PATTERN OF CRANIAL ONTOGENY IN POPULATIONS OF *GORILLA* AND *PAN*

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA
BY

JASON S. MASSEY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

KIERAN P. MCNULTY

June 2018

Acknowledgments

I am so deeply indebted to my advisor Dr. Kieran McNulty. I have known Kieran for many years, and in that time, he has provided me with every opportunity to succeed. My first field experience was at his site in Kenya, and since then he has guided me through stimulating areas of study, introduced me to colleagues that have expanded my research interests, and challenged me to be a better and focused researcher. I am an anthropologist because of him. Likewise, I could not have accomplished this without a strong and dedicated committee. I am so grateful for Drs. Martha Tappen, Michael Wilson, David Fox, and Anthony Weinhaus. The interesting discussions, challenging questions, access to data, and support over the many years have been integral to my success.

I am also indebted to Drs. Bernard Wood and Shannon McFarlin. This dissertation would not exist without their dedicated support, funding, and patience. They have given me access to needed specimens and many summers of exciting fieldwork.

I thank the Department of Anthropology and the community therein for so many years of emotional and academic support. In particular, I would like to thank Kara Kersteter, Nora Last, Megan Whaley, and Barbara London. Additionally, many summers of data collection and fieldwork were funded by numerous block grants and the Graduate Research Partnership Program.

I would like to thank the Evolutionary Anthropology Labs, and in particular John Soderberg and Matt Edling, for access to collections, facilities, and so much technical support with software and 3D scanners.

Thank you to thank the Department of Integrative Biology and Physiology for opening my eyes to teaching anatomy. The Human Anatomy Program, Drs. Anthony Weinhaus, and Mark Cook, did not just allow me to teach anatomy, they guided me toward being an effective and thoughtful educator. They provided teaching when funding was low as well as at times when I needed to write.

I would like to thank the University of Minnesota for supporting my research in many ways. Funding for travel and writing was given through the Thesis Travel Research Grant and the Doctoral Dissertation Fellowship.

Additional funding, including needed travel to Gombe National Park, Tanzania, was provided by the Leakey Foundation. Thank you for 50 years of funding projects such as this one.

I thank the curators and staff of the many museums and institutions that let me visit and collect data: The Royal Museum for Central Africa, Tervuren, Belgium; Powell-Cotton Museum, Birchington-on-Sea, United Kingdom; Royal College of Surgeons, London, United Kingdom; Natural History Museum, London, United Kingdom; Cleveland Museum of Natural History, Cleveland, Ohio. I would also like to thank the numerous field assistants, researchers, and other staff associated with the following organizations: Mountain Gorilla Skeletal Project, Rwanda Development Board – Department of Tourism and Conservation, Dian Fossey Gorilla Fund International's Karisoke Research Center, Mountain Gorilla Veterinary Project, Tanzania Wildlife Research Institute, Tanzania Commission of Science and Technology, Tanzania National Parks, and the Jane Goodall Institute's Gombe Stream Research Centre.

And, of course, I could not do this without unwavering support from my friends and family, particularly my parents and brother. I could not have stayed the course without their unconditional love and encouragement.

Abstract

The biology of African apes provides an important comparative framework for interpreting the evolutionary unfolding of our own species, *Homo sapiens*. Understanding the ontogeny of our closest living relatives is critical, as evolutionary transformations in adult shape ultimately arise through changes in the timing and patterning of growth and development. However, our current knowledge of African ape skeletal ontogeny is deficient in two important respects. First, wild-shot museum specimens lack the single datum necessary for a comprehensive study of ontogeny: *specimen age*. Second, skeletal research on African apes invariably uses samples that are pooled at the subspecies, species, or even genus level.

This work aims to rigorously quantify and compare the patterns of cranial ontogeny in African ape *populations*, utilizing two important new skeletal samples with known ages. Unlike most previous research, this study will use samples assigned to specific populations in order to characterize intraspecific variation in development. This work aims to answer the following questions: 1) how do African ape populations differ in their ontogeny? 2) to what degree do ontogenetic models based on pooled samples diverge from population-level ontogenies? 3) how does ontogeny mediate sexual dimorphism in *Gorilla* and *Pan*?, and 4) which aspects of anatomy provide insight into heterochronic relationships between extant taxa?

Table of Contents

List of Tables

List of Figures

1 Introduction

The biology of African apes provides an important comparative framework for interpreting the evolutionary unfolding of our own species, *Homo sapiens*. Evolutionary transformations in adult shape ultimately arise through changes in the timing and patterning of growth and development. Therefore, understanding the comparative ontogenies of our closest living relatives is critical to investigating how divergent adult shapes were manifested in the fossil record. However, our current knowledge of African ape skeletal ontogeny is deficient in two important respects. First, wild-shot museum specimens lack the single datum necessary for a comprehensive study of ontogeny: *specimen age*. Second, skeletal research on African apes invariably use samples that are pooled at the subspecies, species, or even genus level. In order to construct adequate sample sizes for ontogenetic analyses, researchers mix organisms that otherwise belonged to genetically and morphologically distinct populations (*e.g.*, Leigh and Shea, 1996; McNulty *et al*., 2006; Cofran and Walker, 2017). As a result, this framework of African ape ontogeny that is so important for interpreting the human fossil record is based on unrealistic, biological models that have been neither statistically tested nor adequately characterized.

This dissertation aims to rigorously quantify and compare the patterns of cranial ontogeny in African ape *populations* based on skeletal samples with known age and locality data. Unlike previous research, this study will use samples assigned to specific populations in order to characterize intraspecific variation in growth and development.

1.1 Background

The study of ontogeny has a rich history in the fields of the natural sciences (de Beer, 1958; further reviewed in Gould, 1977). Deriving from earlier work, Haeckel introduced the concept of heterochrony in 1875 (Haeckel, 1875; Gould, 1977). To Haeckel (1875), heterochrony is the displacement in time of ontogenetic appearance of one organ relative to another. This causes a disruption in the normal recapitulation of phylogenetic ontogeny (Gould, 1977). Though compelling, this work was a demonstrable oversimplification of complex biological processes. Haeckel's ideas were modified and improved by subsequent researchers, including de Beer (*e.g.*, 1958; 1959) who pushed the importance of heterochrony, and particularly paedomorphosis, in evolutionary morphogenesis. Nevertheless, such work fell out of favor until Gould (1977; and Alberch *et al*., 1979) revived and formalized the role of ontogeny in evolutionary research by demonstrating that change in adult form must be mediated by changes in growth and development. Gould's work was one impetus for the emergence of evolutionary development, so called "evo-devo," which studies how ontogenies evolve in lineages to create new forms, behaviors, and life histories (Raff, 2007; Laland *et al*., 2014; Antón and Kuzawa, 2017).

Since Gould's *Ontogeny and Phylogeny* (1977), numerous studies have contributed to the study of ontogeny in evolutionary biology, including important works in the field of paleoanthropology (Shea, 1983a, b, 1989; Richtsmeier *et al*., 1993; Godfrey and Sutherland, 1995; Leigh and Shea, 1995, 1996; O'Higgins and Jones, 1998; O'Higgins and Strand Viðarsdóttir, 1999; Antón and Leigh, 2003; Mitteroecker *et al.*,

2004b, 2005; Raff, 2007; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2008). Ontogenetic research in paleoanthropology typically focuses on one of four topics: accurately interpreting the evolutionary significance of juvenile fossils, the evolution of the human-like life history, the way in which ontogeny contributes to sexual dimorphism, and heterochrony.

1.1.1 Evolutionary significance of juvenile fossils

Juvenile specimens are a critical part of the hominin fossil record providing unique windows into the ontogenetic processes of extinct species. For example, the first known African hominin, from Taung, South Africa (Dart, 1925), has been the basis for numerous taxonomic (Dart, 1925; Rak, 1983; Faulk, 2009; Robinson, 2012), ontogenetic (Ackermann and Krovitz, 2002; Cobb and O'Higgins, 2004; Lacruz *et al*., 2005; McNulty *et al*., 2006), and evolutionary studies (Falk *et al*., 2012), including research on the evolutionary development of South African hominins (Gunz, 2012; McNulty 2012). Likewise, subadult hominin KNM-WT 15000 has been a vital component of research on *Homo erectus*, providing important clues about the evolution of human life-history patterns (Antón and Leigh, 2003). Further, the ability to diagnose Neanderthal and human traits in juvenile specimens is imperative to questions about the degree and expression of genetic admixture (Currat and Excoffier, 2004; Trinkaus, 2007; Gunz and Bulygina, 2012).

Properly classifying a juvenile fossil, whether as a holotype for a new species like Taung 1 (Dart, 1925) or MH1 (Berger *et al*., 2010) or part of the hypodigm of an existing one, is an important first step toward assessing a species' ontogenetic trajectory.

However, classifying juvenile fossils necessarily requires detailed models of ontogenetic processes – models based on biologically meaningful samples.

For example, KMN-ER 62000 was referred to *Homo rudolfensis* because its dental arcade and orthognathic face most closely resemble KNM-ER 1470 (Leakey *et al*., 2012). However, because this specimen is a juvenile, it is unclear how the facial morphology used to make this classification might have changed as the last molar erupted and the basisphenoid synchondrosis fused. Specimens discovered more recently from Dikika, Ethiopia (Alemsaged *et al*., 2006), Malapa, South Africa (Berger *et al*., 2010), and Dineledi Chamber, South Africa (Berger *et al*., 2015) have not yet been subject to multiple comprehensive ontogenetic studies but will likewise benefit from contextual information on their growth and development.

1.1.2 Evolution of the human life history pattern

Life history studies the timing of certain biological milestones such as weaning, puberty, reproduction, and death (Sterns, 1976; Charnov, 1993). Primates were among the first orders of mammals studied by life history researchers because of their relationship to humans and because they display, on average, a slow life-history strategy (Harvey and Clutton-Brock, 1985; Harvey *et al*., 1986; Janson and van Schaik, 1993; Jones, 2011). As an order, Primates have long lifespans, few offspring, and take many years to grow to reproductive age compared to other mammals of comparable body size (Harvey and Clutton-Brock, 1985; Harvey *et al*., 1986; Janson and van Schaik, 1993; Jones, 2011). Many hypotheses have been proposed to shed light on the slow life history strategy of primates, and studies have used both mathematical modeling (*e.g.*, Sterns,

1976, 1992; Bogin, 1988; Charnov, 1991, 1993; Charnov and Berrigan, 1993), and empirical data collected on wild or captive primates (*e.g.*, Harvey and Clutton-Brock 1985; Watts, 1985; Janson and van Schaik, 1993; Gurven and Walker, 2006; Jones, 2011) to study this phenomenon.

Charnov (1991, 1993; Charnov and Barrigan, 1993) proposed that, because most mammals do not grow continuously (Bogin, 1988), energy limitations force a trade-off between growth and reproduction that has evolved to optimize reproductive success (Charnov, 1991, 1993). Thus, a typical mammal's life can be broken up into a growth period and a reproductive period. The growth period includes the time from birth to menarche and is characterized as the time during which an organism grows to adult size, plays, and learns adult behaviors (Watts, 1985; Pagel and Harvey, 1993). During this period of life, individuals must allocate all extra energy beyond somatic maintenance to growth. The reproductive period requires that the individual has reached adult body size and has the necessary traits (anatomically, physiologically, and behaviorally) to mate (Pagel and Harvey, 1993; Bogin, 1988, 1997). Therefore, understanding the growth period should explain the basic primate "slowness." As an adult, most mammal's extra energy is diverted from growth and is allocated to reproduction.

In an assessment of life history strategies in primates, Harvey and Clutton-Brock (1985) collected data on 135 species from wild and captive individuals and analyzed 17 life history variables. They found that adult body mass is highly, positively correlated with adult brain size, neonatal mass, neonatal brain size, and interbirth interval. Additionally, neonatal mass is positively correlated with relative gestation length, relative weaning age and relative age at maturity. Pagel and Harvey (1993) argued that selection

for the appropriate body size at maturity sets the age at maturity via the growth law used by Charnov (1991). The juvenile period that arises in primates enables the evolution of social and behavioral traits that may further affect the age at maturation.

Janson and van Schaik (1993) proposed that this juvenile "limbo" is a time between the safety of infantile dependence and the complex world of independent adult life. They argue that the juvenile period is a time of great ecological risks because: 1) there is less dependence on the mother, and 2) juveniles must begin to fit into an ecological role defined by adults, even though they do not have the body size or skill to do so (Janson and van Schaik, 1993). Although a juvenile cannot contribute to its own reproductive success, it can contribute to its survivability by maximizing the chance that it reaches the size or age necessary for breeding.

Godfrey and colleagues (2004) tested the ecological-risk model in lemurs and indriids. On average, species in the family Lemuridae are frugivorous whereas comparably sized species in the Indriidae are folivorous. Godfrey and colleagues (2004) showed that folivores develop faster than similarly sized frugivores in anthropoids. Therefore, the lemurs and indriid developmental strategies are more likely responses to the nutritional quality and the relative abundance of food resources in times of environmental stress (Godfrey *et al*., 2004).

Jones (2011) also proposed that diet stability may be the reason primate development is so slow. Jones (2011) argues that the speed of primate life histories can be explained by the tendency of primates to specialize in high-quality food items which make them susceptible to environmental variability. Because gorillas eat temporally- and spatially-consistent vegetation, they can afford to grow quickly. Faster rates of growth

can be sustained on a lower quality diet if the food is abundant and predicable, over space and time (which is the case for leaves and grasses; Leigh, 1994; Marlowe, 2010). Orangutans, on the other hand, live in an environment of mast fruiting events interspersed with long periods of scarcity (Jaeggi *et al*., 2010; Jones, 2011). Therefore, orangutans follow a "safer" strategy by developing slowly so they are not faced with excessive growth when high-quality food items are scarce. Chimpanzees, like orangutans, are ripe fruit specialists, though their resources are much less seasonal. This allows their life histories to be faster than orangutans, though still slower than gorillas.

Although many life history traits are behavioral or physiological and hence are not preserved in hard-tissue anatomy, a few relevant traits (body size, brain size, and dental development) can be observed in the fossil record. In particular, great strides were made in studies of hominin evolution with the discovery that age-at-death could be reliably estimated in fossil specimens using the microstructure of their teeth (Dean *et al*., 1986; 1993; Bromage and Dean, 1991; Beynon and Dean, 1991; Skinner 1997; Stringer and Dean, 1997; Beynon et al., 1998; Smith *et al*., 2007, 2010; Kelley and Schwartz, 2010, 2012; Smith, 2013; Hogg *et al*., 2015), thereby providing a means to estimate the pace of ontogeny and life history. This methodology allows for the evolution of the human-like life history strategy, or at least the timing, to be studied in fossil specimens (*e.g*., Smith, 1989; Dean, 2006; Smith *et al*., 2007; Kelley and Schwartz, 2010, 2012; but see Robson and Wood, 2008).

However, the results from dental developmental studies have been over-interpreted by the paleoanthropology community: assuming that an ape-like timing of dental development necessarily implies ape-like maturation for the entire skeleton

(Simpson *et al*., 1991; but see, *e.g*., Shea 1983a). With dental maturation as the standard for developmental age (Dean and Wood, 1981; Zelditch et al., 2012), important variations in the growth and development of other anatomical structures are still relatively unknown. To be clear, researchers on dental development have been very precise in interpreting results of their own work. Yet, widespread reliance by other researchers on dental estimates of ontogenetic timing has obscured more interesting relationships among age, size, anatomy, and life history with respect to other parts of the skeleton.

For example, the age of first molar emergence suggests only minor differences between gorillas and chimpanzees in the timing of dental development (Kelley and Schwartz, 2012). Yet, McFarlin and colleagues (2012) demonstrated that Virunga mountain gorilla brain growth achieves 90 percent of adult brain mass at approximately 28 months of life, and full adult mass by 3 to 4 years of age – approximately one year earlier than chimpanzees. This difference, though related to factors specific to the life history of this population (McFarlin *et al*., 2012), would not necessarily be predicted from the timing of dental development. Moreover, the braincase is not a completely modular system. As the neurocranium develops, it will change the shape and position of adjacent anatomy, and the differential timing of these interactions can potentially result in very different morphology. Hence, what is completely unknown but most relevant to fossil studies, is how other aspects of the skull and skeletal ontogeny diverge from the timing of dental eruption: for example, which cranial features mature more quickly, which features mature more slowly? How do these differences result in anatomical variations?

1.1.3 Sexual dimorphism

The ontogeny of sexual dimorphism has been studied for many aspects of anatomy including body mass (McHenry, 1992, 1994; Leigh and Shea 1995, 1996; Ruff, 2002; Plavcan, 2012; Fragaszy *et al*., 2015), canine size (Plavcan *et al*., 1995; Schwartz and Dean, 2001; Leigh *et al.*, 2005), coloration (Breuer *et al*., 2007), postcranial anatomy (Taylor, 1997; Berdnikovs *et al*., 2007; Bastir *et al*, 2014; Garcia-Martinez *et al.*, 2016), and skull shape (Lockwood, 1999; del Castillo *et al*., 2014; Loza *et al.*, 2015; Holton *et al.*, 2016).

In a study of captive African ape body mass, Leigh and Shea (1995, 1996; also Shea, 1985, 1986; Leigh, 1992, 1995) concluded that sexual dimorphism in chimpanzees and gorillas is mediated through fundamental differences in ontogenetic timing (similar to descriptions of the evolutionary altering of ontogenetic timing: heterochrony): *Pan troglodytes* achieves dimorphism through rates of growth between sexes (rate hypermorphosis), whereas sexual dimorphism in *Gorilla gorilla* is obtained through bimaturism, or time hypermorphosis, of growth (*i.e.*, males grow for a longer duration than females). They report that these differences may be brought about by differentiation of ecological risks and male competition, a model that accords with research by Janson and van Schaik (1993; but see Watts and Pusey, 1993; Jones, 2011; Pontzer *et al.*, 2010, 2012). In a study of postcranial elements, however, Taylor (1997) found that male gorillas also exhibit a growth spurt after females, indicating both a duration and rate change in the acquisition of sexual dimorphism.

Schwartz and Dean (2001) investigated rate and duration of canine size dimorphism and found that all species studied (great apes, including humans) primarily

demonstrate bimaturism (or time hypermorphosis) with little evidence of rate hypermorphosis. Finally, McFarlin and colleagues (2012) presented growth data for brain size for *G. b. beringei* housed at Karisoke Research Center. Sexual dimorphism in brain size growth in this population appears to be a consequence of both time (bimaturation) and rate hypermorphosis.

Additional analysis of an expanded number of taxa revealed bimaturism in multimale/multifemale groups (*e.g.*, *Saimiri sciureus*, *Cebus apella*, *Cercopithecus aethiops*, *Cercocebus atys*, *Macaca*, and *Papio papio*), whereas single-male or community groups (*e.g.*, *Cercopithecus diana*, *Cercopithecus mitis*, *Cercopithecus negletctus*, *Erythrocebus patas*, *Mandrillis sphinx*, *Colobus guereza*, *Presbytis entellus*, *Presbytis obscura*) exhibit rate dimorphism (Leigh, 1995). These studies demonstrate that all aspects of anatomy are not governed by the same ontogenetic timing to achieve body size dimorphism. Though timing is not the only mechanism by which one can achieve differences in ontogeny. Altering the duration (timing) and rate of growth contributes to ontogenetic divergences, as well as altering the pattern and magnitude of development.

In fact, studies have shown that global dimorphism in the cranium is also tied to differences in the ontogenetic trajectories (development) in a few aspects of cranial anatomy (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Mitteroecker *et al*, 2004a, b; 2005; Liebermann *et al*, 2007; Hallgrimsson *et al*., 2007a, 2007b).

The subject of this dissertation, the cranium, has been extensively studied in terms of its evolutionary history, ontogeny, and heterochrony (*e.g.*, Mitteroecker et al., 2004a, b, 2005; Lieberman et al 2000, 2007), because of the important functions that it serves: it

houses most of the sense organs; provides passage for cranial nerves; it contains the anterior opening for the digestive and respiratory tracts; and provides protection for the brain. As the degree of shape dimorphism increases during ontogeny, dimorphism can result in radically different anatomical structures despite the constraints of these important functions. Nevertheless, the organism must maintain these crucial functions. Understanding how ontogeny mediates sexual dimorphism in the cranium is important for understanding the relationships of modular units which retain an integrated functionality.

1.1.4 The complicated case of heterochrony

The fourth focus of paleoanthropological research on ontogeny is the study of heterochrony – evolutionary changes in the timing of growth and development through the dissociation of size, shape, and age (Gould, 1977; Shea, 1983b; 1989; Mitteroecker *et al*., 2005; Lieberman *et al.*, 2007; McNulty, 2012). Heterochrony describes changes in the developmental program between ancestors and descendants resulting in differences in size and shape (Gould, 1977). Altering the ancestral population's growth and development can result in descendent morphology being paedomorphic (the descendent at some age resembles the ancestor at a younger age) or peramorphic (the descendant resembles an older form of the ancestor or transcends the ancestral form; Gould 1977; Alberch *et al*., 1979). Several heterochronic processes have been defined and are often characterized using a "clock model" (Gould 1977) or a bivariate plot (Alberch *et al*., 1979; Klingenberg and Spence, 1993; Figure 1.1). These processes act by either altering the rate of growth (neoteny and acceleration), the timing of onset (post- and pre-

displacement), or the timing of offset (progenesis and hyper-morphosis) of an aspect of anatomy (Figure 1.1). Those that result in paedomorphosis are neoteny, progenesis, and post-displacement (Gould 1977; Alberch *et al*., 1979; Klingenberg and Spence, 1993). Processes resulting in peramorphosis are acceleration, hypermophosis (*sensu* Gould, 1977), and pre-displacement (Gould 1977; Alberch *et al*., 1979; Klingenberg and Spence, 1993).

However, work on heterochrony went through a fundamental shift after Gould (1977). Gould's (1977) work was a true decoupling of size, shape, and age where the ancestral processes contributing to growth (size), development (shape), and timing of onset and offset (age) could be independently altered resulting in different descendent morphology. However, Gould failed to recognize that descendent populations need not follow ancestral patterns of growth and development (Godfrey and Sutherland, 1995a). Alberch and colleagues (1979) set out to redefine and formalize the various processes that can result in pera- or paedomorphosis while including the ontogenetic "pertubations" (pre- and post- displacement) omitted by Gould (1977). Alberch and colleagues (1979) created bivariate plots summarizing growth in size or "growth in shape" (development) independent of age without considering size/shape dissociation (Godfrey and Sutherland 1995a).

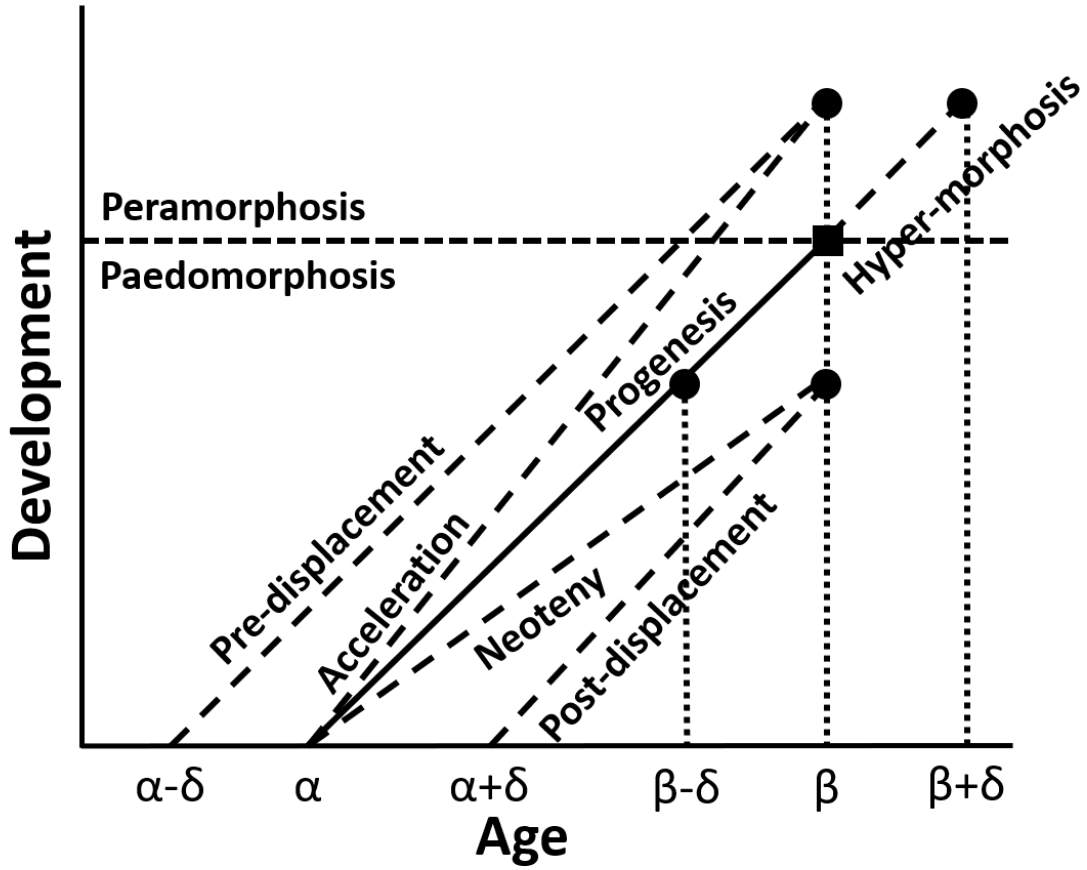

Figure 1.1: Redrawn from Klingenberg and Spence, 1993. Alterations in the rate or timing of growth in an organ or structure can lead to either peramorphic or paedomorphic descendants. The solid line denotes the growth of the ancestor and the square denotes the ancestor's adult form. The dashed lines and the circles denote the descendent ontogenies and adult forms, respectively. Acceleration is an increase and neoteny a decrease in the rate of growth of an organ or structure. Change in onset of growth is represented as pre-displacement (α-δ) or post-displacement (α+δ). Change in offset of growth of a structure is progenesis (β-δ) or hyper-morphosis (β+δ). Any one or combination of these processes can contribute to the alteration of descendant morphology.

Since Gould's (1977) *Ontogeny and Phylogeny*, numerous studies have contributed to the study of ontogeny in evolutionary biology, including important works in the field of paleoanthropology (Shea, 1983a, b, 1989; Godfrey and Sutherland, 1995; Leigh and Shea, 1995, 1996; O'Higgins and Jones, 1998; Antón and Leigh, 2003; Berge

and Penin, 2004; Cobb and O'Higgins, 2007; Mitteroecker *et al.*, 2004a, b, 2005; Raff, 2007; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2001; Bhullar *et al*., 2012; McNulty, 2012; Foth *et al*., 2016; Antón and Kuzawa, 2017; Du *et al*., 2018). In particular, the idea that human evolution is a product of neotenic processes resulting in paedomorphism has generated much debate in paleoanthropology (Shea, 1989; Mitteroecker *et al*., 2004a, b; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2008; Zollikofer and Ponce de León, 2010).

A fundamental obstacle to studying heterochrony in anthropological contexts is that age data are rarely available in museum collections. Since age scales with size up to a certain point, many subsequent studies substituted size for age and focused mainly on the dissociation of size and shape (allometric heterochrony; Godfrey and Sutherland, 1995a). These studies, however, do not consider dissociation of age and size. Shea (1983a) investigated claims that bonobos, common chimpanzees, and gorillas are placed on a continuum of paedo- to peramorphosis using this new approach. He introduced new terms, differentiating hypo/hypermorphosis in components of time (duration) and rate. Time hypo/hypermorphosis is equated to Gould's progenesis and hypermorphosis, based on age of offset and when size and shape are coupled together; rate hypo/hypermorphosis is a special case of neoteny and acceleration (shape is decoupled from age and size) where size and shape are recoupled, but age is decoupled (Shea, 1983a, Alba, 2002). Shea states that the new definitions are meant to focus on the process (neoteny, acceleration, etc.) not the results (pera- and paedomorphosis) of heterochrony. Using this approach, Shea (1983b) argued that differences in cranial morphology in *Pan paniscus*

and *P. troglodytes* resulted from neoteny, stating that the dissociation of skull growth from overall size fits the criterion for neontenic retardation.

The "clock model" or the bivariate plots employed when discussing classical heterochronic processes demonstrate how an aspect of anatomy can be altered evolutionarily to either result in paedomorphic or peramorphic descendants. However, these concepts and descriptions of evolutionary change work best with a single shape variable (Gould, 1977; Alberch *et al*., 1979). And indeed, the majority of classic studies of heterochrony only use a single biological or anatomic shape variable such as a ratio of lengths, size, or angular measures (Gould, 1977; Alberch *et al*., 1979). Modern morphometric techniques on the other hand, especially geometric morphometrics, employ many of variables in order to retain and evaluate the geometric context of biological variation (Bookstein, 1978; 1982; Corner and Richtsmeier, 1991).

As Procrustes approaches to the study of shape distinguish between size and shape (shape being the outcome of a generalized Procrustes analysis; see below), it is appropriate for the analysis of heterochrony. Therefore, for the terminology of Alberch and colleagues to be useful, all shape variables must overlap in shape space (Mitteroecker *et al*., 2004a, b; Lieberman *et al*., 2007; McNulty 2012; Figure 8.1). This is because the original assumption of global heterochrony is that both species (or groups) need to undergo the same process (sequence) of shape change over development (Godfrey and Sutherland, 1995a). The descendant can either elongate or truncate the trajectory (hypermorphosis or progenesis, respectively), or the trajectory can be differently associated with size (or age [neoteny, acceleration, pre-, or post-displacement]; Alberch *et al*., 1979; Mitteroecker *et al*., 2005). Though, importantly, the shape of both groups

must undergo the same sequence of events. Thus, morphometric data can reveal heterochrony only if the ontogenetic trajectories overlap in shape space.

With these caveats in mind, several researchers have tried to devise ways of studying heterochrony using modern techniques (Mitteroecker *et al.*, 2004a, b; 2005; Lieberman *et al*., 2007 Ponce de León and Zollikofer, 2008). Mitteroecker and colleagues (2004a) tested common allometry among the great apes. In contrast to earlier works of Shea (1983a, b), Mitteroecker and colleagues (2004a) showed that pure heterochrony in the ape lineage is falsified as humans do not share a common ontogenetic trajectory. Thus, globally heterochrony cannot be used to explain ontogenetic differences (Shea, 1989; Mitteroecker *et al*., 2004a, b; Liebermann *et al*., 2007). In fact, Mitteroecker and colleagues (2004b) conclude by stating that the complex anatomy of the cranium, which is a set of integrated, semi-autonomous modules, may not conform a single heterochronic process. Thus, global (using all cranial landmarks) heterochrony cannot be used to explain ontogenetic differences and focus should be turned to regionally dissociated heterochrony (Shea, 1989; Mitteroecker *et al*., 2004a, b; Liebermann *et al*., 2007).

To further assess global and regional heterochrony, Mitteroecker *et al*. (2005) studied the pannin ontogenetic trajectories in multivariate shape-space and found that the two species of *Pan* diverge in ontogenetic trajectory early in development, and that three cranial regions (neurocraium, upper and lower face) show distinctly differing trajectories. From this, they rejected hypotheses of global and regional heterochrony to explain ontogenetic differences in the pannins (Mitteroecker *et al.*, 2005).

However, Lieberman and colleagues (2007) argued that the criteria in Mitteroecker and colleagues (2005) was too stringent. Lieberman and colleagues (2007)

tested regional dissociation and found shape differences in the neurocranium and basicranium could be attributed to post-formation (a normal rate and timing of development, however the initial shape of the descendent is underdeveloped; Alba, 2002), but that the face of *Pan paniscus* does not appear to be paedomorphic in the same pattern or extent as the neurocranium and basicraniuim. Thus, while global or pure neoteny is not supported by morphological evidence (Shea, 1989; Mitteroecker *et al*., 2005; Lieberman *et al*., 2007), there are inconsistent results as to whether the cranium exhibits localized heterochrony.

1.2 Evolutionary Changes in Morphology

1.2.1 The integration of ontogeny and evolution

These four major topics are often treated as separate questions within the paleoanthropology community, but in fact are different avenues for addressing the overarching issues of how ontogeny contributes to the biological complexity of hominoid evolution. The interplay between ontogeny and evolution are well documented (Gould, 1977; Raff, 2000, 2007; Laland *et al*., 2014; Antón and Kuzawa, 2017) and suggest that evolutionary changes in morphology must derive at some fundamental level from alterations in the pattern and timing of ontogeny.

However, it is difficult to obtain good sample sizes, and even more difficult to get juvenile samples. Collecting appropriate samples for testing these hypotheses is time- and resource-consuming and obtaining adequate samples for analyses are difficult. The result is that most current studies on morphological ontogeny pool specimens together from museum samples, without regard to population divisions, in order to study growth and

development (*e.g*. Leigh and Shea, 1996; McNulty *et al*., 2006; McNulty, 2012; Cofran and Walker, 2017). By testing ontogenetic hypotheses at the species or subspecies level, researchers are able to acquire appropriate sample sizes, but at the cost of overlooking potentially relevant variation due to infraspecific substructuring.

The assumption of subspecies-, species- or genus-level ontogenetic uniformitarianism was undermined when Strand-Viðarsdóttir and colleagues (O'Higgins and Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al*., 2002; Strand Viðarsdóttir and O'Higgins, 2003) found statistically significant differences in cranial growth and development among different modern human populations. Ignoring such differences – for example, pooling samples derived from different genetic and ontogenetic regimes – is to create ontogenetic models of unknown biological validity or significance.

Groves, (1970, 2003, 2005) and others (Albrecht *et al*., 2003; Miller *et al*., 2004), demonstrated important differences among populations of African ape adult cranial morphology. Since evolutionary changes in adult morphology must come about by changing the pattern and/or timing of ontogeny, these cranial differences are suggestive of distinct population-level patterns of ontogeny. Further, given the relatively recent divergence times of human populations compared to at least some African ape populations, one might expect ontogenetic differences among the latter to be at least as divergent as those documented for modern humans (cf. Strand Viðarsdóttir *et al*., 2002). Although an argument can be made that geographical and ecological dispersion of humans compared to ranges of modern apes explains variation in human ontogeny where in apes it might be more consistent, the fact remains that the variation in ontogeny of our closest living relatives has yet to be documented.

1.2.2 Integrating population-level thinking

Population-level morphological studies are uncommon, but not new to biological anthropology. Groves' early work focused on infraspecific morphological differences in many primates including African apes (Groves, 1967; 1970, 1986; Groves *et al.*, 1992). This work helped to formalize the number of species/subspecies recognized among various primate groups. Uchida (1992) analyzed the intraspecific variation in teeth of living great apes to study fossil Miocene catarrhines. She (Uchida, 1992, 1996) noted that in order to interpret morphological variation among fossils, it is prudent to study variation at several different taxonomic levels (population, subspecies, species, and genus). The conclusions of Uchida's (1992) analysis of great ape populations are clear: subspecies may differ markedly in morphology, which may represent a unique mosaic of characters; and, using one population to represent an entire species is not a representative analog for a temporally and geographically variable fossil species. Likewise, Pilbrow (2003) demonstrated that studying organisms at the level of populations allows one to assess patters of variation without the constraints of taxonomy. Pilbrow (2003, 2006) showed that most of the variation within species of *Pan* is distributed at the level of local populations. Pilbrow (2003, 2010) showed variation among gorillas at the level of demes, with an altitude gradient being the major contributing factor to variation in that case. Gorillas in these separate ecological zones have been shown to be correlated with the amount of fruit in the diet. Robbins and McNeilage (2003) showed that highland Grauer's gorillas incorporate 20 fruit species into their diet, whereas lowland groups incorporate 48 species. Bonobos on the other hand, seem to retain a high level of gene flow among

populations, possibly homogenizing dental variation across the species (Pilbrow and Groves 2013).

Populations in this study are defined based on work by Mayr (1963; 1999), Albrecht and Miller (1993), Albrecht and colleagues (2003) and Miller and colleagues (2004). Specifically, one population is defined as a group of potentially breeding males and females within a formal taxonomic designation of a species or subspecies (Mayr, 1963). However, variation can be further analyzed at lower levels of population taxonomy. Albrecht and Miller (1993) introduced a hierarchical structure in which variation in a population below the level of subspecies could be studied. Accordingly, one could study sexual dimorphism as variation nested within localities (geographically disparate groups of organisms), which themselves are nested within demes (individuals from multiple geographic localities which retain some amount of gene flow and similar ecological zones; cf. Endler, 1977), which are nested within subspecies, which are genetically structured groups within the species (Albrecht and Miller, 1993; Albrecht *et al*., 2003).

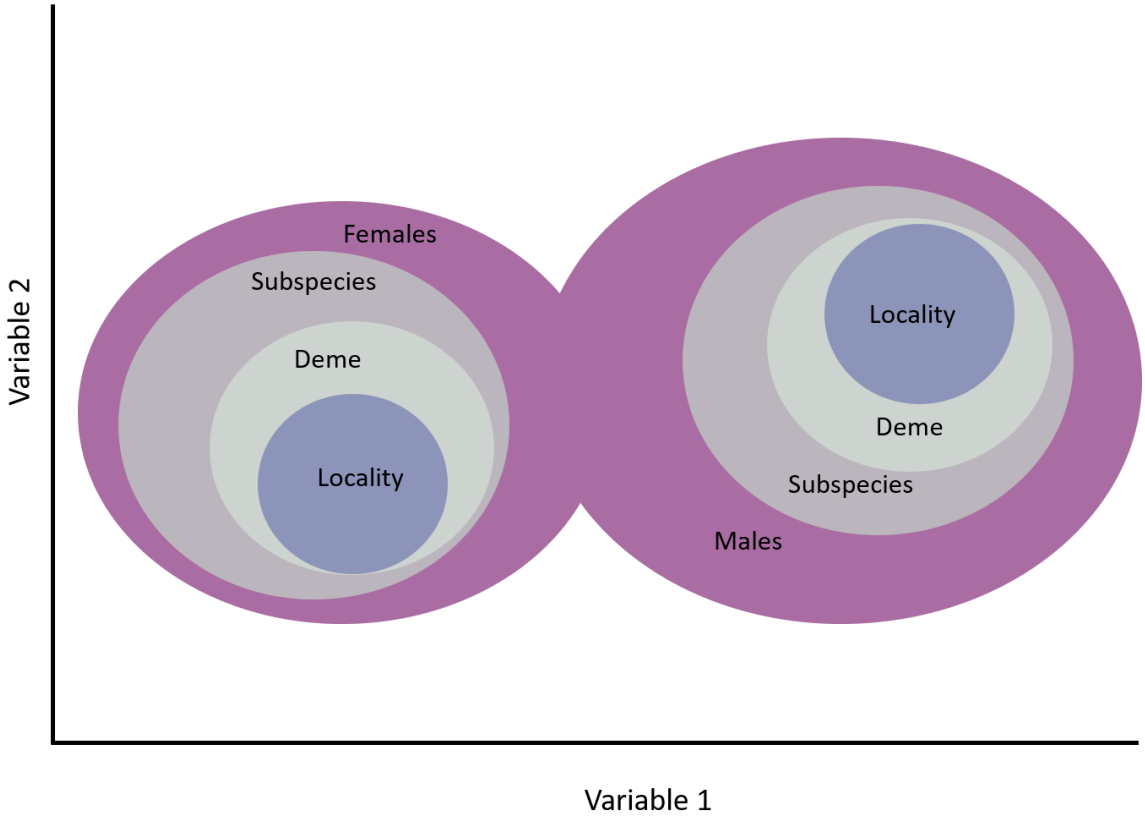

Figure 1.2: Redrawn from Albrecht and Miller 1993. Nested hierarchy of intraspecific (population-level) variation in a sexually dimorphic, polytypic species.

1.3 Hypotheses to be Tested

Expanding on the work of Albrecht and colleagues (Albrecht and Miller, 1993; Albrecht *et al.*, 2003; Miller *et al*., 2004), this project will sample variation at multiple infraspecific levels to assess differences in ontogenetic patterns. The results will characterize ontogeny according to a species' population taxonomy (the biological organization of the species, which is made up of aggregates of populations) and population structure (the geographic arrangement of local populations across the species' range) (Albrecht *et al.*, 2003 and Miller *et al.*, 2004). It will also enable variation among

fossils to be compared to, and measured against, well-characterized levels of infraspecific variation in the modern analog species (Miller *et al*., 2004).

According to this basic research design, this project will answer the following research questions:

1. How do individual populations of African apes differ in their development compared to other conspecific populations? To what degree and in what respects do ontogenetic models based on pooled samples diverge from individual population-level ontogenies?
2. How does ontogenetic trajectories mediate sexual dimorphism in gorillas and chimpanzees? Are these processes similar or different?
3. Can classical Gouldian heterochronic processes be identified in the cranium from analyses of densely-distributed landmark data?

Subsequent chapters will further develop these questions, testing a number of specific hypotheses.

1.3.1 Testable hypotheses: Ontogenetic variation at the population-level

$H1_0$ – Adult cranial morphology does not differ in size and shape among conspecific populations of African apes.

Predictions and Tests – Based on work by Groves and others (Groves, 1970, 2003, 2005, Shea *et al*., 1993; Sarmiento and Oates, 2000; Grubb *et al*., 2003; Gonder *et al*., 2006), rejecting this hypothesis is anticipated for at least some comparisons. Nevertheless, it is important to first test for these differences using the same population-level samples, datasets, and methods that are incorporated throughout the rest of the

project. Differences among groups will be tested using MANOVAs. The high degree of sexual dimorphism in African ape crania dictates that separate analyses be run for males and females in order to avoid comparing mean shapes that lack biological valence.

H2$_0$ – Patterns and magnitudes of growth and development in localized populations are identical to each other and to those reconstructed from samples pooled at subspecies and species levels.

Predictions and Tests – A rejection of this hypothesis is also anticipated based on the work of Strand Viðarsdóttir *et al*. (2002), who found statistically significant differences in cranial ontogeny between populations of modern humans. A study of the ontogenetic trajectories in size-shape space will be undertaken using a principal component analysis of the Procrustes aligned coordinates and the natural logarithm of centroid size (Mitteroecker *et al*., 2004a, b, 2005). Developmental patterns for each sample will also be computed by ordinary least-squares regression of shape variables on log(centroid size), generating a shape trajectory of regression coefficients. Differences between groups will be computed as the multivariate angle between trajectories (arccosine of their vector dot-product) and tested for differences using permutation tests (Good, 2006; O'Higgins and Strand Viðarsdóttir, 1999), following the resampling guidelines of McNulty and colleagues (2006). The magnitude of shape change and ontogenetic differences in size will likewise be tested with permutation tests in the manner described by McNulty and colleagues (2006). As above, males and females will be tested separately.

A simple rejection of the null hypothesis – that trajectories are similar – is potentially misleading in that it implies all aspects of ontogeny are different. To better inform our understanding African ape ontogeny, these analyses will also be run on subsets of data that represent anatomical "modules," as indicated from embryological and functional evidence (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Hallgrimsson *et al*., 2007a, 2007b).

1.3.2 Testable hypotheses: The ontogeny of sexual dimorphism

H3$_0$ – Sexual dimorphism results from the same processes of development in chimpanzees and gorillas.

Predictions and Tests – In a study of body mass in captive African apes, Leigh and Shea (1995, 1996) concluded that sexual dimorphism in chimpanzees and gorillas is mediated through fundamental differences in ontogenetic timing (*i.e.*, heterochrony). This project will contribute to these ideas for different aspects of skull ontogeny, utilizing wild populations of gorillas and chimpanzees with known ages of death: a population of *Gorilla beringei beringei* from Parc National des Volcans, Rwanda, and a population of *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. This hypothesis will be tested globally for the entire skull, as well as regionally using the divisions established above in *H2*. This study will add to the conclusions of Leigh and Shea (1995, 1996) to test the pattern and magnitude of skull development between males and females in populations of wild apes. The duration and rate of overall growth is unlikely to explain

sexual dimorphism in all aspects of the anatomy; therefore, rejection of the null hypothesis is expected.

1.3.3 Testable hypotheses: Finding heterochrony

$H4_0$ – Classic heterochronic mechanisms can describe the relationship between *Pan paniscus* and *Pan troglodytes*.

Predictions and tests – Classical descriptions of heterochrony have been difficult to apply to morphometric datasets: global heterochrony seems to be rejected *in toto*, but the presence of regional heterochrony is still contested (Shea, 1989; Mitteroecker *et al*., 2005; Lieberman *et al*., 2007). Mitteroecker and colleagues (2004b, 2005) showed that in order for descriptions of classical heterochrony to be applied to morphometric data, ontogenetic trajectories must overlap in shape space. This study aims to find groups of landmarks derived from a global dataset to see if any combination can adequately align shape space trajectories so that heterochrony can be further studied. This study is a further test of utilizing classical descriptions of heterochrony using a global landmark dataset. However, this research does not represent one more attempt to test predetermined datasets for heterochrony. Rather, the goal is a systematic reduction of the dataset to see if heterochrony has explanatory power to describe *any* cranial differences between *P. paniscus* and *P. troglodyates*. A rejection of the null hypothesis is anticipated based on these previous works (*e.g.*, Mitteroecker *et al*., 2004a, b, 2005).

To test this, this project will carry out multivariate regressions of shape variables on log(centroid size) to determine whether the ontogenetic trajectories overlap in shape space. If not, then the dataset will be reduced using three study designs evaluating the

differences between groups in regression coefficients at each coordinate. Each of the reduced datasets will be reevaluated in shape space. If any of the reduced datasets have overlapping trajectories in shape space, an evaluation of heterochrony in size-shape space will be performed.

2 Materials and Methods

2.1 Sample

2.1.1 Sample used in analyses

Cranial data from a large ontogenetic sample of African apes were collected cognizant of two types of information needed for this study: individuals retaining known provenience (location of collection), and individuals with known ages at death. Specimens associated with known provenience data came from the Powell-Cotton Museum, Royal College of Surgeons, British Natural History Museum, the Royal Museum for Central Africa, and Cleveland Museum of Natural History. This sample was then divided into populations (as explained below in 2.1.2) based either on the known latitude-longitude position of where the specimen was acquired, or the known locality of acquisition if the exact latitude-longitude was unknown. The total number of specimens scanned was 1200, comprising specimens of *Gorilla gorilla gorilla*, *G. beringei graueri*, *Pan troglodytes troglodytes*, *P. t. schweinfurthii*, and *P. paniscus* (see Table 2.1 for a breakdown by sex and age class). Museum specimens were assigned relative age based on dental development stage (occlusion of sequential tooth positions) and on centroid size. Specimens with known age at death were collected from the Mountain Gorilla Skeletal Project (MGSP) housed at Dian Fossey International's Karisoke Research Center in Rwanda, and from the Jane Goodall Institute's Gombe Stream Research Centre in Tanzania. Specimens from Rwanda (*Gorilla beringei beringei*) and Tanzania (*Pan troglodytes schweinfurthii*) were assigned chronological ages based on reported birth and

death dates, or inferred ages agreed upon by behavioral researchers studying those populations.

2.1.2 Determination of population taxonomy and population history

Specimens were allocated to different populations in order to facilitate hierarchical analyses of infraspecific variation (Albrecht and Miller, 1993; Albrecht *et al*., 2003; Miller *et al*., 2004). Species were subdivided into subspecies, demes, localities, and sexes. While subspecies divisions are often denoted in museum catalogs, demes and localities are typically not. However, many of the specimens scanned for this study retain the relevant records of where they were collected. From these data, the samples were organized into more detailed infraspecific groups.

Elevation was used to separate the specimens of *Gorilla beringei graueri* into separate demes: highland and lowland. Gorillas in these separate ecological zones have been shown to be correlated with amount of fruit in the diet. Robbins and McNeilage (2003) showed that highland Grauer's gorillas incorporate 20 fruit species into their diet, whereas lowland groups incorporate 48 species. Previous analyses on postcrania have shown this to be an important source of variation within this subspecies (Dunn *et al*., 2014; Knigge *et al*., 2015). Based on those studies, an elevation cutoff of 1,500 m delineated highland and lowland Grauer's gorillas.

Most specimens of *Gorilla gorilla gorilla* and *Pan troglodytes troglodytes* were assigned to localities based on proximity to the nearest town or village. However, when latitude-longitude data were available, these coordinates were used to group specimens using a cluster analysis; cluster was constrained to produce four branches in the resulting

dendrogram; and the two known provenience data with the largest samples sizes were used to identify different populations (the largest sample size in each case did not retain latitude-longitude data).

2.2 Digitization Protocols

2.2.1 Scanning

Specimens were digitized with a Breuckmann SmartScan^{3D} white light scanner. Unlike laser scanners, this equipment takes digital photographs as it illuminates and projects patterns on the specimen with a 100-watt halogen lamp. This model has two digital cameras with a 30° triangulation angle spaced approximately 71 cm from the specimen. The two 300 mm cameras used to digitize specimens provide 180 µm resolution.

The majority of specimens underwent three rotations of 10 digital images each to capture the entire surface geometry. Large, male gorillas needed four or five rotations to completely capture their surfaces. The scanning software, Optocat (Optocat, 2012), was configured to capture maximum data (as little data were masked as possible) using a 2½D Fourier filter. Raw data were imported into Geomagic Design X (3D Systems, Inc, 2017) to be aligned and merged into one mesh. Floating polyfaces, and other noise components, were deleted, and each mesh was re-wrapped for the purposes of visualization in a way that does not alter the specimen's point cloud. Finally, holes were filled and final specimens exported for landmarking.

Table 2.1: Sample size for the museum collections divided into sex and age classes. Age classes were based on the occlusion of dentition using known dental eruption sequences: dP4: deciduous 4th premolar, M1: 1st molar, M2: 2nd molar, M3: 3rd molar. Category totals are bolded.

Taxon	**dP4**	**M1**	**M2**	**M3**	**Total**
Gorilla gorilla gorilla					
Unknown	7	19	10	3	**39**
Female	9	16	38	126	**189**
Male	15	17	26	143	**201**
Total	**31**	**52**	**74**	**272**	**429**
Gorilla beringei graueri					
Unknown	14	5		14	**33**
Female		3	5	35	**43**
Male	1	2	4	36	**43**
Total	**15**	**10**	**9**	**85**	**119**
Pan troglodytes troglodytes					
Unknown	30	33	12	24	**99**
Female	8	17	21	125	**171**
Male	6	19	18	56	**99**
Total	**44**	**69**	**51**	**205**	**369**
Pan troglodytes schweinfurthii					
Unknown	16	21	11	28	**76**
Female	2	4	8	8	**22**
Male		3	5	12	**20**
Total	**18**	**28**	**24**	**48**	**118**
Pan paniscus					
Unknown	19	35	9	12	**75**
Female	4	4	12	25	**45**
Male	8	7	11	19	**45**
Total	**31**	**46**	**32**	**56**	**165**
Grand total					**1200**

2.2.2 Landmarking

Finalized 3D models were landmarked in order to digitize specific anatomical features of their three-dimensional geometry. Landmarks were chosen to represent biologically or geometrically homologous points or structures on each specimen (Bookstein, 1991), and collected in Stratovan Checkpoint (Stratovan Corp, 2016). Landmarking 3D meshes results in each specimen, or observation, having its own configuration. Each landmark is associated with three variables: an x-, y-, and z-coordinate. For example, this study utilizes 148 landmarks (Table 11.1, Figure 2.1), so the total number of variables for each observation is 444. Landmarks are chosen in order to sample the anatomy of interest, in this case based on previously published protocols (Frost, 2001; Harvati, 2001; McNulty, 2003; Baab, 2007; Terhune *et al*., 2007; White *et al*., 2012) with additional landmarks added for the purposes of this study (Table 11.1, Figure 2.1). Although only complete specimens were used in this research, occasional missing landmarks were estimated using thin-plate spline interpolations (e.g., Gunz *et al*., 2009) computed in the R statistical package Geomorph (Adams *et al*., 2016).

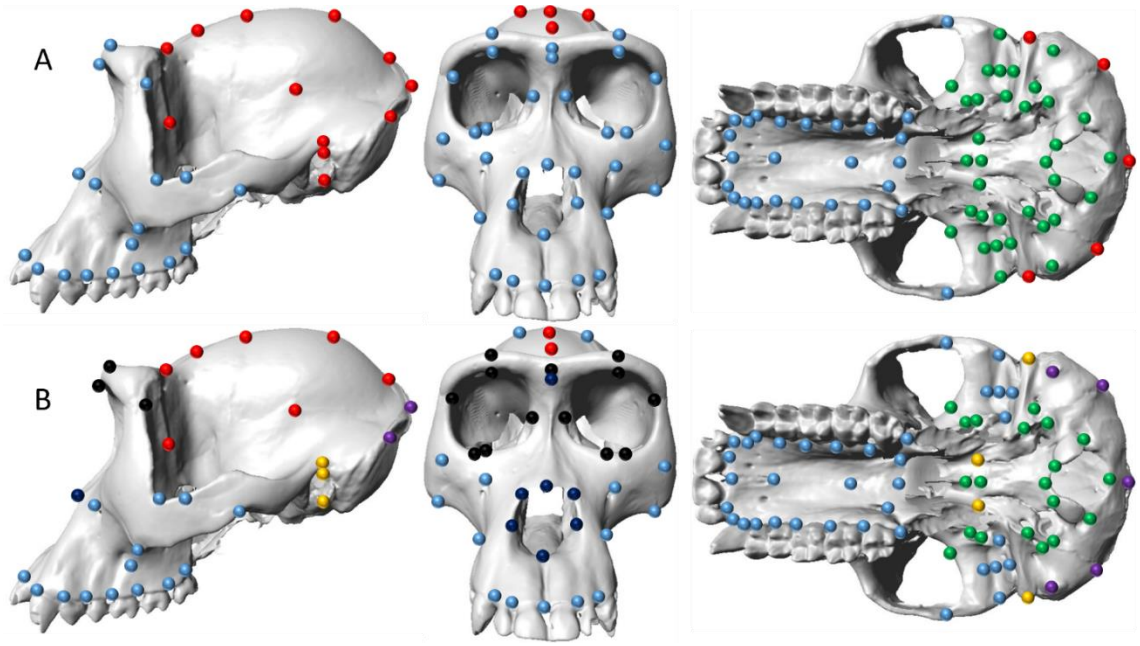

Figure 2.1: Landmark dataset. Each point represents one of the 148 landmarks used in this study. Embryological and functional cranial modules were analyzed separately. A) Embryological modules: blue: viscerocranium, red: neurocranium, green: basicranium. B) Functional modules: green: basicranium, blue: mastication, dark blue: nasal, purple: cervical muscle attachments, red: neurocranium, black: orbit, yellow: petrous.

2.3 Statistical Analyses

2.3.1 Procrustes superimposition

After landmarking, each specimen's configuration resides in its own coordinate system. Thus, any shape differences detected in homologous landmarks would likely be overshadowed by differences in specimens' locations, orientations, and size. Therefore, a Procrustes superimposition was performed to eliminate these nuisance variables across all landmark configurations (Gower, 1975; Kendall, 1977; Rohlf and Slice, 1990). The superimposition method used here was a generalized Procrustes analysis (GPA; Gower, 1975; Rohlf and Slice, 1990; Slice, 1996, 2001), which projects specimens into a common shape space (a new configuration of aligned and size-adjusted landmark

positions) by following three steps. First, the centroid of each specimen (the "center of gravity" of a specimen's landmarks) is translated to the origin of the coordinate system. Then, every specimen is scaled to a unit centroid size (computed as the square root of the sum of squared distances of each landmark in a configuration to that specimen's centroid). Finally, orientation is eliminated by iteratively rotating each specimen about its centroid to minimize the Euclidean distances between homologous landmarks on all specimens to those of a mean configuration (Gower, 1975; Rohlf and Slice, 1990; Slice, 2001). Following GPA, the specimens reside in a common, multidimensional shape space that has known and relatively simple topographic properties (Rohlf, 1999; Slice, 2001).

2.3.2 Embryological and functional modules

Mitteroecker and colleagues (2004a) showed that global (entire cranium) ontogenetic trajectories can diverge in shape space when, in fact, only one or a few regional aspects of anatomy differ. The modular nature of the skull (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Hallgrimsson *et al*., 2007a, 2007b) can confound studies of ontogeny and heterochrony in that results based on a global landmark dataset do not account for which aspects of anatomy create the observed morphological differences (Mitteroecker *et al*, 2004a, 2005; Liebermann *et al*, 2007). Therefore, analyses were performed globally (utilizing the entire cranial landmark dataset: 148 landmarks) and on ten anatomical landmark subsets (Figure 2.1). These subsets, aligned and analyzed separately, were chosen to capture embryological and functional modules defined by

previous researchers (Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Halgrímsson *et al*., 2007b; Goswami and Finarelli, 2016).

Functional complexes were chosen to follow Cheverud and colleagues (Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986), as well as additional anatomical units that contribute to specific functions (*e.g*., the masticatory apparatus, attachments for cervical musculature, the visual apparatus, etc.). Embryological complexes were chosen to represent the three traditionally identified regions of the skull (face, basicranium, and neurocranium; Halgrímsson *et al*., 2007a, b). The skull forms tissue around the developing brain in two major portions, the neuorcranium and the viscerocranium. Each of these divisions is further subdivided into a membranous part and a cartilaginous part based on the type of bone formation they undergo. The neurocranium largely undergoes intramembranous ossification to form the flat bones of the cranial vault. The viscerocranium is derived from the frontonasal process (from neural crest cells) and the first two pharyngeal arches. This portion of the cranium largely undergoes endochondral bone formation to form the maxilla, mandible, ear ossicles, and hyoid. The basicranium is largely thought to anchor the face and braincase together. It is derived from several processes including endochondrally ossified somites contributing to the occipital bone as well as endochondrally ossified temporal and sphenoid bones (Scheuer, 2000; Sadler, 2012).

2.3.3 Geometric morphometric analyses utilized in this study

Statistical analyses were performed in SAS ® software. Testing hypotheses H1 to H3 (ontogenetic variation in population taxonomy) used similar methods and are

described together. Testing hypothesis H4 (assessing heterochrony) used a different set of methods and is, therefore, described separately.

Ontogenetic variation at the level of subspecies, deme, and locality was analyzed on specimens obtained from museum collections that retained information about collection provenience. Where no locality information was provided (or in the case where this information was provided but was not specific enough to categorize into a population), specimens were used as a comparative sample designed to mimic an aggregate sample. These unknown population aggregates are similar to studies that utilize museum collections without regard to population divisions. This design allowed pairwise analyses to be performed on coherent population groups as well as between known populations and unknown, museum-like samples. Ontogenetic variation at the level of sex was analyzed on two African ape populations: *Pan troglodytes schweinfurthii* housed at Gombe National Park, Tanzania and *Gorilla beringei beringei* housed at Volcanoes National Park, Rwanda.

Table 2.2: Functional and embryological complexes with landmarks included in each.

Modules tested	**Landmarks Included (numbers found in appendix: Table 11.2)**
Global landmark dataset	1-148
Embryological modules	
Basicranium	6, 17, 18, 19, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 134, 135, 136, 137, 138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148
Neurocranium	2, 3, 5, 7, 20, 21, 22, 23, 24, 27, 28, 29, 30, 32, 33, 34, 35, 36, 106, 107, 108, 109, 111, 112, 113, 114, 115
Viscerocranium	1, 4, 8, 9, 10, 11, 12, 13, 14, 15, 16, 25, 26, 31, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 70, 71, 72, 73, 74,

	75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 110, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133
Functional Modules	
Basicranium	6, 17, 18, 19, 55, 56, 57, 58, 60, 62, 68, 69, 134, 135, 136, 137, 139, 141, 147, 148
Mastication	11, 12, 13, 14, 15, 16, 25, 26, 28, 31, 33, 37, 38, 44, 45, 46, 48, 51, 52, 53, 54, 63, 64, 65, 66, 67, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 107, 110, 112, 116, 117, 123, 124, 125, 127, 130, 131, 132, 133, 142, 143, 144, 145, 146
Nasal	9, 10, 47, 49, 50, 126, 128, 129
Cervical musculature	20, 32, 61, 111, 140
Neurocranium	5, 7, 8, 21, 22, 23, 24, 27, 29, 30, 34, 106, 108, 109, 113
Orbit	1, 4, 39, 40, 41, 42, 43, 118, 119, 120, 121, 122
Petrous	2, 3, 35, 36, 59, 114, 115, 138

Pairwise differences among adult group means at each taxonomic level (i.e., genus, species, subspecies, deme, locality, and sex) were tested using multivariate analysis of variance (MANOVA). Ontogenetic trajectories were studied visually in size-shape space (Mitteroecker *et al*., 2004a, b, 2005), and statistically using ordinary least-squares regression of shape variables on log(centroid size). Differences in the patterns of development between groups were computed as the multivariate angle between ontogenetic vectors (*i.e*., the arccosine of their vector dot-product). Differences between groups' magnitudes of development, or the amount of shape change, were computed as the absolute value difference in overall shape change from mean specimens in the youngest and oldest age categories.

Multivariate angles and differences in magnitudes were tested for significance using permutation tests (Good, 2006; O'Higgins and Strand Viðarsdóttir, 1999), following the resampling protocol outlined by McNulty and colleagues (2006). That study laid out three possible statistical designs for permutation tests: 1) permuted groups contain an equal number of specimens for each developmental stage, randomizing within their ages classes; 2) permuted groups retained unequal sample sizes (matching original samples), but still randomizing within each developmental stage; and 3) randomly placing specimens into two groups without regard to developmental stage (as is commonly used in the literature; O'Higgins *et al*., 2001; O'Higgins and Collard, 2002; Penin *et al*., 2002; Strand Viðarsdóttir *et al*., 2002; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Cobb and O'Higgins, 2007). McNulty and colleagues (2006) found that the latter design more readily return statistically significant p-values than does the more conservative approach of permuting within developmental stage. Hence, this study employs permutation test that constrain resampling to occur within age classes.

3 Population-level thinking in ontogenetic variation

As mentioned in the first chapter, this dissertation focuses on ontogenetic variation at multiple levels of taxonomy below that of the species. Population-level thinking investigates evolutionary questions that can help elucidate the processes of speciation. I have structured this dissertation to first look at variation in ontogeny at the infraspecific levels of population organization: subspecies, demes, and localities. Following that is an analysis of how ontogeny mediates sexual dimorphism. Finally, I assess whether classical descriptions of heterochrony can be applied to the extant *Pan* species.

The following chapter investigates 1) whether adults of each group differ statistically in the global dataset as well as each cranial module, 2) whether there is variation in ontogenetic trajectories at the population level – below the level at which most studies investigate, 3) whether this variation is important for fossil reconstructions utilizing museum samples, and 4) possible mechanisms for changes in ontogeny between populations.

4 Population-level ontogenetic variation in *Gorilla* and *Pan*

4.1 Introduction

4.1.1 Growth and development

The study of growth and development has been a vital component of biological research since well before Darwin. Developmental recapitulation was a central theory in the late-eightieth and early-nineteenth centuries (reviewed in Gould, 1977), but only later did von Baer (1928) recognize that related species share characteristics early in embryogenesis, diverging morphologically later in ontogeny (reviewed in Mitteroecker, 2004a). These ideas were modified and improved by subsequent researchers, including de Beer (*e.g.*, 1958) who argued the importance of heterochrony, and particularly paedomorphosis, in evolutionary morphogenesis. Nevertheless, such work fell out of favor until Gould (1977) revived and formalized the role of ontogeny in evolutionary research by demonstrating that change in adult form must be mediated by changes in growth and development. This work was one impetus for the emergence of evolutionary development, so called "evo-devo," which studies how ontogenies evolve in lineages to create new forms, behaviors, and life histories (Raff, 2007). Since Gould's *Ontogeny and Phylogeny*, numerous studies have contributed to our understanding of ontogeny in evolutionary biology, including important works in the field of paleoanthropology (Shea, 1983a, b, 1989; Richtsmeier *et al*., 1993; Godfrey and Sutherland, 1995; Leigh and Shea, 1995, 1996; O'Higgins and Jones, 1998; O'Higgins and Strand Viðarsdóttir, 1999; Antón

and Leigh, 2003; Mitteroecker *et al.*, 2004a,b, 2005; Raff, 2007; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2008).

Juvenile specimens are a critical part of the hominin fossil record, providing unique windows into the ontogenetic processes of extinct species. As examples, Taung 1, DIK-1-1, KNM-WT 15000, DNH 35 and 67, and the Mezmaiskaya Neanderthal juvenile have provided important clues about the evolution of human life history patterns and evolutionary development of our lineage (Dart, 1925; Ackermann and Krovitz, 2002; Cobb and O'Higgins, 2004; Antón and Leigh, 2003; Lacruz *et al*., 2005; McNulty *et al*., 2006; Alemsaged *et al*., 2006; Ponce de León *et al*., 2008; Smith *et al*., 2012; Gunz 2012; McNulty 2012). Specimens discovered more recently from Malapa, South Africa (Berger *et al*., 2010), the Turkana Basin, Kenya (Leakey *et al*., 2012), and Dmanisi, Georgia (Rightmire *et al*., 2006; Lordkipanidze *et al*., 2013) will likewise expand our knowledge of hominin evolutionary development but have not yet been subject to multiple comprehensive ontogenetic studies.

Great strides were made in studies of hominin evolution with the discovery that age-at-death could be estimated in fossil specimens using the microstructure of their teeth (Dean *et al*., 1986; 1993; Bromage and Dean, 1991; Beynon and Dean, 1991; Skinner 1997; Stringer and Dean, 1997; Beynon *et al*., 1998; Bolter and Zihlman, 2011; 2012). Because layers of each tooth tissue are secreted at predictable time intervals, leaving a record of growth, these incremental lines can provide reliable age estimates of an individual and therefore the pace of ontogeny and life history in the absence of behavioral data. This methodology led to important contributions to our understanding of hominin growth and development, and has been used to determine the age at death for several

hominin specimens (Dean *et al*., 1986; Bromage and Dean, 1991; Dean *et al*., 1993). These studies also allowed for the study of the evolution of a human-like life history strategy (*e.g*., Smith, 1989; Kelley and Schwartz, 2010, 2012; Schwartz, 2012; but see Robson and Wood, 2008). A comparison of human and primate tooth microstructure concluded that the human-like pattern of life history did not evolve until very recently (Dean *et al*., 2001; Dean, 2006). Finally, Smith *et al*. (2007) concluded that the rate of growth in the juvenile Neanderthal from Scladina, Belgium matured at a rate intermediate between *Homo erectus* and *H. sapiens*. They inferred that this individual had a shorter childhood and accelerated life history compared to *H. sapiens*.

The value of such studies has been immeasurable. However, there are difficulties with the interpretation, or over-interpretation, of these ontogenetic models. Simpson *et al*. (1991) demonstrated that when the bony skeleton of a hominin fossil is compared to an ape-like dental developmental schedule, that fossil will be interpreted as having an ape-like developmental pattern. Yet, if that same fossil is compared to the dental development of a human, that fossil will exhibit a more human developmental pattern. In other words, the choice of analogs used for comparison potentially biases the results (Simpson et al., 1991). Further, results from dental developmental studies have been over-interpreted by some in the paleoanthropology community, assuming that an ape-like timing of dental development necessarily implies ape-like maturation for the entire skeleton (Simpson *et al.*, 1991; but see, *e.g.*, Shea 1983a). With dental maturation as *the standard* for developmental age (Dean and Wood, 1981; Zelditch *et al*., 2012), important variations in the growth and development of other anatomical structures are still relatively unknown.

For example, the age of first molar emergence in gorillas and chimpanzees suggests only minor differences between them in the timing of their dental development (Kelley and Schwartz, 2012). Yet, McFarlin and colleagues (2012) demonstrated that brain growth in Virunga mountain gorilla achieves 90 percent of the adult mass at approximately 28 months, and full adult mass by 3 to 4 years of age; this is approximately a year before chimpanzee brains reach adult mass. This difference, though related to factors about the life history of this population (McFarlin *et al*., 2012), would not necessarily be predicted from the timing of dental development. Moreover, the braincase is not a completely modular system. As the neurocranium develops, it will affect the shape and position of adjacent anatomical structures, and the differential timing of these interactions can potentially result in very different morphological configurations.

Hence, the important discovery of incremental growth in dental microstructures, which enables reliable estimates of age-at-death for extant and fossil specimens, describes only a small part of the evolutionary developmental story in our lineage. It provides a much-needed chronometer for evaluating timing of ontogeny and life history but does not record the ontogenetic dynamics of the entire organism. To be clear, dental development researchers have been very precise in interpreting results of their own work. Yet, widespread reliance by secondary and tertiary researchers on dental estimates of ontogenetic timing has obscured the many potentially interesting relationships among age, size, anatomy, and life history.

4.1.2 Variation below the species-level

A confounding factor in previous ontogenetic analyses is the fact that many (*e.g.*, Leigh and Shea, 1996; McNulty *et al*., 2006; Cofran and Walker, 2017) utilized museum collections pooled together without regard to infraspecific genetic structuring. Because most museum collections lack large samples at early ontogenetic stages, researchers often group specimens for analysis at the subspecies, species, or even genus level (see discussions in Albrecht *et al.*, 2003; Miller *et al.*, 2004). As a result, the framework of African ape ontogeny that is so important for interpreting the human fossil record may be based on unrealistic biological models that have been neither statistically tested nor adequately characterized.

In fact, the assumption of subspecies-, species- or genus-level ontogenetic uniformitarianism has long been suspect given well-documented differences in adult morphology at all of these taxonomic levels (Groves 1970, 2003, 2005; Shea *et al*., 1993; Sarmiento and Oates, 2000; Grubb *et al*., 2003; Albrecht *et al*, 2003; Miller *et al*, 2004; Gonder *et al*., 2006). This has been explicitly demonstrated for human populations, with differences in growth and development leading to differing adult cranial morphologies (O'Higgins and Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al*., 2002; Strand Viðarsdóttir and O'Higgins, 2003).

Given the above analyses (*e.g.*, Strand Viðarsdóttir *et al*., 2002), we might expect the difference in human ontogenies to be due to a cessation of gene flow among these populations allowing each to adapt to particular environments. The divergence of the lineages leading to modern humans from those leading to other species of *Homo* (Neanderthals) occurs between 0.8 and 0.4 Ma (Rieux *et al.*, 2014) and the most recent

dates of modern humans leaving Africa and entering the Levant and Arabia (the spreading of humans into new environments) are 0.085 Ma (Groucutt *et al*., 2018; though possibly as early as 0.194; Hershkovitz *et al*., 2018). For comparison, divergence among western and eastern chimpanzee populations is approximately 0.50 Ma (Gonder *et al*., 2006). Thus, if population-level difference in human ontogeny occurs due to genetic divergence, then ontogenetic differences among certain ape population could be at least as divergent.

4.1.3 Population-level analyses

A population is defined here based on the works by Mayr (1963, 1999), Albrecht and Miller (1993), Albrecht and colleagues (2003) and Miller and colleagues (2004): for example, as a group of potentially breeding males and females within a formal taxonomic designation of a species or subspecies (Mayr, 1963). Albrecht and Miller (1993) introduced a hierarchical structure within which subspecies variation is partitioned into multiple levels population analysis. As such, variation due to sexual dimorphism is nested within localities (geographically disparate groups of organisms), which are nested within demes (individuals from multiple geographic localities which retain some amount of gene flow; Endler, 1977), which are nested within subspecies, and subspecies in turn group together within a formal taxonomically defined species (Albrecht and Miller, 1993; Albrecht *et al*., 2003). Thus, a population is a general term that encompasses multiple levels of variation: subspecies, deme, and locality.

Population-level morphological studies are not new to biological anthropology. Groves' (1967, 1970, 1986; Groves *et al*., 1992) early work focused on infraspecific

morphological differences in many primates including African apes. This work helped to formalize how many species/subspecies are recognized among various primate groups. More recently, Uchida (1992) analyzed the infraspecific dental variation at several taxonomic levels (populations, subspecies, species, and genera) of living great apes to better assess variation in Miocene fossil catarrhines. Her conclusions reinforce the idea that subspecies may differ markedly in morphology, and hence using one population to represent an entire species is not a sufficient benchmark for a temporally and geographically variable fossil species. Likewise, Pilbrow (2003) demonstrated that studying organisms at the level of populations allows one to assess patters of variation without the constraints of taxonomy. Pilbrow (2003, 2006) showed that most of the variation within species of *Pan* can be observed at the level of local populations. Pilbrow (2003, 2010) found similar results among gorillas, with an altitude gradient being the major factor contributing to variation. Bonobos on the other hand, seem to retain a high level of gene flow among populations, possibly homogenizing dental variation across the species (Pilbrow and Groves 2013).

The current study is one part in a broader project, which seeks to address infraspecific ontogenetic variation in *Gorilla* and *Pan*. Specifically, it aims to quantify and compare the patterns and magnitudes of cranial ontogeny in African ape *populations* based on skeletal samples with known locality data. This project is aimed at answering the following research questions: Do individual populations of African apes differ in their ontogenetic trajectories from conspecific populations and from pooled, museum-like samples? If so, which aspects of anatomy differ ontogenetically among closely related populations? This study aims to provide characterizations of intraspecific variation that

reflect a species' population taxonomy (the biological organization of a species made up of aggregates of populations) and population structure (the geographic arrangement of local populations across the species' range) (Albrecht *et al.*, 2003 and Miller *et al.*, 2004).

4.2 Methods

4.2.1 Sample

This study sampled 366 specimens of *Gorilla* and *Pan* (see Table 4.1 for specimen breakdown). Approximately 72% of the sample has known geographic coordinates indicating where each specimen was collected. Where these data do not exist, information from the locality or nearest village was used to group specimens into populations (Albrecht et al., 2003; Miller et. al, 2004). In cases where no locality information is provided (or in the case where this information is provided, but it is not specific enough to categorize into a population), specimens were used as a comparative group designed to mimic an aggregate sample of pooled populations. These unknown population aggregates are similar to samples found in many museum collection and often utilized in studies of ontogeny.

Analyses described below were carried out on two localities of *Pan troglodytes troglodytes*, two localities of *P. paniscus*, and two demes of *Gorilla beringei graueri*. The two localities of central chimpanzees include a cluster of specimens historically collected from Abong Mbang and another near Ebolowa, Cameroon. These two locations are roughly 250 km apart. The bonobo sample was derived from two localities, one near Ilima and one near Ubundu (roughly 500 km apart), Democratic Republic of the Congo. Finally, the Grauer's gorilla demes were separated into highland and lowland groups

using the elevation and latitude/longitude provenience data. Gorillas in these separate ecological zones have been shown to be correlated with amount of fruit in the diet. Robbins and McNeilage (2003) showed that highland Grauer's gorillas incorporate 20 fruit species into their diet, whereas lowland groups incorporate 48 species. The demarcation into highland and lowland groups was 1,500 meters above sea level (following Knigge *et al*., 2015; Mayaux *et al*., 2004), and was chosen based on previous works that found greater dental (Pilbrow, 2010) and postcranial (Knigge *et al.*, 2015) variation in altitude than in geographic locality.

Table 4.1: Population-level profile of sample. Sample size for each population divided into age classes based on dental eruption: dP4 = deciduous dentition in occlusion, M1 = first molar in occlusion, M2 = second molar in occlusion, M3 = third molar in occlusion.

Taxon	**Population**	**dP4**	**M1**	**M2**	**M3**	**Total**
G. b. graueri						
	Highland	12	3	4	15	**34**
	Lowland	3	1	1	22	**27**
P. t. schweinfurthii						
	Unknown provenience	14	23	18	9	**64**
P. t. troglodytes						
	Abong Mbang	2	4	5	17	**28**
	Ebolowa	1	3	7	11	**22**
	Unknown provenience	9	12	8	22	**51**
P. paniscus						
	Ilima	11	15	12	12	**50**
	Ubundu	10	19	14	12	**55**
	Unknown provenience	8	12	5	10	**35**
Total						**366**

The high degree of sexual dimorphism in African apes, and their disparate ontogenetic programs (Lockwood, 1999; del Castillo *et al*., 2014; Loza *et al.*, 2015; Holton *et al.*, 2016), dictates that separate analyses be run for males and females. For this reason, the current study focuses on female ontogenetic variation due to smaller sample sizes for males. However, Cobb and O'Higgins (2007) have shown that pooling sexes in the youngest age classes is statistically justified for cranial morphology and enables one to better characterize these early developmental stages. Therefore, specimens of unknown sex that lacked any permanent molars were included in analyses of females (Cobb and O'Higgins, 2007); no individual with known classification as "male" was used here, regardless of age class.

4.2.2 Data collection

Specimens were digitized with a Breuckmann SmartScan^{3D} white light scanner. The raw data were then imported into Geomagic Design X (3D Systems, Inc, 2017) to be aligned and merged into one mesh. Minor defects in the mesh were corrected or eliminated before exporting the models for further data collection. Finalized 3D models were landmarked in Stratovan Checkpoint (Stratovan Corp, 2016; Bookstein, 1991). This study employed 148 landmarks in order to sample the cranial anatomy of interest. Traditional landmarks were chosen based on previously published studies (Frost, 2001; Harvati, 2001; McNulty, 2003; Baab, 2007; Terhune *et al*., 2007; White *et al*., 2012) with additional landmarks added for the purposes of this project (Figure 4.1).

The Geomorph package in R (Adams *et al*., 2016) was used to estimate missing landmarks using thin-plate spline interpolation (Gunz *et al*., 2009). As is the case in

geometric morphometrics, the raw coordinate data were subjected to a generalized Procrustes analysis to eliminate variation due to the landmark configuration's position, size, and orientation. All other statistical analyses were performed in SAS® software.

4.2.3 Statistical Analysis

Pairwise differences among adult group means at each taxonomic level (*i.e.*, genus, species, subspecies, deme, and locality) were tested using multivariate analysis of variance (MANOVA). Common chimpanzees and bonobos were studied at the level of locality, whereas Grauer's gorillas were studied at the demic-level. The difference here is two-fold. First, the Grauer's gorillas samples size did not allow for locality-level substructing. Second, Results from Pilbrow (2003, 2010) indicated adult differences in the molar morphometrics of populations of gorilla along an elevation gradient. Additionally, Knigge and colleagues (2014) likewise showed similar elevation gradient variation in talar morphology suggesting different locomotor regimes. Similar results (a divergence of shape) are predicted here in the adult sample.

Mitteroecker and colleagues (2004a) showed that global (entire cranium) ontogenetic trajectories can diverge in shape space when, in fact, only one or a few regional aspects of anatomy actually differ. The modular nature of the skull (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Hallgrimsson *et al*., 2007a, 2007b) can confound studies of ontogeny and heterochrony in that results based on the global landmark datasets do not account for which aspects of anatomy create the observed morphological differences (Mitteroecker *et al*, 2004a, 2005; Liebermann *et al*, 2007). Therefore, this study

employed analyses on the global dataset (utilizing the entire cranial landmark dataset) and on ten anatomical landmark subsets. These subsets (aligned and analyzed separately) were chosen to capture embryological and functional modules previously defined (Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Halgrímsson *et al*., 2007b; Goswami and Finarelli, 2016; Figure 4.1).

Adult morphological variation and ontogenetic trajectory variation was first tested at three higher taxonomic levels (results summarized in Table 4.2). Generic variation was tested between *Gorilla* and *Pan*. Species-level variation was tested between *P. paniscus* and *P. troglodytes*. Subspecies-level variation was tested between *P. t. troglodytes* and *P. t. schweinfurthii*. Once variation was detected at these higher taxonomic levels, lower level taxonomic variation (locality and demic level) was tested.

Analyses of ontogenetic trajectories were undertaken using a few different approaches. First, trajectory summaries were assessed by plotting samples in size-shape space, or the principal component ordination of the aligned coordinates with the natural log of centroid size (Mitteroecker *et al*., 2004a, 2005). Typically, the natural logarithm of centroid size (logCS) will have a much larger variance than GPA-aligned coordinates, and thus the first principal component will primarily summarize this variable plus landmark variation associated with size differences (Mitteroecker *et al.*, 2004a). For this reason, visualizing specimen distributions in size-shape space is a useful method for assessing ontogenetic trajectories.

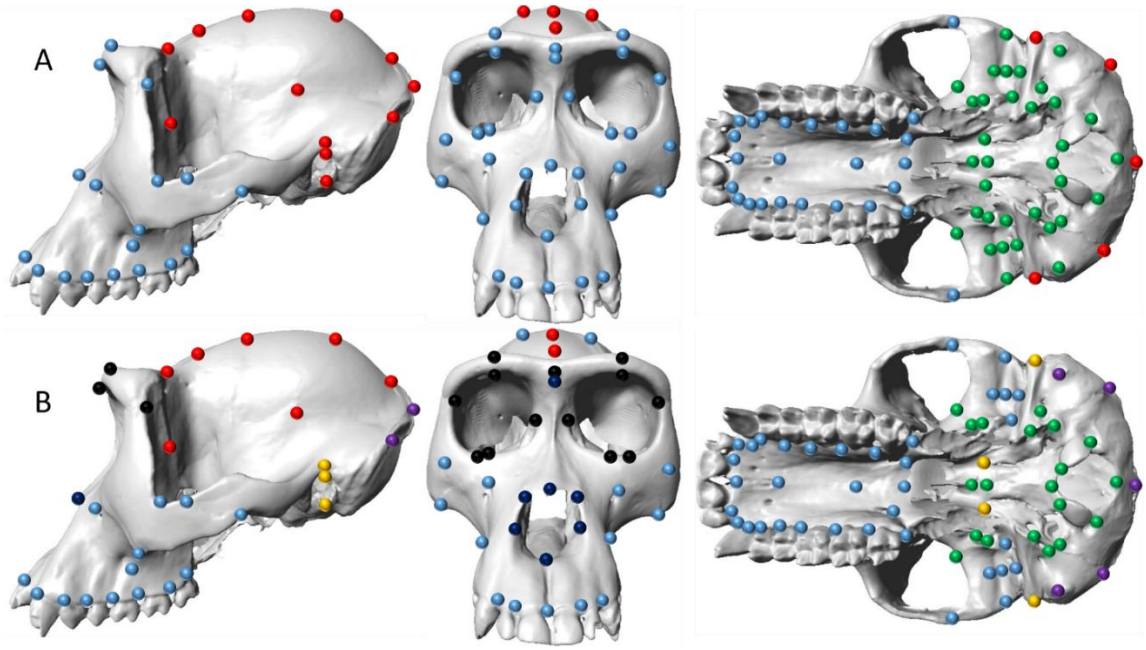

Figure 4.1: Embryological and functional cranial modules analyzed separately. A) Embryological modules: blue = viscerocranium, red = neurocranium, green = basicranium. B) Functional modules: green = basicranium, blue = mastication, dark blue = nasal, purple = cervical muscle attachments, red = neurocranium, black = orbit, yellow = petrous.

Developmental trajectories in each group were quantified by ordinary least-squares regression of shape variables on logCS to produce a vector of shape change corresponding to the direction of growth. Differences between two groups' developmental vectors were computed as the multivariate angle between them (arccosine of their vector dot-product), and tested using permutation tests (e.g., McNulty et al., 2006; Singleton et al., 2012). Differences between groups' magnitudes of development, or the amount of shape change, were computed as the absolute value difference in overall shape change from mean specimens in the youngest and oldest age categories, and likewise were tested with permutation tests.

Although permutation tests are commonplace in statistical analyses (see, *e.g.*, Good, 2006), including studies of landmark data (*e.g.*, O'Higgins and Strand Viðarsdóttir, 1999; O'Higgins *et al*., 2001; O'Higgins and Collard, 2002; Penin *et al*., 2002; Strand Viðarsdóttir *et al*., 2002; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Cobb and O'Higgins, 2007; Drake and Klingenberg, 2008; Rodriguez-Mendoza *et al*., 2011; Weisensee and Jantz, 2011; Klingenberg *et al*., 2012; Martin-Serra *et al*., 2014), this study specifically followed the resampling protocol outlined by McNulty *et al*. (2006). They demonstrated that in circumstances for which there is a dearth of observations representing some aspects of structured variation within a sample (*e.g.*, the youngest age classes in an ontogenetic study), simple models of permutation design are more likely to find statistically significant differences than models which resample with respect to that structured variation (McNulty *et al*., 2006). The current study laid out three possible statistical designs for permutation tests: 1) resampling within age classes, constraining permuted groups to an equal number of specimens for each developmental stage; 2) resampling within age classes, but replicating in permuted groups the original (unequal) sample sizes at each age class; and, 3) ignoring structured variation and resampling randomly across all age classes. Following McNulty *et al*. (2006) and Singleton *et al*. (2012), this study employed the more conservative permutation test (model 1 above) in an attempt to capture true differences in the groups.

4.3 Results

4.3.1 Higher taxonomic level variation

Results for all comparisons at the subspecies level and higher are reported in Table 4.2. Not surprisingly, differences in adult shape using the global landmark dataset and each module were statistically significant at the level of genus and species (Table 4.2).

The results from ontogenetic vectors likewise show statistically significant differences at these levels with one exception: the functional neurocranial module at the species-level comparison ($p=0.063$). In contrast, there were few differences in the magnitudes of shape change. At the genus-level, statistically significant differences in magnitude of developmental change were found in the embryological modules basicranium ($p<0.001$) and in the functional modules basicranium ($p<0.001$), nasal ($p<0.001$), cervical musculature ($p<0.001$), and neurocranium ($p=0.021$). At the species-level, only the embryological viscerocranium ($p=0.022$) and the petrous functional module ($p=0.023$) were statistically significantly different in magnitude.

Pairwise comparison of adult morphology at the subspecies level were statistically different in the global cranium and all cranial modules except cervical musculature ($p=0.7767$). The pattern of ontogenetic shape change was statistically significant in the global dataset ($p=0.041$), as well as in four cranial modules: embryological modules neurocranium ($p=0.011$) and viscerocranium ($p=0.023$), and the functional modules orbit ($p=0.002$) and petrous ($p=0.002$). Statistically significant differences were found in the magnitude of shape change in the functional basicranium ($p=0.014$) and orbit ($p=0.009$).

Table 4.2: Results of statistical tests between groups at the genus, species, and subspecies levels. MANOVA results document statistical differences in adult morphology. Developmental trajectories were tested for differences in both angle (pattern of shape change) and magnitude (amount of shape change) using permutation tests with 1000 replicates. "Global" denotes results from all 148 landmarks; landmark subsets labeled either embryological (E) or functional (F) modules.

Comparison groups by cranial modules		Adult Shape MANOVA (Wilks' Λ)		Angular differences between ontogenetic trajectories		Vector length differences between ontogenetic trajectories	
		F-value	p-value	Angle	p-value	Difference	p-value
Pan – Gorilla							
	Global	191.59	**<0.0001**	18.18°	**<0.001**	0.00071	0.763
E	Basicranium	67.83	**<0.0001**	30.93°	**<0.001**	0.00217	**<0.001**
E	Neurocranium	87.60	**<0.0001**	29.72°	**<0.001**	0.00291	0.124
E	Viscerocranium	182.76	**<0.0001**	23.01°	**<0.001**	0.00139	0.357
F	Basicranium	52.11	**<0.0001**	35.77°	**<0.001**	0.00210	**<0.001**
F	Mastication	152.45	**<0.0001**	16.53°	**<0.001**	0.00011	0.963
F	Nasal	84.05	**<0.0001**	60.05°	**<0.001**	0.01053	**<0.001**
F	Cervical Musculature	44.14	**<0.0001**	70.87°	**<0.001**	0.00185	**<0.001**
F	Neurocranium	91.35	**<0.0001**	34.47°	**<0.001**	0.00160	**0.021**
F	Orbit	8.52	**<0.0001**	39.51°	**<0.001**	0.00060	0.375
F	Petrous	16.35	**<0.0001**	23.37°	**<0.001**	0.00018	0.598
P. troglodytes – P. paniscus							
	Global	45.63	**<0.0001**	13.03°	**<0.001**	0.00132	0.354
E	Basicranium	14.02	**<0.0001**	32.30°	**<0.001**	0.00034	0.326
E	Neurocranium	17.65	**<0.0001**	18.83°	**<0.001**	0.00309	**0.034**
E	Viscerocranium	32.96	**<0.0001**	15.76°	**<0.001**	0.00044	0.679
F	Basicranium	12.38	**<0.0001**	41.27°	**<0.001**	0.00013	0.807
F	Mastication	29.84	**<0.0001**	14.25°	**<0.001**	0.00088	0.550
F	Nasal	7.28	**<0.0001**	35.01°	**0.030**	0.00277	0.073
F	Cervical Musculature	7.66	**<0.0001**	36.40°	**<0.001**	0.00004	0.999
F	Neurocranium	11.90	**<0.0001**	22.19°	0.063	0.00093	0.188
F	Orbit	15.47	**<0.0001**	22.98°	**<0.001**	0.00126	0.192
F	Petrous	8.10	**<0.0001**	24.41°	**<0.001**	0.00082	**0.023**

P. t. troglodytes – P. t. schweinfurthii

	Global	19.83	**<0.0001**	11.35°	**0.041**	0.00842	0.473
E	Basicranium	37.82	**<0.0001**	35.57°	0.096	0.00068	0.030
E	Neurocranium	8.26	**<0.0001**	14.45°	**0.011**	0.00085	0.557
E	Viscerocranium	10.70	**<0.0001**	17.99°	**0.023**	0.00928	0.435
F	Basicranium	25.96	**<0.0001**	45.90°	0.061	0.00131	**0.014**
F	Mastication	2.78	**0.0213**	12.10°	0.046	0.00152	0.280
F	Nasal	157.81	**<0.0001**	35.39°	0.653	0.00379	0.078
F	Cervical Musculature	0.05	0.7767	24.88°	0.391	0.00079	0.456
F	Neurocranium	3.92	**0.0023**	19.28°	0.502	0.00016	0.734
F	Orbit	12.86	**<0.0001**	32.50°	**0.002**	0.00192	**0.009**
F	Petrous	13.53	**<0.0001**	31.06°	**0.002**	0.00036	0.494

4.3.2 Population-level variation

Three population-level comparisons were made, within *Pan troglodytes troglodytes* (Abong Mbang vs. Ebolowa), *P. paniscus paniscus* (Ilima vs. Ubundu), and *Gorilla beringei graueri* (highland vs. lowland). Results of these tests are reported in Table 4.3. Shape differences associated with significantly different developmental trajectories are illustrated in Figures 4.2 and 4.4. Using the global landmark dataset, neither adult morphology, the angles of ontogenetic trajectories nor magnitudes of shape differences were statistically significant for these lower taxonomic comparisons. However, some functional/embryological modules were significantly different (Table 4.3; Figures 4.2 and 4.4)

Between the two populations of *Pan troglodytes troglodytes*, Abong Mbang and Ebolowa chimpanzees showed statistically different adult shapes (p=0.0195) and statistically different pattern of ontogenetic shape change (p=0.003) in the cervical musculature functional module (Figures 4.2 and 4.3). In the magnitude of shape change,

statistically significant difference was reached in the nasal (p=0.012) module. The adult phenotypic differences between these two populations include a wider and more robust nuchal region (Figure 4.2).

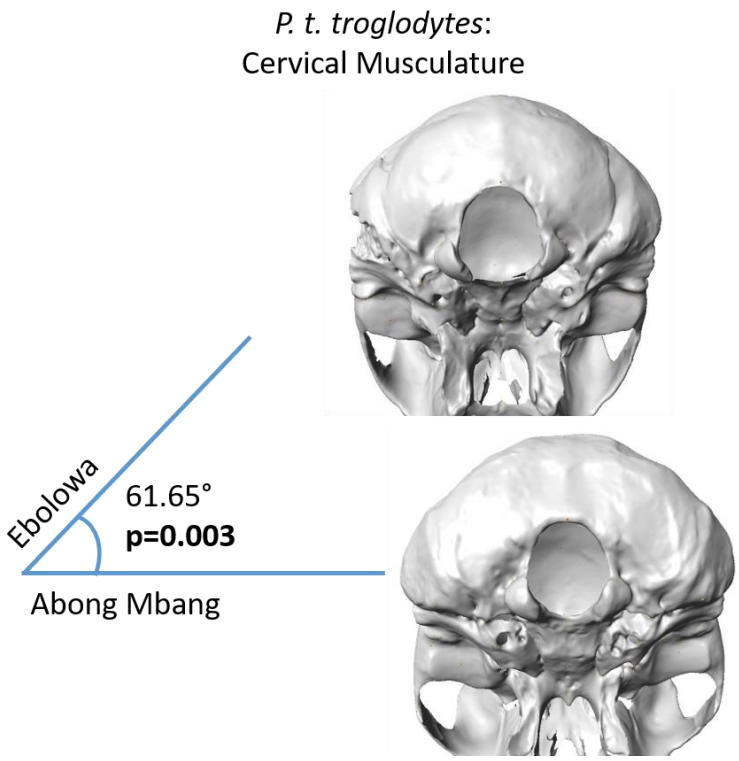

Figure 4.2: Representative adult individuals near the mean shapes in the cervical musculature module between *Pan troglodytes troglodytes* populations.

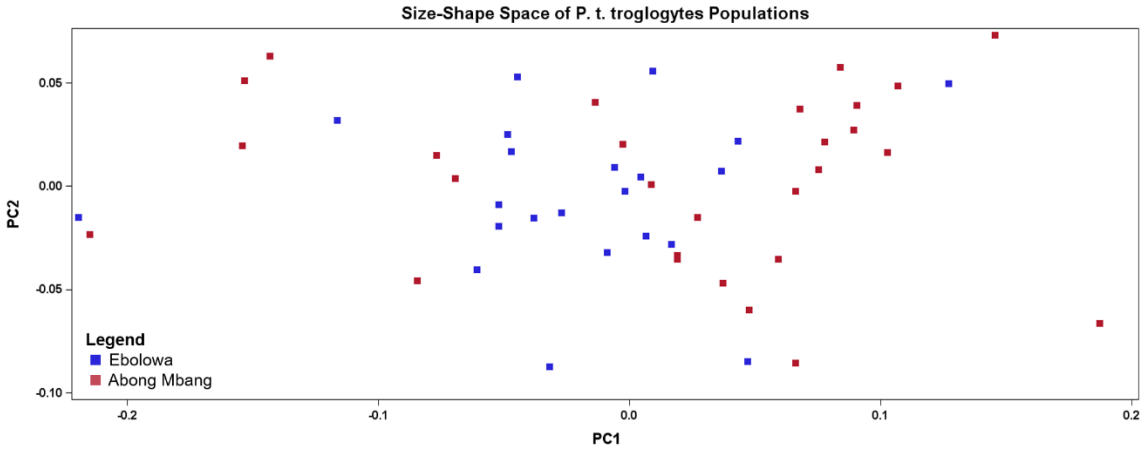

Figure 4.3: Size-shape space of the cervical muscular module in populations of *Pan troglodytes troglodytes*

In populations of *Pan paniscus*, Ilima and Ubundu show statistical differences in adult morphology in two cranial modules: the embryological viscerocranium and the functional nasal module. Ontogenetically these populations differ statistically in the pattern of development in the basicranial (p=0.008) and masticatory functional modules (p=0.022). The magnitude of shape change was found to be statistically different in only the nasal (p=0.014) functional module (Figures 4.4 and 4.5). Ilima has a wider basicranium relative to Ubundu. The zygomatic is flatter anteriorly in Ubundu than Ilima bonobos, but those from Ilima have rounder, less pear-shaped nasal apertures (Figure 4.4).

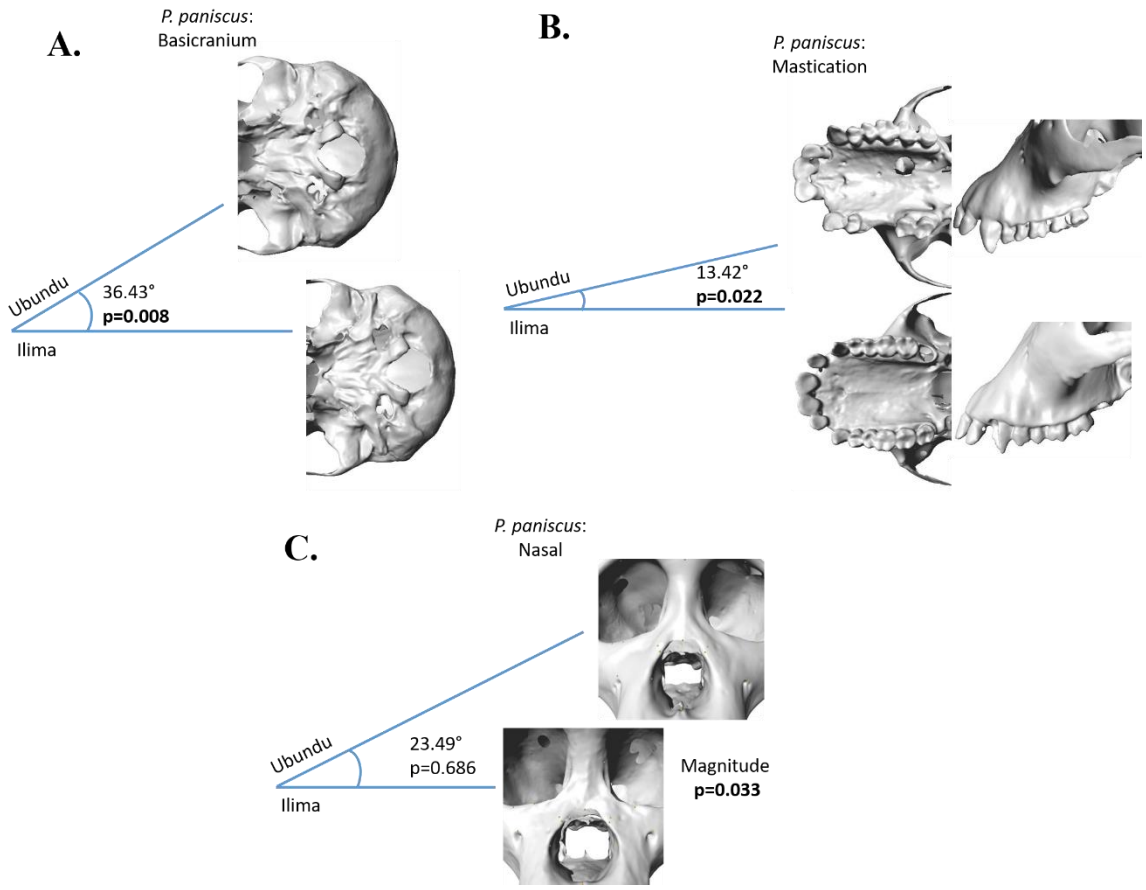

Figure 4.4: Representative individuals near the mean adult shapes for each of the statistically significant trajectories in *Pan paniscus*. A. Adult differences in the basicranium module. B. Adult differences in the mastication module. C. Adult differences in the nasal module.

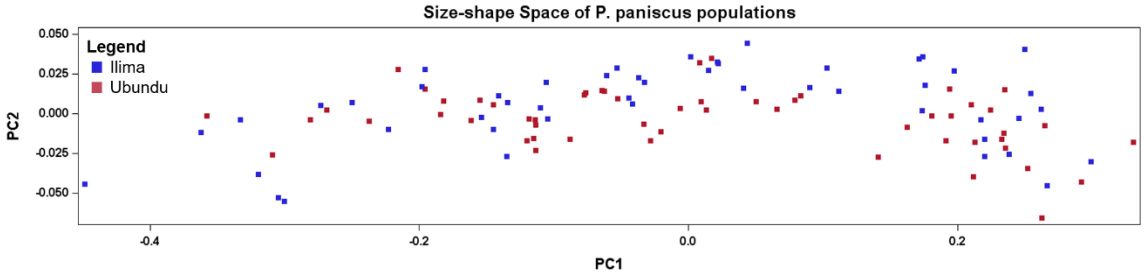

Figure 4.5: Size-shape space of the mastication module in populations of *Pan paniscus*

The demic-level differences in *Gorilla beringei graueri* between highland and lowland populations were statistically significant in five of the adult cranial modules: the basicranial (p=0.0085) and viscerocranial (p=0.0094) embryological modules, and the basicranial (p=0.0104), masticatory (p=0.0124), and nasal (p=0.0169) functional modules. However, neither the angles nor magnitudes of developmental trajectories were found to be statistically different.

Table 4.3: Results of statistical tests at the locality/deme level. MANOVA results document statistical differences in adult morphology. Developmental trajectories were tested for differences in both angle (pattern of shape change) and magnitude (amount of shape change) using permutation tests with 1000 replicates. "Global" denotes results from all 148 landmarks; landmark subsets labeled either embryological (E) or functional (F) modules.

Comparison groups by cranial modules		Adult Shape MANOVA (Wilks' Λ)		Angular differences between ontogenetic trajectories		Vector length differences between ontogenetic trajectories	
		F-value	p-value	Angle	p-value	Difference	p-value
***P. t. troglodytes*: Abong Mbang – Ebolowa**							
	Global	2.21	0.3584	13.08°	0.921	0.00092	0.933
E	Basicranium	2.71	0.0558	39.03°	0.693	0.00021	0.934
E	Neurocranium	2.45	0.0546	15.06°	0.746	0.00191	0.546
E	Viscerocranium	0.72	0.7386	17.12°	0.987	0.00159	0.724
F	Basicranium	2.41	0.0613	44.367°	0.694	0.00051	0.750
F	Mastication	1.90	0.1521	12.55°	0.992	0.00140	0.749
F	Nasal	1.35	0.2815	32.10°	0.824	0.00459	**0.012**
F	Cervical Musculature	3.63	**0.0195**	61.65°	**0.003**	0.00141	0.634
F	Neurocranium	0.95	0.5194	21.84°	0.989	0.00041	0.999
F	Orbit	0.46	0.8960	23.37°	0.947	0.00681	0.052
F	Petrous	0.36	0.8940	17.94°	0.665	0.00108	0.343
***P. paniscus*: Ilima – Ubundu**							

	Global	2.20	0.1311	10.66°	0.173	0.00091	0.389
E	Basicranium	2.65	0.0728	27.21°	0.090	0.00043	0.242
E	Neurocranium	2.61	0.0572	15.51°	0.070	0.00086	0.334
E	Viscerocranium	4.12	**0.0154**	14.39°	0.222	0.00052	0.627
F	Basicranium	2.75	0.0581	36.43°	**0.008**	0.00022	0.501
F	Mastication	2.81	0.0541	13.42°	**0.022**	0.00057	0.675
F	Nasal	4.78	**0.0046**	23.49°	0.686	0.00214	**0.014**
F	Cervical Musculature	1.09	0.3992	9.63°	0.928	0.00070	0.440
F	Neurocranium	0.82	0.5834	19.37°	0.990	0.00086	0.239
F	Orbit	1.20	0.3770	11.69°	0.774	0.00088	0.322
F	Petrous	1.83	0.1493	13.92°	0.247	0.00347	0.111
***G. b. graueri*: Highland – Lowland**							
	Global	2.04	0.0801	14.17°	0.836	0.00351	0.348
E	Basicranium	3.11	**0.0085**	42.51°	0.498	0.00130	0.410
E	Neurocranium	2.06	0.0620	15.07°	0.598	0.00602	0.172
E	Viscerocranium	3.30	**0.0094**	16.66°	0.954	0.00215	0.346
F	Basicranium	3.07	**0.0104**	45.08°	0.809	0.00180	0.507
F	Mastication	3.05	**0.0124**	11.61°	0.989	0.00274	0.374
F	Nasal	0.50	0.8271	21.50°	0.930	0.00069	0.741
F	Cervical Musculature	0.91	0.4897	40.58°	0.216	0.00192	0.236
F	Neurocranium	2.80	**0.0169**	30.89°	0.585	0.00225	0.272
F	Orbit	0.49	0.8503	21.76°	0.658	0.00051	0.677
F	Petrous	2.29	0.0615	16.18°	0.631	0.00025	0.746

4.3.3 Variation between population samples and samples with unknown provenience

Finally, tests for ontogenetic variation between population-level divisions and specimens with unknown locality provenience are summarized in Table 4.4. The two populations of *Pan troglodytes troglodytes* were compared with an aggregate population of unknown locality *P. t. troglodytes* specimens, resulting in statistically significant differences in adult morphology for the global dataset and for many of the cranial modules (all but the petrous modules for both populations). In Abong Mbang

chimpanzees, the pattern of shape change differed significantly in the embryological basicranium (p=0.032). No module reached significance in the magnitude of shape differences. In Ebolowa, the pattern of shape change differed significantly in the functional cervical musulature (p=0.034) and the magnitude of shape change differed significantly in the orbit (P=0.032).

Few differences were found between the *P. paniscus* populations and the aggregate sample. For Ilima, differences were found between adults in functional basicranial shape (p=0.0248), and in the pattern of ontogenetic shape change in the same module (p=0.003). There was a statistically significant difference in the magnitude of shape change in the nasal functional module (p=0.034). Ubundu bonobos only differed from the aggregate in the adult morphology of the nasal complex (p=0.0189). No differences were found between the pattern of shape change or the magnitude of shape differences.

Table 4.4: Results of statistical tests between groups and the aggregate sample. MANOVA results document statistical differences in adult morphology. Developmental trajectories were tested for differences in both angle (pattern of shape change) and magnitude (amount of shape change) using permutation tests with 1000 replicates. "Global" denotes results from all 148 landmarks; landmark subsets labeled either embryological (E) or functional (F) modules.

Comparison groups by cranial modules	Adult Shape MANOVA (Wilks' Λ)		Angular differences between ontogenetic trajectories		Vector length differences between ontogenetic trajectories	
	F-value	p-value	Angle	p-value	Difference	p-value
***P. t. troglodytes*: Abong Mbang – Aggregate**						
Global	35.40	**<0.0001**	14.36°	0.124	0.00154	0.532

E	Basicranium	45.23	<**0.0001**	49.26°	**0.032**	0.00038	0.610
E	Neurocranium	33.17	<**0.0001**	13.36°	0.806	0.00136	0.506
E	Viscerocranium	3.70	**0.0027**	21.45°	0.181	0.00136	0.555
F	Basicranium	50.96	<**0.0001**	71.33°	0.350	0.00026	0.678
F	Mastication	3.05	**0.0089**	16.08°	0.069	0.00084	0.734
F	Nasal	23.36	<**0.0001**	23.87°	0.966	0.01282	0.082
F	Cervical Musculature	3.15	**0.0262**	54.65°	0.552	0.00009	0.965
F	Neurocranium	19.05	<**0.0001**	35.52°	0.518	0.00057	0.767
F	Orbit	4.77	**0.0008**	46.69°	0.214	0.00055	0.834
F	Petrous	1.15	0.3557	23.83°	0.993	0.00086	0.420
***P. t. troglodytes*: Ebolowa – Aggregate**							
	Global	24.35	<**0.0001**	17.14°	0.240	0.00054	0.941
E	Basicranium	38.83	<**0.0001**	46.16°	0.492	0.00080	0.633
E	Neurocranium	18.14	<**0.0001**	19.20°	0.622	0.00074	0.793
E	Viscerocranium	9.90	<**0.0001**	18.31°	0.948	0.00293	0.369
F	Basicranium	47.62	<**0.0001**	90.13°	0.185	0.00021	0.918
F	Mastication	5.12	**0.0007**	15.84°	0.421	0.00058	0.849
F	Nasal	17.70	<**0.0001**	32.56°	0.912	0.01661	0.073
F	Cervical Musculature	3.79	**0.0138**	76.50°	**0.034**	0.00067	0.910
F	Neurocranium	16.53	<**0.0001**	43.09°	0.503	0.00027	0.857
F	Orbit	5.97	**0.0003**	41.82°	0.770	0.00605	**0.032**
F	Petrous	0.19	0.9636	38.08°	0.863	0.00191	0.436
***P. paniscus*: Ilima – Aggregate**							
	Global	2.38	0.1455	10.82°	0.658	0.0001	0.924
E	Basicranium	2.39	0.1249	33.40°	0.118	0.0007	0.176
E	Neurocranium	0.92	0.5454	13.61°	0.548	0.0005	0.788
E	Viscerocranium	1.78	0.1965	15.78°	0.581	0.0004	0.669
F	Basicranium	4.17	**0.0248**	44.52°	**0.003**	0.0005	0.284
F	Mastication	0.66	0.7544	13.39°	0.357	0.0008	0.590
F	Nasal	2.09	0.1135	32.38°	0.524	0.0021	**0.034**
F	Cervical Musculature	0.84	0.5384	19.87°	0.431	0.0002	0.813
F	Neurocranium	0.43	0.8449	22.11°	0.904	0.0007	0.363
F	Orbit	2.63	0.0603	19.05°	0.169	0.0007	0.375
F	Petrous	1.00	0.4733	16.41°	0.212	0.0003	0.460
***P. paniscus*: Ubundu – Aggregate**							

	Global	1.09	0.4772	9.62°	0.508	0.0008	0.485
E	Basicranium	0.93	0.5713	24.64°	0.807	0.0002	0.463
E	Neurocranium	1.64	0.2151	14.66°	0.141	0.0004	0.777
E	Viscerocranium	1.22	0.3876	13.58°	0.408	0.0010	0.469
F	Basicranium	1.44	0.3102	25.85°	0.799	0.0003	0.405
F	Mastication	1.45	0.3035	10.64°	0.439	0.0014	0.273
F	Nasal	3.64	**0.0189**	28.78°	0.229	0.0000	0.999
F	Cervical Musculature	0.71	0.6269	18.39°	0.484	0.0009	0.432
F	Neurocranium	1.50	0.2427	26.88°	0.188	0.0002	0.913
F	Orbit	1.97	0.1362	14.85°	0.722	0.0001	0.854
F	Petrous	0.86	0.5568	15.92°	0.235	0.0001	0.670

4.4 Discussion

4.4.1 Variability in ontogenetic trajectories

The above analyses show variability in morphological ontogeny at all levels of taxonomy. This variability exhibits itself in the global cranial dataset (the cranium as a whole) as well as discrete cranial modules representing embryological and functional anatomies. In every pairwise comparison of populations except one, statistically significant differences were found in the ontogenetic trajectories. These differences, which lead to adult morphological differences, manifested in both the pattern of development and the magnitude of shape difference. The exception is that of the demic-level analysis of *Gorilla beringei graueri*. Here, five of the ten cranial modules significantly differed in adult morphology (Table 4.3), but this was not mirrored by differences in their ontogenetic trajectories. The statistically significant results for the adult morphology echoes the results in Pilbrow (2003, 2010) and Knigge and colleagues (2014) who also found adult differences in molar morphometrics and talar morphology

along an elevation gradient, respectively. However, one potential reason this study could not find statistically significant differences in the ontogenetic trajectories leading to these adult shapes might be statistical power in the youngest age classes.

For the most part, the expectation that ontogeny plays a role in the formation of adult morphological differences is confirmed here. These results show that adult differences seen at many taxonomic levels, including the population-level (Groves 1970, 2003, 2005, Shea *et al.*, 1993; Sarmiento and Oates, 2000; Grubb *et al*., 2003; Albrecht *et al*, 2003; Miller *et al*, 2004; Gonder *et al*., 2006), are acquired in part by ontogenetic differences in the pattern and magnitude of shape change. This study echoes work done on ontogenetic variation in human populations (O'Higgins and Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al*., 2002; Strand Viðarsdóttir and O'Higgins, 2003).

This study has also shown that the aggregation of specimens into genus-, species-, and subspecies-level groupings can create ontogenetic representations that are statistically different from samples taken from known, coherent populations. In particular, the basicranium, neurocranium, nasal, and cervical musculature modules were shown to vary between pooled samples and those from individual localities. The reason for grouping ontogenetic samples into larger amalgamations is clear: increased sample sizes tend to yield more robust statistical results. However, statistically significant differences are not meaningful if they are based on shapes or ontogenetic models that lack biological valence. Studies that collect specimens without regard to population history are at risk of having inconsistent amounts of ontogenetic variation in analog samples.

4.4.2 The relationship of ontogenetic trajectories and differing life histories

Drawing connections between morphological disparity and causes of variation can be difficult. However, morphological variation among adults within these populations seems to manifest itself most consistently in the face and muscular attachment sites (masticatory apparatus, nasal region, and cervical musculature). Avenues of further research should investigate the behavioral or ecological underpinnings that might allow these regions to differ ontogenetically.

It seems likely that differing morphological ontogenetic trajectories are related to differing life history strategies based on ecological pressures imposed on organisms. As Jones (2011) argued, an organism's ontogenetic rate is related to ecological variables such as seasonality and distribution of food resources (also see Janson and van Schaik's [1993] hypothesis on ecological risks). Jones (2011) argues that the speed of primate life histories can be explained by the tendency of primates to specialize in high-quality food items, which makes them susceptible to environmental variability.

For example, because gorillas eat temporally and spatially consistent vegetation, they can afford to grow quickly. Faster rates of growth can be sustained on a lower quality diet if the food is abundant and predicable, spatially and temporally (which is the case for leaves and grasses; Leigh, 1994; Marlowe, 2010). Orangutans, on the other hand, rely on mast fruiting events interspersed with long periods of scarcity (Jaeggi et al., 2010; Jones, 2011). Therefore, orangutans follow a "safer" strategy by developing more slowly so that they do not face extended growth when high-quality foods are unavailable. Chimpanzees, like orangutans, are ripe fruit specialists, though their resources are much

less seasonal. This allows their life histories to be faster than orangutans, though still slower than gorillas.

Marlowe (2010) came to a similar conclusion, that a higher-energy diet results in faster growth. The Hadza grow much more slowly (and to a much smaller body size) than do people in industrial societies (Marlowe, 2010). Marlowe (2010) attributes the faster rate of growth among western societies to the higher quality diet which is available year-round. Hill and Kaplan (1999) have also noted the tendency for "well-fed" populations to grow to maturity faster than others. On average, Ache children adopted by American families grow quicker and to a taller height than comparably aged Ache (Walker and Hill, 2003).

Further evidence that food abundance and quality affect the timing of life history comes from comparisons of wild and captive primates as well as human populations. Borries and colleagues (2001) found that when looking at two populations of *Semnopithecus entellus*, the population with relatively poor nutritional conditions prolonged age at first birth, gestation period, lactation periods and interbirth interval; which has culminated in a more than 50 percent reduction in reproductive rate. Analysis of captive versus wild growth rates in primates has shown that dental emergence rates are accelerated in captive animals where food can be found in abundance (Zihlman and Bolter, 2004; Kelly and Schwartz, 2010; Bolter and Zihlman, 2011). The ideas in Jones (2011) and others (*e.g.*, Janson and van Shaik, 1993; Pontzer *et al.*, 2010, 2012) can be applied to lower levels of taxonomy as well as at the subfamily and genus levels.

This study has shown that there is a statistically significant amount of variation in populations of *Gorilla* and *Pan* in the pattern and magnitude of cranial *development.*

There are multiple ways to achieve divergent adult anatomy. An alteration in the rate and duration of growth and an alteration in the pattern and magnitude of development can achieve very different morphologies. If we can extend the conclusions of Jones (2011) and others studying the ecological variables leading to growth [*e.g.*, Leigh, 1994; Hill and Kaplan, 1999; Borries and colleagues, 2001; Zihlman and Bolter, 2004; Marlowe, 2010; Kelly and Schwartz, 2010; Bolter and Zihlman, 2011) to lower, population-level taxonomy, then perhaps ecological variables are also attributing to the changes in ontogeny presented here. Thus, variation found in this study's cranial modules among these populations point to important new avenues of research for understanding morphological changes that are tied to differing ecological pressures.

4.5 Conclusion

This study has shown that variation in ontogenetic trajectories is anticipated by variation in adult morphology at all levels of taxonomy. This holds true at higher, traditional taxonomy (genus, species) and lower, population-level taxonomy (subspecies, locality). Further, these lower-level differences seem to more consistently manifest in the face and muscular attachments. Finally, this study has shown that aggregate samples taken from multiple museum visits (in order to create larger sample sizes) underestimate the amount of variation in adult morphology and ontogenetic trajectories, in at least aspects of the cranium.

Since well before Darwin, the study of ontogeny and ontogenetic variation has played a central role in our understanding of evolutionary transformations. While such work fell out of favor, Gould helped reintroduced and popularized the study of growth

and development and its importance to study biological change. Since this time, numerous studies have contributed to the study of ontogeny in the extant and extinct primates (*e.g.*, Shea, 1983a, b, 1989; Dean *et al*., 1986, 1993; Bromage and Dean, 1991; Beynon and Dean, 1991; Godfrey and Sutherland, 1995; Leigh and Shea, 1995, 1996; Skinner 1997; Stringer and Dean, 1997; Beynon *et al*., 1998; O'Higgins and Jones, 1998; O'Higgins and Strand Viðarsdóttir, 1999; Mitteroecker *et al.*, 2004a,b, 2005; Raff, 2007; Lieberman *et al*., 2007; Bolter and Zihlman, 2011, 2012). This study has shown that the variation seen in African ape adult morphology (Groves 1970, 2003, 2005; Shea *et al.*, 1993; Sarmiento and Oates, 2000; Grubb *et al*., 2003; Albrecht *et al*, 2003; Miller *et al*, 2004; Gonder *et al*., 2006) comes, as least in part by variation in the ontogenies. Further, this variation can be seen at all levels of traditional taxonomy as well as lower-level population taxonomy. The conclusions drawn here second studies of human population ontogenetic differences (O'Higgins and Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al*., 2002; Strand Viðarsdóttir and O'Higgins, 2003).

Further, these lower-level differences seem to more consistently manifest in the face and muscular attachments (masticatory apparatus, nasal region, cervical musculature). Although variation seen in the pattern and magnitude of development in aspects of the cranium among populations of organisms are difficult to correlate directly to behavioral and/or ecological variables, future avenues of research should be directed to understand the significance of altering these aspects of anatomy ontogenetically to produce distinct adult morphology.

Further, samples that pool specimens from genetically and morphologically distinct populations may be missing the potential variation in population taxonomy and

may compare our fossils to poorly calibrated "yardsticks" (cf. Miller *et al*., 2004). In some aspects of cranial anatomy, this study found that there are statistically significant differences between known provenience samples and aggregate samples mimicking larger datasets derived from visiting many museum samples. As evolutionary change in ontogenetic trajectories is estimated using juvenile fossils, it is our hope that this study will better inform researchers of human evolution about the developmental and functional implications of growth. Namely, aspects of ontogeny can be significantly variable at every level of taxonomy. Further, fossils, sparsely distributed through space and time, add more uncertainty to estimation of growth and development. Therefore, caution should be taken when comparing fossil species to any ontogenetic sample that pools morphologically and genetically distinct populations.

5 The ontogeny of sexual dimorphism

The previous chapter identified ontogenetic variation in female crania at taxonomic levels below that of species. Those results indicate that species-level generalizations of growth and development fail to capture the complexity of ontogeny within the organisms we study, and potentially create artificial models of development through averaging significantly different processes. This is similar to results from human populations (O'Higgins and Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al*., 2002; Strand Viðarsdóttir and O'Higgins, 2003), but the ubiquity of humans in every environment raises questions about whether that degree of variation might be found in ape species with distributions that more closely approximate those of our fossil ancestors. This study highlights a concept anticipated, but largely ignored in the literature: the process of ontogeny is to some degree an adaptation to the ecological variables acting on a population – not a biological constant of a species.

Further, the previous chapter showed that amalgamations of specimens with unknown provenience or from multiple populations (specimens grouped together from museum samples without regard to genetically and morphologically distinct populations), can, at least in some aspects of anatomy, mask the amount of variation in a sample. Therefore, the consequence of studying ontogeny without regard to population history is a misrepresentation of ape ontogeny, which in turn impacts our interpretations of evolutionary development in fossil lineages.

One of the fundamental sources of species variations, manifest even at the smallest population levels, is sexual dimorphism. The next chapter specifically investigates how sexually dimorphic features are obtained through ontogeny. Secondary sexually dimorphic features do not arise until well after weaning in primates. In fact, Cobb and O'Higgins (2007) showed that sex-specific divergence in cranial morphology manifests after the eruption of the second molar. Thus, from the infant state, males and females share an essentially monomorphic cranial morphology. This difference in adult morphology is often attributed to particular competition strategies employed by males and, by proxy, the socioecological roles males and females play in their group system.

In mammals, one sex is typically more robust or has a larger body size than the other. There are multiple ways a species can achieve sexually dimorphic morphology: a change in the pattern of shape change, a change in the magnitude of shape change, or a change in the rate and duration of growth. Morphometrically, these can be calculated as the multivariate angle of the ontogenetic trajectories, the magnitudes of the ontogenetic trajectories, and the timing at which anatomy becomes mature. The following chapter investigates the multivariate angle and magnitude of development in the crania of Karisoke mountain gorillas and Gombe chimpanzees.

6 The ontogeny of cranial sexual dimorphism among individuals housed at Karisoke Research Center and Gombe National Park

6.1 Introduction

African apes are our closest living relatives. Understanding their biology is imperative as they are used as analog species for studying human evolution. One characteristic in which African apes more closely resemble our hominin ancestors than do modern humans is the degree of size and shape sexual dimorphism. Sexual dimorphism and ontogeny have been studied for many aspects of anatomy including body mass (McHenry, 1992, 1994; Leigh and Shea 1995, 1996; Ruff, 2002; Plavcan, 2012; Fragaszy *et al*., 2015), canine size (Plavcan *et al*., 1995; Schwartz and Dean, 2001; Leigh *et al.*, 2005), coloration (Breuer *et al*., 2007), postcranial anatomy (Taylor, 1997; Berdnikovs *et al*., 2007; Bastir *et al*, 2014; Garcia-Martinez *et al.*, 2016), and skull morphology (Richtsmeier *et al.*, 1993; Lockwood, 1999; Plavcan, 2002; del Castillo *et al*., 2014; Loza *et al.*, 2015; Holton *et al.*, 2016).

The interaction between ontogeny and sexual dimorphism, or how ontogeny mediates sexual dimorphism, has likewise been studied on various aspects of anatomy. Schaefer and colleagues (2004) assessed ontogenetic pattern and magnitude of sexual dimorphism in African apes and found that ontogenetic scaling contributes to the development of sexual dimorphism in apes. Cobb and O'Higgins (2007) likewise tested

the contribution of ontogeny to sexual dimorphism. They showed that sexual dimorphism is not present early in development but rather manifests after the eruption of the second permanent molar (Cobb and O'Higgins, 2007). Because the presence of cranial secondary sexual characteristics seems to be mediated through post-natal ontogeny, it is appropriate to study the acquisition of these features via geometric morphometric techniques on post-natal skeletal collections.

In a study of body mass from captive African apes, Leigh and Shea (1995, 1996; also Shea, 1985, 1986; Leigh, 1992, 1995) concluded that sexual dimorphism in chimpanzees and gorillas is mediated through fundamental differences in ontogenetic timing (*i.e.*, heterochrony): *Pan troglodytes* achieves dimorphism through differential rates of growth (rate hypermorphosis), whereas sexual dimorphism in *Gorilla gorilla* is obtained through time hypermorphosis (bimaturism), or differential durations of growth (*i.e.*, males grow longer than females). They report that these differences may be due to differing life histories brought about by differentiation of ecological risks and male competition, a model provided by Janson and and van Schaik (1993) (but see alternative theories presented by Watts and Pusey, 1993; Jones, 2011; and Pontzer, 2010, 2012). Additional analysis of an expanded number of taxa revealed similar results with multimale/multifemale groups (*e.g.*, *Saimiri sciureus*, *Cebus apella*, *Cercopithecus aethiops*, *Cercocebus atys*, *Macaca*, and *Papio hamadryas papio*) showing bimaturism, whereas single-male or community groups (*e.g.*, *Cercopithecus diana*, *Cercopithecus mitis*, *Cercopithecus negletctus*, *Erythrocebus patas*, *Mandrillis sphinx*, *Colobus guereza*, *Presbytis entellus*, *Presbytis obscura*) exhibit rate dimorphism (Leigh, 1995).

In an analysis of postcranial elements, Taylor (1997) found that male gorillas exhibit a growth spurt later in development than do females, indicating that changes in both duration and rate contribute to the acquisition of sexual dimorphism. Schwartz and Dean (2001) investigated rate and duration of canine size dimorphism and found that all species studied (great apes including humans) exhibit mainly bimaturism with little evidence of rate hypermorphosis. Finally, McFarlin and colleagues (2013) presented growth data for brain size for *G. b. beringei* skeletal materials housed at Karisoke Research Center. Sexual dimorphism in brain size growth in this population appears to be a consequence of both bimaturation and rate hypermrophosis.

Together, these studies indicate that sexual dimorphism is likely the result of multiple ontogenetic processes operating across modular anatomical systems. Given the complex functional and structural demands on the cranium (as a host for most sense organs, a conduit for cranial nerves, the anterior opening for both digestive and respiratory tracts, and the housing of the brain), there is no reason to expect the adult cranium is the result of a single ontogenetic process (Mitteroecker *et al*., 2004b). In fact, multivariate ontogenetic trajectories diverge when *aspects* of the anatomy (not the entire cranium) differ ontogenetically (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Mitteroecker *et al*, 2004a,b, 2005; Liebermann *et al*, 2007; Hallgrimsson *et al*., 2007a, b). However, the cranium must nevertheless encompass extensive morphological variation while maintaining these crucial functions. Understanding how ontogeny mediates cranial sexual dimorphism in this regard is important for understanding the relationships of modular units that retain an integrated functionality.

There are multiple ways to achieve sexual dimorphism. Many studies have relied on rate and duration of growth (Leigh and Shea 1995; 1996; Shea, 1985, 1986; Leigh, 1992, 1995 Taylor, 1997; Schwartz and Dean 2001; McFarlin *et al*., 2013), while others have studied pattern and magnitude of development (*e.g.*, Schaefer *et al*., 2004; Cobb and O'Higgins, 2007). The present study tests how ontogeny mediates cranial shape sexual dimorphism by assessing differences in the patterns and magnitudes of male and female developmental vectors. Utilizing wild populations of gorillas and chimpanzees with known ages of death (*Gorilla beringei beringei* from Volcanoes National Park, Rwanda; *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania), ontogenetic trajectories were tested globally for the entire cranium, as well as regionally using embryological and functional cranial modules.

6.2 Materials and Methods

6.2.1 Study sample

This study utilized a sample from two African ape populations (Gombe National Park, Tanzania and Volcanoes National Park, Rwanda), which have been the focus of behavioral research since the 1960s (Table 6.1). Therefore, individuals housed in the skeletal collections from these study sites retain a wealth of information regarding behavior, ecology, diet, and – importantly for studies of ontogeny – known ages at death. This last datum allows for ontogenetic analyses to be conducted on both chronological age as well as age proxies such as overall size (*e.g.*, log centroid size) and dental development. Unknown aged specimens of *Pan troglodytes schweinfurthii* were collected

from the Royal Museum for Central Africa, Belgium to supplement the sample sizes at the youngest ages classes (Table 6.1).

Table 6.1: Profile of sample. Sample size for mountain gorillas and eastern chimpanzees divided into age classes based on dental eruption: dP4 = deciduous dentition in occlusion, M1 = first molar in occlusion, M2 = second molar in occlusion, M3 = third molar in occlusion. Parentheses denote the number of individuals with known age at death for Karisoke mountain gorillas (*G. b. beringei*) and Gombe chimpanzees (*P. t. schweinfurthii*).

Taxon	**Sex**	**dP4**	**M1**	**M2**	**M3**	**Total**
G. b. beringei						
	Male	3 (3)	4 (2)	0	14 (7)	**21 (12)**
	Female	3 (3)	3 (2)	0	21 (9)	**27 (14)**
P. t. schweinfurthii						
	Male	4 (3)	2 (1)	9 (5)	(14)	**29 (23)**
	Female	2	4	8 (1)	28 (20)	**42 (21)**
Total						**119 (70)**

6.2.2 Data collection

Specimens were digitized with a Breuckmann SmartScan^{3D} white light scanner. The raw data were then imported into Geomagic Design X (3D Systems, Inc, 2017) to be aligned and merged into one mesh. Minor defects in the mesh were corrected or eliminated before exporting the models for further data collection. Finalized 3D models were landmarked in Stratovan Checkpoint (Figure 6.1; Stratovan Corp, 2016; Bookstein, 1991). This study employed 148 landmarks in order to sample the cranial anatomy of interest (Figure 6.1, Table 11.1). Traditional landmarks were chosen based on previously published material (Frost, 2001; Harvati, 2001; McNulty, 2003; Baab, 2007; Terhune *et*

al., 2007; White *et al*., 2012) with additional landmarks added for the purposes of this study.

The Geomorph package in R (Adams *et al*., 2016) was used to estimate missing landmarks using thin-plate spline interpolation (Gunz *et al*., 2009). As is the case in geometric morphometrics, the raw coordinate data were subjected to a generalized Procrustes analysis to eliminate variation due to the landmark configuration's position, size, and orientation. All other statistical analyses were performed in SAS® software.

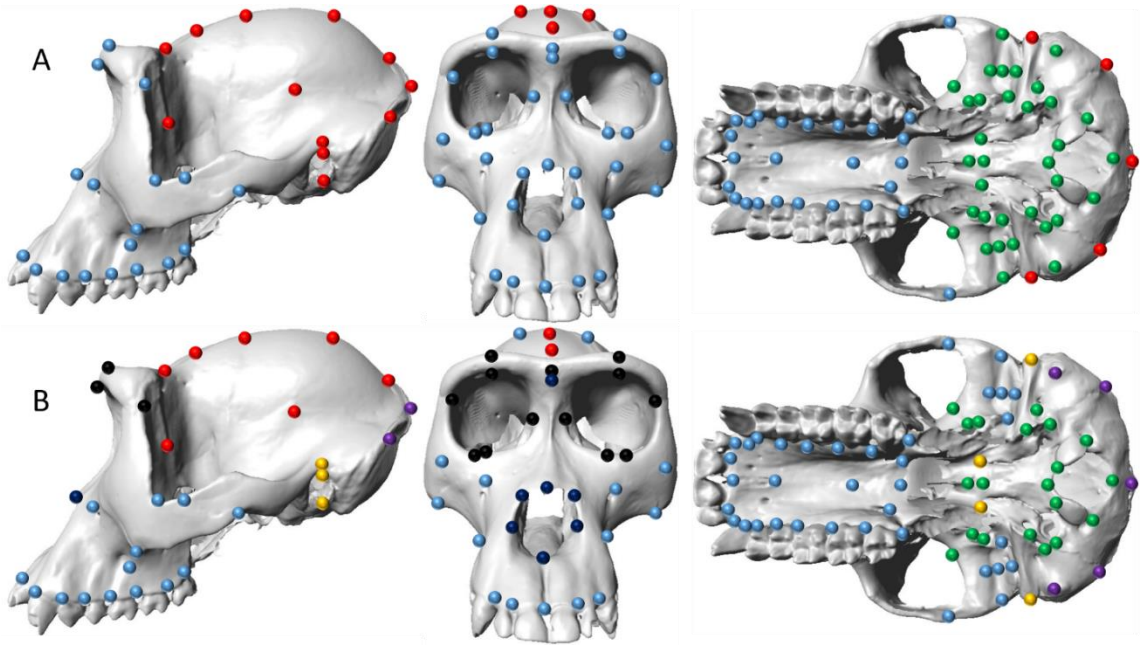

Figure 6.1: Landmark dataset. The global landmark dataset used all 148 landmarks. Analyses were repeated using anatomical subsets of these landmarks: A) Embryological units: blue = viscerocranium, red = neurocranium, green = basicranium. B) Functional units: green = basicranium. B) Functional units: green = basicranium, blue = mastication, dark blue = nasal, purple = cervical muscle attachments, red = neurocranium, black = orbit, yellow = petrous.

6.2.3 Statistical analyses

Pairwise differences between adult male and female group means were tested using multivariate analysis of variance (MANOVA). Mitteroecker and colleagues (2004a,b) showed that global (entire cranium) ontogenetic trajectories can diverge in shape space when, in fact, only one or a few regional aspects of anatomy actually differ. The modular nature of the skull (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Hallgrimsson *et al*., 2007a, 2007b) can confound studies of ontogeny and heterochrony in that results based on the global landmark datasets do not account for which aspects of anatomy create the observed morphological differences (Mitteroecker *et al*, 2004a; 2005; Liebermann *et al*, 2007). Therefore, this study employed analyses on the global dataset (utilizing the entire cranial landmark dataset) and on ten anatomical landmark subsets. These subsets (aligned and analyzed separately) were chosen to capture embryological and functional modules previously defined (Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Halgrímsson *et al*., 2007b; Goswami and Finarelli, 2016; Figure 6.1).

Analyses of ontogenetic trajectories were undertaken using a few different approaches. First, trajectory summaries were assessed by plotting samples in size-shape space, or the principal component ordination of the aligned coordinates with the natural log of centroid size (Mitteroecker *et al*., 2004a, 2005). Typically, the natural logarithm of centroid size (logCS) will have a much larger variance than GPA-aligned coordinates, and thus the first principal component will primarily summarize this variable plus landmark variation associated with size differences (Mitteroecker *et al.*, 2004a). For this

reason, visualizing specimen distributions in size-shape space is a useful method for assessing ontogenetic trajectories.

Developmental trajectories in each group were quantified by ordinary least-squares regression of shape variables on logCS to produce a vector of shape change corresponding to the direction of growth. Differences between the sex's developmental vectors were computed as the multivariate angle between them (arccosine of their vector dot-product), and tested using permutation tests (e.g., McNulty et al., 2006; Singleton et al., 2012). Differences between groups' magnitudes of development, or the amount of shape change, were computed as the absolute value difference in overall shape change from mean specimens in the youngest and oldest age categories, and likewise were tested with permutation tests.

Although permutation tests are commonplace in statistical analyses (see, *e.g.*, Good, 2006), including studies of landmark data (*e.g.*, O'Higgins and Strand Viðarsdóttir, 1999; O'Higgins *et al*., 2001; O'Higgins and Collard, 2002; Penin *et al*., 2002; Strand Viðarsdóttir *et al*., 2002; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Cobb and O'Higgins, 2007; Drake and Klingenberg, 2008; Rodriguez-Mendoza *et al*., 2011; Weisensee and Jantz, 2011; Klingenberg *et al*., 2012; Martin-Serra *et al*., 2014), this study specifically followed the resampling protocol outlined by McNulty *et al*. (2006). They demonstrated that in circumstances for which there is a dearth of observations representing some aspects of structured variation within a sample (*e.g.*, the youngest age classes in an ontogenetic study), simple models of permutation design are more likely to find statistically significant differences than models which resample with respect to that structured variation (McNulty *et al*., 2006). The current

study laid out three possible statistical designs for permutation tests: 1) resampling within age classes, constraining permuted groups to an equal number of specimens for each developmental stage; 2) resampling within age classes, but replicating in permuted groups the original (unequal) sample sizes at each age class; and, 3) ignoring structured variation and resampling randomly across all age classes. Following McNulty et al. (2006) and Singleton et al. (2012), this study employed the more conservative permutation test (model 1 above) in an attempt to capture true differences in the groups.

6.3 Results

6.3.1 Ontogenetic sexual dimorphism in Gorilla beringei beringei

Although there is a statistically significant difference between male and female adult morphology, the global cranium dataset did not show a statistically significant difference in the pattern of ontogenetic change (Figure 6.2; results are presented in Table 6.2).

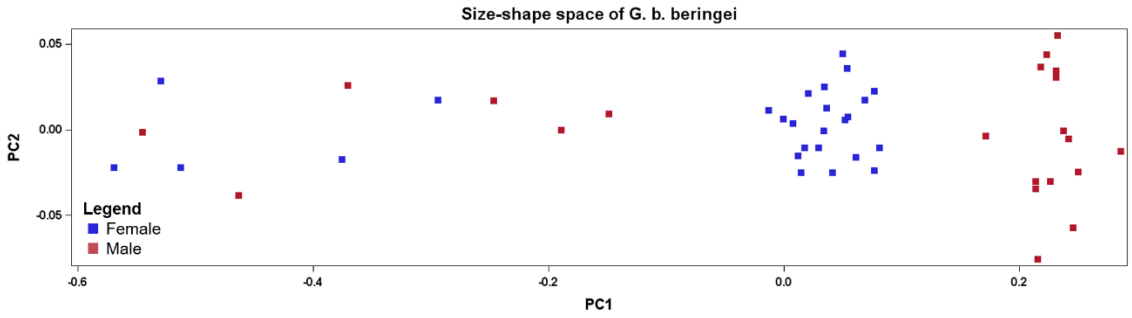

Figure 6.2: Size-shape space *of G. b. beringei* in the global landmark dataset.

Subsetting the landmark dataset into embryological and functional modules, however, does reveal statistically significant differences in the pattern and magnitude of shape change. The functional module cervical musculature displays a statistically significant difference in the pattern of development ($p=0.007$; Figure 6.3). Males display a wider, taller, and more robust nuchal region that consistently forms a compound crest with the sagittal crest (Figure 6.3). Differences in the magnitude of shape change (Figure 6.4) are evidenced by the neurocranium in both the functional ($p=<0.001$) and embryological ($p=0.047$) modules. Here, of course males are distinguished from females by having a sagittal crest, a compound nuchal crest, and deeper post-orbital sulcus (Figure 6.4).

Table 6.2: Results of statistical tests between sex of Karisoke mountain gorillas. MANOVA results document statistical differences in adult morphology. Developmental trajectories were tested for differences in both angle (pattern of shape change) and magnitude (amount of shape change) using permutation tests with 1000 replicates. "Global" denotes results from all 148 landmarks; landmark subsets labeled either embryological (E) or functional (F) modules.

Comparison sex by cranial modules		Adult Shape MANOVA (Wilks' Λ)		Angular differences between ontogenetic trajectories		Vector length differences between ontogenetic trajectories	
		F-value	p-value	Angle	p-value	Difference	p-value
	Global	15.65	**0.0036**	16.46°	0.864	0.00243	0.329
E	Basicranium	15.14	**0.0039**	27.18°	0.518	0.00123	0.332
E	Neurocranium	11.89	**0.0008**	22.10°	0.694	0.00227	**0.047**
E	Viscerocranium	21.22	**0.0048**	24.13°	0.531	0.00301	0.353
F	Basicranium	3.37	0.0763	25.83°	0.689	0.00138	0.410
F	Mastication	7.85	**0.0173**	20.30°	0.736	0.00293	0.378
F	Nasal	10.17	**0.0011**	33.12°	0.123	0.00133	0.294
F	Cervical Musculature	7..47	**0.0037**	54.97°	**0.007**	0.00259	0.184
F	Neurocranium	32.25	**<0.0001**	24.69°	0.186	0.00440	**<0.001**
F	Orbit	2.05	0.1805	22.13°	0.978	0.00017	0.879
F	Petrous	0.45	0.8303	23.18°	0.549	0.00158	0.055

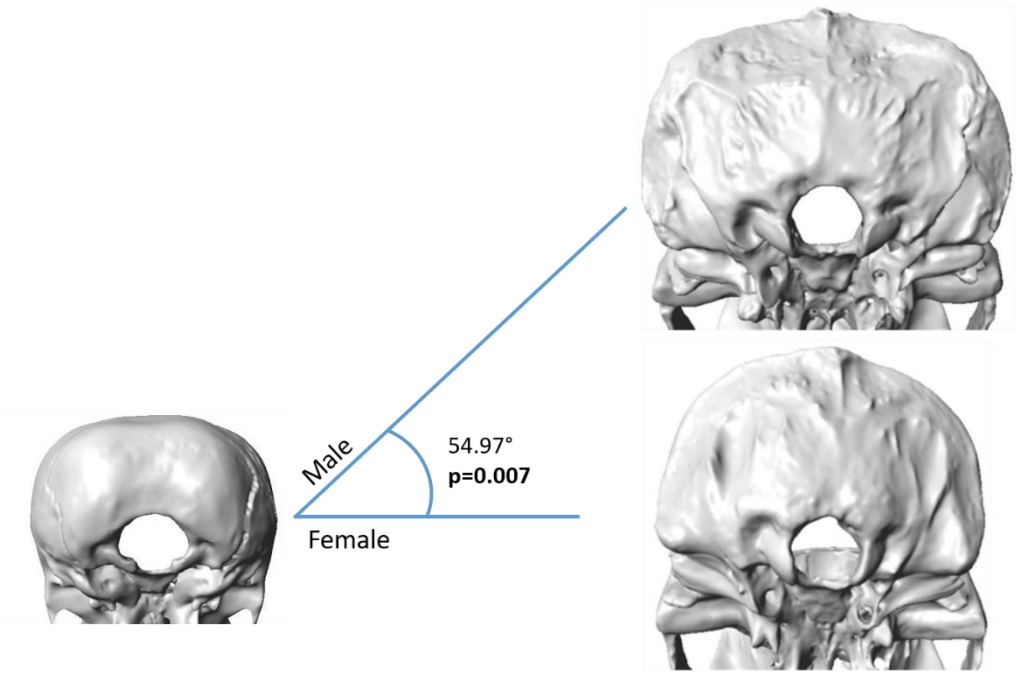

Figure 6.3: Sexual dimorphism in the cervical musculature of *G. b. beringei*, representing statistically significant differences in the pattern of ontogenetic trajectories. Illustrated using representative individuals near the mean shapes for cervical musculature trajectory.

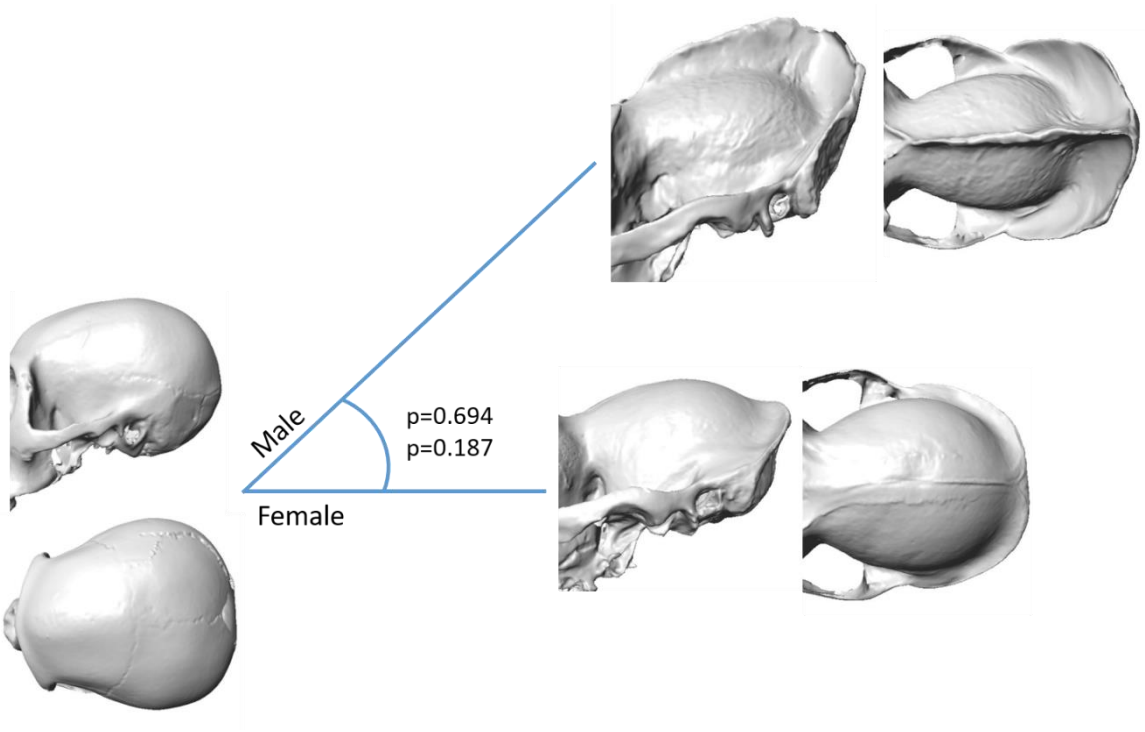

Figure 6.4: Sexual dimorphism in the neurocranium *G. b. beringei*, representing statistically significant differences in the magnitude of shape change. Illustrated using representative individuals near the mean shapes for males (left) and females (right).

6.3.2 Ontogenetic sexual dimorphism in Pan troglodytes schweinfurthii

For chimpanzees, the global dataset likewise showed a statistically significant difference in the adult morphology of males and females (p=0.0011), but no difference in

their ontogenetic trajectories (Figure 6.5). Results from this sample are located in Table 6.3.

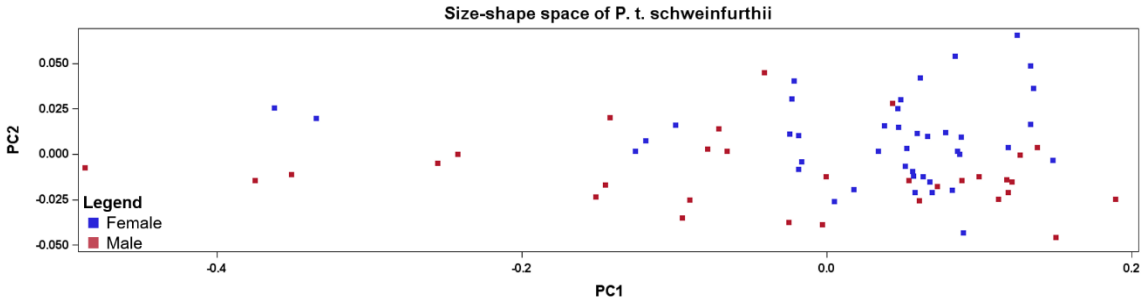

Figure 6.5: Size-shape space of *P. t. schweinfurthii* in the global landmark dataset.

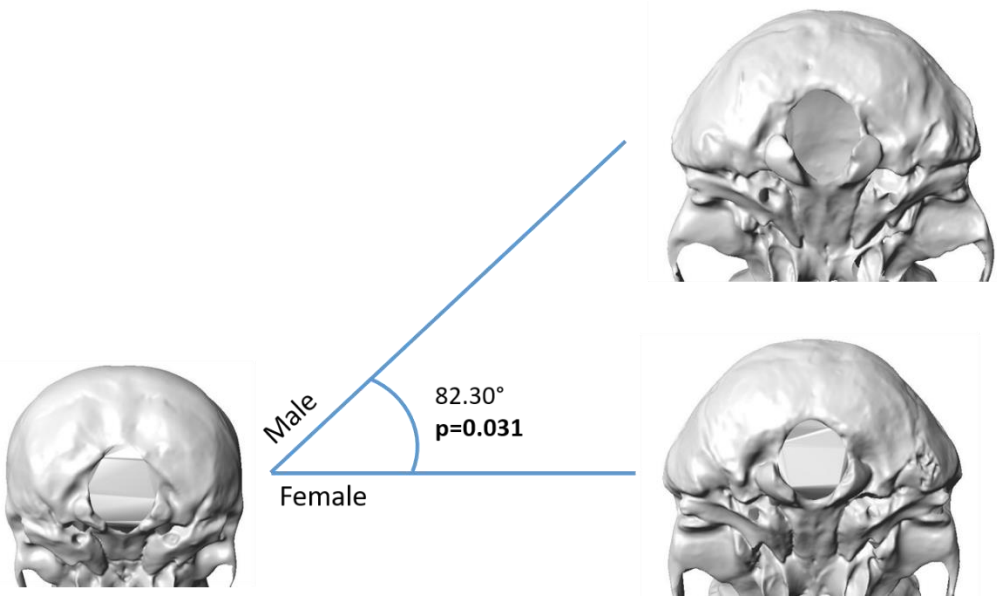

Figure 6.6: Sexual dimorphism in the cervical musculature of Gombe chimpanzees, representing statistically significant differences in the pattern of ontogenetic trajectories. Illustrated using representative individuals near the mean shapes for orbit trajectory.

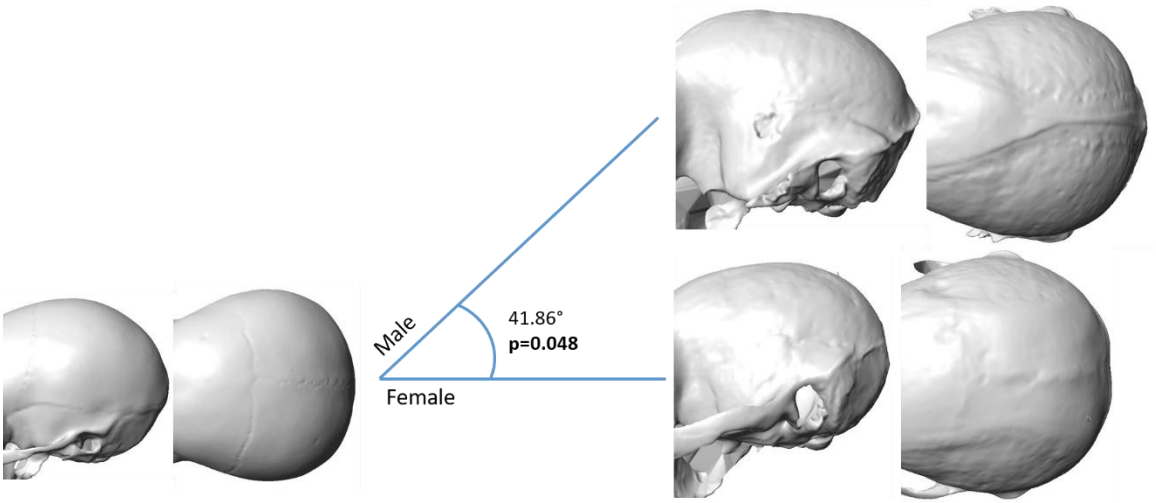

Figure 6.7: Sexual dimorphism in the neurocranium of Gombe chimpanzees, representing statistically significant differences in the magnitude of ontogenetic trajectories. Illustrated using representative individuals near the mean shapes for mastication trajectory.

Adult morphological differences were also displayed in the viscerocranial embryological unit ($p<0.0001$) and the mastication ($p<0.0001$), neurocranial ($p=0.0208$), and orbital ($p=0.0120$) functional modules. Statistically significant differences were found in the pattern of development in the cervical musculature ($p=0.031$) and the neurocranial ($p=0.048$) modules. No statistically significant differences were found in the magnitude of shape change. Males are characterized by having wider and more robust nuchal regions with larger attachments at the mastoid region (Figure 6.6), and longer, lower neurocrania with more pronounced attachments for the temporalis muscles (Figure 6.7).

Table 6.3: Results of statistical tests between sex. MANOVA results document statistical differences in adult morphology. Developmental trajectories were tested for differences in both angle (pattern of shape change) and magnitude (amount of shape change) using permutation tests with 1000 replicates. "Global" denotes results from all 148 landmarks; landmark subsets labeled either embryological (E) or functional (F) modules.

Comparison sex by cranial modules		Adult Shape MANOVA (Wilks' Λ)		Angular differences between ontogenetic trajectories		Vector length differences between ontogenetic trajectories	
		F-value	p-value	Angle	p-value	Difference	p-value
	Global	6.77	**0.0011**	15.40°	0.597	0.00128	0.875
E	Basicranium	1.30	0.3143	47.79°	0.380	0.00092	0.423
E	Neurocranium	2.20	0.0642	17.33°	0.447	0.00421	0.084
E	Viscerocranium	9.30	**<0.0001**	22.08°	0.591	0.00210	0.880
F	Basicranium	1.24	0.3293	72.36°	0.184	0.00047	0.728
F	Mastication	12.44	**<0.0001**	16.83°	0.385	0.00103	0.876
F	Nasal	1.10	0.3900	35.91°	0.799	0.00043	0.954
F	Cervical Musculature	1.03	0.4186	82.30°	**0.031**	0.00094	0.480
F	Neurocranium	2.75	**0.0208**	41.86°	**0.048**	0.00118	0.161
F	Orbit	3.07	**0.0120**	50.84°	0.150	0.00144	0.676
F	Petrous	1.21	0.3335	35.45°	0.116	0.00604	0.575

6.4 Discussion

The way in which ontogeny mediates sexual dimorphism in body size has been attributed to differing growth rates and durations (Leigh and Shea 1995, 1996). Results here indicate that an analysis of growth rate and duration do not fully capture the complexity of sexual dimorphism: different ontogenetic trajectories also lead to sexual dimorphism by differences in both developmental patterns and magnitude of shape change. In addition to body size dimorphism, *Gorilla beringei beringei* obtains sexual dimorphism through altering the pattern and magnitude of development in aspects of the

cranium. *Pan troglodytes schweinfurthii* achieves sexual dimorphism through a difference in the pattern of development in the same aspects of anatomy.

The finding that sexual dimorphism is mediated by both ontogenetic pattern and magnitude has interesting implications to work put forth by Cobb and O'Higgins (2007). They demonstrated that males and females show similar ontogenetic patterns and different ontogenetic scaling until the eruption of the second permanent molar. However, after this developmental stage, ontogenetic patterns between males and females diverge. They conclude that sexual dimorphism is governed by differential ontogenetic trajectories (not scale) primarily after the age of second molar eruption. Results here indicate a difference in the pattern and magnitude of several cranial anatomical units. Though the differences here may be that ontogeny was studied over the entirety of the trajectory where Cobb and O'Higgins (2007) separated their analyses into developmental stage.

Berge and Penin (2004) found adult sexual dimorphism in gorillas and attributed it to an extension of the common growth allometry in males. Their results indicate allometric traits that distinguish male gorillas are increased prognathism, a change in the shape of the nuchal region, and lower, longer cranial vault. However, Berge and Penin (2004) state that their statistical tests only indicate only statistically significant size differences between males and females, not shape differences. Results here indicate that all of the regions mentioned by Berge and Penin (2004) are statistically significantly different in the shape of adult morphology. Further, these shape differences are brought about alterations in ontogeny of males and females. The neurocranium indicates an allometric difference, while the nuchal region (cervical musculature module) indicates a change in the pattern of development.

Pan t. schweinfurthii, as represented by individuals housed at Gombe National Park, obtains sexual dimorphism through altering the pattern of development in the cervical musculature and the neurocranium. Statistically significant differences in the adult morphology of male and female chimpanzees was also observed in the viscerocranium, mastication, orbit, and neurocranial modules; however, explanation of these differences and their possible contribution to the global sexual dimorphism in this population was not observed in the ontogenetic trajectories.

Although Berge and Penin (2004) could not find statistically significant differences in their sample of chimpanzees (due to a small sample size). Cobb and O'Higgins (2007) showed that sexual dimorphism is best attributed to divergent trajectories than an extension or truncation of the ontogenetic scale. This study finds similar results for aspects of the cranium.

The reason for the variation in ontogenetic trajectories among species has historically been tied to socioecological differences in male competition (Wiley, 1974; Jarman, 1983; Janson and van Schaik, 1993). Gorillas live in groups where one male mates with multiple females and exhibit extreme sexual dimorphism via male-male competition (Harcourt *et al*., 1981; Harcourt and Harvey, 1984); however, their societies are not strictly limited to single-male multifemale groups. Mountain gorillas live in more multimale-multifemale groups where mating opportunities for non-dominant, black back males occur more frequently (Vigilant *et al*., 2015). Chimpanzees live in multimale multifemale, fission-fusion groups and males rely more on sperm competition (Harcourt *et al*., 1981; Harcourt and Harvey, 1984). As sexual dimorphism is often used as a proxy for male competition and for inferring aspects of male and female socioecology (Jarmon,

1983; Harcourt and Harvey, 1984; Janson and van Schaik, 1993; Jones, 2011), what is most interesting is that the acquisition of sexually dimorphic features is different in these species. This study indicates that applying a single mechanism, for instance, rate hypermorphosis or bimaturism, may be appropriate for individual traits (*e.g.*, body size), but does not fully capture the complexity of ontogenetic outcomes in adult cranial sexual dimorphism.

However, this study has shown that simply altering the ontogenetic pattern or magnitude of cranial development does not reveal the more complicated aspects anatomical modules. The organism does not alter the global pattern or magnitude of development *(i.e.*, there is not just one mechanism that acts on the entire anatomy); instead, individual aspects of anatomy are altered (in different ways) to produce global adult differences. These differences in cranial anatomy add up to create the global trajectory. As an individual grows, morphology must change in concert with other aspects of anatomy to maintain organismal functionality (Badyaev, 2002). There seems to be little variation in the genetics controlling growth and development (*e.g.*, Badyaev, 2002). However, as ontogeny mediates extreme sexual dimorphism, this work shows that development of an intricate piece of anatomy like the skull is much more complicated than simply maintaining functionality. Thus, the process of ontogeny must not only navigate functionality of the cranium as its morphology changes, it must also balance a complicated interplay of the dimorphic and monomorphic traits that make up the global cranial anatomy in males and females.

6.5 Conclusion

The present study builds on work by Leigh and Shea (1995; 1996; Shea, 1985, 1986, Leigh, 1992, 1995) on the differences in how ontogeny mediates sexual dimorphism among the African ape body size. In addition to body size growth rate and durations, sexual dimorphism is also acquired through patterns and magnitude of shape change. Work on ontogenetic shape change has shown varying results on whether the pattern or both the pattern and magnitude of shape change contributes to sexual shape dimorphism (Schaefer et al., 2004; Berge and Penin, 2004; Cobb and O'Higgins, 2007). The results here indicate that *Gorilla* acquires sexual dimorphism through mostly magnitude differences between male and female ontogenetic trajectories and pattern differences in one cranial modules, while *Pan* acquires sexual dimorphism through a pattern differences in two regions of anatomy.

7 Ontogeny and evolution

In the previous chapter *Gorilla beringei beringei*, as represented by the specimens housed at the Karisoke Research Center, Rwanda were shown to achieve morphological sexual dimorphism by altering the pattern of development in cervical muscular attachment sites. There is also a difference in the magnitude of development in the face and masticatory apparatus. *Pan troglodytes schweinfurthii*, housed at Gombe National Park, Tanzania, however, show statistically significant differences in the pattern of development of the cervical muscular attachment sites and the neurocranium. What is most interesting is that the two genera are not employing a single mechanism for obtaining sexual dimorphism. Development of sex differences in gorillas and chimpanzees focus on different aspects of anatomy and altered those regions in different ways.

The final paper investigates the potential to find heterochronic features in the evolution and divergence of modern taxa. Much work has considered whether differences between extant taxa can be characterized using that lead to either paedomorphosis or peramorphosis. In particular, *Pan paniscus* is often regarded as having a paedomorphic morphology to *Pan troglodytes*. However, studies using multivariate morphometric data reject the notion of pure, classical heterochrony to explain chimpanzee-bonobo differences across the entire cranium; there are contrasting results regarding the possibility that regional dissociated heterochrony can explain some aspects of these differences. A basic problem with diagnosing multivariate heterochrony is that the formal

definitions of heterochronic processes require both taxa to share some aspect of their developmental trajectories: they must have similar shapes at some point during ontogeny. With a large multivariate dataset, the requirements for shape similarity become difficult to meet. As noted in one study, when classic heterochrony is extended into multidimensional studies there has yet to be a case in which it can be properly documented for primates (Mitterocker et al., 2005).

For this reason, the overarching hypothesis testing in the next chapter is not *which* heterochronic signature describes differences between two taxa, but *whether* a heterochronic signature can be found at all. The aim of this study was to find aspects of anatomy, or specific landmarks, that are consistent with a heterochronic explanation, and this was done heuristically by filtering out landmarks that undermine the application of a heterochronic model. However, if no reduction of the data can find a heterochronic signature, then there may be larger issues with how we conceive of heterochrony and ontogenetic evolution, or the methods and sample we employ to study heterochrony.

8 Finding the heterochronic signal through the noise

8.1 Introduction

The study of growth and development has been a vital component of biological research since well before Darwin. Developmental recapitulation first became a central theory in the late-eightieth and early-nineteenth centuries (reviewed in Gould, 1977), but later von Baer (1828) recognized that related species share only early embryogenesis diverging morphologically later in development (reviewed in Mitteroecker *et al.*, 2004a). These ideas were expounded upon by scholars such as Saint-Hilaire and Serres in the 1820s and 1830s, then encapsulated as "ontogeny recapitulates phylogeny" by Ernst Haeckel (reviewed in Gould, 1977).

Deriving from this earlier work, Haeckel introduced the concept of heterochrony in 1875 (Haeckel, 1875; Gould, 1977). To Haeckel, heterochrony is the displacement in time of ontogenetic appearance of one organ relative to another (Haeckel, 1875). This would cause a disruption in the normal recapitulation of phylogenetic ontogeny (Gould, 1977). Though compelling, these works were discovered to be an oversimplification of complex biological processes. These ideas were modified and improved by subsequent researchers, including de Beer (*e.g.*, 1958; 1959) who argued the importance of heterochrony, and particularly paedomorphosis, in evolutionary morphogenesis. Nevertheless, such work fell out of favor until Gould (1977; and Alberch *et al*., 1979) revived and formalized the role of ontogeny in evolutionary research by demonstrating that changes in adult form must be mediated by changes in growth and development.

Gould and others' works were one impetus for the emergence of evolutionary development, so called "evo-devo," which studies how ontogenies evolve in lineages to create new forms, behaviors, and life histories (Raff, 2007; Laland *et al*., 2014; Antón and Kuzawa, 2017).

Heterochrony largely describes the evolutionary relationships of ancestor and descendent size and shape (Gould, 1977). By altering the ancestral population's growth and development, descendent morphology can result in paedomorphosis (the descendent at some age resembles the ancestor at a younger age) or peramorphosis (the adult descendent transcends the ancestor's adult shape; Gould 1977; Alberch *et al*., 1979). Several processes can lead to these results and are typically displayed as a "clock model" (Gould 1977) or a bivariate plot (Figure 1.1; Alberch *et al*., 1979; Klingenberg and Spence, 1993). Processes resulting in paedomorphosis include neoteny, progenesis, and post-displacement (Gould 1977; Alberch *et al*., 1979; Klingenberg and Spence, 1993). Processes resulting in peramorphosis include acceleration, hyper-mophosis, and pre-displacement (Gould 1977; Alberch *et al*., 1979; Klingenberg and Spence, 1993). These processes act by either altering the rate of growth (neoteny and acceleration), the timing of onset (post- and pre-displacement), or the timing of offset (progenesis and hyper-morphosis) of an aspect of anatomy.

However, work on heterochrony went through a fundamental shift after Gould (1977). Gould's (1977) work was a true decoupling of size, shape, and age where the ancestral processes contributing to growth (size), development (shape), and timing of onset and offset (age) could be independently altered resulting in different descendent morphology. However, Gould failed to recognize that descendent populations need not

follow ancestral patterns of growth and development (Godfrey and Sutherland, 1995a). Alberch and colleagues (1979) set out to redefine and formalize the various processes that can result in pera- or paedomorphosis while including the ontogenetic "pertubations" (pre- and post- displacement) omitted by Gould (1977; Godfrey and Sutherland, 1995). They created bivariate plots summarizing age on shape or size on shape (Godfrey and Sutherland 1995a).

Since Gould's *Ontogeny and Phylogeny*, numerous studies have contributed to the study of ontogeny in evolutionary biology, including important works in the field of paleoanthropology (Shea, 1983a; 1983b; 1989; Richsmeier *et al*., 1993; Godfrey and Sutherland, 1995; Leigh and Shea, 1995; 1996; O'Higgins and Jones, 1998; O'Higgins and Strand Viðarsdóttir, 1999; Antón and Leigh, 2003; Berge and Penin, 2004; Cobb and O'Higgins, 2004; Mitteroecker *et al.*, 2004a, b, 2005; McNulty *et al*., 2006; Raff, 2007; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2001; 2008; Bhullar *et al*., 2012; McNulty, 2012; Foth *et al*., 2016; Antón and Kuzawa, 2017; Du *et al*., 2018). In particular, the idea that human evolution is a product of neotenic processes resulting in paedomorphism has generated much debate in paleoanthropology (Shea, 1989; Mitteroecker *et al*., 2004a, b; 2005; Lieberman *et al*., 2007; Zollikofer and Ponce de León, 2010; Ponce de León and Zollikofer, 2008).

Age data, though, are rarely available in museum collections. Since age scales with size up to a certain point, many subsequent studies substituted size for age and focused mainly on the dissociation of size and shape (allometric heterochrony; Godfrey and Sutherland, 1995a). These studies, however, do not consider dissociation of age and size. Shea (1983a) investigated claims that bonobos, common chimpanzees, and gorillas

are placed on a continuum of paedo- to peramorphosis using this new approach. He introduced new terms, differentiating hypo/hypermorphosis in components of time (duration) and rate. This formulation is easier to apply to studies of size and shape when age is not considered. Time hypo/hypermorphosis is equated to Gould's progenesis and hypermorphosis, based on age of offset and when size and shape are coupled together; rate hypo/hypermorphosis is a special case of neoteny and acceleration (shape is decoupled from age and size) where size and shape are recoupled, but age is decoupled (Shea, 1983a, Alba, 2002). Shea states that the new definitions are meant to focus on the process (neoteny, acceleration, etc.) not the results (pera- and paedomorphosis) of heterochrony. Using this approach, Shea (1983b) argued that differences in cranial morphology in *Pan paniscus* and *P. troglodytes* resulted from neoteny, arguing that the dissociation of skull growth from overall size fits the criterion for neontenic retardation.

The "clock model" or the bivariate plots employed when discussing classical heterochronic processes demonstrate how an aspect of anatomy can be altered evolutionarily to either result in paedomorphic or peramorphic descendants. However, these concepts and descriptions of evolutionary change work best with a single shape variable (Gould, 1977; Alberch *et al*., 1979). And indeed, the majority of classic studies of heterochrony only use a single biological or anatomic shape variable such as a ratio of lengths, size, or angular measures (Gould, 1977; Alberch *et al*., 1979). Modern morphometric techniques on the other hand, especially geometric morphometrics, employ many of variables in order to retain and evaluate the geometric context of biological variation (Bookstein, 1978; 1982; Corner and Richtsmeier, 1991).

As Procrustes approaches to the study of shape distinguish between size and shape (shape being the outcome of a generalized Procrustes analysis; see below), it is appropriate for the analysis of heterochrony. Therefore, for the terminology of Alberch and colleagues to be useful, all shape variables must overlap in shape space (Mitteroecker *et al*., 2004a, b; Lieberman *et al*., 2007; McNulty 2012; Figure 8.1). This is because the original assumption of global heterochrony is that both species (or groups) need to undergo the same process (sequence) of shape change over development (Godfrey and Sutherland, 1995a). The descendant can either elongate or truncate the trajectory (hypermorphosis or progenesis, respectively), or the trajectory can be differently associated with size (or age [neoteny, acceleration, pre-, or post-displacement]; Alberch *et al*., 1979; Mitteroecker *et al*., 2005). Though, importantly, the shape of both groups must undergo the same sequence of events. Thus, morphometric data can reveal heterochrony only if the ontogenetic trajectories overlap in shape space.

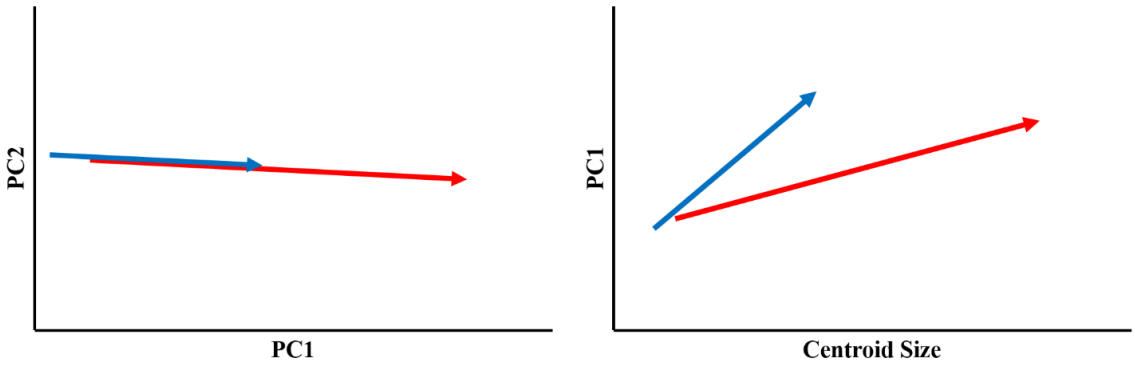

Figure 8.1: Redrawn form Mitteroecker et al., (2004b). Heterochrony is only a tenable description if the trajectories of the two groups overlap in shape space and diverge only in size-shape space.

With these caveats in mind, several researchers have tried to devise ways of studying heterochrony using modern techniques (Mitteroecker *et al.*, 2004a, b; 2005; Lieberman *et al*., 2007 Ponce de León and Zollikofer, 2008). Mitteroecker and colleagues (2004a) tested common allometry among the great apes. In contrast to earlier works of Shea (1983a,b), Mitteroecker and colleagues (2004a) showed that pure heterochrony in the ape lineage is falsified as humans do not share a common ontogenetic trajectory. Thus, globally heterochrony cannot be used to explain ontogenetic differences and focus should be turned to regionally dissociated heterochrony (Shea, 1989; Mitteroecker *et al*., 2004a, b; Liebermann *et al*., 2007).

To further assess global and regional heterochrony, Mitteroecker *et al*. (2005) studied the pannin ontogenetic trajectories in multivariate shape space and found that the two species of *Pan* diverge in ontogenetic trajectory early in development, and that three cranial regions (neurocraium, upper and lower face) also show distinctly differing trajectories. From this, they rejected hypotheses of global and regional heterochrony (Mitteroecker *et al.*, 2005). This should come to no surprise since the complex anatomy of the cranium, which is a set of integrated, semi-autonomous modules, need not conform a single heterochronic process (Mitteroecker and colleagues, 2004b).

Lieberman and colleagues (2007) again tested regional dissociation and found shape differences in the neurocranium best attributable to post-formation (a normal rate and timing of development, however the initial shape of the descendent is underdeveloped; Alba, 2002), but that the face of *Pan paniscus* does not appear to be paedomorphic in the same pattern or degree as the neurocranium. Thus, while global or pure neoteny is not supported by morphological evidence (Shea, 1989; Mitteroecker *et*

al., 2005; Lieberman *et al*., 2007), there are inconsistent results as to whether the cranium exhibits localized heterochrony.

This study is a further test of utilizing classical descriptions of heterochrony using a global landmark dataset. However, the aim here is not to try to find heterochronic signatures using three-dimensional morphometric data, but to systematically reduce the dataset until a heterochronic process can be applied to the results. To clarify, the present study does not test the hypothesis of *which* classical description of heterochrony fits our dataset, but *whether* a systematic manipulation of the data can find relationship that fit the strict requirements of classical heterochrony. As mentioned above, classical descriptions of heterochrony have been difficult to apply to morphometric datasets, global heterochrony seems to be rejected *in toto*, and the presence of regional heterochrony is still contested. This study aims to replicate the conclusions in Mitteroecker and colleagues (2005) for the global landmark dataset, then systematically reduce the landmark number to determine if heterochrony can be found. If successful (*i.e*., a reduction of data finds that the reduced landmark dataset is appropriate for studies of heterochrony), then the reduced dataset could indicate areas or anatomies of the cranium that can be further investigated in all future studies. Data reduction here systematically deletes variables without utilizing *a priori* knowledge of classically defined cranial regions or modules (Moss and Young, 1960; Cheverud, 1982; Cheverud *et al*, 1983; Cheverud and Richtsmeier, 1986; Lieberman *et al*, 2000; Hallgrimsson *et al*., 2007a, 2007b).

If, however, a systematic reduction in the data does not provide any heterochronic relationships (*vis-à-vis*, species' trajectories never overlap in shape space so as to be

further studied) as envisioned by Mitteroecker and colleagues (2005), then the way we conceptualize heterochrony is potentially flawed. Either 1) the methods used to identify heterochronic relationships are inappropriate, 2) the data used to test for heterochrony are inappropriate, or 3) the assumptions and theory underlying the process of evolutionary change through altering developmental pathways is flawed.

8.2 Materials and Methods

8.2.1 Sample

The two species of *Pan* are often used in analyses of heterochrony because wild specimens are numerous in museum collections and *P. paniscus* is often thought of as a paedomorphic version of *P. troglodytes* (Shea, 1983a,b, 1989; Mitteroecker *et al*,. 2004a, b; 2005; Lieberman *et al*., 2007). Several studies have found that the ontogenies of these two species show strong evidence of pure, global heterochrony or regionally dissociated heterochrony (Shea, 1983a,b, 1989; Mitteroecker *et al*,. 2004a, b; 2005; Lieberman *et al*., 2007). For this reason, these two species were chosen here for further analysis (Table 8.1).

Table 8.1: Study Sample Size. Table divided by the number of specimens in each age category used in the study.

Species	**dp4**	**M1**	**M2**	**M3**	**Total**
P. t. troglodytes	15	26	29	58	**128**
P. paniscus	29	46	31	58	**164**
Total	**44**	**72**	**60**	**116**	**292**

8.2.2 Data Collection

Specimens were digitized with a Breuckmann SmartScan^{3D} white light scanner. The raw data were then imported into Geomagic Design X (3D Systems, Inc, 2017) to be aligned and merged into one mesh. Non-anatomical holes were filled before exporting the models for further data collection. Finalized 3D models were landmarked in Stratovan Checkpoint (Figure 8.2; Stratovan Corp, 2016; Bookstein, 1991). This study employed 148 landmarks in order to sample the cranial anatomy of interest. Traditional landmarks were chosen based on previously published material (Frost, 2001; Harvati, 2001; McNulty, 2003; Baab, 2007; Terhune *et al*., 2007; White *et al*., 2012) with additional landmarks added for the purposes of this study.

Geomorph (Adams *et al*., 2016) was used to estimate missing landmarks using thin plate spline interpolations. Data were aligned by generalized Procrustes analysis – to eliminate variation due to the landmark configuration's position, size, and orientation – and then symmetrized using MorphoJ (Klingenberg, 2011). All further analyses were performed in SAS® software on the symmetrized data.

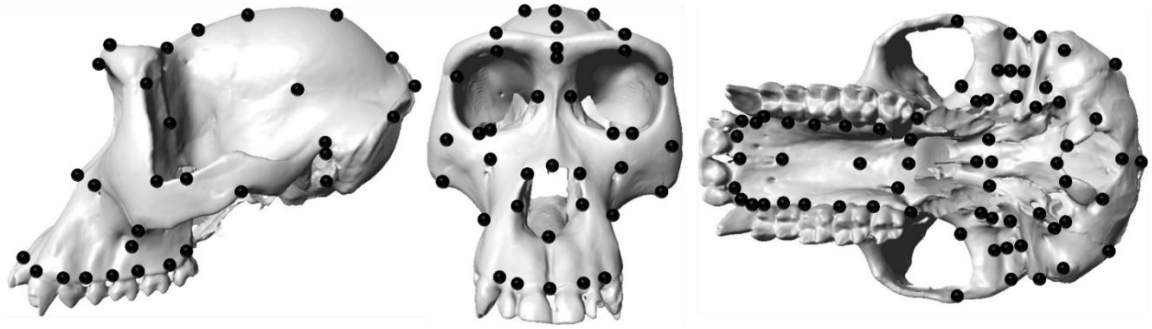

Figure 8.2: Landmark dataset. The global landmark dataset used 148 landmarks from the face, braincase, and cranial base.

8.2.3 Statistical Analysis

Landmark-based geometric morphometrics is a suite of analyses that are designed to preserve geometric integrity of data, allowing a more comprehensive analysis of form and shape. Thus, geometric morphometrics seems to be an ideal tool to study heterochronic shape change in primates. Based on the prescriptive work of Mitteroecker and colleagues (2005), this project employs a combination of visualizations of shape space and permutation tests designed to test whether ontogenetic trajectories are parallel and overlap in shape space. To test for heterochrony, the data were projected into shape space and evaluated visually. If trajectories overlapped in shape space, then further analyses were performed. As Mitteroecker and colleagues (2004a, 2005) demonstrated, the visual evaluation of overlap in the first several principal component scores can be misleading because these axes may not be the optimal rotation to visualize the true trajectories. They prefer, instead, to construct a shape space based on predicted trajectories of specimens calculated from the within-species multivariate regressions on "reasonable size values" of dummy specimens (Mitteroecker *et al.*, 2005: 252). Projected into this space, should be the real specimens. This has the advantage of displaying the optimal rotation of the first three principal components to best visualize the differences in trajectories. If, upon inspection of the first few principal components, the trajectories overlap, this optimally rotated space will be constructed.

A further test for determining whether the trajectories overlap in shape space is to mathematically assess the direction of the trajectories and the amount of overlap. This was done first by computing within-species multivariate regressions of the shape variables on size (natural logarithm of centroid size) and calculating the sum the squared

residuals across both groups. This statistic was permuted 1000 times to evaluate the hypothesis that the ontogenetic vectors are identical in shape space (Mitteroecker *et al*., 2005). Failure to reject the null-hypothesis means that differences is shape could be explained by heterochronic processes involving elongation or truncation of ontogeny when size and shape remain associated. To assess whether species' ontogenies overlap (but are not identical) in shape space involved a similar procedure but permuting the sum of squared (normal) distances of specimens to their trajectory rather than the sum of squared residuals. This allows for the size/shape relationship to be decoupled, testing only for overlap in the trajectories. Failure to reject the null-hypothesis in this case means that heterochronic rate differences may explain differences in the anatomy.

Although permutation tests are commonplace in statistical analyses (see, *e.g*., Good, 2006), including studies of landmark data (*e.g*., O'Higgins and Strand Viðarsdóttir, 1999; O'Higgins *et al*., 2001; O'Higgins and Collard, 2002; Penin *et al*., 2002; Strand Viðarsdóttir *et al*., 2002; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Cobb and O'Higgins, 2007; Drake and Klingenberg, 2008; Rodriguez-Mendoza *et al*., 2011; Weisensee and Jantz, 2011; Klingenberg *et al*., 2012; Martin-Serra *et al*., 2014), this study specifically followed the resampling protocol outlined by McNulty *et al*. (2006). They demonstrated that in circumstances for which there is a dearth of observations representing some aspects of structured variation within a sample (*e.g*., the youngest age classes in an ontogenetic study), simple models of permutation design are more likely to find statistically significant differences than models which resample with respect to that structured variation (McNulty *et al*., 2006). The current study laid out three possible statistical designs for permutation tests: 1) resampling within

age classes, constraining permuted groups to an equal number of specimens for each developmental stage; 2) resampling within age classes, but replicating in permuted groups the original (unequal) sample sizes at each age class; and, 3) ignoring structured variation and resampling randomly across all age classes. Following McNulty et al. (2006) and Singleton et al. (2012), this study employed the more conservative permutation test (model 1 above) in an attempt to capture true differences in the groups.

8.2.4 Data reduction techniques

This study began with evaluating the case of heterochrony in shape space using this study's entire dataset of 148 landmarks (Figure 8.2). As each landmark is a series of three coordinates (X, Y, and Z), this is equivalent to 444 coordinate variables per specimen. To test the overarching hypothesis that heterochrony cannot be detected in the crania of *Pan* species, the analyses outlined above were first performed on the complete dataset, and then on serially reduced datasets after eliminating variables that obscure the signature of heterochronic processes. Importantly, because deleting a single variable (for example, an X coordinate of glabella or a Z coordinate of bregma) has no biological validity, particularly given the arbitrary orientation of specimens following GPA, entire landmarks (X, Y, and Z coordinates) were eliminated if any one of its three coordinates were designated for removal. Following data reduction, resulting datasets were again subjected to the analyses outlined above to determine whether the trajectories are identical or even overlap in shape space.

The first step of data reduction used multivariate regressions of shape coordinates on logCS in both *Pan troglodytes* and *P. paniscus* to produce the species' ontogenetic

trajectories. If the coefficients for these two variables had different signs (+/-), then the regression line for that variable was sloping in the opposite direction, presumably contributing the divergence of the ontogenetic trajectories. These cases, as well as the other coordinates in the corresponding landmarks, we deleted during this step. For example (Table 8.2), the Y of left porion was negative for *P. paniscus* and positive for *P. troglodytes*. In this example, that variable is deleted, and so too the entire landmark.

Table 8.2: An Example of beta coefficients from the first data reduction step. Here, the beta coefficients all are the same sign (+/-) except the Y coordinate of left porion (highlighted). In this case, all of left porion is deleted and the specimens are plotted in shape space again with this landmark omitted.

Landmark	**Variable #**	**β of *P. paniscus***	**β of *P. troglodytes***
Left Orbitale			
X	1	0.031	0.029
Y	2	-0.004	-0.004
Z	3	0.016	0.013
Left Porion			
X	4	0.038	0.039
Y	5	-0.003	0.001
Z	6	0.029	0.023

In the second reduction step, another within-species multivariate regression of the shape variables on logCS was performed on the resultant dataset from the first reduction. In this case, a reduced major axis regression of the beta coefficients was performed (Figure 8.3) and the residuals calculated. For landmarks at which the species were similar to each other, they plotted close to the regression line; when they were different, the magnitude of the residual would increase. Hence, this step eliminated landmarks with

coordinates that fell beyond one standard deviation from the reduced major axis regression.

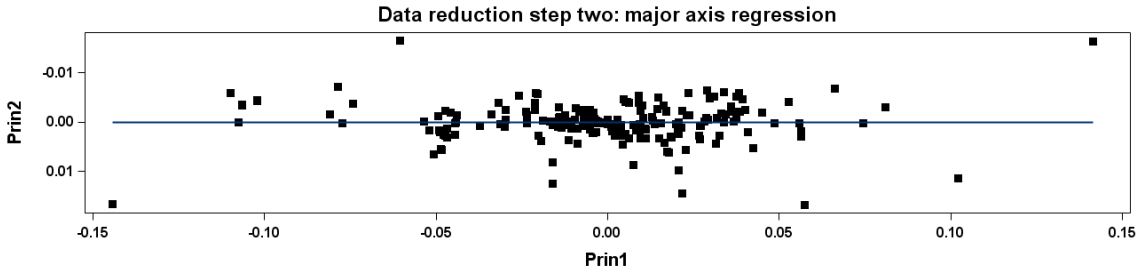

Figure 8.3: Data reduction step two involved a reduced major axis regression of the beta coefficients derived from a within-species regression of shape variables on logCS. Residuals from the regression line were calculated. Variables that exceed one standard deviation were deleted.

Finally, the third reduction in data used a bivariate regression of corresponding variables from each species. For example, the first variable of *P. troglodytes* (left orbitale X) was regressed against the first variable of *P. paniscus* (left orbitale X; Figure 8.4). Here, variables with an insignificant F-value at the level of 0.05 were deleted. The variables that were left have a statistically positive slope indicating that a change in *Pan paniscus* corresponded to a similar change in *Pan troglodytes*. Due to the data reduction in step one, no variable regressions had a negative slope. Again, deleted variables required the entire landmark to be removed from further analysis.

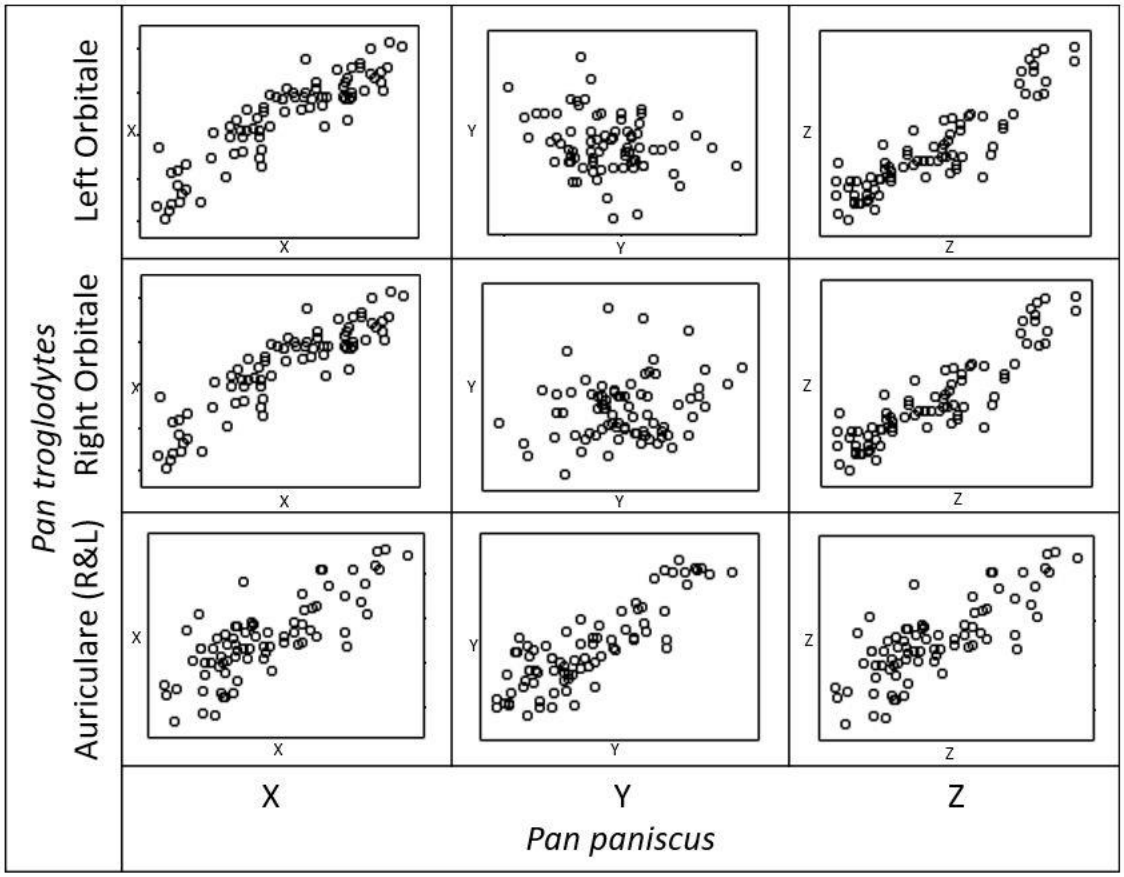

Figure 8.4: An example of three landmarks from step 3. This example shows the bivariate regressions for the X, Y, and Z variables for three landmarks. The variables for *P. paniscus* are located on the x-axes, and *P. troglodytes* on the y-axes. In this example, left and right orbitale would be deleted since one of their variables have an insignificant correlation between the two species (*i.e.*, a unit change in *Pan troglodtyes* does not have a corresponding change in *Pan paniscus*). Auriculare (both right and left) would remain for further testing as it has a statistically significant, positive correlation between the species (*i.e.*, a unit change in *Pan troglodtyes* has a similar change in *Pan paniscus*).

8.3 Results

8.3.1 Initial test of heterochrony

As shown before and here, the global landmark dataset for *Pan troglodytes* and *P. paniscus* do not have overlapping trajectories in shape space (Figure 8.5; Mitteroecker *et al.*, 2005). The multivariate angular difference between the species is 12.39°. However,

the permutation test does not indicate that the two trajectories statistically differ in direction (p=0.898). *Pan troglodytes* shows a longer trajectory than *P. paniscus* (Figure 8.5). This is an indication of elongation/truncation of growth when size and shape remain associated. However, because the visualization of shape space and the permutation test for overlapping trajectories is statistically significant (Figure 8.5; permutation test p=0.006), heterochronic mechanisms that dissociate size and shapes are not applicable. The two species differ at the earliest stage of the development, and this difference diverges throughout adulthood (Figure 8.5). Therefore, differences between species in the cranium as a whole cannot be described using the classic heterochronic relationships as envisioned by Gould (1977) and Alberch and colleagues (1979).

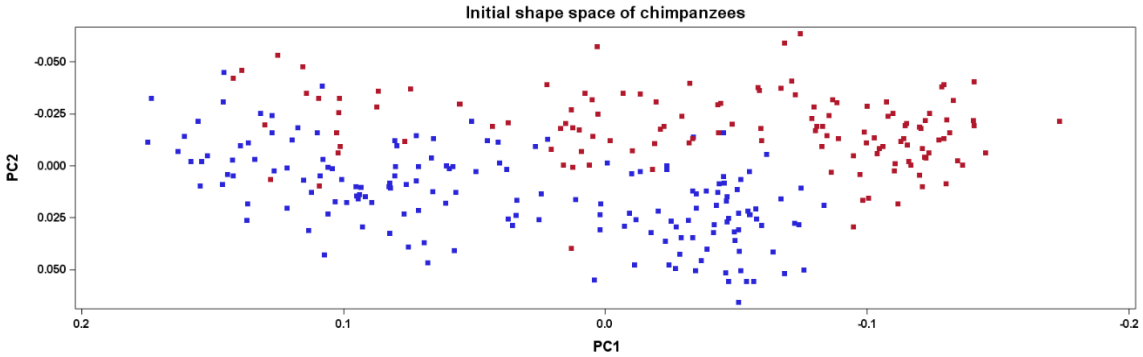

Figure 8.5: Initial test of heterochrony. *Pan paniscus* and *P. troglodytes* do not share a common trajectory in shape space; thus, a classic description of heterochrony cannot be applied.

8.3.2 Data reduction 1: the signs of beta coefficients

In comparing the beta coefficients for *Pan troglodytes* and *P. paniscus*, inconsistencies were found in 47 of the coordinates' signs (+/-). These coordinates, as

well as the landmarks with which they are associated, were deleted from the analysis. The resulting dataset reduced the landmark number to 109 (309 coordinates; Table 8.3).

Heterochrony was again assessed on the new dataset. The multivariate angular difference between the two species was 12.18°. However, a permutation test of the sum of squared residuals was statistically non-significant (p=0.641). By plotting the new, reduced dataset into shape space (Figure 8.6), the visualization indicates that a heterochronic description is again invalid. The two species did not achieve overlapping trajectories in shape space (p=0.003). So, they cannot share a classical heterochronic relationship.

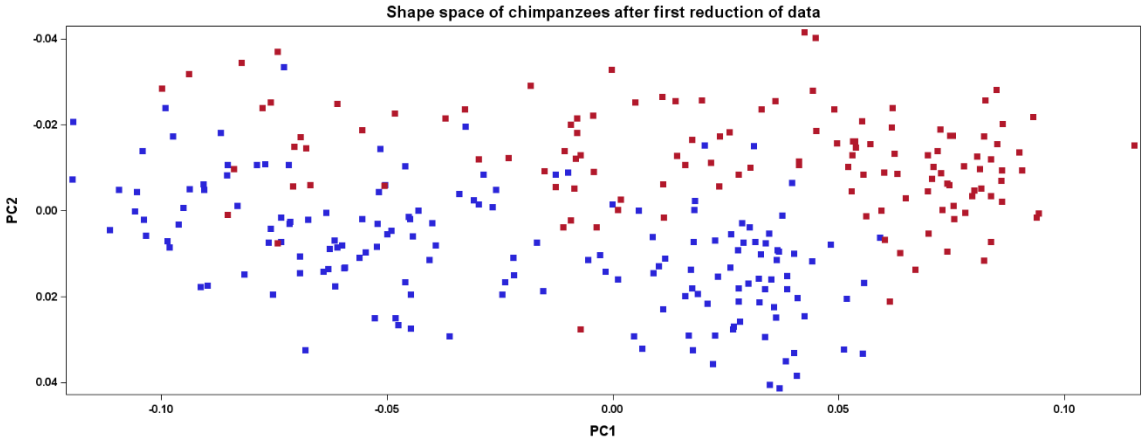

Figure 8.6: Test of heterochrony after the first deletion of landmarks. *Pan paniscus* and *P. troglodytes* do not share a common trajectory in shape space; thus, a heterochronic description to these species still cannot be applied.

8.3.3 Data reduction 2: reduced major axis regression

Shape variables were again regressed on logCS for each species on the resultant landmark number from the initial reduction step. A reduced major axis regression was

performed on the beta coefficients, and the residuals for each coordinate were calculated (Figure 8.3). Coordinates were deleted if their residuals fell beyond one standard deviation. This further reduced the dataset leaving 201 coordinates in this analysis. This corresponds to 67 landmarks (Table 8.3).

The multivariate angular difference between the two species was 11.06°, but a permutation test of the sum of squared residuals was statistically non-significant (p=0.855). By plotting the new, reduced dataset into shape space (Figure 8.7), the visualization indicates that a heterochronic description is again invalid. The two species did not achieve overlapping trajectories in shape space (p=0.037). So, they cannot share a classical heterochronic relationship.

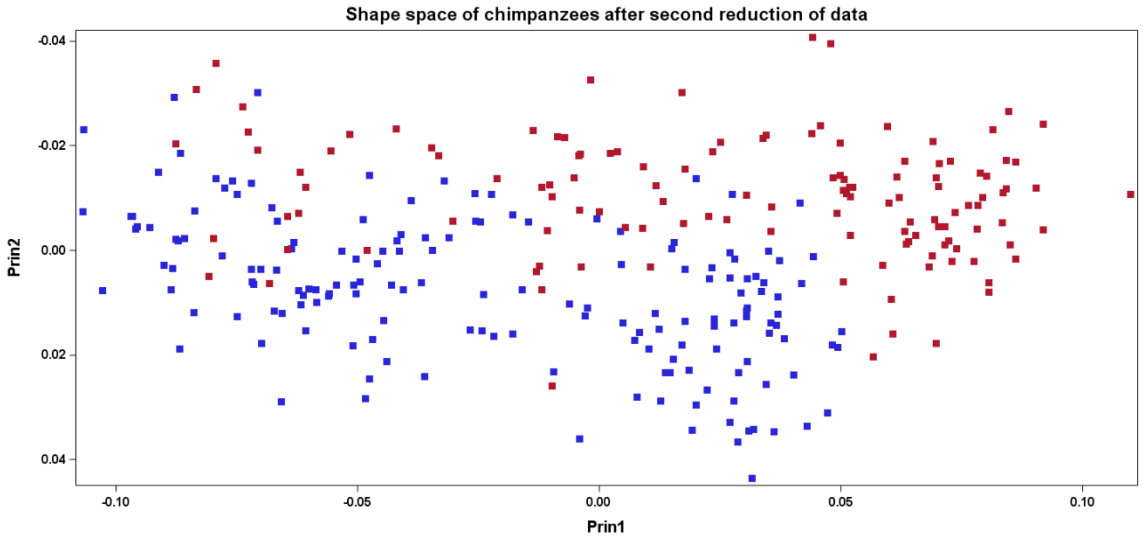

Figure 8.7: Test of heterochrony after the second deletion of landmarks. Pan paniscus and P. troglodytes do not share a common trajectory in shape space; thus, a heterochronic description to these species still cannot be applied.

8.3.4 Data reduction 3: individual variable regressions

In this analysis, each coordinate of *P. troglodytes* with the corresponding coordinate for *P. paniscus* was independently regressed. The coordinates that were left have a statistically positive slope indicating that a unit change in *Pan paniscus* corresponded to a similar change in *Pan troglodytes*. The resulting dataset reduced the landmark number to 30 (Table 8.3).

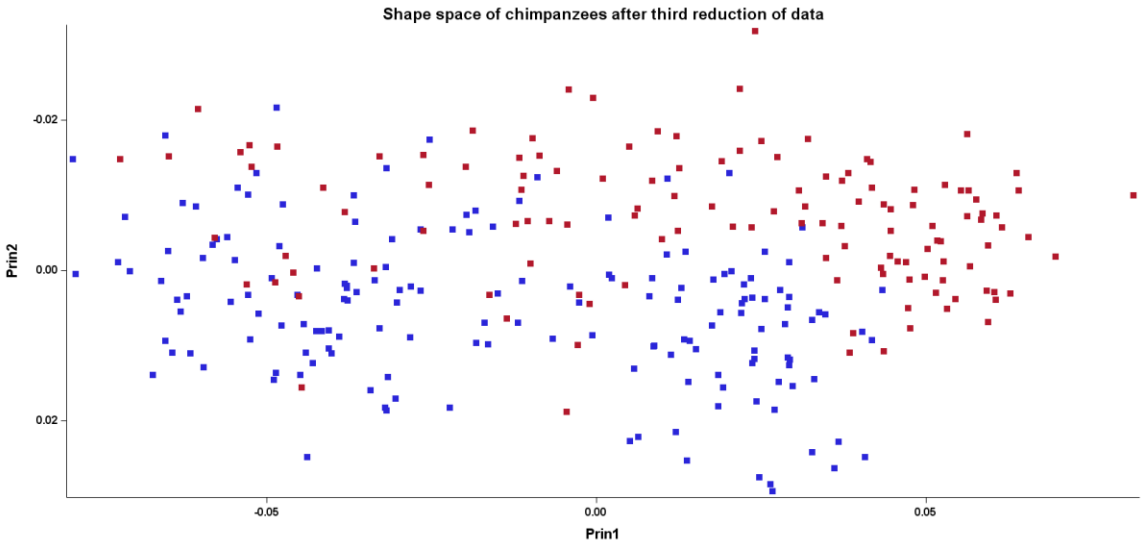

Figure 8.8: Test of heterochrony after the third deletion of landmarks. Pan paniscus and P. troglodytes do not share a common trajectory in shape space; thus, a heterochronic description to these species still cannot be applied.

The multivariate angular difference between the two species was 9.24°. However, a permutation test of the sum of squared residuals was again statistically non-significant (p=0.996). By plotting the new, reduced dataset into shape space (Figure 8.8), the visualization indicates that a heterochronic description is still invalid. The two species did not achieve overlapping trajectories in shape space (p=0.001). *Pan paniscus* and *Pan troglodytes* cannot be described as having a classical heterochronic relationship.

Table 8.3: The data reduction steps, their descriptions, and the number of landmarks (variables) remaining after data reduction.

Data reduction steps	Description	Ending landmark # (Ending Variable #)
1. The signs of beta coefficients	Within-species multivariate regression to obtain two beta coefficients for each coordinate. Coordinates were deleted if their beta coefficient signs were opposite (+/-).	103 (309)
2. Regression of beta coefficients	Within-species multivariate regression. Major axis regression of beta coefficients Coordinates were deleted if residuals 1 standard deviation from the regression fit line.	67 (201)
3. Individual variable regressions	Bivariate regressions performed individually on each coordinate. Coordinates were deleted if they had an insignificant correlation.	56 (168)

8.4 Discussion

The above results from data reduction techniques, which systematically reduce the landmark dataset, show that these attempts were insufficient at finding landmarks that would cause the two species' trajectories to overlap in shape space. Thus, even deliberate attempts to reveal heterochrony in cranial ontogeny between chimpanzees and bonobos were unable to find a group of landmarks that fit the necessary criteria. Given the clear importance of heterochrony in moderating evolutionary shape change, why is it so difficult to detect in a multivariate dataset?

One possibility is that landmark-based geometric morphometrics is not the appropriate tool to detect heterochrony. Mitteroecker and colleagues (2004a) state that multivariate analyses (landmark-based morphometrics or any other kind of analyses

utilizing more than one variable) may be incapable of distinguishing among heterochronic processes that lead to paedomorphosis and peramorphosis. This seems unlikely as geometric morphometrics is particularly tuned to studying not only biological shape, but shape changes and variation by dissociating size and shape (Penin *et al*., 2002; Berge and Penin, 2004; Cobb and O'Higgins, 2004; Mitteroecker *et al*., 2004a, b, 2005). In fact, there has been some success at studying regional heterochrony with multivariate landmark datasets (Mitteroecker *et al.,* 2004a; Lieberman *et al*., 2007; Ponce de León and Zollikofer, 2008). For instance, Lieberman and colleagues (2007) found that the bonobo adult neuro- and basicranium fall within the range of chimpanzee subadults indicating paedomorphosis via postformation. However, studies that have found regional heterochrony have not typically met the criterion of overlapping trajectories in shape space. Lieberman and colleagues (2007) argue that this criterion is too conservative and goes against the original formulation of hypotheses by Gould (1977). However, as outlined by Mitteroecker and colleagues (2005) and here, two groups must share overlapping trajectories in all of shape space to fit the classical descriptions of heterochrony originally outlined by Gould (1977) and others (Alberch *et al*., 1979). This is because the original assumption of global heterochrony is that both species (or groups) need to undergo the same process (sequence) of shape change over development (Godfrey and Sutherland, 1995a).

Another problem may be in the datasets used in most studies: extant hominoids (Shea, 1983a, b, 1989; Mitteroecker *et al,*. 2004a, b; 2005; Lieberman *et al*., 2007). As originally envisioned, heterochrony is the dissociation between shape, age, and size through evolutionary time (Gould 1977). Therefore, it is explicitly tied to an ancestor-

descendant relationships. By using extant species to test hypotheses of heterochrony, we ignore the true ancestor-descendent relationship and reduce heterochronic terminology to mere descriptions of developmental shape changes. Neither *P. paniscus* nor *P. troglodytes* is ancestral to the other, and perhaps should not be modeled that way. A more appropriate test for heterochrony would be to run the above analyses on specimens where the ancestor-descendant relationship is better known or more easily modeled.

For example, Bhullar and colleagues (2012; and later expanded work by Foth *et al*., 2016) investigated heterochronic shifts in dinosaurs including the extant (birds) and extinct theropods. They identified at least four heterochronic shifts in the evolution of birds including both paedomorphic and peramorphic shifts (Bhullar *et al*., 2012). Drake (2011) tested weather dogs are paedomorphic extensions of wolf shapes. While these are evolutionary cousins and not direct ancestor-descendent relationships, it is well established that domesticated dogs are recent descendants of wild wolves. Drake (2011) found that no breed of domestic dog shares a paedomorphic relationship with wolves. Utilizing similar evolutionary relationships, Evin and colleagues (2017) investigated heterochronic processes in the domestication of pigs. In their analysis, they too concluded that domestic pigs are not merely paedomorphic descendants of the wild boar. However, these analyses do not take into account the caveats of geometric morphometric techniques that are presented here and elsewhere (Mitteroecker *et al*., 2004a, b, 2005).

A third possibility is that classical descriptions of heterochronic change are inappropriate to the study of biological organisms. When studying a single shape variable, in two species, heterochrony is almost always a valid description (Mitteroecker *et al*., 2005): the dimensionality of the data do not allow for variations in directions that

could not be accounted for by mechanisms of heterochrony. For instance, a bivariate plot of a length ratio in two species will always resemble one of the plots in Alberch *et al* (1979). However this relationship falls apart when one adds multiple variables to an analysis. As there are no single-variable organisms, does this mean that we should study evolutionary change one variable or ratio at a time? Of course not. Studying biological life using one variable at a time disregards the more complex and interesting biological processes like covariation, integration, and modularity. The cranium is a complex organ with many integrated modules. So, there is no reason why the cranium needs to conform to just one heterochronic process. This holds true with the known mosaic evolution and dissociated heterochrony in primate evolution (Mitteroecker *et al*., 2004a). This mosaic evolution has the very real probability that aspects of cranial anatomy have undergone multiple heterochronic processes, skewing any relationship that might be described as heterochrony (Mitteroecker *et al*., 2004). The result being that one may never find a clear, singular heterochronic signature in the data.

It is the opinion of this author that classical descriptions of heterochronic change can never be applied to biological organisms in a real way. To be clear, the underlying hypothesis that evolutionary change, in part, comes about through alterations in ontogeny have been well documented and is not in question here (Raff 2000, 2007; Laland *et al*., 2014). However, the use of the terms and simplistic mechanisms (like neoteny or progenesis) to explain complex evolutionary transformations is called into question. The study presented here tired multiple steps to coax the data to fit a heterocrhonic model. However, no data reduction technique performed was able overlap the trajectories in shape space. As multiple studies have struggled to find heterochrony (with this study

unable to find it even with manipulation of the data), perhaps it is time to move away from these descriptions.

8.5 Conclusion

This analysis systematically deleted variables in the dataset in order to align the trajectories of *Pan troglodytes* and *P. paniscus* in shape space. The assumption being that once common anatomy can be found that restrict such divergence in shape space, then classical descriptions of heterochronic change can be applied that may define the evolutionary shape transformation in the pannins. However, the intention was not to find and describe landmarks as if stating these anatomies are more or less important to evolvability in hominoids. The present study sought to determine if a heterochronic signature (*i.e.* Gould, 1977; Alberch *et al*., 1979) could ever be found using landmark-based geometric morphometrics.

By systematically reducing the landmark dataset in three separate steps a signature of heterochronic change in the cranial morphology of the pannins was not found. This analysis showed that reducing the dataset as to find anatomy that would overlap the two species' ontogenetic trajectories; thus, displaying a heterochronic relationship, still does not result in a detectable signal. What is the cause of this? First, perhaps the dataset is not applicable to detecting heterochrony. Pannins are not an ideal group to test theories of evolutionary change as they do not share an ancestor-descendent relationship but have been evolving separately for approximately 0.93MA (Hay, 2010). Second, geometric morphometrics may not an ideal toolkit to finding heterochronic shifts in primate evolution. As geometric morphometrics studies shape in multivariate space,

finding any anatomies in complex biological organisms that share a common trajectory in shape space may prove to be an inappropriate and overly conservative criterion. Finally, perhaps the theory and assumptions behind classical, Gouldian heterochrony cannot ever be applied outside of a strict bivariate analysis of shape. Evolution has likely utilized many heterochronic processes as well as paedo-and peramorphic reversals to obtain adult cranial shapes. Thus, finding an evolutionary relationship that can be described using a single heterochronic process is likely extremely rare. Perhaps it is time to move away from descriptions of classical heterochrony (like neoteny and progenesis).

9 Conclusion

The interplay between ontogeny and evolution has been of interest to the anthropological community for decades and to natural philosophers since well before Darwin. Ontogenetic research from many paleoanthropological studies focus on one of four main topics: the evolutionary significance of juvenile fossils, the evolution of the human-like life history, how ontogeny mediates sexual dimorphism, and heterochrony. However, these topics are actually different avenues to understanding the complicated way in which ontogeny plays a role in evolution: alterations in the ontogenetic programs of a population can lead to evolutionary transformations. This dissertation focused on these broader interests in three independent but related studies: population-level variation in ontogeny, how sexually dimorphic characteristics are acquired through ontogeny, and searching for a heterochronic signature utilizing a morphometric dataset.

This dissertation performed three-dimensional shape analysis on African ape crania. Specimens with known provenience data were collected and analyzed with an eye towards population taxonomy (subspecies, locality, deme, and sex). Additionally, two new skeletal collections with known age at death were used from Karisoke Research Center, Rwanda and Gombe National Park, Tanzania.

In chapter four, analyses show variability in morphological ontogeny at all levels of taxonomy. This variability exhibits itself in the global cranial dataset (the cranium as a whole) as well as discrete cranial modules representing embryological and functional anatomies. Statistically significant differences were found in the ontogenetic trajectories

of many of the populations under study. These differences, which lead to adult morphological differences, manifested in both the pattern of development and the magnitude of shape change. This study has also shown that the aggregation of specimens into genus-, species-, and even subspecies-level groupings diminishes the biological complexity of ontogeny. However, as the statistical differences in the adult morphology as well as the statistical differences in the pattern and magnitude of development show, these larger amalgamations are not congruent with contextualized samples. Studies that collect specimens without regard to population history are at risk of having inconsistent amounts of ontogenetic variation in analog samples.

Chapter six contributed to work performed by Leigh and Shea (1995; 1996; Shea, 1985, 1986, Leigh, 1992, 1995) on the differences in how ontogeny mediates sexual dimorphism among the African ape body size. Karisoke mountain gorillas acquire sexual dimorphism through differences in ontogenetic trajectory of the cervical neck muscular attachments and magnitude of shape change in the neurocranium. Gombe chimpanzees acquire sexual dimorphism through a difference in the pattern ontogenetic trajectories two regions of anatomy: the cervical muscular attachments and the neurocranium. This study indicates that applying a single mechanism, for instance, rate hypermorphosis or bimaturism, may be appropriate for individual traits (*e.g.*, body size), but does not fully capture the complexity of ontogenetic outcomes in adult cranial sexual dimorphism. What is most interesting, is that Gombe chimpanzees and Karisoke mountain gorillas exhibit ontogenetic changes in development in the same regions of the cranium, but under different processes (an alteration of pattern or an alteration of magnitude of shape difference)

Chapter eight systematically reduced the landmark dataset utilizing three reduction steps. Here I was not able to find a signature of heterochronic change in the cranial morphology of the pannins. This analysis showed that manipulating the dataset as to coax two species into displaying a heterochronic relationship still does not result in a detectable signal. What is the cause of this? The underlying theory behind classical, Gouldian heterochrony (that evolutionary transformations are in part spurred by changes in the developmental schedule) are correct. However, the simplistic descriptions to describe this evolutionary change (whereby all developmental processes must conform to similar changes to age or size) cannot ever be applied outside of a strict bivariate analysis of shape.

Overall, the results of these analyses contribute to our understanding of how ontogeny and variations in ontogeny lead to evolutionary transformations. Variation in ontogenies lead to adult morphological differences seen in populations documented here and other studies (Groves, 1970, 2003, 2005, Shea *et al*., 1993; Sarmiento and Oates, 2000; Grubb *et al*., 2003; Gonder *et al*., 2006; Pilbrow 2003, 2006, 2010; Pilbrow and Groves 2013; Uchida, 1992, 1996; Knigge *et al*., 2015). The alteration of similar anatomy (through different mechanisms) leads to sexual dimorphism in mountain gorillas and chimpanzees. This contributes to similar studies of growth (Leigh and Shea 1995, 1996) and development (Schaefer *et al*., 2004; Berge and Penin, 2004; Cobb and O'Higgins, 2007) by showing that the pattern and magnitude of development leads to sexually dimorphic anatomy. And previous studies like Mitteroecker (2004b, 2005) were not able to find overlapping trajectories in shape space. Here, the reduction of data to coax overlapping shape trajectories was still insufficient, leading to the conclusion that

classical descriptions of heterochrony (Gould, 1977; Alberch *et al*., 1979) are not likely to ever fit morphological data utilizing multivariate methods.

10 Bibliography

3D Systems, Inc (2017): Geomagic Design X version 2016.1.1.

Ackermann, Rebecca and Krovitz, Gail (2002). Common Pattern of Facial Ontogeny in the Hominid Lineage. *The Anatomical Record*, 269: 142-147.

Adams, Dean; Collyer, Michael; and Sherratt, Emma (2016): Geomorph – Geometric Morphometric Analyses of 2D/3D Landmark Data, version 3.0.0.

Alba, David (2002): Shape and stage in heterochronic models. IN: Minugh-Purvis , N., McNamara, K.J. (Eds.), Human Evolution through Developmental Change. Johns Hopkins University Press, Baltimore, pp. 28-50.

Alberch, P.; Oster, G. F.; Gould, S. J.; Wake, D. B. (1979): Size and Shape in Ontogeny and Phylogeny. *Paleobiology*, 5: 296-317.

Albrecht, Gene and Miller, Joseph (1993): Geographic variation in Primates. IN Kimbel W; Martin L (eds.) Species, Species Concepts and Primate Evolution, Springer, Boston, MA.

Albrecht, Gene; Gelvin, Bruce; Miller, Joseph (2003): The hierarchy of intraspecific craniometric variation in gorillas: A population-thinking approach with implications for fossil species recognition studies. In: Taylor, A.B. & Goldsmith, M.L. (eds.) Gorilla Biology: A Multidisciplinary Perspective. Cambridge: Cambridge U Press, pp. 62-103.

Alemesged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D., & Wynn, J.G. (2006). A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature*, 443: 296-301.

Antón, Susan and Leigh, Steven (2003): Growth and life history in Homo erectus, In: Thompson, J.L., Krovitz, G.L., & Nelson, A.J. (eds.), Patterns of growth and development in the Genus *Homo* (pp. 219-245). Cambridge: Cambridge U Press.

Antón, Susan C. and Kuzawa, Christopher W. (2017): Early *Homo*, plasticity and the extended evolutionary synthesis. *Interface Focus*, 7.

Austad, Steven N. and Fischer, Kathleen E. (1992): Primate Longevity: Its Place in the Mammalian Scheme. *American Journal of Primatology*, 28: 251-261.

Baab, Karen L. (2007): Cranial shape variation in *Homo erectus*. City University of New York, Ph.D. thesis.

Badyaev, Alexaner V. (2002): Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution*:17. 369-378.

Balolia, Katharine L.; Soligo, Christophe; Wood, Bernard (2017): Sagittal crest formation in great apes and gibbons. *Journal of Anatomy*: 230. 820-832.

Bastir, Markus; Higuero, Antonio; Rios, Luis; Garcia Martinez, Danial. (2014): Three-Dimensional Analysis of Sexual Dimorphism in Human Thoracic Vertebrae: Implications for the Respiratory System and Spine Morphology. *American Journal of Physical Anthropology*: 155, 513-521.

Berdnikovs, S.; Bernstein, M.; Metzler, A; German, R.Z. (2007): Pelvic Growth: Ontogeny of Size and Shape Sexual Dimorphism in Rat Pelves. *Journal of Morphology*, 268: 12-22.

Berge, Christine and Penin, Xavier (2004): Ontogenetic Allometry, Heterochrony, and Interspecific Differences in the Skull of African Apes, Using Tridimensional Procrustes Analysis. *American Journal of Physical Anthropology*, 124: 124-138.

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., & Kibii, J.M. (2010). *Australopithecus sediba*: A New Species of *Homo*-Like Australopith from South Africa. *Science*, 328: 195-204.

Berger, L. R., Hawks, J., de Ruiter, D. J., Churchill, S. E., Schmid, P., Delezene, L. K., … Zipfel, B. (2015). Homo naledi, a new species of the genus Homo from the Dinaledi Chamber, South Africa. eLife, 4, e09560. http://doi.org/10.7554/eLife.09560 Beynon, A. D. and Dean, M. C., (1991): Hominid dental development. *Nature*, 351: 196.

Beynon, A. D.; Dean, M. C.; Leakey, M. G.; Reid, D. J.; Walker, A., (1998): Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *Journal of Human Evolution*, 35: 163-209.

Bhullar, Bhart-Anjan S., Marugan-Lobon, Jesus, Racimo, Ferndado, Bever, Gabe S., Rowe, Timothy B., Norell, Mark A., and Abzhanov, Arhat (2012): Birds have paedomorphic dinosaur skulls. *Nature*, 487: 223-226.

Bogin, Barry (1988): Patterns of Human Growth. Cambridge University Press, Cambridge.

Bolter, Debra R. and Zihlman, Adrienne L. (2011): Brief Communication: Dental Development Timing in Captive *Pan paniscus* With Comparisons to *Pan troglodytes*. *American Journal of Physical Anthropology*, 145: 647-652.

Bolter, Debra and Zihlman, Adrienne; (2012): Skeletal Development in *Pan paniscus* with comparisons to *Pan troglodytes*. *American Journal of Physical Anthropology*, 147: 629-636.

Bookstein, Fred L. (1978): The Measurement of Biological Shape and Shape Change. Springer-Verlag, New York.

Bookstein, Fred L. (1982): On the cephalometrics of skeletal change. *American Journal of Orthodontics*, 82: 177-198.

Bookstein, Fred, L. (1991): Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge: Cambridge University Press.

Borries, Carola; Koenig, Andreas; Winkler, Paul (2001): Variation in life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology*, 50: 391-402.

Breuckmann GmbH, (2009). Meersbug, Germany.

Breuer, Thomas; Robbins, Martha M.; Boesch, Christophe. (2007): Using Photogrammetry and Color Scoring to Assess Sexual Dimorphism in Wild Western Gorillas (*Gorilla gorilla*). *American Journal of Physical Anthropology*, 134: 369-382.

Breuer, Thomas; Hockemba, Mireille Breuer-Ndoundou; Olejniczak, Claudia; Parnell, Richard J.; Stokes, Emma J. (2008): Physical Maturation, Life-History Classes and Age Estimates of Free-Ranging Western Gorillas – Insights From Mbeli Bai, Republic of Congo. *American Journal of Primatology*, 70: 1-14.

Bromage, Timothy G. and Dean, M. Christopher, (1991): Re-evaluation of the age at death of immature fossil hominids. *Nature*, 317: 525-527.

Bruner, Emiliano and Manzi, Giorgio (2001): Allometric analysis of the skull in *Pan* and *Gorilla* by geometric morphometrics. *Rivista di Antropologia*, 79: 45-52.

Charnov, Eric L., (1991): Evolution of life history variation among female mammals. *Proceedings for the National Academy of Sciences, USA*, 88: 1134-1137.

Charnov, Eric L., (1993): Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford.

Charnov, Eric L., and David Berrigan, (1993): Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews* 1.6: 191-194.

Cheverud, James M., (1982): Phenotypic, Genetic, and Environmental Morphological Integration in the Cranium. *Evolution*, 36: 499-516.

Cheverud, James M. and Richtsmeier, Joan T. (1986): Finite-Element Scaling Applied to Sexual Dimorphism in Rhesus Macaque (*Macaca Mulatta*) Facial Growth. *Systematic Zoology*, 35: 381-399.

Cheverud, James; Lewis, Jack L; Bachrach, William; Lew, William D. (1983): The Measurement of Form and Variation in Form: An Application of Three-Dimensional Quantitative Morphology by Finite-Element Methods. *American Journal of Physical Anthropology*. 62: 151-165.

Cobb, Samuel N. and O'Higgins, Paul, (2004): Hominins Do Not Share a Common Postnatal Facial Ontogenetic Shape Trajectory. *Journal of Experimental Zoology*, 302B: 302-321.

Cobb, Samuel N. and O'Higgins Paul, (2007): The ontogeny of sexual dimorphism in the facial skeleton of the African apes. *Journal of Human Evolution*, 53: 176-190.

Cofran, Zachary and Walker, Christopher; (2017): Dental development in *Homo naledi*. *Royal Society, Biology Letters*, 13.

Corner, Brian D. and Richtsmeier, Joan, T., (1991): Morphometric Analysis of Craniofacial Growth in *Cebus apella*. *American Journal of Physical Anthropology*, 84: 323-342.

Currat, Mathias and Excoffier, Laurent, (2004): Modern Humans Did Not Admix with Neanderthals during Their Range Expansion into Europe. *PLoS Biology*, 2, 421.

Dart, R.A. (1925). *Australopithecus africanus*: The Man-Ape of South Africa. *Nature*, 115: 195-199.

de Beer, G. R. (1958): Embryos and Ancestors. Oxford Press, Oxford, United Kingdom.

de Beer, G. R., (1959): Paedomorphosis. *Proceedings XV Int. Cong. Zool*., 927-930.

Dean, M. C. (2006): Tooth microstructure tracks the pace of human life-history evolution. *Proceedings of the Royal Society B*, 273: 2799-2808.

Dean, M. C. and Wood, B. A., (1981): Developing Pongid Dentition and Its Use for Ageing Individual Crania in Comparative Cross-Sectional Growth Studies. *Folia Primatologica*, 36: 111-127.

Dean, M. C.; Stringer, C. B.; and Bromage, T. G, (1986): Age at Death of the Neanderthal Child From Devil's Tower, Gibraltar and the Implications for Studies of General Growth and Development of Neanderthals. *American Journal of Physical Anthropology*, 70: 301-309.

Dean, M. C.; Beynon, A. D.; Thackeray, J. F.; and Macho, G. A., (1993): Histological Reconstruction of Dental Development and Age at Death of a Juvenile *Paranthropus robustus* Specimen, SK 63, From Swartkrans, South Africa. *American Journal of Physical Anthropology*, 91: 401-419.

Dean, Christopher et al.; (2001): Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, 414: 628-631.

del Castillo, Daniela L.; Flores, David A.; Cappozzo, Humberto. (2014): Ontogenetic Development and Sexual Dimorphism of *Franciscana* Dolphin Skull: A 3D Geometric Morphometric Approach. *Journal of Morphology*: 275, 1366-1375.

Drake, Abby Grace (2011): Dispelling dog dogma: an investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. *Evolution and Development*, 13: 204-213.

Drake, Abby G. and Klingenberg, C. P., (2008): The pace of morphological change: historical transformation of skull shape in St. Bernard dogs. *Proceedings for the Royal Society of London B* 275: 71-76.

Dryden, I. L., & Mardia, K. V. (1992). Size and shape analysis of landmark data. *Biometrika*, 57-68.

Du, Andrew; Zipkin, Andrew; Hatala, Kevin; Renner, Elizabeth; Baker, Jennifer; Bianchi, Serena; Bernal, Kallista; and Wood, Bernard (2018): Pattern and process in hominin brain size evolution are scale-dependent. *Proceedings for the Royal Society, B*, 285.

Endler, John (1977): Geographic Variation, Speciation, and Clines. Princeton University Press.

Evin, Allowen; Owen, Joseph; Larson, Greger; Debiais-Thibaud, Melanie; Cucchi, Thomas; Strad Vidarsdottir, Una; Dobney, Kieth (2017): A test for paedomorphism in domestic pig cranial morphology. *Biology Letters*, 13.

Faulk, Dean, (2009): The natural endocast of Taung (*Australopithecus africanus*): Insights from the unpublished papers of Raymond Dart. *American Journal of Physical Anthropology*, 140(Supp 49): 49-65.

Faulk, Dean; Zollikofer, Christoph P. E.; Morimoto, Naoki; and Ponce de León, Marcia, (2012): Metopic suture of Taung (*Australopithecus africanus*) and its implications for hominin brain evolution. *Proceedings for the National Academy of Sciences, USA*, 109: 8467-8470.

Foth, Christian; Hedrick, Brandon; Ezcurra, Martin (2016): Cranial ontogenetic variation in early saurischians and the role of heterochrony in the diversification of predatory dinosaurs. *Peer J*, 4.

Fragaszy, Dorothy M.; Izar, Patricia; Qing Liu; Eshchar, Yonat; Young, Leigh Anna; Visalberghi, Elisabetta. (2015): Body Mass in Wild Bearded Capuchins, (*Sapajus libidinosus*): Ontogeny and Sexual Dimorphism. *American Journal of Primatology*: 78, 473-484.

Frost, Stephen (2001): Fossil Cercopithecidae from the Afar Depression, Ethiopia: species systematics and comparison to the Turkana Basin, PhD Dissertation, City University of New York.

Garcia-Martinez, Danial; Torres-Tamayo, Nicole; Torres-Sanchez, Isabel; Garcia-Rio, Francisco; Bastir, Markus. (2016): Morphological and functional implications of sexual dimorphism in the human skeletal thorax. *American Journal of Physical Anthropology*: 161, 467-477.

Godfrey, Laurie R. and Sutherland, Michael R., (1995a): What's growth got to do with it? Process and product in the evolution of ontogeny. *Journal of Human Evolution*, 29: 405-431.

Godfrey, Laurie R. and Sutherland, Michael R., (1995b): Flawed Inference; Why Size-based Tests of Heterochronic Processes Do Not Work. *Journal of Theoretical Biology*, 172: 43-61.

Godfrey, Laurie R. and Sutherland, Michael R., (1996): Paradox of Peramorphic Paedomorphosis: Heterochrony and Human Evolution. *American Journal of Physical Anthropology*, 99: 17-42.

Godfrey, Laurie R.; Samonds, K. E.; Jungers, W. L.; and Sutherland, M. R., (2001): Teeth, Brains, and Primate Life Histories. *American Journal of Physical Anthropology*, 114: 192-214.

Godfrey, L. R.; Samonds, K. E.; Jungers, W. L.; Sutherland, M. R.; and Irwin, M. T. (2004): Ontogenetic correlates of diet in Malagasy Lemurs. *American Journal of Physical Anthropology*, 123: 250-276.

Gonder, Mary; Disotell, Todd; Oates, John (2006). New Genetic Evidence on the Evolution of Chimpanzee Populations and Implications for Taxonomy. *International Journal of Primatology*: 27, 1103-1127.

Good, Philip I. (2006): Resampling Methods: A Practical Guide to Data Analysis, Third Edition. Boston: Birkhäuser.

Goodall, C. R. (1991). Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society, Series B*, 285-339.

Goswami, Anjali; Finarelli, John A. (2016): EMMLi: A maximum likelihood approach to the analysis of modularity. *International Journal of Evolution*: 70, 1622-1637.

Gould, S. J., (1977): Ontogeny and Phylogeny. Cambridge: Harvard University Press.

Gower, J. C. (1975). Generalized Procrustes Analysis. *Psychometrika*, 40(1), 33-51.

Green, Richard et al.: (2010): A Draft Sequence of the Neanderthal Genome. *Science*, 328: 710-722.

Groucutt, Huw, Grun, Rainer, et al., (2018): *Homo sapiens* in Arabia by 85,000 years ago. *Nature Ecology and Evolution*, 2: 800-809.

Groves, Colin (1967): Ecology and taxonomy of the gorilla. *Nature*. 213: 890-893.

Groves (1970). Population systematics of the gorilla. Journal of Zoology, London, 161: 287-300.

Groves, Colin (1986): Systematics of the great apes: IN Swindler, D; Erwin, J (eds.) Comparative primate biology, volume 1: systematics, evolution, and anatomy. New York: Alan R. Liss: 187-217.

Groves (2003). A history of gorilla taxonomy. In: Taylor, A.B. & Goldsmith, M.L. (eds.) Gorilla Biology: A Multidisciplinary Perspective. Cambridge: Cambridge U Press, pp. 15-34.

Groves (2005). Geographic variation with Eastern Chimpanzees (*Pan troglodytes cf. schweinfurthii* Giglioli, 1872). *Australian Primatology*.

Groves, Colin; Westwood, Celia; and Shea, Brian; (1992): Unfinished business: Mahalanobis and a clockwork orang. *Journal of Human Evolution*, 22: 327-340.

Grubb, Peter; Butynski, Thomas; Oates, John; Bearder, Simon; Disotell, Todd; Groves, Colin; Struhsaker, Thomas (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology*, 24: 1301-1357.

Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., and Bookstein, F. L. (2009): Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57: 48-62.

Gunz, P. (2012). Evolutionary relationships among robust and gracile australopiths, an "evo-devo" perspective. *Evol. Bio*. 39: 472-487.

Gunz, Philipp and Bulygina, K., (2012): The Mousterian child from Tesik-Tash is a Neanderthal: A geometric morphometric study of the frontal bone. *American Journal of Physical Anthropology*, 149: 365-379.

Gurven, Michael and Walker, Robert (2006): Energetic demand of multiple dependents and the evolution of slow human growth. *Proceedings for the Royal Society B*, 273: 835-841.

Haeckel, E. (1875): Die Gastrula und die Eifurchung der Thiere. *Jena. Z. Naturwiss*., 9: 402-508.

Hallgrímsson, Benedict; Lieberman, Daniel E.; Young, Nathan M.; Parsons, Trish; Wat, Steven. (2007a): Evolution of covariance in the mammalian skull. IN Bock, Gregory and Goode, Jamie (eds.) *Tinkering: The Microevolution of Development*. London: Wiley.

Hallgrímsson, B.; Lieberman, D. E.; Liu, W.; Ford-Hutchinson, A. F.; Jirik, F. R., (2007b): Epigenetic interactions and the structure of phenotypic variation in the cranium. *Evolution and Development*, 9: 76-91.

Harcourt, A.H.; Harvey, P.H. (1984): Sperm competition, testes size and breeding systems in primates. IN: Sperm Competition and the Evolution of Animal Mating Systems, ed. Smith, RL. 587-600. London: Academic

Harcourt, A.H.; Harvey, P.H.; Larsen, S.G.; Short, R.V. (1981): Testes weight, body weight, and breeding systems in primates. *Nature* 293:55-57.

Harvati, K. (2001): The Neanderthal Problem: 3-D geometric morphometric models of cranial shape variation within and among species. PhD Dissertation, City University of New York.

Harvey, Paul H. and Clutton-Brock, T. H., (1985): Life History Variation in Primates. Evolution, 39: 559-581.

Harvey, Paul H., Marin, R. D., and Clutton-Brock, T. H.; (1986): Life Histories in Comparative Perspective. IN: Primate Societies (Smuts, Barbara B., Cheney, Dorothy L., Seyfarth, Robert M., Wrangham, Richard W., and Struhsaker, Thomas T., eds.). University of Chicago Press, Chicago; 181-196.

Hay, Jody (2010): The Divergence of Chimpanzee Species and Subspecies as Revealed in Mulipopulation Isolation-with-Migration Analyses. *Molecular Biology and Evolution*, 27: 921-933.

Hershkovitz, Israel, Weber, Gerhard, Quam, Rolf, Duval, Mathieu, *et al*, (2018): The earliest modern humans outside Africa. *Science*, 359: 456-459.

Hill, Kim and Kaplan, Hillard (1999): Life History Traits in Humans: Theory and Empirical Studies. *Annual Review of Anthropology*, 28, 397-430.

Hogg, Russell T., Godfrey, Laurie R., Schwartz, Gary T., Dirks, Wendy, Bromage, Timothy G., (2015): Lemur Biorhythms and Life History Evolution. *Plos One*, 10: e0134210.

Holton, Nathan E.; Alsamawi, Ammar; Yokley, Todd R.; Froehle, Andrew W. (2016): The Ontogeny of Nasal Shape: An Analysis of Sexual Dimorphism in a Longitudinal Sample. *American Journal of Physical Anthropology*: 160, 52-61.

Jaeggi, Adrian V.; Dunkel, Lynda P.; van Noordwijk, Maria A.; Wich, Serge A.; Sura, Agnes A. L.; and van Schaik, Carel P. (2010): Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture. *American Journal of Primatology*, 72: 62-71.

Janson, Charles H. and van Schaik, Carel P., (1993): Ecological Risk Aversion in Juvenile Primates: Slow and Steady Wins the Race. IN: Pereira, Michael E. and Fairbanks, Lynn A. (eds.) Juvenile Primates: Life History, Development, and Behavior. Oxford U Press, New York, 57-74.

Jarmon, P. (1983): Mating system and sexual dimorphism in large, terrestrial mammalian herbivores. *Biological Reviews*: 58: 485-520.

Jones, James Holland, (2011): Primates and the Evolution of Long, Slow Life Histories. *Current Biology*, 21: R708-R717.

Kelley, Jay and Schwartz, Gary T., (2010): Dental development and life history in living African and Asian apes. *Proceedings for the National Academy of Science, USA*, 107: 1035-1040.

Kelley, Jay and Schwartz, Gary T., (2012): Life-History Inference in the Early Hominins *Australopithecus* and *Paranthropus*. *International Journal of Primatology*, 33: 1332-1363.

Kendall, D. (1977). The diffusion of shape. *Advances in Applied Probability*, 9, 428-430.

Kendall, D. G. (1989). A survey of the statistical theory of shape. *Statistical Science*, 87-120.

Klingenberg, C. P. (2016). Size, shape, and form: concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, 113-137.

Klingenberg, Christian Peter and Spence, John R. (1993): Heterochrony and Allometry: Lessons from the Water Strider Genus Limnoporus. *Evolution*, 47: 1834-1853.

Klingenberg, C. P., Duttke, S, Whelan, S, Kim, M, (2012): Developmental plasticity, morphological variation and evolvability: a multilevel analysis of morphometric integration in the shape of compound leaves. *Journal of Evolutionary Biology*, 25: 115-129.

Knigge, Ryan P.; Tocheri, Matthew W.; Orr, Caley, M; McNulty, Kieran P. (2015): Three-Dimensional Geometric Morphometric Analysis of Talar Morphology in Extant Gorilla Taxa from Highland and Lowland Habitats. *The Anatomical Record*, 298: 277-290.

Lacruz, Rodrigo; Ramirez Rozzi, Fernando; Bromage, Timothy (2005). Dental enamel hypoplasia, age at death, and weaning in the Taung child. *South African Journal of Science*, 101: 567-569.

Lack, David (1954): The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Laland, Kevin; Uller, Tobias; Feldman, Marcus; Sterelny, Kim; Muller, Gerg; Moczek, Armin; Jablonka, Eva; Odling-Smee, John (2014): The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings for the Royal Society, B*, 282.

Leakey, M.G., Spoor, F., Dean, M.C., Fiebel, C.S., Antón, S.C., Kiarie, C., & Leakey, L. (2012). New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature*, 488: 201-204.

Leigh, Steven R. (1992): Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution*, 23: 27-50.

Leigh, Steven R., (1994): Ontogenetic Correlates of Diet in Anthropoid Primates. *American Journal of Physical Anthropology*, 94: 499-522.

Leigh, Steven R. (1995): Socioecology and the Ontogeny of Sexual Dimrophism in Anthropoid Primates. *American Journal of Physical Anthropology*, 97: 339-356.

Leigh, Steven R. and Shea, Brian T. (1995): Ontogeny and the Evolution of Adult Body Size Dimorphism in Apes. *American Journal of Physical Anthropology*, 36: 37-60.

Leigh, Steven R. and Shea, Brian T. (1996): Ontogeny of Body Size Variation in African Apes. *American Journal of Physical Anthropology*, 99: 43-65.

Leigh, Steven R.; Setchell, Joanna M.; Buchanan, Laurel S. (2005): Ontogenetic Bases of Canine Dimorphism in Anthropoid Primates. *American Journal of Physical Anthropology*: 127, 296-311.

Lieberman, Daniel E.; Ross, Callum F.; Ravosa, Matthew J. (2000): The Primate Cranial Base: Ontogeny, Function, and Integration. *Yearbook of Physical Anthropology*. 43: 117-169.

Lieberman, Daniel E.; Carlo, Julian; Ponce de León, Marcia; Zollikofer, Christoph P. E., (2007): A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos. *Journal of Human Evolution*, 52: 647-662.

Lockwood, Charles A. (1999): Sexual Dimorphism in the Face of *Australopithecus africanus*. *American Journal of Physical Anthropology*, 108: 97-127.

Lordkipanidze, David; Ponce de Leon, Marcia; Margvelashvili, Ann; Rak, Yoel; Rightmire, Philip; Vekua, Abesalom; Zollikofer, Christoph (2013): A complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early *Homo*. *Science*, 342: 326-331.

Loza, C. M.; Scarano, A.C.; Soibelzon, L.H.; Negrete J.; Carlini, A.A. (2015): Morphology of the tympanic-basicranial region in Mirounga leonia (Phocidae, Carnivora), postnatal ontogeny and sexual dimorphism. *Journal of Anatomy*: 226, 354-372.

Marlowe, Frank W. (2010): The Hadza: Hunter-Gatherers of Tanzania. University of California Press, Berkley.

Martin-Serra, A, Figueirido, B, Palmqvist, P, (2014): A three-dimensional analysis of morphological evolution and locomotor performance of carnivoran forelimb. *Plos One*, 9: e85574.

Mayaux, Philippe; Bartholome, Etienne; Fritz, Steffen; and Belward, Alan. (2004): A new land-cover map of Africa for the year 2000. *Journal of Biogeography*, 31: 861-877.

Mayr, Ernst (1963): The taxonomic evaluation of fossil hominids. IN Washburn, S (ed.) Classification and Human Evolution, Aldine, Chicago.

McFarlin, Shannon C.; Barks, Sara K.; Tocheri, Matthew W.; Massey, Jason S.; Erikson, Amandine B.; Fawcett, Katie A.; Stoinski, Tara S.; Hof, Patrick R.; Bromage, Timothy G.; Mudakikwa, Antónie; Cranfield, Michael R.; Sherwood, Chet C., (2012): Early Brain Growth Cessation in Wild Virunga Mountain Gorillas (*Gorilla beringei beringei*). *American Journal of Primatology*, 75: 450-463.

McHenry, Henry M. (1992): Body Size and Proportions in Early Hominids. *American Journal of Physical Anthropology*, 87: 407-431.

McHenry, Henry M. (1994): Behavioral ecological implications of early hominid body size. *Journal of Human Evolution*, 27: 77-87.

McNulty, Kieran P. (2003): Geometric morphometric analyses of extant and fossil hominoid craniofacial morphology. PhD Dissertation, City University of New York.

McNulty, K.P. (2012). Evolutionary Development in *Australopithecus africanus. Evolutionary Biology*: 39, 488-498.

McNulty, Kieran P.; Frost, Stephen, R.; Strait, David S., (2006): Examining affinities of the Taung child by developmental simulation. *Journal of Human Evolution*, 51: 274-296.

Miller, J; Albrecht, G; Gelvin, B (2004). Craniometric variation in early Homo compared to modern gorillas: a population-thinking approach. In: Anapol, F., German. 4.Z., Jablonski, N.G. (Eds.) Shaping Primate Evolution: Form, Function and Behavior. Cambridge U Press, Cambridge, pp. 66-98.

Mitteroecker, Philipp; Gunz, Philipp; Bernhard, M; Schaefer, K; and Bookstein, F., (2004a): Comparison of cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution*, 46: 679-697.

Mitteroecker, Philipp; Gunz, Philipp; Bookstein, Fred L. (2004b): Regional dissociated heterochrony in multivariate analysis. *Annals of Anatomy*, 186: 463-470.

Mitteroecker, Philipp; Gunz, Philipp; and Bookstein, Fred L., (2005): Heterochrony and geometric morphometrics: a comparison of cranial growth in *Pan pansicus* versus *Pan troglodytes*. *Evolution and Development*, 7: 244-258.

Moss, Melvin L; Young, Richard W. (1960): A Functional Approach to Craniology.

O'Higgins, Paul and Jones, Nicholas (1998): Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. *Journal of Anatomy*, 193: 251-272.

O'Higgins, Paul and Strand Viðarsdóttir, Una (1999): New approaches to the quantitative analysis of craniofacial growth and variation. IN: Human growth in the past: studies from bones and teeth. Cambridge: Cambridge University Press: 128-160.

O'Higgins, Paul and Collard, Mark; (2002): Sexual dimorphism and facial growth in papionine monkeys. *Journal of Zoology, London*, 257: 255-272.

O'Higgins, P.; Chadfield, P.; Jones, N.; (2001): Facial growth and the ontogeny of morphological variation within and between the primates *Cebus apella* and *Cercocebus torquatus*. *Journal of Zoology*, 254: 255-272.

Optocat, 2012 version 11.01.06 – 2206.

Pagel, Mark D. and Harvey, Paul H., (1993): Evolution of the Juvenile Period in Mammals. IN: *Juvenile Primates: Life History, Development, and Behavior* (Pereira, Michael E. and Fairbanks, Lynn A. eds.). Oxford University Press, Oxford; 28-37.

Penin, X.; Berge, C.; Baylac, M. (2002): Ontogenetic study of the skull of modern humans and the common chimpanzee: neotenic hypothesis reconsidered with a tridimensional Procrustes analysis. *American Journal of Physical Anthropology*. 118: 50-62.

Pilbrow, Varsha (2003): Dental variation in African apes with implications for understanding patterns of variation in species of fossil apes. PhD Dissertation. New York University.

Pilbrow, Varsha (2006): Population systematics of chimpanzees using molar morphometrics. *Journal of Human Evolution*. 51: 646-662.

Pilbrow, Varsha (2010): Dental and phylogenetic patterns of variation in gorillas. *Journal of Human Evolution*, 59: 16-34.

Pilbrow, Varsha and Groves, Colin (2013): Evidence for Divergence in Populations of Bonobos (*Pan paniscus*) in the Lomami-Lualaba and Kasai-Sanuru Regions Based on Preliminary Analysis of Craniodental Variation. *International Journal of Praimatology*, 34: 1244-1260.

Plavcan, J. Michael (2002): Taxonomic variation in the patterns of craniofacial dimorphism in primates. *Journal of Human Evolution*, 42: 579-608

Plavcan, J. Michael (2012): Body Size, Size Variation, and Sexual Size Dimorphism in Early *Homo*. *Current Anthropology*, 53: 409-423.

Plavcan, J. Michael; van Schaik, Carel P.; Kappeler, Peter M. (1995): Competition, coalitions and canine size in primates. *Journal of Human Evolution*, 28: 245-276.

Ponce de León, Marcia and Zollikofer, Christoph P. E., (2001): Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature*, 412: 534-538

Ponce de León, Marcia and Zollikofer, Christoph P. E., (2008): Neanderthals and modern humans – chimps and bonobos: similarities and differences in development and evolution. IN: Neanderthals Revisited: New Approaches and Perspectives, Harvati, K; and Harrison, T (eds.). Springer, Leipzig, pp. 71-88.

Ponce de León, Marcia S; Golovanova, Lubov; Doronichev, Vladimir; Romanova, Galina; Akazawa, Takeru; Kondo, Osamu; Ishida, Hajime; Zollikofer, Christoph (2008): Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceedings for the National Academy of Sciences, USA*: 105: 13764-13768.

Pontzer, Herman; Raichlen, David A.; Shumaker, Robert W.; Ocobock, Cara; and Wich, Serge A. (2010): Metabolic adaptation for low energy throughput in orangutans. *Proceedings for the National Academy of Sciences, USA*, 1-5.

Pontzer, H., Raichlen, D. A., Wood, B. M., Mabulla, A. Z., Racette, S. B., & Marlowe, F. W. (2012). Hunter-gatherer energetics and human obesity. *Plos one*: 7, 40503.

Raff, R. A. (2000): Evo-devo: the evolution of a new discipline. *Nature Reviews Genetics*, 1: 74-79.

Raff, R. A. (2007): Written in stone: fossils, genes, and evo-devo. *Nature Reviews Genetics*, 8: 911-919.

Rak, Y., (1983): The australopithecine face. New York, Academic Press.

Ravosa, Matthew J. (1991): The Ontogeny of Cranial Sexual Dimorphism in Two Old World Monkeys: *Macaca fasicularis* (Cercopithecinae) and *Nasalis larvatus* (Colobinae). *International Journal of Primatology*, 12: 403-426.

Read, A. F. and Harvey, P. H. (1989): Life history differences among the eutherian radiations. *Journal of Zoology, London*, 219: 329-353.

Richtsmeier, Joan, T; Corner, Brian D.; Grausz, Hannah M.; Cheverud, James M.; Danahey, Steven E. (1993): The role of postnatal growth pattern in the production of facial morphology. *Systematic Biology*, 42: 307-330.

Rieux, Adrien; Eriksson, Anders; Li, Mingkun; Sobkowiak, Benjamin; Weinhert, Lucy A; Warmuth, Vera; Ruiz-Linares, Andres; Manica, Andrea; Balloux, Francois (2014): Improved calibration of the Human Mitochondrial Clock Using Ancient Genomes. *Molecular Biology and Evolution*, 31: 2780-2792.

Rightmire, Philip; Lordkipanidze, David; Vekua, Abesalom (2006): Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *Journal Human Evolution*, 50: 115-141.

Robbins MM, McNeilage A (2003): Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 24:467–491.

Robinson, Chris, (2012): Geometric morphometric analysis of mandibular shape diversity in *Pan*. *Journal of Human Evolution*, 63; 191-204.

Robson, Shannen L. and Wood, Bernard (2008): Hominin life history: reconstruction and evolution. *Journal of Anatomy*, 212: 394-425.

Rodriquez-Mendoza, R, Munoz, M, Saborido-Rey, F, (2011): Ontogenetic allometry of the bluemouth, *Helicolensus dactylopterus dactylopterus* (Teleostei: Scarpaenidae), in the Northeast Atlantic and Mediterranean based on geometric morphometrics. *Hydrobiologica*, 670: 5-22.

Rohlf, F. J. (1996). Morphometric spaces, shape components and the effects of linear transformations. In L. F. Marcus, M. Corti, A. Loy, G. J. Naylor, & D. E. Slice, Advances in Morphometrics (pp. 117-132). New York: Springer Science+Business Media.

Rohlf, F. J. (1999). Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification*, 16, 197-223.

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, 39(1), 40-59.

Ruff C., (2002): Variation in Human Body Size and Shape. *Annual Review of Anthropology*, 31: 211-232.

Sarmiento, Esteban and Oates, John (2000). The Cross River Gorillas: A Distinct Subspecies, Gorilla gorilla diehli, Matschie 1904. *American Museum Novitas*, 3304: 1-55.

The code and data analysis for this dissertation was generated using SAS® software. Copyright, SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA

Schaefer, Katrin; Mitteroecker, Philipp; Gunz, Phillip; Bernhard, Markus; Bookstein, Fred (2004): Craniofacial sexual dimorphism patterns and allometry among extant hominids. *Annals of Anatomy*, 186: 471-478.

Schwartz, Gary T. and Dean, Christopher. (2001): Ontogney of Canine Dimorphism in Extant Hominoids. American *Journal of Physical Anthropology*, 115: 269-283.

Shea, Brian T. (1983a): Allometry and Heterochrony in the African Apes. *American Journal of Physical Anthropology*, 62: 275-289.

Shea, Brian (1983b): Paedomorphosis and Neoteny in the Pygmy Chimpanzee. *Science*, 222: 521-522.

Shea, Brain T. (1985): The Ontogeny of Sexual Dimorphism in the African Apes. *American Journal of Primatology*, 8: 183-188.

Shea, Brian T. (1986): Ontogenetic Approaches to Sexual Dimorphism in Anthropoids. *Human Evolution*, 1: 97-110.

Shea, Brian T., (1989): Heterochrony in human evolution: The case for neonteny reconsidered. *Yearbook of Physical Anthropology*, 32: 690-702.

Shea, Brian; Leigh, Steven; and Groves, Colin (1993). Multivariate craniometric variation in chimpanzees. IN Kimbel, W and Martin, L (eds.) *Species, species concepts, and primate evolution*: 265-296. Springer, Boston.

Simons, Evan A.; Frost, Stephen R. (2016): Constructing cranial ontogenetic trajectories: A comparison of growth, development, and chronological age proxies using a known-age sample of *Macaca mulatta*. *American Journal of Physical Anthropology*, 161: 396-308.

Simpson, Scott W.; Lovejoy, C. Owen; and Meindl, Richard S., (1991): Relative Dental Development in Hominoids and Its Failure to Predict Somatic Growth Velocity. *American Journal of Physical Anthropology*, 86: 113-120.

Singleton, Michele. (2012): Postnatal Cranial Development in Papionin Primates: An Alternative Model for Hominin Evolutionary Development. *Evolutionary Biology*, 39: 499-520.

Skinner, Mark, (1997): Age at death of Gibraltar 2. *Journal of Human Evolution*, 32: 469-470.

Slice, D. E. (1996). Three-dimensional, generalized resistant fitting and the comparison of least-squares and resistant-fit residuals. In L. F. Marcus, M. Corti, A. Loy, G. J. Naylor, & D. E. Slice, Advances in Morphometrics (pp. 179-199). New York: Plenum Press.

Slice, D. (2001). Landmark coordinates aligned by Procrustes analysis do not lie in Kendall's shape space. *Systematic Biology*, 50, 141-149.

Slice, D. E., Bookstein, F. L., Marcus, L. F., & Rohlf, F. J. (1996). A glossary for geometric morphometrics. In L. F. Marcus, M. Corti, A. Loy, G. J. Naylor, & D. E. Slice, Advances in Morphometrics (pp. 531-552). New York: Springer Science .

Smith, B. Holly (1989): Dental Development as a Measure of Life History in Primates. *Evolution*, 43: 683-688.

Smith, Tanya M. (2013): Teeth and Human Life-History Evolution. *Annual Review of Anthropology*, 42: 191-208.

Smith, Tanya M.; Toussaint, Michel; Reid, Donald J.; Olejniczak, Anthony J.; Hublin, Jean-Jacques, (2007): Rapid dental development in a Middle Paleolithic Belgian Neanderthal. *Proceedings for the National Academy of Sciences, USA*, 104: 20220-20225.

Smith, T.M., Tafforeau, P., Reid, D.J., Pouech, J., Lazzari, V., Zermeno, J.P., Guatelli-Steinberg, D., Olejniczak, A.J., Hoffman, A., Radovčić, J., Masrour, M., Toussaint, M., Stringer, C., Hublin, J-J. (2010) Dental evidence for ontogenetic differences between modern humans and Neanderthals. Proc. Natl. Acad. Sci. USA 107:20923-20928.

Smith, Tanya M., Olejniczak, Anthony, J. Zermeno, John P., Tafforeau, Paul, Skinner, Matthew M., Hoffmann, Almut, Radovicic, Jakov, Toussaint, Michel, Kruszynski, Robert, Menter, Colin, Moggi-Cecchi, Jacopo, Glasmacher, Ulrich A., Kullmer, Ottmar, Schrenk, Friedemann, Stringer, Chris, Hublin, Jean-Jacques, (2012): Variation in enamel thickness within the genus *Homo*. *Journal of Human Evolution*, 62: 395-411.

Smith, Tanya M., Machanda, Zarin; Bernard, Andrew B.; Donovan, Ronan M.; Papakyrikos, Amanda M.; Muller, Martin N.; and Wrangham, Richard, (2013): First molar eruption, weaning, and life history in living wild chimpanzees. *Proceedings for the National Academy of Sciences, USA*, 110: 2787-2791.

Stearns, Stephen C. (1976): Life-History Tactics: A Review of the Ideas. *The Quarterly Review of Biology*, 51: 3-47.

Sterns, Stephen C. (1992): The Evolution of Life Histories. Oxford University Press, Oxford.

Strand Viðarsdóttir, Una and O'Higgins, Paul (2003). Developmental variation in the facial skeleton of anatomically modern *Homo sapiens*. In: Patterns of Growth and Development in the Genus *Homo*, Thompsons, J., Krovitz, G., & Nelson, A (eds.). Cambridge: Cambridge U Press. 114-143.

Strand Viðarsdóttir, Una; O'Higgins, Paul; Stringer, Chris (2002): A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *Journal of Anatomy*, 201: 211-229.

Stratovan Corporation (2005-2016): Stratovan Checkpoint version 2016.06.28.0428.

Stringer, C. B., and Dean, M. C., (1997): Age at death of Gibraltar 2 – a reply. *Journal of Human Evolution*, 32: 471-472.

Taylor, Andrea B. (1997): Relative Growth, Ontogeny, and Sexual Dimorphism in *Gorilla* (*Gorilla gorilla gorilla* and *G. b. beringei*): Evolutionary and Ecological Considerations. *American Journal of Primatology*, 43: 1-31.

Terhune, Claire E.; Kimbel, William H.; Lockwood, Charles, A. (2007): Variation and diversity in *Homo erectus*: a 3D geometric morphometric analysis of the temporal bone. *Journal of Human Evolution*, 53: 41-60.

Trinkaus, Erik, (2007): European early modern humans and the fate of Neandertals. *Proceedings of the National Academy of Sciences, USA*, 104: 7367-7372.

Uchida, Akiko (1992): Intra-species variation among the great apes: Implications for taxonomy of fossil hominoids. PhD Dissertation. Harvard University.

Uchida, Akiko (1996): What we don't know about great ape variation. *TREE*, 11: 163-168.

Vigilant, L., Roy, J., Bradley, B. J., Stoneking, C. J., Robbins, M. M., Stoinski, T. S., (2015). Reproductive competition and inbreeding avoidance in a primate species with habitual female dispersal. *Behavioral Ecology and Sociobiology*, 69: 1163-1172.

von Baer, K. E., (1828): Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion (Borntraeger, Koenigsberg).

Walker, Robert and Hill, Kim (2003): Modeling Growth and Senescence in Physical Performance Among the Ache of Eastern Paraguay. *American Journal of Human Biology*, 15: 196-208.

Watts, David P. (1985): Observations on the Ontogeny of Feeding Behavior in Mountain Gorillas (*Gorilla gorilla beringei*). *American Journal of Primatology*, 8: 1-10.

Watts, David P. and Pusey, Anne E. (1993): Behavior or Juvenile and Adolescent Great Apes. IN: Juvenile Primates: Life History, Development, and Behavior (Pereira, Michael E. and Fairbanks, Lynn A. eds.). Oxford University Press, Oxford; 148-167.

Weisensee, K.E. and Jantz, R. L., (2011): Secular change in craniofacial morphology of the Portuguese using geometric morphometrics. *American Journal of Physical Anthropology*, 145: 548-559.

White, Tim D.; Black, Michael T.; Folkens, Pieter A. (2012): Human Osteology 3rd ed. Elsevier.

Wiley, R. H. (1974): Evolution of social organization and life-history patterns among grouse. *Quarterly Review of Biology*, 49: 201-227.

Williams, George C. (1957): Pleiotropy, Natural Selection, and the Evolution of Senescence. Evolution, 11: 398-411.

Williams, George C. (1966): Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. American Naturalist, 100: 687-690.

Zeldich, Miriam Leah; Swiderski, Donald L.; Sheets, H. David, (2012): Geometric Morphometrics for Biologists: A Primer, Second Edition. Elsevier, Amsterdam.

Zihlman, A. L.; Bolter, D; and Boesch, C. (2004): Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *Proceedings for the National Academy of Sciences,USA*, 101: 10541-10543.

Zollikofer, C. P. E. and Ponce de León, M. S., (2004): Kinematics of Cranial Ontogeny: Heterotropy, Heterochrony, and Geometric Morphometric Analysis of Growth Models. *Journal of Experimental Zoology*, 302B: 322-340.

Zollikofer, Christoph P. E. and Ponce de León, Marcia S., (2010): The evolution of hominin ontogenies. *Seminars in Cell & Developmental Biology*, 21: 441-452.

11 Appendix

Table 11.1: List of landmarks used in this study, their abbreviations, and definitions.

Landmark	Abbr.	Definition
Anterior Landmarks		
Glabella	GLA	Most anterior midline point on the frontal bone
Nasion	NAS	Junction of naso-frontal and internasal sutures
Rhinion	RHI	Most inferior point of internasal suture
Frontomalare orbitale	FMO	Junction of frontozygomatic suture and orbital rim
Dacryon	DAC	Junction of the frontal with the maxillolacrimal suture
Zygoorbitale	ZOO	Junction of zygomaticomaxillary suture and the orbital rim
Malar foramen	MAF	Superior margin of the largest malar foramen
Zygomaxillare	ZOM	Most inferior point on the zygomaticomaxillary suture
Superior premaxillary suture	SPS	Most superior aspect of premaxillary suture
Midtorus superior	MTS	Most superior part on the supraorbital torus projected directly above MTI
Midtorus inferior	MTI	Midline point on the superior margin of the orbit
Orbitale	ORB	Most inferior point on the orbital margin
Alare	ALA	Most lateral point on the margin of the nasal aperture
Nasomaxillary suture	NMA	Point at which nasomaxillary sutures meet aperture
Infraorbital foramen	IFO	Superior margin of the largest infraorbital foramen
Anterior nasal spine	ANS	Most anterior insertion of cartilaginous nasal septum
Alveolare	ALV	Most inferior midline point on the bony septum between the central incisors
Lateral Landmarks		
Superior Zygomaticotemporal suture	SZT	Most superior point on the zygomaticotemporal suture of the zygomatic arch
Frontosphenomalare	FSM	Point on external cranial vault where frontal, sphenoid and malar bones join
Frontomalare temporale	FMT	Point where the frontozygomatic suture crosses the temporal line
Stephanion	ST	The intersection of the coronal suture and the inferior temporal line

Buccal interdental points	BID	Contact points for each tooth pair projected laterally to the alveolar margin
Distal M3	DM3	Most distal point on M3 projected laterally to the alveolar margin
Porion	POR	Most superior point on the margin of the external auditory meatus
Auriculare	AUR	Point vertically above the center of the external auditory meatus at the root of the zygomatic process, a few millimeters above porion
Jugale	JUG	Point in the depth of the notch between the temporal and frontal processes of the zygomatic
Malar root	MLR	Point where malar root arises from the maxilla
Mid-temporal squama	MSQ	Point midway along squamosal suture
Zygion	ZYG	Most lateral point on the zygomatic arch
Posterior Landmarks		
Lambda	LDA	Junction of the sagittal and lambdoidal suture
Asterion	AST	Common meeting point of the lambdoid, parietomastoid, and occipitalmastoid sutures
Opisthocranion	OPC	Most posterior midline point on the cranium
Superior Landmarks		
Bregma	BRG	Junction of coronal and sagittal sutures
R/L bregma	L/RBG	Point on the coronal suture just off the sagittal crest onto the neurocranium. When no sagittal crest exists, this point is the same as bregma
Internal bregma	AVBG	The average distance of R and L bregma, or the projection of bregma into the sagittal crest just above the neurocranium. Where no sagittal crest exists, this point is the same as Bregma
Midline post-toral sulcus	MPT	Most inferior midline point of the post-glabellar concavity
Metopion	MET	Point midway between nasion and bregma on the midline
Mid-parietal	MP	Point midway along the parietals on the midline
R/L mid-parietal	L/RMP	Point on the neurocranium and off the sagittal crest projected inferiorly from mid-parietal when the cranium is held in Frankfort Horizontal. When no sagittal crest exists, this point is the same as mid-parietal

Internal mid-parietal	AVMP	The average distance of R and L mid-parietal, or the projection of mid-parietal into the sagittal crest just above the neurocranium. Where no sagittal crest exists, this point is the same as mid-parietal
Inferior Landmarks		
Midline anterior palatine	MAP	Junction of median palatine and transverse palatine sutures
Incisivion	ISV	Most posterior point of oral incisive foramen
Inferior zygomaticotemporal suture	IZS	Most inferior point on the zygomaticotemporal suture of the zygomatic arch
Foramen spinosum	FSP	Point on lateral margin of foramen spinosum
Spheno-palatine suture	SPL	Most inferior point on the suture between palatine and sphenoid bones (on pterygoid process
Spenotemporal suture	TSS	Point where spheotemporal suture passes from squama to cranial base
Lingual interdental points	LID	Contact points for each tooth pair projected medially to the alveolar margin
Lingual most aspect of canine	LAC	Most lingual point on canine projected to the alveolar bone
Maxillary tuberosity	MT	Most posterior point on ‘occlusal’ surface of alveolus
Lateral foramen ovale	LFO	Lateral margin of foramen ovale
Opisthion	OPI	Midline posterior margin of the foramen magnum
Basion	BAS	Midline anterior margin of the foramen magnum
Hormion	HOR	Most posterior midline point on the vomer
Staphylion	STA	Point on the median palatine suture where it intersects with a line drawn between the deepest aspect of the notches at the rear of the palate
Posterior occipital condyle	POC	Most posterior point on long axis of occipital condyle, taken on the articular surface
Anterior occipital condyle	AOC	Most anterior point on the long axis of occipital condyle, taken on the articular surface
Mastoidiale	MAD	Most inferior point on the mastoid process
Stylomastoid foramen	SMF	Posterior border of stylomastoid foramen
Lateral jugular fossa	LJF	Lateral margin of the jugular fossa
Postglenoid	PG	Most inferior point on the postglenoid process
Lateral mandibular fossa	LAF	Most lateral aspect of the mandibular fossa

	Center of mandibular fossa	CMF	Point of intersection of the long axis and the axis perpendicular to the long axis of the mandibular fossa
	Center of articular eminence	CAE	Point on the center of the articular eminence
	Anteriomedial projection of petrous bone	AMP	Most anteriomedial projection of petrous bone
	Lateral carotid canal	LCC	Most lateral point on the margin of the carotid canal
	External acoustic porus	IEA	Most inferior point on the external acoustic porus
	Sphenoidbasion	SB	Midline point on the basisphenoid synchondrosis
	Posterior nasal spine	PNS	Most posterior midline point on the palate
	Orale	OR	Midline point on the median palatine suture interests with a line drawn tangent to the posterior margins of the central incisor alveoli
	Greater palatine foramen	GPF	Most posterior margin of the greater palatine foramen

Table 11.2: Landmarks in analyses. Landmarks are ordered as they were collected in Stratovan Checkpoint. Variable number is the corresponding X, Y, and Z positions of each landmark.

#	Landmark Name	Variable #		
		x	**y**	**z**
1	Left orbitale	1	2	3
2	Left porion	4	5	6
3	Right porion	7	8	9
4	Right orbitale	10	11	12
5	Bregma	13	14	15
6	Basion	16	17	18
7	Glabella	19	20	21
8	Nasion	22	23	24
9	Rhinion	25	26	27
10	Anterior nasal spine	28	29	30
11	Alveolare	31	32	33
12	Orale	34	35	36
13	Incisivion	37	38	39
14	Midline anterior palatine	40	41	42
15	Stphylion	43	44	45
16	Posterior nasal spine	46	47	48
17	Hormion	49	50	51
18	Sphenoidbasion	52	53	54
19	Opisthion	55	56	57
20	Opisthocranion	58	59	60
21	Lambda	61	62	63
22	Mid-parietal	64	65	66
23	Metopion	67	68	69
24	Midline post-toral sulcus	70	71	72
25	Left Superior zygomaticotemporal suture	73	74	75
26	Left Inferior zygomaticotemporal suture	76	77	78
27	Left Frontosphenomalare	79	80	81
28	Left Stephanion	82	83	84
29	Left Bregma	85	86	87
30	Left Midparietal	88	89	90
31	Left Zygion	91	92	93

32	Left Asterion	94	95	96
33	Left Frontomalare temporale	97	98	99
34	Left Mid-temoral squama	100	101	102
35	Left Auriculare	103	104	105
36	Left External acoustic porus	106	107	108
37	Left Jugale	109	110	111
38	Left Malar root	112	113	114
39	Left Frontomalare orbitale	115	116	117
40	Left Dacryon	118	119	120
41	Left Mid-torus inferior	121	122	123
42	Left Mid-torus superior	124	125	126
43	Left Zygoorbitale	127	128	129
44	Left Zygomaxillare	130	131	132
45	Left Malar foramen	133	134	135
46	Left Infraorbital foramen	136	137	138
47	Left Superior premaxillary suture	139	140	141
48	Left Inferior premaxillary suture	142	143	144
49	Left Inferior nasomaxillary suture	145	146	147
50	Left Alare	148	149	150
51	Left Lingual most aspect of canine	151	152	153
52	Left Greater palatine foramen	154	155	156
53	Left Maxillary tuberosity	157	158	159
54	Left Spheno-palatine suture	160	161	162
55	Left Foramen spinosum	163	164	165
56	Left Lateral foramen ovale	166	167	168
57	Left Lateral jugular foramen	169	170	171
58	Left Lateral carotid canal	172	173	174
59	Left Anteriomedial projection of petrous bone	175	176	177
60	Left Temporo-sphenoid suture	178	179	180
61	Left Mastoidiale	181	182	183
62	Left Stylomastoid foramen	184	185	186
63	Left Postglenoid	187	188	189
64	Left Lateral mandibular fossa	190	191	192
65	Left Center of articular eminence	193	194	195
66	Left Medial mandibular fossa	196	197	198

67	Left Center of mandibular fossa	199	200	201
68	Left Anterior occipital condyle	202	203	204
69	Left Posterior occipital condyle	205	206	207
70	Left Distal M3 - Lingual	208	209	210
71	Left Distal M3 - Buccal	211	212	213
72	Left M3 M2	214	215	216
73	Left M2 M1	217	218	219
74	Left M1 P4	220	221	222
75	Left P4 P3	223	224	225
76	Left P3 C	226	227	228
77	Left C I2	229	230	231
78	Left I2 I1	232	233	234
79	I1 I1	235	236	237
80	Right I1 I2	238	239	240
81	Right I2 C	241	242	243
82	Right C P3	244	245	246
83	Right P3 P4	247	248	249
84	Right P4 M1	250	251	252
85	Right M1 M2	253	254	255
86	Right M2 M3	256	257	258
87	Right Distal M3 - Buccal	259	260	261
88	Right Distal M3 - Lingual	262	263	264
89	Left M3 M2	265	266	267
90	Left M2 M1	268	269	270
91	Left M1 P4	271	272	273
92	Left P4 P3	274	275	276
93	Left P3 C	277	278	279
94	Left C I2	280	281	282
95	Left I2 I1	283	284	285
96	I1 I1	286	287	288
97	Right I1 I2	289	290	291
98	Right I2 C	292	293	294
99	Right C P3	295	296	297
100	Right P3 P4	298	299	300
101	Right P4 M1	301	302	303

102	Right M1 M2	304	305	306
103	Right M2 M3	307	308	309
104	Right Superior zygomaticotemporal suture	310	311	312
105	Right Inferior zygomaticotemporal suture	313	314	315
106	Right Frontosphenomalare	316	317	318
107	Right Stephanion	319	320	321
108	Right Bregma	322	323	324
109	Right Midparietal	325	326	327
110	Right Zygion	328	329	330
111	Right Asterion	331	332	333
112	Right Frontomalare temporale	334	335	336
113	Right Mid-temoral squama	337	338	339
114	Right Auriculare	340	341	342
115	Right External acoustic porus	343	344	345
116	Right Jugale	346	347	348
117	Right Malar root	349	350	351
118	Right Frontomalare orbitale	352	353	354
119	Right Dacryon	355	356	357
120	Right Mid-torus inferior	358	359	360
121	Right Mid-torus superior	361	362	363
122	Right Zygoorbitale	364	365	366
123	Right Zygomaxillare	367	368	369
124	Right Malar foramen	370	371	372
125	Right Infraorbital foramen	373	374	375
126	Right Superior premaxillary suture	376	377	378
127	Right Inferior premaxillary suture	379	380	381
128	Right Inferior nasomaxillary suture	382	383	384
129	Right Alare	385	386	387
130	Right Medial most aspect of canine	388	389	390
131	Right Greater palatine foramen	391	392	393
132	Right Maxillary tuberosity	394	395	396
133	Right Spheno-palatine suture	397	398	399
134	Right Foramen spinosum	400	401	402
135	Right Lateral foramen ovale	403	404	405
136	Right Lateral jugular foramen	406	407	408

137	Right Lateral carotid canal	409	410	411
138	Right Anteriomedial projection of petrous bone	412	413	414
139	Right Temporo-sphenoid suture	415	416	417
140	Right Mastoidiale	418	419	420
141	Right Stylomastoid foramen	421	422	423
142	Right Postglenoid	424	425	426
143	Right Lateral mandibular fossa	427	428	429
144	Right Center of articular eminence	430	431	432
145	Right Medial mandibular fossa	433	434	435
146	Right Center of mandibular fossa	436	437	438
147	Right Anterior occipital condyle	439	440	441
148	Right Posterior occipital condyle	442	443	444

Table 11.3: Landmark deletions per study threshold. The "X" denotes that the landmark did not meet the threshold for that method and was deleted from subsequent analyses.

Landmark	Reduction 1	Reduction 2	Reduction 3
Midline landmark			
Bregma		**X**	**X**
Basion		**X**	**X**
Glabella			
Nasion			
Rhinion			
Anterior nasal spine	**X**	**X**	**X**
Alveolare			
Orale		**X**	**X**
Incisivion	**X**	**X**	**X**
Midline anterior palatine			**X**
Staphylion			**X**
Posterior nasal spine			**X**
Hormion		**X**	**X**
Sphenobasion			**X**
Opisthion	**X**	**X**	**X**
Opisthocranion		**X**	**X**
Lambda		**X**	**X**
Mid-parietal			
Metopion			
Midline post-toral sulcus			
Left Landmarks			
Orbitale			**X**
Porion	**X**	**X**	**X**
Superior zygomaticotemporal suture		**X**	**X**
Inferior zygomaticotemporal suture	**X**	**X**	**X**
Frontosphenomalare	**X**	**X**	**X**
Stephanion	**X**	**X**	**X**
Bregma off sagittal crest		**X**	**X**
Midparietal off sagittal crest			**X**
Zygion		**X**	**X**
Asterion			**X**
Frontomalare temporale			**X**
Mid-temporal squama			**X**
Auriculare			
External acoustic porus			
Jugale			**X**
Malar root		**X**	**X**
Frontomalare orbitale	**X**	**X**	**X**
Dacryon	**X**	**X**	**X**
Mid-torus inferior			**X**
Mid-torus superior			**X**
Zygoorbitale	**X**	**X**	**X**
Zygomaxillare			**X**
Malar foramen			
Infraorbital foramen			**X**
Superior premaxillary suture	**X**	**X**	**X**
Inferior premaxillary suture			**X**
Inferior nasomaxillary suture	**X**	**X**	**X**

Alare			X
Lingual most aspect of canine		X	X
Greater palatine foramen	X	X	X
Maxillary tuberosity	X	X	X
Spheno-palatine suture	X	X	X
Foramen spinosum			X
Foramen ovale	X	X	X
Lateral jugular foramen		X	X
Lateral carotid canal		X	X
Anteriomedial projection of petrous			X
Temporo-sphenoid suture			X
Mastoidale		X	X
Stylomastoid foramen		X	X
Postglenoid	X	X	X
Lateral mandibular fossa		X	X
Articular eminence			
Medial mandibular fossa			X
Center of mandibular fossa			X
Anterior occipital condyle		X	X
Posterior occipital condyle		X	X
Distal M3 – lingual	X	X	X
Distal M3 – buccal			
Buccal M3-M2	X	X	X
Buccal M2-M1	X	X	X
Buccal M1-P4			X
Buccal P4-P3			X
Buccal P3-C	X	X	X
Buccal C-I2		X	X
Buccal I2-I1		X	X
Buccal I1-I1		X	X
Lingual M3-M2			X
Lingual M2-M1	X	X	X
Lingual M1-P4	X	X	X
Lingual P4-P3	X	X	X
Lingual P3-C	X	X	X
Lingual C-I2			
Lingual I2-I1			
Lingual I1-I1			
Right Landmarks			
Buccal I1-I2		X	X
Buccal I2-C		X	X
Buccal C-P3	X	X	X
Buccal P3-P4			X
Buccal P4-M1			X
Buccal M1-M2	X	X	X
Buccal M2-M3	X	X	X
Distal M3 – buccal		X	X
Distal M3 – lingual	X	X	X
Lingual I1-I2			
Lingual I2-C			
Lingual C-P3	X	X	X
Lingual P3-P4	X	X	X
Lingual P4-M1	X	X	X
Lingual M1-M2	X	X	X

Lingual M2-M3			X
Orbitale			X
Porion	X	X	X
Superior zygomaticotemporal suture			X
Inferior zygomaticotemporal suture	X	X	X
Frontosphenomalare	X	X	X
Stephanion			
Bregma off sagittal crest		X	X
Midparietal off sagittal crest			X
Zygion		X	X
Asterion		X	X
Frontomalare temporale			X
Mid-temporal squama			
Auriculare			
External acoustic porus			
Jugale			X
Malar root		X	X
Frontomalare orbitale	X	X	X
Dacryon	X	X	X
Mid-torus inferior			X
Mid-torus superior			X
Zygoorbitale	X	X	X
Zygomaxillare			X
Malar foramen			
Infraorbital foramen			X
Superior premaxillary suture	X	X	X
Inferior premaxillary suture			
Inferior nasomaxillary suture	X	X	X
Alare			X
Lingual most aspect of canine		X	X
Greater palatine foramen	X	X	X
Maxillary tuberosity	X	X	X
Spheno-palatine suture	X	X	X
Foramen spinosum			X
Foramen ovale	X	X	X
Lateral jugular foramen		X	X
Lateral carotid canal		X	X
Anteriomedial projection of petrous			X
Temporo-sphenoid suture			X
Mastoidale		X	X
Stylomastoid foramen		X	X
Postglenoid	X	X	X
Lateral mandibular fossa			X
Articular eminence			
Medial mandibular fossa		X	X
Center of mandibular fossa			X
Anterior occipital condyle		X	X
Posterior occipital condyle		X	X