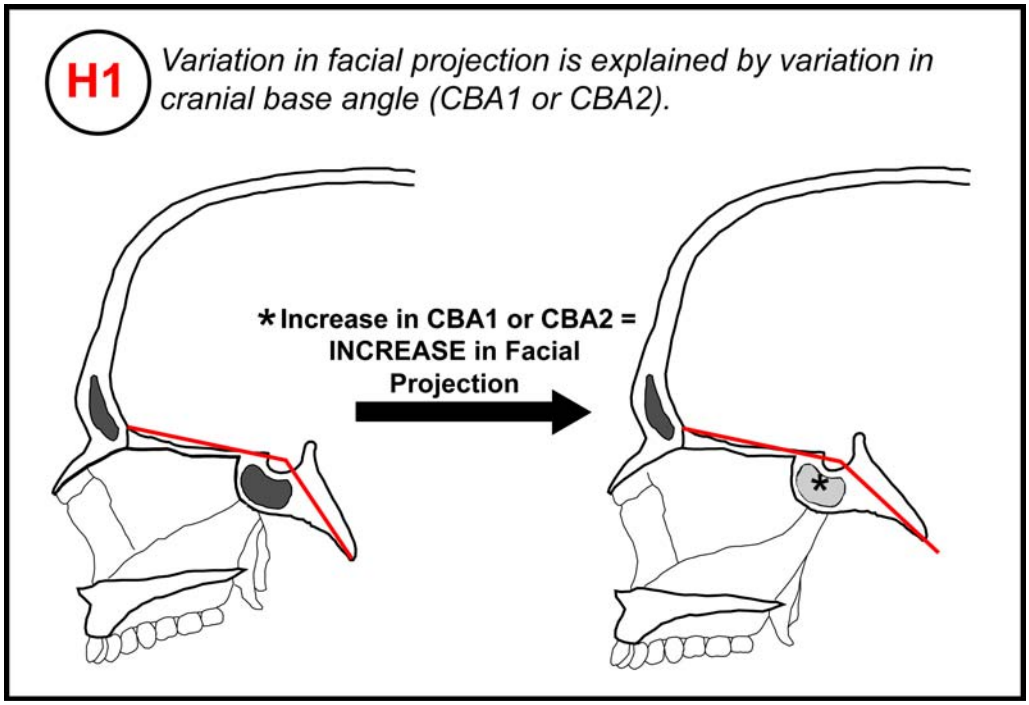


Figure 3.1. Visual depiction of Hypothesis 1 (H1). CBA1 (which is illustrated here) is ~15° greater in the cranium on the right, which also exhibits a greater degree of facial projection than the cranium on the left.

HYPOTHESIS 2

Hypothesis 2 (H2): variation in facial projection (FP1 or FP2) is explained by variation in upper facial length (UFL) (Fig. 3.2).

Upper facial length (i.e., the distance between the PM Plane and nasion) influences variation in facial projection because, all other variables being equal, the longer the anteroposterior dimension of the upper face is, the more the upper face will project anterior to the anterior cranial base. Thus, increases in the upper facial length are predicted to be associated with increases in facial projection.

Prediction 2 (P2): increases in upper facial length (UFL) will be associated with increases in facial projection (FP1 or FP2) (positive correlation).

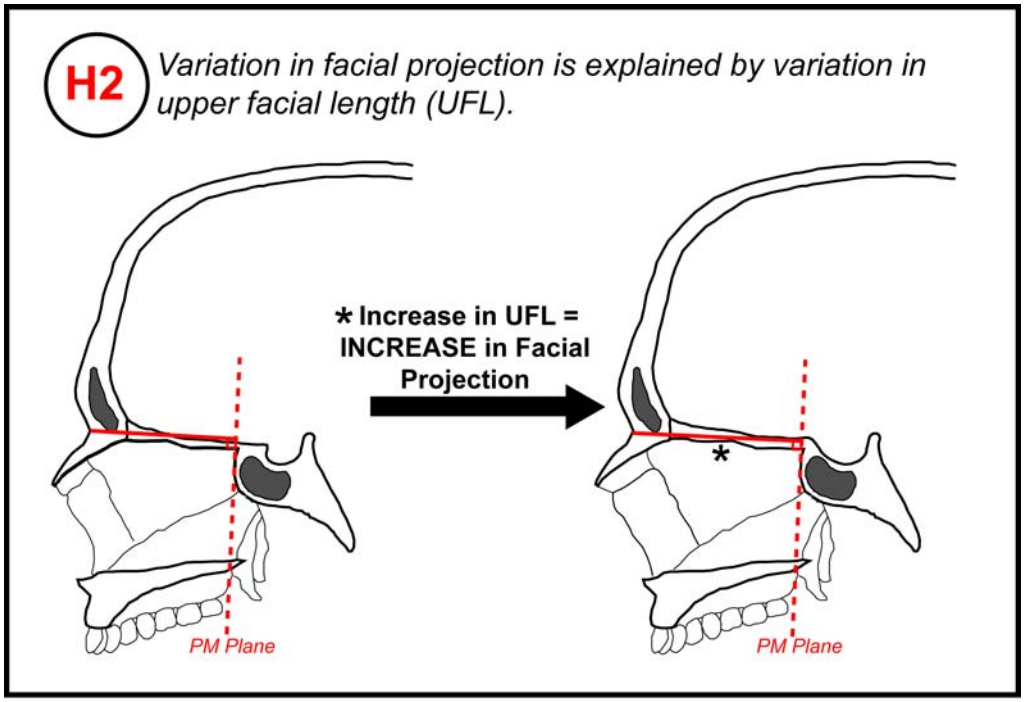


Figure 3.2. Visual depiction of Hypothesis 2 (H2). UFL is ~15% greater in the cranium on the right, which also exhibits a greater degree of facial projection than the cranium on the left.

Criteria for Rejection (CR2): (a) H1 will be rejected if the correlation between facial projection (FP1 or FP2) and upper facial length (UFL) is not significant (at $\alpha = 0.05$) or (b) if the correlation is significant and negative.

HYPOTHESIS 3

Hypothesis 3 (H3): variation in facial projection (FP1 or FP2) is explained by variation in anterior cranial base length (ACBL) (Fig. 3.3).

Anterior cranial base length affects variation in facial projection because, all other variables held constant, if the anterior cranial base length increases in length, a greater proportion of the anteroposterior dimension of the upper face (i.e., upper facial length) can fit below the anterior cranial fossa. Thus, when the anterior cranial base is longer, less of the upper face will project anterior to the anterior cranial base, resulting in reduced facial projection.

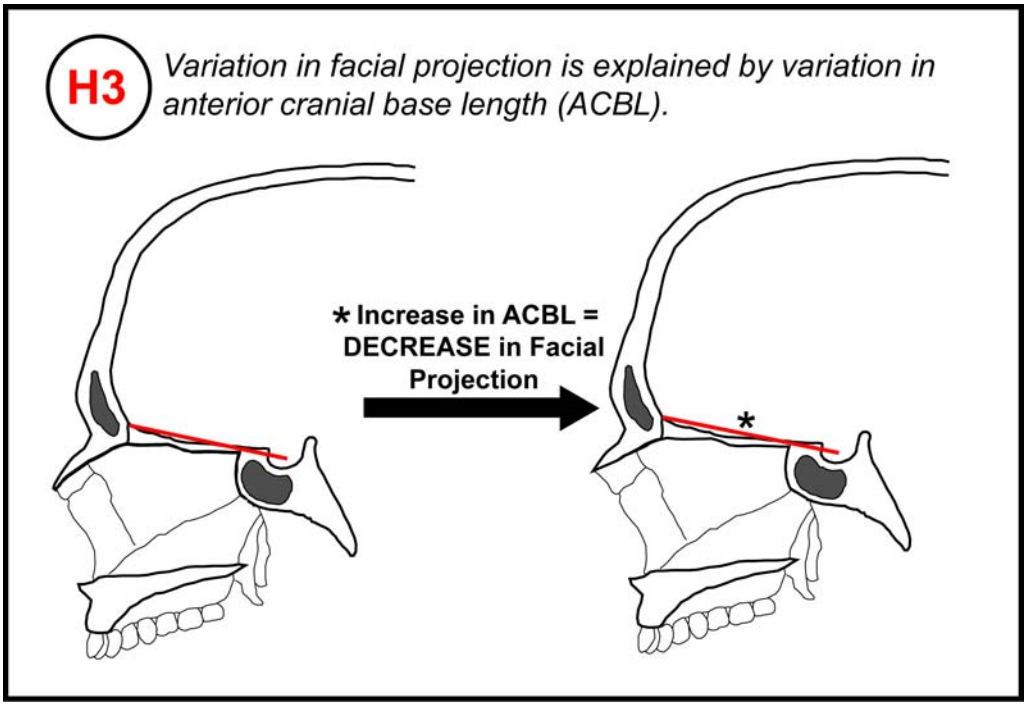


Figure 3.3. Visual depiction of Hypothesis 3 (H3). ACBL is ~30% greater in the cranium on the right, which also exhibits a greater degree of facial projection than the cranium on the left.

Prediction 3 (P3): increases in anterior cranial base length (ACBL) will be associated with decreases in facial projection (FP1 or FP2) (negative correlation).

Criteria for Rejection (CR3): (a) H1 will be rejected if the correlation between facial projection (FP1 or FP2) and anterior cranial base length (ACBL) is not significant (at $\alpha = 0.05$) or (b) if the correlation is significant and positive.

HYPOTHESIS 4

Hypothesis 4 (H4): variation in facial projection (FP1 or FP2) is explained by variation in anterior sphenoid length (ASL) (Fig. 3.4).

Anterior sphenoid length is predicted to influence facial projection because this distance determines the position of the PM Plane relative to sella—i.e., an increase in anterior sphenoid length "pushes" the PM Plane anteriorly (Lieberman, 2000). Because the PM Plane marks the posterior border of the facial block (including the upper face),

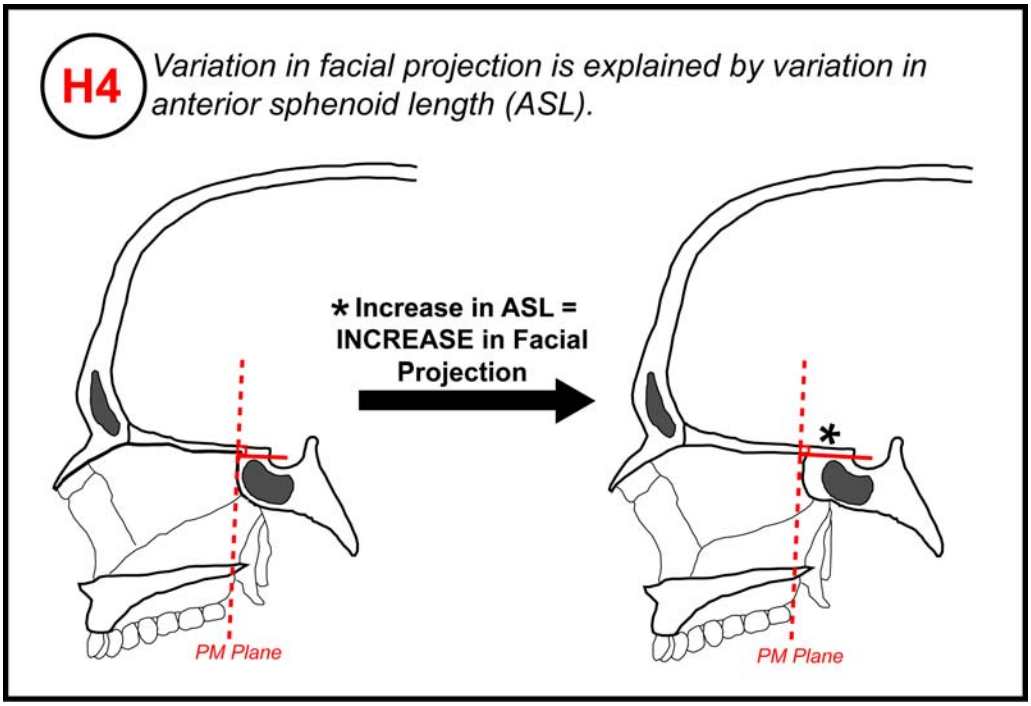


Figure 3.4. Visual depiction of Hypothesis 4 (H4). ASL is ~40% greater in the cranium on the right, which also exhibits a greater degree of facial projection than the cranium on the left.

when all other variables are held constant and anterior sphenoid length is relatively greater, the PM Plane will be more distant from sella, resulting in an increase in facial projection.

Prediction 4 (P4): increases in anterior sphenoid length (ASL) will be associated with increases in facial projection (FP1 or FP2) (positive correlation).

Criteria for Rejection (CR4): (a) H1 will be rejected if the correlation between facial projection (FP1 or FP2) and anterior sphenoid length (ASL) is not significant (at $\alpha = 0.05$) or (b) if the correlation is significant and negative.

HYPOTHESIS 5

Hypothesis 5 (H5): variation in facial projection (FP1 or FP2) is explained by variation in anterior middle cranial fossa length (AMCFL) (Fig. 3.5).

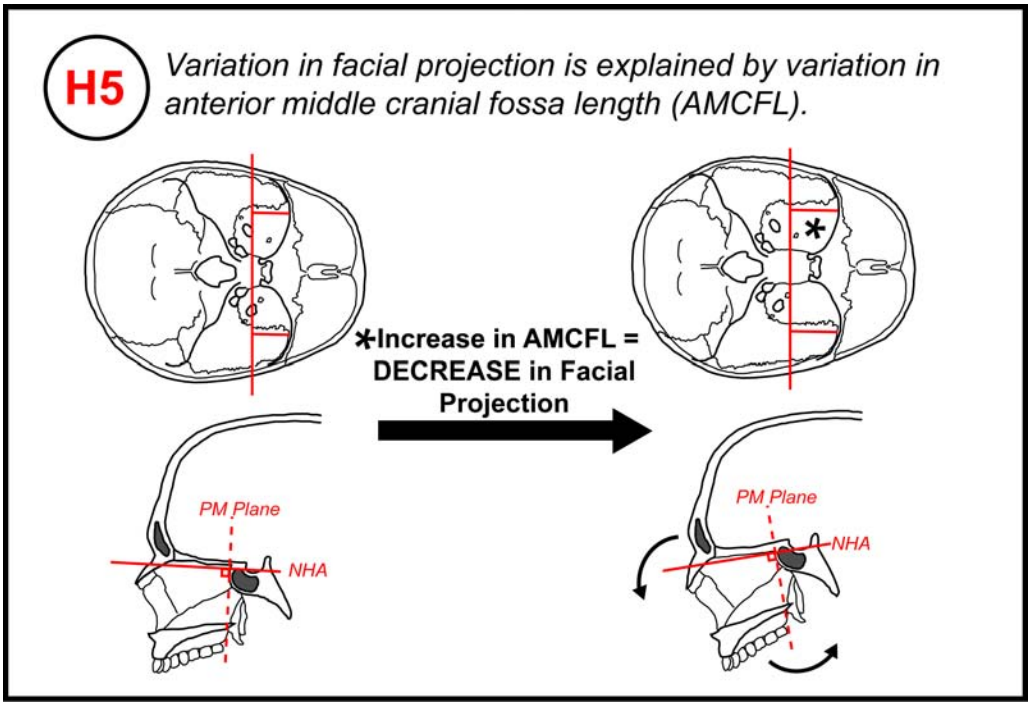


Figure 3.5. Visual depiction of Hypothesis 5 (H5). AMCFL is ~25% greater in the cranium on the right, which also exhibits a greater degree of facial projection than the cranium on the left.

Anterior middle cranial fossa affects variation in facial projection because increasing the length of the anterior middle cranial fossa may cause the PM Plane to rotate ventrally. This ventral rotation of the PM Plane, in turn, causes concomitant rotation of the NHA, resulting in decreased facial projection (see also McCarthy and Lieberman, 2001; McBratney-Owen and Lieberman, 2003; Lieberman, 2008; Bastir et al., 2011).

Prediction 5 (P5): increases in anterior middle cranial fossa length (AMCFL) will be associated with decreases in facial projection (FP1 or FP2) (negative correlation).

Criteria for Rejection (CR5): (a) H1 will be rejected if the correlation between facial projection (FP1 or FP2) and anterior middle cranial fossa length (AMCFL) is not significant (at $\alpha = 0.05$) or (b) if the correlation is significant and positive.

CHAPTER 5—RESULTS

This chapter reports the results of the analytical procedures outlined in the Chapter 3. The chapter begins with a brief overview of the data on facial projection and the results of tests of sexual dimorphism and correlation of variables. This chapter also reports the results of the univariate and multivariate PGLS regression analyses, as well as the results of analyses designed to evaluate the position of *Homo sapiens* relative to patterns in the univariate and multivariate regression analyses.

VARIATION IN FACIAL PROJECTION IN ANTHROPOID PRIMATES

Figure 5.1 presents data on facial projection (FP1 and FP2) using shape-ratios for size adjustment. Based on visual inspection, using this method of size adjustment, platyrrhines, appear to have somewhat greater values for facial projection[1] than catarrhines in FP1 and FP2. For FP1, there is no apparent difference in either measure between hominoids and cercopithecoids (i.e., non-hominoid catarrhines). However, for FP2, cercopithecoids seem to have values for facial projection intermediate between platyrrhines (which are greater than cercopithecoids) and hominoids (which are less than cercopithecoids).

There is not a close agreement between the two measures of facial projection (i.e., FP1 and FP2) using shape-ratios for size adjustment. This is evidenced by the lack of correlation between these measures (see below), but can also be demonstrated by

[1] The majority of analyses (i.e., all analyses except multivariate analyses using cranial size as an independent variable for size adjustment) use size-adjusted variables. For this reason, variables will be referenced without the prefix, "size-adjusted" throughout this chapter. All variables are size-adjusted unless otherwise indicated.

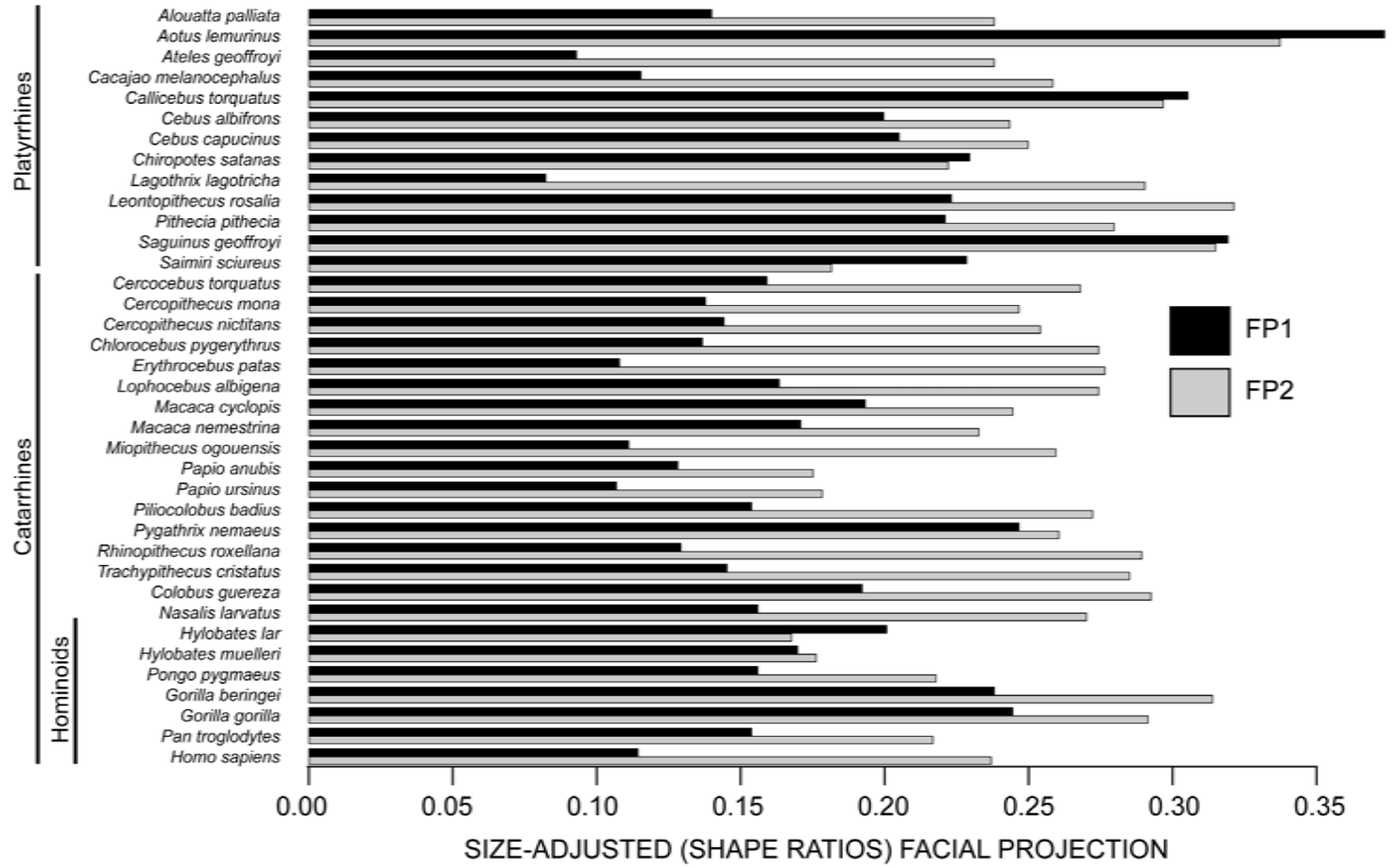


Figure 5.1. Bar chart of size-adjusted facial projection using shape-ratios for size adjustment.

examining the species with the highest and lowest values for facial projection using the two different measures. For FP1, *Aotus lemurinus* has the highest value for facial projection, followed by *Saguinus geoffroyi*, *Callicebus torquatus*, *Pygathrix nemaeus*, and *Gorilla gorilla*. The species with the lowest value for facial projection using FP1 is *Lagothrix lagotricha*, followed by *Ateles geoffroyi*, *Papio ursinus*, *Erythrocebus patas*, and *Miopithecus ogouensis*. For FP2, *Aotus lemurinus* has the highest value for facial projection, followed by *Leontopithecus rosalia*, *Gorilla beringei*, *Saguinus geoffroyi*, and *Callicebus torquatus.* The species with the lowest value for facial projection using FP2 is *Hylobates lar*, followed by *Papio anubis*, *Hylobates muelleri*, *Papio ursinus*, and *Saimiri sciureus*. *Homo sapiens* does not have the lowest value for facial projection for either FP1 or FP2, when shape-ratios are used for size adjustment.

Figure 5.2 presents data on facial projection (FP1 and FP2) using phylogenetically-controlled residuals for size adjustment. Compared to cercopithecoids, platyrrhines have higher values for FP1, as most values for this group are positive. In cercopithecoids, by contrast, most values for FP1 are negative. Hominoids have roughly equal numbers of positive and negative values and include both large negative and large positive values for FP1. For FP2, there are no clear differences between the groups. However, platyrrhines appear to be less variable than hominoids. With the exception of *Papio anubis* and *Papio ursinus*, which have large negative values, cercopithecoids are also less variable than hominoids for FP2.

There is also no close agreement between the two measures of facial projection (i.e., FP1 and FP2) using phylogenetically-controlled residuals for size adjustment. Again, this is evidenced by the lack of correlation between these measures (see below).

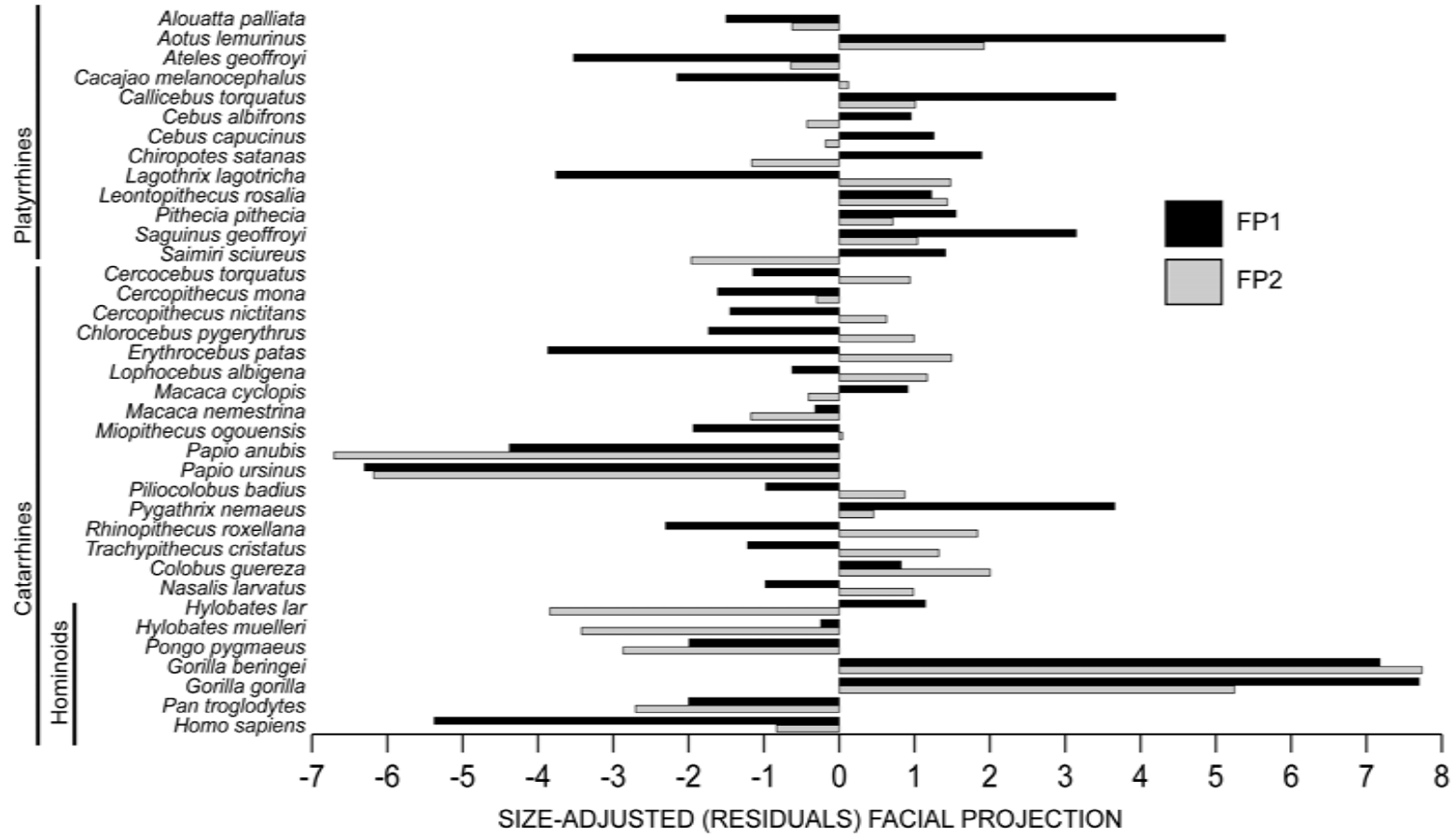


Figure 5.2. Bar chart of size-adjusted facial projection using phylogenetically-controlled residuals for size adjustment.

Using FP1, *Gorilla gorilla* has the highest value for facial projection, followed by *Gorilla beringei*, *Aotus lemurinus*, *Callicebus torquatus*, and *Pygathrix nemaeus*. The species with the lowest value for facial projection using FP1 is *Papio ursinus*, followed by *Homo sapiens*, *Papio anubis*, *Erythrocebus patas*, and *Lagothrix lagotricha.* Using FP2, *Gorilla beringei* has the highest value for facial projection, followed by *G. gorilla*, *Colobus guereza*, *Aotus lemurinus*, and *Rhinopithecus roxellana.* The species with the lowest value for facial projection using FP2 is *Papio anubis*, followed by *P. ursinus*, *Hylobates lar*, *H. muelleri*, and *Pongo pygmaeus*. As with the results for shape-ratios, *Homo sapiens* does not have the lowest value for facial projection for FP1 or FP2 when phylogenetically-controlled residuals are used for size adjustment.

These comparisons also make it clear that the results vary depending on the method used for size adjustment. There is generally no agreement between FP1 and FP2 regardless of whether shape-ratios or phylogenetically-controlled residuals are used for size correction.

Species mean data for all variables are reported in Appendix B.

SEXUAL DIMORPHISM

As discussed in Chapter 3, sexual dimorphism is generally not prevalent in the sample used for this dissertation. Using shape-ratios for size adjustment, the total proportion of significant tests of sexual dimorphism (i.e., considering the number of variable-plus-species combinations that show significant differences between sexes as a proportion of all variable-plus-species combinations [minus variable-plus-species combinations in which small sample sizes precluded comparison]), is 21/234 (9.0%).

Using phylogenetically-controlled residuals, the total proportion of significant tests of sexual dimorphism is 6/191 (3.1%).

There is no clear phylogenetic/taxonomic pattern in sexual dimorphism using either method of size adjustment. Using phylogenetically-controlled residuals, sexual dimorphism is somewhat more prevalent in platyrrhines than catarrhines; however, due to the very low prevalence of sexual dimorphism using this method of size adjustment, this pattern is probably not remarkable. Results of test of sexual dimorphism are reported in Appendix A.

CORRELATION OF VARIABLES

As discussed in Chapter 3, tests of correlation among the variables employed here were carried out for two reasons: (1) to assess the degree of multicollinearity in the multivariate PGLS regression analyses; and (2) to gauge the degree of correlation between variables that are alternative methods for measuring the same anatomical phenomenon—i.e., facial projection (FP1 and FP2), cranial base angle (CBA1 and CBA2), and ASL and AMCFL.

The results of tests of correlation among variables are reported in Appendix C. In general, correlation among the variables is most prevalent when the raw data are considered. This prevalence is relevant to the multivariate PGLS regression analyses that use cranial size as an independent variable as the method for size adjustment, as the raw data are used in these regressions. Correlation among variables is somewhat more prevalent when shape-ratios are used for size adjustment than when phylogenetically-controlled residuals are used.

Table 5.1 reports the results of correlation of sets of variables that are alternative methods for measuring the same anatomical phenomenon. In all units of analysis (i.e., in anthropoids, platyrrhines, catarrhines, and hominoids) and using both methods of size adjustment (i.e., shape-ratios and phylogenetically-controlled residuals), the correlations between CBA1 and CBA2 are highly significant. Likewise, the correlations between ASL and AMCFL are highly significant in all units of analysis and using both methods of size adjustment. However, FP1 and FP2 are not correlated in any unit of analysis when shape-ratios are used for size adjustment, although the correlation approaches significance in anthropoids and platyrrhines. When phylogenetically-controlled residuals are used for size adjustment, FP1 and FP2 are correlated in platyrrhines and hominoids. Thus, it seems that FP1 and FP2 are correlated when phylogenetically-controlled residuals are used for size adjustment, but not when shape-ratios are used.

UNIVARIATE ANALYSES

The results of the univariate PGLS regression analyses are presented in Table 5.2. They show that upper facial length (UFL) is the independent variable that is most often significantly correlated with facial projection. Specifically, UFL is correlated with facial projection in every case except five—i.e., in catarrhines and hominoids using shape-ratios for size adjustment and FP1 as the measure of facial projection, in hominoids using shape-ratios for size adjustment and FP2 as the measure of facial projection, and in platyrrhines and hominoids using phylogenetically-controlled residuals for size adjustment and FP1 as the measure of facial projection. Cranial base angle (measured either as CBA1 or CBA2), ASL, and AMCFL are also correlated with facial projection in

TABLE 5.1. Correlation of variables (FP1 v. FP2, CBA1 v. CBA2, and ASL v. AMCFL). Bolded results are significant at $\alpha = 0.05$.

Size-Adjustment Method: Shape-Ratios						
	FP1 v. FP2		**CBA1 v. CBA2**		**ASL v. AMCFL**	
Unit of Analysis	***r***	***p***	***r***	***p***	***r***	***p***
Anthropoids	0.29	0.07	**0.86**	**<0.01**	**0.83**	**<0.01**
Platyrrhines	0.51	0.06	**0.87**	**<0.01**	**0.76**	**<0.01**
Catarrhines	0.18	0.39	**0.76**	**<0.01**	**0.92**	**<0.01**
Hominoids	0.48	0.23	**0.88**	**<0.01**	**0.90**	**0.01**

Size-Adjustment Method: Phylogenetically-Controlled Residuals						
	FP1 v. FP2		**CBA1 v. CBA2**		**ASL v. AMCFL**	
Unit of Analysis	***r***	***p***	***r***	***p***	***r***	***p***
Anthropoids	0.09	0.58	**0.86**	**<0.01**	**0.87**	**<0.01**
Platyrrhines	**0.56**	**0.04**	**0.87**	**<0.01**	**0.85**	**<0.01**
Catarrhines	-0.08	0.70	**0.76**	**<0.01**	**0.87**	**<0.01**
Hominoids	**0.80**	**0.02**	**0.88**	**<0.01**	**0.91**	**0.01**

TABLE 5.2. Results of univariate PGLS regression analyses. Bolded values are significant at $\alpha = 0.05$. Italicized results indicate that the data were log_{10} transformed. Results in blue indicate that the data were transformed using the Box-Cox transformation. Highlighted results were not normal after transformation. 'NA' denotes comparisons that could not be made due to small sample size.

Size-Adjustment Method: Shape-Ratios

	FP1 v. CBA1					FP1 v. CBA2					FP1 v. ACBL					FP1 v. UFL					FP1 v. ASL					FP1 v. AMCFL				
Unit of Analysis	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***
Anthropoids	37	0.89	0.24	0.15	0.06	37	0.89	0.23	0.16	0.05	37	0.87	0.16	0.36	0.02	**37**	**0.76**	**0.41**	**0.01**	**0.17**	*37*	*0.74*	*0.32*	*0.05*	*0.10*	35	0.87	0.16	0.36	0.02
Platyrrhines	13	0.81	0.29	0.33	0.09	13	0.76	0.31	0.30	0.10	13	0.40	0.58	0.04	0.34	**13**	**0.04**	**0.82**	**<0.01**	**0.66**	13	0.75	-0.23	0.46	0.05	**13**	**0.60**	**-0.56**	**0.05**	**0.32**
Catarrhines	24	0.48	0.30	0.16	0.09	24	0.87	0.33	0.11	0.11	24	0.21	-0.06	0.79	0.00	24	0.24	0.09	0.68	0.01	24	0.20	0.04	0.84	0.00	22	0.00	0.16	0.47	0.03
Hominoids	7	1.00	0.58	0.17	0.34	7	0.00	0.61	0.15	0.37	7	1.00	-0.39	0.38	0.15	7	0.00	0.09	0.85	0.01	7	1.00	-0.43	0.34	0.19	NA	NA	NA	NA	NA

	FP2 v. CBA1					FP2 v. CBA2					FP2 v. ACBL					FP2 v. UFL					FP2 v. ASL					FP2 v. AMCFL				
Unit of Analysis	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***
Anthropoids	37	0.97	0.19	0.25	0.04	37	0.96	0.19	0.27	0.03	37	0.95	0.19	0.27	0.03	**37**	**1.00**	**0.61**	**<0.01**	**0.37**	37	0.98	0.15	0.36	0.02	35	0.96	0.13	0.44	0.02
Platyrrhines	13	0.71	0.43	0.14	0.19	13	0.88	0.25	0.41	0.06	13	0.92	0.01	0.96	0.00	**13**	**0.00**	**0.72**	**0.01**	**0.51**	13	0.92	0.05	0.88	0.00	13	0.87	-0.28	0.36	0.08
Catarrhines	24	0.95	0.18	0.40	0.03	24	0.89	0.21	0.33	0.04	24	1.00	0.12	0.56	0.02	**24**	**1.00**	**0.57**	**<0.01**	**0.32**	24	1.00	0.21	0.32	0.05	22	1.00	0.45	0.04	0.20
Hominoids	7	1.00	-0.04	0.93	<0.01	7	1.00	-0.03	0.94	0.00	7	1.00	-0.66	0.10	0.44	7	1.00	-0.26	0.57	0.07	7	1.00	-0.29	0.54	0.08	NA	NA	NA	NA	NA

Size-Adjustment Method: Phylogenetically-Controlled Residuals

	FP1 v. CBA1					FP1 v. CBA2					FP1 v. ACBL					FP1 v. UFL					FP1 v. ASL					FP1 v. AMCFL				
Unit of Analysis	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***
Anthropoids	**37**	**0.00**	**0.37**	**0.02**	**0.14**	**37**	**0.76**	**0.40**	**0.01**	**0.16**	37	0.56	-0.26	0.11	0.07	**37**	**0.27**	**0.36**	**0.03**	**0.13**	37	0.30	-0.15	0.38	0.02	35	0.00	-0.28	0.11	0.08
Platyrrhines	13	0.42	0.49	0.09	0.24	13	0.21	0.49	0.09	0.24	13	0.00	-0.01	0.99	0.00	13	0.02	0.34	0.26	0.12	**13**	**0.00**	**0.68**	**0.01**	**0.47**	13	0.13	-0.51	0.07	0.26
Catarrhines	24	0.17	0.37	0.07	0.14	**24**	**0.69**	**0.44**	**0.03**	**0.20**	24	0.00	0.09	0.67	0.01	**24**	**0.00**	**0.57**	**<0.01**	**0.32**	24	0.00	0.19	0.37	0.04	22	0.00	-0.06	0.81	0.00
Hominoids	7	1.00	0.68	0.09	0.47	7	1.00	0.69	0.09	0.47	7	1.00	-0.32	0.48	0.10	7	1.00	0.62	0.14	0.39	7	1.00	-0.34	0.45	0.12	NA	NA	NA	NA	NA

	FP2 v. CBA1					FP2 v. CBA2					FP2 v. ACBL					FP2 v. UFL					FP2 v. ASL					FP2 v. AMCFL				
Unit of Analysis	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***	**N**	**ML**	***r***	***p***	***r²***
Anthropoids	37	0.76	0.19	0.26	0.04	37	0.72	0.23	0.17	0.05	37	0.00	-0.04	0.80	0.00	**37**	**0.55**	**0.69**	**<0.01**	**0.48**	37	0.00	0.21	0.22	0.04	35	0.00	0.08	0.63	0.01
Platyrrhines	24	1.00	0.17	0.43	0.03	24	0.97	0.18	0.41	0.03	22	1.00	-0.18	0.41	0.03	**24**	**0.00**	**0.76**	**<0.01**	**0.58**	***24***	***0.00***	***0.62***	***<0.01***	***0.38***	22	1.00	0.41	0.06	0.17
Catarrhines	13	0.00	0.52	0.07	0.27	13	0.00	0.28	0.35	0.08	13	0.52	-0.42	0.16	0.17	**13**	**0.00**	**0.61**	**0.03**	**0.38**	13	0.00	0.09	0.76	0.01	13	0.00	-0.10	0.76	0.01
Hominoids	7	0.84	0.13	0.78	0.02	7	0.00	0.42	0.35	0.17	7	1.00	-0.27	0.55	0.08	**7**	**0.18**	**0.82**	**0.02**	**0.68**	7	0.89	-0.02	0.96	0.00	NA	NA	NA	NA	NA

some cases; however, these variables are less frequently correlated with facial projection than is UFL.

These patterns are also evident in Figure 5.3, which is a "heat map" of the results of the univariate PGLS regression analyses. This figure shows the strength of the correlations in each unit of analysis using both measures of facial projection and both methods of size adjustment. It is clear that, by and large, UFL is moderately to strongly correlated with facial projection (orange and red, respectively in Figure 5.3). CBA1 and CBA2 are weakly correlated with facial projection in the few cases in which the correlation between these variables is significant. ASL and AMCFL are moderately correlated with facial projection in the few cases in which the correlations with facial projection are significant. This figure also shows that the correlations between the independent variables and facial projection are more frequent in cases in which phylogenetically-controlled residuals are used for size adjustment vis-à-vis cases in which shape-ratios are used for size adjustment.

Figure 5.4 is another heat map illustrating the results of the univariate PGLS regression analyses. Unlike Figure 5.3, which is organized according to methods of size adjustment and facial projection measurement, Figure 5.4 is organized by taxonomic group. This figure shows that, in analyses of anthropoids, independent variables that are significantly correlated with facial projection in anthropoids are generally more weakly correlated with facial projection than in other groups. This figure also shows that, among analyses of hominoids, there is only one case in which an independent variable is significantly correlated with facial projection (i.e., UFL when phylogenetically-controlled

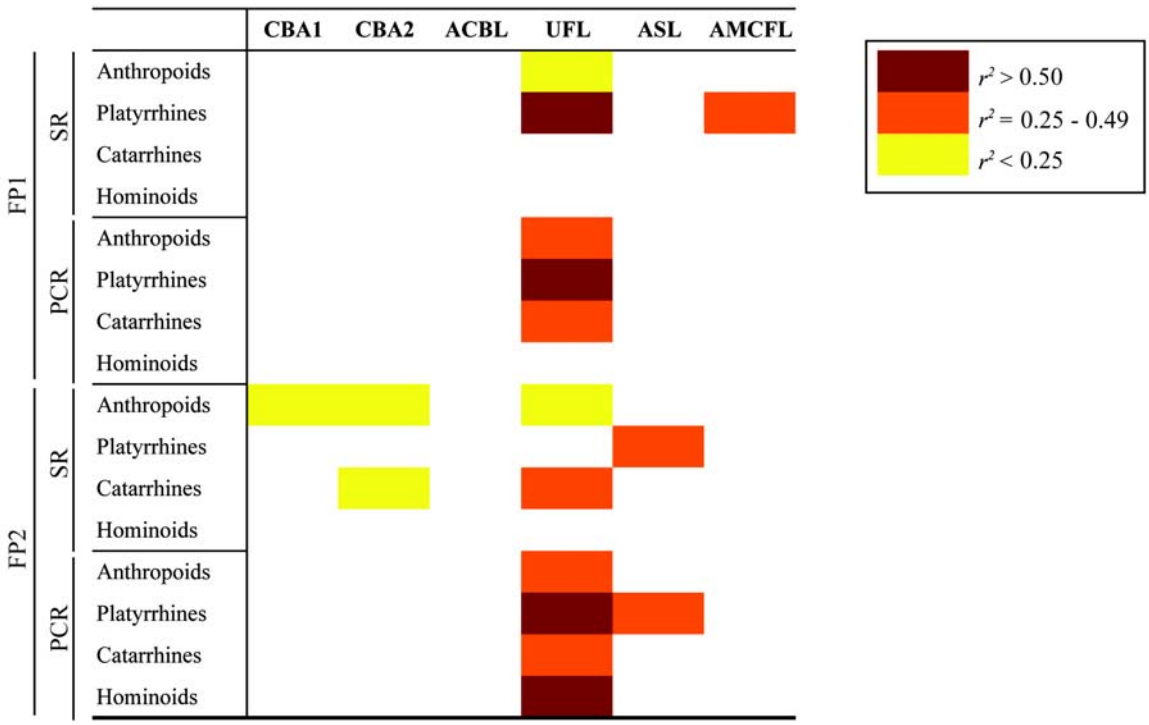


Figure 5.3. 'Heat map' of univariate PGLS regression analyses. Non-significant results and comparisons that could not be made due to small sample sizes are colored white. Significant results are colored yellow ($r^2 < 0.25$), orange ($r^2 = 0.25 – 0.50$), or red ($r^2 > 0.50$). The size adjustment methods (i.e., shape-ratios [SR] or phylogenetically-controlled residuals [PCR]) and the dependent variables (i.e., FP1 or FP2) are indicated on the left side of the figure.

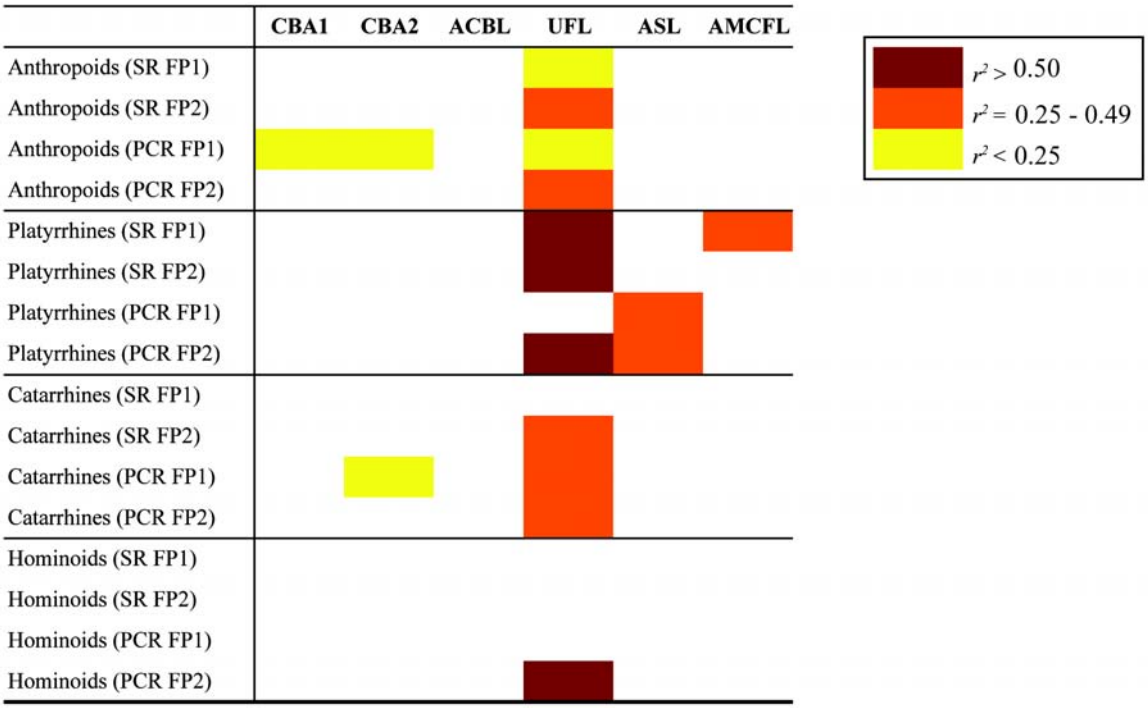


Figure 5.4. 'Heat map' of univariate PGLS regression analyses organized by unit of analysis. Non-significant results and comparisons that could not be made due to small sample sizes are colored white. Significant results are colored yellow ($r^2 < 0.25$), orange ($r^2 = 0.25 – 0.50$), or red ($r^2 > 0.50$). The size adjustment methods (i.e., shape-ratios [SR] or phylogenetically-controlled residuals [PCR]) and the dependent variables (i.e., FP1 or FP2) are indicated on the left side of the figure.

residuals are used for size adjustment and FP2 is used as the measure of facial projection).

Figures 5.5-5.8 are scatterplots of facial projection versus UFL in anthropoids. Figure 5.5 plots FP1 (using shape-ratios for size adjustment) against UFL (using shape-ratios for size adjustment). The relatively wide scatter of the data points around the regression line (as well as the relatively low value of r^2 for this comparison) demonstrates that, while UFL is the best predictor of FP1 in this case, it is only weakly correlated with FP1 ($r^2 = 0.17$. This figure also reiterates the fact that there is no clear phylogenetic pattern in FP1. The only phylogenetic pattern in UFL in this case is that most platyrrhines have higher values for this variable than catarrhines. *Aotus lemurinus* is a possible outlier in the positive direction in this relationship. The phylogenetic signal (indicated by the value ML λ) for this relationship is moderately strong (i.e., 0.76).

Figure 5.6 plots FP2 (using shape-ratios for size adjustment) against UFL (using shape-ratios for size adjustment). As with FP1, the relationship between these two variables is significant but relatively weak ($r^2 = 0.37$). In this relationship, *Saimiri sciureus*, *Hylobates lar*, and *H. muelleri* are possible negative outliers, whereas *Gorilla gorilla* is a possible positive outlier. The phylogenetic signal of this bivariate relationship is very strong, as indicated by the value for ML λ (i.e., 1.00).

Figure 5.7 plots FP1 (using phylogenetically-controlled residuals for size adjustment) against UFL (using phylogenetically-controlled residuals for size adjustment). As in the previous two plots, this relationship is significant but relatively weak ($r^2 = 0.13$). *Gorilla gorilla* and *G. beringei* are possible positive outliers in this

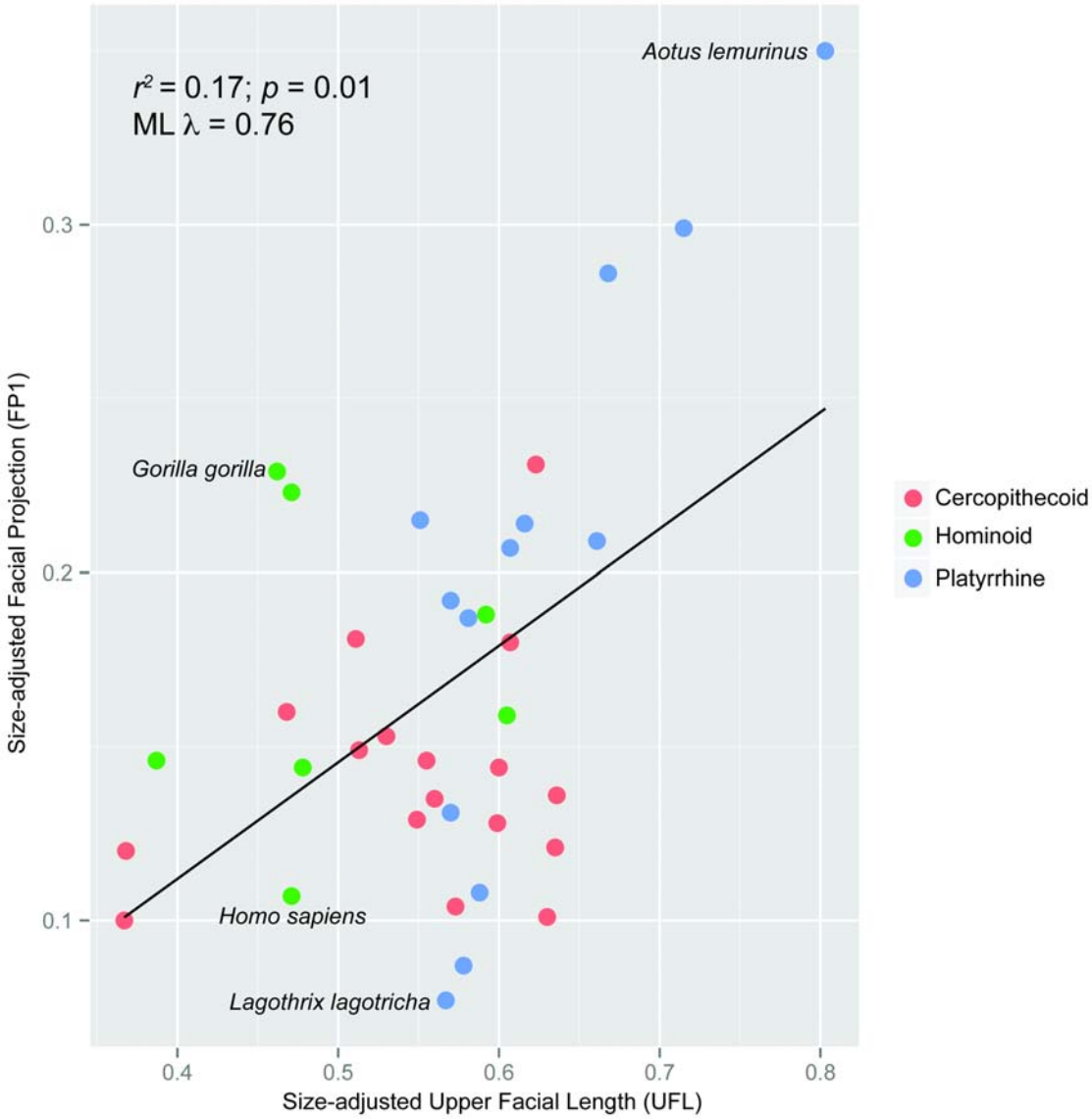


Figure 5.5. Scatterplot of size-adjusted facial projection (FP1) versus size-adjusted upper facial length (UFL) in anthropoids. Shape-ratios were used for size adjustment.

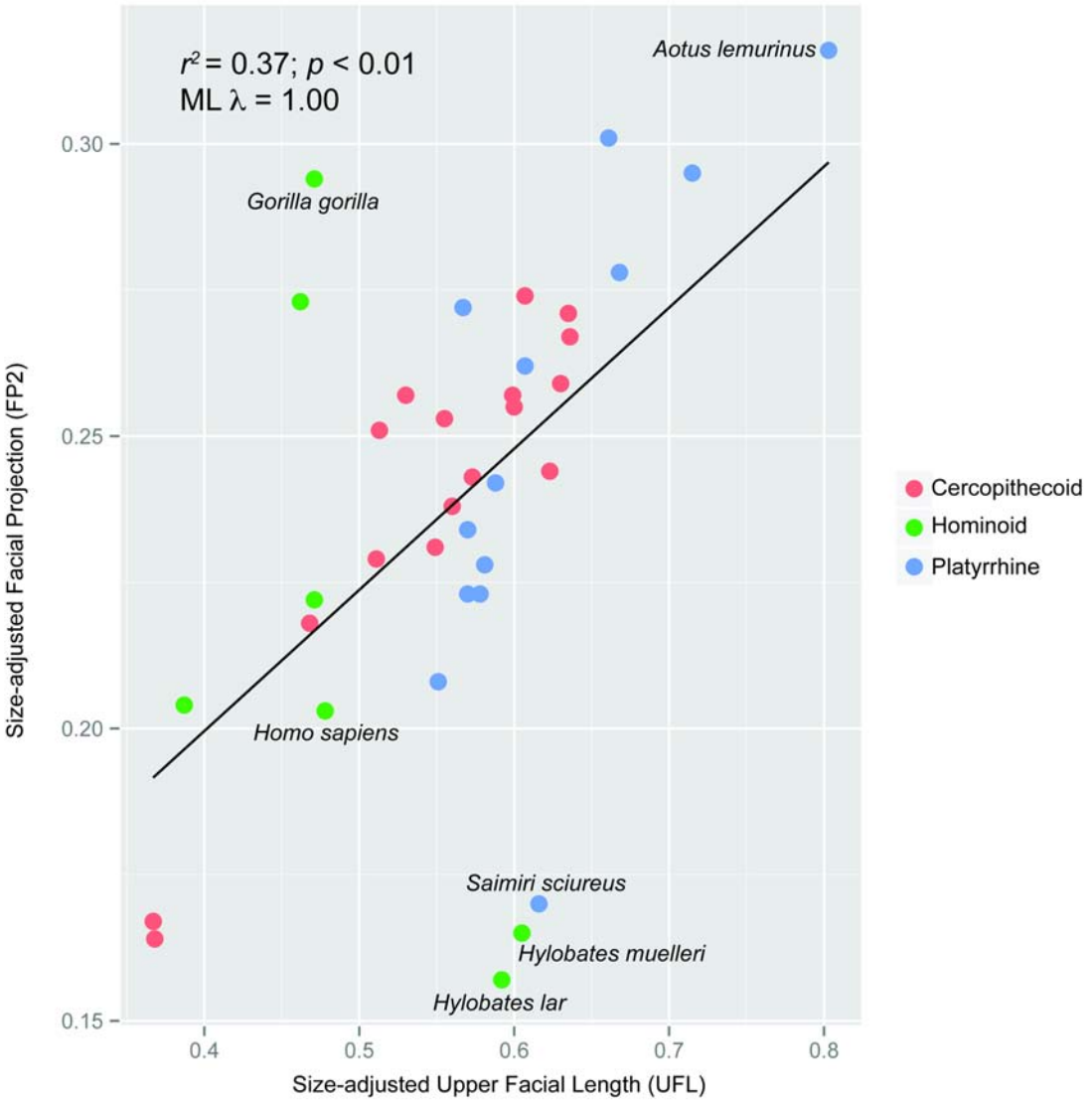


Figure 5.6. Scatterplot of size-adjusted facial projection (FP2) versus size-adjusted upper facial length (UFL) in anthropoids. Shape-ratios were used for size adjustment.

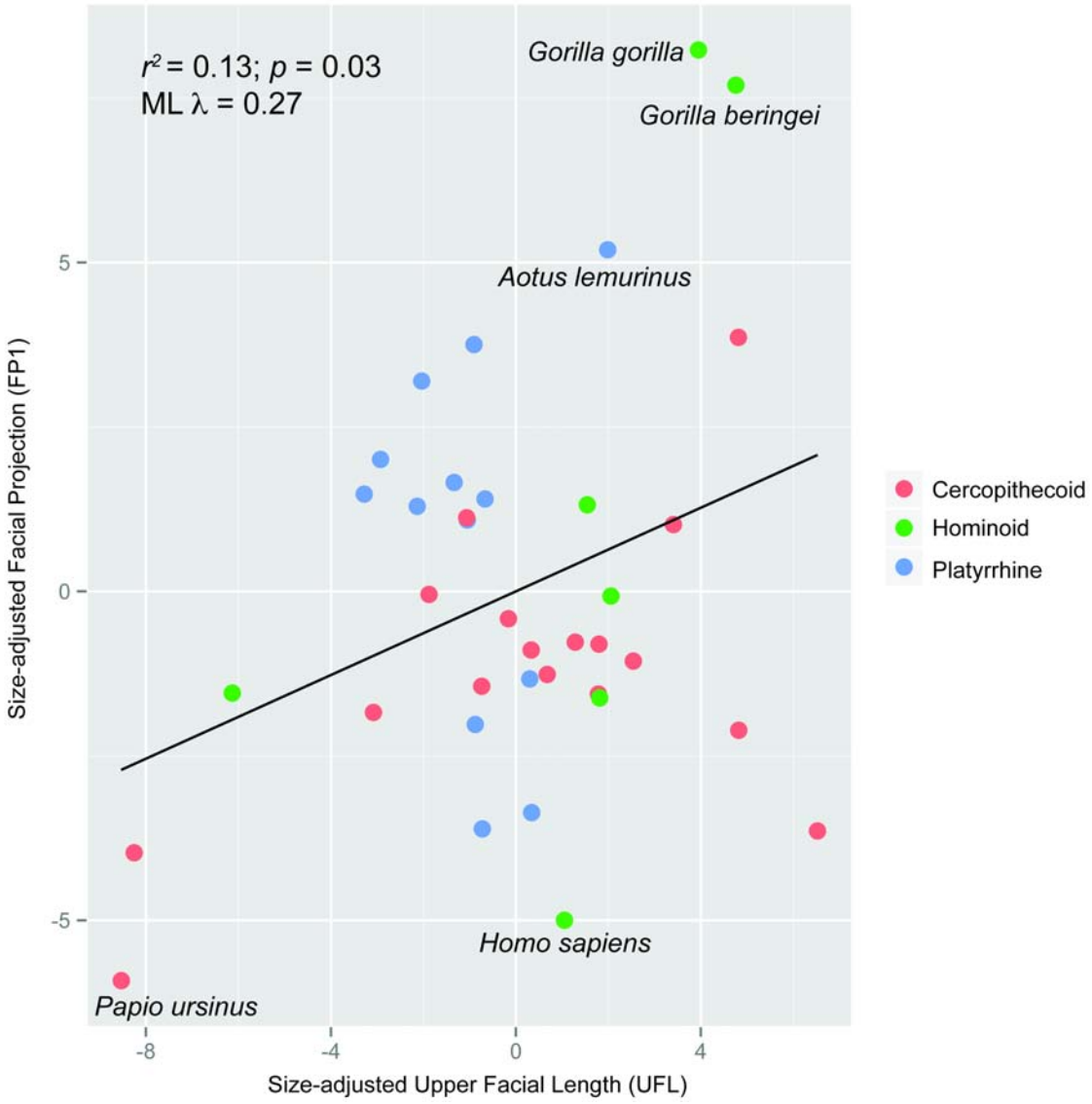


Figure 5.7. Scatterplot of size-adjusted facial projection (FP1) versus size-adjusted upper facial length (UFL) in anthropoids. Phylogenetically-controlled residuals were used for size adjustment.

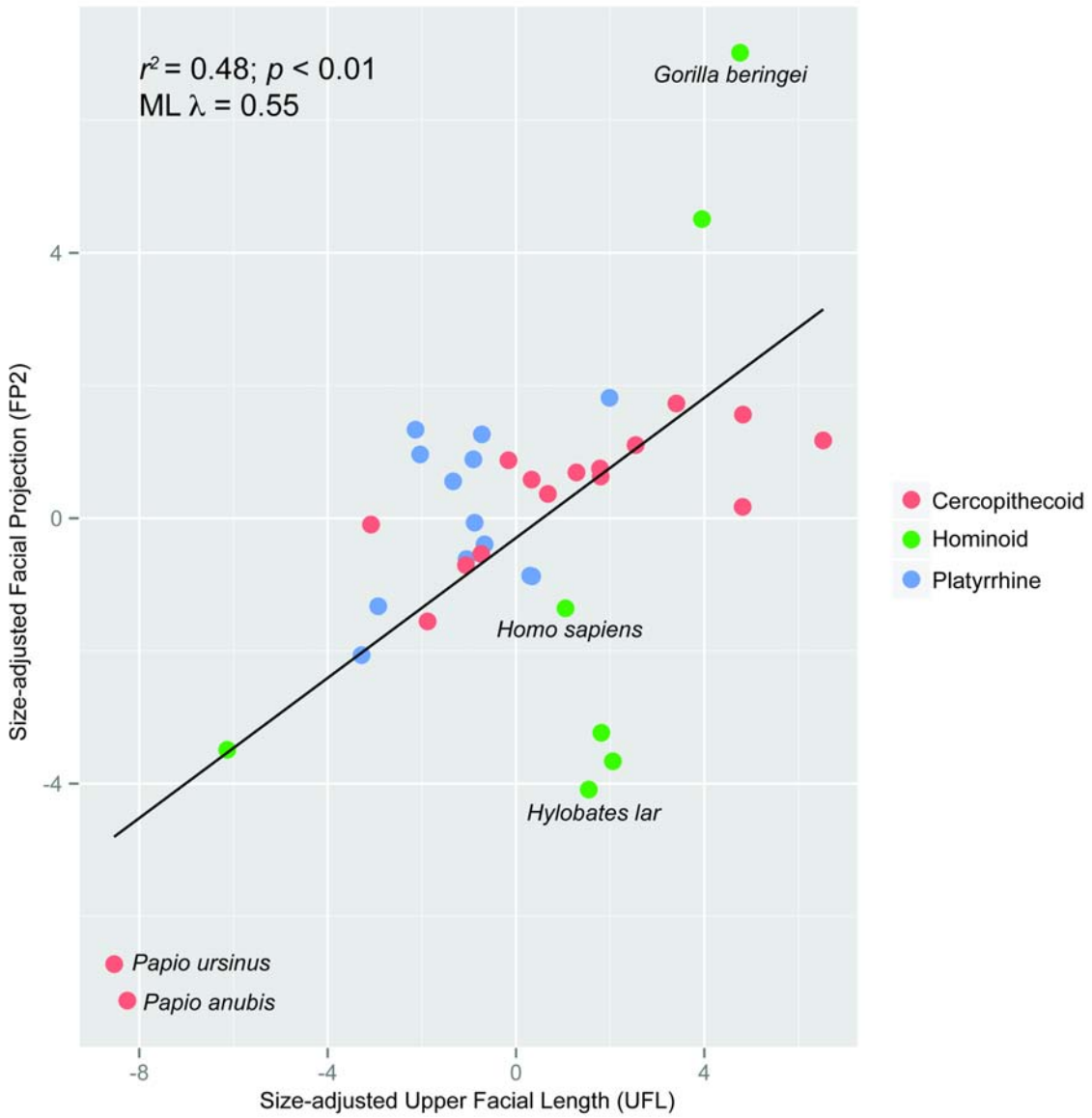


Figure 5.8. Scatterplot of size-adjusted facial projection (FP2) versus size-adjusted upper facial length (UFL) in anthropoids. Phylogenetically-controlled residuals were used for size adjustment.

relationship; *Homo sapiens* and *Papio ursinus* are possible negative outliers. The phylogenetic signal in this relationship is relatively weak (ML $\lambda = 0.17$).

Figure 5.8 is a scatterplot of FP2 (using phylogenetically-controlled residuals for size adjustment) against UFL (using phylogenetically-controlled residuals for size adjustment). This relationship is somewhat tighter than those described above ($r^2 = 0.48$). However, the relationship is still relatively weak, as variation in UFL explains less than half of the variation in FP2, as indicated by the value for r^2. In this plot, *Gorilla beringei* appears to be a positive outlier, and *Hylobates lar* appears to be a negative outlier.

In sum, the univariate PGLS regression analyses demonstrate that UFL is the single best predictor of facial projection in nearly all cases. However, the correlations in each case are relatively weak, and a large proportion of the variation in facial projection is left unexplained in these analyses.

MULTIVARIATE ANALYSES

The results of the multivariate PGLS regression analyses are presented in Tables 5.3-5.8. These tables are organized according to the method of size adjustment (i.e., shape-ratios, phylogenetically-controlled residuals, and cranial size used as an independent variable) and the measure of facial projection (i.e., FP1 and FP2).
In each of these tables, results are reported separated by model. These models are as follows (see Chapter 3 for more information):

(1) Model 1: CBA1, UFL, ASL, and ACBL

(2) Model 2: CBA1, UFL, AMCFL, and ACBL

(3) Model 3: CBA2, UFL, ASL, and ACBL; and

TABLE 5.3. Results of multivariate PGLS regression analyses using shape-ratios for size adjustment and with FP1 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Shape-Ratios

Dependent Variable: FP1

MODEL 1

	WHOLE MODEL				CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	37	0.70	0.15	0.05	0.71	+	NA	0.38	-	NA	0.03	+	NA	0.71	-	NA
Platyrrhines	**13**	**0.00**	**0.59**	**0.02**	0.93	-	NA	0.32	+	NA	0.14	+	NA	0.25	-	NA
Catarrhines	24	*1.00*	*0.20*	*0.10*	*0.16*	+	NA	*0.03*	-	NA	*0.64*	+	NA	***0.03***	**+**	**NA**
Hominoids	7	0.00	0.76	0.16	0.15	+	NA	0.07	+	NA	0.09	+	NA	0.22	+	NA

MODEL 2

	WHOLE MODEL				CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.42**	**<0.01**	0.91	+	NA	0.08	+	NA	0.63	+	NA	**0.01**	**-**	**0.24**
Platyrrhines	**13**	**0.00**	**0.56**	**0.03**	0.72	-	NA	0.46	+	NA	0.32	+	NA	0.39	-	NA
Catarrhines	22	0.00	-0.07	0.64	0.68	+	NA	0.39	+	NA	0.74	-	NA	0.60	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	37	0.69	0.15	0.05	0.83	+	NA	0.38	-	NA	**0.02**	**+**	NA	0.70	-	NA
Platyrrhines	**13**	**0.00**	**0.60**	**0.02**	0.71	+	NA	0.24	+	NA	0.15	+	NA	0.30	-	NA
Catarrhines	24	1.00	0.04	0.21	0.27	+	NA	0.10	-	NA	0.15	+	NA	0.18	+	NA
Hominoids	7	0.00	0.57	0.27	0.28	+	NA	0.14	-	NA	0.73	+	NA	0.32	+	NA

MODEL 4

	WHOLE MODEL				CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**35**	**0.18**	**0.37**	**<0.01**	0.60	-	NA	0.14	+	NA	0.48	+	NA	**0.01**	**-**	**0.19**
Platyrrhines	**13**	**0.13**	**0.55**	**0.03**	0.74	+	NA	0.36	+	NA	0.33	+	NA	0.62	-	NA
Catarrhines	22	0.00	-0.07	0.62	0.60	-	NA	0.34	+	NA	0.90	-	NA	0.42	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 5.4. Results of multivariate PGLS regression using shape-ratios for size adjustment and with FP2 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. Grey highlighted results were not normal after log_{10} and Box-Cox transformations. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Shape-Ratios

Dependent Variable: FP2

MODEL 1

	WHOLE MODEL				CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**37**	**0.70**	**0.19**	**0.03**	0.64	+	NA	**0.04**	-	**0.57**	0.10	+	NA	0.14	+	NA
Platyrrhines	13	0.00	0.31	0.14	0.95	+	NA	0.60	+	NA	0.14	+	NA	0.49	-	NA
Catarrhines	*24*	*1.00*	*0.20*	*0.10*	*0.16*	+	NA	***0.03***	-	**NA**	*0.64*	+	NA	***0.03***	+	**NA**
Hominoids	**7**	**0.00**	**0.99**	**<0.01**	0.49	-	NA	**<0.01**	-	**0.76**	**<0.01**	+	**0.36**	**0.02**	+	**0.02**

MODEL 2

	WHOLE MODEL				CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**35**	**1.00**	**0.83**	**<0.01**	0.32	-	NA	**<0.01**	-	**0.40**	**<0.01**	+	**0.77**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.94**	**<0.01**	**<0.01**	+	**0.07**	**<0.01**	-	**0.23**	**<0.01**	+	**0.66**	<0.01	+	NA
Catarrhines	**22**	**0.23**	**0.89**	**<0.01**	0.78	-	NA	**<0.01**	-	**0.40**	**<0.01**	+	**0.67**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**37**	**0.91**	**0.94**	**<0.01**	0.94	-	NA	**<0.01**	-	**0.58**	**<0.01**	+	**0.87**	**<0.01**	+	**0.28**
Platyrrhines	**13**	**1.00**	**0.89**	**<0.01**	0.89	+	NA	**<0.01**	-	**0.38**	**<0.01**	+	**0.84**	**<0.01**	+	**0.28**
Catarrhines	**24**	**0.00**	**0.97**	**<0.01**	0.44	+	NA	**<0.01**	-	**0.65**	**<0.01**	+	**0.85**	**<0.01**	+	**0.19**
Hominoids	*7*	***0.00***	***>0.99***	***<0.01***	*0.06*	-	NA	***<0.01***	-	***0.80***	***<0.01***	+	***0.23***	***0.01***	+	***<0.01***

MODEL 4

	WHOLE MODEL				CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**35**	**1.00**	**0.84**	**<0.01**	0.08	-	NA	**<0.01**	-	**0.40**	**<0.01**	+	**0.78**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.88**	**<0.01**	0.12	+	NA	**<0.01**	-	**0.29**	**<0.01**	+	**0.82**	<0.01	+	NA
Catarrhines	**22**	**0.00**	**0.90**	**<0.01**	0.71	+	NA	**<0.01**	-	**0.41**	**<0.01**	+	**0.67**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 5.5. Results of multivariate PGLS regression analysis using phylogenetically-controlled residuals for size adjustment and with FP1 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Phylogenetically-Controlled Residuals

Dependent Variable: FP1

MODEL 1

	WHOLE MODEL				CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**37**	**0.56**	**0.37**	**<0.01**	0.46	+	NA	**<0.01**	-	**0.20**	**<0.01**	+	**0.30**	**0.37**	+	**NA**
Platyrrhines	13	0.00	0.34	0.12	0.33	+	NA	0.35	+	NA	0.57	-	NA	0.03	-	NA
Catarrhines	**24**	**0.00**	**0.52**	**<0.01**	**0.03**	+	**0.09**	0.07	-	NA	**<0.01**	+	**0.33**	0.06	+	NA
Hominoids	**7**	**0.00**	**0.95**	**0.03**	**0.02**	+	**0.31**	0.33	-	NA	**0.03**	+	**0.21**	0.07	+	NA

MODEL 2

	WHOLE MODEL				CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	35	0.00	-0.02	0.50	0.81	+	NA	0.73	+	NA	0.79	+	NA	0.13	-	NA
Platyrrhines	13	0.33	-0.03	0.50	0.48	+	NA	0.80	+	NA	0.76	-	NA	0.38	-	NA
Catarrhines	22	0.00	-0.07	0.64	0.44	+	NA	0.43	+	NA	0.85	+	NA	0.51	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	**37**	***0.60***	***0.37***	***<0.01***	*0.66*	+	NA	***<0.01***	-	***0.16***	***<0.01***	+	***0.26***	*0.37*	+	*NA*
Platyrrhines	13	0.00	0.30	0.15	0.48	+	NA	0.40	+	NA	0.81	-	NA	0.06	-	NA
Catarrhines	**24**	***0.79***	***0.49***	***<0.01***	*0.13*	+	NA	***0.02***	-	***0.03***	***<0.01***	+	***0.13***	***0.03***	+	***0.06***
Hominoids	7	0.00	0.85	0.10	0.08	+	NA	0.13	-	NA	0.32	+	NA	0.10	+	NA

MODEL 4

	WHOLE MODEL				CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**	***p***	**Sign,**	**SPR^2**
Anthropoids	35	0.00	0.00	0.43	0.49	-	NA	0.89	+	NA	0.81	+	NA	0.11	-	NA
Platyrrhines	13	0.19	-0.04	0.51	0.51	+	NA	0.76	+	NA	0.96	-	NA	0.52	-	NA
Catarrhines	22	0.00	-0.10	0.73	0.71	-	NA	0.56	+	NA	0.80	+	NA	0.29	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 5.6. Results of multivariate PGLS regression analysis using phylogenetically-controlled residuals for size adjustment and with FP2 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. Grey highlighted results were not normal after log_{10} and Box-Cox transformations. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Phylogentically-Controlled Residuals

Dependent Variable: FP2

MODEL 1

	WHOLE MODEL				CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**
Anthropoids	**37**	**0.57**	**0.97**	**<0.01**	0.89	+	NA	**<0.01**	-	**0.43**	**<0.01**	+	**0.84**	**<0.01**	+	**0.19**
Platyrrhines	**13**	**0.91**	**0.89**	**<0.01**	0.49	+	NA	**<0.01**	-	**0.31**	**<0.01**	+	**0.46**	**<0.01**	+	**0.22**
Catarrhines	**24**	**0.84**	**0.97**	**<0.01**	0.01	-	NA	**<0.01**	-	**0.39**	**<0.01**	+	**0.87**	**<0.01**	+	**0.11**
Hominoids	**7**	**1.00**	**0.96**	**0.03**	0.61	-	NA	**0.04**	-	**0.15**	**0.01**	+	**0.70**	0.06	+	NA

MODEL 2

	WHOLE MODEL				CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.85**	**<0.01**	0.26	-	NA	**<0.01**	-	**0.35**	**<0.01**	+	**0.73**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.90**	**<0.01**	**0.01**	+	**0.05**	**<0.01**	-	**0.18**	**<0.01**	+	**0.49**	<0.01	+	NA
Catarrhines	**22**	**0.00**	**0.87**	**<0.01**	0.02	-	NA	<0.01	+	NA	**<0.01**	+	**0.74**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**
Anthropoids	**37**	**0.59**	**0.97**	**<0.01**	0.88	-	NA	**<0.01**	-	**0.45**	**<0.01**	+	**0.80**	**<0.01**	+	**0.19**
Platyrrhines	**13**	**0.96**	**0.89**	**<0.01**	0.65	+	NA	**<0.01**	-	**0.21**	**<0.01**	+	**0.69**	**<0.01**	+	**0.21**
Catarrhines	**24**	**0.91**	**0.97**	**<0.01**	0.01	-	NA	**<0.01**	-	**0.41**	**<0.01**	+	**0.83**	**<0.01**	+	**0.09**
Hominoids	**7**	**1.00**	**0.92**	**0.05**	0.30	-	NA	**0.05**	-	**0.25**	**0.02**	+	**0.49**	0.15	+	NA

MODEL 4

	WHOLE MODEL				CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**	***p***	**Sign**	**SPR^2**
Anthropoids	**35**	**1.00**	**0.87**	**<0.01**	0.01	-	NA	**<0.01**	-	**0.38**	**<0.01**	+	**0.74**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.85**	**<0.01**	0.07	+	NA	**<0.01**	-	**0.16**	**<0.01**	+	**0.75**	<0.01	+	NA
Catarrhines	**22**	**0.00**	**0.92**	**<0.01**	<0.01	-	NA	**<0.01**	-	**0.44**	**<0.01**	+	**0.78**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 5.7. Results of multivariate PGLS regression analysis using the cranial size proxy (i.e., geometric mean of cranial size measurements) for size adjustment and with FP1 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Cranial Size as Independent Variable

Dependent Variable: FP1

MODEL 1

	WHOLE MODEL				CRANIAL SIZE		CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	***37***	***0.56***	***0.68***	***<0.01***	*0.18*	+	*0.46*	+	NA	***<0.01***	-	***0.05***	***<0.01***	+	***0.07***	*0.37*	+	NA
Platyrrhines	13	0.33	-0.06	0.55	0.79	+	0.51	+	NA	0.78	-	NA	0.42	-	NA	0.82	+	NA
Catarrhines	**24**	**0.00**	**0.87**	**<0.01**	0.99	+	**0.02**	**+**	**0.09**	***0.07***	**-**	NA	**<0.01**	**+**	**0.08**	**0.04**	**+**	**0.03**
Hominoids	7	0.00	0.97	0.12	0.39	-	0.23	+	NA	0.58	-	NA	0.19	+	NA	0.24	+	NA

MODEL 2

	WHOLE MODEL				CRANIAL SIZE		CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.45**	**<0.01**	**0.01**	+	0.99	-	NA	0.70	+	NA	0.80	+	NA	0.14	-	NA
Platyrrhines	13	0.33	-0.06	0.55	0.79	+	0.51	+	NA	0.82	+	NA	0.78	-	NA	0.42	-	NA
Catarrhines	**22**	**0.00**	**0.55**	**<0.01**	0.04	+	0.19	+	NA	0.40	+	NA	0.82	+	NA	0.71	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CRANIAL SIZE		CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	***37***	***0.61***	***0.67***	***<0.01***	*0.17*	+	*0.67*	+	NA	***<0.01***	**-**	***0.06***	***<0.01***	**+**	***0.08***	*0.38*	+	NA
Platyrrhines	13	0.00	0.30	0.19	0.90	+	0.51	+	NA	0.44	+	NA	0.83	-	NA	0.08	-	NA
Catarrhines	**24**	**0.85**	**0.74**	**<0.01**	0.75	+	0.13	+	NA	0.02	+	NA	**<0.01**	**+**	**0.11**	**0.03**	**+**	**-0.05**
Hominoids	**7**	**0.00**	**0.98**	**0.01**	0.44	-	0.08	+	NA	**0.05**	**-**	**0.06**	0.12	+	NA	0.06	+	NA

MODEL 4

	WHOLE MODEL				CRANIAL SIZE		CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.49**	**<0.01**	**0.01**	+	0.17	-	NA	0.87	+	NA	0.75	+	NA	0.05	-	NA
Platyrrhines	13	0.19	-0.06	0.55	0.96	+	0.54	+	NA	0.77	+	NA	0.96	-	NA	0.55	-	NA
Catarrhines	**22**	**0.00**	**0.52**	**<0.01**	**0.04**	**+**	0.59	-	NA	0.62	+	NA	0.78	-	NA	0.28	-	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 5.8. Results of multivariate PGLS regression analysis using the cranial size proxy (i.e., geometric mean of cranial size measurements) to adjust for size and with FP2 as the dependent variable. Bolded values are significant at $\alpha = 0.05$ (significant correlations that are in the opposite direction as predicted are not bolded). Italicized results indicate that the data were log_{10} transformed. Grey highlighted results were not normal after log10 and Box-Cox transformations. 'NA' denotes one of three situations: (1) Comparisons that could not be made due to small sample size; (2) Cases in which SPR^2 was not calculated because the model and/or variable were not statistically significant; or (3) when the variable was significant but the correlation was in the opposite direction as predicted.

Size-Adjustment Method: Cranial Size as Independent Variable

Dependent Variable: FP2

MODEL 1

	WHOLE MODEL				CRANIAL SIZE		CBA1			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**37**	**0.65**	**0.99**	**<0.01**	0.57	-	0.83	-	NA	**<0.01**	-	**0.16**	**<0.01**	+	**0.28**	**<0.01**	+	**0.04**
Platyrrhines	**13**	**0.83**	**0.94**	**<0.01**	0.83	+	0.51	+	NA	**<0.01**	-	**0.11**	**<0.01**	+	**0.14**	**<0.01**	+	**0.10**
Catarrhines	**24**	**0.00**	**>0.99**	**<0.01**	0.14	-	0.24	-	NA	**<0.01**	-	**0.13**	**<0.01**	+	**0.30**	**<0.01**	+	**0.03**
Hominoids	**7**	**0.00**	**>0.99**	**<0.01**	0.53	-	0.12	-	NA	**0.03**	-	**0.01**	**0.01**	+	**0.05**	**0.03**	+	**0.01**

MODEL 2

	WHOLE MODEL				CRANIAL SIZE		CBA1			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.97**	**<0.01**	**<0.01**	+	0.69	+	NA	**<0.01**	-	**0.18**	**<0.01**	+	**0.05**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.97**	**<0.01**	**0.02**	-	**0.01**	+	**0.03**	**<0.01**	-	**0.08**	**<0.01**	+	**0.16**	<0.01	+	NA
Catarrhines	**22**	**0.00**	**0.98**	**<0.01**	**0.01**	+	0.01	-	NA	**<0.01**	-	**0.17**	**<0.01**	+	**0.32**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

MODEL 3

	WHOLE MODEL				CRANIAL SIZE		CBA2			ACBL			UFL			ASL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**37**	**0.77**	**0.99**	**<0.01**	0.60	-	0.45	-	NA	**<0.01**	-	**0.07**	**<0.01**	+	**0.25**	**<0.01**	+	**0.04**
Platyrrhines	**13**	***0.96***	***0.93***	***<0.01***	*0.92*	-	*0.71*	+	NA	***<0.01***	-	***0.10***	***<0.01***	+	***0.35***	***<0.01***	+	***0.11***
Catarrhines	**24**	**0.00**	**<0.99**	**<0.01**	0.26	-	0.16	-	NA	<0.01	+	NA	**<0.01**	+	**0.23**	**<0.01**	+	**0.02**
Hominoids	**7**	**0.00**	**<0.99**	**0.01**	0.34	-	0.16	-	NA	**0.03**	-	**0.02**	**0.02**	+	**0.04**	0.06	+	NA

MODEL 4

	WHOLE MODEL				CRANIAL SIZE		CBA2			ACBL			UFL			AMCFL		
Unit of Analysis	**N**	**ML λ**	**Adj. r^2**	***p***	***p***	**Sign, +/-**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**	***p***	**Sign, +/-**	**SPR^2**
Anthropoids	**35**	**0.00**	**0.97**	**<0.01**	**<0.01**	+	0.40	-	NA	**<0.01**	-	**0.19**	**<0.01**	+	**0.32**	<0.01	+	NA
Platyrrhines	**13**	**0.00**	**0.94**	**<0.01**	**0.04**	-	0.09	+	NA	**<0.01**	-	**0.08**	**<0.01**	+	**0.25**	<0.01	+	NA
Catarrhines	**22**	**0.00**	**0.97**	**<0.01**	**<0.01**	+	0.01	-	NA	**<0.01**	-	**0.19**	**<0.01**	+	**0.33**	<0.01	+	NA
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

(4) Model 4: CBA2, UFL, AMCFL, and ACBL

Using shape-ratios for size adjustment and FP1 as the measure of facial projection, there are very few instances in which models are significant (Table 5.3). All four models are significant when platyrrhines are the unit of analysis. These models explain relatively little of the variation in facial projection, with adjusted r^2 values between 0.55 and 0.60. However, in each of these cases, none of the independent variables are significant predictors of facial projection. When anthropoids are the unit of analysis, Model 2 and 4 are significant, but these correlations also explain relatively little of the variation in facial projection (adjusted r^2 values of 0.42 and 0.37, respectively). In both of these cases, the only significant predictor of facial projection is AMCFL. None of the models are significant when catarrhines and hominoids are the units of analysis.[2]

When shape-ratios are used for size adjustment and FP2 is the measure of facial projection, a majority of the models for a majority of the units of analysis are significant (Table 5.4). Moreover, most of these models explain a relatively large amount of the variation in facial projection. The only exception to this generalization is for Model 1 in anthropoids (adjusted $r^2 = 0.19$). For the remainder of the models, adjusted r^2 values are 0.83 or greater. Cranial Base Angle (measured as either CBA1 or CBA2) is a significant predictor of facial projection in only one model (i.e., CBA2 for Model 2 in platyrrhines). By contrast, ACBL and UFL are significant predictors of facial projection in a majority of the significant models. Anterior Sphenoid Length is only a significant predictor of facial projection for Model 1 in hominoids and in all units of analysis for Model 3. In

[2] It should be noted that, due to difficulty in locating the landmarks to measure AMCFL, sample sizes of hominoids were too small to include this unit of analysis in tests of Models 2 and 4. This fact is true for all combinations of facial projection measure and size adjustment method.

most of the significant models, more than one independent variable is a significant predictor of facial projection, and, in the majority of these cases, UFL is the most important predictor of facial projection (as indicated by SPR^2 values). The only exceptions are for Model 1 in anthropoids and for Model 3 in hominoids; in these cases, the SPR^2 values for ACBL are greater than that of UFL.

When phylogenetically-controlled residuals are used for size adjustment and FP1 is the measure of facial projection (Table 5.5), very few models yield significant results. A notable exception to this generalization is for Model 1, in which all units of analysis except platyrrhines are significant. In addition, for Model 3, in anthropoids and catarrhines, the regressions are significant. The majority of the significant models, with the exception of Model 1 in hominoids (adjusted $r^2 = 0.95$), explain relatively little of the variation in facial projection based on values for adjusted r^2. For all significant models, more than one independent variable is a significant predictor of facial projection, and, in all cases except in Model 1 for hominoids, UFL is the most important predictor of facial projection, based on values of SPR^2. For Model 1 in hominoids, CBA1 is the most important predictor of facial projection.

When phylogenetically-controlled residuals are used for size adjustment and FP2 is the measure of facial projection, all of the models for which analyses can be run are significant (Table 5.6). In addition, these models explain a relatively large amount of the variation in facial projection—adjusted r^2 values range from 0.85 to 0.97. UFL is a significant predictor of facial projection in all cases, and ACBL is a significant predictor of facial projection in all cases except for Model 2 in catarrhines, in which the correlation is significant, but in the opposite direction as predicted. ASL is a significant predictor of

facial projection in all models in which it is included. AMCFL is also a significant predictor of facial projection in all models in which it is included; however, these correlations are all in the opposite direction as predicted. Multiple independent variables are significant in each case except in Model 2 for catarrhines, in which only UFL is significant. In all cases in which more than one independent variable is a significant predictor of facial projection, UFL is the most important predictor of facial projection, based on values for SPR^2.

Table 5.7 reports the results of analyses using cranial size (i.e., the geometric mean of the six cranial size measurements) as an independent variable for size adjustment and FP1 as the measure of facial projection. In these analyses, all models in which anthropoids and catarrhines are the units of analysis are significant. Model 3 in hominoids is also significant. In analyses in which anthropoids and catarrhines are the units of analysis, the models explain a moderate and variable amount of the variation in facial projection—i.e., adjusted r^2 values range from 0.45 to 0.87. Adjusted r^2 values are always greater for models in which catarrhines are the unit of analysis. In the one significant model in which hominoids are the unit of analysis, the model explains a relatively large amount of the variation in facial projection (adjusted $r^2 = 0.98$). UFL is a significant predictor of facial projection in all of the significant models except for Model 4 in both anthropoids and catarrhines. Similarly, ACBL is a significant predictor of facial projection in all significant models, except in Model 2 for anthropoids and catarrhines, in Model 3 for catarrhines, and in Model 4 for anthropoids and catarrhines. In all cases in which there is more than one significant independent variable in a model, UFL is the most important predictor of facial projection (based on values for SPR^2). The only

exception is for Model 1 in catarrhines in which CBA1 is the most important predictor of facial projection.

When cranial size used as an independent variable in the regression analyses is used for size adjustment and FP2 is the measure of facial projection (Table 5.8), all models are significant. Moreover, all of these models explain a relatively large amount of the variation in facial projection (adjusted r^2 values range from 0.93 to >0.99). UFL is a significant predictor of facial projection in every case, and ASL is a significant predictor of facial projection in all models in which it is included (i.e., in Models 1 and 3). ACBL is a significant predictor of facial projection in every case except for Model 3 in catarrhines. In this case, the correlation between ACBL and FP2 is significant, but is in the opposite direction as predicted. CBA is significant in only one model (i.e., CBA1 for Model 2 in platyrrhines). Anterior Middle Cranial Fossa Length is significantly correlated with FP2 in all models in which it is included. However, in each case, the correlation is in the opposite direction as predicted. More than one independent variable is significant in all cases, and, in each case except for Model 2 in anthropoids (in which ACBL is the most important predictor of facial projection), UFL is the most important predictor of facial projection, based on values of SPR^2.

Figures 5.9 and 5.10 are "heat maps" of the multivariate PGLS regressions and provide an overview of these analyses. Figure 5.9 is organized according to the method used for size adjustment and by Model number, whereas Figure 5.10 is organized according to units of analysis. There are very few significant models when FP1 is used as the measure of facial projection (Figure 5.9). In contrast, when FP2 is used as the measure of facial projection, the majority of models are significant. It also clear that, in

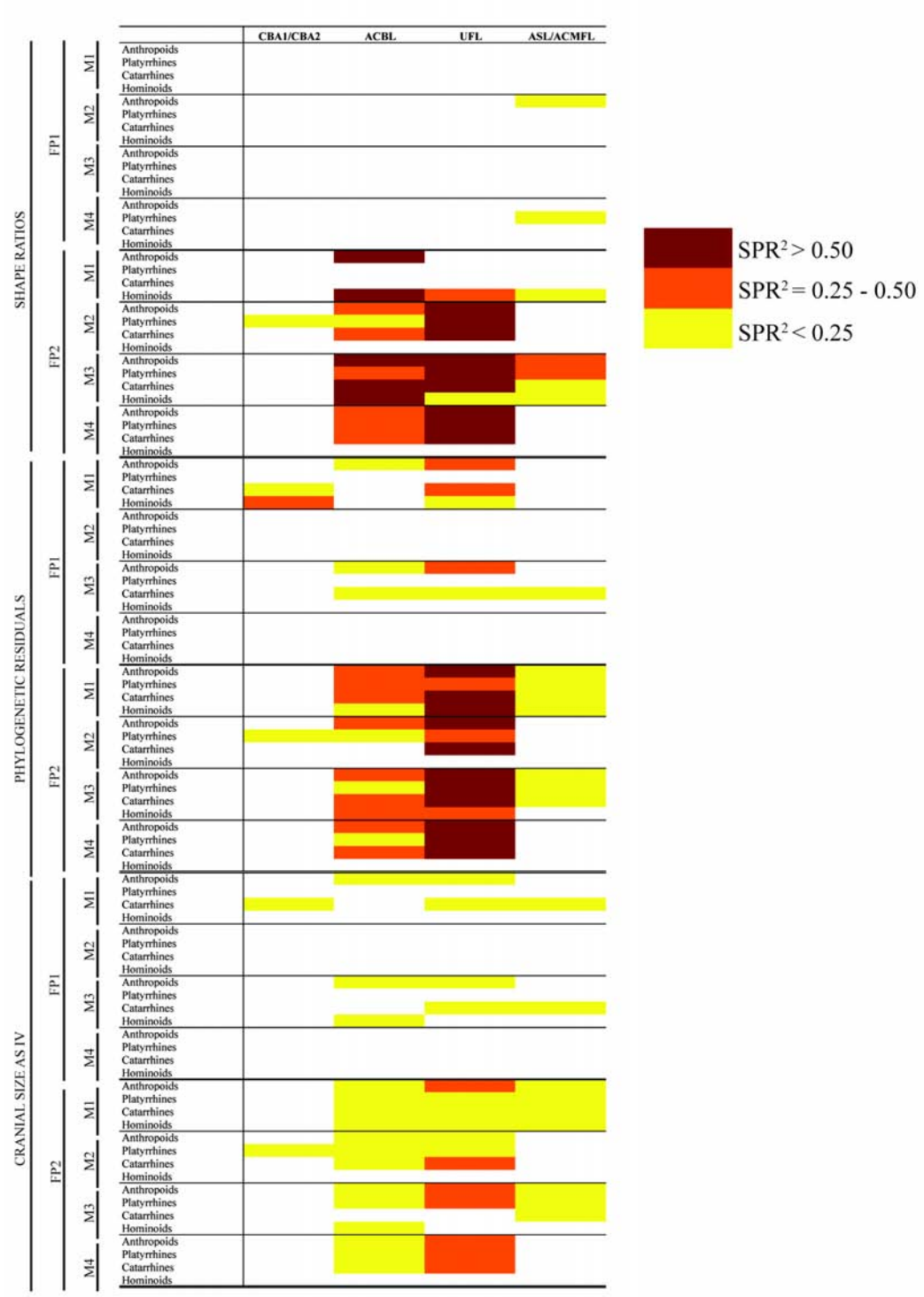


Figure 5.9. 'Heat map' of multivariate PGLS regression analyses. Non-significant results and comparisons that could not be made due to small sample sizes are colored white. Significant results are colored yellow ($SPR^2 < 0.25$), orange ($SPR^2 = 0.25 – 0.50$), or red ($SPR^2 > 0.50$). The size adjustment methods (i.e., shape-ratios, phylogenetically-controlled residuals, or using cranial size as an independent variable) and the dependent variables (i.e., FP1 or FP2) are indicated on the left side of the figure.

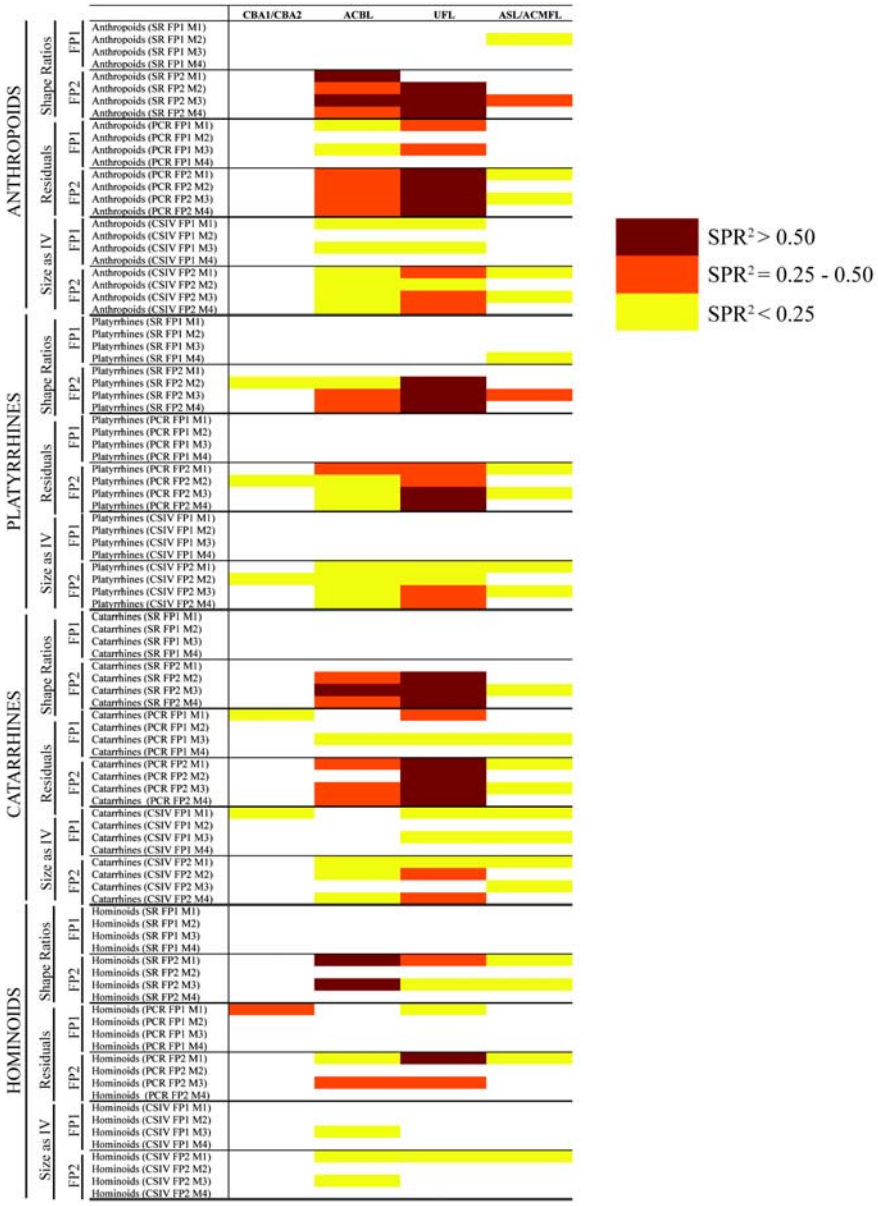


Figure 5.10. 'Heat map' of multivariate PGLS regression analyses organized by unit of analysis. Non-significant results and comparisons that could not be made due to small sample sizes are colored white. Significant results are colored yellow (r^2 < 0.25), orange (r^2 = 0.25 – 0.50), or red (r^2 > 0.50). The size adjustment method (i.e., shape- ratios, phylogenetically-controlled residuals, or cranial size as an independent variable in the multiple regression) and the unit of analysis (i.e., anthropoids, platyrrhines, catarrhines, and hominoids) are indicated on the left side of the figure. This information is also provided parenthetically next to the entry for each analysis. Model numbers are also provided. Abbreviations are as follows: Model number (Model 1 [M1], Model 2 [M2], Model 3 [M3], Model 4 [M4]), size adjustment method (shape- ratios [SR], phylogenetically-controlled residuals [PCR], or cranial size as an independent variable in the multiple regression [CSIV]).

general, UFL and ACBL are the most important predictors of facial projection, and that, largely, UFL is the single best predictor of facial projection in the multivariate analyses. This figure also clearly shows that CBA (measured as CBA1 or CBA2) is generally not an important predictor of facial projection. When viewed according to units of analysis, similar observations can be made (Figure 5.10). Additionally, this figure also shows that the largest proportion of significant models occur when anthropoids are the unit of analysis. There are also a relatively large amount of significant models when platyrrhines and catarrhines are the units of analysis, but these constitute fewer significant models than in cases where anthropoids are the unit of analysis. When hominoids are the unit of analysis, a relatively small number of models are significant.

COMPARING MODELS – AKAIKE'S INFORMATION CRITERION

Akaike's Information Criterion was used to compare univariate and multivariate models to one another. Specifically, for each combination of size adjustment method (i.e., shape-ratios, phylogenetically-controlled residuals, or cranial size as an independent variable) and measurement of facial projection (i.e., FP1 or FP2), the best univariate model (based on r^2 value) was compared to the best multivariate model (based on adjusted r^2). In each case, the model with the lowest value for AICC was deemed the "best" model.

For analysis with FP1 as the measure of facial projection and shape-ratios as a means of size adjustment, the univariate model with UFL as the independent variable was the best model in anthropoids and platyrrhines (Table 5.9). No models (i.e., neither univariate nor multivariate) were significant in this case for catarrhines, and small sample sizes precluded an analysis of hominoids. The best model for anthropoids explains very

TABLE 5.9. Results of model comparison using the Corrected Akaike Information Criterion (AICC) for models using FP1 as the dependent variable. Results indicated in red represent the best model (i.e., lowest AICC value) for each case. In each case, r^2 (for univariate models) or adjusted r^2 (for multivariate models) is provided for the best model. For cases in which the best model was a multivariate model, SPR^2 for all significant independent variables is also provided (bolded variables are those with highest SPR^2 in each case). 'NA' indicates cases in which samples sizes were too small to perform analysis, when there were no significant models, and, for multivariate models, when no independent variables were significant.

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP1

	Univariate		Multivariate		r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Variable**	**AICC**	**Model No.**	**AICC**	**(Best Model)**	**(SPR^2)**
Anthropoids	UFL	-111.22	4	-109.01	0.17	NA
Platyrrhines	UFL	-38.16	3	-27.68	0.66	NA
Catarrhines	NA	NA	NA	NA	NA	NA
Hominoids	NA	NA	NA	NA	NA	NA

Size-Adjustment Method: Phylogenetically-Controlled Residuals
Dependent Variable: FP1

	Univariate		Multivariate		r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Variable**	**AICC**	**Model No.**	**AICC**	**(Best Model)**	**(SPR^2)**
Anthropoids	CBA2	188.63	1	178.99	0.37	ACBL (0.20); UFL (0.30); **ASL (0.37)**
Platyrrhines	ASL	47.37	NA	NA	0.47	NA
Catarrhines	UFL	117.79	1	113.64	0.52	CBA1 (0.09); **UFL (0.33)**
Hominoids	NA	NA	1	81.54	0.95	**CBA1 (0.31)**; UFL (0.21)

Size-Adjustment Method: Cranial Size as Independent Variable
Dependent Variable: FP1

			r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Model No.**	**AIC**	**(Best Model)**	**(SPR^2)**
Anthropoids	2	155.70	0.45	NA[a]
Platyrrhines	NA	NA	NA	NA
Catarrhines	2	103.59	0.55	NA[a]
Hominoids	NA	NA	NA	NA

[a] None of the independent variables were signficant in these models

little of the variation in facial projection ($r^2 = 0.17$), while the best model for platyrrhines explains only a moderate amount of variation in facial projection ($r^2 = 0.66$). In cases in which phylogenetically-controlled residuals are used for size adjustment, a multivariate model (i.e., Model 1) is the best model in anthropoids, catarrhines, and hominoids (see Table 5.9). In platyrrhines, a univariate model (i.e., with ASL as the independent variable) is the best model. In the best model for anthropoids, ASL is the most important predictor of facial projection among the independent variables in the model; ACBL and UFL are also significant predictors of facial projection in anthropoids. In catarrhines, UFL is the most important predictor of facial projection among the independent variables in the model; CBA1 is also a significant predictor of facial projection in catarrhines. In hominoids, the most important predictor of facial projection is CBA1, but UFL is also a significant predictor of facial projection in hominoids. The best models explain a variable amount of variation in facial projection in this case, and the amount of variation explained by the models (based on r^2 or adjusted r^2) increases in taxonomically narrower units of analysis (i.e., the adjusted r^2 value is greater in catarrhines than in anthropoids, and the adjusted r^2 value in hominoids is greater than in catarrhines).

When cranial size is included in the multivariate model as an independent variable to adjust for size, Model 2 is the best model in anthropoids and catarrhines (see Table 5.9). No models were significant in this case in platyrrhines, and small sample sizes precluded an analysis of hominoids. The best models in anthropoids and catarrhines each explain roughly half of the variation in facial projection.

The results of model comparisons when FP2 was used as the measure of facial projection are reported in Table 5.10. When shape-ratios are used for size adjustment,

TABLE 5.10. Results of model comparison using the Corrected Akaike Information Criterion (AICC) for models using FP2 as the dependent variable. Results indicated in red represent the best model (i.e., lowest AICC value) for each case. In each case, r^2 (for univariate models) or adjusted r^2 (for multivariate models) is provided for the best model. For cases in which the best model was a multivariate model, SPR^2 for all significant independent variables is also provided (bolded variables are those with highest SPR^2 in each case). 'NA' indicates cases in which samples sizes are too small to perform analysis, when there were no significant models, and, for multivariate models, when no independent variables are significant.

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP2

	Univariate		Multivariate		r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Variable**	**AIC**	**Model No.**	**AIC**	**(Best Model)**	**(SPR^2)**
Anthropoids	UFL	-150.77	1	-232.53	0.19	ACBL (0.57)
Platyrrhines	UFL	-50.97	2	-71.18	0.94	CBA1 (0.07); ACBL (0.23); **UFL (0.67)**
Catarrhines	UFL	-99.13	3	-165.42	0.97	ACBL (0.65); **UFL (0.85)**; ASL (0.19)
Hominoids	NA	NA	3	-7.96	>0.99	**ACBL (0.80)**; UFL (0.23); ASL (0.01)

Size-Adjustment Method: Phylogentically-Controlled Residuals
Dependent Variable: FP2

	Univariate		Multivariate		r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Variable**	**AIC**	**Model No.**	**AIC**	**(Best Model)**	**(SPR^2)**
Anthropoids	UFL	157.75	4	73.96	0.87	CBA2 (0.02); ACBL (0.38); **UFL (0.74)**
Platyrrhines	UFL	37.43	2	21.86	0.90	CBA1 (0.05); ACBL (0.18); **UFL (0.49)**
Catarrhines	UFL	107.73	3	42.20	0.97	CBA2 (0.01); ACBL (0.41); **UFL (0.83)**; ASL (0.09)
Hominoids	UFL	33.55	3	78.82	0.68	NA

Size-Adjustment Method: Cranial Size as Independent Variable
Dependent Variable: FP2

			r^2 / Adj. r^2	Sig. Independent Variable(s)
Unit of Analysis	**Model No.**	**AIC**	**(Best Model)**	**(SPR^2)**
Anthropoids	3	50.41	0.99	ACBL (0.07); **UFL (0.32)**; ASL (0.04)
Platyrrhines	NA	NA	NA	NA
Catarrhines	3	14.22	<0.99	ACBL (0.08); **UFL (0.23)**; ASL (0.02)
Hominoids	NA	NA	NA	NA

multivariate models are the best models in all units of analysis. In each case, UFL and ACBL are the most important predictors of facial projection among the independent variables in the respective models. In anthropoids, ACBL is the only significant predictor of facial projection. ACBL is also the best predictor of facial projection in the best model for hominoids; UFL and ASL are also significant predictors in this case, but their contributions are less important than that of ACBL. In platyrrhines and catarrhines, UFL is the best predictor of facial projection among the independent variables in the best models. In platyrrhines, CBA1 and ACBL are also significant predictors of facial projection, but these independent variables (particularly CBA1) are less important than UFL. In catarrhines, ACBL and ASL are also significant predictors of facial projection. These independent variables (particularly ASL), however, are less important than UFL. Whereas the best model for anthropoids explains relatively little of the overall variation in facial projection (adjusted $r^2 = 0.19$), the best models for the remaining units of analysis explain a relatively large amount of variation in facial projection (r^2 / adjusted r^2 values are greater than 0.94).

When phylogenetically-controlled residuals are used for size adjustment, multivariate models are again the best models for anthropoids, platyrrhines, and catarrhines (see Table 5.10). In each of these cases, UFL is the best predictor of facial projection among the independent variables in the models. CBA (i.e., CBA1 or CBA2) and ACBL are also significant predictors of facial projection, but these independent variables explain relatively less of the variation in facial projection than UFL. In catarrhines, ASL is also a significant predictor of facial projection, but explains very little

of the overall variation. In hominoids, the best model was the univariate model with UFL as the independent variable. These best models, be they multivariate or univariate ones, explain a moderate to large amount of variation in facial projection (r^2 / adjusted r^2 values range from 0.68 in hominoids to 0.97 in catarrhines).

When cranial size is included in the multivariate model as an independent variable to adjust for size, Model 3 is the best model in anthropoids and catarrhines (see Table 5.10). In both cases, UFL is the best predictor of facial projection among the independent variables in the best models. ACBL and ASL are also significant predictors of facial projection in anthropoids and catarrhines, but these variables explain very little of the overall variation (SPR^2 values range from 0.02 – 0.08) and are thus much less important than UFL. These best models explain a relatively large amount of variation in facial projection (adjusted r^2 values are both 0.99 or greater). There are no significant models for platyrrhines, and small sample sizes precluded an analysis of hominoids.

COMPARING *HOMO SAPIENS* TO REGRESSION MODELS

Against each applicable regression model that was deemed to be the best in each case, two methods were used to compare *Homo sapiens.* In this way, it is possible to determine how closely this species fits the patterns defined by the model. First, 95% prediction intervals for all regressions were calculated for each model (with *Homo sapiens* omitted), and the position of *Homo sapiens* relative to these intervals was evaluated. The second method examined studentized residuals. Specifically, the studentized residual for *Homo sapiens* was calculated in each case; *Homo sapiens* was considered an outlier (i.e., it does not fit the regression model) whenever the absolute value of the residual was greater than three.

Table 5.11 reports the results of these comparisons in analyses in which FP1 was used as the measure of facial projection. Using both methods, *Homo sapiens* fits the best model in all cases except in catarrhines when phylogenetically-controlled residuals are used for size adjustment. In catarrhines, *Homo sapiens* falls outside of the 95% prediction intervals. However, the absolute value of the studentized residual for *Homo sapiens* in this case is less than three, although its value (2.84) closely approaches three.

The results for analyses in which FP2 was used as the measure of facial projection are reported in Table 5.12. In all cases, *Homo sapiens* falls within the 95% prediction intervals of the best model, and the absolute value of the studentized residual for *Homo sapiens* is less than three.

GEOMETRIC MORPHOMETRIC ANALYSIS

The geometric morphometric analysis was designed to explore variation in middle cranial fossa shape and position within the cranial base. Specifically, for each unit of analysis (i.e., anthropoids, platyrrhines, catarrhines, and hominoids), PCs 1-5 from the geometric morphometric analysis were regressed against facial projection. This procedure was conducted for each combination of size adjustment method (i.e., shape-ratios, phylogenetically-controlled residuals, or cranial size as an independent variable) and measurement of facial projection (i.e., FP1 or FP2) (Table 5.13). Of the 80 possible comparisons, there are only six cases in which the correlation between facial projection and one of the PCs is significant. In particular, using shape-ratios for size adjustment, PC1 is significantly correlated with FP1 in anthropoids and PC3 is significantly correlated with FP1 in platyrrhines. In addition, PC1 is significantly correlated with FP2 in anthropoids. Using phylogenetically-controlled residuals for size adjustment, PC3 is

TABLE 5.11. Results of evaluations of position of Homo sapiens *for models using FP1 as the dependent variable. Only the best models (determined using AICC) are considered here. 'Homo sapiens fit' indicates whether or not* Homo sapiens *falls within the 95% prediction intervals. 'Yes' indicates that* Homo sapiens *falls within the 95% prediction intervals; 'No' indicates that* Homo sapiens *falls outside of the 95% prediction intervals. 'NA' indicates cases in which samples sizes were too small to perform analysis or for 'Model No.' in cases in which the best model was a univariate model.*

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP1

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	U	NA	Yes	-0.036
Catarrhines	NA	NA	NA	NA
Hominoids	NA	NA	NA	NA

Size-Adjustment Method: Phylogenetically-Controlled Residuals
Dependent Variable: FP1

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	M	1	Yes	-0.658
Catarrhines	M	1	No	-2.838
Hominoids	M	1	Yes	0.003

Size-Adjustment Method: Cranial Size as Independent Variable
Dependent Variable: FP1

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	NA	2	Yes	0.822
Catarrhines	NA	2	Yes	-1.188
Hominoids	NA	NA	NA	NA

TABLE 5.12. Results of position of Homo sapiens *for models using FP2 as the dependent variable. Only the best models (determined using AICC) are considered here. 'Homo* sapiens *fit' indicates whether or not* Homo sapiens *falls within the 95% prediction intervals. 'Yes' indicates that* Homo sapiens *falls within the 95% prediction intervals; 'No' indicates that* Homo sapiens *falls outside of the 95% prediction intervals. 'NA' indicates cases in which samples sizes were too small to perform analysis or for 'Model No.' in cases in which the best model was a univariate model.*

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP2

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	M	1	Yes	0.008
Catarrhines	M	3	Yes	0.001
Hominoids	M	3	Yes	0.002

Size-Adjustment Method: Phylogentically-Controlled Residuals
Dependent Variable: FP2

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	M	4	Yes	-0.765
Catarrhines	M	3	Yes	0.793
Hominoids	U	NA	Yes	-0.807

Size-Adjustment Method: Cranial Size as Independent Variable
Dependent Variable: FP2

Unit of Analysis	Univariate (U)/ Multivariate (M)	Model No.	*Homo sapiens* Fit (Yes / No)	*Homo sapiens* Studentized Res.
Anthropoids	NA	3	Yes	0.430
Catarrhines	NA	3	Yes	0.291
Hominoids	NA	NA	NA	NA

TABLE 5.13. Results of geometric morphometric analysis. FP1 and FP2 were regressed against PCs 1-5 from the geometric morphometric analysis using PGLS. Bolded values are significant at $\alpha = 0.05$. Italicized results indicate that the data were $\log_{10}$ transformed. Results in blue indicate that the data were transformed using the Box-Cox transformation. 'NA' denotes comparisons that could not be made due to small sample size.

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP1

		FP1 v. PC1				FP1 v. PC2				FP1 v. PC3				FP1 v. PC4				FP1 v. PC5			
Unit of Analysis	**N**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**
Anthropoids	34	**0.90**	**-0.42**	**0.01**	**0.17**	*0.78*	*-0.18*	*0.31*	*0.03*	*0.86*	*0.31*	*0.07*	*0.10*	*0.77*	*-0.09*	*0.61*	*0.01*	*0.81*	*-0.10*	*0.57*	*0.01*
Platyrrhines	13	0.80	-0.41	0.16	0.17	0.76	0.02	0.95	0.00	**1.00**	**0.75**	**<0.01**	**0.56**	0.72	-0.16	0.61	0.03	0.88	-0.48	0.09	0.23
Catarrhines	21	0.54	-0.33	0.14	0.11	0.00	-0.19	0.41	0.04	0.00	-0.40	0.08	0.16	0.00	-0.18	0.44	0.03	0.00	0.22	0.35	0.05
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Size-Adjustment Method: Phylogenetically-Controlled Residuals
Dependent Variable: FP1

		FP1 v. PC1				FP1 v. PC2				FP1 v. PC3				FP1 v. PC4				FP1 v. PC5			
Unit of Analysis	**N**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**
Anthropoids	34	0.70	-0.34	0.05	0.11	0.00	0.05	0.77	0.00	0.00	0.20	0.26	0.04	0.00	0.03	0.85	0.00	0.00	-0.26	0.14	0.07
Platyrrhines	13	0.28	0.37	0.21	0.14	0.20	0.26	0.39	0.07	**0.00**	**0.59**	**0.04**	**0.34**	0.00	0.43	0.14	0.18	0.37	-0.40	0.18	0.16
Catarrhines	21	0.00	0.11	0.65	0.01	0.00	-0.30	0.19	0.09	0.00	-0.30	0.19	0.09	0.00	0.37	0.10	0.13	0.00	0.10	0.66	0.01
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Size-Adjustment Method: Shape-Ratios
Dependent Variable: FP2

		FP2 v. PC1				FP2 v. PC2				FP2 v. PC3				FP2 v. PC4				FP2 v. PC5			
Unit of Analysis	**N**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**
Anthropoids	34	**0.61**	**0.43**	**0.01**	**0.19**	0.95	0.00	0.99	0.00	0.94	0.03	0.87	0.00	0.94	0.08	0.65	0.01	0.96	0.05	0.77	0.00
Platyrrhines	11	0.60	-0.48	0.10	0.23	0.69	0.31	0.31	0.10	1.00	0.20	0.51	0.04	0.93	-0.15	0.62	0.02	1.00	0.31	0.30	0.10
Catarrhines	21	0.69	-0.24	0.30	0.06	0.87	0.10	0.66	0.01	0.93	-0.17	0.47	0.03	0.77	0.32	0.16	0.10	0.87	-0.17	0.46	0.03
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Size-Adjustment Method: Phylogenetically-Controlled Residuals
Dependent Variable: FP2

		FP2 v. PC1				FP2 v. PC2				FP2 v. PC3				FP2 v. PC4				FP2 v. PC5			
Unit of Analysis	**N**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**	**ML**	***r***	***p***	***r*²**
Anthropoids	34	0.76	-0.16	0.38	0.02	0.80	0.09	0.60	0.01	0.76	0.06	0.73	0.00	0.78	0.25	0.15	0.06	0.83	0.22	0.22	0.05
Platyrrhines	13	0.00	-0.52	0.07	0.27	0.00	0.41	0.16	0.17	0.00	-0.11	0.71	0.01	0.00	0.02	0.94	0.00	0.00	0.13	0.67	0.02
Catarrhines	21	1.00	0.03	0.90	0.00	1.00	0.12	0.61	0.01	**1.00**	**-0.20**	**0.38**	**0.04**	1.00	0.20	0.39	0.04	**0.50**	**-0.63**	**0.00**	**0.40**
Hominoids	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

significantly correlated with FP1 in platyrrhines and PC3 and PC5 are significantly correlated with FP2 in catarrhines. In general, these PCs explain relatively little of the variation in facial projection (r^2 values range from 0.04 to 0.56).

Table 5.14 reports the percentage of overall variation that is explained by the PCs that are significantly correlated with facial projection in the respective samples from the geometric morphometric analysis. These results indicate that, with the exception of PC1 in anthropoids, the PCs explain relatively little of the overall variation in the sample (i.e., < 10%). For this reason, PC1 in anthropoids was the only axis that was explored further.

Figure 5.11 is a scatterplot of PC1 against facial projection (i.e., FP1; shape-ratios used for size adjustment) in anthropoids, with accompanying wireframe diagrams illustrating shape variation along this PC axis. Negative values on PC1 characterize species with greater facial projection, whereas positive values characterize species with less facial projection. PC1 also describes differences in the shape and position of the middle cranial fossa. In particular, negative values for PC1 characterize species with anteroposteriorly longer middle cranial fossae that extend more posteriorly within the cranial base. Conversely, positive values for PC1 characterize species with anteroposteriorly shorter middle cranial fossae that extend less far posteriorly within the cranial base. In addition, while all configurations along PC1 exhibit an anterior. projection of the middle cranial fossa, negative values for PC1 characterize species in which this anterior projection is located more laterally on the internal aspect of the cranial base. By contrast, positive values for PC1 characterize species in which the anterior projection of the middle cranial fossa is located more centrally within the middle cranial fossa. The anterior projection is also slightly more pronounced in species occupying the

TABLE 5.14. Principal components (PCs) from the geometric morphometric analysis by unit of analysis and the percentage of overall variation explained by each.

Unit of Analysis	PC	Variation Explained (%)
Anthropoids	1	57.56
Platyrrhines	3	7.38
Catarrhines	3	9.07
Catarrhines	5	3.02

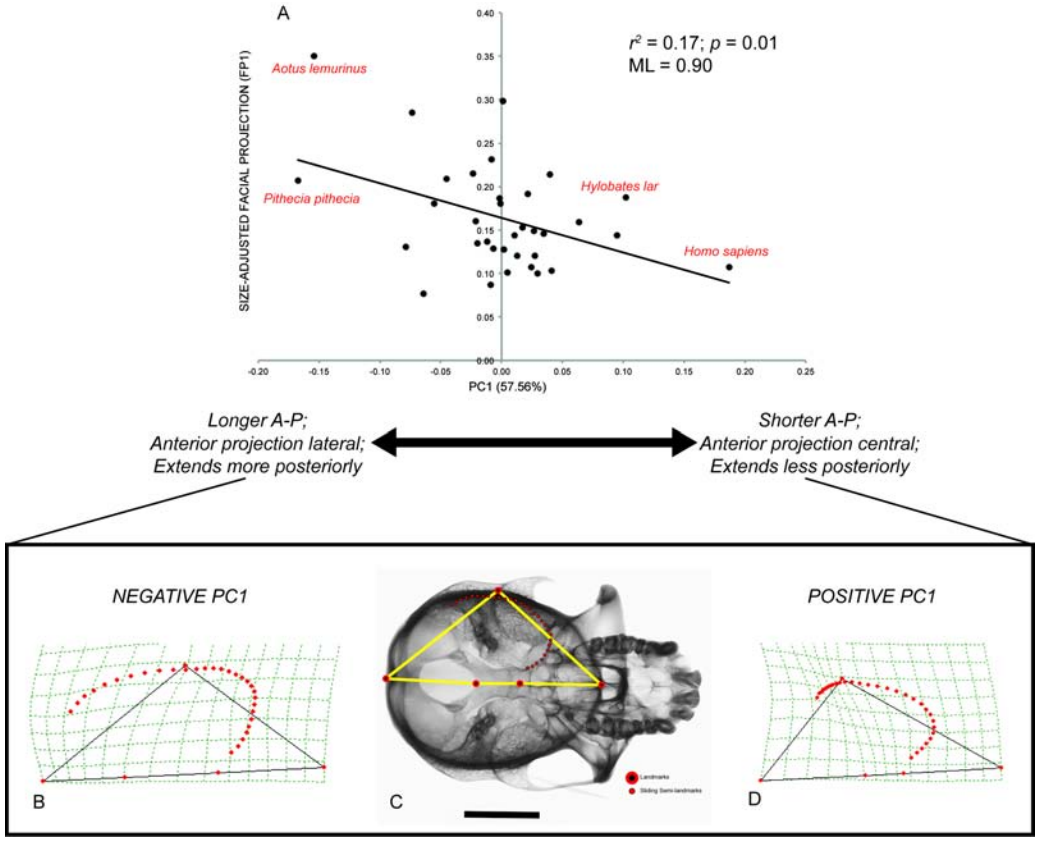


Figure 5.11. Results of geometric morphometric analysis of middle cranial fossa shape and position in anthropoids. A) Scatterplot of size-adjusted facial projection (i.e., FP1; shape-ratios used for size adjustment) vs. PC1. Differences in configurations are listed below A. B) Wireframe diagram of configuration at extreme negative values of PC1. C) Illustration of landmark and semi-landmark locations. Scale bar is 40 mm. D) Wireframe diagram of configuration at extreme positive values of PC1.

positive range of PC1. It is important to note that PC1 is also significantly positively correlated ($r^2 = 0.67$; $p < 0.01$) with centroid size (i.e., the overall size of the landmark configuration in each species). Thus, negative values on PC1 characterize species that possess smaller landmark configurations (i.e., smaller cranial bases), and positive values characterize species that possess larger landmark configurations (i.e., larger cranial bases).

CHAPTER 6—DISCUSSION AND CONCLUSIONS

This chapter summarizes the implications of the results that were presented in the previous chapter. Generally, the results indicated that UFL and ACBL were the best predictors of facial projection. By and large this result was consistent in all analyses. In all cases, *Homo sapiens* was found to fit the patterns apparent in all units of analysis. Methodological issues and their potential consequences for these interpretations are discussed, and the hypotheses presented in Chapter 4 are evaluated. In the context of these considerations, the relevance of the results for studies of human evolution is explored, and final conclusions, including suggestions for future research directions, are provided.

DISCUSSION

Methodological Issues

There are a number of methodological issues that have important implications for the interpretations of the results of this study. The first, and perhaps most important, of these issues is the general lack of correlation between the two measures of facial projection—i.e., FP1 and FP2. As discussed in Chapter 5, the correlation between these variables is somewhat stronger when phylogenetically-controlled residuals are used for size adjustment. However, this difference is slight, as correlations in two of the four units of analysis also approach significance when shape-ratios are used. Regardless of these differences, the fact that a strong correlation between these variables is not ubiquitous (i.e., strong correlation does not occur in all, or nearly all, units of analysis using both methods of size adjustment) suggests that these two measurements of facial projection may describe different anatomical phenomena.

Although both measurements of facial projection describe the anteroposterior position of the upper face relative to the anterior cranial base, these two measurements employ different landmarks to characterize the region of both the upper face and anterior cranial base. FP1 uses foramen caecum point to represent the anteroposterior position of the anterior cranial base and sellion to represent the anteroposterior position of the upper face, whereas FP2 uses the intersection of the superior orbital margin and the anterior cranial fossa to represent the position of the anterior cranial base and the anteriormost point on the inferior orbital margin to mark the position of the upper face. The lack of correlation between FP1 and FP2 in most comparisons, then, is likely due to the fact that important variation is introduced by employing these different landmarks for describing facial projection. In particular, the lack of correlation between FP1 and FP2 is likely due to the fact that the positions of sellion and the most anterior point on the inferior orbit (which represent the location of the upper face in FP1 and FP2, respectively) relative to the position of the anterior cranial base are not correlated. That is, FP1 represents the anterior projection of the orbits, whereas FP2 represents the anterior projection of the structures located between the orbits and associated with the nasal bridge. It is also worth noting that the standard deviations for FP1 are larger in most species than those of FP2 (despite the fact that FP2 is the larger of the two measurements in the majority of cases), suggesting that this measurement may be more variable within species or, alternatively, that FP1 is more difficult to measure precisely. The latter interpretation, however, is less likely because the percent measurement error for the two measurements is nearly identical (see Chapter 3). Although this discussion suggests that FP1 and FP2 may describe somewhat different anatomical features (both of which fit the definition of facial

projection employed here) it is not clear which, if either, of these two measurements should be favored, as neither can be judged to be a "better" description of facial projection, as defined here.

Another potential methodological issue stems directly from the model from which the hypotheses were derived. Specifically, one of the independent variables—i.e., UFL—completely overlaps one of the dependent variables—i.e., FP2. In other words, UFL, which is measured from the PM Plane to sellion, measured perpendicular to the PM Plane, includes the measurement for FP2, which is measured perpendicular to the PM Plane, from foramen caecum to sellion. Therefore, if FP2 increases in length, UFL must increase in length concomitantly because UFL completely overlaps FP2. If UFL increases, however, FP2 may or may not increase in length. In this case, whether or not FP2 must exhibit an increase corresponding to an increase in UFL depends on which portion of UFL—i.e., the posterior portion from the PM Plane to foramen caecum or the anterior portion from foramen caecum to sellion—increases. If the anterior portion of UFL increases in length, then FP2 will exhibit a corresponding increase, and, in this case, UFL and FP2 would be autocorrelated. On the other hand, if the posterior portion of UFL increases, FP2 will not necessarily. In this case, UFL and FP2 would not be autocorrelated. It is therefore clear that, in terms of its predicted relationship with facial projection, the critical portion of UFL is the posterior (non-overlapping) portion. If this portion of UFL (which can be obtained by subtracting FP2 from UFL) is correlated with FP2, it would suggest that this portion of UFL is an important predictor of FP2.

The observation that the posterior portion of UFL is the critical portion of this measurement, however, brings up another similar issue. In particular, the posterior

portion of UFL overlaps to a large degree with ACBL. The non-overlapping portion of UFL and ACBL is the posterior portion of ACBL, measured from sella to the PM Plane. It should be noted that the posterior portion of UFL (from the PM Plane to foramen caecum) is not precisely congruent with the anterior portion of ACBL (from sella to foramen caecum) because the former is measured perpendicular to the PM Plane, and the latter is a direct distance between sella and foramen caecum and is not registered relative to any line. Similarly, the posterior portion of ACBL is not precisely congruent with ASL, which is measured from sella to the PM Plane perpendicular to the PM Plane. However, in both cases, the measurements are likely congruent enough to suggest how this methodological issue may affect the interpretations of the results presented here.

This potential methodological issue may shed important light on the results of this study. Specifically, it may explain why ACBL and UFL are consistently the best predictors of facial projection. For example, UFL and ACBL are the first and second strongest predictors of FP2 in eight out of nine of the best models; the only exception is in anthropoids using shape-ratios for size adjustment, in which case a univariate model (with ACBL as the independent variable) was the best model. The posterior portion of UFL (from the PM Plane to foramen caecum) more or less overlaps with the anterior portion of ACBL (but see above). Moreover, the results of the present study demonstrate that the anterior portion of ACBL, insofar as it can be approximated by ASL, is not a strong predictor of FP2, suggesting instead that the anterior portion of ACBL is likely the portion of this measurement that drives its relationship with FP2. Therefore, the fact that UFL and ACBL are the best predictors of FP2 in the majority of cases may be explained

if this overlapping area (from the PM Plane to foramen caecum) is a strong predictor of FP2. Future research is required to clarify this issue.

The last methodological issue raised by the results of this study is the unexpectedly low values for size-adjusted facial projection in the two species in the genus *Papio* (see Figs. 5.1 and 5.2). These low values are unexpected because visual inspection of radiographs of specimens in these two species suggests that they should have moderate-to-high values for size-adjusted facial projection. The low values for these species is likely due to the fact that they both possess relatively long (anteroposteriorly) facial skeletons (i.e., both have long "muzzles/snouts"). The relatively long facial skeletons in these two species equate to large measurements for three of the six cranial size measurements (i.e., facial height, skull length, and palate length). Consequently, the geometric mean of the cranial size measurements for these two species is relatively large, which, in turn, may underestimate the real degree of facial projection in these two species. It is important to note that, although this issue is most notable in the two *Papio* species, it is likely not limited to them. Rather, this problem probably exists to varying degrees across the sample. As discussed in the next section, it is also likely that the opposite issue (i.e., an overestimation of size-adjusted facial projection in species with relatively small facial skeletons) occurs, as well.

As noted in Chapter 5, a similar issue exists with the values of size-adjusted facial projection in *Homo sapiens*. That is, these values are unexpectedly high regardless of the measurement of facial projection or the method of size adjustment that was employed; however, *Homo sapiens* is one of the species with the five lowest values for size-adjusted facial projection using FP1 and phylogenetically-controlled residuals for size adjustment.

These relatively low values for *Homo sapiens* are unexpected because, as discussed in Chapter 2, many researchers have identified *Homo sapiens* as a species that should exhibit the lowest values for facial projection among anthropoids.

The unexpected values for size-adjusted facial projection in *Homo sapiens* may be due to the fact that the facial skeleton in this species is relatively short anteroposteriorly. Therefore, the values for four of the six cranial size measurements (i.e., facial height, skull length, and palate length) are relatively low. As a result, the geometric mean of the cranial size measurements is relatively small in *Homo sapiens*, resulting in overestimation of size-adjusted facial projection. However, the neurocranium in *Homo sapiens* is relatively tall (supero-inferiorly) and the cranial base is relatively wide, resulting in relatively larger measurements for two of the cranial size measurements (i.e., neurocranial height and cranial width). The effect of these relatively large values may mitigate, to some degree, the small values for the length measurements listed above. In general, the unexpectedly low and high values for size-adjusted facial projection in *Papio* and *Homo sapiens*, respectively, suggests that scaling relationships among the components of the cranium described by the cranial size measurements (as well as the scaling relationship between these variables and measurements of facial projection) may have an important effect on the values of size-adjusted facial projection.

Correlation among the independent variables (see Appendix C) has important implications for the multivariate regression analyses. In particular, as discussed in Chapter 3, one assumption of multiple regression analysis is that the independent variables are not correlated (i.e., the problem of multicollinearity), and, although there is no agreed-upon level/frequency of correlation that signals that this assumption has been

violated, it is instructive to compare the level of correlation among the variables when different methods of size adjustment are used. The level of correlation among the independent variables in the raw data is very high. Thus, the results of multiple regression analyses that are adjusted for size using the geometric mean of the cranial size as an independent variable (which use the raw data), will suffer most severely from the problem of multicollinearity. The level of correlation among the independent variables is much lower when shape-ratios and phylogenetically-controlled residuals are used for size adjustment, with slightly lower levels when the latter are used. The increased correlation among independent variables when shape-ratios are used for size adjustment may be expected because, as discussed in Chapter 3, this method of size adjustment may not eliminate size-related aspects of shape (i.e., allometry). By contrast, using phylogenetically-controlled residuals statistically removes both size and allometry. In other words, unless a given variable scales isometrically with the geometric mean of cranial size, shape-ratios will retain some degree of allometry. The retention of size-related shape variation may cause greater degrees of correlation when shape-ratios are used for size adjustment (i.e., compared to cases in which phylogenetically-controlled residuals are used) because the allometric component of the size-adjusted variables will be autocorrelated.

These results suggest that the problems associated with violating the assumption of noncorrelation among the independent variables will be greatest when cranial size is used as an independent variable to adjust for overall size. This problem is less severe when the other two size adjustment methods are used, but is slightly greater in cases in which shape-ratios are used compared to cases in which phylogenetically-controlled

residuals are used. As discussed in Chapter 3, this problem affects the accuracy of the estimates of regression parameters, including the correlation coefficient, coefficient of determination, adjusted r^2, and SPR^2. The results of the multivariate regression analyses should be interpreted with these facts in mind—i.e., the results from analyses that use a geometric mean of the cranial size for size adjustment should be largely downplayed, and the results of analyses using phylogenetically-controlled residuals should be emphasized somewhat more than those using shape-ratios.

Evaluation of Hypotheses

As reported in the previous chapter, the results relevant to testing each of the five hypotheses vary based on a number of factors, including the measurement of facial projection that is used (i.e., FP1 or FP2), the size adjustment method that is employed, the unit of analysis, whether univariate or multivariate methods are used, and the specific regression model (in the multivariate analyses) that is being considered. Despite this large degree of variation in the results, a synthesis of all results permits some general evaluation of the hypotheses. These evaluations are contextualized within the methodological issues raised above.

Hypothesis 1, which predicts a positive correlation between facial projection and CBA, receives very little support in this study. This fact is true regardless of the measurement of facial projection used, whether multivariate or univariate results are considered, and, by and large, irrespective of the unit of analysis. The only notable exception is that in hominoids, with FP1 as the facial projection measurement and using phylogenetically-controlled residuals for size adjustment, the best model is a multivariate model in which CBA1 is the most important predictor of facial projection (see Table 5.9).

The lack of support for Hypothesis 1 suggests that CBA is generally not an important predictor of facial projection in this sample. Furthermore, this result suggests that relative brain size and the relative size of the facial skeleton—both of which are considered the ultimate causes of variation in CBA (see Chapter 2)—do not contribute greatly to variation in facial projection in any of the units of analysis. Importantly, this fact is true regardless of which measurement of CBA (i.e., CBA1 or CBA2). The result in hominoids discussed above suggests that, at least in this one specific case, CBA is an important predictor of facial projection. The fact that this result was one in which phylogenetically-controlled residuals were used for size adjustment may lend additional credence to these results because the problem of multicollinearity is less severe using this method of size adjustment (see above).

Hypothesis 2 predicts a positive correlation between facial projection and UFL. This hypothesis received relatively strong support in this study. In both univariate and multivariate analyses and regardless of the facial projection measurement used, UFL is frequently significantly correlated with facial projection, and, in many cases, it is a very strong predictor of facial projection (based on r^2 and SPR^2 values). However, UFL is not as important in predicting facial projection in the univariate analyses when catarrhines and hominoids are the units of analysis; this issue will be discussed further in the next section. In the multivariate analyses, UFL is not nearly as frequently an important predictor of facial projection when FP1 is used as the facial projection measure. It should be noted, however, that, in these cases, very few if any independent variables are significant predictors of facial projection. Similarly, UFL is not as frequently an important predictor of facial projection when cranial size is used as an independent

variable to adjust for size. As in the case discussed above, however, very few independent variables are significant in these analyses, and analyses using this method for size adjustment suffer most severely from the problem of multicollinearity (see above), casting some doubt on the applicability of these results. In both of these cases, the fact that UFL is also not a strong predictor of facial projection is less conspicuous. In addition, when multivariate and univariate regression models are compared to determine the best model, UFL is often either the single best predictor (i.e., in cases in which a univariate model is the best model) or a significant predictor (if not the best predictor) of facial projection in cases in which a multivariate model is the best model. Taken together, these results suggest that the anteroposterior length of the upper face plays a very important role in explaining variation in facial projection in all units of analysis.

Hypothesis 3 receives equivocal support from the results of this study. In particular, this hypothesis, which predicts a negative correlation between ACBL and facial projection, receives no support in the univariate analyses. In the multivariate analyses, however, ACBL is frequently a significant and moderately important predictor of facial projection. This is particularly notable when FP2 is used as the measure of facial projection; ACBL is typically neither a significant nor an important predictor of facial projection when FP1 is used. In almost all cases in which ACBL is a significant predictor of facial projection in the multivariate analyses, UFL is also a significant predictor, and, in these cases, UFL is almost always a more important predictor than ACBL. This fact is further supported in comparisons of mutltivariate and univariate models when FP2 is the facial projection measurement, which demonstrate that ACBL and UFL are included in the best models in most cases, and both are frequently

significant predictors in the best models. In the majority of these cases, UFL is a more important predictor of facial projection than ACBL (based on values of SPR^2). A notable exception is in hominoids using FP2 as the measurement of facial projection and shape-ratios for size adjustment. In this case, ACBL is a more important predictor of facial projection than UFL. ACBL is not an important predictor of facial projection in most cases when cranial size is used as an independent variable in multiple regression models for size adjustment. As discussed above, this fact can be dismissed to some degree because this method of size adjustment suffers greatly from the problem of multicollinearity; in addition, very few independent variables are significant/important predictors of facial projection in these analyses. These results suggest that ACBL is a somewhat important predictor of facial projection. However, the importance of ACBL varies depending on the specific analysis being considered. Moreover, this variable is most likely to be an important predictor in multivariate models, especially in models in which UFL is also an important predictor of facial projection.

The results of this study lend very little support for Hypothesis 4, which predicts a positive correlation between ASL and facial projection. Specifically, this hypothesis is not supported in univariate analyses, in which ASL is rarely a significant predictor of facial projection. However, ASL is a significant predictor of FP2 in platyrrhines using both methods of size adjustment. In the multivariate analyses, ASL is infrequently a significant predictor of facial projection, and, in cases in which it is a significant predictor, it is relatively unimportant (based on low SPR^2). One important exception to the generalization that ASL is not an important predictor of facial projection is found in the best model for anthropoids with FP1 as the measure of facial projection and

phylogenetically-controlled residuals used for size adjustment. In this case, ASL is a significant predictor in the best model, and this variable is also the most important predictor of FP1. Despite this exception, the results of this study generally do not suggest that ASL is an important predictor of facial projection.

Hypothesis 5 predicts a negative correlation between ACMFL and facial projection. Similar to Hypothesis 4, this hypothesis receives very little support from the results of the present study. In particular, AMCFL is very rarely correlated with facial projection in the univariate or multivariate analyses; this variable is more frequently correlated with facial projection in the multivariate analyses, but, in these cases, it is never an important predictor (based on SPR^2). The relative unimportance of AMCFL is underscored by the fact that this variable is not a significant predictor in any of the best models.

As reviewed in Chapter 3, Hypotheses 4 and 5 represent different ideas about how increases in the length of the anterior portion of the middle cranial fossa affect the position and orientation of the PM Plane. Put differently, ASL and AMCFL describe the same anatomical phenomenon measured in lateral (ASL) and superior (ACMFL) radiographs. The crucial difference between these hypotheses, however, is that Hypotheses 4 predicts that increases in this dimension will cause the PM Plane to migrate (or "push") anteriorly without rotation, resulting in increases in facial projection, whereas Hypothesis 5 predicts that increases in this dimension will cause the PM Plane to rotate ventrally, which, in turn, causes the NHA to rotate ventrally, resulting in a decrease in facial projection. However, the results presented here—i.e., the general lack of support for either hypothesis—suggest that neither of these predictions hold. Although these

results do not resolve the issue of whether the PM Plane rotates or migrates anteriorly without rotation when the length of the anterior portion of the middle cranial fossa increases in length, they do suggest that neither of these processes is overly important in predicting variation in facial projection in anthropoids.

Although neither Hypothesis 4 nor Hypothesis 5 receive strong support, the results of the geometric morphometric analysis can shed additional light on their respective predictions. In the only noteworthy component of the geometric morphometric analysis (i.e., PC1 in anthropoids using FP1 as the measurement of facial projection; see Fig. 5.11), species that possess greater degrees of facial projection are shown to also exhibit relatively anteroposteriorly longer middle cranial fossae. Conversely, species with lower degrees of facial projection are shown to have shorter and somewhat more anteriorly projecting middle cranial fossae. This result may suggest that, contrary to the results summarized above, increases in AMCFL may be correlated with decreases in facial projection because the species with lower degrees of facial projection exhibit middle cranial fossae that are slightly more anteriorly projecting. If this is true, the anterior projection of the middle cranial fossa causes the PM Plane to rotate ventrally. Because these results also show that species with lower degrees of facial projection also have anteroposteriorly shorter middle cranial fossa, they suggest that these increases are due in large part to an anterior migration of the entire middle cranial fossa (i.e., instead of a lengthening of the middle cranial fossa; see Chapter 3). Bearing in mind the relatively low amount of variation in facial projection that is explained by PC1 ($r^2 = 0.17$), the results of the geometric morphometric analysis do not outweigh the results of the univariate and multivariate analyses, and, by and large, the conclusion that Hypotheses 4

and 5 are not supported is not substantially altered by the geometric morphometric results.

It is important to note that ASL and AMCFL are the only independent variables employed in this study that describe morphology that is located lateral to the midline, as both of these variables are anchored anteriorly by the greater wings of the sphenoid. This fact is relevant because, as discussed in Chapter 2, research has shown that lateral basicranial structures are more closely correlated with the size, shape, and position of the facial skeleton than midline structures and that midline and lateral basicranial structures are not strongly correlated with each other. The results of the present study, however, suggest that variables describing the lateral basicranium are not correlated with facial projection. Although this finding may cast some doubt on previous arguments that suggest the lateral basicranium is a stronger predictor of facial morphology, it should be kept in mind that FP2 is a midline measure. Therefore, it may not be unexpected that lateral basicranial variables are not strongly correlated with FP2—i.e., because lateral basicranial structures may not be good predictors of midline facial morphology. Of course, this explanation cannot resolve the lack of correlation between these lateral basicranial variables and FP1, which represents structures in the upper face that are located lateral to the midline. It is possible that, while lateral basicranial structures are generally better predictors of facial morphology than midline structures, they are not good predictors of the specific aspects of facial morphology investigated here.

Evaluation of Units of Analysis

In addition to evaluation of the individual hypotheses, it is important to summarize the results from analyses of each unit of analysis and discuss their

implications. As in the previous chapter, the mention of any unit of analysis (i.e., anthropoids, platyrrhines, catarrhines, and hominoids) refers to that taxonomic grouping only. That is, unless otherwise specified, when a unit of analysis that colloquially includes narrower units is mentioned, the remarks apply to that specific unit and not to any of the included units.

As in the evaluation of the specific hypotheses, the results vary greatly depending on the specific analysis (i.e., depending on the measurement of facial projection, the size adjustment method, whether univariate or multivariate results are considered, and which specific regression model is being considered). Nevertheless, some generalizations in these results can be identified.

When anthropoids are the unit of analysis, variation in facial projection is explained best by UFL and ACBL. UFL stands out as the most important predictor of facial projection in both the univariate and multivariate analyses, whereas ACBL is generally an important predictor of facial projection only in the multivariate analyses. These variables are frequently significant predictors of facial projection regardless of the size adjustment method that is used. This pattern is apparent regardless of the facial projection measurement used, but ACBL and UFL are much more frequently significant and more important predictors of facial projection when FP2 is used. However, the importance of these models (based on SPR^2 values) is considerably lower when cranial size is used as an independent variable for size adjustment. As discussed above, multicollinearity is a large problem in these analyses; therefore this discrepancy is probably not that important. These two variables also contribute significantly to most of the best models for this unit of analysis, and these variables are also the two most

important predictors of facial projection in most of the best models. It is important to note, however, that, in anthropoids, even the best models explain relatively little of the overall variation in facial projection (based on adjusted r^2 values). The one exception to this occurs when FP2 is used as the measure of facial projection and phylogenetically-controlled residuals are used for size adjustment; in this case, the best model accounts for almost 90% of the variation in facial projection. Taken together, these results suggest that UFL, and, to a somewhat lesser extent, ACBL are the most important predictors of facial projection in anthropoids. Specifically, the results suggest that, when anthropoids are the unit of analysis, increases in facial projection are associated with increases in UFL and decreases in ACBL. These results also suggest, however, that, in general, none of the models explain a considerable amount of the variation in facial projection in anthropoids. In addition, *Homo sapiens* closely conforms to the best models when anthropoids are the unit of analysis, suggesting that this species follows the general trends for anthropoid primates.

The results of the analyses in which platyrrhines are the unit of analysis are very similar to those in which anthropoids are the unit of analysis (see above). In particular, UFL, and to a lesser extent, ACBL are the most important predictors of facial projection in this unit of analysis, as shown in the results of the univariate and multivariate analyses when FP2 is used as the measure of facial projection. However, when FP1 is the measurement of facial projection, very few (if any) variables are significant predictors of facial projection. As with anthropoids, these results are weaker when cranial size is used as an independent variable to adjust for size, but this inconsistency can be largely ignored for the same reasons cited above. The best models for platyrrhines are generally

univariate models with UFL as the independent variable or multivariate models in which UFL and ACBL are the most important predictors of facial projection. Unlike for anthropoids, the best models when platyrrhines are the unit of analysis commonly explain a relatively large amount of the variation in facial projection. In sum, then, UFL and ACBL are the most important predictors of facial projection in both anthropoids and platyrrhines; and, in both cases, increases in facial projection are correlated with increases in UFL and decreases in ACBL. The major difference between these two units of analysis lies in the amount of variation explained by the models in each case.

A similar pattern is apparent in analyses in which catarrhines constitute the unit of analysis. Namely, UFL and ACBL are the most important predictors of facial projection in this unit of analysis when both univariate and multivariate results are considered. This pattern is apparent regardless of the facial projection measurement that is used, but ACBL and UFL are much more frequently significant and much more important predictors of facial projection when FP2 is used. ACBL is generally only a significant predictor of facial projection in multivariate models that also include UFL as an independent variable, and, in these cases, UFL is always a more important predictor of facial projection than ACBL. Again, these findings are less pronounced when cranial size as an independent variable is used for size adjustment. The best models in this case generally explain a relatively large amount of the variation in facial projection (i.e., greater than 90% in the majority of cases). In four of the five cases in which significant models exist, *Homo sapiens* follows the general trends that characterize other catarrhines. This result implies that the factors that explain variation in facial projection in catarrhines more generally, also explain the degree of facial projection in *Homo sapiens*. The lone

exception to this generalization is found when FP1 is used as the measure of facial projection and phylogenetically-controlled residuals are used for size adjustment—i.e., in this case, *Homo sapiens* fall outside the 95% prediction intervals of the best model, suggesting that, in this case, our species does not follow the general trends for catarrhines.

The general pattern in hominoids is that, compared to other units of analysis, very few (if any) independent variables are significant predictors of facial projection. This fact is particularly true in the univariate analyses. Likewise, in the multivariate analyses, when FP1 is used as the measurement of facial projection, very few if any independent variables are significant predictors of facial projection. As in the other units of analysis, UFL and ACBL are the most important predictors of facial projection in hominoids when FP2 is used as the measurement of facial projection, and very few if any independent variables are significant when FP1 is used. For hominoids, however, unlike for other units of analysis, ACBL is frequently a more important predictor of facial projection than UFL. Moreover, CBA is also an important predictor of facial projection in some analyses of hominoids. In fact, in one analysis (i.e., with FP1 as the facial projection measurement and using phylogenetically-controlled residuals for size adjustment), CBA1 is the most important predictor of facial projection in the best model. Most of the best models for hominoids explain a large proportion of the variation in facial projection—i.e., two of the three cases in which sample sizes permitted analysis, the adjusted r^2 value is 0.95 or greater. In the third case, however, the r^2 value is relatively low (0.68). *Homo sapiens* conforms to the general patterns found in hominoids based on evaluation of prediction intervals and studentized residuals.

In general, there are fewer instances in which analyses in hominoids could be conducted (i.e., due to small sample sizes), and this fact may have an important influence on the results in this unit of analysis. Specifically, the sample size for species in hominoids is never more than seven in any analysis, and these small sample sizes may increase the probability of Type I error. In other words, the results may suggest that some independent variables, which would be revealed as significant predictors of facial projection if sample sizes were larger, are not significant.

The results reveal differences in the explanations for variation in facial projection among hominoids, on one hand, and all other anthropoids, on the other. Specifically, unlike for other units of analysis, CBA is an important predictor of facial projection in hominoids, but not for other units of analysis. Moreover, ACBL and UFL are important predictors of variation in facial projection in hominoids and non-hominoids; however, in hominoids, ACBL is a more important predictor of variation in facial projection than UFL, whereas, in all non-hominoid units of analysis, the reverse is true. This finding may suggest that cranial base flexion has a greater effect on variation in facial projection in hominoids due to a phylogenetic change in the relationship between these two phenomena. However, the present data cannot directly address this issue.

As suggested in the preceding paragraphs, the patterns for all units of analysis are generally consistent with each other. In particular, very few independent variables are significant predictors of facial projection when FP1 is used as the measurement of facial projection. Additionally, neither univariate nor multivariate models explain a large proportion of variation in FP1. When FP2 is used as the measurement of facial projection, by contrast, UFL and ACBL are consistently significant predictors of facial

projection, and these variables are usually the most important predictors of facial projection, regardless of the unit of analysis. In the majority of the units of analysis, UFL is a more important predictor of facial projection than ACBL. The best models explain a relatively large amount of variation in facial projection in platyrrhines, catarrhines, and hominoids. In anthropoids, however, the best model explains relatively little of the variation in facial projection. Also, in most cases, *Homo sapiens* fits the general patterns in each unit of analysis, suggesting that facial projection in this species is explained by the same factors that explain facial projection in the respective unit of analysis. As discussed above, hominoids represent a notable exception to these general patterns. Most importantly, in hominoids, CBA (in addition to UFL and ACBL) is also an important predictor of facial projection.

In summary, UFL and ACBL are the most important predictors of facial projection in all of the units of analysis. This finding suggests that increases in facial projection are largely due to increases in the anteroposterior length of the upper face and decreases in the anteroposterior length of the anterior cranial base. The fact that the combination of these two variables is the best explanations of facial projection and are usually included together in significant models is noteworthy because the effect that each of these variables has on facial projection is linked to the effect of the other. Specifically, increases in facial projection are most likely to occur when UFL is increased relative to ACBL or vice-versa. This is true because the ACBL defines the space inferior to which the upper face is situated (see Chapter 2). Therefore, the degree to which the upper face projects anterior to the anterior cranial base (i.e., the degree of facial projection) can be modified by changes in the relative lengths of the anterior cranial base and upper face. In

other words, for a given ACBL, increases in UFL will cause increases in facial projection and vice-versa because, when ACBL is held constant, anteroposteriorly longer upper faces will be located more anteriorly relative to the anterior cranial base than anteroposteriorly shorter upper faces. Likewise, with a given UFL, increases in ACBL will cause decreases in facial projection and vice-versa because, when UFL is held constant, upper faces will be located most posteriorly relative to the anterior cranial base when the space for the upper face in the anteroposterior dimension (i.e., ACBL) is greater. In general, this finding suggests that UFL and ACBL work synergistically to explain variation in facial projection. It is important to reiterate, though, that UFL is generally a more important predictor of facial projection. Therefore, although ACBL also makes an important contribution to variation in facial projection, increases/decreases in UFL are the major explanation of this variation.

These findings are generally consistent with previous studies of variation in facial projection in extant anthropoids. Specifically, these results corroborate Lieberman and colleagues' (Lieberman, 2000; McBratney-Owen and Lieberman, 2003) studies, which suggested that differences in facial projection between *Pan troglodytes* and *Homo sapiens* are underlain primarily by differences in UFL and ACBL. Lieberman and colleagues also argued that these same features are the most important factors that explain intraspecific variation in facial projection. When combined with the results of previous studies, then, the results here suggest that the results of Lieberman and colleagues' narrow comparison are more generalizable, as they also explain differences in facial projection in the much broader sample employed here.

Another important finding provided by the present study is that the proposed explanations do a relatively good job of predicting variation in facial projection when FP2 is used as the measure of facial projection, but not when FP1 is used. As discussed above, these measurements are also not strongly correlated with each other, which might stem from the fact that they describe subtly different anatomical phenomena (i.e., FP1 describes the anterior projection of the orbits, whereas FP2 describes the anterior projection of the structures located between the orbits). The finding that the factors hypothesized to underlie variation in facial projection are good explanations only when FP2 is used as the measure of facial projection may suggest that these factors explain variation in midline structures in the upper face, but do not explain variation in lateral upper facial structures. This finding is perhaps not unexpected because the explanations for variation in facial projection that were tested here are derived from models that use FP2 to describe facial projection.

These findings also have important implications for the causes of variation in facial projection in anthropoids. Namely, they suggest that the most important predictor of facial projection (i.e., UFL) is a factor intrinsic to the facial skeleton. That is, unlike many of the factors that are predicted to influence facial projection, UFL is not linked to the anatomy of the brain or its component parts in any direct way. Thus, the major explanation for variation in facial projection does not invoke modifications of the brain (this point will be discussed further in the context of the human fossil record, see below). However, the other major contributor to variation in facial projection (i.e., ACBL) is linked to the size of the frontal lobes. McCarthy (2004) showed that frontal lobe volume and anterior cranial fossa size scale isometrically. It is important to point out, however,

that ACBL includes portions of the cranial base that comprise both the anterior and middle cranial fossae. Therefore, increases in frontal lobe volume will cause increases in ACBL, but ACBL can also increase in the absence of increases in frontal lobe volume. Put differently, if increases in ACBL are due to increases in the length of the portion of ACBL between sella and the PM Plane (i.e., the middle cranial fossa portion of ACBL), rather than the portion from the PM Plane to foramen caecum point (i.e., the anterior cranial fossa portion of ACBL).

The fact that CBA is an important predictor of facial projection in hominoids is also important. In particular, this finding suggests that, in hominoids, the relative size of the brain and/or facial skeleton may also play important parts in explaining facial projection. Because CBA is an important contributor to variation in facial projection and because CBA is underlain by relative brain size (i.e., increases in relative brain size are associated with decreases in CBA) and relative facial size (i.e., increases in relative facial size are associated with increases in CBA), variation in the relative sizes of the facial skeleton and brain may be important in explaining variation in facial projection in hominoids (and perhaps in hominins, see below).

Implications for the Hominin Fossil Record

The findings outlined above have important implications for studies of the hominin fossil record. In particular, they may provide insights into the causes of variation in facial projection among hominin species and, in so doing, may offer clues to an important aspect of cranial evolution in hominins. The consistency of the results across all units of analysis suggests that the same features explain variation in facial projection regardless of the taxonomic scale at which this variation is considered. That

is, in all units of analysis in this study—from the broadest (i.e., anthropoids) to the narrowest group—the results suggest the UFL and ACBL are the most important predictors of variation in facial projection. Therefore it is likely that the same factors explain variation in facial projection in taxonomic groups that were not included in this study (e.g., hominins). Given the uniformity of the results among the extant anthropoids included here, it is reasonable to invoke the same factors as explanations for variation in facial projection when making inferences about the evolution of facial projection in hominins. Moreover, the fact that *Homo sapiens* generally fits the trends identified in the units of analysis of which it is part suggests that is appropriate to expect that the evolution of extremely reduced facial projection in *Homo sapiens* was also underlain by the same factors identified in this study. Specifically, this logic dictates that UFL and ACBL are the most important factors underlying variation in facial projection in hominins, and that these features also explain the evolution of extreme facial retraction in *Homo sapiens*.

The results in hominoids, however, are probably more relevant to discussions of fossil hominins than those in other units of analysis because this unit of analysis is the narrowest unit and includes the species most closely related to hominins. If the results in hominoids are favored over those in other units of analysis, CBA should also be invoked as an important factor underlying facial projection in hominins (but see below). Moreover, following this logic, CBA should be considered less important than UFL in explaining the evolution of facial projection in hominins.

Having identified the factors that are most likely to explain variation in facial projection in hominins based on the results of this study, it is important to discuss

previous assessments of these factors to further evaluate the likelihood that these features might indeed underlie the evolution of facial projection in hominins.

The potential contribution of CBA to variation in facial projection in hominins is confounded by the fact that the position of *Homo sapiens* relative to other hominin species is currently unresolved. As reviewed in Chapter 2, a difference of opinion exists concerning whether or not *Homo sapiens* possess cranial bases that are less flexed than would be expected for a haplorrhine primate with its relative brain size. Ross and Henneberg (1995) argued that the cranial base in *Homo sapiens* is significantly less flexed than expected based on its relative brain size and found no significant differences in CBA between *Homo sapiens* and the hominin species included in their analysis, despite differences in relative brain size. This finding suggests that significant decreases in CBA did not occur during hominin evolution. However, using a different measure of CBA (see Chapter 3), Spoor (1997) found that *Homo sapiens* does not possess a less flexed cranial base than expected based on its relative brain size, suggesting that CBA may have increased significantly during the course of hominin evolution as relative brain size increased.

If Ross and Henneberg's (1995) argument is correct, it is unlikely that CBA contributed greatly to variation in facial projection among hominins simply because CBA does not vary significantly in this group, whereas the degree of facial projection does. In addition, if this argument is correct, it would be somewhat contrary to the findings presented here, which suggest that CBA is likely to be a contributing factor to variation in facial projection in hominins based on the results in hominoids. On the other hand, if Spoor's (1997) argument is correct, CBA may have contributed to variation in facial

projection in hominins because it suggests that CBA varies significantly among hominins, which is more in accord with the findings of the present study.

The role of UFL in explaining variation in facial projection in hominins—in particular, the reduction in facial projection in *Homo sapiens*—has been evaluated by Lieberman (1998). He found significant differences in UFL between Pleistocene and recent *Homo sapiens*, but he found no significant differences in this measure between Pleistocene *Homo sapiens* and other *Homo* species (i.e., *Homo erectus*/*ergaster*, *Homo heidelbergensis*, and *Homo neanderthalensis*). This finding suggests that UFL decreased over time in *Homo sapiens*, but not at the transition between *Homo sapiens* and its putative ancestor. Moreover, because a reduction in facial projection is already present in Pleistocene *Homo sapiens* (i.e., Lieberman [1998] found no significant differences in facial projection between Pleistocene and recent *Homo sapiens*), UFL likely does not explain the extreme reduction in facial projection in *Homo sapiens*. It should be pointed out, though, that Lieberman's (1998) measurements (at least those of ASL) were later shown to be in error (see Chapter 2). Consequently, it is unclear whether the remaining variables (and associated statistical tests) were also measured/performed incorrectly. This ambiguity is underscored by the fact that Spoor et al.'s (1999) reassessment of Lieberman's (1998) study suggested that a reduction in the overall size of the facial skeleton likely contributed to reduced facial projection in *Homo sapiens* (see O'Higgins et al., 2001). Therefore, in sum, the possibility that UFL contributed to extreme facial retraction in *Homo sapiens* remains somewhat viable.

The role ACBL in explaining the variation in facial projection in hominins is less ambiguous. Lieberman's (1998) study focused on the evolution of cranial form in *Homo*

sapiens, including the dramatic reduction in facial projection in this species, and showed that ACBL differs significantly between Pleistocene and recent *Homo sapiens* and other species in the genus *Homo*. No significant differences were found, however, between Pleistocene and modern *Homo sapiens*. These findings suggest that ACBL may be an important factor underlying the reduction in facial projection in *Homo sapiens*. Moreover, these findings accord well with the results of this study, which suggest that ACBL contributes to variation in facial projection in all anthropoids, regardless of taxonomic scale.

The results of this study are also relevant to understanding the ultimate causes of variation in facial projection in hominins. Prominent among hypotheses about the ultimate causes of variation in facial projection are those that invoke changes in the brain and its components. These arguments are intuitively appealing because they suggest that changes in the relative size of the brain or its components may be related to changes in cognition. Therefore, these arguments provide a potential link between the morphological changes that mark the origin of *Homo sapiens* and the behavioral changes that appear first in the archaeological record associated with the earliest representatives of this species (e.g., O'Connell, 2006; Stiner and Kuhn, 2006; Marean, 2007; McBrearty, 2007; Klein, 2008; Brown et al., 2009). If these arguments are corroborated, it would suggest that selection on brain size and/or architecture account partly for the unique cranial form exhibited by *Homo sapiens* as well as the behavioral novelties associated with these species (e.g., symbolic behavior, complex stone tool armatures, long-chain technological processes, and language).

As discussed in Chapter 2, variation in CBA is associated with relative brain size. Therefore, selection for increased relative brain size may represent an ultimate explanation for variation in facial projection in hominins. However, research has shown that relative brain sizes in *Homo sapiens* and "archaic" *Homo* (i.e., *Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo erectus*/*ergaster*) are not significantly different (Ruff et al., 1997). Moreover, an anteroposterior shorter cranial base (which can cause decreases in CBA by increasing relative brain size (Strait, 1999; see Chapter 2) is shared by all hominins (Kimbel and Rak, 2010; Kimbel et al., 2014).

ACBL may also be associated with variation in the brain or its component parts, and selection for these changes in brain anatomy may then underlie variation in facial projection in hominins. As discussed above, frontal lobe volume has been shown to scale isometrically with anterior cranial fossa length (McCarthy, 2004), and this finding suggests that ACBL may also be related to frontal lobe volume. It is important to note that ACBL can be increased without increasing anterior cranial fossa length—i.e., if the portion of ACBL from sella to the PM Plane increases in length. In addition, although relative frontal lobe volume in hominin species cannot be compared, it has been shown that relative frontal lobe volume in *Homo sapiens* is no greater than in other hominoids (Semendeferi, 2001; Semendeferi et al., 2001; Rilling and Seligman, 2002; Schenker et al., 2005). Therefore it is somewhat unlikely that an increase in frontal lobe volume represents an ultimate cause of variation in facial projection in hominins.

The results of the present study also provide very little support for the hypotheses that link variation in facial projection to the size and shape of the middle cranial fossae and temporal lobes. Specifically, although the geometric morphometric analysis may

offer some support, Hypotheses 4 and 5 are largely refuted by the results here. This finding is important because these hypotheses have suggested a specific adaptive scenario that explains why selection may have favored increased size of the temporal lobes. This scenario suggests that selection favoring the cognitive functions associated with the temporal lobe (e.g., organization of sensory outputs, language, memory, and symbolic thought) may have caused increases in the size of the temporal lobe, which, in turn, caused the temporal lobes to project further anteriorly, resulting, ultimately, in decreases in facial projection (Lieberman, 2008; see also McCarthy and Lieberman, 2001; Bastir et al., 2008). Although this scenario could explain why *Homo sapiens* possesses low degrees of facial projection and anteriorly projecting temporal lobes, it is not supported by the results of the present study. Therefore is it unlikely that the drastic reductions in facial projection in *Homo sapiens* are due to selection on the size and/or shape of the temporal lobes.

Thus, despite their intuitive appeal, further examination suggests that explanations positing changes in brain anatomy as the ultimate causes for variation in facial projection in hominins rather unlikely. Moreover, this finding suggests that, at least in the context of facial projection, selection for changes in the size and/or shape of the brain and its component parts are probably not the ultimate cause of the unique for of the modern human cranium. Consequently, these results do not support a straightforward link between changes in the morphology of the cranium and changes in behavior that are both considered hallmarks of *Homo sapiens*.

Evolutionary changes in UFL are not generally considered to be directly related to changes in the anatomy of the brain. Instead, these changes are thought to be related to

mastication and diet. Specifically, the general trend of diminution in facial skeleton size in hominins (and the reduction of the facial skeleton in *Homo sapiens*, in particular) has been argued to be related to a reduction in the need to withstand strains encountered during chewing (Ross, 2001; Lieberman et al., 2004; Lieberman, 2011; see also Carlson, 1976; Carlson and Van Gerven, 1977). Furthermore, Lieberman (2008) linked these evolutionary changes in facial skeleton size to cooking and/or food preparation, which would make food easier to chew (Lucas, 2004), thereby reducing the strains encountered by the facial skeleton related to mastication. It is important to note, however, that these arguments concern the anatomy of the entire facial skeleton, not the anteroposterior dimension of the upper face specifically, and it is possible for the facial skeleton to reduce in overall size without a concomitant decrease in UFL. Nevertheless, this argument suggests that it is at least plausible that dietary changes during the course of human evolution are an important factor underlying variation in facial projection in hominins and, particularly, the extreme reduction in facial projection in *Homo sapiens*.

Given this discussion, it is possible to offer some speculations regarding the evolution of facial projection in Middle-Late Pleistocene *Homo*. Compared to australopiths, there is an increase in brain size in the genus *Homo*, and this increase in brain size may have caused an increase in cranial base flexion and a concomitant decrease in facial projection. However, as cranial base angle was generally identified as a less important factor than upper facial length and anterior cranial base length in the present study, this interpretation may be questionable. This is particularly true because, as mentioned above, there is some debate about whether there is any significant change in cranial base angle during hominin evolution. If this is true, therefore, it is unlikely that

changes in relative brain size exerted an influence on variation in facial projection in Middle-Late Pleistocene *Homo*.

The advent of cooking may have had an important indirect influence on variation in facial projection in Middle-Late Pleistocene *Homo* (Lieberman, 2008). As discussed above, the practice of cooking food changes the mechanical properties of many foods and, in most cases, makes them easier to chew, and, in terms of the biomechanics of feeding, reduces the strain produced by masticating food (Lucas, 2004). Therefore, insofar as overall facial size is an adaptation for resisting strains encountered in chewing and other non-dietary uses of the masticatory apparatus, cooking may have released the constraint requiring the facial skeleton to be relatively large to resist the strains associated with uncooked foods (Lieberman, 2008).

This explanation, however, cannot explain the relatively large facial skeletons possessed by *Homo heidelbergensis* and *Homo neanderthalensis*, as these two species do not exhibit smaller facial skeletons relative to a *Homo erectus*/*ergaster*-like ancestor. The first solid evidence for the controlled use of fire dates to 250,000 years ago (James, 1989; Brace, 1995; Rowlett, 2000; Goldberg et al., 2001); thus, it is possible that *Homo heidelbergensis* used fire in food preparation, and it is very likely that *Homo neanderthalensis* did so. However, it is also likely that these species engaged in non-dietary behavior using their jaws and teeth, for example holding hides in their anterior dentition while working the hides with both hands. If this is the case, then the strains experienced during these behaviors may explain the relatively large faces in *Homo heidelbergensis* and *Homo neanderthalensis* (Rak, 1986; Demes, 1987; Anton, 1994; O'Connor et al., 2005). Although this view does not necessarily challenge the idea that

the relatively large size of the facial skeleton in *Homo neanderthalensis* was symplesiomorphic (Trinkaus 1987, 2003, 2006), it suggests that, in addition to being a primitive retention, larger facial skeletons may have been favored by selection in this species because it conferred the ability to resist strains from non-dietary use of the masticatory apparatus (Rak, 1986; Demes, 1987; Anton, 1994; O'Connor et al., 2005).

In *Homo sapiens*, in which non-dietary behavior of the masticatory apparatus is not believed to have been widespread and cooking food was prevalent, selection would have no longer favored relatively larger facial skeletons. In other words, relatively large facial skeletons were no longer required to resist the strains encountered by masticating uncooked foods or using their teeth and masticatory apparatuses as tools. Intriguing evidence regarding the epigenetic effects on facial size of a change in diet has been offered by archaeologists studying human groups that experienced a shift from harder to softer foods (Carlson, 1976; Carlson and Van Gerven, 1977; Corruccini, 1999). This research shows a significant trend for a decrease in facial skeleton size associated with a shift from harder to softer foods. Therefore, the extremely reduced degree of facial projection in *Homo sapiens* may be explained by an overall reduction in facial skeleton size that was caused by the adoption of cooking and the absence of non-dietary behaviors involving the masticatory apparatus in this species.

There are two important problems with these speculations. First and foremost, as mentioned above, it is assumed that an overall reduction in facial size in *Homo sapiens* included a reduction in the anteroposterior dimension of the facial skeleton. While this assumption is likely to be true, it is also possible that facial size reduction in *Homo sapiens* primarily involved a reduction in the superoinferior dimension, and that the

anteroposterior length of the facial skeleton was relatively unaffected by this reduction in overall facial size. If this was the case, then the reduction of facial size in *Homo sapiens* would have no relevance for understanding the reduction in facial projection in this species. Secondly, this explanation cannot adequately explain the reduction in overall facial size in *Homo sapiens* (Lieberman, 2008). Although the adoption of cooking and the abandonment of the use of the teeth as tools explains why natural selection no longer favored relatively larger facial skeletons, these factors do not explain why selection favored smaller facial skeletons in *Homo sapiens*. Put differently, this scenario cannot explain why the possession of relatively smaller facial skeletons would have conferred a fitness benefit in *Homo sapiens*. These problems notwithstanding, the speculations presented here provide information with which hypotheses about the evolution of facial projection in Middle-Late Pleistocene hominins can be produced and tested.

CONCLUSIONS

The goal if this dissertation was to investigate variation in facial projection in anthropoid primates. Specifically, this research posed two questions: (1) What factors explain variation in facial projection in anthropoid primates? and (2) Does *Homo sapiens* depart from any apparent patterns identified in anthropoids? Answers to these questions were sought by testing five specific hypotheses that relate this variation to different aspects of the anatomy of the cranial base and facial skeleton. Ultimately, this dissertation aimed to understand more fully variation in facial projection in hominins, and, in particular, the evolution of greatly reduced facial projection in *Homo sapiens*.

The results of this study suggest that UFL, ACBL, and, to a lesser extent CBA are the most important predictors of facial projection in anthropoids. In particular, increases

in facial projection are associated with increases in UFL, decreases in ACBL, and increases in CBA. These variables were consistently significant and important predictors of facial projection in all units of analysis, and these results were consistent in both univariate and multivariate analyses. Importantly, the best models explain a relatively large amount of variation in facial projection in platyrrhine, catarrhines, and hominoids; however, in anthropoids, these models explain relatively little of the variation in facial projection. Furthermore, *Homo sapiens* was shown to fit the general trends in nearly all comparisons, indicating that the factors that reduced facial projection in *Homo sapiens* are underlain by the same factors that explain variation in facial projection in anthropoids and taxonomic sub-groups within anthropoids.

It is reasonable to predict that UFL, ACBL, and CBA explain variation in facial projection in hominins, as well. However, it is currently difficult to discern whether or not CBA can be invoked as an explanation for variation in facial projection in hominins because there is disagreement about whether or significant changes in CBA occurred during the course of human evolution. Therefore, it is also unknown whether relative brain size—which explains variation in CBA—was the ultimate cause of variation in facial projection in hominins. Similarly, it is difficult to substantiate arguments that suggest that increases in frontal lobe volume—which are associated with increases in anterior cranial base length, which, in turn, forms part of ACBL—explain the reduction of facial projection in hominins, culminating in the highly retracted condition found in *Homo sapiens*. For these reasons, proposals that suggest that changes in the anatomy of the brain and/or its component parts are the ultimate explanations for highly reduced facial projection in *Homo sapiens* are unlikely. By contrast the idea that extreme facial

retraction in *Homo sapiens* is ultimately explained by reductions in overall facial size (including reductions in UFL), which may be linked to changes in diet and/or dietary behavior, are more consistent with the current evidence. However, the role of all three of these factors—i.e., UFL, ACBL, and CBA—in modulating facial projection in hominins should be researched further, as none of these explanations can be eliminated. Importantly, though, the combination of these results and previous considerations of variation in facial projection in hominins suggest that explanations that emphasize the role of the brain in this context should be downplayed.

Future research that tests the hypotheses outlined here in samples of fossil hominins is desperately needed. Combined with the data presented here, data on fossil hominins will permit much more nuanced inferences about the causes of variation in facial projection in hominins. In addition, research on the evolution of facial skeleton size in primates would be beneficial, as it would provide further evidence about how and why *Homo sapiens* evolved relatively small facial skeletons. This research is important because, as discussed above, UFL emerges from this study as the most likely predictor of variation in facial projection and it is at least plausible that evolutionary decreases in UFL are linked to overall diminution in facial skeleton size in the hominin lineage.

Previous investigations of this facial projection in anthropoid primates have been hampered by a lack of comparative data. This dissertation has filled this gap, and, in so doing, it has provided a context in which hypotheses about the general trends in anthropoids could be evaluated. In addition, this research assessed the position of *Homo sapiens* in the context of these general trends. Although many new questions have been raised, this research has shown that three variables (UFL, ACBL, and CBA) are the most

important predictors of variation in facial projection in the sample, and it is argued that these features are also likely to be the most important to understanding variation in facial projection in hominins. However, CBA and ACBL are somewhat less likely to be responsible for variation in facial projection in hominins because these features are thought to be related to changes in brain anatomy that do not jibe well with our current understanding of the fossil evidence. Thus, UFL is the most probable explanation for variation in facial projection in hominins and the marked reduction in facial projection in *Homo sapiens*, and is likely linked to the evolutionary reduction in the facial skeleton size. Although it is sure to raise still more questions, future research—in particular, the addition of data from fossil hominin species—promises to shed further light on this issue.

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APPENDIX A

TESTS OF SEXUAL DIMORPHISM

Bolded results indicate significant differences between males and females. Bolded blue results indicate that males were significantly larger than females. Bolded red results indicate that females were significantly larger than males.

Size-Adjustment Method: Shape-Ratios						
Species	**FP1**	**FP2**	**UFL**	**ASL**	**AMCFL**	**ACBL**
Alouatta palliata	**<0.01**	0.25	0.88	0.37	0.42	0.99
Aotus lemurinus	0.81	0.84	0.21	0.66	0.71	0.21
Ateles geoffroyi	0.97	0.76	0.31	0.30	0.42	0.74
Cacajao melanocephalus	0.98	**0.02**	0.10	0.57	0.98	0.62
Callicebus torquatus	0.60	0.17	0.95	0.39	0.63	0.72
Cebus albifrons	0.79	0.53	0.14	0.19	0.06	0.86
Cebus capucinus	0.18	0.75	0.10	**0.05**	0.30	0.12
Chiropotes satanas	0.25	**0.03**	0.36	0.14	0.46	0.28
Lagothrix lagotricha	0.15	0.99	1.00	0.59	0.10	0.72
Leontopithecus rosalia	0.95	**0.03**	0.31	**0.01**	0.43	0.14
Pithecia pithecia	0.80	0.10	0.11	0.96	NA	0.22
Saguinus geoffroyi	0.21	0.39	0.57	0.28	0.61	0.55
Saimiri sciureus	0.50	0.18	0.54	0.78	NA	0.08
Cercocebus torquatus	1.00	0.51	0.81	**0.04**	0.15	0.10
Cercopithecus mona	NA	NA	NA	NA	NA	NA
Cercopithecus nictitans	0.22	0.57	0.45	0.65	0.28	0.28
Chlorocebus pygerythrus	0.69	0.80	0.61	0.45	**0.02**	**<0.01**
Erythrocebus patas	0.09	0.91	0.90	0.25	0.53	0.70
Lophocebus albigena	0.67	0.48	0.75	0.90	0.77	0.39
Macaca cyclopis	0.96	**0.76**	0.83	0.92	0.50	0.52
Macaca nemestrina	0.09	**<0.01**	0.29	**0.02**	0.06	**0.05**
Miopithecus ogouensis	0.50	0.75	0.28	0.88	0.69	0.21
Papio anubis	NA	NA	NA	NA	NA	NA
Papio ursinus	0.25	0.84	**0.04**	0.05	0.62	**0.01**
Colobus guereza	0.97	0.72	0.45	0.47	0.31	0.70
Nasalis larvatus	**0.02**	0.95	0.06	0.08	0.08	**<0.01**
Piliocolobus badius	0.36	0.59	0.88	0.08	0.05	0.35
Procolobus verus	NA	NA	NA	NA	NA	NA
Pygathrix nemaeus	NA	NA	NA	NA	NA	NA
Rhinopithecus roxellana	NA	NA	NA	NA	NA	NA
Simias concolor	NA	NA	NA	NA	NA	NA
Trachypithecus cristatus	0.98	0.14	0.63	0.21	0.20	**<0.01**
Gorilla beringei	**<0.01**	0.24	0.32	0.09	NA	**0.01**
Gorilla gorilla	0.25	0.71	0.65	0.99	NA	0.06
Homo sapiens	0.80	0.80	0.34	0.08	0.61	0.43
Hylobates lar	0.37	0.75	0.47	0.16	0.71	0.43
Hylobates muelleri	0.22	0.34	0.15	0.75	0.83	0.43
Pan troglodytes	0.37	**0.63**	0.44	0.44	0.78	0.70
Pongo pygmaeus	0.45	0.27	0.48	0.90	0.92	0.75

NOTES: (1) Bolded values are significant at $\alpha = 0.05$; (2) Red values indicate that female values were significantly greater then male values; (3) Blue values indicate that male values were significantly greater than female values

Size-Adjustment Method: Phylogentically-Controlled Residuals						
Species	**FP1**	**FP2**	**UFL**	**ASL**	**AMCFL**	**ACBL**
Alouatta palliata	0.80	0.45	0.69	0.97	0.96	0.28
Aotus lemurinus	0.60	0.86	0.11	0.85	0.59	0.21
Ateles geoffroyi	0.93	0.75	0.32	0.27	0.43	0.73
Cacajao melanocephalus	0.76	0.11	0.20	0.24	0.93	0.49
Callicebus torquatus	0.60	0.27	0.98	0.39	0.58	0.79
Cebus albifrons	0.26	0.58	0.22	0.34	0.40	0.92
Cebus capucinus	0.58	0.80	0.85	0.49	0.92	0.84
Chiropotes satanas	0.31	**0.03**	0.32	0.13	0.90	0.78
Lagothrix lagotricha	0.06	0.31	0.97	0.96	0.14	0.62
Leontopithecus rosalia	0.70	**0.02**	0.37	**0.02**	0.14	0.08
Pithecia pithecia	0.50	0.22	0.13	0.88	NA	0.31
Saguinus geoffroyi	0.26	0.86	0.82	0.30	0.53	0.35
Saimiri sciureus	0.22	0.74	0.33	0.70	NA	0.58
Cercocebus torquatus	0.30	0.16	**0.04**	0.52	0.37	0.13
Cercopithecus mona	NA	NA	NA	NA	NA	NA
Cercopithecus nictitans	0.19	0.45	0.45	0.92	0.90	0.84
Chlorocebus pygerythrus	0.60	0.77	0.27	0.42	0.35	0.59
Erythrocebus patas		0.32	0.87	0.68	0.37	0.50
Lophocebus albigena	0.62	0.49	0.65	0.09	0.55	0.95
Macaca cyclopis	0.48	0.69	0.86	0.73	0.22	0.83
Macaca nemestrina		0.96	0.99	0.56	0.61	0.46
Miopithecus ogouensis	0.32	0.61	0.13	0.76	0.48	
Papio anubis	NA	NA	NA	NA	NA	NA
Papio ursinus		0.08	0.97	0.78	0.90	0.13
Colobus guereza	0.78	0.54	0.91	0.63	0.94	1.00
Nasalis larvatus	0.90	0.95	0.94	0.35	0.48	0.64
Piliocolobus badius	0.40	0.72	0.43	0.23	0.23	0.77
Procolobus verus	NA	NA	NA	NA	NA	NA
Pygathrix nemaeus	NA	NA	NA	NA	NA	NA
Rhinopithecus roxellana	NA	NA	NA	NA	NA	NA
Simias concolor	NA	NA	NA	NA	NA	NA
Trachypithecus cristatus	0.92	0.24	0.31	0.20	0.44	0.12
Gorilla beringei	0.91	0.88	0.94	0.86	NA	0.81
Gorilla gorilla	0.34	0.13	0.12	1.00	NA	0.41
Homo sapiens	0.96	0.98	0.24	**0.02**	0.44	0.07
Hylobates lar	0.38	0.73	0.98	0.50	0.61	0.72
Hylobates muelleri	0.91	0.23	0.08	0.62	0.78	0.93
Pan troglodytes	0.89	**0.03**	0.92	0.97	0.84	0.19
Pongo pygmaeus	0.29	0.65	0.44	0.62	0.97	0.40

NOTES: (1) Bolded values are significant at $\alpha = 0.05$; (2) Red values indicate that female values were significantly greater then male values; (3) Blue values indicate that male values were significantly greater than female values

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APPENDIX B

RAW DATA – SPECIES MEANS AND STANDARD DEVIATIONS

Raw (i.e. non size-adjusted) species means and standard deviations.

	GEOMEAN[a]		CBA1		CBA2		FP1		FP2		ACBL		UFL		ASL		AMCFL	
SPECIES	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Alouatta palliata	47.43	2.92	178.63	2.04	182.92	5.45	6.28	2.02	10.61	1.44	28.31	1.89	27.02	1.97	11.16	1.08	10.14	0.86
Aotus lemurinus	26.98	0.57	178.96	3.28	180.89	2.14	9.45	1.02	8.53	0.67	18.25	0.96	21.66	0.65	4.99	0.80	4.00	0.35
Ateles geoffroyi	45.92	1.58	169.57	2.06	162.76	4.42	4.00	1.62	10.25	1.30	28.17	1.80	26.54	1.47	11.74	1.04	11.08	1.16
Cacajao melanocephalus	39.07	1.06	168.92	1.91	170.79	3.64	4.22	1.79	9.46	0.88	22.57	1.08	22.96	1.29	8.93	0.57	8.79	1.08
Callicebus torquatus	29.22	1.11	169.39	3.29	171.61	2.73	8.38	2.48	8.12	0.87	18.66	1.37	19.54	1.18	7.16	0.96	6.67	0.68
Cebus albifrons	39.39	1.72	170.56	3.23	169.53	4.79	7.38	2.04	8.99	0.87	24.74	1.37	22.90	2.22	9.07	0.97	9.29	0.77
Cebus capucinus	43.01	2.13	172.16	2.51	171.23	3.51	8.29	1.97	10.05	0.99	26.38	1.33	24.53	2.04	10.45	0.84	10.86	1.10
Chiropotes satanas	36.04	1.14	170.96	2.34	172.70	2.94	7.75	1.57	7.49	1.55	20.83	1.20	19.87	1.72	8.32	0.58	8.22	1.04
Lagothrix lagotricha	43.47	1.45	172.68	3.34	172.51	3.54	3.35	1.93	11.82	0.94	24.73	1.82	24.63	1.09	11.92	1.09	11.34	0.92
Leontopithecus rosalia	26.10	0.93	172.65	2.38	170.47	3.61	5.41	1.11	7.84	0.73	18.37	1.11	17.23	0.84	8.44	0.51	6.79	0.60
Pithecia pithecia	34.41	1.72	176.43	1.05	176.38	1.95	7.13	2.19	9.00	0.75	19.86	1.17	20.90	1.15	7.58	0.48	7.24	0.29
Saguinus geoffroyi	22.51	0.52	171.04	1.95	169.80	2.01	6.73	0.92	6.63	0.56	16.21	0.84	16.10	0.43	6.61	0.58	5.10	0.48
Saimiri sciureus	26.11	1.05	166.71	2.57	169.56	1.94	5.60	0.86	4.44	0.68	18.83	0.84	16.09	0.90	6.83	0.65	6.21	0.40
Trachypithecus cristatus	44.24	1.73	167.49	1.85	161.27	3.12	6.03	1.91	11.84	1.27	25.82	1.18	28.16	1.10	9.20	1.01	9.07	0.71
Colobus guereza	52.54	2.45	172.55	2.78	163.23	2.90	9.46	2.01	14.40	1.36	28.37	2.52	31.89	1.92	10.54	1.23	11.48	1.15
Nasalis larvatus	55.53	4.58	166.04	2.89	157.47	4.20	8.16	2.33	14.05	1.71	29.38	1.92	30.80	2.33	12.18	0.94	12.63	1.06
Piliocolobus badius	47.68	2.55	165.57	2.16	155.34	4.91	6.85	1.80	12.16	2.07	27.40	2.11	28.60	2.00	10.37	0.83	10.62	1.27
Pygathrix nemaeus	54.51	1.24	153.78	6.30	142.57	1.84	12.63	2.50	13.30	1.61	33.61	1.98	33.97	0.92	12.61	0.71	11.80	1.03
Rhinopithecus roxellana	52.27	1.42	157.93	4.49	150.62	2.57	6.29	1.72	14.17	2.12	30.61	1.77	33.21	1.37	11.08	0.85	11.51	2.04
Cercocebus torquatus	64.99	10.28	158.79	2.16	168.07	2.50	9.59	1.42	16.15	1.81	30.57	1.73	33.10	3.48	13.03	0.89	12.71	1.16
Cercopithecus mona	47.38	3.91	167.35	2.70	170.76	2.94	6.16	1.92	10.93	1.43	25.83	1.63	25.96	2.41	10.11	0.92	10.35	1.10
Cercopithecus nictitans	50.64	3.17	169.01	2.91	172.19	2.74	6.87	1.32	12.59	1.97	27.43	1.82	28.50	2.38	10.95	1.12	11.33	1.14
Chlorocebus pygerythrus	48.02	3.62	161.32	3.52	161.88	3.07	6.15	1.56	12.36	1.72	26.35	1.58	28.71	2.12	9.95	1.11	9.52	1.10
Erythrocebus patas	59.26	6.32	160.02	5.26	162.95	3.44	5.91	1.43	15.41	2.34	32.14	2.41	37.32	4.14	10.21	0.66	10.13	0.85
Lophocebus albigena	55.35	5.11	161.40	0.96	162.19	0.94	8.49	1.84	14.20	2.21	27.09	1.75	29.29	2.21	11.31	0.71	11.16	1.52
Macaca cyclopis	56.04	3.88	161.87	1.57	160.02	4.89	10.14	1.78	12.78	1.04	27.30	1.97	28.63	2.38	10.85	0.92	10.78	0.90
Macaca nemestrina	69.12	6.27	160.69	3.62	159.14	3.50	11.12	2.71	14.97	0.87	29.59	2.61	32.32	2.88	11.95	1.52	12.89	1.92
Miopithecus ogouensis	31.86	1.22	164.39	2.72	166.27	2.70	3.22	1.13	7.75	0.75	19.15	0.84	18.27	1.07	7.51	0.67	7.72	0.80
Papio anubis	96.56	8.66	154.90	3.26	154.45	4.10	11.68	2.50	15.65	2.63	35.06	2.75	35.40	2.24	15.22	2.02	14.49	1.44
Papio ursinus	93.21	11.25	157.40	2.53	154.51	3.91	9.19	2.00	15.42	1.87	34.07	2.82	33.97	2.87	14.65	1.57	14.68	2.28
Hylobates lar	48.25	1.67	168.30	2.37	155.02	3.99	9.06	2.31	7.58	1.29	31.91	2.12	28.55	1.61	10.79	1.50	10.52	1.85
Hylobates muelleri	47.77	1.47	169.22	3.08	158.78	4.52	7.59	1.85	7.89	1.57	31.96	2.25	28.90	2.20	10.70	1.26	10.89	1.77
Pongo pygmaeus	105.42	8.89	160.73	1.55	134.64	3.45	15.56	5.90	21.50	2.91	37.84	4.36	40.57	4.43	17.95	6.13	16.21	3.12
Gorilla beringei	120.60	11.78	159.11	3.13	149.34	5.26	27.29	7.49	35.55	5.57	41.99	4.24	56.70	5.66	19.84	4.64	-	-
Gorilla gorilla	123.71	9.64	157.03	2.12	151.29	3.80	28.33	8.62	33.76	5.45	46.33	4.04	56.96	5.75	22.58	3.29	-	-
Pan troglodytes	91.68	4.25	157.42	2.38	154.75	3.96	13.24	2.46	18.55	2.01	40.61	3.29	43.78	1.46	15.17	2.68	16.61	1.96
Homo sapiens	90.99	5.12	137.02	2.13	114.13	6.44	9.74	3.19	20.27	4.15	44.85	5.91	42.79	5.78	20.71	2.70	23.40	3.53

[a] Geometric mean of six cranial size measurements

APPENDIX C

CORRELATION OF VARIABLES

Tests of correlation between all variables (pair-wise comparisons) in all units of analysis (i.e., anthropoids, platyrrhines, catarrhines, and hominoids) and all variables using both methods of size-adjustment. Bolded results indicate significant correlations at a = 0.05.

Size-Adjustment Method: Shape-Ratios

Anthropoids

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.31	0.05												
FP2	0.21	0.21	0.29	0.07										
UFL	**0.58**	**<0.01**	**0.53**	**<0.01**	**0.48**	**<0.01**								
ASL	**0.41**	**0.01**	0.28	0.09	0.17	0.29	**0.59**	**<0.01**						
CBA2	**0.86**	**<0.01**	0.24	0.15	0.23	0.15	**0.50**	**<0.01**	0.33	0.04				
AMCFL	0.21	0.22	0.04	0.80	0.10	0.54	**0.36**	**0.03**	**0.83**	**<0.01**	0.10	0.54		
ACBL	**0.56**	**<0.01**	**0.43**	**0.01**	0.09	0.57	**0.87**	**<0.01**	**0.81**	**<0.01**	**0.46**	**<0.01**	**0.64**	**<0.01**

Platyrrhines

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.03	0.93												
FP2	0.51	0.06	0.32	0.27										
UFL	0.19	0.52	**0.82**	**0.00**	**0.61**	**0.02**								
ASL	-0.48	0.08	0.00	1.00	0.00	1.00	0.02	0.93						
CBA2	**0.87**	**<0.01**	0.08	0.78	0.34	0.24	0.14	0.63	**-0.58**	**0.03**				
AMCFL	**-0.66**	**0.01**	-0.43	0.13	-0.38	0.18	**-0.55**	**0.04**	**0.76**	**<0.01**	**-0.69**	**0.01**		
ACBL	-0.37	0.19	**0.67**	**0.01**	0.01	0.98	**0.65**	**0.01**	**0.56**	**0.04**	-0.38	0.18	0.10	0.73

Catarrhines

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.16	0.45												
FP2	0.00	1.00	0.18	0.39										
UFL	**0.47**	**0.02**	0.09	0.66	0.37	0.07								
ASL	0.20	0.34	0.04	0.85	0.13	0.54	**0.70**	**<0.01**						
CBA2	**0.76**	**<0.01**	-0.07	0.75	0.12	0.58	0.35	0.08	0.05	0.83				
AMCFL	0.15	0.50	0.21	0.34	0.27	0.22	**0.62**	**<0.01**	**0.92**	**<0.01**	**-0.04**	**<0.01**		
ACBL	**0.44**	**0.03**	-0.01	0.98	-0.03	0.87	**0.89**	**<0.01**	**0.84**	**<0.01**	**0.26**	**<0.01**	**0.76**	**<0.01**

Hominoids

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.49	0.21												
FP2	-0.43	0.29	0.48	0.23										
UFL	0.60	0.12	0.17	0.69	-0.58	0.13								
ASL	0.04	0.93	-0.28	0.50	-0.59	0.13	**0.71**	**0.05**						
CBA2	**0.88**	**<0.01**	0.62	0.10	-0.21	0.62	0.61	0.11	-0.08	0.85				
AMCFL	-0.17	0.75	0.04	0.93	-0.06	0.92	0.64	0.17	**0.90**	**0.01**	**-0.07**	**<0.01**		
ACBL	0.48	0.23	-0.15	0.73	**-0.81**	**0.02**	**0.93**	**<0.01**	**0.85**	**0.01**	0.38	0.14	**0.68**	**<0.01**

Size-Adjustment Method: Phylogentically-Controlled Residuals

Anthropoids

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.27	0.10												
FP2	0.09	0.58	**0.55**	**<0.01**										
UFL	-0.25	0.13	0.28	0.09	**0.57**	**0.00**								
ASL	-0.20	0.23	-0.06	0.74	0.19	0.24	0.24	0.14						
CBA2	**0.86**	**<0.01**	0.18	0.28	0.11	0.51	-0.31	0.05	**-0.34**	**0.04**				
AMCFL	-0.26	0.12	-0.17	0.32	0.20	0.23	**0.42**	**0.01**	**0.87**	**<0.01**	**-0.36**	**0.03**		
ACBL	-0.42	0.01	-0.15	0.35	-0.08	0.65	**0.70**	**0.00**	**0.51**	**<0.01**	**-0.56**	**<0.01**	**0.64**	**<0.01**

Platyrrhines

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.44	0.12												
FP2	**0.56**	**0.04**	0.06	0.83										
UFL	**0.61**	**0.02**	0.36	0.21	**0.64**	**0.01**								
ASL	-0.43	0.13	**-0.69**	**0.01**	0.00	1.00	-0.45	0.11						
CBA2	**0.87**	**<0.01**	0.48	0.08	0.38	0.18	0.47	0.09	-0.56	0.04				
AMCFL	**-0.67**	**0.01**	-0.52	0.06	-0.18	0.53	**-0.67**	**0.01**	**0.85**	**<0.01**	**-0.72**	**<0.01**		
ACBL	-0.24	0.41	-0.04	0.88	-0.36	0.20	0.08	0.79	0.32	0.26	-0.36	0.20	0.21	0.47

Catarrhines

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	0.34	0.09												
FP2	-0.08	0.70	**0.62**	**<0.01**										
UFL	-0.08	0.69	**0.59**	**<0.01**	**0.71**	**<0.01**								
ASL	**-0.43**	**0.03**	0.21	0.32	0.27	0.19	0.40	0.05						
CBA2	**0.76**	**0.00**	0.18	0.40	-0.03	0.88	-0.17	0.42	**-0.60**	**<0.01**				
AMCFL	**-0.44**	**0.04**	-0.04	0.85	0.17	0.43	0.42	0.05	**0.90**	**<0.01**	**-0.57**	**<0.01**		
ACBL	-0.34	0.09	0.15	0.47	0.04	0.84	**0.64**	**0.00**	**0.67**	**<0.01**	**-0.55**	**0.00**	**0.71**	**<0.01**

Hominoids

	CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
FP1	**0.79**	**0.02**												
FP2	0.35	0.40	**0.80**	**0.02**										
UFL	0.15	0.72	0.61	0.11	**0.83**	**0.01**								
ASL	-0.66	0.07	-0.27	0.53	0.06	0.88	0.09	0.83						
CBA2	**0.88**	**<0.01**	**0.82**	**0.01**	0.47	0.24	0.49	0.22	-0.66	0.07				
AMCFL	-0.69	0.13	-0.24	0.65	0.29	0.57	0.45	0.36	**0.91**	**0.01**	-0.54	0.27		
ACBL	-0.63	0.10	-0.24	0.56	0.06	0.89	0.42	0.30	0.78	0.02	-0.37	0.36	**0.95**	**<0.01**

Raw Data

Anthropoids

	Cranial Size		CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
CBA1	**-0.66**	**<0.01**														
FP1	**0.80**	**<0.01**	**-0.39**	**0.02**												
FP2	**0.92**	**<0.01**	**-0.57**	**<0.01**	**0.87**	**<0.01**										
UFL	**0.94**	**<0.01**	**-0.62**	**<0.01**	**0.82**	**<0.01**	**0.94**	**<0.01**								
ASL	**0.95**	**<0.01**	**-0.69**	**<0.01**	**0.75**	**<0.01**	**0.89**	**<0.01**	**0.92**	**<0.01**						
CBA2	**-0.66**	**<0.01**	**0.86**	**<0.01**	**-0.44**	**0.01**	**-0.56**	**<0.01**	**-0.64**	**<0.01**	**-0.73**	**<0.01**				
AMCFL	**0.89**	**<0.01**	**-0.73**	**<0.01**	**0.53**	**<0.01**	**0.85**	**<0.01**	**0.88**	**<0.01**	**0.97**	**<0.01**	**-0.77**	**<0.01**		
ACBL	**0.91**	**<0.01**	**-0.68**	**<0.01**	**0.69**	**<0.01**	**0.82**	**<0.01**	**0.88**	**<0.01**	**0.94**	**<0.01**	**0.74**	**<0.01**	**0.94**	**<0.01**

Catarrhines

	Cranial Size		CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
CBA1	**-0.54**	**0.01**														
FP1	**0.85**	**<0.01**	-0.27	0.20												
FP2	**0.89**	**<0.01**	**-0.44**	**0.03**	**0.91**	**<0.01**										
UFL	**0.90**	**<0.01**	**-0.47**	**0.02**	**0.90**	**<0.01**	**0.94**	**<0.01**								
ASL	**0.94**	**<0.01**	**-0.63**	**<0.01**	**0.83**	**<0.01**	**0.87**	**<0.01**	**0.90**	**<0.01**						
CBA2	**-0.53**	**0.01**	**0.76**	**<0.01**	-0.35	0.09	**-0.41**	**0.04**	**-0.50**	**0.01**	**-0.68**	**<0.01**				
AMCFL	**0.81**	**<0.01**	**-0.71**	**<0.01**	**0.62**	**<0.01**	**0.76**	**<0.01**	**0.82**	**<0.01**	**0.96**	**<0.01**	**-0.78**	**<0.01**		
ACBL	**0.86**	**0.00**	**-0.58**	**<0.01**	**0.77**	**<0.01**	**0.76**	**<0.01**	**0.91**	**<0.01**	**0.93**	**<0.01**	**-0.68**	**<0.01**	**0.90**	**<0.01**

Hominoids

	Cranial Size		CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
CBA1	-0.53	0.18														
FP1	**0.86**	**0.01**	-0.14	0.74												
FP2	**0.97**	**<0.01**	-0.45	0.26	**0.94**	**<0.01**										
UFL	**0.95**	**<0.01**	-0.47	0.24	**0.92**	**<0.01**	**0.98**	**<0.01**								
ASL	**0.93**	**<0.01**	**-0.74**	**0.04**	**0.74**	**0.04**	**0.90**	**<0.01**	**0.89**	**<0.01**						
CBA2	-0.38	0.36	**0.88**	**<0.01**	0.05	0.91	-0.27	0.53	-0.22	0.61	-0.60	0.12				
AMCFL	**0.75**	**0.09**	**-0.94**	**<0.01**	0.31	0.56	**0.83**	**0.04**	**0.85**	**0.03**	**0.94**	**<0.01**	**-0.86**	**0.03**		
ACBL	**0.86**	**0.01**	**-0.78**	**0.02**	**0.66**	**0.07**	**0.84**	**0.01**	**0.88**	**<0.01**	**0.94**	**<0.01**	-0.52	0.19	**0.98**	**<0.01**

Platyrrhines

	Cranial Size		CBA1		FP1		FP2		UFL		ASL		CBA2		AMCFL	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
CBA1	0.28	0.33														
FP1	-0.33	0.26	0.32	0.26												
FP2	**0.85**	**<0.01**	0.53	0.05	-0.24	0.40										
UFL	**0.95**	**<0.01**	0.46	0.10	-0.20	0.50	**0.91**	**<0.01**								
ASL	**0.89**	**<0.01**	0.07	0.82	**-0.59**	**0.03**	**0.76**	**<0.01**	**0.77**	**<0.01**						
CBA2	0.20	0.50	**0.87**	**<0.01**	0.39	0.17	0.37	0.20	0.34	0.24	-0.07	0.80				
AMCFL	**0.93**	**<0.01**	0.02	0.94	-0.48	0.08	**0.76**	**<0.01**	**0.00**	**<0.01**	**0.97**	**<0.01**	-0.08	0.80		
ACBL	**0.97**	**<0.01**	0.22	0.45	-0.33	0.26	**0.77**	**<0.01**	**0.92**	**<0.01**	**0.90**	**<0.01**	**0.11**	**0.72**	**0.92**	**<0.01**