Mandibular Growth in *Australopithecus robustus*

by

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Abstract

Mandibular growth in *Australopithecus robustus*

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This dissertation tests the hypothesis that humans' unique pattern of growth was present in our fossil relative, *Australopithecus robustus*. Growth and development encompass the mechanisms and processes that bring about morphological variation and adaptation. Growth is also an important life history variable influencing both an animal's energy requirements and how it is treated by predators and conspecifics. Humans' unique pattern of growth, featuring long juvenile and childhood phases of slow growth followed by an adolescent growth spurt, is critical to the acquisition of language and culture. Unfortunately, the fragmentary and cross-sectional nature of fossil samples makes it difficult to ascertain the evolution of this pattern.

A novel randomization method, the ζ□□□□□□□ test, is developed to statistically test the null hypothesis that patterns of ontogenetic variation cannot be distinguished in the mandibles of humans and *A. robustus*. This species is not a direct human ancestor, but is closely related with a recent common ancestor and its mandible comprises the largest ontogenetic series of an early hominid. The ζ test compares age-related changes between pairs of specimens, and so maximizes information obtained from

fossil samples compared with traditional methods. This method can be extended to test other hypotheses with datasets do not meet assumptions of traditional statistics.

Results of the ζ test indicate *A*. *robustus* mandibular growth differs from humans' during two periods. First, prior to the eruption of the first permanent teeth, *A*. *robustus*' corpus breadth increases much more than humans'. Second, the *A*. *robustus* mandible increases in most dimensions in the time between the eruption of the first and second permanent molars, whereas human mandibular size tends to increase more after the second molar is occluded. These results suggest that the human pattern of growth was not shared with *A*. *robustus*, and provide the first statistical evidence for differences in skeletal size growth between humans and an early Pleistocene hominid. These findings are discussed in terms of life history and evolutionary developmental biology, including the possibility of early weaning, the influence of the developing dentition, and bone functional adaptation in *A*. *robustus*.

Chapter 1

Introduction

Processes of growth and development are the proximate mechanisms responsible for humankind's unique biology and behaviors. The goal of this dissertation is to increase our understanding of growth and development in early hominid evolution, to better understand how and when the human condition evolved. The most direct evidence for this must come from the fossil record (Raff, 2007), and despite a large number of hominid fossils at various stages of ontogeny, there is still much to be learned about how humans' extinct ancestors and relatives grew up. Some of the gaps in our knowledge lie in the nature of fossil samples – subadults and adequate representations of ontogenetic series are relatively rare – while others lie in the methods with which ontogenetic studies have been carried out. In order to provide new evidence as to the evolution of human development, this dissertation presents a new method for analyzing patterns of growth in fossil samples, comparing the amount of size change between dental eruptions in mandibles of humans and our extinct relative *Australopithecus robustus*. This chapter introduces this species, and previews the content of this contribution to paleoanthropology.

Kissing Cousins.

The earliest age of the Pleistocene epoch, from 2.58-1.81 million years ago (mya; Gibbard et al., 2010), was a key time in hominid evolution. This period saw the rise of at

least two contemporaneous and sympatric lineages: the genus *Homo* (Leakey et al., 1964), our ancestors, and a lineage of "robust" *Australopithecus* in both East (Leakey and Leakey, 1964; Leakey and Walker, 1976) and South Africa (Broom, 1938; Broom and Robinson, 1949). These lineages likely share a common ancestor in a 'gracile' australopith (or "australopithecine," referring to any species in the genus *Australopithecus*) such as *Australopithecus afarensis* or *africanus*, and can be distinguished largely on the basis of the development of the masticatory apparatus. Fossils attributed to *Homo* generally have more lightly built jaws, smaller muscle attachments, and smaller postcanine teeth than the robust australopiths: hence the term "robust" refers only to craniodental characteristics. Because of this gross similarity, robust australopiths are often grouped together in the genus *Paranthropus* (e.g. Strait and Grine, 2004), although the implied monophyly is uncertain on anatomical (Rak, 1983; Kimbel et al., 1988; McCollum, 1999; but see Suwa et al., 1997) and ecological or trophic grounds (Ungar et al., 2008; van der Merwe et al., 2008; Cerling et al., 2011).

This research examines similarities in the pattern growth (i.e. the amount of size change between dental eruptions) in members of each of these lineages, the extinct *Australopithecus robustus* and modern humans (*Homo sapiens*). The *A. robustus* mandibular sample is the largest ontogenetic series of an early Pleistocene hominid, and this species is very closely related to humans sharing a recent common ancestor. *A. robustus* fossils are known from a number of Pleistocene sites in the Sterkfontein Valley in South Africa. The type specimen, the partial skull TM 1517, comes from the B deposits of the Kromdraai site (Broom, 1938), but the bulk of this species' fossils are from the nearby site of Swartkrans (Broom, 1949; Brain, 1981, 2004). The Swartkrans

australopiths were initially distinguished as a separate species, *Paranthropus crassidens* (Broom, 1949; Grine, 1982), but most now consider these remains to be conspecific with the Kromdraai B remains (Brain, 1981; Fuller, 1996; Kaszycka, 2002; Cofran and Thackeray, 2010).

More recently, some remarkable findings from other Sterkfontein valley sites have been attributed to *A. robustus*. Two hominid teeth are known from the site of Gondolin (Menter et al., 1999). Of these, GDA-2 is a lower second molar (M_2) larger than any other South African australopith molar, but within the range of the East African "hyper-robust" *A. boisei*. In addition, DNH 7 is the most complete skull (cranium and mandible) attributed to *A. robustus*, coming from the site of Drimolen (Keyser, 2000; Keyser et al., 2000). Finally, COB 101 a partial (and crushed) cranium comes from the site of Cooper's Cave (Steininger et al., 2008). *A. robustus*-bearing deposits from all these sites, including Swartkrans and Kromdraai, are probably roughly contemporaneous (Herries et al., 2009; Pickering et al., 2011). However, for reasons discussed in Chapter 3, the present analysis focuses on the *A. robustus* mandibular series from Swartkrans only.

Figure 1. The *Australopithecus robustus* ontogenetic series from Swartkrans. From youngest to oldest, these include: (bottom row, left to right) SK 438, 64, 3978, 62, 61, 63; (top row, left to right) SK 25, 55b, SKX 4446, SK 843, 6, and SKW 5. SK 1587 is not pictured.

The *A. robustus* face is generally interpreted in terms of its adaptive capabilities for processing a variable diet, relying at least occasionally on hard-objects like nuts and/or requiring prolonged periods of chewing (Robinson, 1954; Rak, 1983; Wolpoff, 1999; Teaford and Ungar, 2000; Grine et al., 2012). From a functional standpoint, the species' jaws and face are adapted to creating high bite forces across the molars and premolars. Tall mandibular rami provide a lever advantage to the medial pterygoid muscles and to the masseter muscle laterally, for generating largely vertical chewing forces (Rak and Hylander, 2008). Tall rami also reduce gape (i.e. the ability to accommodate a large food bolus), which results in more evenly distributed forces throughout the length tooth row.

Consistent with its powerful chewing capabilities, mechanical properties of *A. robustus*' bony mandible itself allow it to withstand high stresses from mastication (Wolpoff, 1975; White, 1977). For instance, the ramus is strengthened against vertical bending forces from the temporalis muscle by a pronounced endocoronoid buttress. The mandibular symphysis is buttressed with superior and inferior 'tori,' keeping the symphysis from wish-boning during mastication. More distally, the corpus is resistant to transverse bending and torsion forces due to the distribution of cortical bone about a relatively broad cross-section (Daegling, 1989; Daegling and Grine, 1991; Grine and Daegling, 1993). The broad corpus in many cases takes on a nearly circular cross-section, a geometry that theoretically increases strength against torsion and mediolateral bending, although it is the distribution of cortical bone about this cross-section that actually determines the corpus' strength.

In light of *A. robustus*' masticatory capabilities, discerning the species' actual diet has been difficult (reviewed in Grine et al., 2012). Analysis of microscopic wear on the molar and premolar teeth of *A. robustus* suggest a diet including more hard-objects than *Australopithecus africanus* (a South African hominid predating and possibly ancestral to *A. robustus*), but there is overlap between the two species (Scott et al., 2005). In addition, both these species are indistinguishable from South African early *Homo* in their ratios of dietary carbon isotopes, a chemical signature that can discern only broad dietary categories (Lee-thorp et al., 2000; Lee-Thorp and Sponheimer, 2006; Ungar and Sponheimer, 2011). Finally, there is mounting evidence that *A. robustus* subsisted to some degree on termites, which it would have obtained using bone tools such as those found at Swartkrans and Drimolen (Backwell and D'Errico, 2001; Lesnik and Thackeray, 2007; Backwell and d' Errico, 2008; Lesnik, 2011 a-b). Suffice it to say, the derived facial anatomy of *A. robustus* betrays what was probably a rather broad diet in this early hominid (Pickering, 2006).

This dissertation tests the null hypothesis that patterns of mandibular growth in humans and *A. robustus* cannot be distinguished. This hypothesis is a basic but important place to investigate growth in this extinct hominid. Such a comparison allows inferences to be made about how *A. robustus*' developmental biology and life history. Subadult fossils make up a large proportion of this species' craniodental hypodigm (Brain 1981), and so it is surprising that these have not yet been used to analyze patterns of size change in *A. robustus* (for *adult* growth, see Lockwood et al., 2007).

Chapter 2 presents the theoretical and analytical reasons for analyzing mandibular growth in *A. robustus*. The research question about mandibular growth in *A. robustus* is

situated in two bodies of theory. First, from the view of evolutionary developmental biology (Raff, 2000), understanding how the *A. robustus* mandible attains its unique morphology helps elucidate the (adaptive) reasons for adult anatomy. Second, from a life history perspective, patterns of growth are part of an animal's adaption to survive in its ecological circumstances (Smith and Tompkins, 1995). Human growth reflects key aspects of humans' unique adaptation relying on language and culture (Bogin, 1999, 2009; Locke and Bogin, 2006), and so comparing patterns of growth in humans with *A. robustus* can help elucidate the origins of this adaptation. I conclude with a brief discussion of the null hypothesis, explaining the reasoning behind the null approach given the issues with using cross-sectional data.

Chapter 3 describes in more detail the human and fossil samples, and the methods employed to study them. The study will focus on *A. robustus* from Swartkrans, as well as a prehistoric human population from modern Ohio. Although there are numerous well-established ways to study growth cross-sectionally, none of these is sufficient to understand ontogenetic variation in the *A. robustus* mandibular sample. The remainder of Chapter 3 describes why the fossil sample necessitates a new approach, and then presents a novel method, which I call the ζ test, for assessing patterns of ontogenetic variation in fossil samples based on randomization/resampling statistics (Efron and Tibshirani, 1991; Sokal and Rohlf, 1995; Manly, 2007).

Chapter 4 presents the performance and results of the ζ test. The chapter begins by documenting the analytical behavior of this new procedure, first in terms of the metric chosen to describe overall mandibular size, and then in terms of the randomization strategy. Patterns of size change are then compared between humans and *A. robustus*,

first for the overall size metric and then for the individual metric traits examined. The chapter ends with a qualitative description of ontogenetic changes to the *A. robustus* symphysis.

Chapter 5 discusses the significance of these findings. The chapter begins with a discussion of the ζ test as an analytical procedure, reviewing why the new method was necessary and how it performed in light of its assumptions and the limitations of a cross-sectional sample. Next I treat the results in terms of evo-devo, examining the potential effects of early weaning, biomechanical adaptation, and dental development on *A. robustus* jaw growth. Finally, I discuss the implications for *A. robustus* life history.

Chapter 6 then summarizes and synthesizes the previous chapters, noting the significance of the present study and making suggestions for future work. Just as this dissertation is based on maximizing the information obtained from fossil samples, these suggestions focus on the development of methods rather than awaiting an expanded fossil record. Even though much of the *A. robustus* sample studied here has been known for as much as 60 years, it is my belief that there is still much to be learned from these and other familiar fossils.

Chapter 2

Background and Theoretical Contexts

This study compares mandibular growth in *Australopithecus robustus* with that of modern humans, and the purpose of this chapter is to present the theoretical underpinnings of the research question of whether their patterns can be distinguished. The chapter discusses the biological and theoretical contexts for the research question and hypothesis. First, from the perspective of evolutionary developmental biology ("evo-devo"), it is of interest to know when and how morphological differences between these species arise. Second, from the perspective of life history theory (Stearns, 1977, 2000; Smith and Tompkins, 1995; Robson and Wood, 2008), patterns of growth are part of an organism's adaptation for meeting the energetic demands of its lifestyle; human life history has several unique attributes including our pattern of growth (Bogin, 1999; Leigh, 2001). I conclude with a brief discussion of cross-sectional data and the strengths of this study.

2.1 Evolutionary Developmental Biology

This study is directly relevant to human evo-devo because it examines how and why anatomical differences between humans and *A. robustus* arise in ontogeny. This section therefore discusses the possible developmental bases of human and *A. robustus* adult mandibular morphology. Special attention is given to the issue of making inferences about growth from the fossil record, and why the *A. robustus* sample is well suited for

this. I then discuss specific hypotheses that have previously been proposed for *A. robustus* jaw development, and how this study can address them.

Evo-devo is a multifaceted field of biology that seeks to understand how growth and development are modified to effect evolution (Raff, 2000, 2007). Patterns of growth are important in evolution because no animal is able to thrive and reproduce at the size and shape it is at birth; adult form arises through processes of growth and development. Because a requirement of evolution by natural selection is for individuals to vary in their potential to survive and reproduce, and growth and development are essentially responsible for an animal's phenotype, ontogeny is an important mediator of evolution (Gould, 1977). As the preeminent biologist Leigh Van Valen stated, "A plausible argument could be made that evolution is the control of development by ecology" (Van Valen, 1973: 488). A developmental perspective therefore helps elucidate the evolutionary significance of similarities and differences between species. A comparison of the growth processes resulting in species' similarities and differences is an ideal focus for the evo-devo approach. At the molecular level, most fundamental developmental processes are shared in common (e.g. conserved) among distantly related organisms (Gilbert et al., 1996; Held, 2010). For instance, although mammalian teeth vary considerably in size and shape, the same processes underlie the formation of enamel and the delineation of cusps in all mammals (Mccollum and Sharpe, 2001), which is key to recognizing homologies (Hall, 2007).

But just how such homologous features (such as jaws) can be made to look different even though they develop through homologous processes is a central question in evo-devo. This question is often framed in terms of how species-specific morphologies

arise: species may also resemble one another at some point early in ontogeny postnatal but thereafter follow divergent ontogenies leading to differences between adults (Fig. 2.1A; Gould, 1977; Alberch et al., 1979; Cobb and O'Higgins, 2004). Some species differences may be established early in life (e.g. embryonically), but then follow basically the same trajectories of size/shape change postnatally (Fig. 2.1B).

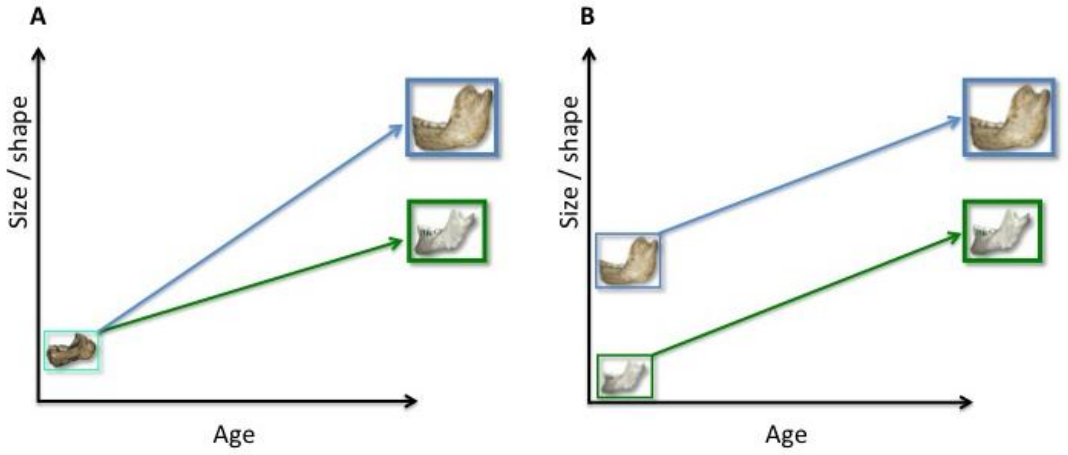

Figure 2.1. Schematic of how species' morphology might arise in ontogeny.

The fossil record necessarily limits studies of ontogenetic evolution to the postnatal growth period, and so the importance of pre- versus postnatal growth is the dichotomized framework employed by many evo-devo examinations of hominid craniofacial variation (e.g. Ackermann and Krovitz, 2002; Zollikofer and Ponce de León, 2004). This framework reasonably assumes that evidence of parallel postnatal ontogenetic trajectories between different species is evidence that prenatal growth is the critical period for determining species morphology. And in fact, a good deal of these studies have indicated that morphological differences between species or populations are present either prenatally or early in postnatal morphology, rather than arising later during growth (Daegling, 1996; Ponce de Leon and Zollikofer, 2001; Ackermann and Krovitz, 2002; Mitteroecker et al., 2004; Zollikofer and Ponce de León, 2004; Rook and

O'Higgins, 2005; Bulygina et al., 2006; Mcnulty et al., 2006; Fukase and Suwa, 2008). Analyses of prenatal skeletal growth are rare, but do suggest that a great deal of morphological differentiation between species occurs during this period (Zumpano and Richtsmeier, 2003; Coquerelle et al., 2010a; Rafiq et al., 2012).

A major limitation to most previous studies of early hominid craniofacial growth (Richtsmeier and Walker, 1993; Ackermann and Krovitz, 2002; McNulty et al., 2006) is that the nature of the fossil record limits many analyses to inferences of growth between a single developmental stage and adulthood. These sole-subadult samples are usually older than infants (e.g. Taung, KNM-WT 15000). This limited sampling almost certainly overlooks major changes in growth patterns that are evident from longitudinal studies, such as are known to happen during human growth in stature and body mass (Tanner, 1951; Hochberg, 2012).

The present study, utilizing the relatively complete ontogenetic series of *A. robustus* mandibles, has the advantage of sampling multiple points in ontogeny and thereby provides a more nuanced glimpse into just how similar or different postnatal growth patterns truly are between humans and an early hominid. Also, some age groups (see Chapter 3) are represented by more than one *A. robustus* mandible, which sheds some light on variation in patterns of growth in this species; this is important since studies of fossil ontogeny suffer from limited sample sizes, underestimating variation within and between age groups (Cobb and O'Higgins, 2004).

Adult mandibles of humans and *A. robustus* are quite different in size and shape, and so an ontogenetic comparison allows one to examine just how these species differences arise. Although these species' mandibular corpora overlap in height, the *A.*

robustus corpus can be twice as broad as humans' (Daegling 1989). The *A. robustus* ramus is also absolutely and relatively taller than humans' (Broom and Robinson, 1952; Bromage, 1989; Rak, et al. 2007; Rak and Hylander, 2008). To be sure, each species' mandible is adapted to generating and withstanding quite different masticatory forces. Nevertheless, all hominids share early canine development and eruption contrasting with living apes (Mann, 1975; Simpson et al., 1990; Smith, 1994). Small anterior tooth size, coupled with anteriorly-placed zygomatic bones, give *A. robustus* a relatively flat ("orthognathic") face, similar to humans but in contrast to earlier australopithecines (Simpson et al. 1990; McCollum 1999).

The similarities between these two hominids – relatively small anterior teeth and a non-projecting face – may arise through similar developmental mechanisms and processes. Facial growth and development occur as the hard and soft-tissues of the face enlarge and are displaced away from the brain case (Moss and Young, 1960; Enlow and Hans, 1996). In order to compensate for this displacement and maintain functional coherence of facial components, bone deposition occurs at facial sutures, and the outer surfaces of bone remodel by deposition and resorption throughout ontogeny. Because humans and *A. robustus* have small canines and incisors, their faces do not need to undergo as much anterior growth as apes or gracile australopithecines (Simpson et al. 1990). As a result, the incisive suture, which allows the anterior face to grow forward, fuses relatively early in humans and *A. robustus* (Braga, 1998).

Patterns of periosteal facial bone remodeling are also similar between *A. robustus* and modern humans, shared to the exclusion of 'gracile' *Australopithecus* and early *Homo* (Bromage, 1989; McCollum, 2008). For example, the anterior surface of the

mandible is largely depository throughout ontogeny in chimpanzees (*Pan troglodytes*; Johnson et al. 1976) and non-robust hominids (Bromage, 1989), reflecting these species' prognathism and predominantly forward direction of facial growth. The anterior alveolar surface is fully resorptive in humans (Enlow and Harris, 1964), and in *A. robustus* this surface is depository medially but resorptive laterally (Bromage, 1989). As with the incisive suture, this locus of resorption reflects the fairly orthognathic face in humans and *A. robustus*. Thus, sutural and periosteal growth processes of the anterior face seem to track the size and development of the anterior teeth (Simpson et al., 1990). These similarities in form and process lead to the hypothesis that anteroposterior length dimensions of the jaw including the symphyseal region should follow similar patterns of size change in each species, at least until the eruption of the permanent incisors.

Whether such "morphogenetic interpretations" of hominid facial remodeling fields can be translated to global ontogenetic changes (Bromage 1989: 759), or rather whether these fields reflect merely "local surface sculpting" (McCollum, 2008: 12), has not yet been tested. O'Higgins and Jones (1998) could not reject the hypothesis that the position of growth fields of bony remodeling across ontogeny is mirrored by facial shape change during growth in the monkey *Cercocebus torquatus*. Further complicating our understanding of craniofacial growth, the relationship between growth fields and size-shape change has been called into question because of great intraspecific and intrasexual variation at any given age (Wealthall, 2002; Mccollum, 2008). In addition, McCollum (2008: 12-13) argued that the remodeling fields on the maxilla of *A. robustus* reflect local topographic change, and are not responsible for creating the orthognathic facial profile superficially similar to modern humans. While the present study cannot directly examine

this question, if the results indicate divergent ontogenies in light of the similar distribution of growth fields in *A*. *robustus* and humans, this would undermine a causal relationship between superficial growth fields and global shape change.

The gross differences between *A*. *robustus* and human jaws also inform predictions about growth patterns. During the ontogeny of humans and apes, the height of the posterior face increases more than the front, resulting in the apparent rotation of the mandible relative to the cranial base (Björk, 1955; Björk and Skieller, 1972; Bromage, 1989; McCollum and Ward, 1997; Wang et al., 2009). As a result, the angle between the (horizontal) corpus and (vertical) ramus usually decreases across ontogeny. Because adult *A*. *robustus* have very tall rami (Broom and Robinson 1952; Rak and Hylander, 2008), Bromage (1989) reasoned that *A*. *robustus* likely experienced greater mandibular rotation during postnatal ontogeny than do humans (Fig 2.2). This hypothesis is difficult to test given the lack of rami in the fossil sample, but may be addressed roughly using other measures of facial height. Similarly, the thick corpus of *A*. *robustus* could be a characteristic that is present in the youngest infants, or may it arise later during postnatal growth.

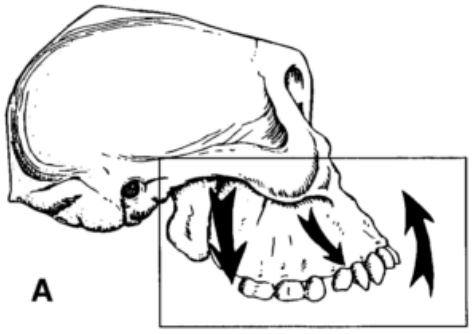

Figure 2.2. Schematic of facial rotation in *A. robustus* (Fig 3. from Mccollum 1997). The mandibular ramus (not shown, but in the area of the left-most arrow) increases in height relatively more than the mandibular symphysis anteriorly (in the area of the smaller middle arrow).

The present study therefore contributes important information to evo-devo debates about how and when differences or similarities in species morphology arise. While the most proximate bases of development, such as bone and tooth morphogenesis, are known to be conserved across taxa, the question is open as to whether more global aspects of facial growth are similarly conserved. The **null hypothesis of conserved developmental patterns in human and *A. robustus*** makes testable predictions. A first prediction is that no species differences in size change should be found for any trait. Second, if differences are found, they should occur across all traits (or at least most of them), and be of similar magnitude. In this scenario, ontogenetic differences are heterochronic, e.g. related to shifts in the rate/timing of development (Gould, 1977, 2000), rather than absolutely deviations in how and where bony growth occurs. Contrarily, the rejection of the null hypothesis would support the **alternate hypothesis of divergent ontogenetic trajectories**. This alternate hypothesis is rather open and so makes few specific predictions, except that that the species differences described above should be reflected in only a subset of traits.

2.3 Life History Theory

The analysis of mandibular growth in *A. robustus* will also address the evolution of human life history. This section begins by reviewing the role of growth in life history. I then discuss the more and less unique aspects of modern human life history. Next, I review the fossil evidence for the evolution of human life history and growth. Finally, I describe why the present study address and/or overcomes many of the shortcomings of

previous studies, and conclude with predictions about the outcome of this analysis based on life history theory.

Growth is more than merely the means by which adult form arises, it is a key aspect of an organism's life history (Smith and Tompkins, 1995). Life history theory stipulates that the timing of major events in an organism's life is part of an optimal strategy to survive and reproduce. This assumes an organism will only have limited energy during its lifetime, and this must be partitioned among requirements of growth, maintenance and reproduction (Smith and Tompkins, 1995). Given the necessity of these tradeoffs, it should be possible to predict patterns of covariation between these variables. Because human life history is remarkable in a number of ways, situating growth in this context can thus help us understand the evolutionary origins of the human adaptive strategy.

Bodily growth is important for life history because it is a process that requires a great deal of energy from outside the organism. This is notably problematic because a developing animal is dependent on available resources, and must also allocate energy to fight infection, forage, develop the physical (e.g. neural) and practical bases for social life (among primates at least), travel, and avoid being preyed upon (Smith and Tompkins, 1995). The energetic requirements of growth are thus shared with other biological systems, and an individual's optimal adaptive strategy at any given time may be to divvy resources between these systems differently than at other times. The changing challenges and advantages to survival that arise during ontogeny theoretically necessitate that a species' ontogeny be well suited to its ecological and social circumstances. As such, an

animal's energy expenditure toward growth, specifically rates and/or duration thereof, must be in accord with these changing ecological and adaptive demands.

Human Growth and Life History

The human adaptive strategy, relying on symbolic language and culture, distinguishes us from our primate relatives, and this uniqueness is marked in several aspects of our biology. Most notably, our brains are much larger than expected for our body size, and account for upwards of 20% of an adult human's basal metabolic rate compared with less than 10% in other Primates (Leonard and Robertson, 1992, 1996; Aiello and Wheeler, 1995). This expensive organ both allows and necessitates our sociolinguistic strategy, and is almost certainly related to our pattern of growth: while primates in general grow slowly compared with other mammals of comparable size (Charnov and Berrigan, 1993; Kaplan et al., 2000; Walker et al., 2006 b), humans grow most slowly of all, having both the absolute longest ontogeny of any primate, as well as a longer ontogeny than expected for a primate of our size (Bogin and Smith, 1996; Leigh, 2001). This protraction of maturation is not equally distributed across the subadult period. Rather, human maturational stages and growth rates appear to reflect the energetic requirements of developing the brain, or using it to develop social-linguistic skills critical to being a successful adult (Allman and Hasenstaub, 1999).

The neonatal human brain averages 382 cm^2, only some 30% adult size at birth compared with 40% adult size in our closest relatives, chimpanzees (DeSilva and Lesnik, 2006, 2008). This smaller proportion nevertheless equates to an *absolutely* larger size than a neonatal chimpanzee's. To reach an average adult size of over 1200 cm^3, human

infants retain rapid (fetal) brain growth rates into the first year postnatal life (Dobbing and Sands, 1979), which then sharply decelerate soon thereafter (Coqueugniot et al., 2004; Leigh, 2006; Coqueugniot and Hublin, 2012). Growing such a large brain can require up to 60% of an infant's energetic expenditure (Leonard et al., 2003), and to offset some of this cost human infants are absolutely and relatively fatter than most other species (Leonard et al. 2003; DeSilva, 2011; Hochberg 2012). In light of this high cost, humans tend to wean offspring at a relatively young age: 2.5 years on average (between 2-4 years globally) among human natural-fertility populations compared with at least four years among living apes (Kaplan et al., 2000; Kennedy, 2005). Bodily growth rates of human infants, while relatively high, are rapidly decelerating during this time (Bogin, 1999; Hochberg, 2012).

Infancy ends with the completion of weaning and is followed by the childhood stage (Bogin, 1999, 2009). One thing that makes this period unique to humans is that the weaned child has only its deciduous teeth, whereas in most mammals completed weaning roughly coincides with the full eruption of the first permanent molar tooth (Smith and Tompkins, 1995; Bogin, 1999). Most other animals are able to forage for themselves at this stage of maturation, but a growing child is poorly equipped to handle adult foods and is highly dependent upon others for acquiring and preparing its food. The child's costly brain, however, is still growing, albeit not as rapidly as during infancy (Leigh, 2006). Growth of the body slows significantly and stabilizes to a relatively low level during this period (Hochberg, 2012). Because of these features, the childhood period has been argued to be uniquely human (Bogin, 1999).

Childhood ends with the eruption of the first permanent teeth (first molars and incisors; Bogin, 1999), usually between the ages of five and seven years in humans (Liversidge, 2003). Bodily growth rates, decelerating through infancy and childhood, reach their lowest levels during this time, the juvenile stage. The human brain has essentially finished *size* growth during by this time (Leigh 2006). Nevertheless, this is still an important period for neural and cognitive development in humans (Campbell, 2006, 2011), coinciding with the behavioral period known as 'middle childhood' to developmental psychologists (Monge and Mann, 2010). Around the time the brain stops growing, the *zona reticularis* within the adrenal gland matures, beginning a steady increase in circulating levels of the neurotransmitter dehydroepiandrosterone (DHEA) and DHEA sulfate (DHEAS; Campbell 2006). This shift in hormone levels is referred to as adrenarche.

Campbell (2006, 2011) notes that DHEA/S are involved in the development of the cerebral cortex from this time until early adulthood. This is thus an especially important time for a child's social development (reviewed in Monge and Mann, 2010). Juveniles begin to acquire reasoning skills, and an understanding of self and the difference between right and wrong, and they begin forming relationships with people other than their parents. In short, this is the time when children begin learning social norms and become integrated into society. Human middle childhood (juvenility) has two other unique correlates with life history. First, the period lasts about 1.5 times longer in humans compared with chimpanzees, providing youngsters with extra time to develop important social, linguistic and foraging behaviors (Kaplan et al., 2000). In addition, this time coincides with a "quiescent period" (or hiatus) in dental development exclusively seen in

humans (Eveleth and Tanner, 1988) and fossil hominids (Mann 1975; Monge and Mann, 2010).

Middle childhood (juvenility) ends with the onset of puberty, the activation of the hypothalamic-pituitary-gonadal axis, resulting in high levels of sex hormones (Hochberg 2012). This marks the final stage of ontogeny, adolescence, which spans the 5-10 years between puberty and adulthood. Adolescent growth contrasts with the generally slow bodily growth during the childhood and juvenile stages. Rather, humans experience a brief growth spurt during which linear skeletal growth rates are at their highest since infancy (Eveleth and Tanner 1988; Bogin 1999; Walker et al. 2006b), shortly after which growth in stature is complete. While many primates experience a spurt in body *mass* around puberty (Leigh 1996), none experiences the rapid increase in *skeletal dimensions* seen in humans (Watts and Gavan, 1982; Bogin, 1999; Hamada and Udono, 2002).

Adolescence is not only important for somatic growth, but it also marks sexual and neural development and a final time when youths can learn critical social behaviors (Bogin and Smith, 1996; Bogin, 1999, 2003, 2009; Locke and Bogin, 2006). Many though not all brain centers, such as the fornix, finish maturing during this time (Hochberg 2012). Adolescents tend to take greater interest in adult activities (Kaplan et al. 2000) and adopt more social uses of language (Locke and Bogin, 2006). Bogin (2003) has further argued that sex differences in the timing, intensity and duration of the adolescent growth spurt promote each sex's "sociosexual" development, facilitating a smooth transition to adult social status. The adolescent growth spurt occurs earlier in girls than boys, making the former appear relatively more mature and so helping them enter into adult social, sexual and economic spheres. Boys, on the other hand, usually begin the

spurt later and it lasts longer compared with girls. This may serve to make adolescent boys' social behavioral mistakes better tolerated by adults who perceive them as boys when they are trying to act more like men.

Relevant to this study, the most remarkable aspect of human ontogeny and somatic growth compared with other primates is our exceptionally long childhood-juvenile period (Leigh and Park, 1998), with concomitant delay in the onset of reproduction: age at first birth averages around 20 years in human many societies, compared with just under 15 years in chimpanzees (Bogin, 1999; Kaplan, et al. 2000). (Some human societies, however, reproduce at earlier ages comparable to chimpanzees, e.g. Filipino Aeta: Migliano et al., 2007; Venezuelan Pumé: Kramer and Greaves, 2010) A long, drawn-out pre-reproductive period is risky from an evolutionary perspective as the delay increases the chance of dying before reproduction, and it may potentially reduce the duration of the reproductive career (Crespi, 2011). Despite the risk of this strategy, the lifetime fitness (i.e. reproductive) consequences can be compensated by our potential to have multiple dependent offspring of different ages (Gurven and Walker, 2006), to reduce the interbirth interval by early weaning, and to have greatly reduced (especially subadult) mortality (Kaplan et al. 2000). What is further unique about this strategy is that the energetic burden of caring for developing youths is not confined to the parents, but older siblings and other family members usually play a crucial role (Hawkes et al., 1998; Kaplan et al., 2000; Bogin, 2003).

In conclusion, human bodily growth is inextricably connected with the energetic and cognitive requirements of developing a large brain capable of high cognitive (i.e. social) function. In the early subadult period (i.e. infancy and childhood) energy is

preferentially devoted to the brain over the body. Bodily growth rates remain low during the subsequent juvenile period, partly in order to provide ample time to begin practicing complex social and foraging behaviors, and partly to offset the energetic costs for caretakers. This 'middle childhood' is essential to humans' sociocultural adaptation. The final stage of growth, adolescence, includes a brief 'spurt' of growth to attain adult body size and is important for youths' incorporation into adult society. Despite the importance of the human pattern of bodily growth to our adaptive strategy, it is still unclear just how early in hominid evolution this pattern arose, or whether all aspects of this pattern appeared at once or piecemeal over the course of evolution.

Early Hominid Life History

In the absence of complete fossil hominid populations, researchers have used a number of lines of evidence to make inferences about the evolution of hominid life history and growth. Lovejoy (1981, 2009) hypothesized that the defining feature of hominids, bipedalism, accounted for our origins and evolutionary success because it increased offspring survivorship. Lovejoy noted that living humans have the potential for higher lifetime fertility than the great apes for two main reasons. First, great apes have a much higher juvenile mortality rate than modern humans. Second, great apes have fairly long intervals between successful births compared with modern human hunter-gatherers. While these are the central tendencies for these species, it should be noted that there is overlap between the ape and human interbirth intervals (Kaplan et al. 2000; Robson and Wood 2008). The ape pattern results in their relatively low reproductive rates and slow population growth, which can create substantial adaptive hurdles in seasonally fluctuating

ecosystems like those of the late Miocene (Lovejoy 1981). Basal hominids, Lovejoy argued, overcame this 'demographic dilemma' with a novel strategy in which a male provisioned a monogamously pair-bonded female and their dependents (i.e. a nuclear family) with resources. Familial provisioning allowed hominids to wean infants early and reduce their interbirth interval (Kaplan et al. 2000; Kennedy 2005; Humphrey 2010). This system implies that early hominids would have cared for multiple offspring at a time.

Under the cooperative breeding and provisioning implied by Lovejoy's (1981) model, selection would favor slow growth rates during childhood to offset the energetic demands of dependent offspring on (provisioning) parents (Gurven and Walker, 2006), especially at hominids' relatively large body sizes (McHenry and Coffing, 2000). Great ape growth rates, on the other hand, are relatively higher than humans' throughout a shorter ontogeny (Walker et al. 2006a). Thus, unique aspects of *modern* human life history are hypothesized to be in place at the onset of hominid origins. Consistent with this hypothesis, DeSilva (2011) showed that humans give birth to relatively large neonates, up to 5-6% of mother's mass compared to only around 3% in chimpanzees. Estimating neonatal and adult female body mass for extinct hominids, DeSilva further found that relatively large (i.e. human-like) neonates characterized hominids as early as *Australopithecus afarensis* (3-4 million years ago). Thus, one aspect of the human life history strategy (birthing large infants) seems to have been present very early in human evolution, raising the possibility that other behavioral and ontogenetic aspects of the strategy may have been in place as well.

Contrary to this prediction, however, many researchers have argued that early hominids would *not* have experienced a human-like pattern (e.g. duration or rates) of

growth. First, early hominids' diminutive adult brain sizes, less than 600 cm^3 compared with over 1200 cm^3 in living humans (Holloway, 2008; Coqueugniot and Hublin, 2011), hint that early hominids would not have had a long growth period like humans. The human adaptive strategy relying on language and culture necessitate large brains for the storage and processing of such complex information (but see Brown et al., 2004, for a recent, small-brained tool-maker). This cognitive skill set is hypothesized to be related to the prolongation of human growth, as it will take a long time to learn the complex skills necessary to be an at least competent member of society (Mann 1975; Allman and Hasenstaub, 1999; Bogin 1999; Kaplan et al., 2000; Bogin, 2003; Bogin and Locke, 2006). Australopithecines' smaller brains suggest a lack of human-like behavioral capacities, meaning a prolonged subadult period would be both unnecessary for survival and evolutionarily risky. Alternatively, slow and prolonged juvenile growth could have been required for australopithecines to learn complex behaviors *because* of their small brains (i.e. learning may take longer; Wolpoff 1999).

A fast, non-human-like ontogeny was further argued for australopithecines based on the observed correlation between brain size and various life history parameters at supra-generic taxonomic levels (e.g. BH Smith 1989). Sacher (1978) found that variation in adult brain size appeared to be explained in part by variance in lifespan across mammals. Building on Sacher's work, BH Smith (1989, 1991; RJ Smith et al., 1995) further explored the correlations between brain size and other life history variables in primates. Brain size was found to correlate fairly highly with age at M_1 eruption ($r = 0.99$ among anthropoid species; Smith 1991), which roughly marks the end of weaning in mammals except humans. Smith (1989, 1991) used the relationships between brain size

and other life history variables to predict that early hominids' small brains imply that they would have erupted their M_1s and weaned at younger ages than humans, with the implication that overall growth was like non-human apes. RJ Smith et al. (1995) came to similar conclusions, however they urged caution when using such correlations to predict hominid life history because of error inherent in statistical models and the inescapable uncertainty of how early hominids would truly fit linear models based on a wide range of living species.

In addition to the correlation between age at M_1 eruption and adult brain size, teeth have been used extensively to make inferences about the evolution of hominid growth and life history. This is due in part to the fact that teeth and jaws are some of the most durable and so well-represented elements in the fossil record, as well as the fact the fact that teeth form and erupt in predictable patterns making it possible to estimate individuals' relative stage in ontogeny, if not chronological age. An assumption of these studies, usually implicit but sometimes explicit (Bromage and Dean, 1985), is that anywhere dental development is more like modern humans or apes, bodily or skeletal growth is also more like that group (Conroy & Vannier, 1991a-b; Smith, 1994).

Human dental development is distinguished from that of the other apes by 1) first permanent molar formation and eruption at roughly the same time as the permanent incisors, as opposed to long before the incisors; 2) a canine that forms and erupts prior to the second molars, as opposed to coincident with or after the third molar (M_3 or "wisdom tooth"); and 3) delayed molar formation, especially of the M_3, such that the formation of adjacent molar crowns do not overlap with one another (Mann, 1975; Anemone et al., 1996; Kuykendall, 1996).

Evidence for dichotomized 'ape-like' and 'human-like' patterns have been sought in relatively complete dentitions of early hominids. Mann (1975) examined the sequence of dental development in *A. robustus* from Swartkrans, and found he could not distinguish the fossil pattern from that of humans. The *A. robustus* sample showed a human-like pattern of spacing between molar crown formation and eruption (viz. M_3). Mann therefore concluded that *A. robustus*, and presumably early other hominids, probably had prolonged maturation like humans, but this was soon called into question.

First, patterns of tooth formation in (non-robust) early hominids were argued to match chimpanzee standards better than humans (although none of the studies were directly comparable to Mann's analysis of the Swartkrans fossils). If a fossil juvenile preserves more than one developing tooth, one can examine each tooth's development relative to the other teeth, and these patterns can then be compared with known patterns and sequences of crown formation in living apes and humans. From here, Smith (1994b: 308) reasoned that, "developmental scores of an individual's teeth are…more likely to agree when scores are assigned from standards based on the individual's correct species or group." For fossils, this implies that better conformation to one species' dental standard equates with overall (e.g. somatic) developmental similarity to that species.

Smith (1986, 1993, 1994a-b) found that teeth of gracile australopithecines and early *Homo* tended to provide more similar age estimates when using chimpanzee compared with human standards, while *A. robustus* and *boisei* actually conformed better to the human standards. The principle deviation of the gracile australopiths from the human pattern was that permanent incisor and canine formation was delayed relative to first molar development and eruption (Conroy and Vannier 1991a-b), e.g. point 1 two

paragraphs above. However, as Simpson and colleagues (1990) point out, this probably due to the larger anterior teeth of these species compared with humans and robust australopithecines, rather than to each species' rates of bodily growth. Moreover, several patterns said to be ape-like, and found in gracile australopiths (i.e. delayed eruption of the permanent incisors relative to first molars, or canines relative to second molars), do not actually completely distinguish apes from humans: while these may be rare in the Euro-Americans on which human standards are developed, they are not uncommon in other populations (Garn and Koski, 1957; Dahlberg and Menegaz-Bock, 1958; Mann, 1988; Wolpoff et al., 1988; Liversidge, 2003). Key to this discussion – Mann's (1975) important observation of a human-like relationship between successive molar formations was never falsified.

Early hominids were also argued to show ape-like maturation on the basis of the study of dental histology. Perikymata and striae of Retzius are lines found on the surfaces of and within tooth crowns, respectively, reflecting the deposition of enamel during the formation of the crown (Guatelli-steinberg, 2009; Tafforeau et al., 2012); perikymata are merely the manifestations of striae of Retzius that reach the crown surface. If the periodicity with which these lines are formed can be known (it ranges from 6-12 days in humans and apes), it is theoretically possible to count these lines and estimate the actual time it took a tooth crown to form (Bromage and Dean, 1985). These crown formation times can then be inferred to reflect overall maturation period. As such, several studies have estimated shorter crown formation times in early hominids compared with humans, and therefore inferred that prolonged maturation had not evolved by the early Pleistocene

(Bromage and Dean, 1985; Beynon and Dean, 1988; Dean et al., 2001; Lacruz et al., 2006, 2008).

A major problem with this technique is that the link between (estimated) tooth formation and growth rates is yet to be firmly established. For instance, the earliest studies argued that incisor crown formation times were shorter in hominids compared with humans, and that they therefore experienced a rapid, ape-like pattern of growth. However, as Mann and colleagues (1990) pointed out, not only do nearly all hominid incisor perikymata counts fall within the impressive range of modern humans, but do ape incisor crowns do not form more rapidly than humans, which was key to the argument that rapid crown formation equated with rapid ontogeny. Similarly, histology-based estimates of molar crown formation times overlap between humans and apes, and in some cases ape crowns have an even longer estimated formation time than humans' (Macho and Wood; Macho, 2001; Smith et al., 2007). This is important given the staggered molar crown formation identified by Mann (1975). Thus, even if dental histology can be used to accurately estimate how long a crown took to form or to estimate an individual's age at death (e.g. Antoine et al., 2009), the relationship between crown formation time and overall maturation rate is probably not tenable.

In summary, studies of dental development in living and extinct hominids have been very informative, but insofar as they tell us anything about life history (e.g. Smith, 1991), dental data alone are not sufficient to make inferences about overall patterns of bodily growth. As Simpson and colleagues (1991: 119) state, these data tell "nothing about the pattern at which [a hominid's] component structures will grow. These are more likely to vary directly with the directional selective milieu that is responsible for their

emergent adaptations." In other words, even if early hominids formed their teeth relatively rapidly, this alone cannot be used to distinguish ape or human patterns of somatic growth.

Skeletal Growth in Early Hominids

Rather than extrapolating growth inferences from teeth or brains to the rest of the body, it may be more useful to examine actual patterns of bony size change across ontogeny. To date, however, there are only a handful of studies of growth in early hominids (i.e. *Australopithecus* and early *Homo*) that have actually utilized *skeletal* size data in conjunction with dental indicators of age. While these studies have been informative in their own right, they nevertheless have various limitations. In this section, these studies are summarized and critiqued, ending with a summary of how the present study builds off of and improves upon these previous works.

Some evidence about ontogenetic size change in *Australopithecus* comes from pelvic remains fossils of *A. africanus*. Berge (1998) compared of iliac growth in African apes (including humans) and *A. africanus*. Significant from a life history perspective, she noted that the adolescent female *A. africanus* ilium (represented by MLD 7) is essentially the same size as what she then considered a young adult female (Sts 14); because this pattern of age-related size variation was common in her ape but not human samples, Berge reasonably concluded *A. africanus* did not follow a human-like pattern of size (or shape) growth. However, Robinson (1972: 76) noted that the distance from the acetabulum to the ischial tuberosity was only 8.0 mm compared with Sts 14's 16.1 mm, raising joint possibility of both a large amount of remaining growth and/or individual

variation in ischial length. Berge and Gommery (1999) later described the Sts 14 pelvic bones as showing several markers of immaturity (viz. unfused epiphyses). The revised assessment of skeletal maturity for Sts 14 both lowers the age disparity between it and MLD 7, and leaves open the question of just how much growth was left in either of these subadults.

Tardieu's (1998) analysis of African ape and early hominid distal femoral growth also suggested early hominids differed from living humans. Tardieu found that distal femora of East African australopithecines (*A. afarensis* and *A. boisei*) do not display the 'squared' shape characteristic of human adults, and which arises through adolescent growth. Rather, these australopiths' distal femora more closely resembled human children. Fossil femora attributed to the genus *Homo*, on the other hand, displayed a more adult human-like morphology. Tardieu thus concluded that australopithecines likely did not experience a human-like adolescent spurt in skeletal growth. While this inference seems reasonable given her fossil sample, it can only be fully tested with an ontogenetic series of femora that the fossil record currently does not afford.

Many studies other of skeletal growth and development of hominids in the early Pleistocene have necessarily focused on a single specimen, KNM-WT 15000. This is one of the only nearly complete skeletons of *Homo erectus*, belonging to an adolescent male from around 1.5 million years ago (Brown et al., 1985; Gathogo and Brown, 2006), slightly postdating *A. robustus*. Well-preserved adult and adolescent partial skeletons from the 1.8 million year old site of Dmanisi are known (Lordkipanidze et al., 2007), but these have yet to be used to assess postcranial growth in this sample (but see Van Arsdale et al., 2012 for treatment of skeletal maturation).

BH Smith (1993) compared age estimates for the KNM-WT 15000 based on published skeletal and dental maturation standards for modern humans and chimpanzees. Estimating this individual's age using ape skeletal and dental standards each provided fairly consistent results, around 8 years at death. Human standards, however, gave very different results: a human showing the same stage of dental development as WT 15000 would tend to be 10-11 years old, while a human of the same skeletal development would be closer to 13 years. Smith took the concordance of the estimates based on the chimpanzee model, and discordance of estimates based on a human model, to indicate that overall growth in *H. erectus* would have been chimpanzee-like.

While interesting, Smith's (1993) study could not fully statistically take into account variation *within* each species, as the skeletal and developmental standards she used were derived from single population averages that do not incorporate natural intraspecific variation, which is known to be extensive in humans (Eveleth and Tanner, 1988; Liversidge, 2003; Walker et al., 2006 a). The "fit" of WT 15000 to either ape or human standards is difficult to interpret without knowing just how much overlap there is between chimpanzee and human patterns of skeletal versus dental maturation (i.e. Wolpoff et al., 1988; Zihlman et al., 2004; Monge et al., 2007). Moreover, the human skeletal and dental standards used were developed on different samples, and so it was unclear just how modern humans vary in the relationship between dental and skeletal maturation.

To this end, Clegg and Aiello (1999) and SL Smith (2004) examined the disparity between skeletal and dental maturation in samples of recent humans whose actual chronological ages were known. Both of these studies found that the 2 year disparity

between skeletal and dental age estimates seen in WT 15000 were not uncommon in modern humans, although it was commoner for dental to be advanced over skeletal development, the opposite of the fossil. Clegg and Aiello's (1999) study has since been criticized for utilizing broken archaeological specimens (Dean and Smith, 2009), but SL Smith's (2004) findings remain unchallenged. Her results corroborate other studies showing that skeletal and dental maturation are not especially tightly linked, and so estimates of an individual's age using both systems will often provide different results (Lewis and Garn, 1960; Cardoso, 2007).

It is further problematic to make the assumption that early hominid fossils will conform to either a chimpanzee or a human model of development only. While either is a reasonable and testable null hypothesis, it is not clear which model, if either, actually best fits early hominids. As a result, some studies run their analysis twice – once assuming a human-like pattern of growth and development and again assuming a chimpanzee model. For example, Antón and Leigh (2003) examined growth rates of facial dimensions in small samples of *Homo erectus*, specifically looking for evidence of a human-like acceleration at adolescence. They plotted the facial height measurements against age, once assigning ages based on a human model of dental development, and then again with a chimpanzee model. They found negative/ambiguous evidence for an adolescent acceleration if *H. erectus* erupted their teeth at the same ages as humans, but a chimpanzee-model of dental development, rather ironically, suggested a marked acceleration in facial growth at adolescence. This is because their dependent variable (facial height) stayed the same while the independent variable (age) was shortened in a chimpanzee model relative to a human one; humans experience developmental

milestones on average around 1.8 times later than (captive) chimpanzees (Smith 1993). If *H*. *erectus* was ape-like in dental development then the species may have been human-like in skeletal growth, whereas a human-like pattern of dental development would imply a chimp-like (more linear) pattern of skeletal growth.

In a statistically rigorous analysis of mandibular growth in an early Pleistocene hominid, Van Arsdale (2006) examined patterns of age- and sex-related variation in the early *Homo erectus* mandibles from the 1.8 million year old site of Dmanisi. This sample contains a large adult (D2600, one of the largest Pleistocene *Homo* mandibles), and both an early and a late adolescent. Using resampling methods similar to those employed in the present study, Van Arsdale found that age- and sex-related variation in ten out of 31 traits in the Dmanisi mandibles exceeded levels of variation in human and chimpanzee samples. This finding is consistent with other studies of adolescent growth in the face of *H*. *erectus*, concluding that a good deal of size change occurs between adolescence and adulthood in the species, possibly indicating a human-like growth spurt (Richtsmeier and Walker 1993; Antón and Leigh 2003).

While the ape-human maturation rate contrast is useful from a comparative standpoint, it also sets up a false dichotomy between the biology of different groups (i.e. Simpson et al. 1991). Traditionally in anthropology, humans have been said to have a "slow" life history (Walker et al., 2006a) compared to apes and others with a more fast-paced life cycle. While this is true for many of the populations studied from developed nations, not all human populations follow the purportedly slow human pattern (Walker et al., 2006; Migliano et al., 2007 Kraemer and Greaves, 2010). Regardless, the resulting expectation for fossil hominids, then, has often been either an ape-like life history, or one

intermediate between (some) humans and chimpanzees (Smith, 1993; Bogin and Smith, 1996; Bogin 1999; Dean et al. 2001; Graves et al., 2010). But as shown for *H. erectus* (Van Arsdale 2006), mandibular growth between adolescence and adulthood exceeded the variation seen in human and chimpanzee samples, and so could not be said to be like either species. It is therefore timely to reappraise hominid skeletal vis-à-vis dental development.

This dissertation will therefore contribute important information about the antiquity of human life history. From this perspective, human growth is most remarkable in that there are a number of growth stages each with its own characteristic rate of size change. As in section 2.1 (evo-devo), the **null hypothesis of identical patterns of growth (and therefore life history) between humans and *A. robustus*** predicts that each species should undergo the same amount of *overall* size change between eruption stages. Rejection of this null hypothesis would support the **alternate hypothesis that patterns of overall size change differ between these species**. Again, as in section 2.1, this alternate hypothesis is rather open and makes few specific predictions. As human growth has been argued to be especially unique in featuring childhood and adolescent periods of relatively slow and rapid growth, respectively, a reasonable alternate hypothesis predicts that *A. robustus* should evince greater size change between eruption stages prior to puberty (i.e. M_2 eruption; Chapter 3), and less size change thereafter.

2.3 A Small, Cross-Sectional Sample

Although the Swartkrans *A. robustus* mandibles are the most complete subadult age series of any part of the skeleton in the fossil record of early Pleistocene hominids,

the sample still presents special analytical challenges. Fossil assemblages are necessarily cross-sectional, sampling different individuals of varying ages (i.e. a cross-section of a population), in contrast with longitudinal data that follow individuals across multiple time points. Analytically, cross-sectional data charting change in size with age assume that the younger individuals could have 'grown into' the older (Fig. 2.3). With cross-sectional data, the many sources of individual variation – such as sex, health and idiosyncrasy – could obscure individual patterns of growth, most notably dampening the effects of changes in growth rate (Leigh, 1996; German, 2004). Comparisons can also imply unrealistic patterns of growth for a population (e.g. the dashed blue line in Fig 2.1). Adding to difficulties, fossils are differently preserved, so not all individuals can be compared for all the same (measurable) features.

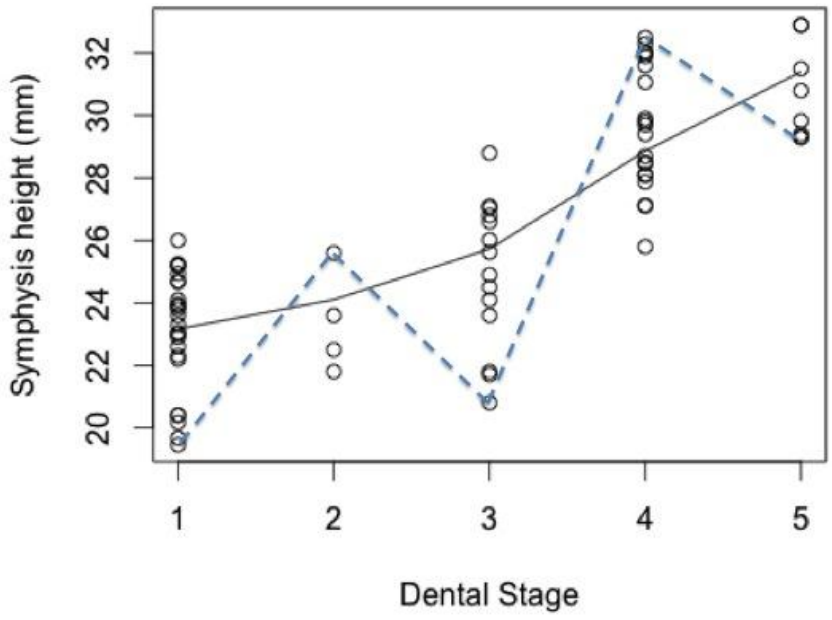

Figure 2.3. Sampling possibilities created by cross-sectional data. Data are humans only. The solid black line is the lowess regression fitted to the data, while the dashed blue line is one of many hypothetical growth trajectories implied by cross-sectional sampling.

Nevertheless, cross sectional data are preferable for this study. It is logistically very challenging to amass large longitudinal datasets, and so the sample sizes afforded to

cross-sectional data make them likelier to indicate the central tendencies of a population (Dahlberg and Menegaz-Bock, 1958). This is important, as the individual (longitudinal) variation in growth alluded to above precludes the specification of any single human growth model; there are myriad ways and reasons fossil variation *could* differ from any humans (e.g. Lee and Wolpoff, 2005), just as there are myriad ways humans might differ from one another. Related, the relatively small fossil sample size raises the issue of how well it may represent the species' normal ontogeny. The null approach adopted here is ideal because it simply asks whether the fossil pattern of variation is likely to be found within a larger, similarly cross-sectional referent.

These aspects of fossil preservation and sampling led to the development of a new method to compare patterns of growth in cross-sectional samples with missing data (Chapter 3). The null hypothesis predicts that between successive dental eruptions, human and fossil jaws will show the same proportional size difference. Statistically, this predicts that the size difference between any differently aged pair of *A. robustus* mandibles is likely to be seen in a randomly-selected pair of humans at comparable stages of dental development as the fossils. Because specimens cannot always be compared for the same sets of traits, pairwise comparisons are critical to maximizing the information from the fossil sample (Lee and Wolpoff, 2005).

In sum, this research adopts the null approach to comparing ontogenetic variation in humans and *A. robustus*. Cross-sectional data, such as are only available for extinct species, have the downside of potentially obfuscating individual patterns of growth, but they are ideal for statistically comparing patterns of variation between samples. Limiting the comparison to humans only yields a straightforward and interpretable result, which is

important in an ontogenetic study already making multiple comparisons between several different age groups. The human comparison directly addresses the question of whether one can identify growth correlates of *human* life history early in the fossil record. If this null hypothesis cannot be rejected then comparison with other species tells nothing about the evolution of human life history.

Conclusion

The fossil record is critical for reconstructing and understanding the evolution of human growth and development. The fragmentary and cross-sectional nature of fossil samples is best handled with a null hypothesis testing approach, asking whether the fossil pattern of ontogenetic variation has a high or low chance of being sampled from a large human reference population. The randomization-based comparative method to be presented herein is designed specifically to test this hypothesis and maximize the information gleaned from the fossil sample. Conceptually, this hypothesis has important implications for human evo-devo and life history.

The *A. robustus* sample contains individuals across nearly the entire subadult growth period, and so is better suited than other early hominid samples to address the evo-devo question of whether species differences and similarities arise largely during pre- versus postnatal growth, and whether species follow identical patterns of postnatal shape change. While this question has been examined for hominids previously (e.g. Ackermann and Krovitz, 2002), the current study uses a more complete fossil sample and a novel method test these alternatives more rigorously than earlier studies could.

This study will also facilitate a better understanding the evolution of human life history. Our unique pattern of growth is a key part of our life history, characterized by a prolonged period of slow growth prior to puberty followed by an adolescent acceleration. This pattern is essential for allowing youngsters the opportunity to learn necessary social skills while minimizing energy requirements. While the antiquity of the human pattern has been investigated extensively by numerous researchers, these studies were hindered by logical and methodological issues, either looking in the wrong skeletal places or utilizing insufficient samples. If the null hypothesis cannot be rejected, this may imply that the human pattern of growth was established by the early Pleistocene (although the failure to reject would not necessarily imply the converse).

The present study has many advantages over previous analyses of growth in extinct hominids. Many earlier studies did not to take into account variation within species. Some of these works fail to capture an adequate example of past population variation because they limit their analysis to one or two fossils. Many studies also failed to account for intraspecific variation by relying on dichotomous models or standards of dental development. Related, some studies did not statistically test whether hominid growth patterns could be distinguished from referent species (Cobb and O'Higgins 2004), but instead simply plotted measurements against age and then made inferences based on visual inspection of these plots (e.g. Ponce de León and Zollikofer 2000; Thompson and Nelson, 2000; Antón and Leigh 2003).

The present analysis is designed to avoid many of the obfuscating factors faced by previous studies of hominid ontogeny. By adopting a statistical hypothesis-testing framework and comparing *A. robustus* only with a large sample of modern humans, this

study is ideally poised to address questions about the evolution of hominid development and life history. The null hypothesis predicts that each species follows the same pattern of size change. For evo-devo, an alternative hypothesis is that characteristic morphologies might arise through differences in the growth of only a subset of traits. For life history, rejection of the null hypothesis would represent the first *skeletal* evidence that an early hominid may not have had the same pattern of growth as humans, a claim that at present is based almost entirely on inferences from dental development. This study will therefore make an important contribution to paleoanthropology regardless of the analysis' outcomes.

Chapter 3

Materials and Methods

The evolution of human development and life history is addressed with the hypothesis that ontogenetic variation among *A. robustus* and recent humans cannot be distinguished. This is tested by comparing patterns of size change in ontogenetic series of mandibles of each species, using a new test designed especially for small, fragmentary samples. This chapter describes the background of each of the species samples, as well as the rationale for their selection. Mandibles in each species are further subdivided into five equivalent age groups based on stages of dental eruption. I then describe the metric variables that will be compared in each sample, explaining why these data are most appropriate for the analysis. Finally, I describe the logic and logistics of the new randomization procedure used to compare patterns of age-related change in each species.

Samples

Australopithecus robustus. The fossil sample is comprised of 13 individuals spanning from infancy to late adolescence with the last permanent molar in the early stages of eruption (Table 3.1). These fossils are from the early Pleistocene site of Swartkrans in South Africa (Broom, 1949; Broom and Robinson, 1952; Brain, 1981, 2004; Sutton et al., 2009; Pickering et al., 2012). The hominid fossils studied come from Member 1 with an additional specimen from Member 2.

Cave sites like Swartkrans have a great deal of uncertainty about their depositional contexts and absolute age. These caves lack volcanic sediments that can be used to estimate absolute ages with accurate and reliable radiometric techniques like argon-argon dating (Ludwig and Renne, 2000; Herries et al., 2009). Moreover, caves can be exposed at any time, raising the possibility that Swartkrans' early Pleistocene deposits may be contaminated by small infillings long post-dating the bulk of the deposit (Broom and Robinson, 1949; Brain, 1981, 2004).

Herries and colleagues (2009) recently reviewed attempts to date Swartkrans and other South African cave sites. Comparison of Swartkrans' non-hominid fauna with that from radiometrically-dated East African sites suggests the majority of Member 1 was deposited between 2.0-1.6 mya, whereas Member 2 may be closer to 1.4-1.5 mya. However, the presence of both relatively primitive and advanced taxa in Members 1-3 could indicate each deposit accumulated contemporaneously between 2-1 mya. Absolute dating techniques such as electron spin resonance and uranium-lead (U-Pb) have been employed on tooth enamel from Swartkrans fossils (Balter et al., 2008). These methods suggest that Members 1-2 date to around 1.8 and 1.5 mya, respectively, but the error ranges of these estimates are great and overlap for each member. More recently, Pickering and colleagues (2011) obtained new U-Pb estimates for the flowstones both under- and overlying Member 1, and were able to bracket the accumulation of Member 1 to between 2.33-1.64 mya.

In sum, it is quite possible that the *A. robustus* sample examined here is the result of a relatively short period of deposition, but this cannot be said for certain. Both faunal correlations and absolute dating techniques provide consistent estimates that Member 1

may be slightly older than Member 2, but the composition of each deposit is similar enough to be consistent with idea that the members being contemporaneous (de Ruiter, 2003; Brain, 2004; Herries et al., 2009). All but one of the fossils examined come from Member 1, which may be constrained to between 1.8-1.6 mya (Pickering et al., 2011). SKX 4446, the only fossil examined from Member 2, has been shown to be very similar to other *A. robustus* mandibles from the site (Grine, 2005), suggesting that even if time averaging were an issue here, it is probably not a major contributor to variability within the sample.

Swartkrans Deposit	*A. robustus* mandibles
Member 1	SK 6, 25, 55b, 61, 62, 63, 64, 438, 843, 1587, 3978, SKW 5
Member 2	SKX 4446

Table 3.1. Provenience and catalog numbers of *Australopithecus robustus* specimens in this analysis.

A. robustus mandibular remains are also known from the nearby site of Drimolen (Keyser et al., 2000), which was probably deposited around the same time as Swartkrans. Mandibular fossils from Drimolen will not be considered in this analysis, however, as these fossils are not yet available for study. This may not be a problem for present analysis, as Drimolen contains few subadult individuals that address ontogenetic variation in *Australopithecus robustus* (Moggi-Cecchi et al., 2010). DNH 44 from Drimolen is a right mandibular corpus and partial ramus of an individual whose dm_2 is as incompletely erupted as SK 438 from Swartkrans. Comparison of SK 438 fossil with the published pictures of DNH 44 suggests that these infants share the same size and proportions. DNH 46 is a partial right mandibular corpus with an occluded rdm_2 and RM_1. The M_1 cusps of DNH 46 are worn and flattened, compared with the freshly erupted M_1s of the Swartkrans mandible SK 63 (which is virtually complete). DNH 46 is therefore probably a little older than SK 63, and again comparisons of the latter with published

photographs of the former (Moggi-Cecchi et al., 2010) give the impression of similar overall size and shape. The only other subadult jaw from Drimolen is DNH 12, a small fragment of posterolateral right mandibular corpus of an adolescent with the RM_3 nearing alveolar eruption. No measurements can be taken on this mandible save for perhaps an estimate of the width of the extramolar sulcus. Thus, only two fossils (DNH 44 and 46) from Drimolen are potentially useful to the study of mandibular ontogeny in *A. robustus*.

It may be appropriate to omit the Drimolen fossils in any event, as they might represent a population distinct from Swartkrans. Dental remains from Drimolen are, for the most part, on the lower end of the Swartkrans range of variation (Moggi-Cecchi et al. 2010), which could reflect systematic differences in body size between hominids at the two sites. In line with this, when Keyser (2000) described the complete female skull (DNH 7) from the site, he noted it was "noticeably smaller" than SK 48 and most other Swartkrans craniodental fossils that were erstwhile considered female; Lockwood and colleagues (2007) have since suggested SK 48 and others may actually have been small adult males. Thus, it is possible although not certain that Drimolen *A. robustus* were generally smaller-bodied than those from Swartkrans, implying differences in growth and age-related variation between the two sites; this would be an interesting hypothesis to test in the future.

A. robustus specimens from Kromdraai are also omitted from this study. The type specimen of *Paranthropus* (*Australopithecus*) *robustus* (Broom, 1938) is not included because it belonged to a young adult (as judged by an M_3 in occlusion), while the present analysis focuses on subadult growth prior to occlusion of M_3. The other subadult *A.*

robustus from the site, TM 1536, is also omitted because it does not preserve measurable anatomy to be compared with the other fossils.

Modern humans. The human sample includes 122 subadults from the site of Libben in Ohio (Lovejoy et al., 1977). Libben is radiocarbon dated to between 800–1100 CE, and was probably continuously occupied during this time. The site is located on the Portage River near Lake Erie, and would have been at the edge of a swamp during its occupation. The site spans over 30,000 square feet and has yielded remains of over 1,300 individuals. Libben was an egalitarian society, and there is no indication of preferential or differential burial of certain individuals or groups (Meindl et al., 2008).

Fauna from the site point to a large animal protein component to the diet, based largely on trap-and-weir hunting of small animals and fish, and there is an odd dearth of vegetables aside from wild rice (Lovejoy et al., 1977; Meindl et al., 2008). Lovejoy and colleagues (1977: 291) report there may have been "marginal corn agriculture at some time," but this appears not to have been a major component (Meindl et al., 2008). Archaeology and paleodemography of the site indicate that adults must have endured extremely high work loads to support what was a healthy and robust population (Howell, 1982). Important for this study, growth of the long bones at Libben appears to have been comparable to other humans both prehistoric (Mensforth, 1985) and modern (Lovejoy et al., 1990).

Libben was selected as a comparative sample for three main reasons. First, subsistence was based on fishing, hunting and gathering (Lovejoy et al., 1977), so individuals' growth would not have been affected by the nutritional and adaptive changes associated with recent agriculture and domestication (Wood et al., 1992; Okazaki, 2004;

Sardi et al., 2006). The high incidence of dental crowding and malocclusion between upper and lower teeth in recent compared with prehistoric human populations has been attributed a more easily processed diet in the former (e.g. Begg, 1954; Beecher and Corruccini, 1981; von Cramon-Taubadel, 2011). Reduced masticatory demands for recent humans fail to stimulate adequate bony jaw growth, and reduce the rate and degree of interproximal wear between adjacent teeth. This is not an issue within the Libben sample, which shows higher than modern interproximal wear and normal occlusion consistent with their non-modern diet.

The second reason Libben was selected is because it is one of the largest skeletal populations. Of 1,327 skeletons from the site, 122 subadults preserved measurable mandibles. With at least 10 individuals in each eruption stage, the sample used here is large enough to provide a reliable estimation of variation within stages (Table 3.2). Finally, Libben alone was selected as a modern referent in order to minimize any effects of population variation in growth (Eveleth and Tanner, 1988; Walker et al., 2006a. For example, Holmes and Ruff (2010) were able to detect expected differences in mandibular growth between two prehistoric North American human populations (n=42 and n=60) with contrasting diets. Intraspecific variation could be unpredictable and random, could artificially inflate sample variance, and could thereby increase the likelihood of failing to reject the null hypothesis. Libben was therefore selected because it provides a sufficiently large sample and represents a single, continuous occupation of hunter-gatherers (Lovejoy et al., 1977).

Dental Eruption Stages

One reason the mandible makes an ideal element for the study of growth is that the presence of developing and erupting teeth (and the bony alveolus containing them) reflect an individual's age and maturity. Calendar ages can be difficult to estimate because of variation both within and between populations in the ages at which children's teeth form and erupt (Dalhberg and Menegaz-Bock, 1958; Wolpoff, 1979; Hägg and Taranger, 1981; Eveleth and Tanner, 1988; Tompkins, 1996; Liversidge, 2003). Although it is possible to assign chronological ages to each mandible studied, there is not a clear answer to which (if any) population standard is best to use.

In contrast to the great variation in the ages at which humans erupt various teeth (Wolpoff, 1979; Liversidge, 2003), the *sequence* in which teeth emerge into the mouth is fairly consistent. For instance, the first permanent molars and incisors always erupt before the second molars and incisors. Important for life history, the eruption of certain teeth roughly coincides with other developmental milestones (Hägg and Taranger, 1981; Kraemer et al., 1982; Smith, 1991, 1993; Bogin, 1999; Zihlman et al., 2007; Hochberg, 2012), allowing the growth period to be divided into developmental stages. For instance, Humphrey (2010) notes that the full occlusion of the deciduous dentition roughly coincides with the end of the nursing period in many human populations. The first permanent molar erupts around the age that weaning is complete in most mammals, to facilitate a weanling's adoption of an adult diet (Smith 1991); humans are a glaring exception to this. Some studies have also found the eruption of the second molar corresponds (though fairly roughly) with the onset of behavioral, skeletal and hormonal correlates of puberty in humans (Hägg and Taranger, 1982) and chimpanzees (Kraemer et al., 1982, Zihlman et al., 2007).

This analysis therefore places individuals into age groups based on stages of dental eruption (e.g. Krogman, 1931a-c), as these are directly comparable across populations and hominid taxa. Eruption is a continuous process wherein a tooth emerges out of its bony crypt (alveolar eruption) and then past the gums (gingival eruption), and comes into contact with its maxillary counterpart (occlusal eruption), although the process continues even after teeth are fully occluded (Wolpoff, 1979). Skeletal remains can only document occlusal and alveolar eruption, and so teeth are treated here as either unerupted (still within a crypt), erupted through the alveolus but not in occlusion, or fully occlusally erupted. With these eruption criteria, eruption stages are defined so as to maximize the number of age groups and minimize the potential overlap between groups. Samples are divided into as many stages as possible such that specimens in one stage can be assumed likely to be less mature, chronologically or developmentally, than those in the next group.

The analysis concerns only growth prior to adulthood as defined by full occlusion of the last molar (M_3). Lockwood and colleagues (2007) have suggested that *A. robustus* males continued growing through adulthood while females did not, resulting in higher levels of sexual dimorphism than in humans. Adults are thus excluded from this analysis to minimize the possible effects age- and sex-related variation.

Eruption Stages

Individuals are assigned to the following groups defined by dental eruption:

Eruption stage	*A. robustus*	Humans
1: Deciduous m_2 erupting/occluded	3	36
2: M_1/I_1 erupting but not in	2	10

occlusion		
3: M_1 occluded but M_2 unerupted/unoccluded	1	32
4: M_2 occluded but M_3 unerupted	6	33
5: M_3 erupting but not occluded	1	11
total	**13**	**122**

Table 3.2. Sample sizes for each eruption stage.

Eruption Stage 1: The youngest specimens in the fossil sample are either about to complete (SK 438) or have just completed (SK 64 and 3978) the eruption and occlusion of their deciduous dentition, with only light attrition of preserved teeth. The dm_2 of SK 438 is not quite to full occlusion, and there is no visible wear on its cusp tips, whereas these tips are only slightly worn and rounded in SK 64 and 3978. These three fossils show identical development of unerupted permanent teeth where they can be compared (P_4 and M_1; Conroy and Vannier 1991a), and none shows signs of exfoliation of the di_1 or of I_1/M_1 eruption. SK 438 is thus probably slightly younger than the other two fossils which are of comparable age.

A limited human sample whose dm_2 was in a similar stage of eruption as SK 438 (n = 5) precluded division of this subsample into two groups; this would be an interesting comparison for future work with a larger sample. **Eruption stage 1 is defined, then, as a deciduous dentition, either fully erupted or with dm_2 nearing full occlusion, and prior to the exfoliation of the di_1 or eruption of the I_1/M_1.**

Eruption Stage 2: The next youngest *A. robustus* are SK 61 and 62, which have completely erupted deciduous dentitions and are in the earliest eruption stages of M_1 and I_1, respectively. Each of these jaws is noticeably larger and more robust (i.e. thicker corpora) than both SK 64 and 3978, and their teeth much more worn. **Eruption stage 2 is**

thus defined by an I_1 and/or M_1 in the process of erupting, but not yet in full occlusion.

Eruption Stage 3: A single *A. robustus*, SK 63, is in this category as its M_1 is freshly occluded and its incisors in the process of erupting. **Eruption stage 3 is defined by full occlusion of I_{1-2} and/or M_1, but prior to the exfoliation of the deciduous canines or molars or eruption of any other permanent teeth**.

Eruption Stage 4: The next oldest group of fossils includes six individuals with various stages of premolar and M_2 eruption and occlusion, and of different levels of preservation. It is problematic to create distinct eruption stages based on P_{3-4}/M_2, because of inter- and intraspecific variation in their eruption sequence. Modern humans tend to erupt the premolars before M_2, although there is variation in this sequence (Garn and Koski, 1957; Smith, 1994; Liversidge, 2003). Australopithecines and great apes, on the other hand, tend to erupt M_2 before the premolars (Schultz, 1960; Smith, 1994). While this latter pattern characterizes most of these six *A. robustus*, the fossil sample suggests P_{3-4}/M_2 sequence polymorphism was present in this species, since the M_2 of SK 55b is freshly occluded but the dm_2 are retained. Given this polymorphism, and the temporal proximity of the eruption of these teeth, it is impossible to create distinct dental categories based on the eruption of these teeth. Thus, **eruption stage 4 is defined by an M_1 in occlusion, premolar(s) and/or M_2 erupting or occluded, and M_3 showing no sign of beginning eruption.**

Eruption Stage 5: This stage includes a single fossil, SKW 5, whose adult teeth are all occluded save for the M_3, which had probably just broken through the gum line but are unworn, indicating they had not come into full occlusion (cf. Grine and Daegling, 1993). Thus, **the fifth and final eruption stage is defined by a completely occluded permanent dentition up to the M_2, with M_3 in the process of erupting without having reached occlusion.**

In sum, the *A. robustus* and human samples are each divided into five comparable subgroups based on dental eruption. Whereas there is a large amount of intra- and interpopulation variation in the chronological ages at which these stages are attained, dental eruption is more closely related to the growth process and life history. Thus, the stages are sequential, but do not necessarily the same in time span. These stages, and not chronological ages, are directly comparable between samples, and so provide the basis for comparing ontogenetic variation in the mandibles of each species.

Variables for Analysis

There are a number of ways to measure size and shape, and to assess growth in these measures statistically. However, the nature of fossil samples places severe limitations on analytical options. The present study examines 29 linear measurements that describe mandibular size and shape (Table 3.3). The 29 traits can be broadly divided into five categories: [1] corpus (including symphysis) breadth, [2] corpus (including symphysis) height, [3] anteroposterior mandibular length, [4] anterior mandibular breadth, and [5] ramus height and anteroposterior length. Many of these measurements will

covary and be slightly redundant – for instance corpus height at P_4 compared with the height between P_{3-4} – but these both are necessary to maximize the number of comparisons that can be made between fragmentary fossil individuals; redundancy is minimized by the unfortunate fact that the one thing that fossil samples have a lot of is missing data. Where possible, only an individual's left side was measured, although data from the right side were used if the data from left side were absent. Measurements were taken to the nearest 0.10 mm with digital sliding calipers, made of plastic so as not to damage precious fossils and delicate subadult bones.

To assess measurement error, each of the 29 measurements was taken three times on each fossil, and on a subset (n=48) of the humans encompassing all eruption stages. Most measurements differed by 0.0-0.2 mm between replications, and the difference between the maximum and minimum triplicates rarely (<1% of the time) exceeded 1.0 mm. For the fossils and this subset of individuals, the average value of the replications was used in the analysis.

In addition to these 29 traits, a pairwise size metric, the geometric mean of the measurements shared by pairs of specimens, is also examined (Jungers et al., 1995). This is calculated as the n^{th} root of the product of n traits. This metric serves a two main purposes. First, it is of interest to summarize the size of an individual with a single number, as size is an important life history variable. Second, and related, not all specimens preserve the same traits, so defining size in terms of traits shared by *pairs* of specimens maximizes the ontogenetic information that can be taken from the sample.

While the analysis of linear measurements has been eclipsed in recent years by descriptions of shape based on configurations of three-dimensional landmark coordinates

(geometric morphometrics, or GM), linear measurements are more appropriate for the present study. GM has been used to compare mandibular growth between groups (e.g. Franchi et al., 2001, 2007; Coquerelle et al. 2010b, 2011), but will not be used in this analysis for two main reasons. First, GM requires that shapes (defined by 2- or 3-dimensional landmark coordinates) be superimposed on one another before they can be compared in a multivariate "shape space," but the choice of superimposition technique is fairly arbitrary and affects the results of an analysis (Lele and Richtsmeier, 2001). The principle superimposition method is generalized Procrustes analysis (Rohlf, 1990), which centers a set of shapes on their centroids (the point in space closest to all other landmarks), after removing the effects of size and shape. This procedure thereby distributes shape variation equally across landmarks.

This superimposition is biologically unrealistic for modeling facial growth, especially in an ontogenetic series – the mandible does not simply enlarge equally in all directions throughout the growth process (Enlow and Hans, 1996). The mandible initially has space only for the developing deciduous dentition, and so space for the additional and replacement teeth is added by differential growth in different anatomical regions. Histological and X-ray based implant studies of mandibular growth in humans (Enlow and Harris, 1964; Johnson et al., 1972; Enlow and Hans, 1996) have shown that the growing mandibular corpus accommodates new teeth distal to the dm_2/P_4 by adding bone at the corpus-ramus junction. During growth the corpus itself "drifts" anteriorly with the oral tissues surrounding it, and so bone is deposited at its posterior extent to maintain functional contact with the ramus. Thus, an ontogenetic series of mandibles will

necessarily contain missing data, as subadults will lack data taken at the positions of teeth that have not yet erupted – because these positions literally do not exist yet.

Second and more importantly, GM and multivariate statistics are not employed here because they are not appropriate for small samples with missing data. As mentioned above, the traditional superimposition method analyzes shapes in a unique multivariate "shape space" defined by complete configurations of landmarks (Rohlf, 1990). Comparing these superimposed shapes in samples with missing data is impossible because different landmark configurations would occupy different shape spaces. The shape-space constraint characterizes traditional multivariate statistics beyond landmark-based GM.

The necessity to have complete specimens severely limits the scope of traditional methods, causing many researchers to restrict their samples to include only the few, more complete fossils. This strategy does not take advantage of the potentially useful information found in the more fragmentary specimens. Moreover, it often limits questions of growth to examining only the starting and end-points of growth, blind to patterns of growth between these time points. In addition, the variance of traits in small fossil samples typically violates the assumptions of parametric and multivariate statistical tests commonly used in studies of growth (Ackermann, 2005; Ahern et al., 2005).

In the present study, the variables of interest are thus linear measurements that can be taken on very fragmentary fossils. Growth is measured here as the proportional size change between eruption stages, that is the ratio of the older divided by the younger individual. This strategy is similar to that used in Euclidean Distance Matrix Analysis (EDMA; Richtsmeier and Lele, 1993; Lele and Richtsmeier, 2001; Richtsmeier et al.,

2002). A ratio as opposed to an absolute size difference between stages is used, because the *A*. *robustus* mandible attains an absolutely larger adult size than any human, and growth rates at a given time must be somehow proportional to size at the time (Huxley, 1932; Tanner, 1951). For instance, if the absolutely smaller human mandible undergoes an adolescent growth spurt during which it achieves a large proportion of its overall size, but the absolute size increase is the same in the already-larger *A*. *robustus*, the significance of this human spurt would be lost if growth were measured as an absolute and not relative change.

Comparisons across age groups raise special issues of homology. Mandibles with deciduous teeth contain crypts with developing crowns and roots, whereas in older individuals these teeth may be erupted and the crypts gone. In this study, tooth positions occupied by deciduous and permanent counterparts are considered homologous (e.g. corpus height at dm_2 is comparable to height at P_4; Table 3.3). The growing mandibular corpus elongates to accommodate additional teeth by deposition posteriorly at the lingual tuberosity, which causes tooth positions anterior thereto to migrate anteriorly (Enlow and Hans, 1996). Thus, even though teeth in these positions may be different at different eruption stages, the actual location of these teeth is the same. Similarly, measurements are taken on younger specimens at the positions of unerupted permanent molars where these can be determined.

In summary, data for this study include 29 linear measurements describing mandibular size and shape, plus a size metric that quantifies the size of individuals based on only those traits shared between pairs of specimens. These variables were selected because they allow fragmentary individuals to be examined and compared whereas

multivariate GM cannot handle so much missing data as in the present ontogenetic samples. Growth in these variables is measured as the ratio between older and younger individuals as determined by dental eruption.

Analysis of growth in A. robustus

The pattern of ontogenetic variation displayed by the fossils must be situated within a statistical framework – just how do mandibular size and shape change in ontogeny, and just how likely or unlikely is it to find the *A. robustus* pattern of variation within a similarly-sized and -preserved sample of modern humans? This section describes difficulties inherent in analyzing growth in fossil samples, and presents a new test using resampling (viz. exact randomization; Sokal and Rohlf, 1995; Manly, 2007) to compare the small ontogenetic series of *A. robustus* mandibles with the larger human sample.

The nature of fossil samples requires analytical methods beyond the traditional (parametric) growth curve – multivariate or univariate (but see Martín-González et al. 2012 for a recent resampling-based treatment). If fossils samples were complete and large enough, one way to make comparisons would be to create a growth curve by plotting trait values against age. From there, an exponential mathematical model approximate age-related changes could be fit to these data (Laird, 1967; Jolicoeur et al., 1991), and the null hypothesis that two groups follow the same growth trajectory or curve could then be tested by comparing each group's residuals from the modeled line (e.g. Holmes and Ruff 2011). When examining growth of many variables at once, multivariate regression or angles between principal components can be used to test for differences between groups (e.g. Cobb and O'Higgins 2004).

Trait ID	Mandibular Measurement
Corpus breadth: taken perpendicular to the base of the corpus	
X223	Breadth at P3
X225	Breadth at septum between P3-4
X227	Breadth at P4
X229	Breadth at septum between P4-M1
X231	Breadth at M1
X233	Breadth at septum between M1-M2
X235	Breadth at M2
X709	Breadth at symphysis, parallel to its long axis
Corpus height: taken perpendicular to the base of the corpus*	
X301	Height at mental foramen
X313	Height at septum between P3-4
X315	Height at P4
X317	Height at septum between P4-M1
X319	Height at M1
X321	Height at septum between M1-2
X323	Height at M2
X331	Height-mental foramen to base
X333*	Distance from mental foramen to the nearest point on alveolar margin
X355	Height from alveolar margin perpendicular to basal ramus-corpus junction
X711	Height at symphysis
Anteroposterior mandibular lengths	
X401	Distal P4 to infradentale
X403	Posterior condyle to distal-lingual I2
X404	Distance from the center of the mental foramen to the posterior edge of the lingual tuberosity
X415	Distance from the anterior margin of the mandibular foramen to distal-lingual P4
Anterior mandibular breadths	
X501	Bimental breadth
X502	Bi-canine breadth (external)
X510	Bi-canine breadth (internal)
X511	Bi-P_3 breadth, internal
Ramus height and length	
X603	Posterior ramus margin on the alveolar plane to septum between P_{3-4}
X607	Perpendicular distance from the mandibular foramen to the inferior ramus margin

Table 3.3. List and description of measurements. Measurements involving the permanent P_{3-4} correspond to the deciduous teeth they replace, dm_{1-2}, respectively, in juveniles.

But such a strategy cannot be done with the current samples. As described above, multivariate methods cannot handle missing data characteristic of fossil samples. And because not all individuals preserve all traits, not all traits can be studied throughout the entire growth period in the same way. For instance, a few corpus dimensions (e.g. height at P_4) can be measured throughout the entire *A. robustus* ontogenetic series, but many other variables are unevenly and sporadically distributed across eruption stages. This means that no single growth curve (uni- or multivariate) will describe growth in all variables. If some traits are present in only two stages this would only imply linear growth, and it would be inappropriate to model this with mathematical growth curve with as many parameters as the models used for traits sampling more of the growth period. Given these limitations of fossil samples, novel techniques for the study of growth are presented here.

Resampling or randomization methods are computationally intensive statistical techniques that provide flexible and rather assumption-free means of testing hypotheses about growth in fossil samples (Manly, 2007; Mattfeldt, 2011). Resampling works by randomly drawing individuals from a large comparative sample to create a subsample that matches the fossil sample in size and composition (i.e. preservation), and then computing a test statistic that describes the randomized sample. This random sampling is then repeated a large number of times (e.g. >10,000) to generate an empirical distribution of test statistics, providing a basis for understanding the likelihood of observing the fossil pattern in the comparative sample. The present study resamples an excessive number of times to obtain all possible combinations of specimens, and discards redundant observations, making this an exact randomization test (Sokal and Rohlf, 1995). This has

an advantage over parametric statistics that make assumptions about sample variation (Potvin and Roff, 1993) and rely on theoretical distributions of test statistics. Moreover, randomization *alone* allows inclusion of fossil fragments that are generally viewed as useless for more traditional statistical analyses, making the most of what little biological variation is preserved in fossil datasets.

Randomization/resamplng thus makes it possible to test a null hypothesis that two patterns of variation are identical. To be sure, a failure to reject the null hypothesis may not indicate identity in growth, but rather could reflect the limitations of the fossil sample itself. Rejection of the hypothesis would also need to be treated with caution because of the potential for Type I statistical error (rejection of a hypothesis when it is in fact true). Thus, the validity of the randomization method described below was tested by running the procedure on the human sample alone, the logic being that a sample compared with itself should show no difference on average. The results of the validation are presented in Chapter 4.

The Randomization Procedure

This section outlines the randomization procedure used to make statistical inferences about differences in patterns of growth between *A. robustus* and humans. All analyses are written in the statistical computing package *R* (R Development Core Team, 2011), and can be found in Appendix III.

Recall that 'growth' is defined here as the proportional size change between eruption stages, and that patterns of mandibular growth in *A. robustus* can only be inferred from 13 individuals. Some pairs of these fossils will preserve more traits than

other pairs, some may share no traits in common, and different pairs will preserve different sets of traits. To maximize the amount of growth-related information that can be gleaned from this sample, the analysis makes pairwise comparisons of proportional size change between *every possible combination* of fossil pairs. This set of all possible proportional changes in *A. robustus* is then sought in the set of all possible pairwise changes that can be resampled in the cross-sectional ontogenetic sample of modern humans from Libben. This strategy situates the fossil pattern of ontogenetic variation within the context of human variation for hypothesis testing.

Proportional changes in size are examined for a pairwise size metric, in addition to the 29 individual traits. This metric allows an individual's different measurements to be summarized with a single number. As this analysis relies on pairwise comparisons, and not all individuals preserve all the same traits, this size metric is calculated as the geometric mean (Darroch and Mosimann, 1985) of all the measurements that a set of individuals shares in common (cf. Lockwood 1999; Gordon et al., 2008). This means that an individual may be described by many size metrics depending on the pairwise comparison, and that 'size' is not necessarily homologous between comparisons. However, as detailed in the algorithm description below, the size metric need only be homologous within pairwise comparisons.

The resampling algorithm is performed for each trait including the pairwise size metric. This algorithm is schematized in Figure 3.1, and works as follows:

1. Randomly select two *A. robustus* mandibles in different eruption stages, and then randomly select two human mandibles so that the pair matches the fossils' stages. Record the following metadata (Table 3.4): identities of which fossils and which

humans are the older or younger of the pair, and the individuals' eruption stages and the number of traits they preserve in common (k).

2. Calculate a **test statistic ζ**, describing the species difference in the amount of relative change in size between the eruption stages (*nota bene*: ζ is not the within-species proportional changes themselves). Recall that when calculating ζ for the pairwise size metric, this must be based only on the set of traits all four resampled individuals share. If k>0, the ratio is calculated first by taking the ratio of the older to younger individual in each species. Then take the difference, ζ, between the *A. robustus* ratio minus the human ratio:

$$\zeta = [(R_{OLDER} / R_{YOUNGER}) - (H_{OLDER} / H_{YOUNGER})].$$

As the absolute difference between two ratios, ζ=0 means no difference in proportional size change, while positive values indicate that *A. robustus* underwent greater relative size change in this comparison, and negative values the opposite.

Because the analysis is based on cross-sectional data, it is possible that in a randomly selected pair, the older individual may be smaller than the younger individual (Fig. 2.3, Appendix I), whereas growth implies an increase in size. To prevent this biologically unrealistic situation, if a ratio of older to younger is less than 1 (older is smaller), the ratio is set to 1, indicating no size change between eruption stages for the species in that comparison. The human sample is large and there can great overlap in size between individuals in different eruption stages, whereas there tends to be less overlap between *A. robustus* in different stages (Appendix I). This means that the human sample is more likely to give the impression of negative growth than the fossils, and this fix therefore obviates the overestimation of ζ in such cases.

3. Repeat a large number of times (e.g. 300,000) to ensure that every possible pairwise comparison is made. For each trait, if 0 is within 95% of the randomized ζ statistics, the null hypothesis cannot be rejected for the trait. That is, if 0 is outside the randomized 95% confidence interval, there are statistically sufficient grounds to reject the null hypothesis in favor of an alternate hypothesis of different patterns of size-change between species.

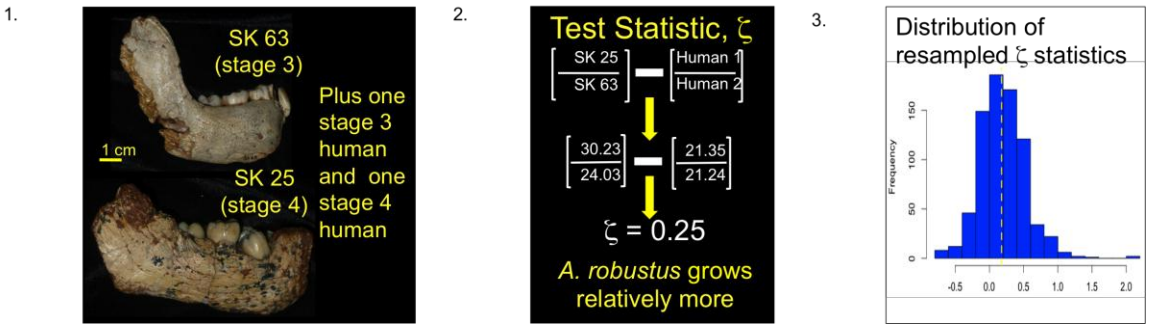

Figure 3.1. The randomization strategy employed in the ζ test.

Resampled data (including metadata) are stored in a matrix with variables as columns and resampled iterations as rows (described in Table 3.4). Iterations that returned NA values (no traits shared between resampled individuals) are discarded. Because the identities of resampled individuals are recorded in each iteration, redundant comparisons consisting of the same two fossils and two humans are removed, making the test an exact randomization procedure. Although it is computationally inefficient to store sample metadata (identities of resampled individuals), this is an important step for ensuring that the program works as intended. Moreover, anyone who is interested in checking whether and how the procedure worked may do so by reviewing the metadata, as the results matrices (even retaining redundant comparisons) are available upon request.

Metadatum	Description
tr	Trait used to calculate size change difference (ζ), individual or the pairwise size metric. The trait is listed according to its number preceded by X (e.g. X223).

k	Number of traits shared by resampled individuals, used to calculate pairwise size metric
a1-2	Eruption stage of the younger (a1) and older (a2) individual of a resampled pair.
da	Difference in eruption stages between resampled pair, e.g. da=1 when the pair includes stages 1 and 2, da=3 when the pair includes stages 2-5, etc.
f1-2	Identities of each fossil, f1 corresponding to the younger and f2 to the older of the two.
h1-2	Identities of each human, h1 corresponding to the younger and h2 to the older of the two.

Table 3.4. Sample metadata (aside from the ζ statistic) stored for each resampled comparison

Summary and Conclusions

Fossil samples present two major challenges to statistical analysis and inference, small sizes and copious missing data. Rather than ask whether *A. robustus* conforms to a specific growth model of growth or pattern of shape change, the present study asks the more basic question of whether two patterns of variation can be distinguished. A novel randomization procedure was presented to quantify and statistically test this question: is the proportional size difference between any pair of *A. robustus* mandibles likely to be seen in a randomly-selected pair of humans at comparable stages of dental eruption as the fossils?

The pattern of *A. robustus* ontogenetic variation is sought in an ontogenetic series of human mandibles from the archaeological population from Libben. This comparative sample was chosen because it is large (n=122 mandibles with at least 10 individuals in each of five dental eruption stages), homogeneous and preagricultural. Comparison was limited to a single human population because this study is concerned with the evolution of human growth and life history. This narrow focus moreover prevents any potential artificial inflation of variance in the human sample due to natural and unpredictable inter-population variation.

A. robustus and humans were compared for patterns of size change between five dental eruption stages, spanning from having only an erupted deciduous dentition to just before the last permanent tooth (M_3) comes into occlusion. Eruption stages are directly comparable between species, and correlated with the growth process and other aspects of life history. The ontogenetic series ceases before adulthood, marked by the full occlusion of M_3, because of the great range of variation in the age at which M_3 comes into occlusion in humans, and because of the potentially confounding effects of high sexual dimorphism in adult *A. robustus*.

Fossil samples, small and missing lots of data, cannot be analyzed using current multivariate methods including landmark-based geometric morphometrics. The present study therefore examined 29 linear measurements and a pairwise size metric based on these variables. These data can allow all measurable fragments – not just the most complete specimens – to be included in a randomization analysis. The ζ test presented above resamples *pairs* of individuals, which uniquely allows it to analyze ontogenetic variation in small, fragmentary fossil samples. The null hypothesis predicts that resampled ζ statistics, which measure the difference in relative size change between pairs of *A. robustus* and humans, will equal zero (no difference) on average.

Failure to reject the null hypothesis could occur for two main reasons: first, the fossil sample may appear to fit a human pattern in light of an actual difference in growth, due to the small fossil sample size. Alternatively, failure to reject the hypothesis may indicate true similarity. Rejection of the hypothesis, however, would strongly indicate differences in patterns of growth between species. Either outcome would provide new

information for paleoanthropology, about the limitations of present fossil samples and methods, and about the paleobiology of *A. robustus*.

Chapter 4

Results of the ζ Test

"Postnatally, the mandible undergoes more variation in shape and greater increase in size than any other facial bone." (Scheuer and Black, 2000: 144)

This chapter presents the results of the ζ test, testing whether patterns of relative change in size can be distinguished in cross-sectional series of human and *A. robustus* mandibles. As this is a novel procedure, the first section (4.1) investigates the behavior of the ζ test. First I examine whether the pairwise size metric (the geometric mean of the set of measurements a pair of specimens shares) is an appropriate measure of size and can be used compare individuals. Next, I assess the behavior of the ζ test, by using it to compare the human sample with itself. This examines the likelihood of rejecting a null hypothesis when it is true. I also examine the potential effects of specimen preservation and the difference in eruption stages being compared on the outcome of the analysis.

Section 4.2 then presents the results of the ζ test comparing the amount of relative change in overall size, measured with the pairwise size metric, between humans and *A. robustus*. Relative change in size is first treated across all possible comparisons, and then focusing on comparisons of individuals in successive eruption stages (i.e. across ontogeny). I also investigate the relationship between the value of the ζ statistic and resampled metadata.

Section 4.3 presents the results of the ζ test for differences in size change of individual traits, presented in five anatomical categories (Table 3.3). As in sections 4.1-2,

ζ statistics for each trait are first treated across all comparisons, followed by comparisons between successive eruption stages. The section ends with a qualitative description of the ontogenetic changes to the anterior corpus (and symphysis) of *A. robustus*, as the complex topography of the region could not be reliably measured with the present techniques.

4.1 Validation of the ζ Test

The ζ test is novel in that it analyzes patterns of change (i.e. age-related) by randomly sampling differently (dentally) aged pairs of individuals, which is necessary with fossil samples in which not all individuals preserve all the same traits. The ζ statistic measures whether the proportional size change between dental eruptions is the same in both *A. robustus* and humans, and is expressed as the difference between the ratios: $\zeta = [(\mathbf{R}_{OLDER} / \mathbf{R}_{YOUNGER}) - (\mathbf{H}_{OLDER} / \mathbf{H}_{YOUNGER})]$, where R and H are an *A. robustus* and human mandible, respectively. Even though this analysis is not the first to use the geometric mean of several measurements to compare fragmentary samples (i.e. Lockwood, 1999; Gordon, et al. 2008), this has not been done in an ontogenetic context. The purpose of this section is therefore to establish the validity of both the pairwise size metric and the randomization methods employed by the ζ test, to show that it can be used to compare humans with *A. robustus*.

Measuring size

With the present samples, focusing on any single trait for the study of growth will require some fossils to be left out, and there are too fossils to prefer approach. A pairwise

size metric, based on whatever trait or traits a pair (or pairs) of specimens preserve in common will maximize the number of comparisons that can be made between age groups. As such, size may be measured differently between different pairs of individuals. This could be problematic because it is not clear how such a size metric behaves analytically. A simple visual comparison human and *A. robustus* mandibles shows that *A. robustus* adults are larger than humans but this gross size difference is less marked in the youngest mandibles. The pairwise size metric ought to be able to detect this pattern.

To examine whether patterns of size difference can be detected using the pairwise size metric, the ζ test described in Chapter 3 is modified to extract all individual pairwise sizes that can be calculated within eruption stages. First, a fossil and human in the same stage are selected at random. If the pair shares at least two traits in common, each individual's size is calculated as the geometric mean of these measurements; pairs with fewer than two shared traits are discarded. There are only 360 possible pairwise fossil-human comparisons (e.g. Table 3.2), but the procedure resamples 5,000 pairs to ensure full coverage, and redundant observations are discarded.

Of the 360 possible pairwise comparisons, 300 shared at least two traits in common from which to measure size (Fig. 4.1). Of the 300 pairs, the *A. robustus* is larger than the human in all but 10 (3.33%), and all of these occur within eruption stage 1. These pairwise sizes can be plotted against eruption stage, similar to a growth curve (Fig 4.2). Overall size overlaps considerably in eruption stage 1, less so in stages 2-3, and finally *A. robustus* sizes are completely outside the upper limits of the human size ranges in eruption stages 4-5. By eruption stage 3 the average *A. robustus* size (calculated solely

from comparing SK 63 with humans) is larger than most humans, even those in stages 4-5 (Table 4.1).

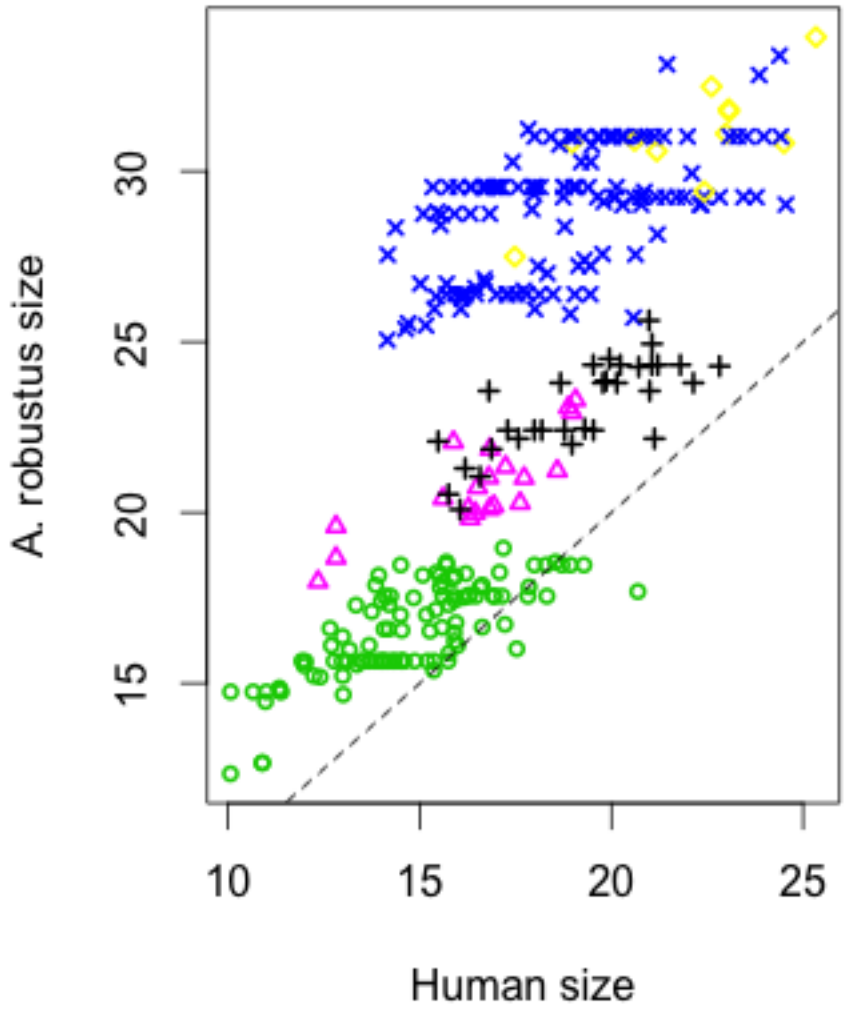

Figure 4.1. Comparison of *A. robustus* and human pairwise size metrics (geometric mean of measurements shared in pairwise comparisons). Each point represents a pairwise comparison, with the *A. robustus* size on the y-axis and the human size on the x axis. Colors correspond to eruption stages: Green = stage 1, Purple = stage 2, Black = stage 3, Blue = stage 4, Yellow = stage 5. The dashed black line indicates identity in size (y=x).

The trajectory of the human sizes across eruption stages (green box and whiskers in Fig. 4.2) is comparable to published growth curves for body mass and stature in humans (Eveleth and Tanner, 1988). There is a general increase in size up to eruption stage 3 (occlusion of the M_1), and a relatively large increase in size by eruption stage 5 (alveolar eruption of M_3) similar to the adolescent growth spurt. An important difference,

however, is that average mandible size is relatively stagnant between stages 3-4, whereas stature and mass growth increase relatively slowly during this period in published growth curves. Note also that in this cross-sectional sample there is a very large range of variation in stage 4, and the median human size is slightly lower than in the preceding period.

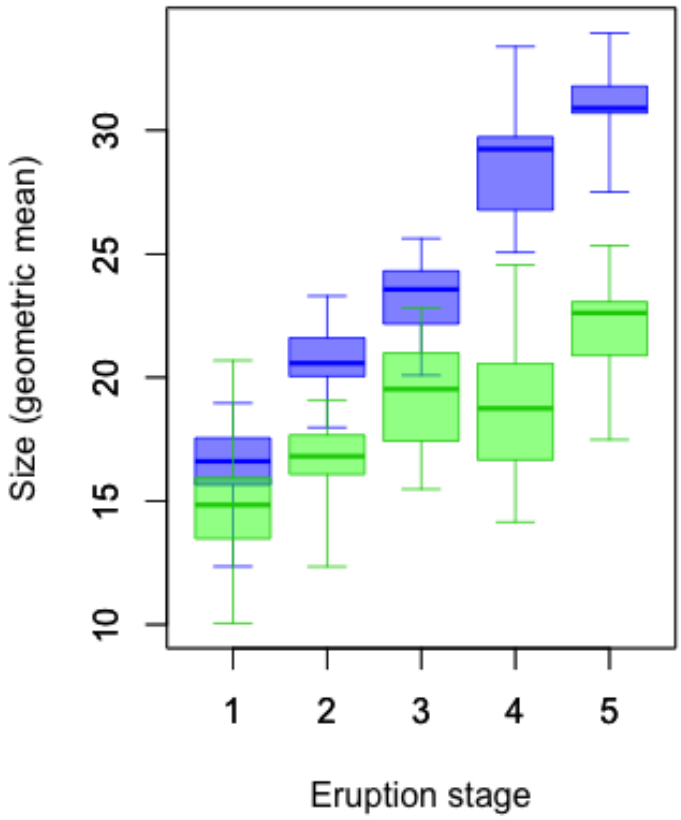

Figure 4.2. *A. robustus* (blue) and human (green) pairwise sizes across ontogeny. Individuals' size may be represented more than once within any stage. Boxes include the 50% quartiles, solid dark lines within boxes are medians, and whiskers extend to the maximum and minimum values.

	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
A. robustus	16.6 (1.36)	20.8 (1.39)	23.1 (1.35)	28.8 (1.86)	31.0 (1.65)
Humans	14.8 (2.14)	16.5 (1.95)	19.2 (2.03)	18.7 (2.54)	22.0 (2.31)

Table 4.1. Species' average pairwise size in each eruption stage: Mean (σ). Pairwise size is measured as the geometric mean of whatever traits a resampled *A. robustus*-human pair shares in common.

This is probably due only partly to sample size, stage 4 being the largest subsample for humans and *A. robustus*. High variation is probably also due to both sexual and ontogenetic variation. Eruption stage 4 is defined by the full occlusion of M_2, which

occurs in a second wave of dental eruptions that roughly coincides with the onset of puberty, prior to the adolescent growth spurt in height and weight (Hägg and Taranger, 1981). There is a great deal of variation in the timing, duration and rate of adolescent growth. The female spurt tends to be earlier, shorter and less intense (lower growth rates) than males', and so sex differences in size and shape become apparent usually around this time, even for the mandible (Coquerelle et al., 2011). Thus, I believe that size shows the most variation in eruption stage 4 because it includes both boys and girls at slightly different stages of skeletal or mandibular growth, although sex is unknown (not estimated) for most Libben subadults.

The distribution of human mandible sizes across eruption stages is thus similar to expectations from known human bodily growth patterns. Similarly, the distribution of *A. robustus* mandible sizes is consistent with visual comparisons of the actual fossils. It is therefore reasonable to measure an individual's size as the geometric mean of the traits it shares with another, which is at the heart of the ζ test.

Randomization methods

In any statistical test, one runs the risk of rejecting a true hypothesis (Type I error) and failing to reject a false hypothesis (Type II; Sokal and Rohlf, 1995). The risk of type II error cannot be assessed in the present case, as this is the very question being examined in the first place (whether *A. robustus* and humans can be distinguished). However, the risk of Type I error can be assessed by comparing the human sample with itself: ζ statistics calculated from within a single sample ought to equal 0 on average.

To assess the risk of Type I error, the randomization procedure described in Chapter 3 is modified to compare humans with humans for the overall size metric (geometric mean). As in the original procedure, two *A*. *robustus* in different eruption stages are randomly sampled. Next, four humans are resampled with replacement (as opposed to only two), two for each of the stages sampled. The four humans are stripped down to the traits shared between all four and the two fossils, to maintain similarity with fossil preservation. The ζ statistic is then computed based solely on the humans – is there any difference in relative size change between two randomly sampled pairs of humans at different eruption stages? Ideally, the test statistics should cluster around 0, as individuals within a single population should provide the same signal of size change. Humans were resampled 100,000 times with replacement to ensure all possible comparisons are obtained, and redundant comparisons were removed.

Period between eruption stages	**n unique resampled**	**Median k**	**ζ (mean)**	**ζ 95% CI**	**P $_{\zeta \leq 0}$ (1-tailed)**
All Possible Combinations	58,709	5	-0.0005	-0.398,0.394	0.530
1-2	6,383	5	-0.004	-0.264,0.264	0.526
2-3	2,007	6	-0.0005	-0.262,0.262	0.534
3-4	5,984	6	0.002	-0.307,0.298	0.535
4-5	6,751	8	0.002	-0.289,0.291	0.543

Table 4.2. ζ statistics for the overall size metric comparing the human sample with itself.

Note that in this validation analysis, even though *A*. robustus is not involved in the calculation of the ζ statistic, two fossils are nonetheless resampled to determine the number of traits used to calculated size (geometric mean). This is important because the human sample is generally better preserved than the fossils, meaning that randomly selected humans will usually have more traits in common than with fragmentary fossils. If the outcome of the test has anything to do with the number of traits shared, this step

will ensure fossil-like preservation, and is therefore more true to the testing conditions when using fossils.

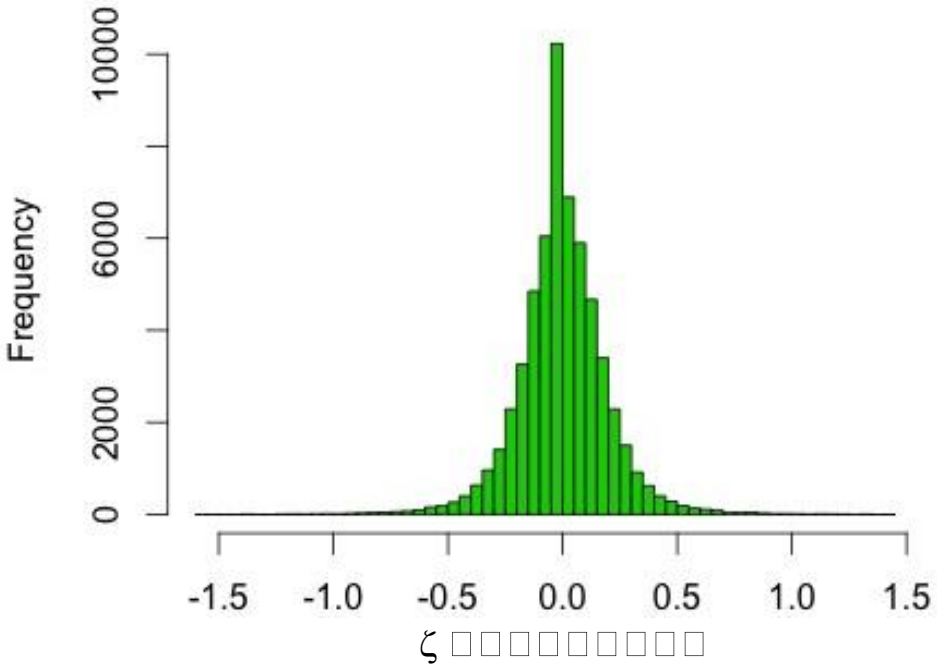

Figure 4.3. ζ statistics for the overall size metric for all pairwise combinations of differently-aged humans. ζ=0 means no difference between resampled pairs.

Results indicate that the ζ test is unlikely to reject the null hypothesis (no difference between groups) when it is true. Of 100,000 iterations, the procedure returned 58,709 unique comparisons. The mean ζ=-0.0005, and the median is 0 (Table 4.2, Fig. 4.3). Moreover, although this distribution is symmetrical about a mean of 0, it is not normal, but rather appears exponential, heavily weighted toward the mean with long tails. This indicates that within a single sample, the ζ test is unlikely to indicate divergent patterns of growth. However, the great range of ζ statistics (and long distribution tails) reflects the ontogenetic variation inherent in cross-sectional samples.

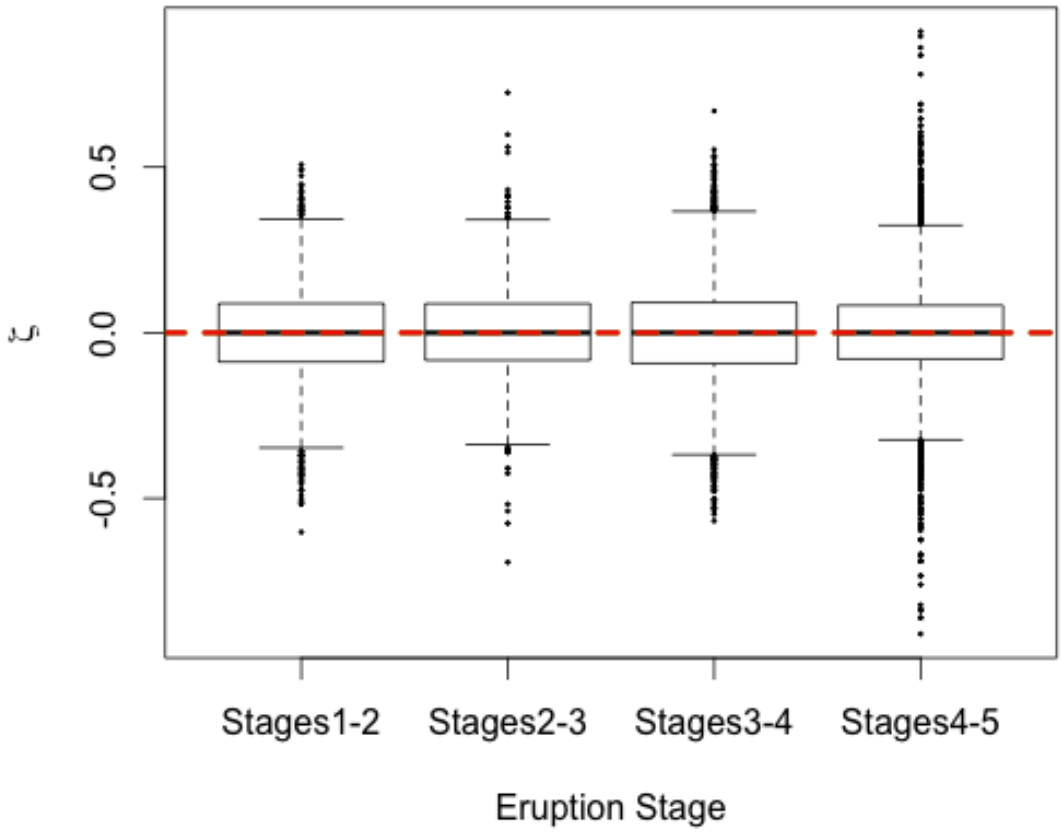

Figure 4.4 ζ statistic for the overall size metric comparing successive dental eruption stages. The red dashed line indicates ζ=0. Boxes include the 50% quartiles, dots are outliers, and solid black lines in each box are medians.

The same pattern emerges when comparing ζ statistics across ontogeny, i.e. between subsequent eruption stages (Table 4.2). For each pairwise comparison between successive stages, the mean ζ is essentially 0, although there is a large range of values as is clear from Figure 4.4. This demonstrates that within a cross-sectional sample such as the one employed here, normal individual variation can create the appearance of many patterns or amounts of growth between dental eruptions. This highlights the importance of comparing the small fossil sample with a larger reference sample, rather than making inferences based on the fossils themselves. For instance, the variation in ζ statistics describing size change between eruption stages across ontogeny (Fig 4.4) shows that it is

possible (though highly unlikely) for a small subsample of humans from Libben to appear to follow a different pattern of growth than the rest of the sample (cf. Fig. 3.1).

Table 4.3 shows the rank correlations (Kendall's tau) between the ζ statistic and metadata, da (the difference between a pair's eruption stages) and k (the number of traits used to calculate the ζ statistic), in each resampled comparison. ζ statistics calculated from the human sample are not correlated with either da or k. There is a small but statistically significant negative correlation between the difference between individuals' eruption stage and the number of traits they share. Each of these relationships and their influence on the ζ statistic are discussed in more detail below.

Variable	ζ	da	k
ζ	-	0.949	0.658
da	-0.0002	-	**2.2E-16**
k	-0.001	**-0.146**	-

Table 4.3. Relationship between resampled ζ and metadata. Kendall's tau rank correlations are below the diagonal and the statistical significance is above. **Bold** cells are statistically significant.

The Effects of Preservation, k

Part of what makes the ζ test for overall size unique is that by calculating 'size' as the geometric mean of the traits shared between resampled specimens, it is able to make sample-based inferences even though a large amount of data is missing (e.g. Gordon et al. 2008). But because ζ is calculated from different sets of measurements depending on the pairwise comparison, this means overall size is not necessarily homologous across all comparisons. It is therefore possible that the number (and types) of traits used to calculate ζ in a given comparison will have an influence on the value and distribution of ζ statistics.

Figure 4.5 shows the distribution of how many traits were used to calculate all ζ statistics. The distribution shows a clear bias toward a small number of traits being preserved in common between specimens. Across the nearly 59,000 comparisons, a

median of five traits are shared and used to calculate size for a given comparison. Although there were 29 traits examined in this analysis, the most that any resampled set of individuals (six: four humans plus two fossils) shared was 20 traits, and this was in only seven (0.01%) of all possible comparisons. While most sizes were calculated off of more than just one trait, nevertheless there are 10,887 comparisons (18.5%) for which k=1. Although the k=1 subset is sizeable, it does not exert too great an influence the results: when excluding this subset, the median number of traits increases from five to only six traits; the mean ζ value shifts from -0.0004 to -0.0003; and the median ζ is still 0.

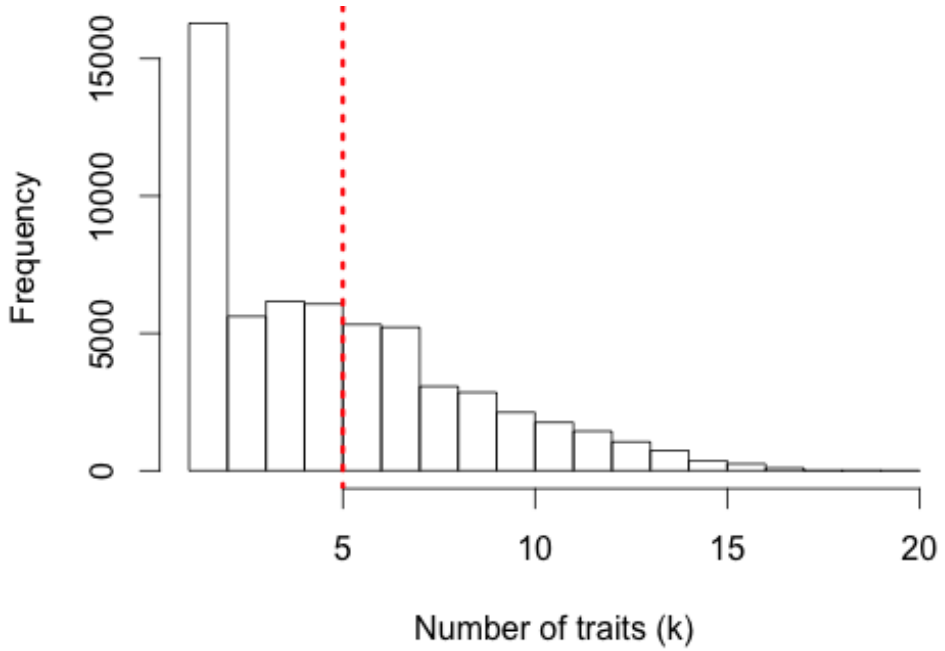

Figure 4.5. The number of traits shared between individuals in the ζ test validation. These k traits were used to calculate the 58,709 ζ statistics. The red dashed line is the sample median.

No matter how many traits are shared, the resampled ζ statistics cluster around ζ =0 (Fig. 4.6), hence the low rank correlation between ζ and k in Table 4.3. But while there is no relationship between k and ζ, Figure 4.6 suggests a relationship between k and the *variance* in ζ. This is because chance preservation of fossils means that two specimens are more likely not to preserve features than to share them, so that there is a

negative correlation between k and the number of individuals sharing k traits (tau=-0.937, $P_{\zeta \leq 0}=0.137E^{-13}$).

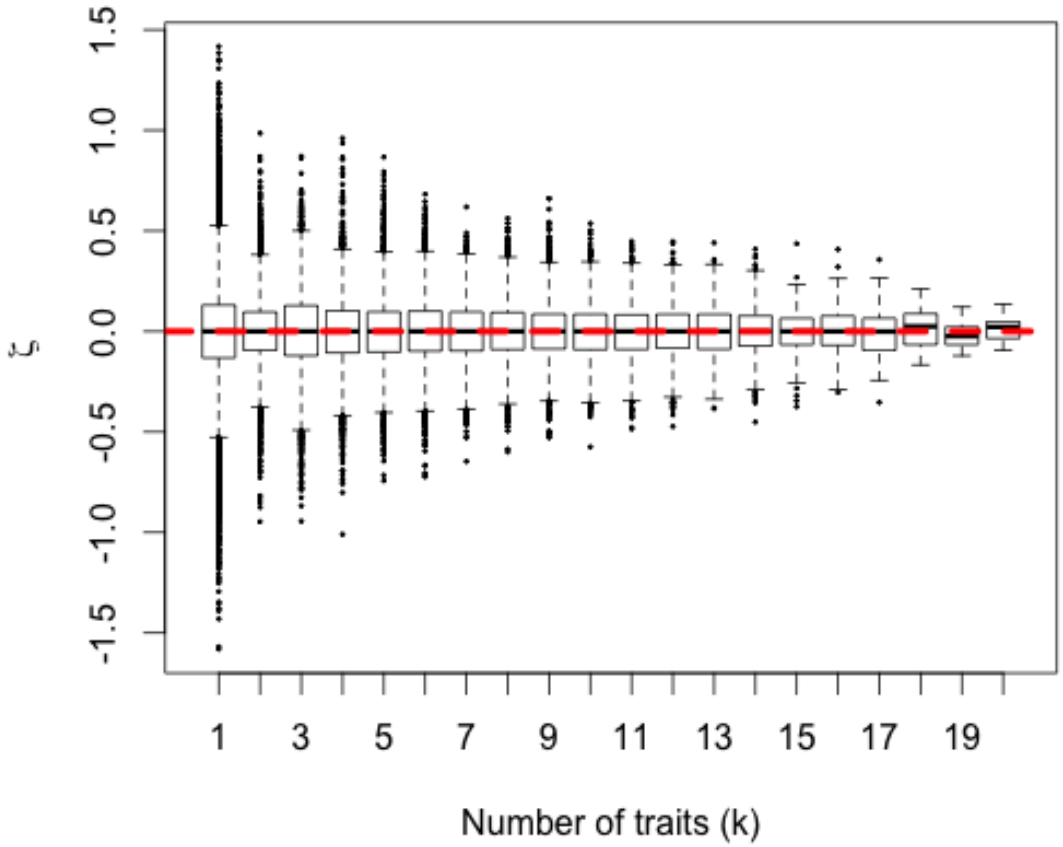

Figure 4.6. The influence of the number of traits (k) on the value ζ statistics in the test validation. The red dashed line indicates ζ=0. Boxes include the 50% quartiles, dots are outliers, and solid black lines are medians.

Because the variation in ζ decreases as k increases (Fig. 4.6), this suggests that the *absolute value* of ζ depends on the number of traits used. In fact, the rank correlation between k and the absolute value of ζ is tau=-0.091 ($P_{\zeta \leq 0}=2.2E^{-16}$). This significant, negative correlation contrasts with the lack of correlation between (raw) ζ and k, but it should be noted that the correlation is nevertheless still fairly low. The central tendency is for ζ to be close or equal to zero, only the length of the distribution tails become absolutely larger as fewer traits are sampled. Thus, the influence of trait number on the

magnitude of measured difference in size change seems to be very small in the present case.

In summary, preservation is capricious in skeletal samples, and so the potential influence of the number of traits (k) used to measure differences in size change was investigated. Most comparisons are based on a relatively small number of traits, and there is a weak negative correlation between the *absolute* magnitude of ζ and the number of traits used to calculate this value. On the whole, however, the ζ statistic averages 0 across different age intervals, regardless of the number of traits shared between individuals. Effects of preservation appear to have little influence on the analytical outcomes, at least when a single population is compared with itself. However, when comparing two populations that do differ in patterns of growth, it is theoretically possible for preservation to influence the results of the ζ test. For instance, if species are similar in the growth of some traits but not others, preservation bias may favor, say, those traits that grow similarly in each group. In this case, ζ values close or equal to 0 would be overrepresented. This is one of the main issues that led to the present study, and the storage of resampled metadata allows the influence of preservation to be assessed in such a situation.

The Effects of Difference in Eruption Stage, da

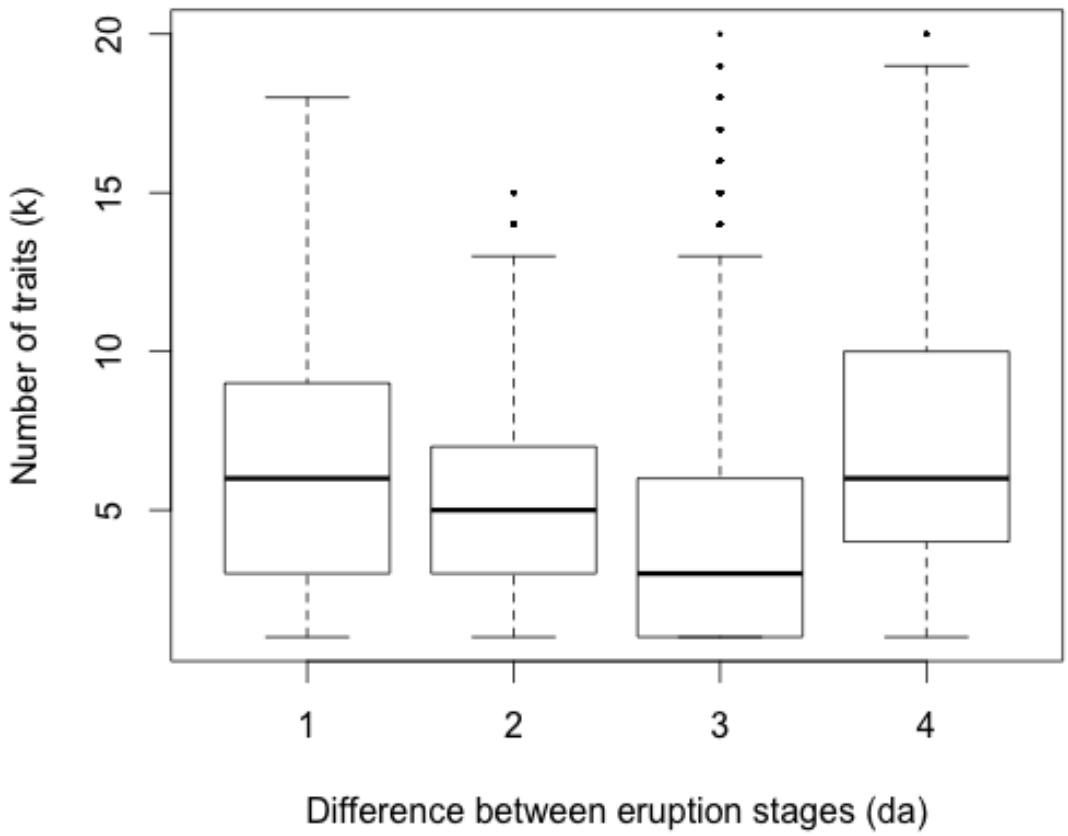

Figure 4.7. The number of traits (k) shared between specimens spanning different eruption stages. For instance da=1 includes comparisons based on eruption stages 1-2, 2-3, 3-4, and 4-5. Boxes include the 50% quartiles, dots are outliers, and solid black lines are medians.

The difference between eruption stages (da) used to calculate ζ could also potentially influence the value of ζ. There is basically no correlation between ζ and da, as shown in Table 4.3. However, there is a modest rank correlation (tau=0.112, $P_{\zeta \leq 0}=2.2E^{-16}$) between the *absolute value* of ζ and da, as with k above. This modest relationship may be explained, at least in part, by the weak but negative and significant rank correlation between da and k (Fig 4.7). Recall that even though the average ζ=0 for all possible values of k, the *variance* in ζ decreases as k increases. The outliers to this relationship are the comparisons for which da=4, which measures size change between eruption stages 1 and 5 (i.e. across the whole of ontogeny). The relatively complete fossils SK 3978 and SKW 5 are in eruption stages 1 and 5, respectively, and the pair preserves 21 of the

possible 29 traits in common. Thus, the difference between eruption stages, da, itself probably exerts little or no influence on the value of ζ. The modest negative correlation between da and the absolute value of ζ is most likely due to the (weak) relationship between ζ and k and between k and da.

Summary of the ζ test validation

The ζ test, examining potential species differences in patterns of overall mandibular size change, was validated by first demonstrating that the pairwise size metric adequately reflects both inter- and intraspecific variation in mandibular size (Figs. 4.1-2), suggesting it is an appropriate size measure for the analysis. The ζ test was then used to compare the human sample with itself, to test whether the method performs according to null predictions: ζ statistics should indicate no difference between randomly sampled pairs of individuals from a single species – or better, a temporally constrained population such as we have with Libben (Lovejoy et al., 1977). As predicted, ζ statistics in the validation cluster around 0 (no difference), although some specific comparisons would suggest substantial age-related differences. For the most part, the value of ζ is hardly influenced by either preservation (the number of traits, k, shared in common between resampled individuals), or the eruption stages (viz. their difference, da) of the individuals used in a given comparison. There is a tendency for older individuals to preserve better and therefore have data for more traits. As a result, the most notable relationships detected were between k and da, as well as between the *absolute value* of ζ and both these metadata, but these relationships were weak.

The ζ test was designed to analyze differences between groups in overall size change between various (dental) ages, in the presence of large amounts of missing data. The validation of the test presented here suggests that this procedure can be extended to the compare *A. robustus* and human samples.

4.2: Species differences in overall size change

This section presents the results of the ζ test of the null hypothesis of indistinguishable patterns of age-related variation in humans and *A. robustus*. The first part compares patterns of overall mandibular size change for the pairwise size metric. As in section 4.1, the results of the ζ test across all possible comparisons are first presented, followed by results from comparisons of individuals in successive eruption stages (i.e. across ontogeny). The section ends by examining the influence of resampled metadata (number of traits shared, difference between a pair's eruption stages) on the value of the ζ statistic.

Results of the ζ test comparing change in overall size

All Possible Comparisons

A total of 29,148 unique human-*A. robustus* comparisons can be made with the present sample sizes and preservation (Table 4.4, Fig. 4.8). Mean ζ=0.310 (median = 0.299) for these comparisons, indicating that the amount of relative size change between eruption stages is greater in *A. robustus* than it is in humans on average. This difference is not statistically significant at the traditional $p \leq 0.05$ level, meaning the hypothesis of indistinguishable size change is not rejected. Nevertheless, the likelihood of seeing such a

large size difference in a human sample is still quite low ($P_{\zeta \leq 0}$=0.124), and it will be shown below that species differences in size change are not the equal between all eruption stages.

Period between eruption stages	n unique resampled	Median k	Mean ζ	Median ζ	ζ 95% CI	Probability ζ≤0 (1-tailed)
All possible comparisons	29,148	5	0.310	0.299	-0.178,0.908	0.124
1-2	2,120	6	0.147	0.155	-0.081,0.305	0.095
2-3	625	9	-0.051	-0.035	-0.261,0.050	0.635
3-4	4,091	7	**0.317**	**0.314**	**0.020,0.574**	**0.019**
4-5	1,985	8	-0.057	-0.021	-0.380,0.141	0.768
1-3	2,432	7	0.127	0.138	-0.146,0.342	0.162
1-4	13,139	4	**0.457**	**0.459**	**-0.096,1.11**	**0.042**
1-5	1,156	9	**0.452**	**0.461**	**0.153,0.712**	**0.002**
2-4	3,031	6	0.202	0.226	-0.240,0.520	0.151
2-5	220	13	**0.159**	**0.166**	**-0.019,0.312**	**0.045**
3-5	349	13	**0.267**	**0.269**	**0.047,0.451**	**0.017**

Table 4.4. Species difference in relative change for the pairwise size metric (geometric mean). **Bold** values indicate that less under 5% the exact randomized distribution is less than or equal to 0 ($P_{\zeta \leq 0}$).

Results corroborate visual comparison of infant and adult *A. robustus* mandibles, which shows that this species clearly underwent greater *absolute* size change than humans during postnatal ontogeny (Table 4.1, Fig. 4.2). The greater absolute and relative size change undergone by the *A. robustus* mandible is exemplified in ζ statistics calculated from individuals in eruption stage 1 to stages 4 and 5 (i.e. periods 1-4 and 1-5 respectively; Table 4.4). These comparisons have the highest mean ζ values, both above 0.450 versus the overall average of 0.310 across all possible comparisons. The ζ distributions for these two periods (both separately and combined) are significantly greater than 0 at $p<0.05$. Period 1-5 has the lowest probability of ζ being less than or equal to 0 (i.e. greater relative size change in humans), and is one of only three dental periods in which 0 is completely outside the 95% confidence interval of the ζ distribution.

In contrast, there is negligible difference between species in relative size change between eruption stages 4-5 (discussed below).

This and the great concordance between the mean ζ for periods 1-4 and 1-5 indicate that the bulk of mandibular growth (as implied by the present sample) in *A. robustus* takes place by the time the second molar has come into occlusion, a dental milestone that roughly corresponds with the onset of behavioral and hormonal cues of adolescence (Hochberg, 2012).

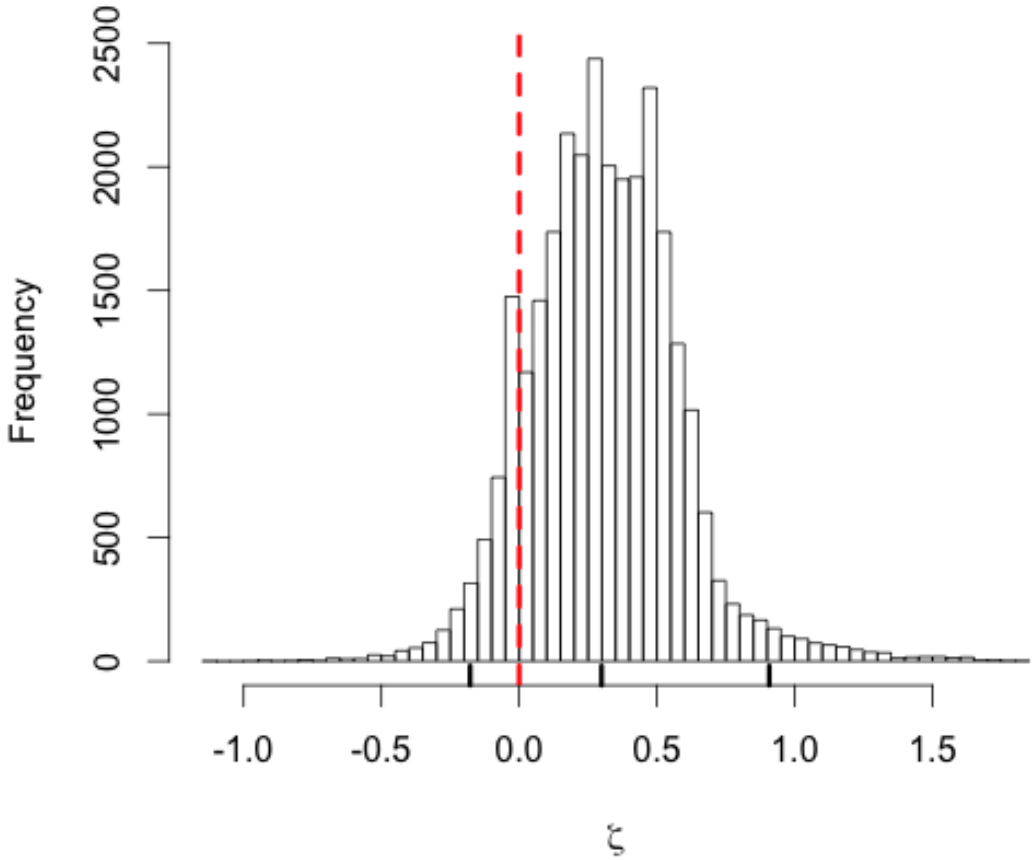

Figure 4.8. ζ statistics for species difference in overall size change between all eruption stages. The red dashed line indicates ζ=0 (no difference between species), and the three bars in the rug indicate the 95% confidence interval (-0.178,0.907) and median (0.299) of the (exact) randomized distribution.

Eruption stages 1 and 4 have the largest sample sizes for both species (Table 3.2), and as such these allow the largest number of unique ζ statistics to be calculated (45% of

all 22,060 comparisons). Not surprisingly, this period contains both the largest and the smallest values of D, and shows the largest variance in D. For instance, the upper 95% confidence limit for this period is 1.11, whereas all other periods' upper limit is less than 1 (Table 4.4). A good deal (31%) of the ζ statistics for period 1-4 were calculated from only k=1 trait, which somewhat misses the point of the ζ test measuring size as a summary of several traits. If the resampled ζs comparing period 1-4 for which k=1 are omitted, the mean ζ drops only mildly (from 0.457 to 0.436), but the standard deviation decreases noticeably from 0.278 to 0.174. Importantly, 0 is no longer within 95% of the exact randomized distribution for which k>1 (n=9,118). In summary, even though there is great variation in ζ statistics for period 1-4, the period's better-preserved individuals indicate that *A. robustus* undergoes much larger amount of change in mandibular size than humans by eruption stage 4 (full occlusion of M_2).

In contrast with the large period 1-4 distribution, there are only 1,156 ζ statistics for period 1-5. Nevertheless, this period contains two relatively well-preserved fossils, SK 3978 in stage 1 and SKW 5 in stage 5, who preserve 21 traits in common. Period 1-5 thus significantly represents both the youngest and oldest age groups, and two of the most complete fossils in the analysis. Because of this pair, the median k=9 traits for this period which is high in comparison with the rest of the resampled statistics (overall median k=5). The n=388 comparisons including this fossil pair have a fairly high mean ζ=0.368±0.122. Because more traits tend to be used to calculate ζ in period 1-5, which samples the beginning and end points of this age series, this period provides a good estimate of the difference in overall size change that occurs in the mandible of each species.

In summary, the distribution of ζ statistics from all possible pairwise comparisons of individuals reveals a general tendency for *A. robustus* to undergo greater size change between eruption stages than modern humans, reflected in a clear bias toward positive values of ζ. In all but two periods between eruption stages (2-3 and 4-5) the mean ζ is greater than 0, with just over 12% of all ζ statistics indicating greater relative size change in humans compared with *A. robustus*. The pervasive tendency for greater *relative* size increase in *A. robustus* gets compounded across ontogeny, so that by the end of the subadult period, the *A. robustus* mandible has undergone significantly greater size increase than a human on average. Period 1-5 contains some of the best-preserved fossils in this analysis, and so overall size is generally based on more traits than for other dental eruption periods. Period 1-4 contains a relatively large number of fossils, and although these are comprised nearly entirely of corpora, they reveal individual variation within an eruption stage. Taken together, these data indicate that the *A. robustus* mandible increases in size substantially more than humans do prior to alveolar eruption of M_3.

Successive Eruption Stages

Of all ζ statistics, 8,821 were between successive eruption stages. This set of stage-successive statistics provides the most fine scale view of potential ontogenetic variation between species. This is significant from a life history standpoint because these dental eruption landmarks roughly coincide with other ontogenetic milestones.

There are two periods in which *A. robustus* and human mandibles show very different amounts of relative size change. First, between eruption stages 1-2, the mean ζ=0.147 ($P_{\zeta \leq 0}$=0.095; Table 4.4). While this difference is not significant at the traditional

($P_{\zeta \leq 0}$=0.05) level, it is nevertheless very unlikely for the amount of relative size change seen in *A. robustus* between eruption stages 1-2 to be sampled from a single human population. A more notable and significant difference between species occurs between eruption stages 3-4, where mean ζ=0.317 ($P_{\zeta \leq 0}$=0.019). In the other two successive periods (stages 2-3 and 4-5) the mean and median ζ are negative but not significantly different from 0 ($P_{\zeta \leq 0}$=0.635 and 0.768, respectively).

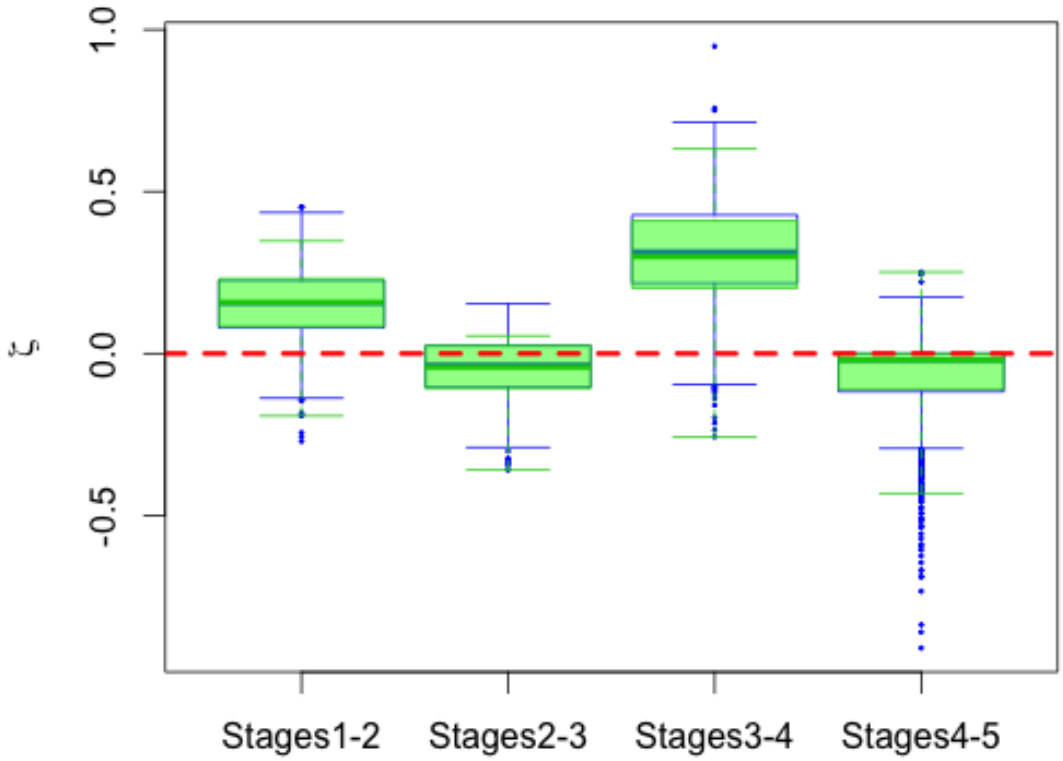

Figure 4.9. ζ statistics for interspecific difference in relative size change between successive eruption stages. The red dashed line indicates ζ=0 (no difference between species). The blue boxes include all 8,821 unique resampled statistics between successive dental eruption stages. Overlain on these in green is the subset of this group (n=6,377) for which k≥5 traits (the sample median). Note that the k≥5 distributions overlap with the full-sample distribution, but with reduced variation (i.e. less deviation from ζ=0). Boxes include the 50% quartiles, dots are outliers, and thick blue/green lines are medians.

Figure 4.9 shows the distribution of ζ statistics between successive eruption stages. This depicts the degree to which each species deviates from a common pattern of size change across ontogeny. Reflecting *relative* change in size, the ζ test is able to compare humans with *A. robustus* in light of the latter's increasingly larger sizes. This figure

therefore illustrates how disparate patterns of size change result in *A*. *robustus* achieving a much larger adult size than humans: both species' stage 1 mandibles overlap in overall size, but *A*. *robustus* generally undergoes a relatively greater change in size by eruption stage 2. The now absolutely larger *A*. *robustus* mandible then undergoes a relatively greater amount of size change between stages 3-4, accentuating the species difference in overall mandibular size. Even though ζ statistics for periods 2-3 and 4-5 tend to be negative on average, this is not enough for human mandibular size to 'catch up' with *A*. *robustus* overall size. The ζ test therefore indicates that compared with modern humans, *A*. *robustus* experienced two 'spurts' of greater change in overall size of the mandible.

Influences on ζ

Table 4.5 shows the Kendall's tau rank correlations between resampled ζ statistics and metadata (da and k) and their significance. All of these variables are significantly correlated with one another. This is quite unlike the correlation matrix for the ζ test validation (Table 4.3), in which correlations were generally low and insignificant. These relationships are examined in more detail below.

Variable	ζ	da	k
ζ	-	**2.2E-16**	**2.2E-16**
da	**0.407**	-	**2.2E-16**
k	**-0.167**	**-0.196**	-

Table 4.5. Relationship between resampled ζ and metadata. Kendall's tau rank correlations are below the diagonal and the significance is above. All correlations are significant.

The Effects of Preservation, k

The median number of traits shared between individuals across all comparisons is 5. As in the test validation, a good deal of these statistics (21%) are based on only k=1

trait. ζ statistics in the k=1 subset exceed the range of observed ζ statistics for all other values of k (Fig. 4.10). Excluding these, the median number of traits shared rises only to k=6, and the average ζ statistic decreases from 0.301 to 0.293.

There is a general, but by no means universal, tendency for ζ to decrease with increasing numbers of traits used to calculate size. A least squares regression of ζ against k yields the line ζ = -0.016*k + 0.406, and although this low slope is significantly different from 0 (F=1,792 on 1 and 29,146 df, p=2.2E-16), only a small amount of the variation in ζ is explained by k (r^2=0.058).

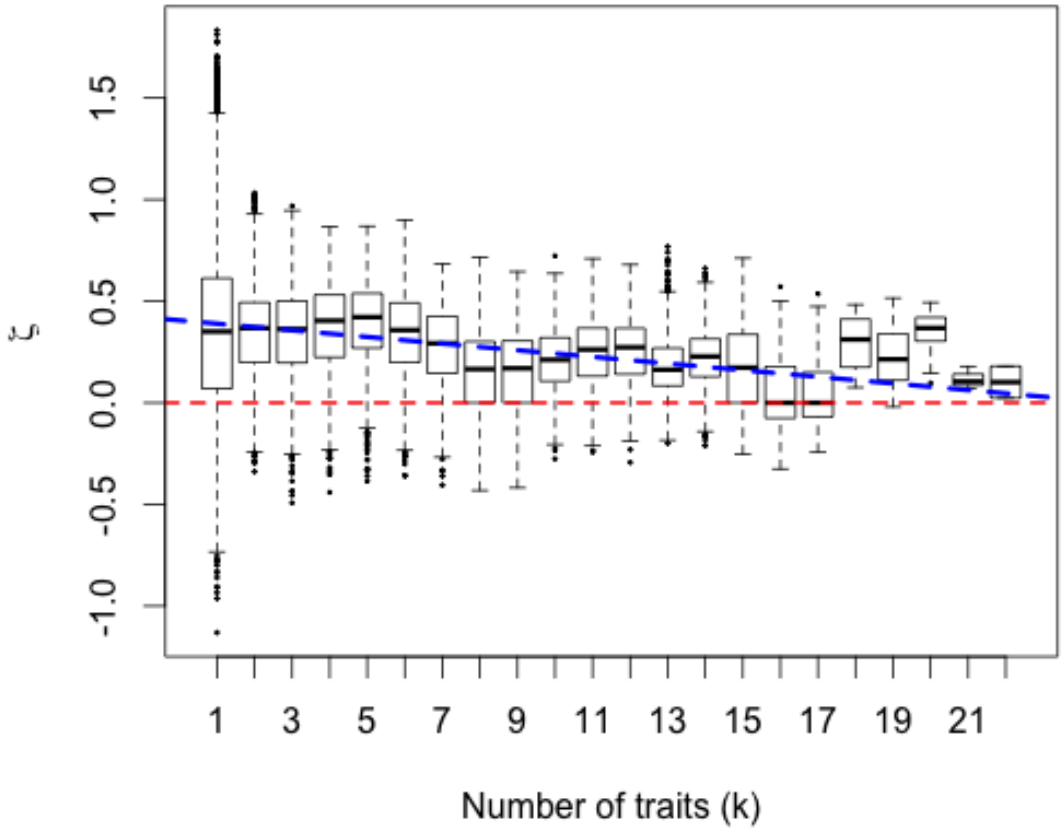

Figure 4.10: The effects of preservation on the value of ζ. The red dotted line indicates ζ=0, and the blue dashed line is the least squares regression line of ζ against k. Boxes include the 50% quartiles, dots are outliers, and thick blue/green lines are medians.

A clear exception to the tendency of decreasing D with increasing numbers of traits occurs for the n=79 comparisons where k=18-20. This group has a mean ζ of 0.294,

close to the mean for all possible comparisons. Reference to the results matrix (not included here due to its large size, but available upon request) indicates that the fossil comparisons in this set include only SK 3978 (eruption stage 1), SK 62 (eruption stage 2) and SKW 5 (eruption stage 5). The n=44 comparisons involving SK 3978 and SKW 5 have a higher mean ζ (0.374) than the other comparisons in the subset (period 1-2 mean ζ=0.182; period 2-5 mean ζ=0.136). Even though ζ statistics for periods 1-5 and 2-5 have similar variation ($\sigma_{1\text{-}5}$=0.093, $\sigma_{1\text{-}4}$=0.082), the period 2-5 statistics are shifted to lower values of ζ compared to period 1-5. Thus, this subset of resampled statistics for which k=18-20 shows a similar pattern to the overall results (Table 4.4). The difference in mean ζ for periods 1-5 and 2-5 highlights both the greater amount of overall size change seen in *A. robustus* between eruption stages 1-2 (Fig. 4.10) and overall between stages 1-5.

Also deviant from the weak relationship between ζ and k are comparisons based on k=16-17 traits. This subset (n=302) has a mean ζ=0.040 and median ζ=0. The relatively low average ζ in this subsample is driven by the n=192 comparisons including SKX 4446 in eruption stage 4 and SKW 5 in stage 5: for the subset k=16-17, all but three of the 180 ζ statistics less than or equal to 0 are based on this pair, and the mean ζ for this pair alone is -0.066. The remaining ζ statistics in the subset k=16-17 are based on periods 1-2, 1-5 and 2-5, and have a mean ζ=0.226, echoing the findings in the previous paragraph. This subset thus underscores the key findings described above: the comparisons of SKX 4446 and SKW 5 indicate relative size increase between eruption stages 4-5 is hardly different between humans and *A. robustus*, with humans actually showing slightly more size change. Nearly all other comparisons in this subset reflect relatively greater size change in *A. robustus* during infancy and across all ontogeny. That

these comparisons are based off a large number of traits bolsters the rest of the results, relying on larger resampled distributions but based on fewer traits.

The Effects of Difference in Eruption Stages, da

While the difference between resampled individuals' eruption stages was shown to have negligible effects on D in the test validation, there is a significant, positive rank correlation between D and da in comparisons of humans with *A. robustus* (Table 4.6). Inspection of Fig. 4.11 indicates this is not a strong or causal relationship. Rather, it is driven by the fact that comparisons between individuals relatively close in eruption stage age (da=1-2) generally have a lower D than those spanning a greater part of ontogeny (da=3-4). This is consistent with findings described above, namely that *A. robustus* tends to undergo greater size change between eruption stages, and this tendency compounds so that the *A. robustus* mandible achieves a much larger adult size than humans.

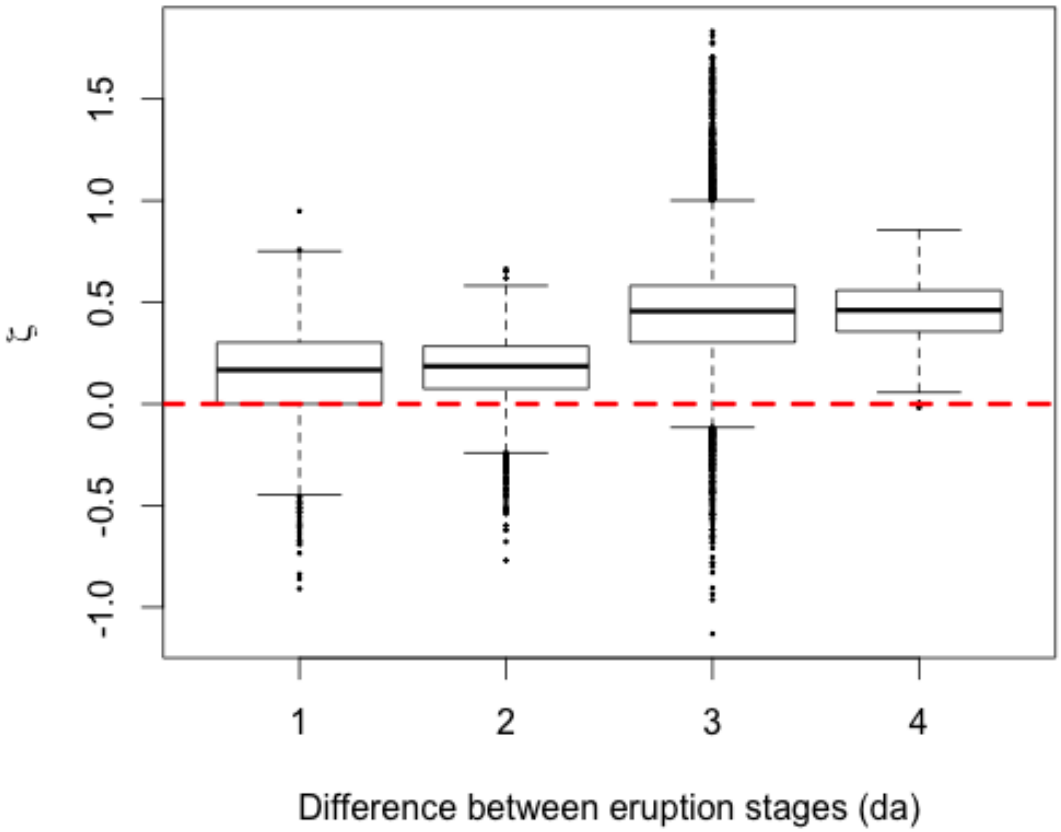

Figure 4.11. Distribution of ζ for each difference between eruption stages. The red dotted line indicates ζ =0. Boxes include the 50% quartiles, dots are outliers, and thick black lines are medians.

Summary of Species Difference in Overall Size Change

Results of the ζ test indicate that *A. robustus* undergoes more size change between eruption stages on average compared with humans. Most but not all periods between stages show positive D values. This is most notable in comparisons of the amount of size change between the beginning and end of the ontogenetic sequence (periods 1-4 and 1-5). The effects of the tendency for greater size change in *A. robustus* get compounded such that by the end of ontogeny, *A. robustus* has undergone a much greater change in overall size compared with humans. This size difference is accomplished by relatively greater size change in *A. robustus* during periods 1-2 (not significant) and 3-4 (significant), and negligible difference between periods 2-3 and 4-5.

There are significant rank correlations between ζ and sample metadata da and k. The relationship between D and da is due to the fairly well preserved fossils in eruption stages 1-2 and 5. This relationship cannot fully explain the negative correlation between ζ and k, and is not easily explained due to the high output of the ζ test. Nevertheless, the inverse relationship between preservation (k) and the value of ζ explains only a small amount of the variation in ζ. Moreover, in spite of the relationship, there is a tendency for ζ to be greater than zero across all possible values of k, save for the subset in which k=16-17, which is biased toward period 4-5 when there is little size difference between *A. robustus* fossils (SKX 4446 and SKW 5).

4.3: Species Differences in Individual Traits

In addition to examining changes in overall size using the pairwise size metric, the ζ test was run for all 29 mandibular measurements on their own (Table 3.2), comparing every possible set of human and *A. robustus* pairs. This section summarizes these results, presented in five anatomical categories: [1] corpus (including symphysis) height, [2] corpus (including symphysis) breadth, [3] overall mandibular length, [4] overall mandibular breadth, and [5] ramus height and length. These findings are summarized in Tables 4.6-7, and in Figure 4.12. Results are also interpreted in the context of the raw data for each trait, which are presented graphically in the Appendix I.

The results matrix of all ζ statistics for each trait contains 117,200 rows (unique resampled comparisons), and nine columns for the output variables/metadata (Table 3.3). Table 4.6 summarizes these results. It is clear from the table that comparisons are unequally distributed across traits and age groups. For instance, corpus heights and

breadths are fairly well represented, whereas other types of measurements are not as well sampled. This disparity in trait representation is due to a relative overrepresentation of mandibular corpora, and the fact that younger individuals are necessarily missing many variables because they had not yet developed by the time the individual died.

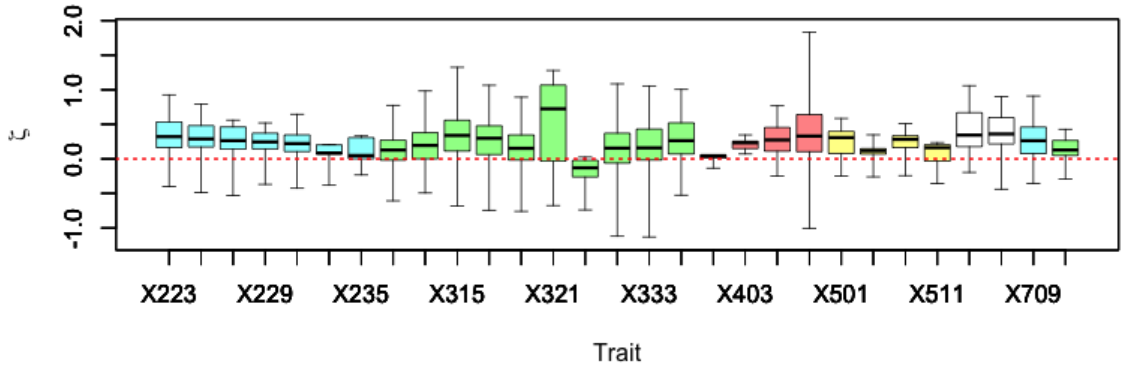

Figure 4.12. The distributions of all possible interspecific ζ statistics for each individual trait. Trait ID numbers and descriptions can be found in Tables 3.2 and 4.6-7. Boxes are color-coded according to anatomical category: Blue=corpus breadths, Green=corpus heights, Red=anteroposterior mandible lengths, Yellow=overall mandibular breadths, White=ramus. Traits X709 and X711 (far right) are measures of symphysis breadth and height, respectively. Boxes include the 50% quartiles, whiskers span the entire range of values, and thick black lines are medians.

Corpus breadths (traits X223-235 and -709)

There are eight measures of corpus breadth, including at the mandibular symphysis and at seven positions along the length of the corpus from the P_3 to the M_2. As could be predicted from visual comparison of fossil and human mandibles, average ζ statistics for each trait in this group tend to be positive (i.e. greater relative jaw breadth growth in *A. robustus*), although not 'significantly' so, as 0 is within the 95% confidence interval for each trait. Nevertheless, the general probability of D being less than or equal to 0 is fairly low ($p \leq 0.181$) for all breadth measures except at the position of M_2. Fewer than 9% of the resampled ζ statistics for breadth at P_3, P_4 or M_1 are less than 0. When considering relative size change across all eruption stage comparisons, the ζ test fails to reject the null hypothesis of indistinguishable patterns of corpus breadth change; but this

is certainly not the case when considering patterns of change only between successive eruption stages.

In *A. robustus*, the mandibular corpus widens at every tooth position throughout ontogeny, but usually with little or no increase between eruption stages 4-5 (Table 4.7 and Appendix I). As with the pairwise size metric, positive ζ values tend to cluster within periods 1-2 and 3-4. In period 1-2, not a single one of the n=930 ζ statistics for breadth at P_3 is less than 0.042: in other words, in this cross-sectional sample of humans, one will never sample as great an increase in breadth at P_3 as is seen in *A. robustus* in period 1-2. Also during this period, breadths at more anterior tooth positions have higher average ζ values, with very low probabilities of resampling $\zeta \leq 0$ (i.e. *A. robustus* showing significantly greater relative size change).

The sole measurement deviating from this pattern during period 1-2 is corpus breadth at the alveolar septum between P_4 (or dm_2) and M_1. This is due largely to comparisons involving SK 3978 (eruption stage 1), which has a larger breadth at this position than the other fossils in stage 1 (SK 64 and 438), and thereby giving the impression of smaller size increases. (Interestingly, SK 3978 shows no sign of P_4 crypt formation or germ calcification; Conroy and Vannier, 1991b) As a result, ζ statistics involving SK 3978 average -0.010 (σ=0.091), much lower than the distributions of ζ statistics involving SK 64 (mean= 0.051, σ=0.092) and SK 438 (mean=0.123, σ=0.092). Omitting ζ statistics based on SK 3978, the mean ζ increases to 0.092 ($P_{\zeta \leq 0}$=0.182).

Corpus breadths in period 3-4 also produce fairly high, positive ζ statistics. As in period 1-2, the species difference in size change is larger for more anterior tooth positions than for around the M_1 more posteriorly. Mean ζ for the anterior breadths in period 3-4

are high and more similar to one another than they are in period 1-2. Posteriorly, the species difference in corpus breadth increase at M_1 and between $M_{1\text{-}2}$ is not nearly as substantial as it is anteriorly. As the corpus had already become much broader in *A. robustus* than humans by eruption stage 2, the (significantly) high ζ statistics for corpus breadths in period 3-4 means that the *A. robustus* corpus becomes even more relatively broad compared with humans.

ζ statistics for corpus breadths in periods 2-3 and 4-5 are quite different from the other periods. Nearly all traits have *negative* mean ζ values, indicating that humans undergo greater relative increase in corpus breadth in these periods. These ζ distributions, however, all center fairly close to ζ =0. During period 2-3, the ζ statistics for the anterior three corpus breadths average just under 0, but posterior to these ζ for breadth at M_1 averages just above 0. Similarly, during period 4-5, ζ statistics for corpus breadth anterior to M_1 are always negative, but ζ statistics are positive at M_1 (nearly significantly) and M_2. Thus, the ζ test indicates that during periods 2-3 and 4-5, *A. robustus* and humans experience similar change in corpus breadth anterior to the M_1 but *A. robustus* undergoes (equivocally) greater size change posteriorly.

Trait ID	Trait	n	Mean ζ	Minimum, Maximum	95% CI	P ζ≤0
All traits		117,200	0.256	-1.13,1.83	-0.288,0.933	0.193
X223	Breadth at P_3	4,509	0.362	-0.402,0.927	-0.081,0.927	0.081
X225	Breadth at P_{3-4}	4,959	0.311	-0.488,0.793	-0.096,0.793	0.114
X227	Breadth at P_4	11,282	0.277	-0.531,0.561	-0.069,0.561	0.082
X229	Breadth at P_4-M_1	9,761	0.242	-0.370,0.520	-0.085,0.520	0.125
X231	Breadth at M_1	8,541	0.228	-0.043,0.648	-0.073,0.601	0.067
X233	Breadth at M_1-M_2	896	0.105	-0.382,0.203	-0.144,0.203	0.123
X235	Breadth at M_2	677	0.102	-0.233,0.332	-0.123,0.331	0.440
X709	Breadth at symphysis	1,297	0.280	-0.354,0.990	-0.150,0.802	0.181
X301	Height at mental foramen	6,506	0.125	-0.607,0.775	-0.276,0.560	0.303
X313	Height at P_{3-4}	7,690	0.201	-0.494,0.982	-0.259,0.761	0.252
X315	Height at P_4	11,904	0.352	-0.681,1.33	-0.235,1.06	0.161
X317	Height at P_4-M_1	10,525	0.269	-0.744,1.06	-0.291,0.780	0.205
X319	Height at M_1	5,398	0.158	-0.760,0.892	-0.343,0.636	0.284
X321	Height at M_{1-2}	2,724	0.534	-0.676,1.28	-0.404,1.28	0.331
X323	Height at M_2	736	-0.159	-0.739,0.025	-0.497,0.025	0.861
X331	Height-mental foramen to base	10,019	0.156	-1.12,1.09	-0.532,0.882	0.330
X333	Height-mental foramen to alveolar margin	5,652	0.202	-1.13,1.056	-0.494,0.945	0.332
X355	Posteromedial corpus height	4,556	0.295	-0.525,1.00	-0.250,0.888	0.170
X711	Height at symphysis	282	0.133	-0.290,0.428	-0.181,0.376	0.199
X401	Length from P_4-M_1 to Infradentale	104	0.022	-0.134,0.055	-0.113,0.055	0.173
X403	Length from the condyle to I_2-C	14	0.211	0.070,0.347	0.084,0.332	0
X404	Length from the mental foramen to lingual tuberosity	2,481	0.282	-0.251,0.767	-0.102,0.671	0.100
X415	Length from mandibular foramen to P_{3-4}	5,036	0.401	-1.00,1.83	-0.378,1.44	0.152

X501	Bimental breadth	327	0.244	-0.245,0.585	0.178,0.525	0.187
X502	Bi canine breadth (external)	84	0.112	-0.261,0.348	-0.185,0.238	0.119
X510	Bi canine breadth (internal)	124	0.259	-0.243,0.508	-0.115,0.507	0.065
X511	Bi-P3 breadth, internal	172	0.084	-0.357,0.236	-0.248,0.236	0.291
X603	Ramus posterior margin to P_{3-4}	258	0.399	-0.196,1.06	-0.151,1.00	0.127
X607	Ramus height from mylohyoid foramen to base	686	0.396	-0.439,0.899	-0.124,0.899	0.071

Table 4.6. Summary of ζ statistics comparing humans and *A. robustus* for each trait, across all age comparisons.

		Period 1-2		Period 2-3		Period 3-4		Period 4-5	
Trait ID	**Trait**	**mean**	**P ζ≤0 (n)**	**mean**	**P ζ≤0 (n)**	**mean**	**P ζ≤0 (n)**	**mean**	**P ζ≤0 (n)**
All traits		0.135	0.199 (11,053)	-0.056	0.579 (3,950)	0.301	0.091 (15,712)	-0.045	0.719 (11,561)
X223	Breadth at P_3	**0.304**	0 (930)	-0.021	0.368 (365)	**0.261**	0.011 (281)	**-0.053**	1 (191)
X225	Breadth at P_{3-4}	**0.247**	0.007 (907)	-0.04	0.725 (411)	**0.258**	0.012 (396)	**-0.052**	1 (213)
X227	Breadth at P_4	0.112	0.073 (1,675)	-0.022	0.353 (476)	**0.231**	0.023 (863)	**-0.048**	1 (489)
X229	Breadth at P_4-M_1	0.062	0.275 (1,438)					**-0.025**	1 (767)
X231	Breadth at M_1	**0.147**	0.030 (436)	0.043	0.190 (210)	0.029	0.270 (1,342)	0.120	0.053 (756)
X233	Breadth at M_1-M_2					0.105	0.123 (896)		
X235	Breadth at M_2							0.101	0.440 (677)
X709	Breadth at symphysis	**0.315**	0.021 (291)					**-0.052**	1 (146)
X301	Height at mental foramen	0.061	0.324 (552)	-0.090	0.828 (303)	0.183	0.112 (850)	-0.081	0.858 (660)
X313	Height at P_{3-4}	0.048	0.392 (564)	-0.070	0.651 (281)	0.248	0.080 (1,126)	-0.083	0.846 (729)
X315	Height at P_4	0.095	0.317 (1,006)	-0.045	0.588 (362)	**0.319**	0.020 (1,372)	**-0.131**	0.962 (679)

X317	Height at P_4-M_1	-0.070	0.629 (642)	-0.0008	0.411 (387)	**0.333**	0.026 (1,823)	-0.127	0.946 (905)
X319	Height at M_1			-0.051	0.519 (376)	0.251	0.105	-0.095	0.733 (1,004)
X321	Height at M_{1-2}					**0.971**	0 (1,491)	-0.111	0.834 (1,081)
X323	Height at M_2							-0.159	0.861 (736)
X331	Height-mental foramen to base	0.120	0.317 (961)	-0.182	0.837 (484)	0.274	0.119 (1,330)	0.028	0.489 (767)
X333	Height-mental foramen to alveolar margin	0.222	0.230 (513)					**-0.141**	1 (638)
X355	Posteromedial corpus height	0.181	0.101 (328)	**-0.128**	1 (134)	0.346	0.055 (488)	0.063	0.356 (407)
X711	Height at symphysis	0.127	0.171 (117)						
X401	Length from P_4-M_1 to Infradentale	0.019	0.209 (43)						
X403	Length from the condyle to I_2-C								
X404	Length from the mental foramen to lingual tuberosity	0.126	0.162 (284)	-0.042	0.553 (132)	**0.270**	0.005 (219)	0.002	0.333 (198)
X415	Length from mandibular foramen to P_{3-4}					0.264	0.068 (1,225)	0.045	0.330 (512)
X501	Bimental breadth	**0.361**	0 (163)						
X502	Bi canine breadth (external)	**0.121**	0 (31)						
X510	Bi canine breadth (internal)	0.188	0.137 (51)						
X511	Bi-P3 breadth, internal	**0.181**	0 (73)						
X603	Ramus posterior margin to P_{3-4}	**0.251**	0 (48)	-0.094	0.897 (29)				

X607	Ramus height from mylohyoid foramen to base					0.276	0.083 (216)		

Table 4.7. ζ statistics comparing humans and *A. robustus* for each trait between successive eruption stages. Empty cells mean no comparisons could be resampled for successive eruption stages. **Bold** values indicate that fewer than 5% the exact randomized distribution is less than or equal to 0 ($P_{\zeta \leq 0}$).

It is not clear how the position of the root of the ramus contributes to species differences in corpus breadth growth (Table 4.8). In dental stage 1, the root flanks the dm_2 in both species. By stage 2 the root migrates posteriorly in humans to flank the M_1, and then the distal M_1 by stage 3. However, in *A. robustus* the root contributes to corpus breadth at the dm_2 up to stage 3. Importantly, ζ statistics are lowest (i.e. not significantly positive) around dm_2 in period 1-2, and the higher and more significant ζs are by the dm_1 and symphysis. In addition, mean ζ is modestly (but significantly) positive for breadth at the (unerupted) M_1 at this time. The significant differences between species in breadth increase at M_1 and dm_1 during this time suggest that M_1 and P_3 crown development is at least partly responsible for the difference, and irrespective of the position of the ramus root.

Eruption stage	*A. robustus*	Humans
1	Mesial dm_2	dm_2-M_1
2	mid dm_2	M_1
3	Distal dm_2	Distal M_1
4	mid/distal M_1	$M_{1\text{-}2}$
5	mid M_1	$M_{1\text{-}2}$

Table 4.8. Position of the ramus root across eruption stages in each species.

However, the different position of the ramus root may contribute to species differences in corpus breadth growth later in ontogeny. The only positive mean ζ for corpus breadth in period 2-3 occurs at the position of M_1. During this period, the root of the ramus migrates from the mid-M_1 to flank the more distal portion of the tooth in humans, whereas it continues to flank the dm_2 in *A. robustus*. It is tempting to conclude the greater breadth increase in *A. robustus* here is due to humans' loss of the ramus root

laterally, but it should be noted that mean ζ is neither very high nor significantly positive (mean ζ=0.043, $P_{\zeta \leq 0}$=0.190).

Summary of corpus breadth. Whereas the *A*. *robustus* mandible can be characterized by generally increasing breadth through subadult ontogeny, the human corpus tends to broaden only modestly, if at all, in this cross-sectional sample. The species differ most in the amount of size change between eruption stages 1-2 and 3-4. In addition, size change at the more anterior tooth positions (P_{3-4}) generally show greater species difference than posterior positions (M_{1-2}). As ζ measures differences in *relative* size change, the relatively greater breadth increase of *A*. *robustus* during period 3-4 is all the more remarkable since it compounds a species difference in breadth established earlier during ontogeny. As a result, the modest disparity in corpus breadth between species early on quickly gets amplified during ontogeny. Even though species differences in relative size change are small in toward the end of subadulthood (period 4-5), the posterior corpus at M_1 of *A*. *robustus* undergoes slightly more size increase than humans, due to the more anterior presence of the ramus on the corpus of in the former.

Corpus heights (traits 301-355 and 711)

There are 11 measurements of corpus height including at the symphysis and at 10 other positions along the length of the corpus. Corpus heights are very well represented in this fragmentary sample, with anywhere from 2,700-11,904 unique ζ statistics for all but two height measures. Plots of raw data hint that amounts of relative height increase are similar between species, although *A*. *robustus* heights are often shifted to higher values

(Appendix I). The ζ test (for all possible comparisons) indicates that although *A. robustus* tends to experience greater relative increase in height at most positions, it is not uncommon for humans to show at least as much change as *A. robustus* for all measures of corpus height (Table 4.6, Fig. 4.15).

Across all possible comparisons of size change in corpus height (Table 4.6), height at M_2 sticks out as having a highly negative mean ζ of -0.159. This trait is represented only in eruption stages 4-5, a time when humans undergo relatively greater size change in not only height at M_2 but also overall size and most other mandibular measurements. This result must be treated with caution since there is only one *A. robustus* in stage 5.

During eruption period 3-4, all height measures have positive mean ζ values. There is a very low chance (0-10%) of sampling *A. robustus*-like corpus height increases in the human sample, and many species differences are statistically significant. Most notably, height between the first and second permanent molars experiences a much greater size increase than humans on average (mean ζ=0.971), and of n=1,491 unique comparisons for this trait and time period, the lowest value of ζ=0.162. That so many measures show such non-trivial differences between species may reflect a global size increase during this period, but it could also relate to the development of molar tooth roots within the corpus.

Similar to results for corpus breadth, ζ statistics for each height measurement tend to be positive in periods 1-2 and 3-4, but negative in periods 2-3 and 4-5. In period 2-3, mean ζ is only slightly negative for most height measurements, but markedly more negative for height from the mental foramen to the corpus base and height at the

posteromedial margin of the corpus (i.e. lingual tuberosity). For this latter height, humans always undergo greater size change than *A. robustus*, though this is based a small sample (n=134) compared to other traits.

In period 4-5, humans on average undergo a greater amount of relative change in nearly all aspects of corpus height, and for many traits there is only a small chance of sampling human-like size change from the smaller *A. robustus* sample. The most pronounced difference between species in height change during this period occurs around the P_4 and mesial M_1. Here, mean ζ ranges from -0.08 to -0.13, and the difference is significant for height at P_4 ($P_{\zeta \leq 0}$=0.038). Interestingly, each species is indistinguishable in the amount of height change at the position of the mental foramen, but mean ζ=0.141 for the height from the mental foramen to the alveolar margin. Humans in eruption stages 4-5 overlap entirely in this measure of alveolar height, whereas the sole *A. robustus* in stage 5 has a shorter height here than *A. robustus* in stage 4. As a result, ζ statistics for this period 4-5 can never be greater than 0 (Chapter 3.3). Thus, the significant difference between species in alveolar height growth in period 4-5 is likely an artifact of sampling and may not be indicative of an actual biological difference.

Summary of corpus height. The ζ test indicates that the amount and pattern of change in corpus height across ontogeny are fairly similar between humans and *A. robustus*, but there are still interesting differences. Again, because the ζ statistic is a relative measure, the fact that the *A. robustus* corpus is generally at or above humans' height range for most measures means that similar amounts of relative size change between species (i.e. ζ is not significantly different from 0) nevertheless allow *A. robustus* to attain a greater

height than humans by stage 5 for some measures. In addition, the predominantly positive (and significant) ζ statistics in period 3-4 followed by predominantly negative ζ statistics in period 4-5, indicates that each species differs in the timing of a mandibular height 'spurt,' *A. robustus* accomplishing a greater amount of height growth prior the full occlusion of M_2 and humans thereafter.

Overall lengths (traits 401-415)

There are four measurements of overall mandibular length. Two are poorly represented in the sample, and so their results should be viewed with caution. The first of these, the length from the alveolar septum anterior to M_1 to the point between the central incisors, fails to distinguish species. This may support the prediction made in Chapter 2, that the relatively small canines and incisors of humans and *A. robustus* might be reflected in similar patterns of jaw growth in this region (e.g. Simpson et al., 1990). However, it also agrees with John Hunter's over 200 year-old observation, that the distance between the symphysis and the "sixth tooth" (dm_2/P_4) does not change through ontogeny (Meikle, 2002). Moreover this is based on only 43 comparisons (Table 4.7)

The second of the less well-preserved length measurements, the length from the posterior mandibular condyle to the septum anterior to C_1, is only preserved in two specimens in the fossil sample, SK 63 in eruption stage 3 and SKW 5 in stage 5. This measurement reflects the length and depth of the oral cavity, and as such could be one of the most informative traits, were it not for the fact it is poorly represented in the fossil sample. The ζ test shows that humans never increase this measurement as much as *A. robustus*, but this result remains open to question since it is based on only 14

comparisons. Thus, the ζ test performed on these poorly represented traits suggests that species are indistinguishable in terms of size change of anterior mandibular length, but that the size of the oral cavity in *A. robustus* increases in size more than humans during ontogeny.

The other two mandibular length measurements are based on the more posterior corpus, and so are very well sampled. Across all possible comparisons, ζ statistics for average from 0.28-0.40, although these are not significant below the level of $P_{\zeta \leq 0}$=0.10 (Table 4.7). The only one of these two measurements to be preserved across all successive dental periods is the length from the mental foramen to the posterior edge of the lingual tuberosity. The species difference in this trait across ontogeny is similar to other results – *A. robustus* undergoes greater size change in periods 1-2 and 3-4, but species are nearly indistinguishable in the amount of size change in periods 2-3 and 4-5. However, only in period 3-4 could the ζ test statistically distinguish species' amount of size change. The other well-sampled length measurement, from the mandibular foramen to the septum anterior to M_1, also undergoes greater size change in *A. robustus* ($P_{\zeta \leq 0}$=0.068).

Summary of overall lengths. The ζ test indicates that the *A. robustus* mandible increases in antero-posterior length more greatly than humans across ontogeny. Species could not be distinguished, however, in the length of the anterior corpus (anterior M_1 to infradentale), which also measures mediolateral (unilateral) mandibular breadth. These results are not unexpected given these species' tooth sizes. The larger molars and premolars of *A. robustus* necessitate a longer jaw. Anterior tooth size is less disparate in

humans and *A. robustus* and so it is not unexpected for them to show similar patterns of relative size change in the length of the anterior jaw (Simpson et al., 1990). The only successive dental period in which species could be distinguished in terms of length growth is period 3-4: during this period, both humans and *A. robustus* must create space for the developing M_3 crown. Thus, at least some aspects of anteroposterior mandible growth probably reflect species differences in tooth size.

Overall (bilateral) breadths (traits 501-511)

Bilateral breadth measurements require relatively complete mandibles, and only four fossil individuals, in stages 1, 2 and 5, meet this criterion. Moreover, preservation limits measurements to the anterior aspect of the mandible, no further posterior than the P_4. Humans tend to have wider mandibles (at least anteriorly) than *A. robustus* throughout ontogeny, though the difference reduces over time (Appendix I). Overall increases in overall breadth tend to be greater in *A. robustus*, but these do not reach statistical significance at $p \leq 0.05$ (Table 4.7).

The only successive growth interval in which comparisons can be made is period 1-2. During this time, all measures of overall breadth show greater relative size change in *A. robustus*, and for three of these traits humans never achieve as much size increase as *A. robustus* (Table 4.8-9). An important caveat, however, is that these results are based on relatively few comparisons (n=31-163). These increases in overall breadth likely reflect the great increase in corpus breadth seen in *A. robustus* during this period. Corroborating this, the ζ test detects great differences between species in periods 1-2 and 1-5, but differences are much smaller in period 2-5. In fact, the ζ test suggests *humans* undergo

greater change in the distance between the lingual margins of the premolars in period 2-5 (mean ζ=-0.120, $P_{\zeta \leq 0}$=0.959, or the probability that $\zeta \geq 0$ =0.041). *A. robustus* undergoes greater size change between the lingual margins of the canines in this time (mean ζ=-0.175, $P_{\zeta \leq 0}$=0.024). This difference between species is explicable by the facts that *A. robustus* premolars are very large compared to humans', and that the posterior tooth rows are nearly parallel in *A. robustus* but parabolic (i.e. premolars more divergent) in humans. Caution is warranted here, however, as each of these traits is represented by only 42-49 comparisons.

Summary of overall breadth. The few bilateral breadth comparisons that can be made seem to reflect two biological phenomena. First, the *A. robustus* mandible is not as broad as humans' early in ontogeny, and it reaches the lower end of the human range of variation by stage 5 via greater relative breadth increase across ontogeny. Second, most of the increase in *A. robustus*' overall breadth reflects the drastic thickening of the corpus that occurs in period 1-2.

Ramus height & length (traits 603 and 607)

The ramus is delicate compared with the mandibular corpus, and so it is poorly represented in the present samples. Two measurements were selected that reflect the height and anteroposterior length of the ramus, and each of them undergoes almost 40% greater size increase in *A. robustus* across all possible comparisons, although with the small sample sizes, neither of these differences are significant below $P_{\zeta \leq 0}$=0.05.

The length of the ramus is approximated by the distance from the posterior ramus margin (on the alveolar plane) to the septum between the P_{3-4} (or dm_{1-2}). Looking across ontogeny (Appendix I, Table 4.8), ramus length growth is much greater in *A. robustus* in period 1-2, and at some point between periods 3-5. As no stage 4 *A. robustus* preserves this measurement it is unclear whether the second great length increase occurs only or chiefly in either period 3-4 or 4-5, or in both. Although ζ statistics for this trait are based on a relatively small amount of comparisons (n=258 for all possible comparisons), the size differences between species suggests that increased sample sizes would not erase the growth differences detected.

The height of the ramus is approximated by the distance from the mandibular foramen to the inferior ramus margin, and is also fairly poorly preserved in the fossil sample (present only in eruption stages 1, 3 and 4). Between stages 1-3, *A. robustus* tends to undergo greater height increase than humans, though not significantly so. During period 3-4, mean ζ=0.276 ($P_{\zeta \leq 0}$=0.083) though again this difference is not quite statistically significant. However, these two periods of greater relative size increase result in the *A. robustus* undergoing a much greater relative increase in height between eruption stages 1-4 (mean ζ=0.628), with a very low chance of sampling *A. robustus* levels of change in the human sample ($P_{\zeta \leq 0}$=0.007).

Summary of ramus height and length. The ζ test indicates that patterns of ramus growth differ between species in a manner similar to that for other traits. The *A. robustus* ramus is positioned relatively anteriorly on the corpus, such that it tends to flank the erupted

molars posteriorly to a greater extent than in humans (Table 4.8). As a result, greater length growth in *A. robustus* probably at least partly reflects this species' large tooth sizes.

Summary of the ζ test for individual traits

Most traits tend to undergo greater relative size change in *A. robustus*, and for all but one trait, the average ζ statistic is positive. Still, in the present cross-sectional data set, ζ=0 is well within the range of values for all but one trait (Table 4.7); this outlier is based on only n=14 comparisons and so must be interpreted cautiously. The distribution of ζ statistics for all traits in successive eruption stages is practically identical to the distribution of ζ statistics for the pairwise size metric, but with more variation (Fig. 4.13).

The only successive interval in which any ζ statistic is most likely to be greater than 0 is period 3-4. The mean ζ for all traits within this period is a rather high 0.301, albeit not quite significant ($P_{\zeta \leq 0}$=0.091). Seventeen of the full 29 traits can be examined during period 3-4 and all but five of these traits are positive at p≤0.100 (i.e. ζ≤0 for no more than 10% of all unique resampled comparisons). Thus, the significantly positive ζ for the pairwise size metric (section 4.2) seems to reflect a global increase in size affecting nearly every part of the *A. robustus* mandible during this time. Period 1-2 also has a relatively high average ζ, with less than 20% of the unique resampled statistics less than or equal to 0. Compared with period 3-4, fewer traits in period 1-2 show such large difference in size change between species. Traits with generally high D values during this period tend to be concentrated in the breadth of the corpus, suggesting this is a time of as corpus shape, as opposed to overall size, change.

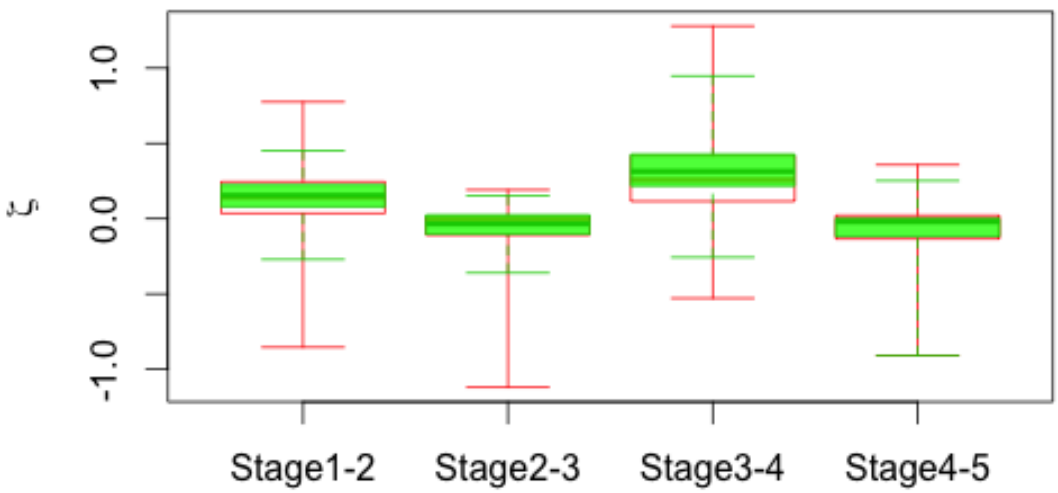

Figure 4.13. Comparison of the ζ statistic for individual traits and for the pairwise size metric across ontogeny. The red box and whiskers are statistics for all individual trait, calculated between successive eruption stages. Overlain in green are the similar ζ statistics for the overall size metric, calculated from two or more traits (cf. Fig. 4.9). Boxes include the 50% quartiles, whiskers span the entire ranges of values, and thick red/green lines are medians.

These results reflect two chief differences in patterns of mandibular size change between humans and *A. robustus*. First, during period 1-2, the *A. robustus* corpus becomes markedly thicker than humans', driving the positive ζ statistics for the pairwise size metric in section 4.2. The *A. robustus* corpus maintains larger relative increases in breadth than humans through ontogeny, resulting in a very thick jaw. The human pattern of change in corpus breadth across ontogeny is quite different from *A. robustus*'. For measures at relatively anterior tooth positions (e.g. by the premolars), corpus breadth appears either to stay constant or even decrease (Appendix I), at least in this cross-sectional sample. During infancy and early childhood (i.e. stages 1-3), the erupted deciduous, and emergent permanent, molars are the posterior-most teeth, flanked laterally by the ramus. As the mandible lengthens during growth by addition of bone at the corpus-ramus junction (Enlow and Hans, 1996), the ramus contributes less and less to these anteriorly displaced tooth positions (Table 4.8). The corpus, independent of the ramus, is of essentially the same size across ontogeny. Consistent with this pattern, for more

posterior tooth positions where breadth generally increases during earlier eruption stages in humans, average breadth actually decreases between eruption stages 4-5, as the ramus contributes less to corpus breadth.

Second, after the *A. robustus* mandible becomes much thicker (e.g. "robust") by eruption stage 2, patterns of size and shape change are similar between species until period 3-4, when *A. robustus* advances to adult values for most traits (and the pairwise size metric). Positive D values are distributed across all types of mandibular traits during this time, meaning this may not be so much a time of *shape* as global *size* change. Interestingly, ζ statistics for many traits tend to be negative – albeit weakly and not significantly – for period 4-5, suggesting a delay in global size change for humans compared with *A. robustus*.

Symphysis and anterior corpus: Qualitative description

Results of the resampling analysis agree well with qualitative (visual) observations of the fossil sample. However, not all aspects of mandibular shape and anatomy could be captured with linear metrics. The complex contours of the mandibular symphysis made it difficult to obtain homologous measures on all specimens preserving the region. The issue of homology is further raised by the disparate posterior symphysis anatomies of humans and *A. robustus*. This section therefore qualitatively describes changes that occur to the *A. robustus* anterior corpus and symphysis.

A. robustus and human mandibles in eruption stage 1, with only the deciduous dentition, appear just broad enough to house the erupted deciduous molars. That is, the bony corpus is barely broader than the deciduous molar(s) it surrounds. This holds for all

three stage 1 *A*. *robustus* included in this study, as well as the similarly aged SK 852 (whose preservation precluded accurate measurement, though it is very similar to SK 3978). Stage 2 *A*. *robustus* mandibles (SK 61 and 62), however, are noticeably larger than those in stage 1, and whereas in humans the difference is not nearly as marked. Much of this marked size increase anteriorly reflects development of the corpus lingual to the deciduous molars and symphysis. Indeed, the most drastic differences in corpus breadth growth during period 1-2 occur around the premolars and symphysis (Table 4.7).

The posterior contour of the symphysis assumes a more posterior relative position across ontogeny. The post-incisive plane, as measured from infradentale to the point where the lingual surface begins to dip inferiorly toward the genial fossa, is about 4.0 mm shorter in SK 3978 than in SK 61 and 62. Where it is preserved in eruption stages 1-3, the inferior transverse torus is poorly developed, barely projecting posteriorly beyond the genial fossa and extending to the antero-posterior level of the dm_1 when viewed superiorly. The posterior symphysis is not preserved in the youngest stage 4 fossils, SK 25 and 55b (whose M_2s are freshly in occlusion and premolars in the process of erupting), although it is probably at the same relative position as in stages 1-3. However, by the time the permanent premolars are occluded later in stage 4 (as judged by SK 6 and SKX 4446), the inferior torus has migrated posteriorly to the position of the P_4. In all older *A*. *robustus* (SKW 5 in stage 5 and adult *A*. *robustus*), the inferior torus is also extended to the antero-posterior level of P_4.

As the inferior torus migrates posteriorly, the anterior contour of the symphysis assumes a more vertical profile across ontogeny. In stages 1-3, the anterior surface arcs postero-inferiorly, beginning relatively high on the symphysis in lateral view. This

surface is poorly preserved in stage 4 (SK 25 and SKX 4446), but the superior part of the contour becomes more vertical anterior to the incisor roots. In SKW 5 and all adult mandibles where the anterior symphysis can be observed, its contour is vertical with the posterior arc beginning lower than the mental foramina when viewed laterally. In SKX 4446 the corpus is broken just laterally to the symphysis, revealing the anterior contour does not merely cover the incisor roots, but rather cortical bone becomes thicker inferiorly (i.e. the root appears procumbent relative to the vertical symphysis anterior to it).

The increasing verticality of the anterior symphysis coupled with a posteriorly migrating posterior symphysis is how *A*. robustus obtains a relatively thick and robust symphysis through growth. Symphyseal development observed in these fossils is in accordance with Bromage's (1989) morphogenetic interpretations of bony remodeling fields. Bromage found both the anterior and posterior symphysis was to be depository in *A*. *robustus* subadult mandibles, and interpreted this pattern of deposition to reflect a postero-superior direction of growth at this surface. The mesial migration of the postcanine teeth caused by interproximal attrition further amplifies the apparent posterior migration of the symphysis.

Summary of Results

Poor preservation and small sample sizes for *A*. *robustus* necessitated the development of a new procedure, the ζ test, to compare patterns of age-related size change with humans. The ζ test compares the amount of relative change in size between dental eruptions, by resampling all possible pairs of *A*. *robustus* and humans: $\zeta = [(\mathbf{R}_{\mathbf{OLDER}}$

$/ \mathbf{R}_{\mathbf{YOUNGER}}) - (\mathbf{H}_{\mathbf{OLDER}} / \mathbf{H}_{\mathbf{YOUNGER}})]$. This chapter presented the validation and results of this new method.

The first section demonstrated that both the pairwise size metric and the ζ test perform as expected. First, the pairwise size metric – the geometric mean of the set of traits shared by pairs of specimens – was used as a way of comparing the overall size individuals when they do not all preserve the same traits. The metric both distinguished human and *A. robustus* sizes across dental stages, and the human 'sizes' were shown to correspond well with humans' characteristic pattern of body size change (Table 4.1, Fig. 4.2). Next, the ζ test was used to compare the human sample with itself to assess the risk of type I statistical error. As expected, the test generally pointed to a common pattern of size change within the human sample (Table 4.2, Figs. 4.3-4). The range of ζ statistics in the test validation, while not as great as in comparisons of humans with *A. robustus*, nevertheless demonstrates the effects of variation inherent to a cross-sectional sample. Finally, preservation and the difference in eruption status between individuals have a negligible influence on the value of the ζ statistic (Table 4.3, Figs. 4.5-7). Variation in ζ tends to decrease as more traits were used to measure size, though this is likely due in part to the fact that more specimens are likelier to share fewer traits.

The next section presented the results of the ζ test comparing human and *A. robustus* mandibles for the pairwise size metric. The test detected notable differences in patterns of size change between these species (Table 4.4, Fig. 4.8). Species overlap in size in the first eruption stage, but by eruption stage 5 the *A. robustus* mandible has enlarged much more than humans' (Fig. 4.1). This difference in relative change was not evenly distributed across ontogeny (Fig. 4.9). *A. robustus* size increases more during

periods 1-2 and 3-4 and there is a very low chance (1-10%) of randomly sampling a human pair so different in size as comparably aged *A. robustus*. Conversely, humans tend to increase relatively more than *A. robustus* in periods 2-4 and 4-5, although the species differences in these latter periods are not as large or significant as the differences in periods 1-2 and 3-4. Resampled metadata (preservation, k, and difference in eruption stage, da) had significant rank correlations with the value of ζ □□□□□□□□□□□. However, these correlations are fairly low, explaining little variance in ζ, and appear to reflect sample preservation more than the performance of the ζ test itself (Figs. 4.10-11).

As shown in the final section, results of the ζ test for individual traits were similar to results for the pairwise size metric (Fig. 4.13). Across all age comparisons, all traits but one (corpus height at M_2) undergo greater size change on average in *A. robustus* (Fig. 4.12), though none of these differences are statistically significant at the traditional threshold (Table 4.6). Looking at these traits between successive dental eruptions revealed significant differences between species' patterns of size change (Table 4.7). Principally, period 1-2 is the time when *A. robustus*' corpus and symphysis become much broader than humans, while period 4-5 sees a more global size increase in *A. robustus*. At least some species differences in size change of individual traits likely reflects the need for *A. robustus* to accommodate much larger postcanine teeth than humans.

Chapter 5

Implications of *A. robustus* Mandibular Growth

The present work contributes both a new method and new results of interest to the field of anthropology. This chapter discusses the importance of these contributions, treated in three parts. First, I review the reasoning of the ζ test and its performance in comparing both a single sample with itself, and humans with the extinct *A. robustus*. Although the ζ test was able to detect differences in patterns of size change between these species, the study was hampered by certain limitations that could be reexamined in future work. Second, I discuss the implications of the results for evolutionary developmental biology. Evo-devo asks how species' distinct morphologies arise during development, and so it is important that the ζ test was able to detect ontogenetic differences between each species. Finally, I discuss the implications for the reconstruction of hominid life history. The results presented here allow inferences to be made about life history variables including growth rates and maturation landmarks, which ultimately addresses the question of the antiquity of the human life history strategy.

5.1 The ζ test

Motivation for the ζ Test

When two groups are compared, a statistical argument can be laid out as to the significance of the comparison – are the groups more similar or different than expected by chance? Because of the abysmal likelihood for any animal to fossilize after it dies,

fossils present major challenges to statistical analysis. For one, sparse samples mean that natural variation is likely to be underestimated. Moreover, the one thing of which there is a lot in a fossil sample is missing data.

Resampling and randomization statistical techniques have become common and successful means of analyzing and comparing groups in the past few decades. This is because personal computers have become faster and more available, and statistical programming languages such as **R** have become increasingly available (e.g. free) and user-friendly. As noted by Sokal and Rohlf (1995) nearly 20 years ago, resampling methods allow anyone to break the bonds of parametric statistics relying on a theoretical distribution of some test statistic, to create empirical distributions of any kind of test statistic they can imagine. As a result, a whole world of previously unavailable research questions has opened to paleoanthropologists.

While randomization has helped address the issue of fossils samples not meeting certain theoretical distributions, that fossil samples likely underestimate normal biological variation can never be avoided. Poor sampling has thus largely precluded the statistical treatment of ontogeny in fossil samples. The ζ test was therefore conceived with these challenges in mind: first, how does one compare multiple traits in multiple individuals across multiple ages, in light of copious missing data? Second, given the present *A. robustus* series, can one reject the hypothesis of indistinguishable patterns of size change with age? This raises the corollary question of whether the distinct aspects of longitudinal growth – specifically changing growth rates – can be discerned from cross-sectional samples.

One of the motivations for devising the ζ test was the desire to extract as much information as possible about mandibular growth from a sample with a large amount of missing data. In the present dataset of up to 29 measurements in 122 humans and 13 *A. robustus*, 47% of the cells are missing data. Missing data are a problem for paleontology and anthropology, and researchers have dealt with this in different ways. The simplest way is to limit the analysis to only complete specimens. In studies of hominid ontogeny, this means comparing size or shape changes between a single developmental stage and adulthood (e.g. Richtsmeier and Walker, 1993; McNulty et al., 2006). This has the downside of further underestimating intraspecific variation in fossil samples, and especially reduces the number of ontogenetic comparisons that can be made. However, it does avoid assumptions (and often subjectivity) required by imputation methods that include fragmentary individuals by estimating their missing values (Mundry, 1999; Strauss and Atanassov, 2006). Imputation, however, is inappropriate in the present dataset as there is too large an amount of missing data.

Rather than specifically limiting fossil to complete specimens, or to adding error to the analysis by essentially guessing missing values, the ζ test was devised to assess patterns of variation by making as few assumptions as possible. The test simply asks how probable it is to sample the same pattern of age-related variation in the fossil sample from a larger reference sample of living humans. The test assumes nothing about the underlying pattern of growth in either species, but it does make a few other assumptions that do bear on the test's outcome. These are reviewed below and discussed in terms of the test's shortcomings and successes.

Assumption 1: Cross-sectional Data Represent Realistic Patterns of Growth

The ζ test essentially boils down the question of early hominid ontogeny to one of sampling: where ontogenetic variation can be compared between humans and *A. robustus*, how likely are the two to be distinguishable? The key assumption made here is that any individual could have grown to be the size of another individual in a later eruption stage. This assumes that patterns of size change detected in the cross-sectional samples for each species reflect actual patterns of longitudinal (i.e. individual) growth. The human growth curve in height and weight is unique among animals, but individual growth patterns can be so variable that 'the' human growth curve gets lost in the noise of cross-sectional data (Tanner, 1951; Leigh, 1996). The necessarily cross-sectional nature of skeletal samples therefore raises two important and related problems for statistically comparing samples. First, the *A. robustus* sample could be small enough that it may not adequately capture the species' pattern of growth. Second, the human sample may be large and variable enough that it could encompass the fossil pattern of ontogenetic variation, potentially resulting in the acceptance of a false null hypothesis.

These two points may not be problematic for the present study. Results presented in Chapter 4 demonstrate that the ζ test is an effective means of comparing patterns of size change in skeletal samples. The validation analysis showed that the test will generally indicate no difference between groups when patterns of size change are in fact similar. Furthermore, the test indicated clear (though not always statistically significant) differences in patterns of size change between humans and *A. robustus*, consistent with visual appraisals of each species' jaws.

That results of the intraspecific (validation) and interspecific analyses differ strongly suggests that that the interspecific differences detected are real biological phenomena rather than artifacts of sampling. Figure 5.1 compares the ζ statistics from both the human-*A. robustus* and test validation distributions, highlighting the magnitude of difference in relative size change between *A. robustus* and humans. The distribution of ζ statistics from the validation (in green; cf. fig. 5.1) is centered at ζ=0, whereas the human-*A. robustus* distribution is shifted to the right of the human-only distribution, reflecting the fact that on average there is greater overall size difference between eruption stages in *A. robustus* compared with modern humans. This holds true no matter how many traits are used (Fig. 5.2). In addition, the human-only distribution is symmetrical while the human-*A. robustus* distribution has a longer right tail (i.e. a small group of relatively high ζ statistics).

This difference between randomized distributions is not an artifact of there being twice as many human-human comparisons as human-*A. robustus* comparisons. For instance, if ζ statistics from the validation distribution (n=58,709) are resampled 5,000 times to match the size of the human-*A. robustus* distribution (n=29,148), the average ζ never exceeds 0.003. This is still lower than 12.6% of the human-*A. robustus* ζ statistics, and nowhere near the interspecific mean ζ (0.310). Thus, the ζ test strongly points to different patterns of growth even though the human-*A. robustus* distribution was not quite 'significantly' different from 0.

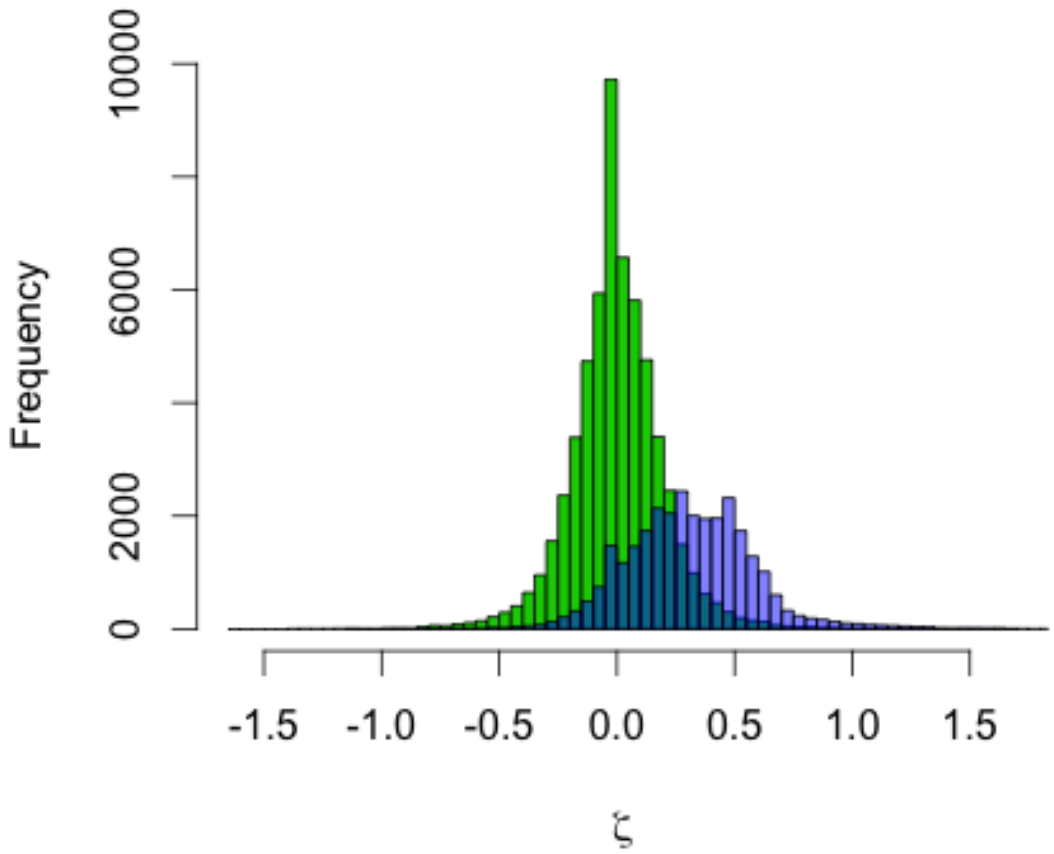

Figure 5.1. Distribution of ζ statistics measuring difference in overall size change, from the validation and interspecific tests. The green distribution is that from the validation comparing the human sample with itself (cf. Fig. 4.3). The blue distribution contains all unique ζ statistics comparing overall size change between humans and *A. robustus* (cf. Fig 4.9).

Assumptions built into the ζ test also raise the question of whether the species differences implied by the test accurately reflect each species' growth. It was assumed that any specimen in one eruption stage could grow to the size of specimens in any older stage. However, in a cross-sectional sample with overlap in size between individuals in different eruption stages, this means that it is conceivable to sample an unrealistic shrinking between dental stages (Fig. 2.3). To address this, the 'growth ratio' of older to younger was set equal to 1 in the calculation of the ζ statistic in such cases (e.g. Fig. 3.1). This potentially introduces bias into the calculation of ζ, since ratios less than one are altered but higher ratios are not.

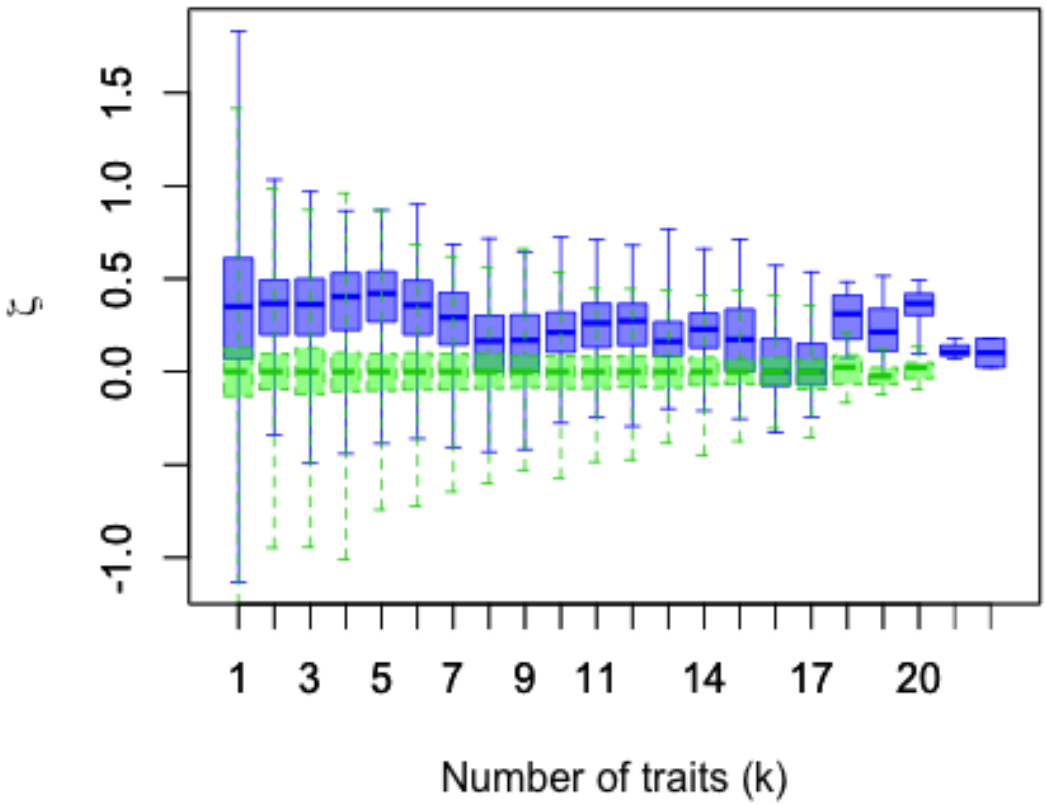

Figure 5. 2. The relationship between the value of D and the number of traits used to calculate D. The results of the validation are in green while the results of the human-*A. robustus* analysis are in blue. Boxes include the 50% quartiles, whiskers include the entire ranges of values, and thick blue/green lines are medians.

However, in the development of the ζ test I found the results to be essentially the same no matter how I treated growth ratios less than one. I ran three trials of 50,000 resamplings each, in which such 'negative growth' ratios were either [1] not altered at all, [2] omitted, or [3] coerced to 1 (as in the results presented here). In trials [1] and [3], in which negative growth ratios were retained, there were about 22,000 unique comparisons, compared to just under 18,000 when negative growth ratios were omitted. The mean and range of ζ were very similar regardless, as were the probabilities of ζ being less than or equal to 0 (cf. Table 4.4). Thus, the fix used in the present study (trial [3]) does not seem introduce substantial bias in the present case. That the results of all three trials agree

showcases the flexibility of the ζ test, that it can be altered to incorporate different assumptions (e.g. whether shrinking is possible during growth).

In spite of the apparent success of the ζ test, it is still subject to the difficulties of cross-sectional data. The ζ test detected a substantial amount of intraspecific variation in age-related size change for humans (e.g. Figs. 4.3-4), creating a substantial amount of overlap between species in patterns of size change (Figs. 4.8-9). Even though the ζ test depicted regular differences between species in size change, within the cross-sectional human sample it is not impossible to randomly sample an *A. robustus*-like pattern of age-related size change, for both the pairwise size metric and individual traits.

This issue with cross-sectional data is highlighted by the ζ statistics for corpus breadth at the septum between P_4-M_1 between eruption stages 1-2 (Chapter 4.3.1). Even though SK 3978 and 64 are in the same eruption stage (stage 1) and show identical stages of tooth crown formation (Conroy and Vannier, 1991b), the former is larger than the latter for most traits they share in common. Intraspecific variation within this age group is such that the results of the test could differ substantially depending on which fossil is used to calculate ζ. In contrast, breadth at P_4-M_1 is similar between the only two fossils in stage 2 (SK 61 and 62), so that ζ statistics do not differ depending on which individual is used. It is therefore possible that an increased *A. robustus* sample size might erase any difference between humans and *A. robustus* detected by the ζ test. In this regard, it could be informative to add the *A. robustus* subadults from Drimolen to the analysis (insofar as these fossil samples can be realistically combined).

Assumption 2: Ages and Stages

The analysis assumes that the amount of time between eruption stages is the same (or at least proportional) in each species, but this may not be the case. The greater size increase of *A. robustus* mandibles during periods 1-2 and 3-4, for example, would not be as remarkable if the absolute duration of these periods were much longer in *A. robustus* than in humans. Conversely, several authors have argued on the basis of dental development that australopithecine ontogeny was a rapid, more similar to living apes than humans (e.g. Dean et al., 1993). While this could still imply a similar relative amount of time between eruption stages, it would make the greater magnitude of size increase in *A. robustus* in periods 1-2 and 3-4 even more dramatic.

However, eruption stages are more important than chronological ages from a life history standpoint, as these stages are roughly coincident with other maturational events in humans and apes (Bogin, 1999; Zihlman et al., 2007; Hochberg, 2012 b). Given the similarity between humans and *A. robustus* in molar crown development (Mann 1975) and eruption (Smith, 1986), the assumption of proportional time between eruption stages seems reasonable. In addition, dental development in wild chimpanzees of known age has been shown to be slightly later than published captive standards, slightly blurring the distinction between ape-like versus human-like developmental timing (Zihlman et al., 2004; Smith et al., 2010)

Assumption 3: A Mixed-Sex Sample

This study made no assumptions about sex, but rather pooled the entire subadult mandibular samples of *A. robustus* and the humans from Libben. For one thing, the sex of fossils can almost never be known with certainty, except in cases of especially large or

small individuals. For instance, the *A. robustus* cranium SK 48 has been interpreted as female based on canine size (Wolpoff, 1999), but as male when compared with smaller cranial remains (Lockwood et al., 2007). Sex of the human subadults from Libben is also uncertain in most cases, as they lack adequate postcrania (viz. innominates) for sexing. Even if it were possible to reliably estimate the sex of fossil mandibles, sexual size dimorphism tends not to appear until after the time of puberty in most species, including humans and apes; the present analysis assumes the same is true in *A. robustus* but this is still a hypothesis. Pooling sexes also has the benefit of keeping the fossil sample as large as possible.

The results presented in Chapter 4 reveal a large range of size variation within eruption stages (Appendix I). This is especially true for the stage 4 subsample, as this period roughly coincides with puberty and there is great individual and sexual variation in the timing of the pubertal growth spurt. As mentioned above, sex cannot usually be reliably determined for subadults before puberty, and so sex is neither known nor estimated for most individuals. The great range of sizes (individual traits and the size metric) and associated ζ statistics during eruption stage 4 (e.g. Fig. 4.2) is consistent with this pattern. The similarly large range in stage 1 is less explicable by sexual dimorphism, and it is probable that much of the size variation may reflect age variation within eruption stages.

The potential influence of sex variation on the results is most salient for eruption stages 3 and 5, which are each represented by only one fossil (SK 63 and SKW 5, respectively). SK 63 is very similar in size and anatomy to stage 2 *A. robustus* and is smaller than stage 4 *A. robustus* for most measurements; ζ statistics were slightly

negative (but not significantly different from 0) for period 2-3 but were significantly positive for period 3-4. Similarly, SKW 5 is also fairly small, within or below the range of stage 4 *A. robustus* for many mandibular dimensions (Appendix I), and similar in size to small adult mandibles such as SK 74 and SKX 5013; ζ statistics for period 4-5 were slightly negative (but again not significantly different from 0). If either of these fossils is especially small for their eruption stage (i.e. due to sexual size dimorphism; see below), this would reduce the difference between species' growth detected in this study. It may therefore be worth investigating whether teeth can be used to estimate individuals' sex, the difficulty being that not all specimens preserve the same teeth. However, an enlarged fossil sample is necessary to adequately assess specimens' sex and this potential influence on *A. robustus* growth.

Summary of the ζ Test

The ζ test is a novel means of comparing patterns of variation in the face of small samples and large amounts of missing data. The test (for the pairwise size metric) behaved as expected when comparing patterns of size change in the human sample with itself, and contrarily pointed toward differences between humans and *A. robustus*. It should be remembered that the test was run exactly the same in both the validation and interspecific analyses, yet the outcomes were quite different in each. In addition, the test comparing size change for individual traits further pointed to differences between species that are consistent with gross differences between species' mandibles. Using this new test, the present study is the first to present both statistical and skeletal evidence for different patterns of bodily size change between a human and australopithecine sample.

Even though the ζ test strongly pointed toward species differences in patterns of size change, viz. between eruption stages 1-2 and stages 3-4, many of these differences were not statistically significant at the traditional $p<0.05$ level. This cautions against interpreting the results as a clear indication of species differences, but can be at least partly explained by the test's three key assumptions: 1) species' true patterns of growth and development can be represented with cross-sectional data; 2) the time between dental eruptions is comparable/proportional between species; and 3) species' patterns of sexual dimorphism will not influence the comparison of growth between samples. The ability of the ζ test to detect differences between humans and *A. robustus* shows that these were safe assumptions to make given the limitations of the samples used. However, the species differences detected here may be validated or refuted by future fossil discoveries and advances in methods for sexing and aging skeletal samples.

5.2 Evo-devo

Chapter 2.2 presented the null hypothesis of conserved developmental processes shared by *A. robustus* and humans, which predicts either that each species should not differ in size change for any trait, or that each trait would differ similarly between species across all traits. The alternate hypothesis of different postnatal development predicts that species differences should be found for only a subset of traits. The ζ test for individual traits (Chapter 4.3) rejects the null in favor of the alternate hypothesis. This section discusses the implications of this result for hominid evo-devo, examining whether differences might be explained by jaw biomechanics and adaptation, or by tooth size and development. I then revisit the predictions from morphogenetic hypotheses of facial

growth that could not be directly examined in this study (Bromage, 1989; McCollum, 2008). I also suggest different ways of addressing questions arising from this study.

The ζ test was used to compare the *A. robustus* and human patterns of relative size change for individual traits across ontogeny. For most traits, the amount of relative change in size between dental eruptions in *A. robustus* can be found in a human sample, with the exception of the time between eruption stages 3-4 and less often between stages 1-2. Between stages 1-2, *A.* robustus experiences significantly greater increases in both corpus and overall mandibular breadth, and in corpus length posterior to the mental foramen. Between stages 3-4 the *A. robustus* mandible exhibits significantly greater increases in the ramus and most aspects of corpus height, corpus breadth around the premolars, and corpus length. Thus stages 1-2 appear to be the period during which the *A. robustus* mandible becomes characteristically "robust," and stages 3-4 witness a greater global size increase than is usually seen in humans.

One of the most notable findings of this study is that the *A. robustus* mandibular corpus becomes markedly more robust than humans early in postnatal ontogeny, rather than prenatally. Many other studies of comparative craniofacial growth have found that different groups (species or populations within species) can be distinguished in the earliest age groups (e.g. Fukase & Suwa, 2008; Ponce de Leon & Zollikofer, 2001). Consistent with these studies, the present study demonstrates that some key differences in the mandibles of humans and *A. robustus* are established early in postnatal growth.

During eruption stage 1, both species overlap in corpus height and breadth, though the few *A. robustus* values tend fall in the high end of the human range (Appendix I). In addition, unique features such as the human chin are present by the time of birth

and are notably absent in the youngest *A. robustus*. The youngest specimens in this eruption stage have their deciduous teeth nearly fully erupted, which means that at least two years of postnatal growth have occurred prior to this eruption stage (by human standards; Liversidge, 2003). Thus, even though species' mandibles are distinct in the earliest eruption stage, it cannot be definitively said that such differences were established prenatally.

Postnatally, between eruption stages 1 and 2, each species follows similar patterns of relative height change, but *A. robustus*' corpus breadth increases more than humans (Table 4.6). This relationship can be examined with the "robusticity" shape index of corpus breadth divided by height at a given tooth position (Daegling, 1989; Teaford & Ungar, 2000). Even though robusticity throughout most of the corpus decreases in both species across ontogeny (Appendix II), the *A. robustus* decreases are usually not as substantial as those implied by the human cross-sectional sample. The ζ test therefore points to an important role of postnatal ontogeny in creating the robust *A. robustus* jaw and humans' relatively gracile one. This raises the question of *why* the *A. robustus* corpus becomes so remarkably broad compared with humans.

Below, I review several possible reasons for this species difference. The relatively broad *A. robustus* mandibular corpus has been interpreted as being adapted to withstand large stresses generated during chewing (Wolpoff, 1975; White, 1977; Daegling, 1989; Teaford & Ungar, 2000). This anatomy could be the direct result of bone itself responding adaptively to the use of the mandible during ontogeny. More indirectly, the growth difference could be genetically determined, inherent to the mandibular development of the species, because of natural selection to create a robust corpus. Also

indirectly related to diet, the larger postcanine teeth of *A. robustus* may necessitate housing in a larger jaw. In this case, the species differences in changing mandibular breadth and robusticity may reflect size of the developing dentition rather than biomechanical adaptations. Not all these possibilities are necessarily mutually exclusive, and each is treated below.

Jaw Biomechanics and Feeding Adaptation.

As discussed in Chapter 1, the *A. robustus* mandible is able to help generate, and then withstand, large muscle forces associated with chewing. This strength is provided by a relatively broad (i.e. "robust") corpus and symphysis, as well as the distribution of cortical bone thereabout. Because human and *A. robustus* mandibular shapes reflect different biomechanical properties, it is possible that growth differences between these species reflect divergent dietary demands. Indeed, Taylor (2002) found that African ape (*Pan* and *Gorilla*) mandibles generally grew so as to increase resistance to masticatory stresses across ontogeny.

However, biomechanical inferences, especially related to ontogeny, must be made cautiously. Taylor (2002, 2006) also found that not all differences in shape (and shape change) between species were fully predictable from their dietary differences. Similarly, Daegling (1989, 1996) warned that anatomical differences between African apes do not necessarily correspond to significant biomechanical differences. Daegling (1989, 2007) has also shown that raw corpus breadth measures and the "robusticity index" are poor predictors of strength against torsion and bending, stressing that while a robust shape may create a cross-section strong against twisting and bending, the distribution of cortical

bone about the cross-section is key to determining strength. Finally, Daegling and Hylander (2000) review the case that the robust australopithecine mandible is actually overdesigned for handling quotidian chewing forces; some inferred biomechanical advantages of the *A. robustus* may instead be non-adaptive 'spandrels' (Gould and Lewontin, 1979). The following discussion treats the robust corpora of subadult *A. robustus* as having greater strength than humans, a reasonable supposition that must be hypothetical until data on cortical bone distribution are available to more accurately estimate the strength of *A. robustus* youths' jaws (Daegling, 1989; Taylor, 2006).

If the relatively more robust corpus of *A. robustus* reflects a functional adaptation to chewing stresses experienced in life, the relative increase in *A. robustus*' (inferred) corpus strength during period 1-2 could reflect early weaning and early adoption of an adult diet in this species. Indeed, *A. robustus* deciduous teeth experience a great deal of (dietary) wear prior to M_1 eruption and it has been suggested that this pattern is indicative of early weaning (Aiello et al., 1991). Aiello and colleagues likened this pattern with extant gorillas rather than early-weaning humans. That is, they interpreted early weaning to be indicative of a relatively fast overall life history and short maturation period like gorillas, rather than a truncated infancy like in humans.

However, in support of a more human-like pattern of weaning, McKinley (1971) found that the estimated survivorship curve of *A. robustus* from Swartkrans and Kromdraai could be best explained by an estimated age at sexual maturity of 11 years and interbirth interval (i.e. time from birth to weaning plus gestation) of 3-4 years (maximum). This is significant because this spacing is at the low end of the wild chimpanzee (Marsden et al., 2006) and gorilla ranges (Kennedy, 2005; Robbins et al., 2009), but the

(modeled) age at sexual maturity is comparable to chimpanzees' and slightly older than gorillas'. Short birth spacing would have been key to *A. robustus*' reproductive success and maintenance of a viable population in light of high mortality and short life spans (Wolpoff, 1979; Lovejoy 1981). Little other work on *A. robustus* paleodemography has been done, but the issue deserves further attention, especially given increased mandibular samples (Brain, 1981, 2004; Sutton et al., 2009; Keyser et al., 2000; Pickering et al., 2012) since McKinley's (1971) study.

Further evidence as to potential early weaning in *A. robustus* could also come from a more systematic and comprehensive examination of patterns of macro- and microwear on deciduous teeth. Aiello and colleagues (1991) compared australopiths only to extant apes. Examining a wider range of variation within and between species, including other hominids or species that wean at different ages (i.e. early), could help shed considerable light on the relationship between weaning and tooth wear (e.g., Bullington, 1991) in early hominids. An important difference between humans' and gorillas' early weaning is that in humans it is accompanied by specially prepared, high quality foods for weanlings (Sellen, 2007), whereas a gorilla weanling would be ingesting harder foods like adults do (Kennedy, 2005; Humphrey 2010). This predicts that macroscopic levels of deciduous wear should be greater in gorillas than humans, providing a baseline for understanding the likelihood and nature of early weaning in *A. robustus* and other early hominids. However, the large variability in practices of weaning, juvenile feeding and diet across human populations (Sellen, 2007), highlights the need to examine multiple human samples (viz. prehistoric populations).

The isotopic composition of teeth could provide further information about possible early weaning in hominids. Carbon, nitrogen and other elements from an animal's diet contribute to the development of the animal's various tissues, including teeth (reviewed in Ungar & Sponheimer, 2011). All plants discriminate against the ^{13}C isotope in favor of ^{12}C in photosynthesis, but do so differently such that leafy plans (C_3 pathway) have lower ratio of $^{13/12}C$ than sedges and tropical grasses (C_4 pathway). The carbon isotopes ratios (expressed as $\delta^{13}C$) within animal teeth have been shown to be effective discriminators of different types of diet. Animals eating C_4 plants will tend to have higher $\delta^{13}C$ values than animals that eat leaves and fruits.

Analysis of the isotopic composition of *A. robustus* teeth shows a wide range of $\delta^{13}C$ values, suggesting the hominid had a rather variable, generalized diet (Lee-thorp & Sponheimer, 2006; Ungar & Sponheimer, 2011). Sponheimer and colleagues (2006) further analyzed the isotopic composition of enamel across the crown height of individual *A. robustus* teeth, thus examining dietary variation within an individual over the time the tooth was developing. Values of $\delta^{13}C$ varied in all four *A. robustus* teeth sampled, and in two of these showed a fairly stable decrease in $\delta^{13}C$. Of these two, one was an M_3 and the other an unspecified molar: the former would not have been formed during infancy and the full transition to an adult diet, and the latter may have been but this cannot be known for sure.

A similar analysis of the isotopic composition of *A. robustus* tooth crowns could therefore shed light on the question of early weaning in this species. For instance, I_1 and P_3 crowns would have been forming during period 1-2 when *A. robustus* first experiences a drastic increase in corpus breadth (Conroy and Vannier, 1991b). A 'longitudinal'

analysis of these teeth in *A. robustus* could test the null hypothesis that $\delta^{13}C$ values will be consistent throughout the height of the crown. Alternatively, a consistent change in in $\delta^{13}C$ values within teeth could provide evidence of weaning during this time. However, carbon isotope ratios can indicate a general dietary tendency (e.g. leaves vs. grasses), but cannot unequivocally tell exactly what an animal was eating and when. Nevertheless, it would be very informative to further investigate the relationship between jaw growth and the isotopic correlates of diet.

Regardless if hypothesis of early weaning in *A. robustus* is correct, the question still remains *why* the corpus so drastically broadens (and presumably strengthens) during this time. On the one hand, the (inferred) increased strength of the *A. robustus* mandibular corpus relative to humans during period 1-2 could be genetically programmed into the species' development. Presumably this could be due to natural selection acting on subadults, favoring those who can achieve foraging independence from older individuals earlier. Unfortunately, this is a rather untestable hypothesis. On the other hand, *A. robustus* early increase in corpus breadth may reflect a mechanical response of bone to the adoption of an adult-like diet. It is difficult to distinguish which of these two is most likely, if either.

The Influence of Developing Teeth

Dietary differences between humans and *A. robustus* are reflected in the size and morphology of each species' teeth (Wolpoff, 1975). In Chapter 2 it was predicted that because humans and *A. robustus* have small canines and incisors compared with other hominids and hominoids, they may show similar patterns of size change in the anterior

corpus; this prediction was borne out, although it was based on a small number of comparisons. Conversely, *A. robustus*' massive molars and premolars might drive some of the differences in posterior corpus length and breadth between species (Wolpoff 1975; Plavcan & Daegling, 2006). The present study could not test this relationship directly, but knowledge of tooth crown formation in *A. robustus* (Conroy and Vannier, 1991) hints that some of the differences in corpus growth between *A. robustus* and humans may well result from differences in the size of the developing permanent dentition.

The ζ test comparing growth in length of the posterior corpus is consistent with the hypothesis that some aspects of jaw growth reflect the development of the dentition. The distance from the mental foramen to the distal-lingual margin of the lingual tuberosity could be compared across all successive eruption stages, but indicated significant differences in size change only during period 3-4 (Table 4.7). This measurement tracks the growth of the lingual tuberosity, which must grow posteriorly to accommodate the molar crypts and crowns as they develop (Enlow and Hans 1996). The lingual tuberosity of the only *A. robustus* in stage 3 (SK 63) encloses a partially developed M_2 crown, and there is no hint of M_3 crown formation distally (Mann, 1975; Conroy & Vannier, 1991b). By eruption stage 4, the *A. robustus* lingual tuberosity has extended posteriorly to surround a developing M_3 crown in all but one specimen (SK 25, the least mature and presumably youngest in stage 4). It is therefore reasonable to connect species differences in corpus length growth to reflect the development of differently sized M_3s.

The ζ test is more equivocal as to the influence of M_2 crown formation for species differences in posterior corpus length growth during period 1-2. While *A. robustus* does

undergo greater length increase than humans here, the difference is not significant ($P_{\zeta \leq 0}$=0.162). None of the stage 1 *A. robustus* shows evidence that the M_2 has begun to form, but the only stage 2 fossil preserving the distal corpus (SK 62) has formed at least the upper portion of the M_2 crown. Results therefore hint that developing large tooth (viz. molar) crowns may be responsible for some differences in jaw growth between humans and *A. robustus*, but this deserves further testing.

Results are also equivocal as to whether *A. robustus*' large postcanine teeth drive its relatively large increases in corpus breadth. Between eruption stages 1-2, the ζ test indicates that *A. robustus* generally undergoes greater relative change in corpus breadth at P_4 (mean ζ=0.112, p=0.073). Of the three *A. robustus* in eruption stage 1, none of them has any development of an unerupted P_4 crown (Conroy and Vannier 1991b). The two *A. robustus* in stage 2 have developed at least part of this crown, however, meaning some if not all of the crown's adult breadth had been attained. It is therefore plausible that appearance and development of the P_4 crown drives some of the growth in corpus breadth between these eruption stages.

But at the same time (period 1-2), the ζ test shows a significant species differences in breadth growth at the positions of the (unerupted) P_3 and M_1, and these tooth crowns are already partially formed in stage 1 *A. robustus*. While the P_3 and M_1 suggest tooth crown formation may be less involved in driving corpus breadth growth, it is also possible that *root* formation is involved. For example, later in development, the P_4 root of SK 6 (stage 4) becomes buccolingually broader than the crown, which interestingly corresponds with *A. robustus*' significantly greater increase in corpus breadth at this position in periods 3-4 (Table 4.7).

It was beyond the scope of the present study to examine the relationship between tooth formation and hominid jaw growth in more detail, but results are consistent with other studies more directly analyzing the relationship in other taxa. Boughner and Dean (2004) tested whether space in the growing jaw influences the initiation of molar crown formation, in *Pan* species and baboons (*Papio hamadryas*). They found that the length of the corpus always provided "excess" crypt space distal to the mineralizing molar crowns, and that posterior corpus length increased most when the M_3 crown began to mineralize. Moreover, the size of this space and its elongation were greater in *Papio* than in *Pan*, consistent with the longer molar teeth in the former genus. Similarly, Fukase & Suwa (2010) found that the faster-growing incisors of recent Japanese mandibles compared with archaeological samples was concomitant with faster anterior corpus height growth in the recent mandibles.

In summary, the present study did not directly examine whether the formation of tooth crowns influences size growth of the mandible, but it is very likely that at least some differences between mandibular growth between *A. robustus* and humans (i.e. in length) reflect the development of *A. robustus*' large postcanine teeth. Future research should therefore examine the relationship between jaw and tooth crown development across a wider range of taxa, especially including megadont species like australopiths. In such a study, CT data could be used to obtain mandibular metrics such as those employed here, combined with absolute measures of tooth crown width, enamel thickness, root size, crypt size, and thickness of cortical versus trabecular bone around developing teeth in subadults.

Mandibular Growth Rotations

The very tall ramus of *A. robustus* has led to the hypothesis that this species undergoes substantial postnatal growth rotation of the mandible and rest of the face (Fig. 2.2; Bromage, 1989; McCollum, 1997, 2008). McCollum (1999) has even suggested that other aspects of the robust australopithecine face, including its thick hard palate and highly hafted face onto the braincase, are merely developmental byproducts of this rotation. Facial rotation is generally measured using angles between parts of *complete* jaws and faces (e.g. Björk, 1969; Björk and Skieller, 1972; Solow and Houston, 1988; Wang et al., 2009), but such data cannot be collected on the majority of the fossil sample. Because facial rotation is essentially a phenomenon of disparate height increase between the front and back of the jaw (Björk and Skieller, 1972), rotation may instead be indirectly addressed by comparing ζ test results for anterior and posterior mandibular heights.

The most anterior and posterior corpus heights in this study are at the symphysis (X711) and ramus (X607), respectively. Across all possible comparisons (Table 4.6) the mean ζ is greater for ramus height than symphysis height (Fig. 5.3), consistent with greater rotation in *A. robustus*. Across ontogeny (i.e. periods 1-4 or 1-5), average ζ for each trait is very different. The ζ test indicates that symphysis height increases more in *A. robustus* than humans from period 1-5 (ζ=0.215, $P_{\zeta \leq 0}$= 0.056, n=107). This period could not be assessed for ramus height, but it can in period 1-4, when mean ζ=0.628 ($P_{\zeta \leq 0}$=0.007, n=285). ζ for ramus height is much greater and significantly higher than 0 compared with ζ for symphysis height, consistent with a larger growth rotation in *A. robustus*. Unfortunately, poor fossil preservation means that these two measurements

cannot be fully compared either within individuals or across ontogeny (Table 4.7), making it difficult to define when and how exactly this difference is brought about.

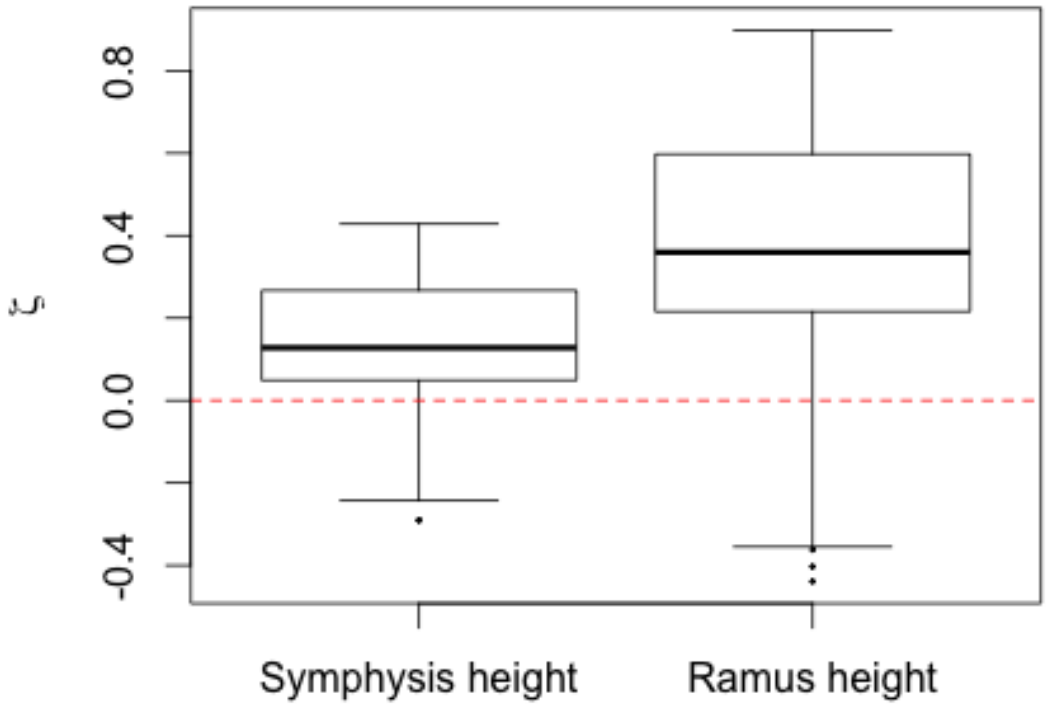

Figure 5.3. All ζ statistics for height at the mandibular symphysis and at the ramus. Boxes include the 50% quartiles, dots are outliers, and solid black lines are medians.

The ζ test does provide evidence to suggest that the greater rotation in *A*. robustus may occur mostly during period 3-4. Early in ontogeny, ζ statistics for both ramus and symphysis height are very similar and not significantly greater than 0 (symphysis height in period 1-2: mean ζ=0.127, $P_{\zeta \leq 0}$==0.171; ramus height in period 1-3: mean ζ=0.177, $P_{\zeta \leq 0}$=0.157). Species differences, if they truly exist, are proportional in the front and back of the mandible, implying no difference between species in the amount of rotation. The amount of relative size increase anteriorly at the symphysis in each species is essentially the same from eruption stage 2-5 (mean ζ=-0.004, $P_{\zeta \leq 0}$=0.527, n=58). Ramus height is not preserved in exactly the same eruption stages, but during period 3-4 ramus height increases much more in *A*. *robustus* than humans on average (mean ζ=0.276, $P_{\zeta \leq 0}$=0.083,

n=216). Taken together, this suggests that anterior and posterior facial growth rates are similar in each species prior to eruption stage 4, but between period 3-4 growth of the *A. robustus* posterior face is relatively faster than the in front compared with humans. In other words, the rate of facial rotation may be similar between species until period 3-4 when *A. robustus*' face rotates faster. The inferred rotation pattern of *A. robustus* differs from the human pattern of rotation, which is usually greatest prior to the eruption of permanent teeth (i.e. period 1-3; Karlsen, 1997; Wang et al. 2009).

The fragmentary fossil record prevents a more definitive and rigorous study of rotation. The ζ test lends support, albeit somewhat equivocal, to the hypothesis of greater facial rotation in *A. robustus* than humans during postnatal growth. Species differences in facial height growth across ontogeny probably contribute to this difference, but there is modest evidence that the bulk of the extra rotation in *A. robustus* occurs during period 3-4, along with the greater overall mandibular growth that occurs in this species.

Bone Remodeling Fields

The proximate mechanisms of mandibular size and shape change are the differential deposition and resorption of bone on its surfaces (Enlow and Harris, 1964). The distribution of these depository and resorptive fields on the faces of different species are consistent with the anatomical differences between them (O'Higgins and Jones, 1998). For instance, the development of humans' pronounced chin is reflected in bone deposition around the symphysis inferiorly but resorption superiorly around the anterior alveolar margin. In prognathic taxa such as *A. africanus*, chimpanzees and macaques, the entire surface is depository (Johnson et al., 1976; Bromage, 1989; Enlow and Hans,

1996). Fields of bony remodeling thus reflects the different vectors of growth in these different facial types: forward in prognathic species and more downward and forward in humans.

Results of the present study are consistent with Bromage's (1989) interpretations of *A. robustus* facial growth based on remodeling fields. Bromage interpreted the resorptive surface of the maxillary clivus and anterolateral mandibular corpus of *A. robustus* to indicate a facial rotation and downward component of facial growth in this species, similar to modern humans but unlike more prognathic taxa. Consistent with this interpretation, the ζ tests suggest *A. robustus*' mandible and face may have experienced a greater anterior rotation than modern humans. Similarly, humans' slender mandibular corpora have a large resorptive surface medially extending from the submandibular fossa beneath the premolars to the ramus posteriorly (Enlow and Hans 1996). This region in *A. robustus* is depository (Bromage 1989), consistent with this species' greater increases in corpus breadth compared with modern humans detected by the ζ test.

Even though Bromage's (1989) interpretations were borne out by the ζ test, the distribution of remodeling fields alone cannot account for the species differences in the magnitude of size changes detected by the ζ test (e.g. McCollum, 2008). As Bromage (1989) recognized, the *rate* of deposition and resorption within these fields is another important variable influencing bony size and shape change. The mandibular corpus, like the shafts of long bones, grows by bone deposition on the external (periosteal) surface and resorption of the internal (endosteal) surface. A reasonable hypothesis would be that *A. robustus* and humans differ in the rate at which these surfaces deposit and resorb bone (cf. the discussion of jaw biomechanical development above).

To test this and other hypotheses about the morphogenetic mechanisms underlying *A. robustus* mandibular growth, Synchrotron micro-computed tomography may eventually prove a useful way of investigating fossil histology beneath the bony surface. This is currently the highest-resolution tomographic technique, and has been used to study the histology in recent and fossil teeth (Tafforeau et al., 2012), as well as histology of recent human bone (Cooper et al., 2011; Pacureanu et al., 2012). The technology is quite expensive, and so has yet to be used extensively on bony fossil material (but see Mazurier et al. 2006; Carlson et al. 2011). This imaging technology has yet to be used to examine the pattern and process of bone growth and remodeling in fossils similar to the classic studies of Enlow and others using ground sections (Enlow, 1962; Enlow and Harris, 1964; Enlow et al., 1971; but see Houssaye et al., 2010 for application to living snakes).

Summary of Evo-Devo

Differences between humans and *A. robustus* in the growth of individual mandibular measurements seem ultimately reflect dietary differences between these species. On the one hand, corpus breadth increases more, and more rapidly, in *A. robustus*. This theoretically increases the mechanical strength of the corpus and symphysis to withstand high forces generated during chewing. This is a hypothesis that merits testing by analyzing cortical bone thickness and distribution about the corpus in developing the jaws of *A. robustus* and other taxa (cf. Daegling and Grine, 1991). On the other hand, length of the posterior corpus increases more in *A. robustus* than humans, concomitant with the former's larger (e.g. longer) teeth. It is possible that differences in

corpus breadth growth between species also reflect the development of differently sized postcanine teeth breadth, although evidence here is equivocal. Tooth size differences cannot account for species differences in breadth growth at the symphysis (Table 4.7), suggesting a biomechanical explanation is more viable for this region (White, 1977).

The test detected a greater degree of facial rotation during growth, perhaps chiefly during period 3-4, and greater rates of corpus thickening in *A. robustus*, as predicted from models of facial morphogenesis (Bromage 1989). These results should be interpreted with a degree of caution, since the inferred mandibular rotation was based on comparing ζ statistics for different corpus heights, rather than testing a true measure of 'rotatedness' in individuals. While the broadening of the *A. robustus* mandibular corpus throughout ontogeny is consistent the species' pattern of mandibular remodeling fields, the severity of this broadening is not necessarily predicted on this basis (McCollum, 2008).

The present research indicates an important role for postnatal ontogeny in creating the morphological differences between *A. robustus* and humans, and raises a number of research questions that deserve treatment in the future. Future studies should employ state of the art computed tomography (CT) imaging techniques to better quantify patterns and rates of bone growth in these hominids. CT data have been extensively used to analyze bony macrostructure for decades, but the technology is now capable of viewing microstructure as well. These new sources of data, combined with novel analyses such as the ζ test, open the door to countless new and interesting questions in anthropology and evolutionary and developmental biology.

5.3 Hominid Life History

Chapter 2.2 presented the null hypothesis that aspects of modern human life history, namely patterns of growth, were identical between humans and *A. robustus*, which would suggest that the human pattern was established by the early Pleistocene. This hypothesis predicts humans and *A. robustus* jaws would follow the same pattern of overall size change between eruption stages, but the results presented in Chapter 4.2 rejected this hypothesis. This section discusses the implications of this result for hominid life history. I begin by addressing the extrapolation of inferences from the mandible to bodily growth. I then discuss this study's findings in terms of whether *A. robustus* may have experienced the unique aspects of human life history stages, including childhood, middle childhood and adolescence. Finally, I treat the proposal that *A. robustus* males continued growth into adulthood, in terms of the outcome of the ζ test as well as data from adult *A. robustus* not presented above.

Results of the ζ test corroborate the visual assessment that the *A. robustus* mandible undergoes much greater increase in overall size prior to the occlusion of the third molar compared with modern humans. This size change is concentrated in two periods, first prior to the full occlusion of the first molar and then between the eruptions of the first and second molars. Before situating these results in the context of hominid life history, it should be noted that one must be careful extrapolating results from *mandibular* size to inferences about *body* size.

A working assumption of the study is that mandibular growth reflects the same processes as the rest of the body, and several studies have shown this to be the case (Bergersen, 1972; Lewis et al. 1985; Franchi et al., 2001, 2007; Antón and Leigh, 2003). Recently, Coquerelle and colleagues (2010b, 2011) examined development of sexual

dimorphism in a cross-sectional sample of recent human mandibles. While their study did not directly compare mandibular and bodily growth, their multivariate mandibular size and shape growth curves (2011: Fig. 3a-b) are similar to published growth curves for mass and stature in living humans (e.g. Bogin 2009, Walker et al. 2006): rates of change (for size and shape) decelerate until around five years of age, level out until puberty (around age 10-12) when there is a short spurt after which growth decelerates or ceases. Sex differences in mandibular growth also mirrored those in bodily growth.

Chapter 4.1 showed that the pairwise size metric used in this study is also consistent with patterns of human body size change (Fig. 4.2). However, it was also shown that the *A. robustus* mandible becomes much larger than humans despite starting at similar sizes in stage 1. Body size estimates for *A. robustus* adults, based on isolated postcrania, range from 30-40 kg (McHenry and Coffing, 2000; Pickering et al., 2012). Most human populations are larger than this (Eveleth and Tanner, 1988), so it cannot strictly be that mandibular growth reflects body growth the exact same way in these species (Wood and Aiello, 1998). In this regard, it is important that the ζ statistic measures *relative* change in size between dental eruptions, minimizing the effects of the absolute size differences between species at later stages of eruption.

With this caveat in mind, the following discussion interprets the results of the analysis in terms of humans' life history stages, proxied by dental eruption (Bogin 1999, Hochberg 2012). The discussion focuses chiefly on the results of the ζ test for the pairwise size metric between successive eruption stages as a proxy for body size since this is an important life history variable (Robson and Wood 2008). Although the

dichotomization of 'ape- or human-like' was decried above, these models are contrasted here to illustrate the unique aspects of humans' pattern of growth.

Infancy or Childhood?

The period between eruption stages 1-3 roughly corresponds with the infant period of chimpanzees, in which the subadult feeds mostly by nursing (Zihlman et al., 2007). Humans, on the other hand, tend to wean from nursing long before the first molar begins erupting (i.e. early in eruption stage 1). Because of this unique dependency, the time from weaning to first molar eruption in humans is considered an evolutionarily novel growth phase, childhood, and present only in humans (Bogin 1997, 1999; Hochberg 2012). Humans rapidly decelerate bodily growth rates at this time, whereas (captive) chimpanzee growth accelerates in this period (Walker et al., 2006b). Mandibular size change in dental eruption periods 1-2 and 2-3, then, could be thought of as representing earlier and later phases of childhood growth, respectively, in humans, but representing infant growth in other apes.

During period 1-3, the *A. robustus* mandible undergoes greater size change than humans' on average, and there is a fairly low probability of sampling a pair of period 1-3 humans as different in size as pairs of *A. robustus* (mean ζ=0.126, $P_{\zeta \leq 0}$=0.158). However, one cannot reject the null hypothesis of indistinguishable growth patterns between period 1-3 overall. Looking at periods 1-2 and 2-3 specifically make it difficult to interpret this weak rejection.

In period 1-2, mean ζ for the pairwise size metric is 0.149 ($P_{\zeta \leq 0}$=0.091), but during period 2-3, the species' patterns of size change are less distinct (Table 4.4). If

these differences in size increase reflect bodily growth rate differences between species, this could argue against *A. robustus* having slow, human-like growth rates during childhood. The high average ζ statistic in period 1-2 followed by near-zero average ζ in period 2-3 could suggest either a delayed deceleration in body growth compared to humans, or possibly an acceleration in period 1-2 similar to chimpanzees. Along these lines, Bastir and Rosas (2004: 506) using geometric morphometric methods found that chimpanzees' mandibular size increases more rapidly than humans' both prior to the eruption of M_1 and thence to M_2 emergence (cf. periods 1-3 and 3-4 in this study).

Alternatively, the differences between species' mandibular growth in period 1-3 may be less directly related to body size, as discussed earlier in section 5.1. The high average ζ statistics during period 1-2 are driven by the significantly positive D values for measures of corpus breadth (Table 4.7). As this is the time when the species' megadont M_2 and P_4 crowns begin forming, the severe mandibular size change in *A. robustus* may simply be a reflection of having large postcanine teeth. An additional possibility, relevant to life history, is that these young mandibles were capable of, and used for, processing an adult-like diet. If this is the case, this may be a marker of relatively early weaning in this species, as described above.

Early weaning is an important part of the human adaptive strategy, as it allows females to reduce the time that ovulation is suppressed due to lactation, thereby decreasing the amount of time between births (Lovejoy, 1981; Kaplan et al., 2000). Human children are not fully equipped handle an adult diet, given their small deciduous teeth and digestive tracts, and so weaned children are highly reliant on older individuals to obtain and prepare their food for them (Sellen, 2007). If the robusticity of stage 2 *A.*

robustus mandibles provides comparable bending and torsion strength to adults, as suggested in section 5.2, this could indicate *A. robustus* weanlings were more independent foragers than humans of comparable dental age.

This study's implications for whether *A. robustus* experienced a human-like childhood or ape-like later infancy depend on a number of things. Depending on how mandibular growth tracks that of the body, ζ statistics between period 1-2 and 2-3 could imply more rapid growth than in humans before permanent teeth begin erupting in period 2-3. Alternatively, because ζ statistics in period 1-2 reflect differences confined largely to corpus breadth growth, this could imply that overall (i.e. body) growth and relative age at weaning are similar between these hominids. These alternatives cannot be distinguished in the present study, nor are they mutually exclusive (cf. section 5.2 above).

Juvenility or Middle Childhood?

The period between eruption stages 3-4 corresponds with the juvenile period of humans and other primates (Bogin 1999). This period lasts from the time of M_1 eruption until puberty, roughly from 4-8 years of age in wild chimpanzees (Pusey 1990; Zihlman et al. 2004, 2007), and around 6-11 years in most human populations (Bogin 2009; Walker et al. 2006). During this time chimpanzees continue high bodily growth rates from the preceding infancy period (Pusey et al. 2005; Walker et al. 2006).

In humans, however, bodily growth rates usually descend to their lowest levels of all ontogeny (Walker et al. 2006a-b, Hochberg 2012). This is also a time critical period of social development in humans, known to psychologists as "middle childhood" (Mann and Monge 2010; Campbell, 2006, 2011). One developmental marker of the beginning of

middle childhood, seen only in humans and other hominids, is a 'quiescent period,' a delay of a few years between the eruption of the permanent incisors on the one hand, and the canines, premolars and M_2 on the other (Liversidge 2003; Mann and Monge 2010). Slow growth during the juvenile/childhood phase is critical to the human adaptive strategy because it reduces the energetic demands on the older individuals who must help feed multiple dependent offspring (Gurven and Walker 2006). This relative (but not total) freedom from foraging allows human youngsters additional time to learn social behaviors and cultural mores (Mann and Monge 2010; Hochberg 2012). The hallmark of human juvenility, or middle childhood, is therefore the preferential devotion of energies to social and cognitive development over body size growth compared with apes.

The high, significantly positive D distributions for both the pairwise size metric and individual traits between eruption stages 3-4 suggest that *A. robustus* likely underwent greater size increase than humans – a juvenile and not middle childhood stage. This is the only period in which the ζ test detected a significant difference in overall size between species ($P_{\zeta \leq 0}$=0.019), and reflects size change throughout the mandible (Table 4.7). Period 3-4 stands out as the only successive eruption period in which *A. robustus'* corpus height increases significantly more than humans'.

Mann (1975) and others (Mann et al. 1990; Mann and Monge 2010) have argued that all hominid juveniles to date show a human-like quiescent period of no dental eruptions, indicative of a middle childhood. If so, then the drastic difference in mandibular, and possibly body, size increase between humans and *A. robustus* would imply that the nature of middle childhood has changed since the early Pleistocene. Slow growth of human children during this time has been viewed as an adaptation to reduce

energetic requirements of multiple dependent offspring (Gurven and Walker 2006; Bogin 2009). The present results would therefore suggest *A*. *robustus* juveniles would have been more independent than human juveniles, consistent with some interpretations of mandibular growth during childhood described above.

It should be noted that this result relies on a sole stage 3 *A*. *robustus* (SK 63). This specimen is more similar in size and morphology to SK 61 and 62 (stage 2) than to stage 4 fossils (Appendix II). If SK 63 is on the small end of the true range of *A*. *robustus* variation at this stage of tooth eruption, then the difference from humans in overall size change may not be so great as indicated by this study.

In sum, results of the ζ test for pairwise size during period 3-4 are consistent with relatively rapid, ape-like growth during the juvenile period in *A*. *robustus*. While rapid juvenile growth for early hominids was suggested on the basis of dental development as it was understood over 20 years ago (e.g. Bromage and Dean 1985; but see Mann et al. 1990 for the problem with their inference), the present study is the first to strongly indicate this for an australopithecine skeletal element. Nevertheless, further study of the relationship between dental development (within the crypt) and mandibular growth, especially in megadont taxa like *A*. *robustus*, may well show this difference to reflect tooth size and not bodily growth (see section 5.2 above). Moreover, given the stronger size similarity between SK 63 and stage 2 *A*. *robustus*, if additional *A*. *robustus* mandibles in eruption stage 3 (M_1 recently occluded), this would reduce the apparent difference between humans and *A*. *robustus* in growth in this period.

Adolescence

The final period of subadult growth examined in the present study, early adolescence, is represented by eruption stages 4-5 (prior to full occlusion of M_3). This period lasts from around 8-10 years in wild chimpanzees (Pusey 1990; Zihlman et al. 2007), but around 11-15 in recent, well-nourished human populations. Humans are unique among primates in that a growth spurt in body size is delayed until around age 10-12 and 12-14 years in girls and boys, respectively (Bogin 1999; Leigh 2001). Moreover, while body mass spurts are known to occur in other species (viz. males; Leigh 1996), none experiences the marked increase in linear skeletal dimensions seen in human limbs (Bogin 1999; Hamada and Udono 2002) and jaws (Bergersen 1972; Anton and Leigh 2003; Franchi et al. 2007; Coquerelle et al. 2011).

Whereas period 3-4 saw the greatest increase in overall size of *A. robustus* mandibles, there is little to no size increase in most mandibular measurements in period 4-5 (Table 4.7). In contrast, corpus height at several positions undergoes a non-trivially, and occasionally significantly, greater size change in humans than in *A. robustus*. This pattern of significantly positive ζ statistics in period 3-4 and mildly negative ζ statistics in period 4-5, is very similar to the difference in mandibular size change between humans and chimpanzees detected using geometric morphometrics (Bastir and Rosas, 2004). As this mandibular pattern is similar to published difference in these species' body mass growth curves (Walker et al., 2006) the results of the ζ test are consistent with expectations of an adolescent spurt in humans but not *A. robustus*. However, this may be due at least in part to the fact that only a single fossil (SKW 5) is represented by this stage, so it is possible that an expanded fossil sample would give a different impression.

Beyond subadult growth

The only other study of growth in *A. robustus* compared age-related size variation in adult maxillae and mandibles from Swartkrans, Drimolen and Kromdraai (Lockwood et al., 2007). In that study, adults were ranked by age based on tooth wear, and by size based largely on visual appraisal. Larger maxillae tended to be older but there were a few old and small specimens, whereas mandibles tended to increase in size across all age groups. Lockwood and colleagues interpreted the pattern of maxillary variation to reflect bimaturism, in which females achieve adult size prior to adulthood while whereas males continue growth into adulthood, resulting in increasing levels of sexual dimorphism. Bimaturism is known to occur for body mass among many living primates including non-human great apes (gorillas and bonobos: Leigh and Shea, 1996), and has concomitantly been found in the facial skeleton of orangutans and gorillas (Randall, 1943; Shea, 1985; Masterson and Leutenegger, 1992; McCollum and Ward, 1997; Daegling, 1996; Schaefer et al., 2004; Hens, 2005; Cobb and Higgins, 2007).

The present study cannot refute or confirm the claim of bimaturism in *A. robustus*, since adults were not studied and individuals' sexes are unknown in the fossil and human samples. The sex of the oldest subadult (and therefore most pertinent to this question) analyzed here, SKW 5, is fairly ambiguous. This specimen is among the smallest of the otherwise fully adult mandibles (as judged by M_3 occlusion) analyzed by Lockwood and colleagues (2007), which might support the argument of bimaturism if the specimen is male. To this end, its corpus is one of the broadest in the Swartkrans *A. robustus* sample. However, its height is among the shortest (cf. Grine and Daegling 1993), even compared with younger (stage 4) specimens (Appendix 1). Indeed, the specimen may well be

female: it is even (visually) smaller than DNH 7 from Drimolen, the very small fossil off which Lockwood and colleagues base their claims of sex in *A. robustus*. SKW 5's dental dimensions also fall in the lower end of the entire range of *A. robustus* from the Swartkrans, Kromdraai and Drimolen sites (Moggi-Cecchi et al. 2010). In short, the claim of bimaturism can only be tested against a larger fossil sample with more secure sex identification than are available at present.

The pattern of subadult growth in *A. robustus* implied by the ζ test is not inconsistent with the hypothesis of bimaturism, whereas extended male growth would seem less likely if the *A. robustus* pattern of size change were similar/identical to humans' since humans do no show as marked bimaturism as gorillas or orangutans. Metric data from adult *A. robustus* (not presented above) also do not refute the hypothesis. The lingual tuberosity is an important locus of mandibular growth, elongating the corpus anteriorly by deposition on its posterior surface (Enlow and Harris, 1964; Enlow and Hans 1996). Linear distances from points along the alveolar margin to the distal-lingual margin of the lingual tuberosity are around 5.0 mm shorter on SKW 5 than measurable adults with M_3 erupted (SK 23, SK 34 an SK 12). Within the adults, however, these increase only modestly with age as assessed by tooth wear (<3.0 mm).

There is equivocal and modest support for the hypothesis of bimaturism in the mandible of *A. robustus*. An alternative hypothesis to bimaturism is that *A. robustus* adult facial variation is the result of natural selection for larger adults to live longer than smaller ones. Distinguishing these hypotheses is not easy given fossil samples, especially because these hypotheses are not necessarily mutually exclusive. The evidence presented here and by Lockwood and others (2007) lend modest or equivocal support to the claim

of bimaturism, and the question should be explored further by comparing *A. robustus* with known bimaturing species such as mandrills, orangutans and gorillas, as well as with other species showing different degrees of adult growth.

Summary of Life History

Investigating the antiquity of the human life history strategy was a major impetus for the analysis of mandibular growth in *Australopithecus robustus*. One of the most unique aspects of this strategy is a long period of bodily growth with non-linear rates: in most populations, bodily growth slows during childhood, rises briefly around the time of puberty and then comes to a halt; this pattern is seen in no other animal (Eveleth and Tanner 1991; Bogin 1999; Walker et al. 2006). In contrast, both wild (Pusey et al., 2005) and captive (Walker et al., 2006a) chimpanzees and other African apes (Leigh and Shea, 1996) have relatively high growth rates throughout ontogeny.

Life history inferences are cautiously made on the basis of the size and shape of the mandible, chiefly as measured by the pairwise size metric (Chapter 3). Previous analyses of human mandibular growth (Bergersen 1972; Franchi et al. 2007; Coquerelle et al. 2011) suggest the size and shape of the mandible changes in a manner similar to the body, and the pairwise size metric used in the present study also patterns by eruption stage as expected based on human bodily growth. Although the *A. robustus* mandible becomes much larger than humans', the effect of this on the analysis is minimized because the ζ statistic, as the difference between two ratios, is a measure of relative and not absolute size change.

Important for life history, *A. robustus*' mandible experiences its most dramatic size change during period 3-4, whereas the greater size change occurs in period 4-5 for the human sample. This does not necessarily preclude the presence of a human-like 'middle-childhood' as assessed by dental development (Mann and Monge 2010), but it does imply an important difference between humans and *A. robustus* at this stage of maturation. If *A. robustus* were as dependent as modern humans of comparable age, such rapid growth would entail a larger amount of energy, obtained from parents and other caretakers (Gurven and Walker, 2006). Rather, juvenile production (food acquisition) in *A. robustus* may have been high as in other animals and unlike humans (Kaplan et al. 2000). Concomitant with a relatively early, dramatic increase in size, a human-like adolescent growth spurt probably was not present in *A. robustus*. Finally, results of the present study could be consistent with early weaning (Aiello et al., 1991) and extended male growth (Lockwood et al., 2007), but they certainly do not confirm these claims.

Summary of *A. robustus* mandibular growth

This chapter reviewed the implications of this study for paleoanthropology. The first contribution is a novel statistical procedure, the ζ test, to assess patterns of variation in skeletal samples otherwise less amenable to study. The test makes few assumptions, and performs as expected and intended: the test did not distinguish the human pattern from itself, yet it was able to detect a number of ways that the *A. robustus* pattern differed from humans. Nevertheless, some aspects of cross-sectional sampling cannot be overcome by the test, especially when individual sex and age cannot be known.

The differences in patterns of mandibular growth detected by the ζ test further contribute to our understanding of hominid evolutionary developmental biology and life history. For evo-devo, results show how *A. robustus*' unique adult mandibular anatomy is attained through growth. The *A. robustus* mandible rapidly becomes broad early in ontogeny, prior to the eruption of the first molar. This change could be due to the development of large tooth crowns within the mandibular corpus, and/or to prepare the infant for the mechanical stresses resulting from of a normal diet following nursing. Results were also consistent with predictions of more extreme facial rotation (due to "posterior facial hypertrophy"; McCollum 1997: 380), and corpus thickening based on observed patterns of periosteal bone deposition and resorption (Bromage 1989; McCollum 1999).

Results also provide the first clear skeletal evidence suggesting that the human pattern of growth, important to our life history strategy, was not present in the early Pleistocene hominid *A. robustus*. In contrast with the human pattern of growth, *A. robustus*' mandible grew relatively more rapidly during the juvenile period (stages 3-4) rather than delaying a growth spurt until adolescence (stages 4-5). The pattern of differences in size change between humans and *A. robustus* is similar to that found comparing mandibular growth in humans and living chimpanzees (Bastir and Rosas 2004), who are known to differ from humans in body mass growth the same way (Pusey et a. 2005; Walker et al. 2006b).

The present study therefore provides important evidence about both life history and mandibular (size and shape) growth in *A. robustus*. At the same time, the test raises a number of questions about the nature of these patterns that could very feasibly be

followed up. The evidence for the possibility of early weaning in *A*. *robustus* (Aiello et al. 1991) can be further sought in dental microwear studies of the Swartkrans juveniles, as well as in the bone histology and biomechanics of their jaws. And to repeat the adage of paleo-anthropology: additional fossils sample will be crucial to definitively show whether the patterns of growth detected by the present study are correct.

Chapter 6

A Look Back and Ahead

This dissertation provides new insights into the biology of *Australopithecus robustus*. In light of this study's success in elucidating the patterns of size and shape change in the *A. robustus* mandible, with implications for hominid development and life history, a number of questions remain or arise from this work. The purpose of this chapter is therefore to review the rationale and results of the present investigation into patterns of growth. I conclude by suggesting future research directions stemming from this work.

Chapter 1 introduced the species under consideration, *A. robustus*. Adult jaws of this species are large and robust, and while evidence is equivocal as to this species' exact diet, it is clear that its mandibular morphology was capable of withstanding the stress and strains of powerful and prolonged chewing. This analysis thus asked how and when this anatomy was created during subadult growth. This hardy anatomy also ensured relatively good preservation, creating the best hominid sample on which to conduct an ontogenetic study. This sample is therefore uniquely poised among early Pleistocene hominid skeletal elements, to test the hypothesis that patterns of size change cannot be distinguished from humans'.

Chapter 2 discussed the motivations for statistically comparing size change in the mandibles of humans and *A. robustus*. The *A. robustus* sample is better suited than any other early hominid sample to address the evo-devo question of whether species

differences come about. This is often framed in terms of whether differences are present early (i.e. prenatally), and whether patterns of shape change are basically the same between species. Although this question has been asked of the earlier hominid *Australopithecus africanus* (e.g. Ackermann and Krovitz, 2002; McNulty et al., 2006), these studies have relied on a single subadult fossil (the Taung skull, in eruption stage 3) and 1-3 adults of unknown age. Such a strategy, focusing on the most complete specimens, underestimates static variation within age groups and necessarily ignores ontogenetic variation between age groups.

Important for life history, this study was also better suited to ask whether the unique human patterns of size change (i.e. growth rates) were present in an early hominid. Our pattern of growth, characterized by a childhood/juvenile period slow growth followed by an adolescent spurt, is essential for both providing youth enough time to learn necessary social and linguistic skills, while also minimizing energy requirements. Most studies of early hominid life history have relied on extrapolating inferences from *dental* development to the rest of the skeleton, which is problematic conceptually (i.e. ape and human body growth rates differ markedly in spite of similar tooth crown formation times). Those studies that did employ skeletal elements (viz. faces and jaws) either relied on a sole fossil subadult, and/or on a dichotomous 'ape- or human-like' framework that hindered the interpretation of results.

Utilizing a the relatively large *A. robustus* ontogenetic series of mandibles and a new statistical test, this study was designed to avoid many of the difficulties and issues faced by previous studies of hominid ontogeny. Testing the null hypothesis that *A. robustus* could not be distinguished from humans in terms of size change between dental

eruptions, this analysis was devised to have more easily interpretable results for the evo-devo and life history of an early hominid species. For evo-devo, this hypothesis implied that anatomical differences between humans and *A. robustus* were established early in development, and that species followed the same pattern of size/shape change. For life history, the null hypothesis implied that the human growth pattern, and possibly other aspects of life history, would be shared with *A. robustus* as a homology.

Chapter 3 described the materials and methods used to test this hypothesis. Fossil samples have prevented rigorous ontogenetic analysis because of small sizes and copious missing data. The *A. robustus* mandibular series from the site of Swartkrans suffers least from these challenges of all early hominid ontogenetic series. The pattern of *A. robustus* ontogenetic variation was sought in a sample of human mandibles from the prehistoric American site of Libben (800-1100 CE; Lovejoy et al., 1977). This sample was chosen because it is among the largest skeletal 'populations,' and appears to have come from an egalitarian hunter-gatherer population (Meindl et al., 2008). Mandibles of humans and *A. robustus* were assigned to one of five dental eruption stages spanning from the completion of the deciduous dentition to just before the occlusion of M_3, as eruption stages are comparable between species and correlated with life history events. Data for this analysis were 29 linear measurements and a pairwise size metric (the geometric mean) computed from these variables, allowing all measurable fossils to be included in the study.

Even though the *A. robustus* mandibular series is relatively complete for a fossil sample, it cannot be analyzed by traditional analytical methods, such as geometric morphometrics and other multivariate statistical techniques. These methods require both

complete specimens, and make assumptions about sample variation that fossil assemblages do not meet. Chapter 3 therefore presented the ζ test, which compares two samples for the relative amount of change in size that occurs between dental eruption stages. The ζ test resamples *pairs* of individuals in each sample, and calculates a test statistic as the difference between the *A*. *robustus* and human growth ratios: $\zeta = [(R_{OLDER} / R_{YOUNGER}) - (H_{OLDER} / H_{YOUNGER})]$. This randomization procedure was run an excessive number of iterations, so that all possible comparisons were made and redundant observations could be removed (i.e. exact randomization). The null hypothesis predicts that resampled ζ statistics will equal zero (no difference between species) on average.

The ζ test was run for the pairwise size metric, based on whatever traits are shared between resampled pairs of specimens, and for every individual trait. The ζ test for the pairwise size metric is important logistically for comparing fragmentary fossils and theoretically for assessing life history, while the ζ test for individual traits is important for analyzing shape change vis-à-vis evo-devo. By describing growth in terms of pairwise comparisons, the ζ test is uniquely able to include all relevant fossils, not just the most complete ones. Rather than specifying any specific pattern or model of growth (e.g. 'ape- or human-like'), the test simply asks whether the fossil pattern of variation is possible or likely to be sampled in a larger human reference.

Chapter 4 demonstrated that the ζ test is appropriate for, and capable of, comparing samples, and presented the results of the test comparing patterns of mandibular size change in humans and *A*. *robustus*. The first section demonstrated that both the pairwise size metric and the ζ test perform as expected. The size metric, which was calculated based on only the measurements shared between pairs of specimens,

distinguished human and *A. robustus* sizes across ontogeny, according well with visual appraisal of each species' mandibles. Importantly, the pattern of change in the human 'sizes' appeared to roughly mirror our pattern of bodily growth; stage 4 human sizes tended to be a little smaller than those in stage 3, an artifact of the cross-sectional sample, but this effect was minimized with a fix to the calculation of the ζ statistic preventing 'negative growth.'

Next, the ζ test was validated by comparing the human sample with itself, to assess whether the test would detect a difference when none existed (e.g. Type I statistical error). The test failed to distinguish the human sample from itself, as resampled ζ □tatistics equaled 0 on average. However, there was a wide range of ζ values in the test validation, underscoring the effects of natural variation within a species on a cross-sectional sample. Preservation and the difference in eruption status between resampled individuals have a negligible influence on the value of the ζ statistic.

The second section of Chapter 4 presented the results of the ζ test comparing human and *A. robustus* mandibles for the pairwise size metric. There were two successive eruption periods in which the amount of size change was notably different between species, ζ being positive in each case (i.e. *A. robustus* grew more). First, *A. robustus* size was found to increase more during period 1-2, with only a 10% chance of sampling such size change in the human sample. Second and more notably, during period 3-4 there was only a 1% chance of randomly sampling a human pair so different in size as comparably aged *A. robustus*. In the other two successive periods (2-3 and 4-5), the average ζ was slightly negative (i.e. humans grew more) but not significantly different from 0. The two periods of greater size change in *A. robustus* resulted in *A. robustus* undergoing much

more size change, becoming much larger, than humans between the first and last eruption stages. In contrast to the validation analysis comparing humans with humans, resampled metadata (preservation, k, and difference in eruption stage, da) had significant rank correlations with the value of ζ in the interspecific comparison. However, these correlations were low and explained little variance in ζ. Rather, the correlations seem simply to reflect the fact that the *A. robustus* mandible becomes much larger than humans.

As shown in the third section of Chapter 4, results of the ζ test for individual traits were similar to results for the pairwise size metric. Most traits tend to undergo greater size change in *A. robustus*, though none of these was statistically significant. However, between successive eruption stages, *A. robustus*' anterior corpus and symphysis become significantly broader than humans', driving the positive ζ for the pairwise size metric in this period (growth changes to the anterior corpus were also described qualitatively at the end of the section). In period 3-4, it was shown that most aspects of the mandible undergo greater size change in *A. robustus*, a period of overall size change compared to the change more in shape during period 1-2.

The ζ test was therefore able to detect important growth differences between humans and *A.* robustus, and Chapter 5 reviewed the implications for paleoanthropology. First, this study contributes a novel statistical procedure, the ζ test, for analyzing fossil samples. The test made few assumptions about the nature of each cross-sectional sample, which do not appear to have strongly influenced the results. However, the single fossils in each dental stage 3 and 5 warrant caution in making two of the assumptions: first, that cross-sectional samples accurately depict characteristic longitudinal growth of individuals in each species, and second that sex variation in growth has a negligible influence on the

outcome of the ζ test. Each of the fossils in these two stages is of comparable overall size and anatomy to fossils in the eruption stages immediately previous. Future fossil discoveries are necessary to determine whether these two fossils are rather small for their age, and whether this would be due to sex.

The second section of Chapter 5 discussed the implications of the analysis for evo-devo. Some aspects of species' morphology, such as the topography of the mandibular symphysis, are distinct between species in the earliest dental stage. Although human and *A. robustus* mandibles are of comparable size when only the deciduous dentition is erupted, the *A. robustus* jaw rapidly becomes broad early in ontogeny, prior to the eruption of the first molar. Results of this study therefore indicate that neither of the idealized trajectories depicted in Figure 2.1 fully describes the growth differences between human and *A. robustus* mandibles. Rather, some species differences were probably established at younger ages than those analyzed here, while other differences came about or were amplified later in ontogeny. *A. robustus*' characteristic corpus robustness and relatively tall ramus (and 'rotated' jaw), for instance, arise at different times later in postnatal growth.

The most notable difference in shape growth between species relates to *A. robustus*' great corpus broadening between eruption stages 1-2, which could reflect several biological phenomena, not necessarily mutually exclusive. First, this could relate to the development of the species' megadont postcanine teeth. Species differences in corpus length growth almost certainly reflected different tooth sizes, but this is less clear for corpus breadth growth. Second, the anatomy attained by eruption stage 2 may reflect a biomechanical response to processing the species' diet. In turn, this corpus broadening

could be taken to indicate early weaning in this species. It was beyond the scope of this analysis to examine all these possibilities, but future work should investigate these further (see below).

The last section of Chapter 5 discussed the implications of this study's results for life history. Results also provide the first statistical, skeletal evidence that humans' characteristic pattern of growth was not present in an early Pleistocene hominid. In contrast to the greater size change in *A. robustus* in period 1-2 which was due entirely to corpus breadth growth, greater growth is spread across the entire *A. robustus* mandible during period 3-4, suggesting this is truly a major size and not shape change. In humans, period 3-4 is described as 'middle childhood' with slow growth. That *A. robustus* grew more during this time suggests that period 3-4 was a juvenile stage rather than a human-like middle childhood (or that its middle childhood was qualitatively very different from humans'), and that this species did not have a delayed adolescent growth spurt similar to humans. However, as noted above, this result rests on two relatively small fossils in each stages 3 and 5.

Future analyses

The present study thus provides some of the clearest evidence for differences in skeletal growth and development between humans and a closely related sister species, raising a number of questions to be addressed by future research. It was noted in Chapter 5 that the present findings may be consistent with the hypothesis of early weaning in *A. robustus*, as proposed by Aiello and colleagues (1991) on the basis of deciduous tooth wear. More direct evidence of such a subsistence shift could come from an ontogenetic

analysis of deciduous tooth microwear, as well as longitudinal analyses of the carbon isotopic composition of teeth forming during this period (cf. Sponheimer et al. 2006).

In addition, if *A. robustus*' great corpus breadth increase between eruption stages 1-2 reflected a biomechanical adaptation resulting from early weaning, this hypothesis could only really be tested by knowing the distribution of cortical bone about the mandibular corpus (Daegling 1991, 2007). The internal anatomy of fossil specimens can be obtained from CT scans (e.g. Conroy and Vannier 1991), and so a future study following from this dissertation would be to use CT data to examine the development of corpus strength in *A. robustus*, humans and other apes (cf. Holmes and Ruff, 2010).

Indeed the study of growth patterns more generally could benefit from the use of 'virtual' methods of data collection and analysis (Weber, 2001). In Chapters 4-5, it was demonstrated that at least some of the differences in human and *A. robustus* mandibular growth are probably due to their differently sized molar crowns and roots, but this relationship could not be directly examined in this analysis for lack of access to the internal anatomy of most specimens. CT data, however, would allow a direct examination of the covariation between corpus growth and tooth crown and root development (e.g. Boughner and Dean 2004; Coquerelle et al. 2010b, 2011).

Thus, an intriguing avenue for future research is the potential use of high-resolution micro-CT (i.e. synchrotron) to analyze bone histology (Mazurier et al., 2006). The external surfaces of fossils have been examined for the telltale signs of bone deposition and resorption via microscopy (Bromage 1989; McCollum, 2008; Martinez-Maza et al. 2010, 2011; Kraniotioi et al. 2011), but the endosteal surfaces of bones are also important sites of growth. If the bony shape changes of the *A. robustus* mandibular

corpus identified in this study are adaptive responses to loads experienced during, say, weaning, virtual bone histology could help identify the mechanism by which this happens (e.g. rapid periosteal deposition and/or reduced endosteal resorption).

Although synchrotron micro-CT has been able to examine the sub-micron structure of recent bones (Cooper et al., 2011; Pacureanu et al. 2012), the mineralization of individual fossils will always influence the usefulness of radiographic imaging (Mann 1975; Smith and Tafforeau 2008; Smith et al., 2012). Many of the important histological signatures of bone modeling and remodeling identified in ground sections involve subtle differences in mineralization between older versus newer bone (e.g. Enlow, 1962). The fossilization process alters the mineral structure of bones and teeth, which has already raised difficulties in the analysis of dental microstructure. It has yet to be shown that the histological signatures of bony growth can be identified in any fossil using micro-CT.

While much can be learned with new techniques for data collection, this study also shows that novel analytical methods also promise to help extract novel information from fossil samples. The ζ test is a new addition to an already large body of randomization/resampling procedures designed to make statistical inferences about fragmentary samples (e.g. Lockwood, 1999; Braga and Francis, 2003; Lee and Wolpoff, 2003; Van Arsdale, 2006; Gordon et al., 2008; Lague et al., 2008; Royer et al., 2009; DeSilva, 2011). The analysis relied on making pairwise comparisons between individuals, and was shown to be a powerful means of analyzing a fragmentary sample such as the *A. robustus* ontogenetic series.

However, it could be argued that a more accurate randomization procedure would have calculated test statistics based on resampled humans that *exactly* matched the *entire*

fossil sample size and composition. In other words, future analyses could rather resample humans to exactly match the fossil sample: 13 specimens with the exact same number of individuals in each eruption stage as the fossils (Table 3.2). Such an analysis may be difficult to operationalize, as a single test statistic cannot adequately describe the myriad possible comparisons between different eruption stages. However, multiple test statistics, such as one for each comparison between successive eruption stages, could be extracted with each resampling iteration (e.g. as was done with for resampled metadata).

Along these lines, Martín-González and colleagues (2012) recently used resampling to estimate growth curve parameters describing postnatal growth from birth to around 5 years in modern humans and Neandertals. This team used isolated femora and tibiae of Neandertal subadults from throughout Eurasia to estimate each individual's height, and these estimates were plotted against individuals' chronological ages as estimated from human skeletal and dental maturation standards. Because of uncertainty in both the height and age estimates, they resampled all different estimated ages and heights for each individual fossil, and calculated the parameters of the growth curve based on these data. They then compared these with empirical height growth curves in recent human populations. Thus, rather than calculating a single test statistic such as ζ to describe their resampled group, Martín-González et al. estimated several statistics (growth curve parameters).

An important difference between the present study and the clever Neandertal-human growth comparison (Martín-González et al., 2012) is that these authors used resampling to estimate the Neandertal growth curve, but not to statistically compare the resulting model parameters with human models (visually, the resampled curves were

distinct). Poor and disparate preservation of the *A. robustus* mandibular sample, however, precluded such an across-ontogeny resampling strategy. It was argued to be unnecessary and inappropriate to calculate growth curves for the present study, but it could be very informative to combine the techniques of the present study and those of Martín-González et al. (2012). That is, to develop test statistics that simultaneously describe the entire growth period (e.g. Martín-González et al., 2012) and statistically compare two samples (e.g. this study).

The ζ test as executed here relied on linear measurements to describe size and shape, but the test could be extended to other metrics and data. The present study did not make use of any 'pairwise *shape* metric' as it had for size, because such a metric would not be easily interpretable in this ontogenetic context. Questions about taxonomic or sex-related variation in fossil samples, however, could be easily treated with the ζ test including a pairwise shape metric specialized for missing data. Such metrics exist for linear measurement data, for instance log $s.e._m$ (Thackeray et al., 1997), STET (Wolpoff and Lee, 2001; Lee and Wolpoff, 2005; Lee 2011), and correlation coefficients (Lague et al., 2008). It could also be useful to develop such a metric for 3D landmark (i.e. geometric morphometric) shape data as well.

Conclusion

This study adopted a null hypothesis testing approach to the study of mandibular growth in *A. robustus*. In addition to demonstrating important differences in mandibular growth between humans and *A. robustus*, this dissertation further demonstrated how randomization procedures can be developed to test new and interesting hypotheses about

old fossils. The ζ test presented here was used to compare patterns of ontogenetic variation, but it can easily be extended to all kinds of other questions and datasets. These methods will only be as effective as samples allow, and some hypotheses remain testable only by the discovery of new fossils. But as demonstrated and discussed in this dissertation, even long-known fossils are waiting for their secrets to be revealed by new methods and technologies.

Appendix I: Raw data plotted against eruption stage

Mandibular corpus breadths

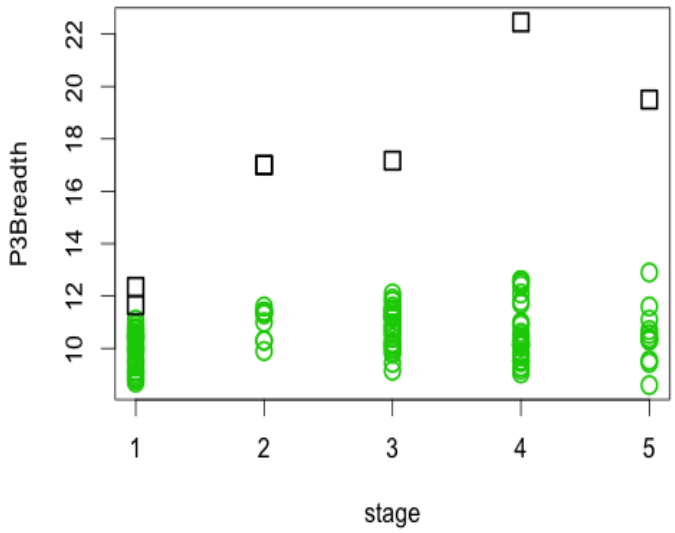

Figure A1.1: Corpus breadth at the position of the P_3 (X223). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

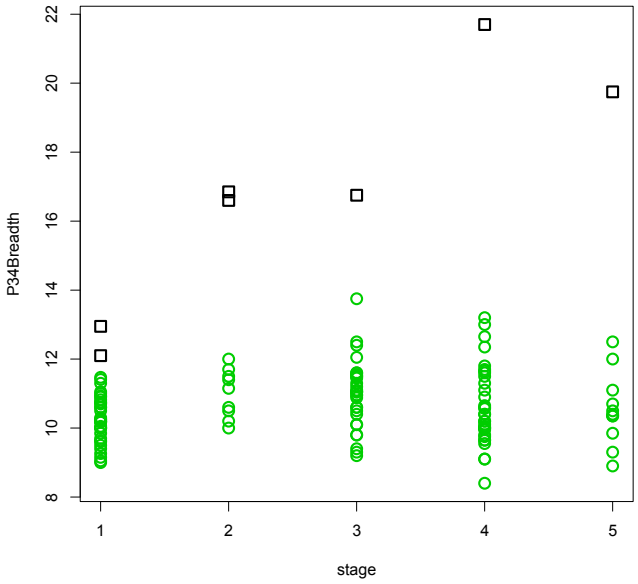

Figure A1.2: Corpus breadth at the position of the $P_{3\text{-}4}$ (X225). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

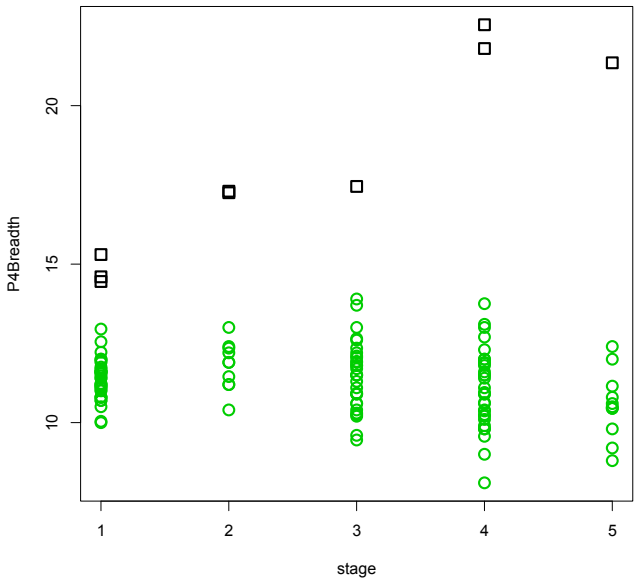

Figure A1.3: Corpus breadth at the position of the P_4 (X227). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

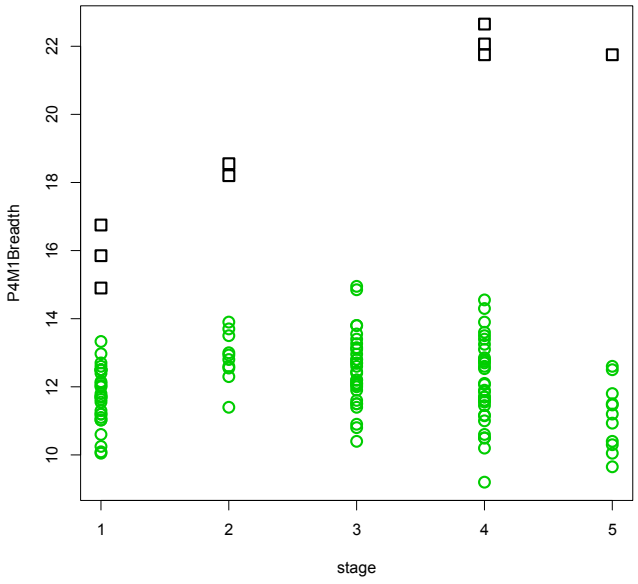

Figure A1.4: Corpus breadth at the position of the P_4-M_1 (X229). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

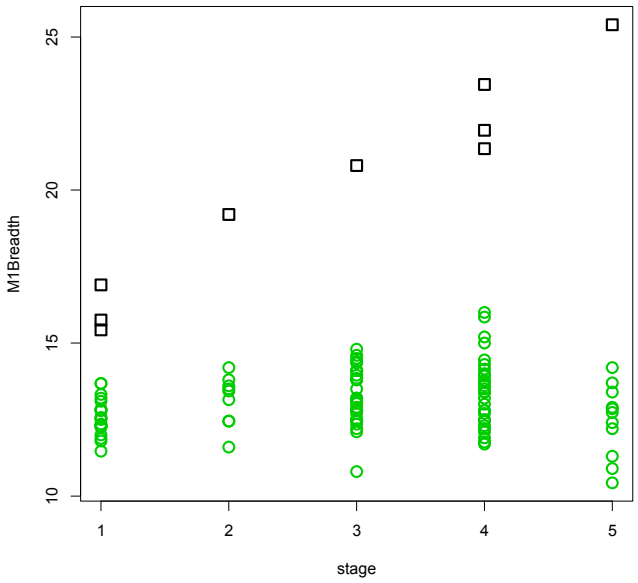

Figure A1.5: Corpus breadth at the position of the M_1 (X231). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

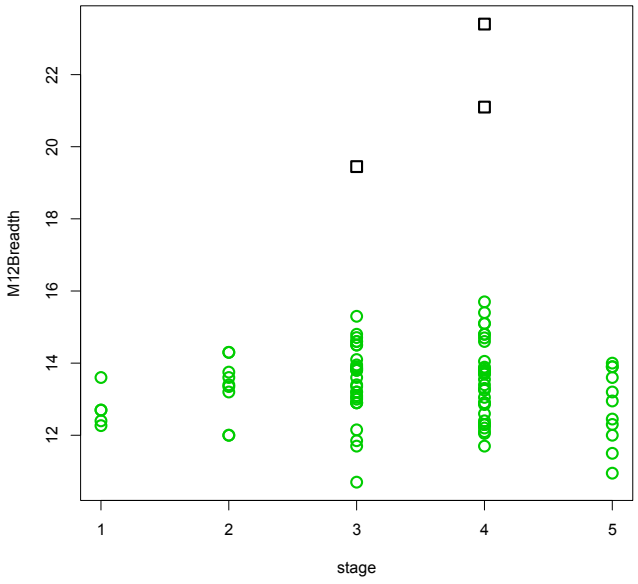

Figure A1.6: Corpus breadth at the position of the $M_{1\text{-}2}$ (X233). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

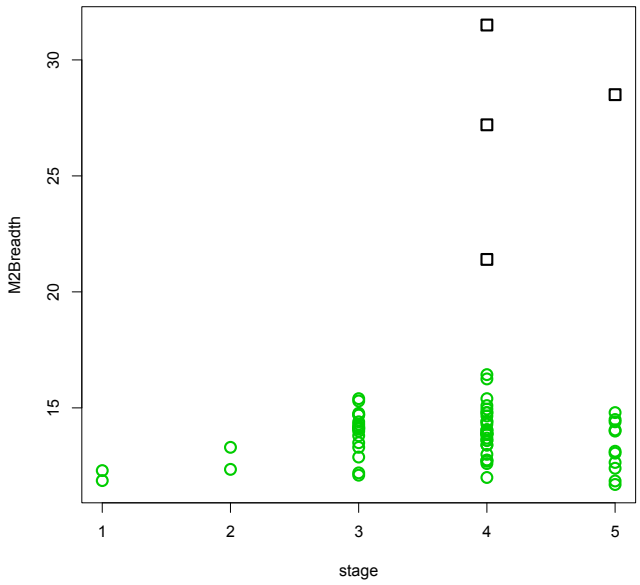

Figure A1.7: Corpus breadth at the position of the M_2 (X235). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

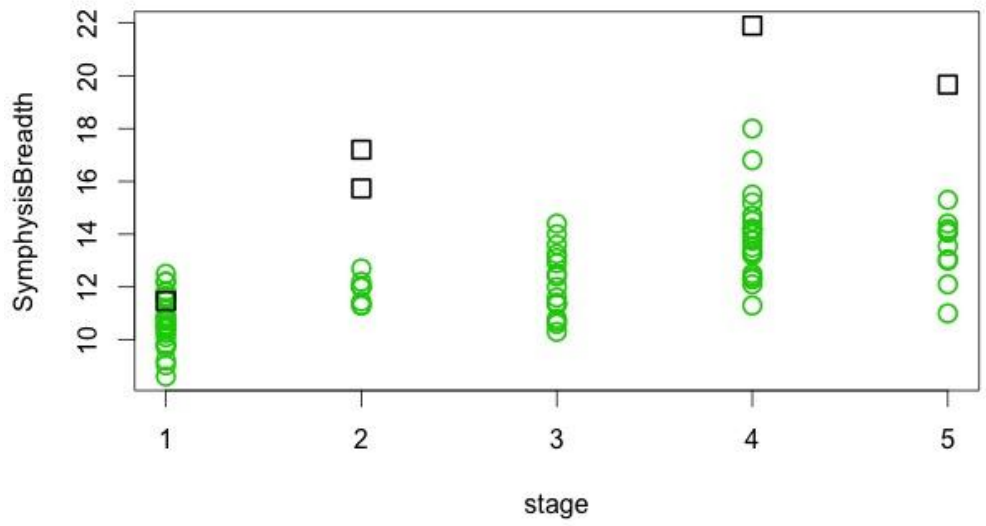

Figure A1.8: Corpus breadth at the mandibular symphysis (X709). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

Mandibular corpus heights

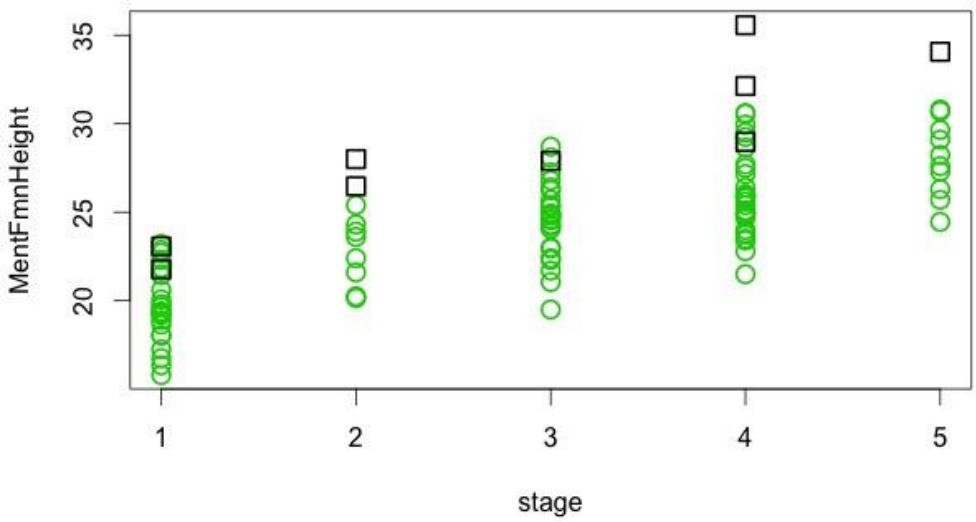

Figure A1.9: Corpus height at the position of the mental foramen (X301). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

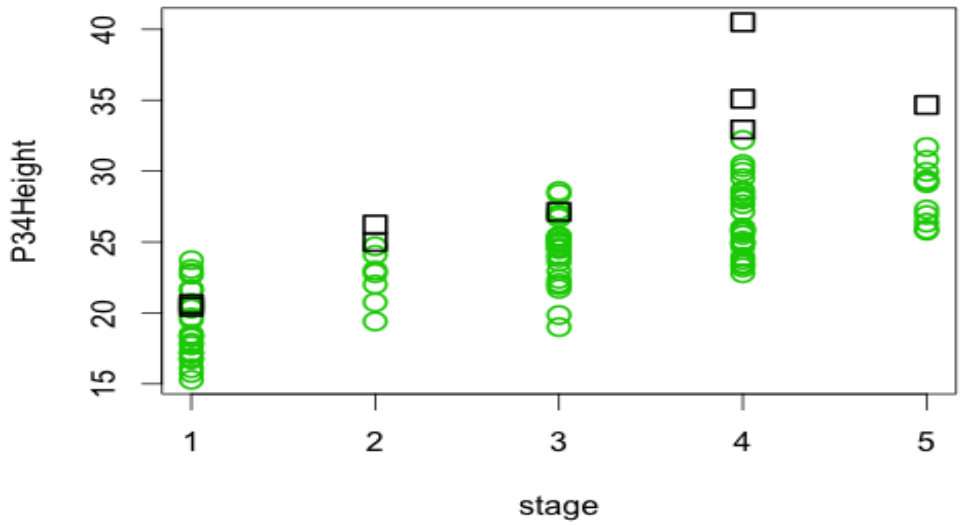

Figure A1.10: Corpus height at the position between P_{3-4} (X313). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

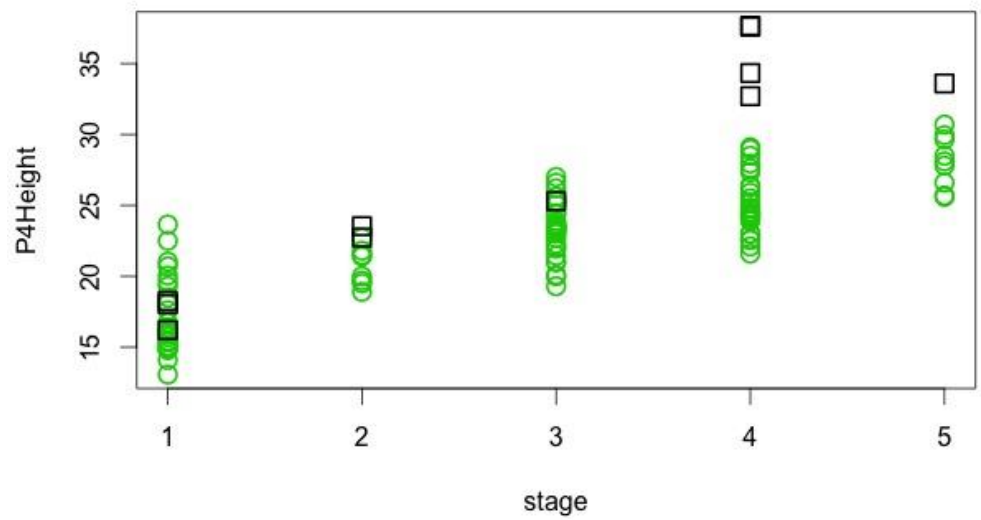

Figure A1.11: Corpus height at the position of P_4 (X315). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

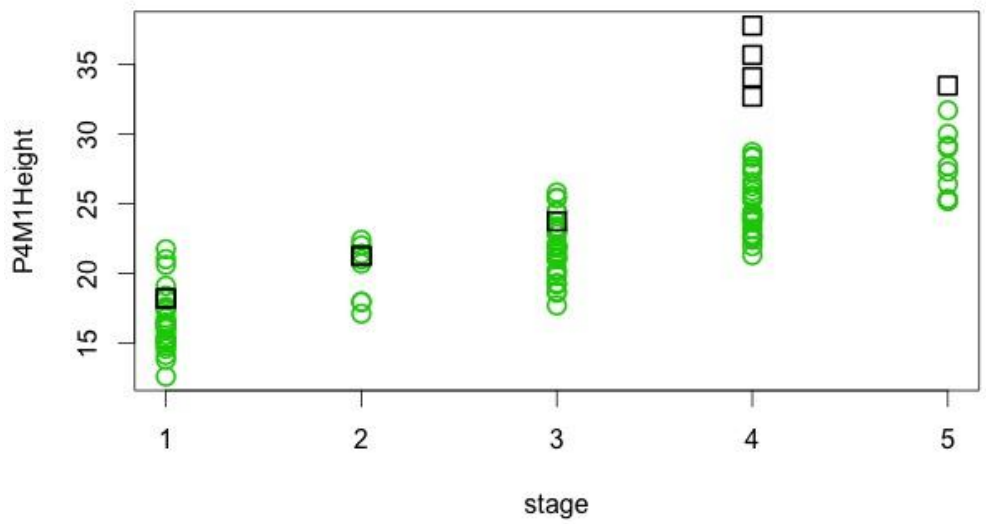

Figure A1.12: Corpus height at the position between P_4-M_1 (X313). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

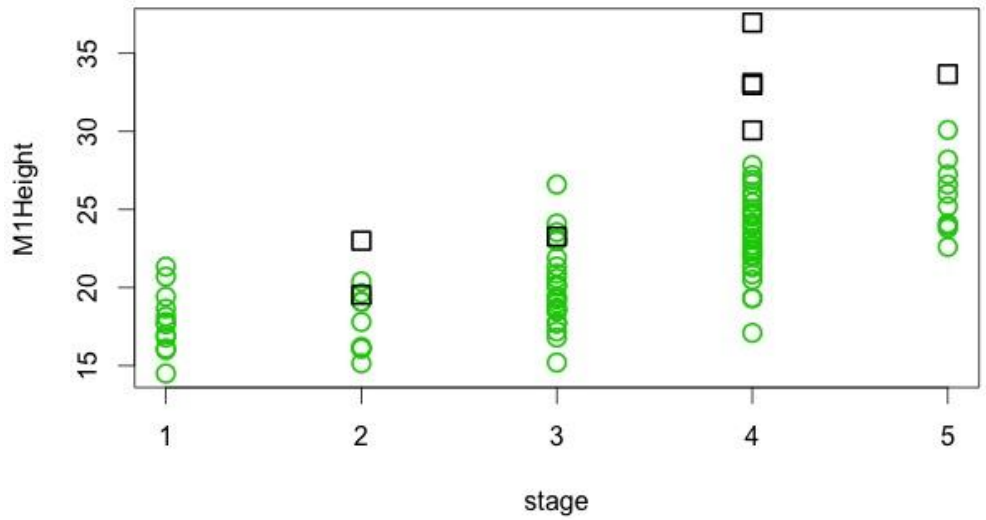

Figure A1.13: Corpus height at the position at M_1 (X319). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

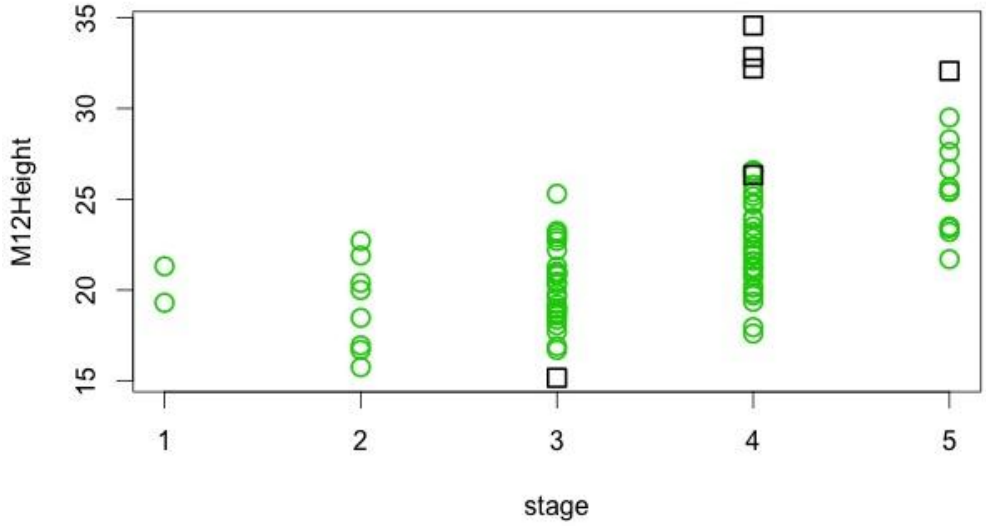

Figure A1.14: Corpus height at the position between $M_{1\text{-}2}$ (X321). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

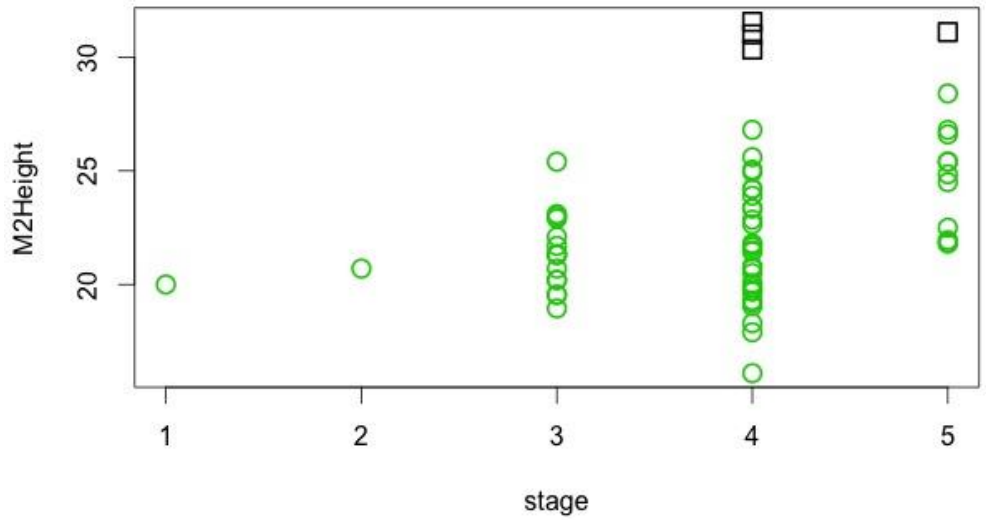

Figure A1.15: Corpus height at the position between M_2 (X323). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

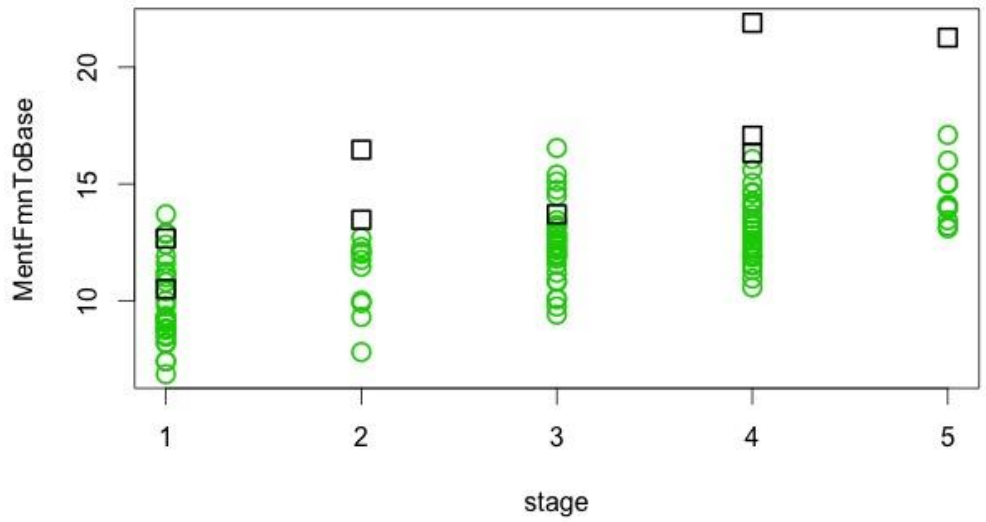

Figure A1.16: Height from the mental foramen to the corpus base (X331). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

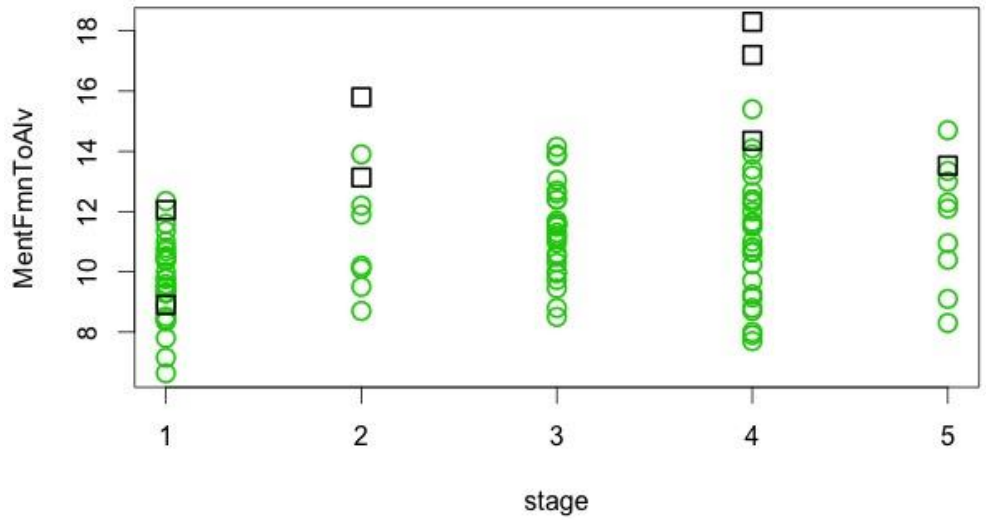

Figure A1.17: Height from the mental foramen to the alveolar margin (X333). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

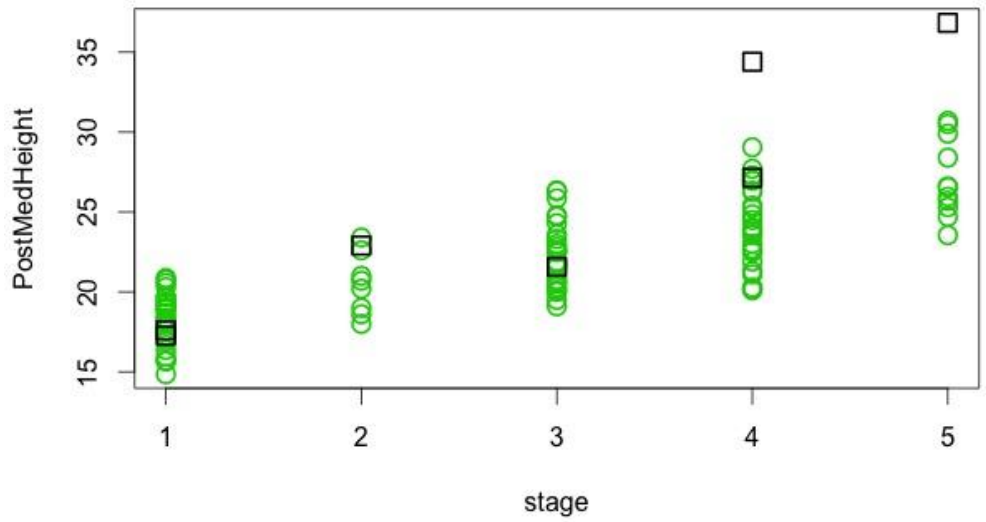

Figure A1.18: Height of the posteromedial corpus, from the base at the ramus-corpus junction to the alveolar margin (X355). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

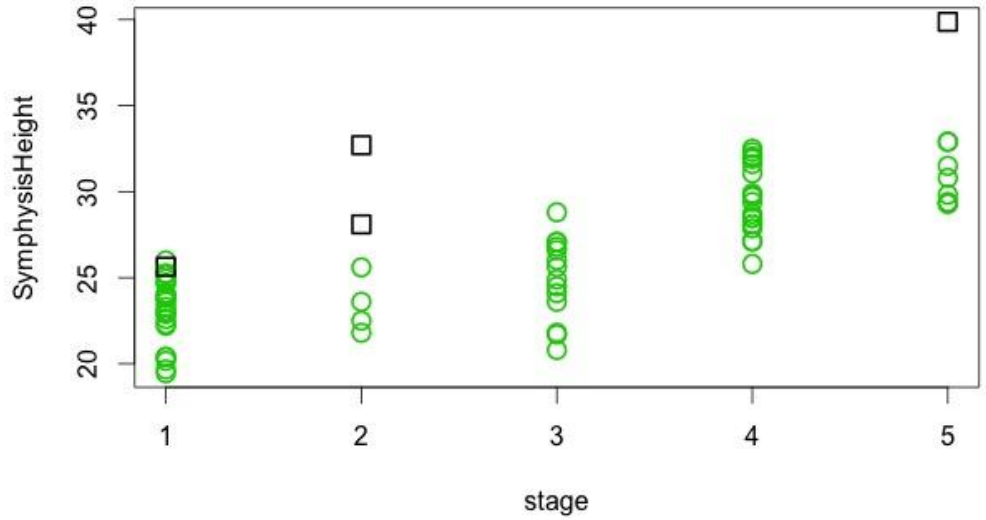

Figure A1.19: Corpus height at the mandibular symphysis (X711). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

Mandibular corpus lengths

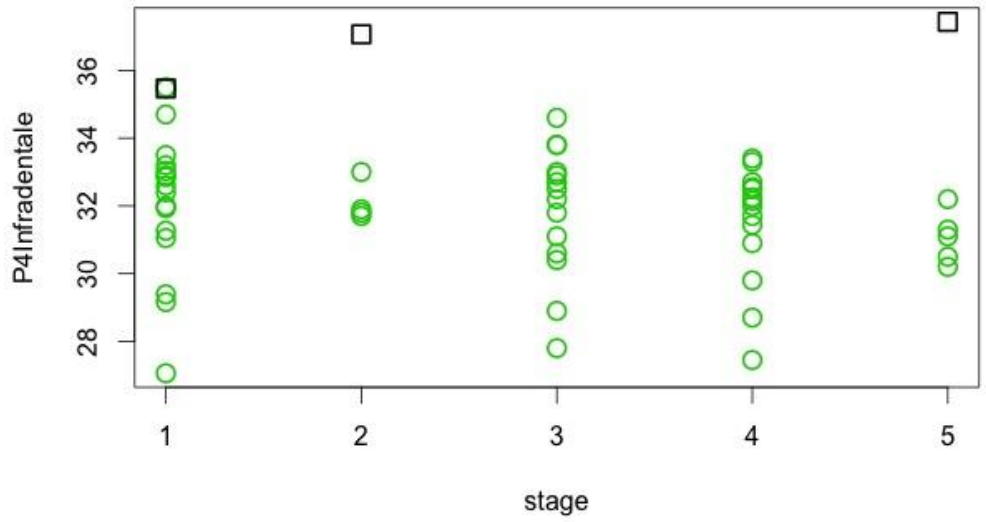

Figure A1.20: Corpus length from infradentale to the alveolar septum between P_4-M_1 (X401). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters. Note that two *A. robustus* share the largest measurement in stage 1.

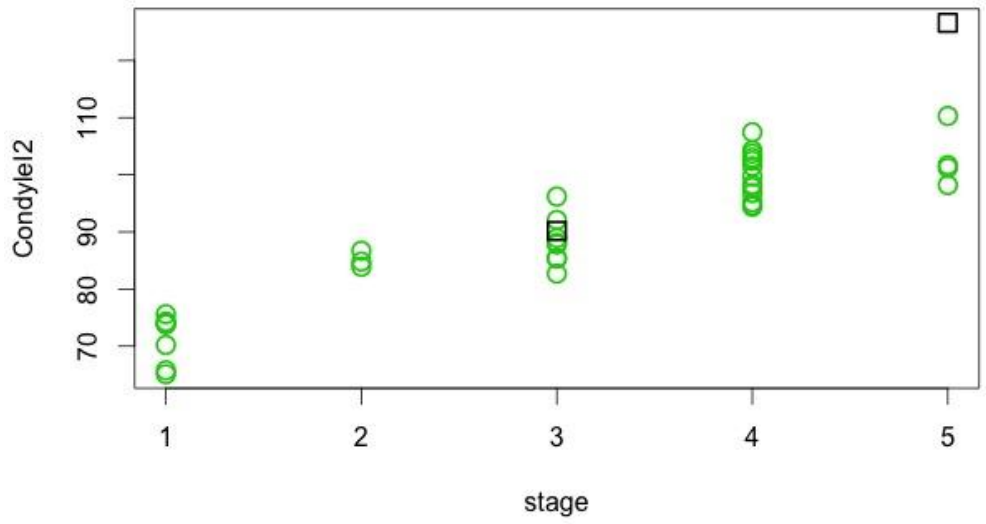

Figure A1.21: Mandibular length from the posterior condyle to the septum between I_2-C_1 (X403). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

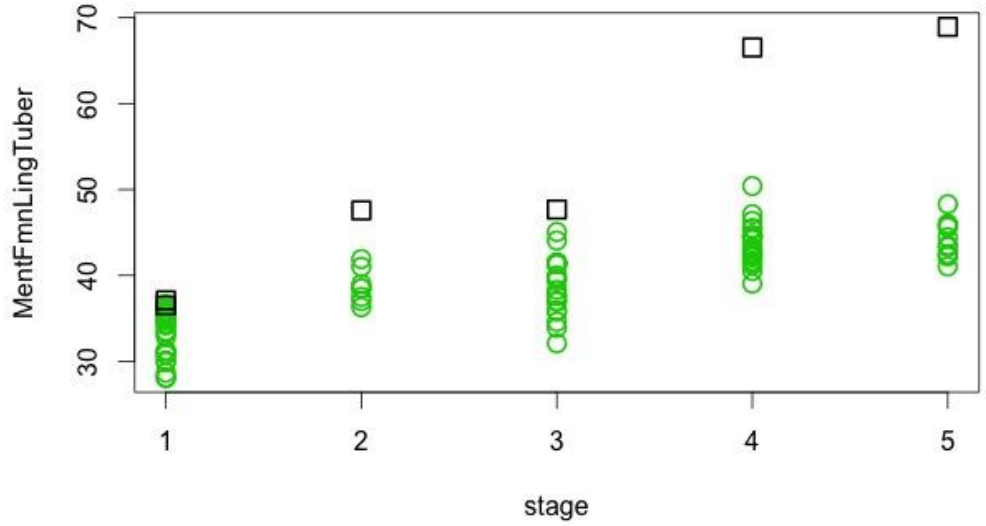

Figure A1.22: Corpus length from the posteromedial margin of the lingual tuberosity to the mental foramen (X404). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

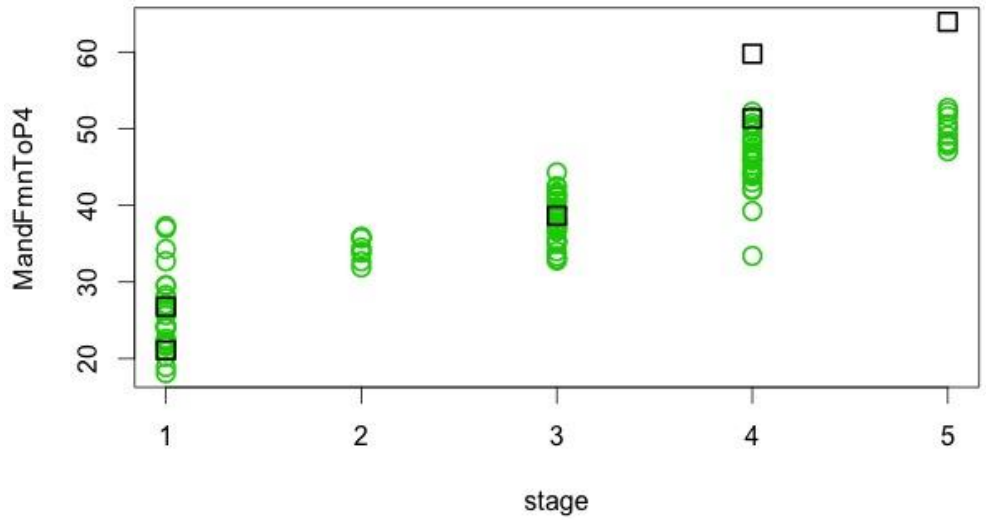

Figure A1.23: Corpus length from the anterior margin of the mandibular foramen to the lingual alveolar septum between the P_4-M_1 (X415). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

Overall mandibular breadths

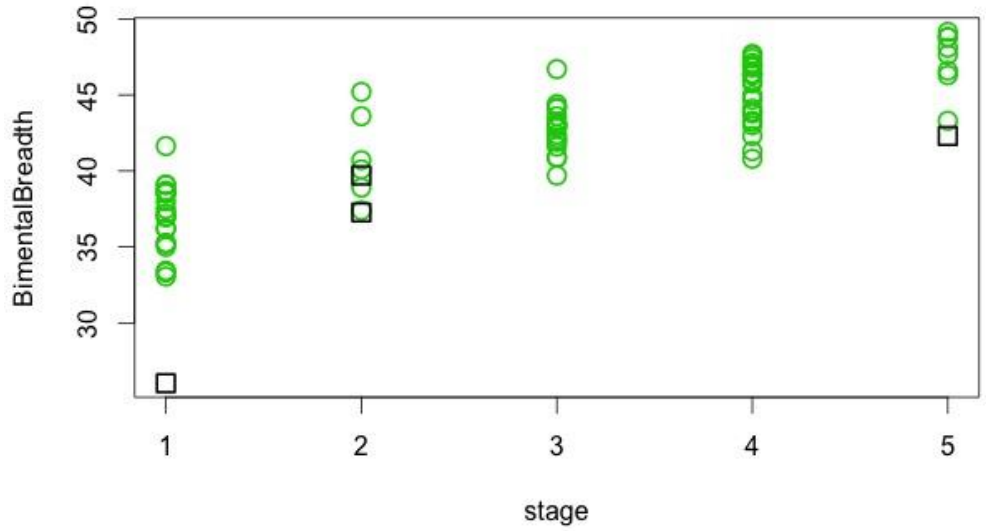

Figure A1.24: Mandibular breadth between the left and right mental foramina (X501). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

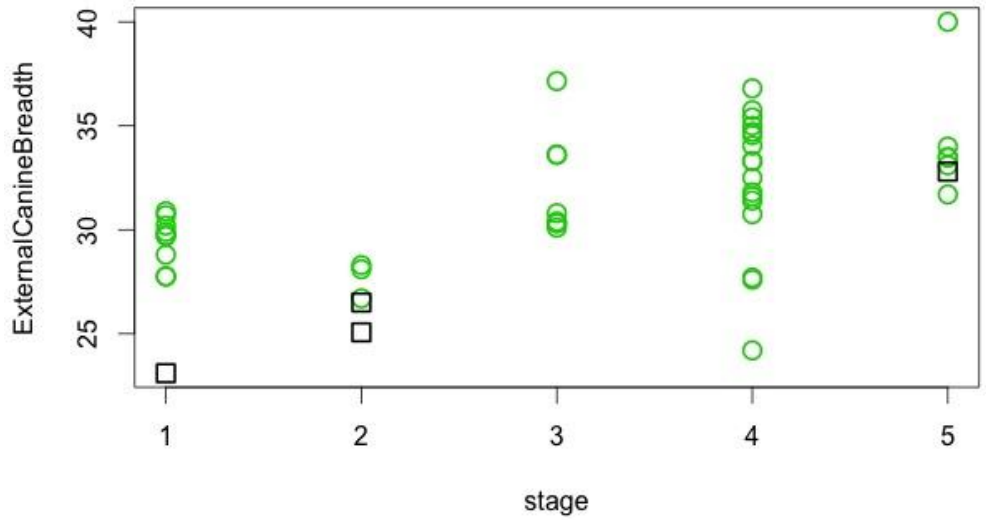

Figure A1.25: Mandibular breadth between the left and right C_1-P_3 septa (labial; X502). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

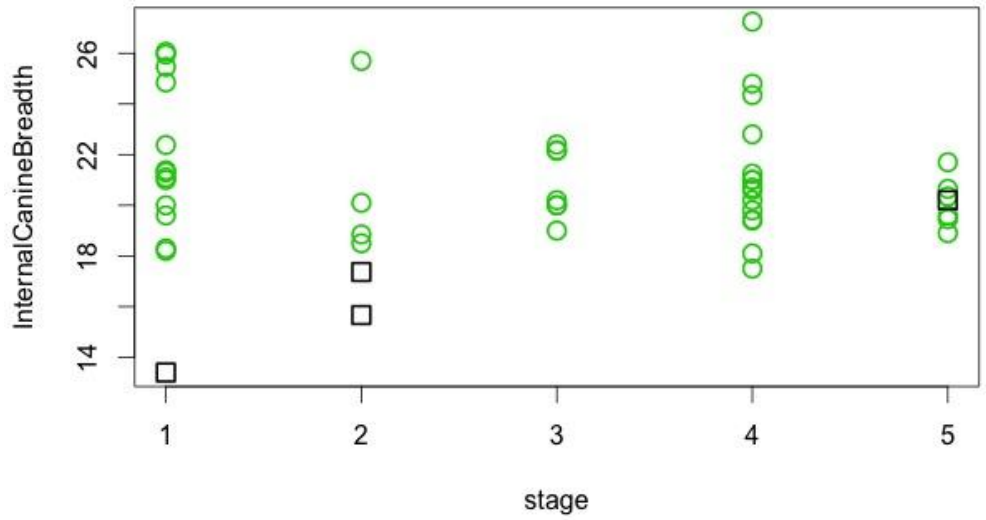

Figure A1.26: Mandibular breadth between the left and right C_1-P_3 septa (lingual; X502). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

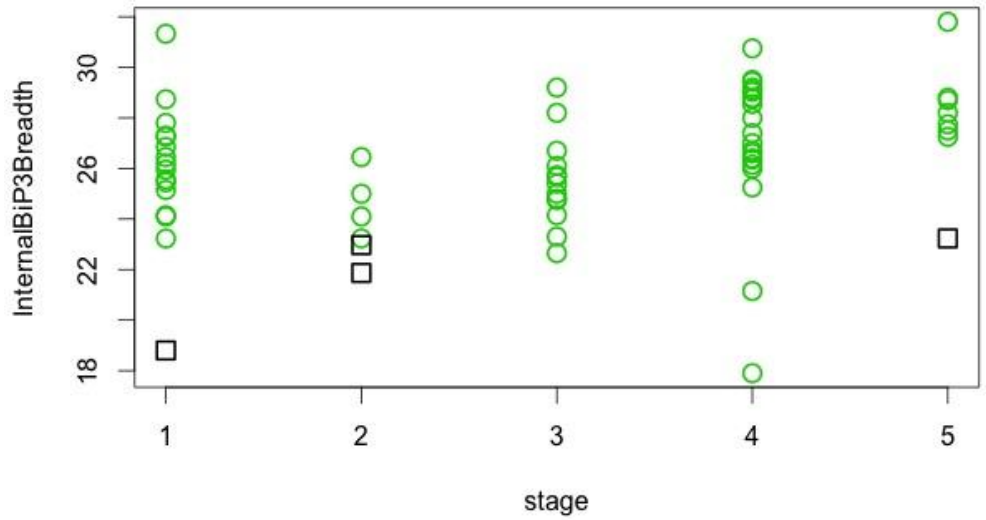

Figure A1.27: Mandibular breadth between the left and right P_3-P_4 septa (labial; X502). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

Ramus length and height

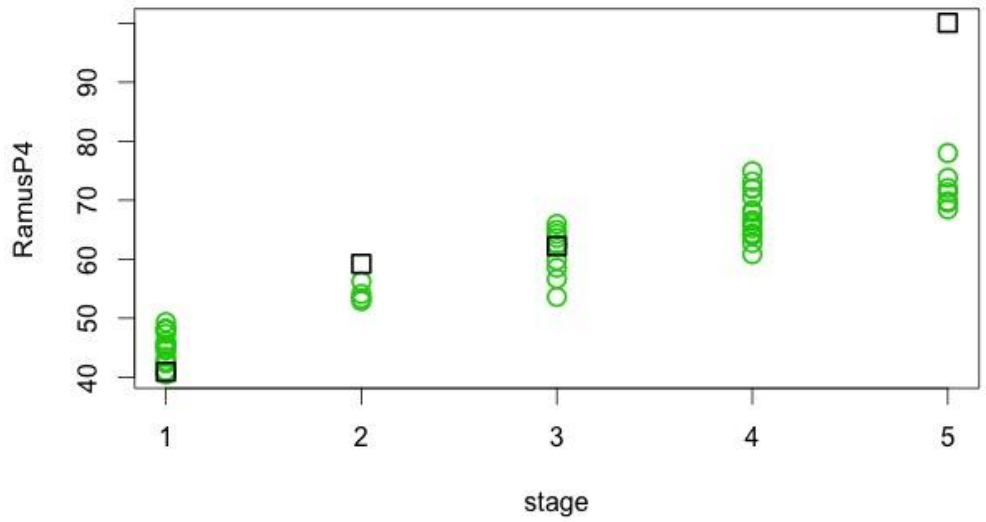

Figure A1.28: Length from the posterior ramus margin to the (X603). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

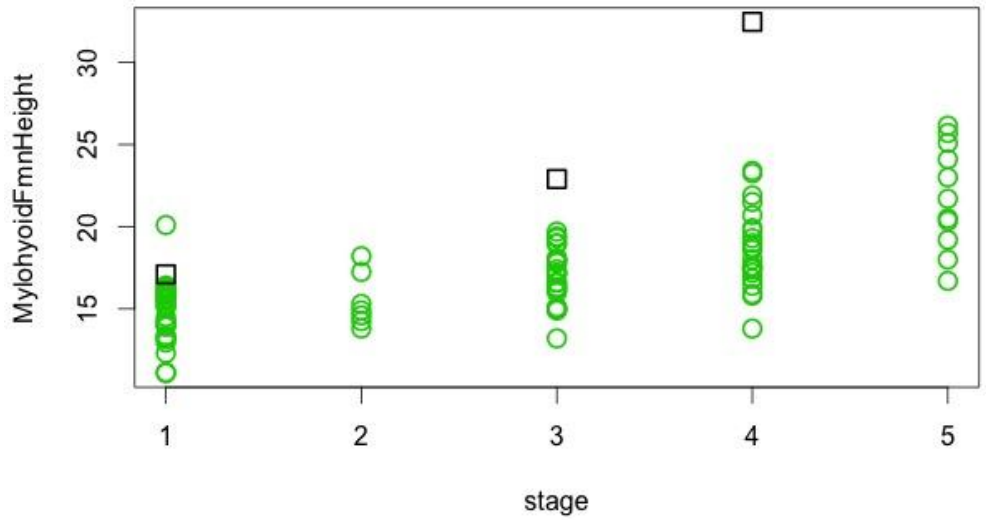

Figure A1.29: Height from the mandibular foramen to the ramus base (X607). Green circles are modern humans and black squares are *A. robustus*. Measurements are in millimeters.

Appendix II: Mandibular corpus robusticity

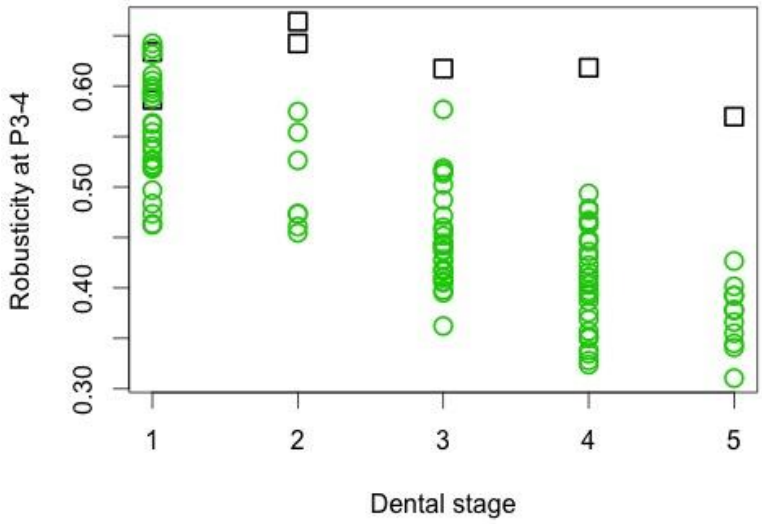

Figure A2.1: Corpus robusticity (breadth / height) at the position between the P_{3-4}. Green circles are modern humans and black squares are *A. robustus*.

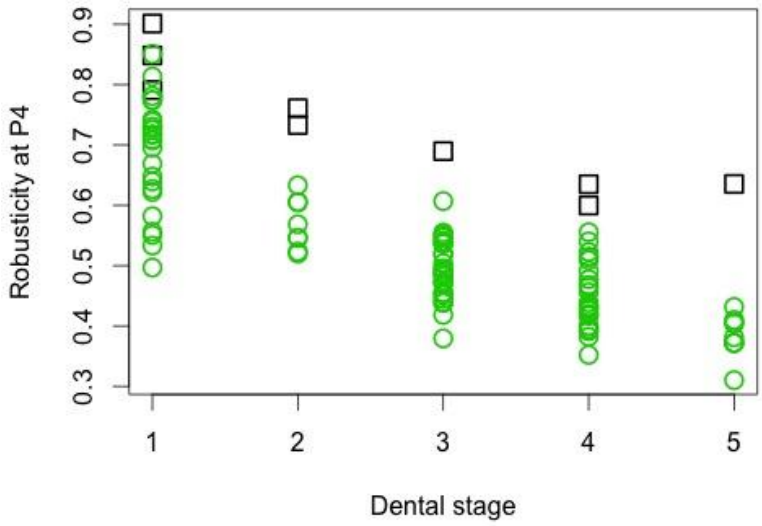

Figure A2.2: Corpus robusticity (breadth / height) at the position of P_4. Green circles are modern humans and black squares are *A. robustus*.

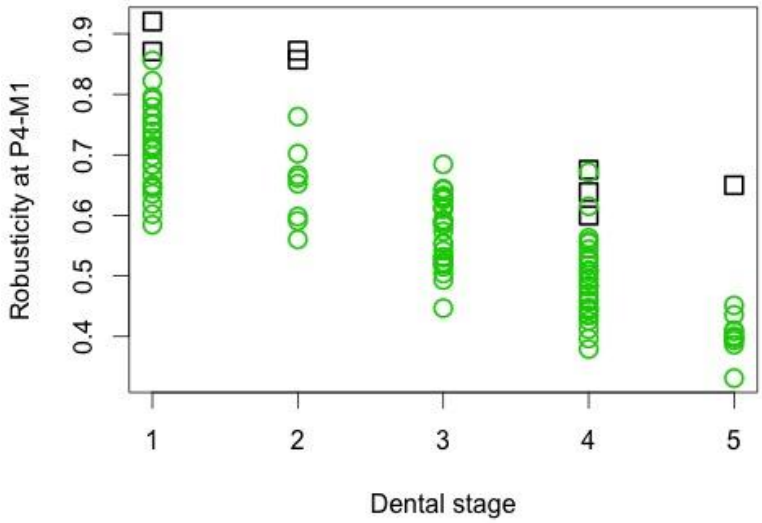

Figure A2.3: Corpus robusticity (breadth / height) at the position between the P_4-M_1. Green circles are modern humans and black squares are *A. robustus*.

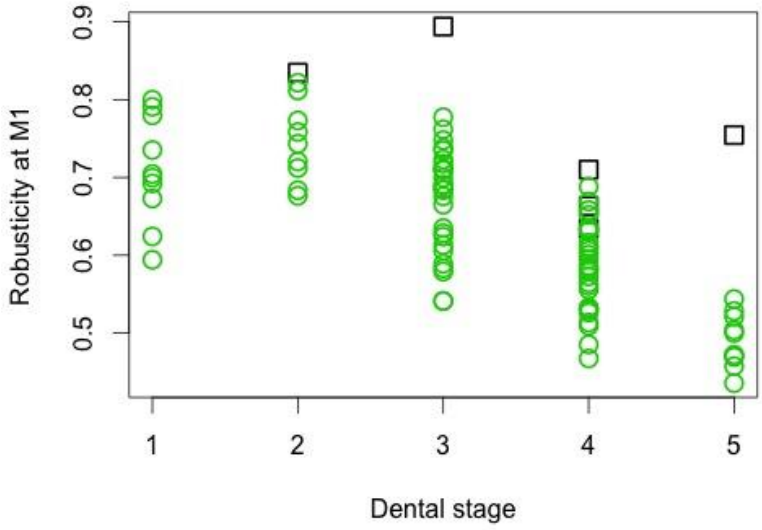

Figure A2.4: Corpus robusticity (breadth / height) at the position of M_1. Green circles are modern humans and black squares are *A. robustus*.

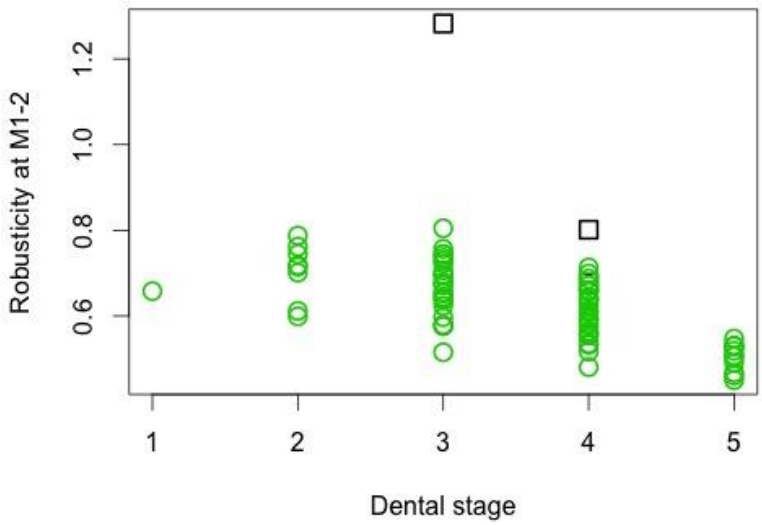

Figure A2.5: Corpus robusticity (breadth / height) at the position between the $M_{1\text{-}2}$. Green circles are modern humans and black squares are *A. robustus*.

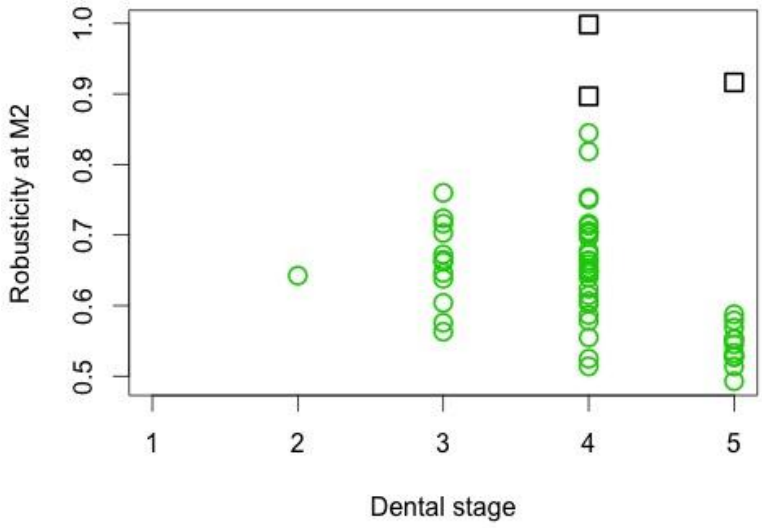

Figure A2.6: Corpus robusticity (breadth / height) at the position of M_2. Green circles are modern humans and black squares are *A. robustus*.

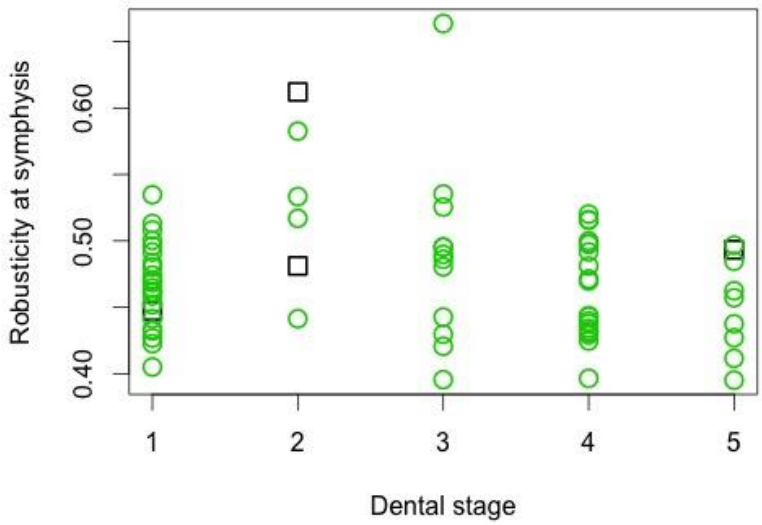

Figure A2.6: Corpus robusticity (breadth / height) at the mandibular symphysis. Green circles are modern humans and black squares are *A. robustus*.

Appendix III: R Code for Analyses

Instructions for using this code are given in this font (Times New Roman), whereas the actual code is in Monaco font.

```
setwd("")  # Enter the name of the directory of data file
 data = data.frame(read.csv(""))
```

To begin, read in the .csv format data file as a data.frame by typing the file name into the quotation marks above. Individuals should be rows, the first column should be their ages, and the remaining columns the measurements/variables. Divide this data.frame into two, one for the fossils (rob) and one for the referent (lib). The next line of code transposes these so that in each data.frame, the individuals are columns and their measurements make up the rows. These will be resampled in the following codes.

```
p.lib = data.frame(t(lib)); p.rob=data.frame(t(rob))
```

Function to calculate the geometric mean (pairwise size metric)

```
GM = function(r1)  {
  prod(r1)^(1/nrow(r1))
 }
```

Declare the variables to be resampled

```
D = NA          # test statistic of size difference
k = NA          # number of traits
a1 = NA; a2 = NA     # ages in the comparison. Later can be used to examine
 differences between specific age groups
f1 = NA; f2 = NA; h1 = NA; h2 = NA  # store each of the individuals each
 iteration
```

Validation of ζ test for the pairwise size metric (Chapter 4.1)

```
for (i in 1:75000)  {
 r1 = sample(p.rob,1); r2 = sample(p.rob[,p.rob[1,]!=r1[1,1]],1) # 2 robusti
    l1 = sample(p.lib[,p.lib[1,]==r1[1,1]],2,replace=T)   # getting 2, w
 replacement
   l2 = sample(p.lib[,p.lib[1,]==r2[1,1]],2,replace=T)
 sub = data.frame(na.omit(cbind(r1,r2,l1,l2)))
    k[i]= nrow(sub)-1;   # number of traits
 # ordered subset by age
   if (sub[1,1]<sub[1,2])  {ry=(sub[3]); ro=(sub[5])} else {ry=(sub[5]);
 ro=(sub[3])}
   if (sub[1,1]<sub[1,2])  {hy =(sub[4]); ho=(sub[6])} else {hy=(sub[6]);
 ho=(sub[4])}
     s2 = data.frame(cbind(ry,ro,hy,ho))
       a1[i] = s2[1,1]; a2[i] = s2[1,2] ; # extract ages now while you still
 can!
      s2=s2[2:nrow(s2),]
 # calculate ratios, and correct for 'negative growth if necessary; block out if
 making no assumptions
    if (k[i]==0)  {gml = NA; gmr = NA}  else {
```

```
      gmr=GM(s2[2])/GM(s2[1]); if (gmr<1) {gmr = 1}   # {=1} or {=NA} makes
 assumption about growth &/or sampling
      gml=GM(s2[4])/GM(s2[3]); if (gml<1) {gml = 1}
    }
 # calculate test statistic
    if (k[i] == 0) {D[i]= NA}  else {
     D[i] = gmr-gml
   }
  # extract information about subsample
    if (k[i]==0) {f1[i] = NA; f2[i] = NA; h1[i] = NA; h2[i]=NA} else {
      f1[i]=names(ry); f2[i]=names(ro); h1[i]=names(hy); h2[i]=names(ho)
      }
} #   #   #   #   #   #   #       FIN!
```

ζ test for the pairwise size metric (Chapter 4.2)

```
for (i in 1:50000)  {
# randomly grab 2 differently aged robustus and 2 humans
 r1 = sample(p.rob,1); r2 = sample(p.rob[,p.rob[1,]!=r1[1,1]],1)
    l1 = sample(p.lib[,p.lib[1,]==r1[1,1]],1)
   l2 = sample(p.lib[,p.lib[1,]==r2[1,1]],1)
 sub = data.frame(na.omit(cbind(r1,r2,l1,l2)))
    k[i] = nrow(sub)-1;   # number of traits
 # ordered subset by age
   if (sub[1,1]<sub[1,2])  {ry=(sub[1]); ro=(sub[2])} else {ry=(sub[2]);
 ro=(sub[1])}
   if (sub[1,1]<sub[1,2])  {hy =(sub[3]); ho=(sub[4])} else {hy=(sub[4]);
 ho=(sub[3])}
     s2 = data.frame(cbind(ry,ro,hy,ho))
       a1[i] = s2[1,1]; a2[i] = s2[1,2] ; # extract ages now while you still
 can!
      s2=s2[2:nrow(s2),]
 # calculate ratios, and correct for 'negative growth if necessary; block out if
 making no assumptions
if (k[i]==0)  {gml = NA; gmr = NA}  else {
      gmr=GM(s2[2])/GM(s2[1]); if (gmr<1) {gmr = 1}
      gml=GM(s2[4])/GM(s2[3]); if (gml<1) {gml = 1}
    }
 # calculate test statistic
    if (k[i] == 0) {D[i]= NA}  else {
     D[i] = gmr-gml
   }
  # extract information about subsample
    if (k[i]==0) {f1[i] = NA; f2[i] = NA; h1[i] = NA; h2[i]=NA} else {
      f1[i]=names(ry); f2[i]=names(ro); h1[i]=names(hy); h2[i]=names(ho)
      }
} #   #   #   #   #   #   #       FIN!
```

ζ test for individual traits (Chapter 4.3)

```
for (i in 1:300000)  {
# randomly grab 2 differently aged robustus & 2 humans
r1 = sample(p.rob,1); r2 = sample(p.rob[,p.rob[1,]!=r1[1,1]],1)
    l1 = sample(p.lib[,p.lib[1,]==r1[1,1]],1)
   l2 = sample(p.lib[,p.lib[1,]==r2[1,1]],1)
 sub = data.frame(na.omit(cbind(r1,r2,l1,l2)))
    k[i] = nrow(sub)-1;   # number of traits
 # ordered subset by age
   if (sub[1,1]<sub[1,2])  {ry=(sub[1]); ro=(sub[2])} else {ry=(sub[2]);
 ro=(sub[1])}
   if (sub[1,1]<sub[1,2])  {hy =(sub[3]); ho=(sub[4])} else {hy=(sub[4]);
 ho=(sub[3])}
     s2 = data.frame(cbind(ry,ro,hy,ho))
```

```
      a1[i] = s2[1,1]; a2[i] = s2[1,2] ; # extract ages now while you still
 can!
      s2=s2[2:nrow(s2),]
 # pick a random variable
 v = s2[sample(1:nrow(s2),1),]
     if (k[i]==0) {tr[i]=NA} else tr[i]= row.names(v[1,])  # which trait?
 # calculate species' ratios, with ratios <1 set equal to 1
    if (k[i]==0)  {gml = NA; gmr = NA}  else {
      gmr=v[1,2]/v[1,1]; if (gmr<1) {gmr = 1}
      gml=(v[1,4])/(v[1,3]); if (gml<1) {gml = 1}
    }
 # calculate test statistic
    if (k[i] == 0) {D[i]= NA}  else {D[i] = gmr-gml}
  # extract information about subsample
    if (k[i]==0) {f1[i] = NA; f2[i] = NA; h1[i] = NA; h2[i]=NA} else {
      f1[i]=names(ry); f2[i]=names(ro); h1[i]=names(hy); h2[i]=names(ho)
      }
} #   #   #   #   #   #   #       FIN!
```

Save a copy

For each of the above resampling procedures, the output can be stored as a .csv file for future analysis in Excel, R, etc.

```
da = a2-a1  # difference between pair's age groups
total = data.frame(na.omit(cbind(tr,D,k,a1,da,f1,f2,h1,h2)))  # all the
 resampled data in a nice matrix
write.csv(total,file="output.csv")
```

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