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**Growth and Development in the Genus *Pan*: a Life-History Approach**

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**Conrad Brimacombe BSc MSc**

**Department of Archaeology**

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**Abstract**

Comparative analysis between extant apes and modern humans has for decades been used to inform the understanding of how humans have evolved their present life-history patterns. Such studies have specifically focused on skeletal life-history as patterns of skeletal development may be represented in fossil human ancestors. Theoretical approaches to analyzing life-history have invoked the principles of heterochrony where changes in growth rate and sequences of maturational events have been proposed to explain differences between *Pan* and *Homo*. Debate has arisen as to whether humans demonstrate neoteny (retention of sub-adult features into adult form), hypermorphosis (attainment of adult form prior to complete maturation) or a mixture of both. This debate remains unresolved partly due to incomplete data for development in *Pan* and lack of integration of data for different skeletal sub-systems such as dental development and epiphyseal fusion. The objective of this study is to improve upon the present state of knowledge by evaluating skeletal development in a sample of *Pan troglodytes* and *Pan paniscus* from osteological collections.

The sample used in this study consisted of 177 *Pan troglodytes* and 37 *Pan paniscus* individuals sourced from the Powell-Cotton Museum (United Kingdom), the Museum of Central Africa (Belgium), and the Adolph Schultz Collection at University of Zurich (Switzerland). The majority of individuals were wild-shot. Epiphyseal fusion was assessed using a method based on McKern and Stewart. Radiographs were taken for mandibular dentition. Dentition was assessed by the Demirjian method for 8 teeth. Length was measured for all long-bones.

Data were analysed for three major parameters of skeletal growth, these being growth rate, sequence of maturational events, and allometric change. Comparisons between chimpanzees and bonobos found these two species to be essentially the same in terms of measured skeletal maturation parameters. Analysis of *Pan paniscus* was more limited due to smaller sample size. Comparison between *Pan* and *Homo* focused primarily on comparison between chimpanzees and humans due to sample size limitations for *Pan paniscus*. Comparisons of sequences found broad similarities between these two species in terms of epiphyseal fusion events. Comparisons of fusion sequences and dental maturation showed some differences, especially in the later stages of maturation for these two systems. Epiphyseal fusion event timing was also considered in the context of proportional change in length of long-bones. It was found that the relative timing of fusion events as proportion of growth in length was the same for both chimpanzees and humans. Estimates of chronological age of fusion were produced for epiphyses analysed in prior studies as well as additional centres not previously evaluated. This was done using Kuykendall’s regression equation for 8 teeth. Estimates for age of fusion determined in this study closely matched the data for sites observed in prior studies using known-age samples. This indicates that the estimates for age for previously undocumented sites in the present study are likely accurate.

The implications of these results for theoretical approaches to studying growth as well as the study of fossil hominids are discussed. Humans appear more divergent from apes when maturational events are considered in the context of chronological years. Comparisons based strictly on maturational events suggest that the differences in growth rate may distort the perception of how large differences in life-history pattern actually are.

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# Introduction

## The problem with sub-adult skeletal and dental development in paleoanthropology

Our knowledge of the origins of the human species has greatly expanded in recent decades. With new fossil evidence being found on a continual basis, what is known about our predecessors since the split between the human lineage and other extant apes continues to change and evolve. A great amount of this research has focused on morphological differences between species and adaptive changes such as the shift towards bipedalism, brain expansion and an extended period of maturation. Much interest has focused on the environmental and behavioural reasons for these adaptations with many well-supported theories having been proffered. However, it has been less clear how these changes are manifest in skeletal evidence for growth and development and there is a good reason for a lack of lucidity in the understanding of this topic. This derives from the fact that understanding changes in skeletal development necessarily requires large samples of sub-adult individuals of different ages from a single species, preferably at a single point in geological time. Even with the size of the fossil record growing on a continual basis, the satisfaction of such requirements is still extremely unlikely if not impossible. Researchers must instead rely on evidence from a scattering of sub-adult specimens spanning different species over large periods of time and space. Such specimens include well-known examples such as the Nariokotome Boy and the Sediba and Dikika specimens (Alemseged *et al.* 2006, Berger *et al.* 2010).

The above mentioned specimens only provide a snapshot of development. They are single individuals frozen at one specific stage of an ongoing process. Developmental parameters from long-deceased human ancestors will never be uncovered by compiling statistics from a small scattering of bones. As such research in the field has been forced to rely on comparing these individuals to developmental patterns of extant humans. The understanding of modern human development is quite advanced but using these data for comparison with fossil remains has been deemed questionable because of the inherent nature of this type of information. Variation is a critical component that must be accounted for in any such comparison. Patterns of growth found for extant humans have been ascertained by the use of large data sets which rely on patterns determined by statistics of central tendency. However, it is well understood from such studies that individuals can exhibit variation in pattern and timing of developmental events caused either by genetic or environmental factors. The case of the Nariokotome *Homo ergaster* specimen (KNM-WT 15000) is both a well-known and pertinent example of the ambiguity that such variation may present. In this individual it was found that the pattern of skeletal fusion shown differed from an expected normal human pattern but was not outside of the range of modern human outliers (Smith 2004). In other words, the Nariokotome specimen’s parent population may or may not have been developmentally analogous to modern humans. Without further information the problem cannot be solved.

This type of difficulty has drawn some researchers to comparisons of modern humans with closely related extant primate species to ascertain where consistencies lie and deviations from shared patterns occur. These patterns may help to identify where changes have developed and where shared primate traits are expected. The underlying logic is that if a trait is shared between two closely related extant species then it is likely that their ancestor also exhibited this same trait. Even though this strategy is very good, from a cladistic perspective it is not foolproof. Traits may develop by convergence whereby the same phenotype has been arrived at twice in two independently evolving species. It is even possible that a trait has disappeared and then re-appeared such as has been observed for the maxillary sinus in some old world monkeys (Rae *et al.* 2002). However, the most important fact to keep in mind is that this method of comparison provides the most tenable pattern of shared and derived traits.

For humans, it has been established that our closest living relatives are chimpanzees and bonobos (Kumar *et al*. 2005, Raaum *et al*. 2005, Stumpf 2007). It is these two species to which research has focused for furthering the understanding of development in human fossil ancestors. This brings us to the key objective of this study. A large body of research on chimpanzees and bonobos has in the past been produced but there remains much still to be understood with many gaps in integration of skeletal developmental parameters. This study seeks to close some of these gaps in knowledge and provide further insights into developmental pattern comparisons between humans and our closest living relatives. This will allow for the refinement of models for what is observed in the fossil record.

## The main objectives of this study

This study will evaluate the level of concordance in pattern and timing of skeletal development between *Pan troglodytes* and *Pan paniscus* and will compare these aspects to humans (*Homo sapiens*). The applicability of theoretical models of growth will be assessed. This will be achieved by documenting the pattern and relative timing of specific skeletal growth parameters. Three aspects of skeletal growth will be considered; epiphyseal fusion (the union of growth plates to the ends of the bone), dental mineralization, and long-bone growth in length in a comparatively large sample ofthese two *Pan* species. Prior studies have focused more narrowly on regional developmental patterns such as hand/wrist and foot bone epiphyseal fusion (e.g., Hamada and Chatani 2003, Watts 1971, 1985, Winkler 1996), dental development (e.g., Anemone *et al*. 1991, Kuykendall 1996, Kuykendall *et al*. 1992, Smith *et al*. 2010, Zihlman 2004), and immature morphology (e.g., Gavan 1971, Hamada *et al.* 1996, Watts 1982). Holistic studies incorporating both dental development and a broad spectrum of epiphyses are rare with only a few researchers attempting this approach using small sample sizes (Bolter and Zihlman 2012, King 2004, Zihlman *et al*. 2007). King (2004) reinforced through discriminant function analysis that there are broadly related trends among apes and Bolter and Zihlman (2012) have provided approximate ranges fusion for both species using a sample of only 10 *Pan troglodytes* and 8 *Pan paniscus* individuals. Even though these studies have been useful for providing a general range of fusion events and an expectation of some broad similarities between all three species, there is still not a clear understanding of fusion sequence and concise timing for fusion events. This is due to the mitigating effect of the small sample sizes used in these studies. There is also a lack of information relating growth rates to fusion sequences and timing.

The present study attempts to improve this situation by the analysis of a cross-sectional sample of 177 *Pan troglodytes* and 37 *Pan paniscus* individuals found in skeletal collections at the Museum of Central Africa, The Powell Cotton Museum, and the University of Zurich. Three main categories of data were evaluated: epiphyseal fusion, dental development, and length of long-bones. Dental mineralization was assessed using the Demirjian (1973) method and used as a scale for maturational development relative to epiphyseal fusion and long-bone growth. Epiphyseal fusion was assessed using a system similar to that employed by Zihlman *et al*. (2007). Fusion events were seriated and sequences within dental and skeletal development compared. Long-bone length data were used in conjunction with dental score which permitted the generation of growth curves by linear regression analysis. Having both length and epiphyseal fusion sequence data from the same sample facilitated the simultaneous integration of dimensional change and maturational pattern. Not only could a sequence of fusion events be produced, but the relative timing of these events could be scaled to changes in long-bone length. These data were compared and contrasted between the two species of *Pan* and the extensive data already in existence for *Homo.*

## The contribution this study will make to modelling of growth and development in hominins

Humans demonstrate an extended period of maturation relative to chimpanzees, bonobos, and other apes (Hill 1993) and have developed a longer lifespan (de Magalhães and Church 2007). Humans experience an extension of sub-adult stages including the addition of childhood and adolescent stages (Bogin and Smith 1996). This has meant that there are differences in growth curves both in terms of duration and rates between the two species. These differences have made direct comparisons of maturational sequences using chronological time as a reference problematic. It is known that in chimpanzees the third molar is complete and in occlusion only shortly after the second molar (Kuykendall and Conroy 1996). Given what is known about chimpanzee growth, this event is likely contemporaneous with or precedes complete skeletal maturation. Research on bonobo dentition and maturation has suggested similar results (Bolter and Zihlman 2012). In humans the third molar emerges either later than or near the end of complete skeletal maturation (Scheuer and Black 2000, Schaefer *et al*.2009, Sciulli 2007). The paucity of chimpanzee data has meant that it cannot be conclusively determined that these species are different. It remains to be determined if such differences of development are also shared between chimpanzees and bonobos. It is such questions that this study aims to address.

Pattern and rate of growth: Heterochrony

Explaining developmental patterns has been approached using different models. These models all fall under the area of developmental theory referred to as heterochrony, which is the study of changes in rates and patterns (sequences) of growth (Rice 1997). This topic will be discussed in detail in Chapter 2. Here two key variables shall be briefly introduced: the pattern of development and the rate of development. The *pattern* of development relates to developmental sequences such as dental eruption and epiphyseal fusion. The *rate* of development refers to the functional relationship between time and growth. These concepts are not independent but past research has tended to analyse them independently. Skeletal elements grow at different rates and their completion is determined by fusion of the epiphysis to the diaphysis. An organism can be looked upon as a system in which the entire process of growth functions as a unit. To illustrate this point, it is known that chimpanzees and bonobos attain adult proportions earlier than humans with respect to chronological time (Hamada *et al.* 1996). However, it is unclear if the means of having achieved this maturity represents an accelerated version of the same pattern or if the pattern is markedly different within this shorter timeframe. Delineating between these concepts is difficult, especially with the amount of inherent individual variation that exists. Having the foundation of long-bone lengths, fusion sequences, and dental development will allow for the pursuit of greater clarity within this topic.

The following are some specific topics of interest that this study will address having both dimensional change and sequence data concomitantly:

##### 1. Morphological change

Here the concern is with the dimensional changes, particularly the relative lengths of bones. The aim is to know how the pattern of different relative lengths of bones is arrived at and how these patterns are represented in skeletal fusion and growth rate.

##### 2. Behavioural and locomotory adaptations

This topic is not independent of morphological change. It involves the additional effects that behavior has on skeletal maturation. It remains to be seen if particular epiphyses that are more precocious than others fuse earlier in order to stabilise joints due to positional behavioural demands. Differences in pattern and timing of ossification centre appearance have been implicated as support for this suggestion (Blomquist 2009, Dainton and Macho 1999, Hunt 1991, 1992). It is not entirely clear if the growth rates of bones are related to such adaptations. In humans, for example, more growth in length occurs at the distal end of a radius than the proximal with the same pattern occuring for the ulna but the reverse being observed for the humerus (Schaefer *et al*.2009, Scheuer and Black 2000). This pattern is generally observed for mammals as a group. However, some studies have found small differences in pattern for individual elements in primates and this has been associated with behavioural patterns (Bolter 2011). It may be speculated that the precocious fusion of epiphyses at the elbow might relate to the need for structural stability in that joint as a consequence of behavioural patterning as early in development as possible. If this is the case then more suspensory primates may place higher priority for earlier fusion of this joint. The provision of sequence and relative timing data from this study will permit inferences to be made in relation to locomotory patterns and dimensional change.

Determining the shared and derived nature of developmental patterns has consequences for what may be inferred about locomotion in fossil ancestors. In recent time this has become a topic of greater interest with current research suggesting that the human and chimpanzee last common ancestor may have been less of a direct analogue of modern extant apes than was once though (Lovejoy *et al.* 2009). When large changes occur in relative timing and rate of maturation, and when these deviations are correlated with differences in behavioural patterning, models may be generated that describe how this ancestor might have appeared.

##### 3. Comparisons of developmental sequences and rates of growth.

As mentioned above, heterochrony may be broken down into two major areas of study: rates of growth and sequences of developmental events. Linking developmental sequences to chronological time informs these theories about the state of development relative to the growth in size or shape. Many of the terms of this subject rely on development relative to the age at which sexual maturity is reached. It has been established for some time that humans differ from chimpanzees in both rate and duration of overall somatic growth (Bogin 1997). Some sequences of developmental events have been determined such as dental development (Kuykendall 1996) but this linkage between rates and sequences is incomplete. This study seeks to bridge many of these gaps by clarifying epiphyseal fusion sequences in the context of dental sequences and dimensional growth.

## Study approach

As noted in section 1.2, this study will evaluate epiphyseal fusion, dental development, and long-bone growth in 177 *Pan troglodytes* and 37 *Pan paniscus* individuals from osteological collections. This study both builds and expands upon past research, which will be defined in Chapter 2: Background. In the context of this past research, it was decided to evaluate dental development using the Demirjian method (Demirjian *et al*. 1973) applied to radiographs of mandibular dentition. This produced summary dental scores comparable with known age samples used by Kuykendall and Conroy (1996). Epiphyseal fusion was recorded using a multi-stage scoring system similar to those that has been used for human studies. Long-bone length was evaluated using an osteometric board, with orientation normalized to set criteria. These data were collected for both sides of the skeleton in order to maximize data entries when skeletal elements were missing from one side or the other, as is common with many osteological collections.

## Chapter overview

Chapter 2 (Background) provides the context in which this research is situated. This chapter is broken into two major sections. The first section is an overview of developmental theory and how it has been applied to chimpanzee, bonobo, and human growth. There is a lack of consensus as to which developmental parameters define differences between the two genera and how these differences have affected adult form. This is discussed. The second half of this chapter describes what is known for humans, chimpanzees, and bonobos for each developmental variable evaluated in this study, these being dentition, epiphyseal fusion and long-bone growth. For each of these variables the effects of sex, population affinities, and nutritional stress are evaluated. Comparisons between these species are then considered, highlighting gaps in knowledge.

Chapter 3 (Materials and Methods) is divided into three section. First, a descriptive analysis of the materials used is pursued (Section 3.1). The geographic origins, state of preservation, completeness, and general demographic data are detailed. Second, the methodology used to collect the data is outlined with justification provided for each procedure (Section 3.2). Third, due to the complex nature of these data, a series of procedures are carried out in order to begin the analysis and to ensure robusticity of the data. These procedures are described in sections 3.3. Sections 3.4 to 3.6 demonstrate how these procedures were carried out in greater detail.

Chapter 4 (General Results) presents the the general results for epiphyseal fusion sequences and long-bone growth in *Pan troglodytes* and *Pan paniscus*. The two major sections of this chapter are concerned with growth rates and sequences within *Pan*. Epiphyseal fusion as plotted against dental score is explored and the limitations of this approach highlighted. Fusion sequences are also seriated without dental score for *Pan troglodytes*. Allometric relationships are explored for long-bone growth and growth curves for each long-bone plotted.

Chapter 5 (Comparisons of growth standards between *Pan* and *Homo*) investigates comparisons between chimpanzee, bonobos, and humans, including comparisons with prior studies of all three species. Such past studies often collected data in different ways and the effects of these differing methodologies must be analysed. This chapter begins by producing estimated chronological ages of fusion from dental scores and compares the results of this analysis to the data provided by to Bolter and Zihlman (2012). An expanded list of estimated chronological ages for the epiphyses in this study are presented. Seriated sequences of fusion are compared to Schaefer and Black’s (2007) modular sequence for human epiphyseal fusion. Following this, an analysis of the relative position of dental and epiphyseal fusion sequences is considered. For the last part of this chapter, a comparison of long-bone lengths relative to epiphyseal fusion events is pursued by considering the timing of fusion events as a proportion of growth in length.

Chapter 6 (Discussion) considers the implications of new information provided in the previous two chapters. This chapter is broken into two section. The first section considers how the results of this study may be situated within the context of developmental theory. How well these data inform debates relating to growth rate and pattern is assessed. The second section considers what the implication these results have for the study of fossil hominids. The Nariokotome *Homo ergaster* specimens is a pertinent example and an analysis of this individual is discussed.

Chapter 7 (Concluding Remarks) provides an assessment of the general findings of this study. The implications that this new information has for the study of developmental theory is discussed. The consequences for the study of fossil hominids are also reviewed. Suggestions for further research are made.

# Background

## Theoretical approaches to growth

This study observes growth for three separate systems of development; epiphyseal fusion, dentition, and long-bone length. These three systems have factored largely in developmental modelling alongside other variables not directly measured in this research. To begin this discussion fundamental concepts are defined followed by an introduction of the applications of heterochrony and developmental theory.

### Fundamental concepts: measuring skeletal growth

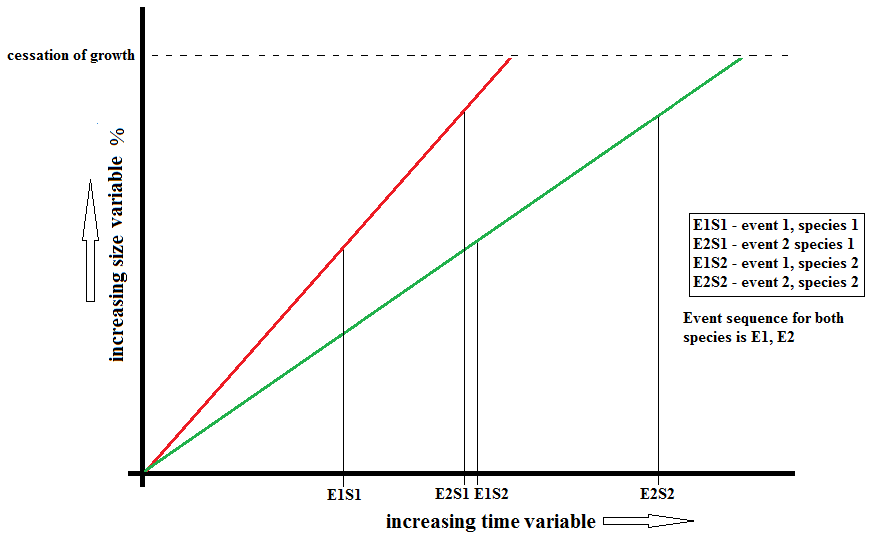
All living organisms, including mammals, grow and develop according to a set of instructions given by their genotype. In recent years molecular biology has undergone a veritable revolution in decoding these instructions and finding out how these systems works. Many regulators of growth such as IGF-I (e.g., Chia *et al.* 2006) have been identified and research within the field will continue to improve the understanding of development at a molecular level. However, the study of genetics is still far from being able to describe growth in terms of morphology and the triggers for ossification and fusion events. Present understanding is able to identify the function of individual proteins and hormones, as well as the consequences of mutation in the genes that code for them, but the complete picture required to establish exactly how these systems work at a molecular level is still missing. Thus, the understanding of growth is still dependent on looking for patterns in what is physically observable, which in this study is bones. The mammalian world is replete with variation in skeletal morphology and diversity but there remain the same intrinsic structures. All of the bones found in a human can be found in for example a baboon, despite differences in shape and proportion. The study of growth relies on assessing modifications of these structures and explaining such changes by proposed adaptative mechanisms.

For skeletal growth there are two basic variables to consider: growth rate and event sequence patterns. Growth rate will be considered first. This may refer to overall somatic growth of an organism as a proportion of final adult size or the relative growth of specific elements. Overall somatic growth is often measured as a function of mass vs. time or another general measure such as anterior trunk length. Examples of such studies for chimpanzees include Hamada *et al.* 1996, Hamada *et al.* 2003, Hamada and Udono 2002, and Schultz 1960. These types of measures are informative in the sense that they take into account the effect of many different systems at once. It is known that chimpanzees and humans gain mass at different rates and for different durations of time. Humans have specific sub-adult stages, specifically childhood and adolescence, which are believed to have been specifically selected for in the human lineage and are not shared with *Pan* (Bogin 1997). Thus, the study of this key variable suggests that all of the more specific systems of skeletal development must likewise be developing at different rates.

The next step of an analysis of growth rates is to consider how different growth rate is manifest in comparisons of specific elements. This may be expressed as a functional relationship between two or more elements. For example, human cranial growth is much in advance of post-cranial growth (Leigh 2004). Growth rates may also differ even within single skeletal elements. For example, in humans and mammals generally, bone growth at the proximal humerus contributes to the majority of growth in length and matures years after cessation in growth of the distal portion (Scheuer and Black 2004). Both ends of this bone contribute to growth in length but at different rates and for different periods of time. Changes in the relative length of bones during growth, if they are present, may also relate to such differences in growth rates between differing elements.

Sequences in development are marked by distinct maturational events such as the formation of ossification centres, tooth emergence, and epiphyseal fusion. Examples of such sequences are provided for humans in many reference texts (e.g., Schaefer *et al.* 2009, Scheuer and Black 2004). These events do not occur simultaneously during growth and are found to follow a predictable order. Particular sub-systems appear to have sequences that are independent from each other such as dental development and skeletal fusion. This has notably been observed in stressed human populations where dental and skeletal development deviate from one another (Demirjian *et al.* 1985, Lewis and Garn 1960,Smith 1991).

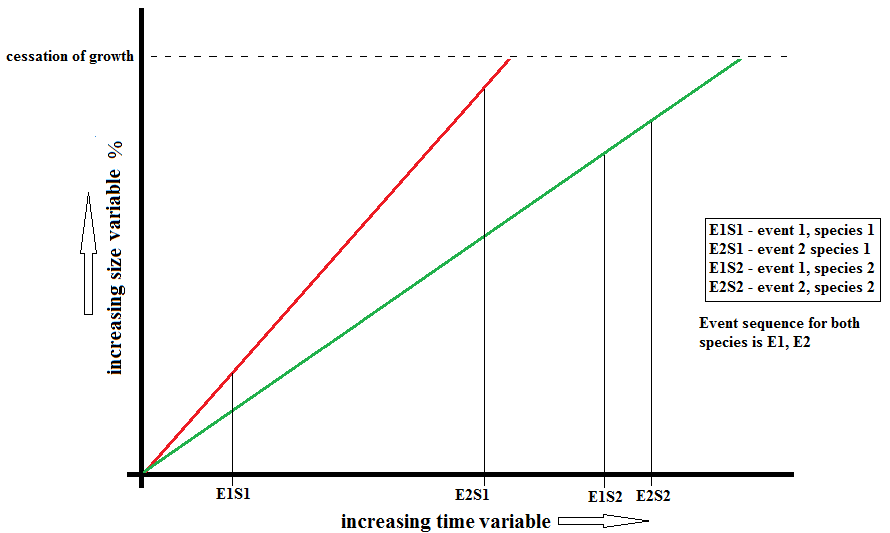
The differences between developmental sequences and rates of growth require some further discussion. Consider a hypothetical example where two species have exactly the same pattern of epiphyseal fusion but one species matures in half the time that the other does. Figure 2.1 illustrates how this may be represented in these species. Each species has a different rate of growth but exactly the same sequence of maturational events.

**Figure 2.1** Maturational events in two hypothetical species of differing growth rates where species 1 (red line) reaches specific maturational events more rapidly than species 2 (green line).

Both events occurred in the same order and at the same relative time in growth (Figure 2.1). Event 1 occurred at 50% and event 2 at 80% of growth. Thus, in this case the only difference is the relative time it took for these events to occur. Growth rate relative to time differs, as does duration of growth but maturational sequences are identical. In addition to this, it can be stated that these maturational events occur at the same time as a proportion of length. Figure 2.2 illustrates inconsistent relative growth.

In Figure 2.2 the event sequence is again identical but the relative timing and rates of growth rates are different between the two species. A third potential scenario would be when the two growth curves superimposed, indicating that growth rate and duration were identical for both species but the sequences differed. These figures illustrate that studying pattern independent of growth rate and time can be misleading when comparing species, although this approach is frequently employed. Both the rate of growth rate and sequence of events need to be considered in conjunction in order to gain a more complete understanding of development.

\*Species 1 (red line) reaches specific maturational events more rapidly than species 2 (green line) and experiences event 1 (E1S1) relatively earlier than species 2.

**Figure 2.2** Maturational events in two hypothetical species of differing growth rates and differing relative timing of sequence events.

### Developmental Theory

In this section the theoretical terminology used to study growth will be presented. How these terms have been applied to comparisons between chimpanzees, bonobos, and humans will be discussed. As noted in Chapter 1, the subject within developmental biology that studies the effects of changes in event timing and rate of growth is known as heterochrony. Heterochrony focuses changes in size and shape through developmental processes. Rice (1997) defined different types of processes that are included within this subject:

1. Progenesis: The achievement of sexual maturity before attaining the adult form.

2. Hypermorphosis: The achievement of adult form prior to sexual maturity.

3. Neoteny: Retention of juvenile traits.

4. Acceleration: Increased rates of development.

5. Sequence heterochrony: Changes in time of onset of events

Some further clarification of these terms is warranted. Progenesis implies that early sexual maturation is positively selected and can lead to precocious reproduction at an earlier phase of growth. Neoteny suggests that traits from sub-adults are maintained through to adult individuals. Therefore the time of attainment of adulthood relative to sexual maturity may or may not change, but it is simply that certain traits remain sub-adult in appearance. Hypermorphosis, conversely implies that an adult state is attained prior to sexual maturity. It may be applied to either the entire organism or individual anatomical features with the latter being a more common usage. Bogin (1997) defines hypermorphosis as the extention of earlier growth stages while neoteny is the retention of lower, or earlier stages into adulthood. Neither progenesis nor acceleration tend to be discussed independently when describing humans. The focus is instead on neoteny and hypermorphosis. Humans are progenetic in the sense that they reach physical sexual maturity prior to complete skeletal maturity. However, this is not unique to this species and is common in many mammalian taxa including primates (Kilborn *et al.* 2002).

The analysis of sequence heterochrony relies on the study of pre- and post-displacement, or in other words the changing of order of events (Bininda-Emonds *et al*. 2002, Jeffery *et al*. 2002, King 2004, Nunn and Smith 1998, Richardson *et al*. 2001, Smith 2001 2002, Velhagen 1997). Many examples of sequence heterochrony studies may be found in the literature including Goswami (2007), King (2004), and Smirthwaite (2007). In the context of skeletal development, this area of study makes particular use of epiphyseal fusion and dental sequences of development. As shall be discussed in section 2.4.6, King’s (2004) study incorporating both of these sequence variables is of particular relevance for the study of sequence heterochrony in primates.

Allometric scaling

Allometric scaling refers to changes in the proportionate size of elements relative to the size of the whole organism. Differences between adults are generally much better studied than differences between sub-adult individuals. Changes in allometry are related to imposed biomechanical and behavioural constraints (Schmidt-Nielsen 1984, Small 1996). When two species with differing adult proportions are compared, it is necessary to consider whether the difference between them develops during growth from a sub-adult of the same dimensions or if these species are born with already differing proportions. This is a phenomenon known as ontogenetic scaling. There has been much discussion considering issues of scaling with respect to both size and shape (e.g., Gould 1977, Persson *et al*. 1998, Ravosa and Daniel 2010).

Combining allometric scaling and maturational sequences

Determining the relationship between maturational events and growth parameters is complex. Various models have been used to try and calibrate maturational events relative to body proportions, and to compare these variables between ancestors and descendents (Klingenberg 1998). It has been suggested that there is not a strong relationship between skeletal maturational pattern and significant changes in size for closely related species (Godfrey and Sutherland 1995), as shown by Roth (1984) who studied skeletal development in elephant species. Roth showed that these species varied dramatically in size but the size changes did not necessarily correlate to any specific changes in pattern of skeletal and dental development. Dwarfed species especially did not exhibit paedomorphic patterns (retention of juvenile traits in adult forms, i.e. neoteny) but simply appeared to be scaled-down versions of larger species. This study may seem like a convincing case in point, although it is only drawn from one dwarfed taxon from which there was sufficient data. It is not evidence that other dwarfed taxa necessarily behave in this manner. However, a bigger challenge for this type of research is that it requires a diverse set of samples from multiple species for robust conclusions to be made. This type of information across appropriately related taxa is still limited.

The application of ontogenetic theory to the study of human evolution

Ontogenetic theory as applied to humans has centred primarily on comparisons between chimpanzees and humans. This is because chimpanzees are a closely related species to humans but also remains morphologically and behaviourally distinct. While bonobos are equally closely related to humans, comparisons with this species are relatively rare but fall into a similar category of study due to bonobos branching away from chimpanzees after the divergence of *Homo*-*Pan*. Adding to the differences between chimpanzees and humans, it has been observed that these species achieve adult form at different times and at different rates. This particular point has been discussed at length with some level of disagreement persisting to the current state of research.

Attempts at unified theories based on neoteny and hypermorphosis

In the 1990s there was a thrust towards producing a unified theory of growth. The subject was extensively debated but disagreement and a lack of consensus remained and persists to the present day. The concept that humans exhibit neoteny has been proposed multiple times and is the oldest proposed explanations for how the species differs from other apes. As discussed by Bogin (1997), the most substantial proponent of this concept was Gould (1981) who provided a case based more on behavioural observations than anatomical ones. Essentially the curiosity and learning behaviours of young primates is brought forward to adulthood in humans.

The popular impression that young chimpanzees appear more ‘human-like’ has led the expectation of sub-adult feature retention. However, the investigation of neoteny in terms of general anatomy has had limited application. There have been some studies of facial morphology that have pointed towards humans retaining sub-adult cranial features into adult form (e.g., Bastir and Rosas 2004, Penin *et al*. 2002). Bufill *et al.* (2011) have suggested that humans maintain neurologically immature state of synaptic connection formation. Apart from the study of cranio-facial growth, the application of neoteny to humans relies on little other anatomical evidence. The simplicity of the concept may have limitations when applied to post-cranial growth. The convention that defines complete maturation of a bone is fusion of its epiphyses. In this sense, neoteny clearly doesn’t apply to humans or apes as they both always mature. However, whether individual elements demonstrate ‘temporary neoteny’ in that an element may grow longer or stay in an immature state for a greater period of time is entirely possible. A pertinent example of this would be the temporally very late fusion of the medial clavicle in humans. Additionally, the argument that dimensional differences during growth indicate neoteny is difficult to prove. Evidence may be presented as a slowing of growth in an element, resulting in a difference for the adult. Whether this is simply a difference between species or a specific retention of sub-adult features is debatable.

The application of neoteny to humans has been challenged in the past for growth rate and for dimensional change. McKinney and McNamara (1991), Parker (1996), and Vrba (1996) argued that humans are instead hypermorphic; they are not persistent subadults but are actually developmentally delayed adults. That is, there is not retention of subadult features into later stages but rather that the adult stages are delayed. These studies again considered overall somatic growth rates as well as cognitive and social rationale for their conclusions. Vrba (1996) went further and posited that this longer period of growth permitted the distortions in body shape between ancestor and descendant we see today. However, the theory that humans are hypermorphic has also been challenged. Shea (1989), Godfrey and Sutherland (1996) and Mitteroecker *et al.* (2004) have reasoned that neither theory sufficiently explains the patterns of growth and allometry in humans. Shea (1989) allowed for neoteny to be potentially present for cranio-facial dimensions. Mitteroecker *et al.* (2004) have taken the opposing view after comparing chimpanzee and human cranial dimensions and concluded that this is not the case. These studies refuting neoteny and hypermorphosis have cited allometric contradictions as evidence against both theories.

In the last decade there has been a decline in attempts to describe human development by a unified theory with perhaps the exception of neoteny in cranio-facial growth, although this too is not without dispute. It seems a reasonable conclusion to draw that differences in growth are inherently more complex than the definitions these terms permit. Thus far neither allometry nor overall somatic growth rate appear to conform to generalised theories of heterochrony either analysed separately or combined. It appears that the size and shape of humans are not strictly the consequence of augmented growth rate but undoubtedly the result of independent selection acting on different anatomical regions and processes. This result points towards the requirement for a more detailed understanding of each developmental process.

Allometric scaling in chimpanzees, bonobos, and humans

Theories of heterochrony may not work well when attempting to integrate data from allometric scaling but the results of such studies are in themselves very useful for understanding developmental change. Shea’s (1989) argument against heterochrony was based on the list of papers that he produced over the previous decade (e.g., Shea 1981, 1983, 1984, 1985, 1989). The details of Shea’s research are discussed in sections 2.6.2 to 2.6.4 when studies of long-bone length are considered. To summarise, Shea (1981) found that *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla* showed broad similarities in overall growth rates but differences in development of individuals bones were both interspecific and intraspecific. These differences had effects on the eventual adult dimensions, which have been more commonly compared. For example, both chimpanzee and gorilla adults have longer upper as opposed to lower limbs. However, during development chimpanzees achieve this difference by greater growth of the distal radius whereas gorillas attain this difference by growth of both the radius and humerus, resulting in a difference of adult inter-membral index (ratio between limb segments). With respect to humans, Shea (1983) noted that differences related to bipedalism certainly do not align with concepts of neoteny and there are allometric reasons in support of this. When examining Shea’s (1981) data, it is clear that *Pan* and *Gorilla* have different limb proportions when compared to humans from birth. Even though Shea’s work was published over 30 years ago and our understanding has improved since then, these studies remain effectively the only source of information available for allometry and growth of these species. Critically, they provide evidence that growth in specific bones for chimpanzees, bonobos, and humans does not necessarily follow a universal pattern, an observation that has implications for reconstructing phylogenetic relationships from growth data. This idea is quite important for the analysis of data from the current study and no studies since have provided further information in this regard.

Sequence heterochrony: the incomplete picture for chimpanzees, bonobos and humans

There has been limited discussion of sequence heterochrony for chimpanzees in a focused theoretical manner. The only two studies which directly address the topic are King (2004) and Blomquist (2009). Blomquist (2009) used radiographic data from Pyle and Sontag (1943), Nissen and Riesen (1949), and Gavan (1953) to evaluate the appearance of ossification centres in hand and wrist bones relative to time using event-pair cracking methods. He suggested that shifts in timing of ossification centre appearance may be related to locomotory differences between chimpanzees and humans. King (2004) used discriminant function analysis to cluster dental and epiphyseal fusion data for 16 different primate species (species and sample size listed in Table 2.1). King’s (2004) methodology did not provide a seriation of fusion events relative to dental development. However, the results of his discriminant function analysis provided useful insights. Distances were determined between groups, with the Hominidae, Hylobatidae, and Cercopithecidae families being distinguishable. Apes tended to cluster together and chimpanzees were distinguished from gorillas.

**Table 2.1** Species and sample sizes used by King (2004).

|  |  |
| --- | --- |
| **species** | **sample size** |
| *Euoticus elegantulus* | 47 |
| *Lepilemur edwardsi* | 19 |
| *Perodicticus potto* | 44 |
| *Propithecus verreauxi* | 20 |
| *Aotus trivirgatus* | 47 |
| *Saguinus nigricollis* | 30 |
| *Saimiri sciureus* | 55 |
| *Cercopithecus ascanius* | 66 |
| *Chlorocebus aethiops* | 36 |
| *Lophocebus albigena* | 80 |
| *Macaca fascicularis* | 80 |
| *Nasalis larvatus* | 42 |
| *Trachypithecus cristatus* | 101 |
| *Gorilla gorilla* | 78 |
| *Hylobates lar* | 98 |
| *Pan troglodytes* | 86 |

The lack of theoretical application of sequence heterochrony aside from these studies is undoubtedly due to the scarcity of data. As shall be explored in detail in section 2.4.6 for epiphyseal fusion in chimpanzees, the present data are too limited to be able to assess epiphyseal fusion relative to dental developmental sequences and bonobos have been even less studied. Not only is epiphyseal fusion data lacking, but also further sequence data such as ossification and other embryological patterns. As noted previously, dental developmental schedules for both for emergence and mineralization are known for chimpanzees and bonobos (e.g., Boughner and Dean 2012, Conroy 1991, Kuykendall *et al*. 1992). Keene (1991) provided some theoretical discussion based on tooth emergence but this did not necessarily contribute to a changed perspective when comparing dental scheduling for the studies that followed. Dental sequences are very useful in their own right but differences observed are limited. How dental and skeletal systems relate to each other is necessary for a complete analysis and the data presently available for skeletal sequences is too unrefined to provide exact sequences.

### How this study can contribute to the theory of growth

The objective of this study, as outlined in Chapter 1, is to acquire new data such that developmental patterns in chimpanzees and bonobos can be better understood for the purposes of assessing fossil hominids. The intention is not to explicitly define these species within the concepts of heterochrony but the analysis of these data implicitly ties in these theories of growth. As discussed above, models of human and chimpanzees growth have been proffered within the context of developmental theory but there remains some level of disagreement. In this study data on dentition, epiphyseal fusion, and long-bone growth are collected. Dental and skeletal fusion data when combined will provide further evidence for comparing sequences of growth in chimpanzees, bonobos and humans. The addition of long-bone length will help define these by providing dimensional data that can be associated with fusion events. Such data are unique to this study and may inform questions that consider fusion sequences relative to dimensional change. Specifically, sequences may be considered with respect to proportionate growth in length. Being able to dissociate these variables (fusion sequence and length) from time allows for observation of these elements as a function purely of maturational development.

## Organisation of sections for each species

For each of the main aspects of growth addressed in this study (epiphyseal fusion, dental development, and long bone growth) the following topics will be addressed:

1. The underlying physiology of epiphyseal fusion, dental development, and long-bone growth;
2. A review of all prior studies for each of chimpanzees, bonobos, and humans, outlining what is known versus unknown;
3. Comparison of captive versus wild populations;
4. A review of the known effects of pathological conditions on skeletal systems.

It should be noted that for humans, captive and wild are not an applicable set of categories. Here, the same types of physiological effects are discussed under the topics of stressed vs. healthy populations.

## Epiphyseal fusion

In this section what is known about epiphyseal fusion plates and their function in growth will be introduced. This will start with a brief overview of the evolved functional aspects of epiphyses (section 2.3.1) followed by a consideration of epiphyseal fusion plate physiology (section 2.3.2). Developing from this basis, epiphyseal fusion sequences in mammals (section 2.4.3), primates in general (2.3.4) and lastly epiphyseal fusion sequences in *Homo* and *Pan* (sections 2.3.5-2.3.9) will be presented.

### The physiology of growth and fusion

Calcified bone forms on one of two types of pre-osseous templates: fibrous membranes, from which we derive the term intramembranous ossification and hyaline cartilage, from which we achieve endochondral ossification. The reason for two distinct types of pre-osseous template is not entirely clear. It has been speculated that fibrous membranes may be present for more rapid ossification in long bones (Holden 1882, Last 1973), although more recently it has been suggested that intramembranous ossification may be a more ancestral type of ossification derived from dermal bone, and as such endochondral ossification may have been derived from this original method of bone formation (Morriss-Kay 2001).

Intramembranous ossification is mainly described in embryonic development, although it does actually continue throughout life (Scheuer and Black 2000). For the purposes of studying epiphyseal fusion sequence and timing, it is endochondral ossification at the end of the diaphysis (the shaft or mid-section of the bone) that is observed. There is distinction between these two types of bone formation. This is especially because long bone formation is in fact intramembranous in origin at early stages of primary centre formation both before and after birth (Scheuer and Black 2000) and it is only later, when it comes to describing the epiphyseal regions of joint formation when strictly endochondral ossification is observed.

There are three distinct functional types of epiphysis: pressure, traction, and atavistic. Only the first two of these are of significant interest in paleoanthropological and archaeological contexts. Pressure epiphyses are necessary to allay stresses through the joint such that longitudinal growth can continue without damage to the diaphysis (Parsons 1905, Smith 1962). The forces in joints follow geometric increases with the size of the animal. These changes are apparent in the morphology of the epiphyseal region as the relative area of the joint surface covered by the plate increases rapidly with age. Examples of such joints include the wrist, knee, and ankle. Traction epiphyses occur at some major muscle insertion sites such as the femoral lesser trochanter and the humeral medial epicondyle of the humerus (Salter and Harris 1963). Atavistic epiphyses are any epiphyses that do not fall into the previous two categories such as costal notch flakes and may have been part of structures that existed at earlier evolutionary stages (Haines 1940, Scheuer and Black 2000).

Fusion at epiphyses is likely be triggered at least in part by hormonal influences. There is a long list of growth factors that have been discovered linked to somatic growth in humans. Endocrine examples include growth hormone (GH), insulin like growth factor I (IGF I), high-affinity growth hormone-binding protein (high-affinity GH-BP) (Shea 1992, Wang *et al.* 1999). Determining the direct link between these substances and epiphyseal closure is not as clear as their effect on overall body growth. Oestrogen is known to correlate with bone maturation while testosterone correlates with cartilagenous growth (Feuillan *et al.* 1999, Ogden 1979). The difference in timing of maturation in human males and females whereby males are consistently delayed compared with females may be related to these two hormonal influences. However, the factors that govern fusion at any particular site are likely not controlled solely by hormonal influences (Weise 2001). Most bones cease growth at different times with many centres, such as the clavicle in humans, fusing long after sexual maturation has occurred. A more recent theory of local control suggests that there is no hormonal control (Nilsson and Baron 2004). Rather, fusion is mediated by entirely intrinsic factors within the growth plate whereby stem-like cells have finite limits on growth potential. Stevens *et al.* (1999) provided some evidence that supports such a theory. They transplanted epiphyseal fusion plates using allografts between individuals of New Zealand white female rabbits, and found that fusion was mediated by the plate as the timing of fusion was dependent on the age of the donor plate and not the recipient. This raises the prospect of several different models. It could be that there is a standard number of cell reproductions and oestrogen shuts this process down early while testosterone extends it. It could be that females have fewer cells to add and oestrogen levels are purely coincidental. It may also be that females have fewer cells and oestrogen accelerates their rate of deposition. The reality is that the true nature of this is simply not known. However, it is likely that growth hormones play some role as evidence from domestic animals demonstrates large effects of introduced hormones and modifications of the pituitary gland (Scanes 1999). Irrespective of the exact nature of hormonal control, it seems that their effects are systemic and that relative fusion timing is controlled locally with pre-programmed senecence for each plate. In other words, growth hormones are mediators of the overall rate and duration of growth but the plates themselves retain their particular schedule of growth cessation relative to other plates.

### Epiphyseal fusion studies from the mammalian world

Mammalian skeletal elements are highly conserved and the same bony elements are present in most species. The differences in morphology observed are the consequence of changes in length and shape of the same elements rather than the generation of new ones. Sometimes bones are lost such as the digits of ungulates. Long bones are generally conserved. Similar to the presence of these bones, fusion centres are also typically conserved. Long bones always have proximal and distal epiphyses. Metacarpals and phalanges have fusion plates at only one end for all terrestrial and marine mammals with only notable exception being cetaceans (Ogden *et al.* 1981).

There have been studies of epiphyseal fusion in several different species of mammal. Sources of current data are often derived from species of economic relevance and ease of access such as livestock (e.g., Noddle 1974), pets (e.g., Sumner-Smith 1966, Smith 1969, Zuck 1938), and animals prevalent in laboratories (e.g., Kaufman 1992, Weise 2001, Witschi 1962). These can problematic due to the high level of human-related selection which has created significant genetic bottlenecks. Some species, such as dogs, have experienced substantial modification to size and allometry and it would seem unlikely that patterns of growth and development would remain completely unaffected. Studies of epiphyseal fusion sequencing in wild species are less common and are also selective with respect to which mammalian taxa are of interest. Comprehensive studies looking at the entire range of epiphyses include North American bighorn sheep, (Walker 1987), bison (Koch 1935), grizzly bears (Weinstock 2009), and whales (Ogden *et al*. 1979). Primate species have also been considered (e.g., Cheverud 1981, King 2004, Wintheiser *et al.* 1977). Studies of specific epiphyses only include the radius and ulna in elk (Knight 1966), fox (Sullivan and Haugen 1976) and deer (Lewall and Cowan 1963). Studies of specific locations have considered some primate species (e.g., Michejda 1987; Newell-Morris and Tarrant 1978; Newell-Morris *et. al.* 1980, Schultz 1941, Watts 1971), with King (2004) presenting a more comprehensive study including a larger number of ossification centres in 16 primate species.

Sample size remains the largest fundamental limitation of such studies. The analyses of these data are also made problematic by large amounts of individual variation and sequence polymorphisms, whereby the sequence of two events is commonly interchanged within a single species (Colbert and Rowe 2008). Larger sample sizes are required to resolve these difficulties and it is only for humans that there is sufficiently extensive data.

King’s (2004) study using discriminant function analysis resolved differences between species within the same taxon and also between taxa in primates. This approach considered sequences of both dental and skeletal fusion which makes distinctions unclear in the sense that some of the differences may be dental-skeletal shifts. Whether shifts are in pattern or relative timing compared to other maturational sequences, the results are still very important. They are of particular note because the same data collection and statistical methodology was applied to a single sample. This level of systematic comparison does not exist for comparing other mammalian taxa to each other. Even though there is some information available for different species, the data are too sparsely reported for overall trends to be observed.

### Epiphyseal fusion in primates

Primate epiphyseal fusion has been studied for a patchy array of different species and with varying breadth of fusion centres considered. Typically the species studied have been those which are most easily accessed or are of particular interest. For example, both radiographic and dry bone studies have been used for *Macaca mulatta* and *M. fuscata* epiphyseal fusion centres (Hayama 1965, Michejda 1987, Van Wagenen and Asling 1958, Watts 1971). Both of these species havehad their skeletal fusion patterns studied sufficiently in depth for skeletal maturation to be compared. Hayama (1965) and van Wagenen and Asling (1958)have suggested that there are no differences in fusion pattern and timing between these two macaque species. Other primate genera that have been studied include squirrel monkeys (Galliari 1988), tamarins (Glassman 1983), and baboons (Bramblett 1969). Studies of apes include orang-utans (Schultz 1941, Winkler 1996). All of the aforementioned studies have looked at a comprehensive survey of epiphyseal closure with the exception of Schultz (1941) and Winkler (1996) who only considered fusions occurring in the hand/wrist. There is a lack of studies examining fusion in gorillas and gibbons, although growth in dental and other tissues of the former have been examined quite closely.

Patterns and trends

Research that summarises general trends in primate epiphyseal closure relies on incomplete data. Despite this, some general modelling has been presented. With respect to the pattern of fusion, Kerley (1966), Schultz (1940, 1944), Shigehara (1980) and Todd (1930) all remarked that there is a general sequence for limb fusion in primates, including humans. The pattern, from earliest to latest was as follows: elbow, hip, ankle, knee, wrist, shoulder. This included all of the epiphyses in each region. For example, the elbow included the distal humerus and the humeral medial epicondyle. It has been observed in humans and other primates that this sequence of commonly observed epiphyseal closure does not vary. These commonly observed epiphyses tend to be on long-bones and with a special focus on the wrist. Comprehensive studies are not numerous enough to find inconsistencies between regions such as hand, foot, ankle, and torso fusion events. As previously mentioned, King (2004) surveyed a larger collection of fusion sites by means of discriminant function analysis. He did not produce a seriation of fusion events for each species, and his samples were possibly not large enough for each species to do so with any measurable statistical confidence. However, the discriminant function distinctions found between species suggested that enough consistent variation is present for differences to be predicted if larger samples of epiphyses are compared between different primate taxa.

Epiphyseal fusion sequences always show consistent patterns at a species level. Deviations from the standard pattern are known as sequence polymorphisms. These have been particularly well-documented in humans with the most common of these highlighted in reference texts such as Scheuer and Black (2004). In reality, sequence polymorphisms can be found for almost every epiphysis in humans. The rates of occurrence vary depending on how temporally close together two given epiphysis are. Schaefer and Black (2007) provided a modular sequence of fusion events for human males that included pre- and post- event shifts. For example, the fusion of the humeral medial epicondyle usually precedes the lesser trochanter and is preceded by the femoral head and proximal radius. In a minority of cases this epiphysis is proceeded by the lesser trochanter or precedes the femoral head or proximal radius (Schaefer and Black 2007). Any combination of these variations is potentially observed in an individual. These variations in order are likely consequent of only small differences in timing of fusion onset for closely overlapping events. Schaefer and Black’s (2007) modular sequence for humans was observed only after after collecting data from hundreds of individuals. Consequently, knowledge of sequence polymorphisms for other primates remains unstudied. Observation is limited due to the impracticality of collecting data from hundreds of skeletonized individuals. Simply determining basic sequences for limb and torso fusion is difficult enough without sufficiently large samples.

### Epiphyseal fusion in humans

This section will discuss the types of studies that have been conducted (radiographic and dry bone) and will consider the methodological robusticity of these techniques. Humans of European ancestry are the most extensively studied group and are the source of most data on epiphyseal fusion. Some research of non-European populations has been considered and comparisons with these studies will be discussed.

Radiography and dry-bone studies

Studies of human epiphyseal fusion patterning have been carried out extensively over the past century using both radiographic and dry-bone techniques. The use of radiographic methods has declined in recent decades due to health concerns. Liberal use of radiographic methods in the mid-twentieth century allowed for a number of longitudinal studies to be undertaken. The earliest of these examined a series of Australian children for a larger number of fusion sites (Flecker 1932). Large scale radiographic longitudinal studies have also been conducted including research at the University of Colorado (e.g., Hansman and Maresh 1961), The Brush Foundation at Case Western Reserve University (e.g., Greulich and Pyle 1959, Hewitt and Acheson 1961, Pyle and Hoerr 1955), The Fels Institute at Yellow Springs Ohio (e.g., Garn *et al.* 1967), and the Oxford Child Health Survey (Tanner *et al.* 1983, 2001). From these studies several roentgenographic atlases were produced, including an atlas for the development of the hand and wrist (Greulich and Pyle 1959), the foot and ankle (Hoerr *et al.* 1962), the distal humerus, proximal radius, and ulna (Brodeur *et al.* 1981), and the patella, distal femur, proximal tibia and fibula (Pyle and Hoerr 1955). Tanner *et al*. (1983, 2001) and Greulich and Pyle (1959) produced methodologies for assessment of skeletal age.

Cross-sectional radiographic studies have been less numerous than longitudinal studies. More cross-sectional studies have used dry-bone, as opposed to radiography. Studies of dry bone using of skeletal collections from archaeological sources are naturally cross-sectional. Most of the cross-sectional studies have supplemented or evaluated the atlas methods previously mentioned (e.g., Cockshott and Park 1983, Cundy *et al*. 1988). Subsequent literature produced using radiographic methods has been conducted with the purpose of improving clinical and forensic data on radiographic assessment (e.g., Flores-Mir *et al.* 2004, Schmeling *et al*. 2004). These studies tend to be limited to specific regions that are easily observed such as hand/wrist fusion.

There are some notable limitations to radiography. The method provides images with only a two-dimensional perspective and fusion state can only be evaluated by what can be seen in this image. There has been variation reported with respect to initiation and completion of fusion (Scheuer and Black 2000) and it is very likely that these differences are partly due to uncertainties as a result of methodology. McKern and Stewart (1957) consistently reported older ages for completion of fusion for many sites on dry bone than had been reported in the radiographic literature. This effect may be the result of final-stage fusion scars simply not being visible in radiographs. Problems with radiography were considered in depth during the collection of early radiographic data by Mainland (1953, 1954, 1957), who looked at systematic error, variable error, and comparisons of methods of assessment of roentgenograms. Error in radiographic studies has also been analyzed by Cockshott and Park (1983) who looked at literature data and studies carried out at McMaster University on hand bones and the sacro-iliac joint. Their advice was the use of a more refined statistical approach using kappa statistics in future studies. Cundy *et al*. (1988) use the Greulich and Pyle method in a study looking at children with leg length discrepancies, which were analysed by several radiologists using the Greulich and Pyle atlas, finding significant variation in terms of age assessment.

The assessment techniques used in the early radiographic studies of the 1950’s and 1960’s have been significantly criticised. Acheson (1954, 1957) pointed out that radiographic assessment techniques required the assumption that there was a rigidly fixed order of sequence events, which biased against variation in sequence order. Acheson also criticised the emphasis on chronological as opposed to maturational age. Garn and Rohmann (1963) and Garn *et al.* (1965) showed that wrist ossification centres in early postnatal life were not normally distributed, but were in fact quite skewed towards late infancy. Epiphyseal union likewise showed skewedness, with much longer tails to the older side of the distribution. Such criticisms led to the Tanner method for assessing skeletal maturity from radiographs (Tanner *et al.*1983, 2001) which, instead of comparing to standardized photographs, used the addition of bone elements to produce a maturity score. The Tanner-Whitehouse method has undergone several revisions that are conventionally referred to as TW2 (Tanner-Whitehouse 2) (Tanner *et al*. 1983) and the most recent version TW3 (Tanner-Whitehouse 3) (Tanner *et al*. 2001). The Tanner-Whitehouse method for assessing skeletal maturity is presently the most commonly used for assessing skeletal maturation from radiographs. No application of the aforementioned method has precipitated any large change in accepted timings of fusion events in studies since the 1980s. This may be partly to do with the decline of radiographic work but also when the data that already exists are combined with dry-bone information, there is enough refinement for sequence timings to be estimated with an acceptable level of precision.

A number of dry bone studies have been conducted in addition to radiographic studies, resulting in a large body of data. Epiphyseal fusion had been observed on bones for centuries but the earliest studies which systematically attempted to produce sequences of union were done by Stevenson (1924) and Todd (1930). These studies used samples of European ancestry, which were not always of known-age from the Western Reserve University (Stevenson 1924, Todd 1930). Stevenson (1924) and Todd (1930) looked at a wide range of sites including all the proximal and distal epiphyses of long bones as well as epiphyses on the pelvis. These were followed by a landmark study by McKern and Stewart (1957) of older sub-adults (ages 17-23 years) from American-Korean War dead. They examined virtually everything in the cranial and post-cranial skeleton. In the half century that followed, more studies were conducted for all skeletal elements (e.g., Cardoso 2008, Coqueugniot and Weaver 2007, Schaefer 2008, Webb and Suchey 1985). Modular sequence patterns whereby a seriation of fusion events irrespective of time have been done by Schaefer and Black (2007). Summary data are available in compiled volumes for both forensic and osteological applications such as Scheuer and Black (2004) and Schaefer *et al.* (2009).

Comparisons of different human populations

Even though many studies have focused on humans of European ancestry, there have been number of studies examining non-western populations. Stewart (1934) looked at Native Americans and Inuit using dry bone observations. No substantial differences were noted at that time. The majority of non-western population studies have been from the late twentieth century. A selection of these are listed in Table 2.2. Most of these projects have been cross-sectional radiographic studies using the TW2 and TW3 methodologies (Tanner *et al.*  1983, 2001). Studies of skeletal maturity over the last several decades include examples from northwest India, Japan, and China (see Table 2.2). In Indian children, multiple radiographic studies have reported union times for a variety of fusion centres. Fusion has been evaluated using the TW2 method for the hand/wrist in large samples (Prakash and Cameron 1981) as well as in various other sites such as the proximal humerus, iliac crest, ischial tuberosity, femoral head (Jit and Singh 1971), elbow, and wrist (Sahni *et al*. 1995) (Table 2.2). With respect to differences observed, Prakash and Cameron (1981) noted that carpal maturity differed between their Indian sample and the British standard, with girls reaching carpal maturity at the same times as British girls, but boys showed retardation in comparison to standards for British boys. The amount of deviation varied with age. Jit and Kaur (1989) also determined some differences between northwest Indian and western populations in terms of timing of fusion in sternebrae, finding slightly earlier times for different stages in the Indian populations. Differences in other populations have also been observed using the TW2 methodology. Ashizawa *et al*. (1996) using a large sample of nearly 1500 Japanese children, noted that their sample population attained adult stages one to two years earlier than Belgian (Beunen *et al*. 1990), British (Tanner *et al*. 1983), southern Chinese (Ye *et al*. 1992) and north Indian standards (Prakash and Cameron 1981, Prakash and Pathmanathan 1991).

**Table 2.2** Studies of epiphyseal fusion sequences across different human populations.

|  |  |  |  |
| --- | --- | --- | --- |
| **country** | **study** | **sample size** | **skeletal elements observed** |
| India | Jit and Singh 1971 | ?1. | proximal humerus, iliac crest, ischial tuberosity, and femoral head |
| Sahni *et al*. 1995 | 149 | elbow and wrist joints in girls |
| Prakash and Cameron 1981 | 298 | hand/wrist |
| Jit and Kaur 1989 | 1018 | fusion in sternebrae |
| Japan | Ashizawa *et al*. 1996 | 1457 | hand/wrist |
| Belgium | Beunen *et al.* 1990 | 9698 | hand/wrist |
| China | Ye *et al*. 1992 | 2122 | hand/wrist |

1. Not defined in publication.

The differences that have been observed only relate to age of epiphyseal maturity, as opposed to pattern of fusion. Fusion sequences between these populations did not differ. Schmeling *et al*. (2000) analyzed the results from over 80 radiographic studies conducted on multiple populations, both theoretically healthy and deprived, finding that the order of events does not correlate with specific ethnic groups. Chronological delays of maturation observed in some studies of supposedly healthy populations were most likely due to unforseen environmental stresses not accounted for in such studies. Evidence from individuals of the same ethnic group maturing in different geographic regions supports this argument (Schmeling *et al*. 2000).

It is notable that the majority of these studies consider only hand and wrist fusion. This anatomical area is easy to radiograph and is routinely observed. Large-scale studies comparable to those of western populations encompassing the complete range of fusion sites are lacking, and there is a paucity of dry-bone studies. There are small differences in human skeletal proportions that are related to climatic effects (Ruff 2002) such as the shorter limbs of people living in colder climates. There are not enough complete data sets from these populations to assess whether these variations in allometry have consequences for the sequence order of fusion, although the work of Stewart (1934) suggests no notable deviations exist.

In most aspects of anatomy humans follow consistent patterns between populations. Given that individual variation can lead to ambiguity in small samples, it would seem necessary that large sample sizes would be required for any tendency towards sequence and age abnormalities to become apparent, if they exist at all. The current data suggest that humans as a species encompassing all populations demonstate a consistent pattern of epiphyseal closure. Minor variations in age of maturity have been observed which are likely the result of adverse or beneficial environmental conditions.

Past studies on stressed populations

Even though there exist sufficient data to model healthy human populations, a discussion of the effects of stress and nutritional deficiencies observed in humans is warranted. As shall be shown in section 2.4.6, the effects stress and nutritional deficiency are less well known for chimpanzees and bonobos. Since humans are very closely related, the patterns observed in this species may be informative for the study of deficiencies in *Pan*. This is especially relevant for osteological collections where the history of individuals prior to death is often less clear.

There have been a number of epiphyseal fusion studies assessing living populations undergoing nutritional stress that have considered variables such as weight, stature, cognitive abilities, dental eruption stage and degree of skeletal maturation. The effects on growth due of different forms of nutritional stress such as deficiencies in energy, fat, protein, and minerals are outlined by Roche and Sun (2003). The majority of studies examining skeletal maturation have done so using only radiographic imaging of hand/wrist fusion (e.g., Bogin and MacVean 1983, Bogin *et al*. 1989, Lampl *et al*. 1978, Stini 1969). Studies of archaeological populations have typically looked at the effects of nutritional stress on the pattern of dental eruption, skeletal maturity and predicted stature (e.g., Albert and Greene 1999, Prendergast Moore *et al*. 1986, Stout and Lueck 1995).

Early studies found readily apparent differences. Greulich (1957) compared growth and skeletal maturation of children of Japanese ancestry born in the United States with those born in Japan. These data were collected not long after the Second World War when Japan was in the process of rebuilding and nutritional standards were known to be poor. It was found that the skeletal maturity of Japanese-born children was delayed between 6 and 24 months when compared to the American-born children (Greulich 1957). Sex differences in maturational delay were found by Stini (1969) who examined maturity in Columbian children experiencing nutritional stress. Males were found to be more delayed than females. Later studies include Bogin and MacVean (1983) and Bogin *et al*. (1989) who looked at Guatemalan children, finding a similar pattern of delays in skeletal maturation of the hand/wrist. Again, males showed greater retardation when compared to females. It has become generally accepted that nutritional stress incurs delays in skeletal maturation and that there are sex differences in the severity of these delays. Males appear to be more susceptible to stress delays than females (Stinson 1985, Wells 2000). Studies in other animals also suggest that this pattern is true for many different species (Katz 1980, Lucas 1998, Smart 1977, 1986). Why this disparity exists has been the subject of debate. It has been suggested that the ability to buffer environmental stress is more critical for females due to reproductive demands. Attempts have been made to fit this into the Trivers-Willard hypothesis (Trivers and Willard 1973), where there is genetic selection to favour male health in good environments and male morbidity in bad environments. Evidence from studies looking at sex ratios in various socio-economic groups appears to support this theory (e.g., Almond and Edlund 2007).

Another very important observation of stressed populations is that post-cranial skeletal maturation is affected more severely than dental maturation (Cardoso 2007, Garn and Rohmann 1966, Lasker 1969, Roberts 1981). Dry-bone archaeological studies where multiple maturational indicators have been analyzed often show this pattern (e.g., Prendergast Moore *et al*. 1986). The effect of nutritional deficiencies on the development of the dentition is discussed in section 2.5.2. In osteological research the use of dental age in sub-adults is often preferred to skeletal age when a population is assumed to be under stress (Ubelaker 1987, 1989). In the absence of other evidence, when an individual shows much more advanced dental development when compared to skeletal age, it may be reasonable to consider that there may be something problematic occurring.

Summary of human epiphyseal fusion

For humans there is a large body of data charting the timing and pattern of epiphyseal fusion. These data are derived from both radiographic and dry-bone studies which when combined have provided a reasonable degree of precision in estimation as well as demonstrating the types and level of variation between individuals. Populations have been found to vary slightly with regards to chronological timing of fusion but not sequence. Most of this variation has been considered to be more likely a result of unforseen environmental factors than genetic ones. Nutritional stress has an effect on the timing of fusion but not the overall pattern, with delays appearing to slow down the entire system. Skeletal growth is more susceptible to nutritional stress than dental development.

### Epiphyseal fusion in chimpanzees

There have been both radiographic and dry-bone studies examining epiphyseal fusion in wild and captive chimpanzees, in addition to one histological study (Kerley 1966). These studies have varied in the breadth of epiphyses considered and sample sizes used. The earliest work was done by Schultz (1940) who noted that long bone epiphyses fused between the ages of 7 and 11 years. Kerley’s (1966) histological work used a sample of known-age chimpanzees to observe epiphyseal maturation in 12 femora and 8 humerii. Kerley’s (1966) sample also provided radiographic observations of epiphyseal fusion for other epiphyses which will be discussed below in the context of Bolter and Zihlman’s (2012) study. Subsequent radiographic and dry-bone work has been completed for specific sites. For example, radiographic studies of hand/wrist and foot epiphyseal fusion centres include Hamada *et al.* (1998), Hamada and Chatani (2003), Nissen and Riesen (1949a,b), and Watts (1971, 1985) using captive populations. Table 2.3 provides a list of studies that include epiphyseal fusion and the regions that were assessed.

**Table 2.3** Previous studies of *Pan troglodytes* epiphyseal fusion.

|  |  |  |  |
| --- | --- | --- | --- |
| **skeletal region** | **study** | **type of study** | **sample size** |
| hand/wrist | Gavan 1953 | radiographic | 16 |
| hand/wrist and foot | Hamada *et al.* 1998 | radiographic | 65 |
|  | Hamada and Chatani 2003 | radiographic | 12 |
|  | Nissen and Riesen 1949a,b | radiographic | 16 |
|  | Watts 1971, 1985 | radiographic | ?1. |
| olecranon, proximal and distal humerus | Schultz 1940 | dry-bone | 63 |
| distal epiphyses of limb bones | Winkler 1996 | dry-bone | 10 |
| histology of distal humerus, acetabulum and acromial process | Kerley 1966 | histological | 30 |
| multiple post-cranial fusion sites | Bolter and Zihlman 2012 | dry-bone | 10 |
| (more than one region of the skeleton) | Kerley 1966 | radiographic | 10 |
|  | King 2004 | dry-bone | 86 |
|  | Zihlman *et al.* 2007 | dry-bone | 22 |

1. These values have not been obtained.

It is evident from Table 2.3 that the majority of past studies of specific skeletal elements have focused on hand/wrist and easily observable limb epiphyses. The lack of diversity in different skeletal elements among different studies has meant that a cohesive picture of fusion cannot be ascertained by combining results. There is also a mixture of radiographic and dry-bone research, with radiographic observation exclusive to hand/wrist fusion. The differing sources for the samples of each of these specific element studies also leaves open the possibility of inconsistency between samples due to unanticipated environmental variables such as nutritional stress.

There have been only four mutiple post-cranial fusion site studies, these being Bolter and Zihlman (2012), Kerley (1966), King (2004) and Zihlman *et al.* (2007). As noted previously, King (2004) was not concerned with producing a seriation of fusion events or estimating ages, but rather with placing chimpanzees in the context other primates using discriminant function analysis. As such he made no contribution to describing the pattern of fusion in chimpanzees other than providing insights as to what should be expected given known patterns in other primates. Chimpanzees clustered apart from African monkeys and were distinct from gorillas. The limitation of including both dentition and epiphyseal fusion in the analysis is that it was not possible to determine if these distinctions stemmed from dental or epiphyseal fusion sequence differences. With fusion patterns not explicitly defined in other species it is not possible to deduce fusion patterns in chimpanzees by these observations alone.

Of multiple skeletal region studies, the study that provided information for the most comprehensive list of epiphyses was Kerley (1966) who listed state of fusion for 31 different epiphyses (Table 2.4). However, the determination of fusion sequences in this study was fundamentally limited by sample size for younger age ranges and the number of individuals used for assessing these epiphyses was only 10, as opposed to the entire sample used for histology which was 30. For most epiphyses only one or two individuals was observed to be fusing and for 7 epiphyses no individuals were observed as fusing at all. As such, Kerley’s (1966) data only provides very approximate ages for fusion of elements other than those of later stage. For those of later stages, typically only 5 or 6 individuals contributed data, although with a high degree of overlap sequences were not discernable.

**Table 2.4** Fusion centres observed by Kerley (1966).

|  |  |
| --- | --- |
| **fusion centres observed by Kerley (1966)** | |
| proximal humerus | lumbar vertebrae |
| distal humerus | iliac crest |
| humeral medial epicondyle | triradiate |
| proximal radius | ischium |
| distal radius | femoral head |
| proximal ulna | greater trochanter |
| distal ulna | lesser trochanter |
| metacarpal heads 2-5 | distal femur |
| phalanges (hand) | proximal tibia |
| medial border of scapula | distal tibia |
| acromium | proximal fibula |
| coracoid | distal fibula |
| medial clavicle | calcaneus |
| ribs | metatarsal heads 2-5 |
| cervical vertebrae | phalanges (foot) |
| thoracic vertebrae |  |

Kerley’s (1966) data were very useful for suggesting which epiphyses fall later within the sequence of fusion. These epiphyses were clearly the proximal humerus, the medial border of the scapula, the ischium, the iliac crest, and the medial clavicle. However, Kerley’s sample was derived purely from captive individuals while Zihlman *et al*.’s (2007) more recent work has added comparison with wild individuals for a more limited number of epiphyses. The epiphyses recorded by Zihlman *et al*. (2007) are shown in Table 2.5.

**Table 2.5** Fusion sites recorded by Zihlman *et al.* (2007).

|  |  |
| --- | --- |
| **bone** | **epiphysis** |
| pelvis | ischio-pubic ramus |
| ilium to pubis |
| ilium to ischium |
| pubis to ischium |
| humerus | proximal |
| medial1. |
| distal |
| radius, ulna, tibia, fibula | proximal |
| distal |
| femur | greater trochanter |
| lesser trochanter |
| distal |

1. It is assumed here that medial implies the humeral medial epicondyle.

Zihlman *et al*.’s (2007) sample consisted of 22 individuals, although those that had observable fusion and dental features reduced the measured sample to 9. The estimated age of these individuals relied on tooth emergence which only provided ranges of estimated age. These data did provide some basic dental landmarks by which point fusion had occurred for certain epiphyses based on single individuals. For example, for one individual that had emergence of the permanent canine (approximate age 10.5 to 12.5 years) the triradiate, proximal femur, and distal humerus had all fused. The basic trends that these data could produce were limited to the obervations in Table 2.6.

**Table 2.6** Zihlman *et al*.’s (2007) skeletal maturity in wild chimpanzees.

|  |  |
| --- | --- |
| **skeletal element** | **wild (years)** |
| distal humerus fully fused | female1.: before 12.5 |
| male: before 13.5 |
| acetabulum fully fused | female2.: before 12.5 |
| male: before 14.5 |
| distal femur fully fused | female: before 16.5 |
| male: before 14.5 |
| humeral head fully fused | female: before 16.5 |
| male: before 14.5 |

1. Missing data for one of the three individuals sampled (aged 10.5)
2. Missing data for one of the three individuals sampled (aged 10.5)

Bolter and Zihlman (2012) provided further data from 5 captive individuals, used for a comparison with *Pan paniscus*. They also provided a comparative table for the epiphyses observed including Kerley (1966). This comparison is reproduced in below in Table 2.7.

**Table 2.7** Reproduced comparison of estimated ages for fusion events in Bolter and Zihlman (2012), Kerley (1966), and Zihlman *et al.* (2007) as presented by Bolter and Zihlman (2012).

|  |  |  |  |
| --- | --- | --- | --- |
| **skeletal element** | **Bolter and Zihlman 2012, captive, age in years, *N* = 5** | **Kerley 1966, captives from Yerkes, age in year, *N* = 101.** | **Zihlman *et al*. 2007, wild from Tai National Park, age in years, *N* = 9** |
| ischio-pubic ramus | <0.83 years | n/a | 0.74< *x* <3.76 |
| distal humerus | <6.74 | partial 6–7 | 7.96b< *x* <10 |
| acetabulum | <6.74 | partial 7 | 5.19< *x*c <11.38 |
| proximal radius | 7.3d | partial 9 | 11.38< *x* <12 |
| coracoid | 7.3< *x* <8.54 | partial 9 | 10< *x* <11.38 |
| proximal femur | 7.3< *x* <8.54 | partial 9 | 11.38< *x* <12 |
| distal tibia | <8.54 | partial 9 | 11.38< *x* <12 |
| proximal tibia | partial 8.54 | partial 9-14 | >12 |
| humeral head | 8.54< *x* <11.68 | partial 9-14 | >12 |
| acromial process | 8.54< *x* <11.68 | <10 | >12 |
| iliac crest | partial 11.68 | partial 9-14 | >12 |

1. Bolter and Zihlman’s (2012) comparison was with the same size present for these epiphyses only. Kerley (1966) had small amounts of data for epiphyses that Bolter and Zihlman (2012) did not analyse, although these were very limited to only a few individuals.

Zihlman *et al*. (2007) suggested that older ages of fusion were being observed in their sample. It could be argued given the ranges presented by Kerley (1966) and Bolter and Zihlman (2012) that the ‘real world’ population ranges for captive and wild could easily overlap. With such small sample sizes there were no statistical means to test these assertions. It is worth noting that Bolter and Zihlman’s (2012) captive sample produced ranges younger than Kerley’s (1966) captive sample, potentially indicating the level of variability between small-sample studies.

It is worth noting the level of agreement between specific element studies and the mutiple skeletal region studies considered above. The timings observed in these radiographic studies are generally consistent with the captive range presented in Bolter and Zihlman (2012) and Kerley (1966). Radiographic studies have always only considered captive individuals.

Sex differences

Prior studies have not considered sex differences either for the specific elements observed in radiographic studies, or in the multiple skeletal region studies with the exception of Zihlman *et al*. (2007). They noted differences in chronological age of fusion for the epiphyses observed. It is likely that sample size limitations have prevented meaningful comparisons by sex. The ranges of fusion in terms of years likely overlap and sufficiently large samples are required. There is no comprehensive analysis suggesting differences in sequence between sexes.

Summary

To summarize chimpanzee epiphyseal fusion data, there exist data providing probable ranges of time for fusion of specific elements. Hand/wrist fusion timing has been studied relatively extensively and estimations of timing may be obtained from the aforementioned radiographic studies in Table 2.3. More comprehensive studies of epiphyseal fusion provide wider ranges of fusion timing and are reliant on small sample sizes. Landmark ages by which certain fusion events are likely to have occurred have been proposed but no more precise sequence of events has been observed due to the limitations of the data.

### Epiphyseal fusion in bonobos

The data for skeletal maturation in *Pan paniscus* are much more limited than what exists for its congeneric *Pan troglodytes*. The only study that has focused on bonobo epiphyseal fusion is Bolter and Zihlman (2012) which was based on only 8 individuals. Five of these were from captivity and of known age at death (0.83, 6.74, 7.30, 8.54 and 11.68 years respectively). The remaining three were wild caught and of unknown age. They were aged using dental eruption (Bolter and Zilhman 2012). The spread of ages of these individuals could be considered conducive to a ‘snapshot’ approach of different developmental stages. However, with several year gaps between individuals, especially between later years, this approach was only able to provide very broad estimates. The exact sequence of fusion remained unspecified.

### Comparisons between chimpanzees and bonobos

The aforementioned study by Bolter and Zihlman (2012) is the only comparison of skeletal fusion between the two species that has been completed. As mentioned in section 2.3.6, the timing of fusion for bonobos was derived from a small sample (*N* = 8). The only information these data could provide were some generalized timings of fusion over a period of several years. These data are reproduced in Table 2.8. It should be noted that only 5 of the 8 bonobos observed by Bolter and Zihlman (2012) were used for the comparison and were the ones of known age from captivity.

**Table 2.8** Data comparing chimpanzee and bonobo epiphyseal fusion reproduced from Bolter and Zihlman (2012).

|  |  |  |  |
| --- | --- | --- | --- |
| **skeletal element** | ***Pan paniscus*** | ***Pan troglodytes*** | ***Pan troglodytes*** |
| **captive, age in years (*N* = 5)** | **captive from Yerkes, Kerley 1966, age in years (*N* = 10)** | **Wild from Tai National Park, age in years (*N* = 9)** |
| ischio-pubic ramus | before 0.83 | n/a | 0.74 to 3.76 |
| distal humerus | before 6.74 | partial 6–7 | 7.96 to 10 |
| acetabulum | before 6.74 | partial 7 | 5.19 to 11.38 |
| proximal radius | 7.3 | partial 9 | 11.38 to 12 |
| coracoid process | 7.3 to 8.54 | partial 9 | 10 to 11.38 |
| proximal femur | 7.3 to 8.54 | partial 9 | 11.38 to 12 |
| distal tibia | before 8.54 | partial 9 | 11.38 to 12 |
| proximal tibia | ≈ 8.54 | partial 9-14 | after 12 |
| humeral head | 8.54 to 11.68 | partial 9-14 | after 12 |
| acromial process | 8.54 to 11.68 | <10 | after 12 |
| iliac crest | ≈ 11.68 | partial 9-14 | after 12 |

Bolter and Zihlman (2012) concluded that fusion timings for chimpanzees and bonobos appear to overlap and that the pattern is very similar. They suggested that there may be some slight differences in timing of fusion of the knee joint and the hip between the two species, although there were only two *Pan paniscus* individuals used to make this assessment. What may be drawn from this study is that any substantive deviations in patterning between these species should not be expected. All other evidence of ape and other primate skeletal maturation discussed to this point would support this. Bolter and Zihlman’s (2012) study is a good starting point although limited by sample size. There still remain no studies that compare the two species using more precisely estimated times for fusion.

### Comparisons between chimpanzees, bonobos and humans

Comparisons between chimpanzees and bonobos have been noted in the previous section (section 2.3.7) and it has been assessed that based on the data from Bolter and Zihlman (2012) that the two species are likely similar in pattern given the limited evidence. As far as the state of current research, bonobos fit within a *Pan* pattern of maturation as set by *Pan troglodytes*. As such, comparisons of either *Pan* species to humans are expected to demonstrate the same results. It may be noted that there have been no direct comparisons of bonobo epiphyseal maturation to humans. Given this assumption of equivalence for skeletal maturational patterns in *Pan*, there remains only one comparison in which analysis within the literature may be explored and that is between chimpanzees and humans.

Comparing chimpanzee and human epiphyseal fusion patterns using prior studies is complicated by the differing rates of growth relative to chronological years. Chimpanzees have a shorter overall growth period and a more linear rate of growth (e.g., Hamada *et al.* 1996, Hamada and Chatani 2003, Shea 1981). These differences have effects on the relative timing of epiphyseal fusion events in terms of calendar years. Differences in growth rate and duration introduce inherent problems for studies only looking at single or a few epiphyses. In theory, attempting a proper comparison would require time to be scaled to see if fusion events occur at the same point of growth. The human growth curve has for some time been known to require a minimum of several polynomials to model (Bock and Thissen 1976, Karlberg 1985) and there exists no quantified functional relationship comparing the two species aside from illustrations of growth curve shape. When it is known that the functions are not exactly the same, which indeed they are not, there is no way of knowing if these events are scaled or if they are distorted without the use of a higher-resolution growth parameter that may be scaled to chronological years. The relationship between dental mineralization and chronological years is well-known for chimpanzees but this approach has not been taken for the aforementioned studies of chimpanzee epiphyseal fusion. This may potentially be a consequence of logistical constraints for radiography. Irrespective of whatever reasons may be behind this, only dental emergence reference points are available which provide a much more coarse approximation to age due to this method only producing groupings of epiphyses by periods of years between emergence events. Potentially as a result of the limitation of growth rate differences between the species, single-region studies simply report the ages at which these events occurred without considering comparison to humans. Multiple skeletal-region studies (Bolter and Zihlman 2012, King 2004, and Zihlman *et al*.2007) have had more potential to make comparison to humans at the levels of sequences but none have had sufficient data to complete such an analysis. King’s (2004) methodology did not include human data and focused on sequence relationships within other primate lineages. Bolter and Zihlman (2012) focused exclusively on chimpanzees and bonobos. Zihlman *et al*. (2007) provided ranges of fusion for the individuals in the sample but their study was more concerned with discussing the differences between males and females and comparisons between wild and captive animals. Kerley (1966) was the only study that made direct comment on comparing chimpanzee to human epiphyseal fusion using original data. Kerley (1966) suggested that fusion times for the acetabulum, the distal humerus, and the acromial process may be earlier in sequence for chimpanzees than that reported for humans. Kerley’s (1966) data set was too small to test this assertion.

## Dental development

The study of dental development is both a complex and diverse topic. The use of such information for this study is limited to understanding mineralization and estimated chronological ages of attainment for particular mineralization stages. However, functional morphology and other such parameters such as emergence do play a role in determining selective pressure on growth patterns and as such this section will situate chimpanzee, bonobo, and human dental development within general primate dental patterns. There are known differences between chimpanzee, bonobo and human dentition with respect to emergence chronology and mineralization (Boughner and Dean 2012, Kuykendall and Conroy 1996) and these must be clarified for comparisons to be made. Further study including dental emergence may also shed light on sequence differences.

### Primate dentition and dental development

The depth of information avaliable about primate dentition is variable, depending greatly on species and genera. The largest body of data pertain to great apes. However, general dental patterning and emergence has been assessed in a variety of species.

***2.4.1.a Dental formula***

Compared to other mammalian groups, the dental formula of primates has shown reduction in tooth number over time (Martin 1990). Extant primate dentition follows a pattern with a maximum number of teeth in each category for incisors, canines, premolars and molars of 2.1.3.3. Platyrrhine species show either 2.1.3.2 or 2.1.3.3 while catarrhines follow 2.1.2.3 (Fleagle 1998, Kinsey 1997). Being catarrhine primates, chimpanzees, bonobos, and humans all share the same dental formula.

***2.4.1.b Morphology***

Primate dentition can be morphologically distinct depending on dietary adaptations (e.g., Fleagle and McGraw 1999, Kinzey 1984, 1992). Primate diets vary from folivory to frugivory and various types of omnivory (Fleagle 1999, Nystrom and Ashmore 2008). An analysis of these differences is not directly relevant in the context of this study but it is important to describe morphological differences related to the species used in this study. Chimpanzees and bonobos have more substantial canines when compared to humans. Aside from this one marked difference, the morphology of the dentition is largely similar apart from some minor variation in cusp patterns and some differences in enamel thickness. This likely relates both to recent ancestry and all three species retaining an relatively omnivorous dietary pattern. Chimpanzee and bonobo dentition is also much larger than that of humans as a proportion of body size and facial dimensions, resulting in significant prognathism. Human dental morphology is atypical of a primate species with regards to dimensions and level of non-metric and morphological variation. Size differences may be due to the effects of craniofacial reduction (Bermúdez De Castro and Nicolas 1995, Calcagno and Gibson 1988).

***2.4.1.c Emergence***

A general sequence of emergence for primates was reported by Schultz (1935) and was determined using a number of primate genera including *Cebus, Ateles, Papio, Cercopithecus, Pongo, Hylobates, Pan* and *Gorilla*, using dry-bone observation. This sequence, from earliest to latest, followed the pattern of second decidous molar, first molar, central incisor, lateral incisor, second molar, premolars, canine, and lastly, third molar. This pattern became and has generally remained accepted as a general sequence of primate dental development with further studies refining this using larger sample sizes. General sequences are to be expected among groups of related species but differences appear when observing individuals species in further detail with regards to such variables as crown and root completion times and scheduling relative to other ontogentic events. There are few species where this level of detail is available. It should be noted that humans diverge from this pattern in unusual ways, a fact that is reviewed in section 2.4.2.

***2.4.1.d Radiographic and other studies***

More detailed study of particular primate species has been done for organgutans (e.g., Beynon *et al*. 1991, Dean and Wood 1981), gorillas (e.g., Beynon *et al*. 1991, Kelley and Schwartz 2010,Simpson *et al*. 1992), chimpanzees (e.g., Kuykendall *et al*. 1992, Kuykendall and Conroy 1996, Nissen and Riesen 1964, Zihlman *et al*. 2004), macaques (e.g., Nass 1977), and baboons (e.g., Dirks *et al*. 2002, Phillips-Conroy and Jolly 1988). These include radiographic and histological studies with some studies looking at known-age samples. Humans have been intensively studied with regards to emergence and mineralization patterning as well as chronological scheduling.

### Dental development in humans

In the following sections (2.4.2, 2.4.3 and 2.4.4) chimpanzee, bonobo, and human dental development is considered in greater detail. Provided is an overview of what is known regarding emergence, mineralization and chronological scheduling. Several variables known to affect dental development in these species are also introduced. Sex differences and population differences have been examined, as well as wild versus captive, or in the case of humans, nutritionally stressed versus healthy populations have been considered and these variables are known to have effects.

***2.4.2.a Human dental development***

Dental development in humans has been extensively analysed in both the clinical and anthropological literature. Patterns for mineralization, emergence, and chronological scheduling of permanent teeth are well known. Histological analysis considering perikymata has also been pursued (FitzGerald 1998, Huda and Bowman 1995). Large sample statistics were compiled in the mid-twentieth century by researchers such as Moorrees *et al.* (1963) and Simson and Kunos (1998) among others. This wealth of information is compiled in reference texts such as Scheuer and Black (2000) and Schaefer *et al.* (2009) as well as countless anthropological textbooks such as White (2000). Methods evaluating the morphology and dimensions of teeth either by radiographic of dry-bone observation include Demirjian (1973), Liversidge *et al.* (1998), and Smith *et al.* (1994).

***2.4.2.b Differences by sex in humans***

In humans there are well-documented differences in developmental timing between males and females (Demirjian and Leveseque 1980, Lewis and Garn 1960, Liversidge 2003, Scheuer and Black 2000). Males are consistently delayed relative to females. These delays correspond to equivalent deviations in skeletal development and attainment of maturity (Scheuer and Black 2000). Differences between the sexes relate only to timing of development as opposed to pattern. Such differences are consistent for emergence and root completion, for which there is ample data from both categories.

***2.4.2.c Human intra-species differences***

Variation of both emergence and root completion in both sexes has been explored in multiple populations (e.g., Simpson and Kunos 1998, Liversidge and Speechly 2001, Monge *et al.* 2007). Significant differences in terms of timing have been found between different populations and slight variations in relative timing of sequences have been shown. These differences are often not without dispute as there are clearly sources of error from both unforseen variables in the sample populations such as nutitional and environmental stresses and problems with variable application of methodology. Comparisons of the application of certain methods such as the Demirjian method have been made using different populations (e.g., Koshy and Tandon 1998, Liversidge *et al.* 2006, Nykänen *et al* 1998, Teivens and Mörnstad 2001b) as well as refinement and comparison to other methods (Chaillet and Demirjian 2004, Teivens and Mörnstad H. 2001a). The true nature of population differences may be difficult to confidently articulate. Liversidge and Speechly (2001) evaluated ethnically British children in comparison to ethnically non-British children in the UK and found no significant differences. Reid and Dean (2006) considered enamel striae of retzius in African and European populations finding that these populations largely overlapped. They concluded that histological analysis of enamel mineralization showed less variation than radiographic methods.

For the purposes of this study it is assumed that the differences between populations is not significant for the application of the Demirjian method and that there exists a standard human pattern. Differences for each sex will be taken from those formulas used by Demirjian for comparison to chimpanzees and bonobos.

### Dental development in chimpanzees

Data exist for both wild and captive chimpanzees. Radiographic, dry-bone, and histological studies have been pursued. Dry-bone studies on emergence include Conroy and Mahoney (1991), Kuykendall *et al*. (1992) and Nissen and Riesen (1964) among others. Emergence sequence patterns are established for both wild and captive populations (Smith *et al.* 2013) with considerations of differences between wild and captive emergence timings (Smith and Boesch 2011, Smith *et al.* 2010). Histological work on chimpanzee dentition has been done by Smith *et al.* (2007). Radiographic studies have improved the overall picture of dental development (Anemone *et al.* 1991, Dean and Wood 1981, Smith *et al.* 2010). Studies using known-age individuals include Kuykendall (1996) and Kuykendall and Conroy (1996). These studies used the Demirjian method on captive populations and provide a chronological age estimation for individuals based on root development for both summary scores and individual tooth scores. Comparisons between histology and radiographic studies have suggested that radiographic estimations are largely correct, although they tend to underestimate age slightly (Reid *et al*. 1998). The sequence of complete root mineralization in chimpanzees has been found to be M1 I1 I2 P3 P4 M2 C M3 (Kuykendall 1996) and the sequence of emergence M1 I1 I2 M2 P3 P4 C M3 (Conroy and Mahoney 1991).

***2.4.3.a Captive vs. wild***

It has been suggested that there exists a difference between wild and captive individuals with regards to mineralization as well as emergence. Zihlman (2004) compared Kuykendall’s (1996) assessment of captive ages and suggested that there are differences in development in terms of chronological age of maturation between wild and captive specimens. Smith *et al.* (2010) have challenged this finding whereby some of the ages of the wild specimens were questioned and it was suggested the Kuykendall’s (1996) ages were still very applicable for wild samples. Based on evidence from humans, it would be expected that differences in diet and stress would have an impact on the chronological timing of development. The precise nature of the delays debated by Smith *et al.* (2010) are interesting. It is important to recognise that the delays between captive and wild specimens are not extreme and there is no evidence to suggest changes in sequence pattern. Both captive and wild data are equally as applicable in this regard.

**Table 2.9** Data from Zihlman *et al*.’s (2007) dental delays of wild chimpanzees.

|  |  |  |
| --- | --- | --- |
| **tooth emergence** | **wild chimpanzees (Taï) (years)** | **captive chimpanzees (years)** |
| M1 | ~ 4 | 2.7 – 4.1(1) |
| M2 | ~8 | 5.3 – 7.3(1) |
| M3 | ~12.5 | no data available (10.5(2)) |

1. Conroy and Mahoney 1991

2. Estimated from Schwartz *et al*. 2000

***2.4.3.b Sex differences in chimpanzees***

Differences in dental development between males and females are documented for developmental timing (Kuykendall 1996, Kuykendall *et al.* 1992). It is evident that the overall pattern of dental development is effectively the same for males and females but that the chronological timing of development is consistently delayed in males (Kuykendall 1996). The only exception to consistency in pattern may be the canine where there appear to be larger relative delays in development in males. It has been suggested that emergence timing differences are consistent with this male pattern of delayed chronological development (Zihlman 2004).

***2.4.3.c Population differences in chimpanzees***

Variation in dental developmental patterning for chimpanzees sub-species has not been extensively studied apart from some very simple observations such as molar morphology (Swindler *et al.* 1998). Many of the studies determining *Pan troglodytes* dental emergence and mineralization patterns have used samples with a mix of individuals from different sub-species. When considering that the aforementioned studies of chimpanzee dental development largely agree with each other and use individuals from all different sub-species, it would be expected by inference that any direct comparison of population sub-groups would most likely show no large deviations. For the purposes of this study, we will assume that there are no differences.

### Dental development in bonobos

There is sufficient information available on bonobo dentition to provide a confident assessment of dental development. Research that has been conducted includes histology (Ramirez and Lacruz 2007), radiographic studies (e.g., Boughner *et al*. 2012, Dean and Wood 1981), and emergence (Bolter and Zihlman 2011, Kinzey 1984). Bougher *et al*. (2012) and Dean and Wood (1981) did not use samples of known age for detemining mineralization sequence. However, there is sufficient data in terms of chronological landmarks such as molar emergence timing to harmonize mineralization pattern and chronological age with some degree of certainty.

***2.4.4.a Sex differences in bonobo dentition***

Direct comparisons between males and females with respect to chronological timing have not been made. Boughner *et al*.’s (2012) study had sufficient sample size to test for overt differences in sequence between males and females but this study did not pursue this approach. In this context ‘overt’ is given to mean highly consistent differences as opposed to small variations in frequencies of certain polymorphisms which may often be difficult to discern, even in much larger studies. Given the combined nature of Boughner *et al*.’s (2012) sample it appears that it was assumed that this species did not show differences between the sexes. There is no further evidence that there are differences in either timing or sequence of dental development between males and females in bonobos.

***2.4.4.b Sequence differences between studies of bonobo dentition:***

Ramirez *et al.* (2007) found slightly different results to Boughner *et al.* (2012) but these may have been consequent of the sampling methods using mandibular vs. maxillary teeth, with the maxilla tending to show more advanced development. There were also some slight contradictions in the results between Bolter and Zihlman (2011) and Boughner *et al*. (2012). Bolter and Zihlman (2012) found the sequence [M1 I1 P4 M2 I2] P3 C M3 for the mandibular dentition while Boughner and Dean (2012) determined the sequence to be M1 I1 I2 [P3 P4] M2 C M3. In this context [] enclose teeth that may show sequence polymorphisms, or in other words, changes in sequence order. Those teeth outside the brackets do not vary in order. Again, these differences may be the result of sample size issues with that of Boughner and Dean (2012) being substantially larger.

***2.4.4.c Population differences in bonobo dentition***

There are no studies that exist that compare different populations of *Pan paniscus*. It is inferred and may be expected that no substantial population variability is likely to be observed due to the much more restricted range of this species.

### Comparisons between chimpanzees and bonobos

It has been suggested that the pattern of dental development in bonobos does not differ significantly from chimpanzees (Boughner and Dean 2004 and Boughner *et al*. 2012). Minor variations in emergence and mineralization sequence have been reported between chimpanzees and bonobos. Boughner *et al.* (2012) found that in bonobos the P3 began to mineralize before the canine whereas in chimpanzees the canine and the P3 mineralized at the same time. They found that these differences were only characterised for the initiation of mineralization but not the completion sequence of teeth. A possible exception was that the P3 and P4 completed mineralization at the same time in *Pan paniscus*, while there was an offset in *Pan troglodytes* with P3 completing before P4. Table 2.10 illustrates differences in completion timing found in emergence and mineralization. It should be noted that this table does not indicate reported polymorphisms for the sake of simplicity, and the level of polymorphisms do vary between studies.

**Table 2.10** Sequence variations in completion order reported for mandibular *Pan paniscus* and comparison to *Pan troglodytes*.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **species (study)** |  |  |  |  | **order** | |  |  |
| 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th |
| *P. paniscus* emergence (Bolter and Zihlman 2011) | [M1 | I1 | P4 | M2 | I2] | P3 | C | M3 |
| *P. paniscus* emergence (Kinzey 1984) | M1 | I1 | M2 | [I2 | P3 | P4] | C | M3 |
| *P. paniscus* mineralization (Boughner *et al*. 2012) | M1 | I1 | [I2 | P3 | P4] | M2 | C | M3 |
| *P. troglodytes* mineralization (Kuykendall 1996) | M1 | I1 | I2 | P3 | P4 | M2 | C | M3 |
| *P.* *troglodytes* emergence (Conroy and Mahoney 1991) | M1 | I1 | I2 | M2 | P3 | P4 | C | M3 |

Boughner *et al.* (2012) compared bonobos to chimpanzees and determined that there were no statistically significant differences between the two species with regards to root mineralization pattern. This finding allows for the application of the same scale of dental score to both *Pan paniscus* and *Pan troglodytes*. It should be noted that individual variation, although not statistically significant, does show some patterning with the delay of the second incisor in bonobos relative to chimpanzees. This was also noted by Kinzey (1984). In addition it appears that there is some consistency in the deviation between the emergence of M2 and the mineralization of M2 in both species.

The data for bonobos explored by Boughner *et al*. (2012) did not use individuals of known age. Present knowledge of the chronological timing of dental development relies solely on Bolter and Zihlman (2011, 2012). Similarly to other overall observations of growth and development, chimpanzee and bonobos dental development appears to follow effectively the same chronologic scheduling of dental development.

### Comparisons between chimpanzees, bonobos and humans

Given the previous comparison of chimpanzees and bonobos, these species will be considered to be effectively the same with regards to emergence timing and mineralization sequences. Comparisons between chimpanzees and humans considering both timing and sequence of mineralization have been made in the past. Comparisons for these two species also exist for for timing and sequence of dental emergence.

***2.4.6.a Emergence and mineralization***

For mineralization, Kuykendall and Conroy (1996) noted some significant shifts in sequence between chimpanzees and human dental mineralization. Notable was the delayed crown formation of the canine and the earlier maturation of the first molar in chimpanzees. For the canine, this was potentially a result of the difference in size of these teeth between the two species. The difference was quite extreme, with chimpanzees having substantially larger canines. There were also some other very important differences. Table 2.11 demonstrates human, chimpanzee, and bonobo emergence and mineralzation sequences. It is evident that there is also a polymorphism for M1 and I1 in humans from one study (Garn 1987). The second molar also deviates later in sequence in humans compared to chimpanzees and bonobos.

**Table 2.11** Chimpanzee, bonobo, and human emergence and mineralization sequences.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **species/study** |  |  |  |  | **order** | |  |  |
| 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th |
| *P. paniscus* emergence (Bolter and Zihlman 2011) | [1.M1 | I1 | P4 | M2 | I21.] | P3 | C | M3 |
| *P. paniscus* emergence (Kinzey 1984) | M1 | I1 | M2 | [I2 | P3 | P4] | C | M3 |
| *P. paniscus* mineralization (Boughner and Dean 2012) | M1 | I1 | [I2 | P3 | P4] | M2 | C | M3 |
| *P. troglodytes* mineralization (Kuykendall 1996) | M1 | I1 | I2 | P3 | P4 | M2 | C | M3 |
| *P. troglodytes* mineralization (Kuykendall and Conroy 1996) | M1 | I1 | I2 | [P3 | P4 | M2] | C | M3 |
| *P. troglodytes* emergence (Conroy and Mahoney 1991) | M1 | I1 | I2 | M2 | P3 | P4 | C | M3 |
| *H. sapiens* emergence (Haavikko 1970) | I1 | M1 | I2 | C | P3 | P4 | M2 | M3 |
| *H. sapiens* mineralization (Demirjian and Levesque 1980) | I1 | M1 | I2 | C | P3 | P4 | M2 | M3 |
| *H. sapiens* mandibular eruption (Smith and Garn 1987) | [M1 | I1] | I2 | [C | P1] | [P2 | M2] | - |

1. Teeth for which polymorphisms occur are bracketed by [,].

***2.4.6.b Polymorphisms***

Changes in sequence order of specific teeth found in an individual relative to the expected pattern for their species are referred to as polymorphisms. Humans have been the most extensively studied species for this phenomena and some regularities have been observed. Sequence polymorphisms have been reported by Diamonti and Townsend (2003), Garn *et al.* (1973), Liversidge and Speechley (2001), Nonaka *et al.* (1990), and Smith and Garn (1987). These studies have often used quite larges samples. For example, Smith and Garn (1987) looked at human sequence polymorphisms in a large sample of 6,000 black and white Americans. They found polymorphisms for the mandible at [M1 I1] I2 [C P1] [P2 M2] with [M1 I1] shifts the most common. Diamonti and Townsend (2003) found similar results using a sample of 8,676 children from Australia whom were said to be typically of European ancestry. Studies of children from other populations include South Asians (Kaul *et al*.1975), Japanese (Nonaka *et al* 1990), Malays (Hussin *et al.* 2007) among others. The prevalence rate for the [M1 I1] polymorphism appear to vary from 30% to 50%. The [C P1] [P2 M2] polymorphisms appeared in all groups but less frequently and consistently. The aforementioned studies of other populations have tended to find similar results. Many of the differences observed in these studies have been criticized for inconsistencies in definitions and methodological considerations such radiographic observation techniques (Braga and Heuze 2007).

It is clear that human teeth are suceptible to sequence changes of emergence with relatively high frequencies. The frequency of sequence changes in chimpanzees and bonobos is less clear when considering the studies in Table 2.11. Neither mineralization sequences or polymorphisms agree between studies. There is not enough data to evaluate if the species of *Pan* share the same level of variability as humans. Given that smaller human studies of only several hundred individuals often retain a level of uncertainty as a consequence of sample size, it may be inferred that exceptionally larger samples are critical for finding trends. Another important perspective to consider is sequences of mineralization irrespective of time. Braga and Heuze (2007) considered human teeth by looking at modularity using X-rays of 2089 human children, finding that the incisors and post-incisors may behave as variably independent subsets of teeth. They suggested that a full understanding of sequence variability should not necessarily assume independence of teeth. Emergence and mineralization may also not correlate. Kuykendall and Conroy (1996) found that this may be true for chimpanzees.

The observed variability in polymorphisms for chimpanzees and bonobos appears more likely a consequence of uncertainty caused by small sample rather than an actual species-level difference. It will be assumed for the purposes of this study that these species do not consistently differ in their polymorphic centres and that their dental development schedules are the same. It may also be suggested that the observation of polymorphisms with the sample sized used in this study may or may not have any statistical relevance. Although it has not been directly tested by any of the aforementioned studies, there is no indication that changes in sequence necessarily affect dental score relative to chronological time.

***2.4.6.c Chronological scheduling***

Due to the requirement of known-age samples, tying dental development to calendar years has been studied much less extensively for chimpanzees and bonobos than sequences of mineralization and emergence. The best data for providing estimated ages of completion for chimpanzees come from Kuykendall (1996), Kuykendall *et al.* (1992), and Kuykendall and Conroy (1996). As an anatomical reference, it has been found that the third molar is in occlusion prior to the fusion of the proximal humerus (Bolter and Zihlman 2012, Zihlman *et al*. 2007). Other studies that link chronological time to mineralization have been completed as well (e.g., Anemone *et al*. 1996, Smith *et al*. 2007). For bonobos, there is reliance on the compartively small sample sizes of Bolter and Zihlman (2011, 2012). The data provided by these studies do suggest that there is no remarkable deviation between chimpanzees and bonobos with regards to overall period of dental maturation.

### Assessment of environmental factors affecting dental development: Pathology and systemic stress

It has been found in humans that that the dentition is less affected by systemic insult than is skeletal growth (Demirjian *et al.* 1985, Lewis and Garn 1960, Smith 1991). Archaeological studies comparing skeletal maturation and dental development have found the same result (Cardoso 2007). For chimpanzees there is less data and for bonobos there is none at all. It has been suggest that in primates captive individuals demonstrate advanced dental emergence (Phillips-Conroy and Jolly 1988). Zihlman *et al.* (2004, 2007) compared wild and captive chimpanzee dental developmental, finding that captive individuals were much more advanced when compared to the wild sample. These studies made the assumption that wild individuals were more stressed than captive. These findings were refuted by Smith *et al.* (2010) who re-assessed the same material with some additional individuals. They found that wild and captive emergence timings greatly overlap. Smith *et al.* (2010) also used radiographic methods to further clarify their results. It is important to keep in mind that ‘captive’ and ‘wild’ are not direct analogues of ‘healthy’ and ‘stressed’ and with other environmental variables likely, these studies are inherently ambiguous. Aside from these comparisons, there exist no studies with well-defined stressed and unstressed individuals. Smith *et al.*’s (2010) results may be important for the interpretation of results of studies such as this one where mixed captive and wild individuals are included. Although it cannot be demonstrated that the nutritional status of their sample mirrors that of other skeletal collections, their conclusions suggest that large deviations between captive and wild groups should not be expected.

## Long bone growth in length: Introduction

There are two main factors to consider with respect to long-bone growth and these stem from two separate questions. First, changes in allometry between species and the achievement of these difference during growth must be considered. Mere observation suggests that adult humans limb proportions deviate from the patterns seen in adult chimpanzees and bonobos. It has also been demonstrated that adult bonobos and chimpanzees differ slightly from each other with bonobos having slightly longer femora and feet as well as scapular dimensions (Coolidge and Shea 1982, Shea 1984). However, these differences are slight in comparison with the difference between *Pan* and *Homo*. These differences in allometry have been linked to locomotor behaviour. Humans are strictly bipedal while chimpanzees and bonobos exhibit suspensory and knuckle-walking behaviour. Bonobos may also be somewhat more arboreal with regards to suspensory behaviour than chimpanzees (Doran 1993). It has been observed that differences in proportions of long-bones remain constant from birth to adulthood (Shea 1981).

The second factor to be considered is growth rate. Growth rate comparisons and associated modelling has been the subject of considerable discussion as noted in section 2.1. Humans show notable deviations when compared to chimpanzees and bonobos, particularly an extended adolescence (Bogin 1999b). This will be explored in section 2.5.4.

### Long bone growth rates in humans

Similarly to all other aspects of human growth, changes in bone length have been well-documented. Studies using large samples conducted in the late twentieth century established general patterns of long-bone length. Both pre- and post-natal values were determined using cross sectional and longitudinal data. Such studies for pre-natal growth include Fazekas and Kósa (1978) and Jeanty (1983). Post-natal length values were determined for all long bones by Maresh (1970). Other studies looking at individuals bones or groups of bones include Ghantus (1951) and Gindhart (1973). More recent longitudinal study results are provided by Smith and Buschang (2005). Data of this nature are compiled in edited volumes such as Scheuer and Black (2004) and Schaefer *et al.* (2009).

***2.5.1.a Sex differences***

Humans are sexually dimorphic with adult females smaller than males on average, although there is considerable overlap between the two sexes. Similarly to other primates, females mature in advance of males. Compiled data from sources such as Scheuer and Black (2004) and Schaefer *et al.* (2009) demonstrate earlier female maturation and subsequent male catch-up growth. These patterns result in differences in size and timing of maturation between the sexes.

***2.5.1.b Population variation***

Humans have been known to exhibit differing long-bone allometry and a number of comparisons have been made between different adult populations (e.g., Holliday and Ruff 2001). The majority of differences appear to relate to tibial length and correlate with different climate conditions. Sub-adult variation in different population groups have been considered by archaeological studies (e.g., Mensforth 1985, Miles and Bulman 1994). Minor deviations have been found with regards to changes in length relative to skeletal maturity. However, within such studies it can often be difficult to differentiate between the effects of nutritional stress on long-bone growth and actual differences related to healthy population affinities. Archaeological populations can also provide less-than-optimal sample sizes and no records about the individual during life. The causal factors underlying the minor variations observed are unlikely to be related to activity. It has been argued that climate affects post-cranial limb-length (Holliday 1997, Newman 1953, Pearson 2000, Ruff 1994, Weaver and Steudel-Numbers 2005). Genetic drift may also be a possibility, although this has not been investigated. For the purposes of this study the standards provided by reference texts such as Scheuer and Black (2004) and Schaefer *et al* (2009) will be used.

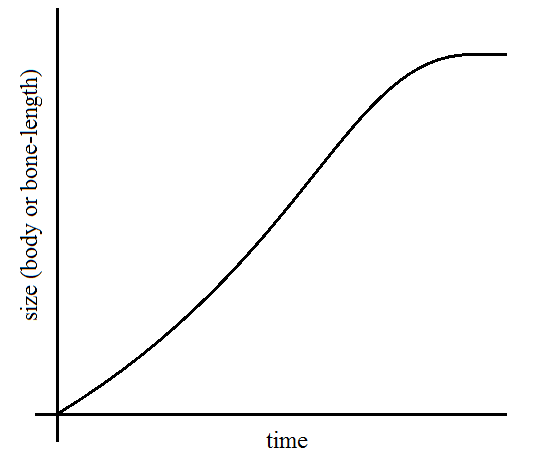
***2.5.1.c Stressed populations***

Some studies have attempted to explore the effects of nutritional stress (e.g., Jantz and Owsley 1984, Hoppa 1992). Retardation of skeletal growth and reduced adult stature as a result of nutritional stress has been documented (Bogin 1999a). Within the context of this study, reliable data from healthy populations are available but it is worth noting in the context of such evidence that relative delays are statistically significant for human populations. Similarly to dental development, this does not prove that such effects are also true for chimpanzees and bonobos, but given the physiological similarity between the two species, it is certainly a worthy point to note.

### Long bone growth rates in chimpanzees

General patterns of growth in chimpanzee long-bones have been studied in both longitudinal and cross sectional samples for both wild and captive animals. The majority of this work has tended to be cross-sectional with longitudinal studies only looking at captive individuals using small sample sizes. Early cross-sectional work was completed by Shea (1981) and early longitudinal work with captive specimens by Gavan (1953) and Smith *et al.* (1975). General discussion of growth rate can be found in Watts and Gavan (1982). Leigh and Shea (1996) performed non-parametric regression analysis on a large sample of chimpanzees and have produced body weight functions. It should be noted that long-bone growth as a function of Demirjian dental score has not been examined in prior studies.

Chimpanzee growth relative to calendar years follows a curve with a slight slowing of rate in juvenile or mid-growth stages and a slight increase of rate at adolecsence, or near the completion of growth, after which there is a dramatic slowing. This observation is both in terms of long-bone length and overall body weight. Figure 2.3 demonstrates what a typical growth rate progression for chimpanzees looks like.

**Figure 2.3** Demonstration of growth rate pattern of chimpanzee size relative to chronological time.

***2.5.2.a Sex differences***

Shea (1981) compared chimpanzees to gorillas and bonobos using dental emergence. He also provided detailed analyses of growth rates of different indicies and assessment by sex. Females were typically advanced in growth relative to males with subsequent catch-up growth exhibited by males. Cross-sectional work by Zihlman *et al.* (1990) and Zihlman *et al.* (2007) has confirmed the patterns found by Shea (1981). Size differences between adult males and females is only slight in chimpanzees (Richmond and Jungers 1995) and is unlikely to be distinguishable in sub-adult dimensional growth.

***2.5.2.b Populations differences***

Analysis of the allometric differences between adults of different sub-species has been made (Morbeck and Zihlman 1989). However, no studies have compared long-bone growth in different sub-species of chimpanzees.

***2.5.2.c Comparisons of captive and wild:***

It has been argued that there are differences between wild and captive chimpanzees with respect to growth rate and final adult dimensions. In humans it has been well-documented that nutritional differences have a significant impact on both rate of growth and final adult height, which is a consequence of reduced limb length (Bogin 1988, 1991). Evidence in humans has relied on comparisons between extant populations and known low socio-economic status archaeological populations. Similarly to dental development, for chimpanzees it has been proposed that wild populations are more stressed than captive ones and that the same principles of delay and reduced growth found in humans applies. Kimura and Hamada (1996) have confirmed this assertion when they found advanced development of long bones in captive chimpanzees relative to wild samples. They also found that captive individuals were larger than wild individuals at cessation of growth, a particular feature that has been noted by others (Coe *et al.* 1979, Hamada *et al.* 1996, Kraemer *et al.* 1982, Matsuzawa *et al.* 1990, Zihlman *et al.* 1990). It appears that unlike dental development there are clear distinctions between captive and wild for this species with respect to long-bone growth.

### Long bone growth rates in bonobos

Similar to other aspects of development, research on long bone growth in bonobos is more limited. Data are available for adult dimensions (Coolidge 1933, Coolidge and Shea 1982, Shea 1983). Studies of adult dimensions have usually been conducted with the objective of comparison with chimpanzees. Studies providing dimensional information on growth in sub-adult bonobos are limited to Shea (1981, 1983, 1984). Shea analysed limb dimensions and overall somatic growth. The sample used was quite small (*N* = 7). Based on these data, it became evident that bonobo growth rates were similar to that of chimpanzees. With such limited data, it is evident that captive and wild comparisons have not been made. There are again no different populations available for comparison.

### Comparisons between chimpanzees, bonobos, and humans

As mentioned in section 2.6.3, Shea (1981, 1983, 1984) compared sub-adult bonobos and chimpanzees. These studies are the only direct comparisons between the two species with respect to growth rates. At present, however, it can only be concluded that bonobo and chimpanzee long-bone growth rates are effectively the same.

In section 2.1 growth rates and allometry were discussed. There are evidently many comparisons of overall somatic growth such as Hamada *et al.* (1996), Hamada and Udono (2002), Schultz (1960), among others. Adult dimensions are well-documented and adult allometry has been considered in the context of differing locomotor behaviour between humans and chimpanzees (e.g., Jungers 1982, Myatt *et al.* 2011). As noted in section 2.5.2, dimensions and rates for growth of individual long-bones have been determined by Shea (1981, 1983, 1984). Despite differences in growth rates making comparisons problematic, Shea (1983) suggested that humans do not develop their bipedally adapted long-bone dimensions during growth, rather, these exist from birth.

Due to the relatively large samples of sub-adult individuals that are required, no further studies have pursued sub-adult allometric change comparisons beyond Shea’s work. Much more research has been done comparing cranial allometry, as mentioned in section 2.1. This lack of study depth may relate to craniometric variables being less tied to locomotion than post-cranial ones. Shea’s evidence also suggests that static allometry consistency between chimpanzee sub-adults and adults indicates that further research into sub-adult allometry would not likely provide any additional insights.

## Summary of current knowledge of Homo and Pan life history variables

In this chapter a wide range of topics have been covered discussing growth and development in *Homo* and *Pan*. Key variables from each section will now be summarised.

### Summary of developmental theory

The concept of heterochrony has been introduced and changes in growth rate and pattern have been considered. Within this subject the concepts of neoteny and hypermorphosis have been explored. These have been used to explain the difference between human and ape development. The debate over the validity of each was considered and it was demonstrated that there is no widespread agreement with respect to these issue. It is clear that for some areas such as sequence heterochrony and the comparison of different systems that more data are required. This study will assist in making up some of these deficiencies.

### Summary of epiphyseal fusion

It is clear that comprehensive data exist for humans with sequence timing well-established. Sex difference in terms of fusion timing have been observed. Current research suggests that population affinities are unlikely to affect pattern of fusion. Populations in which minor differences have been observed have tended to also be stressed populations and as such make results less reliable. Nutritional stress has also been shown to delay fusion timing.

For chimpanzees most epiphyseal fusion sites have been observed at some point but sample sizes and levels of precision for age ranges vary dramatically. Methodology is also inconsistent between studies. As such, a well-defined sequences using a large sample size have yet to be achieved. Population comparisons have not been considered for epiphyseal fusion in chimpanzees. Comparisons of captive vs. wild have shown some differences, although sample size limitations have rendered the level of deviation unclear.

For bonobos the only work on epiphyseal fusion sites has been Bolter and Zihlman (2012). Data for the effect of stress on growth has not been acquired. There are no population sub-groups to compare for this species.

Differences between species/sub-species:

Epiphyseal fusion comparisons between chimpanzees and bonobos are limited to Bolter and Zihlman (2012). This study found that there were generally no differences between the species. However, the sample size was small and only very generalized ranges were obtained for fusion timing. Comparisons of chimpanzees to humans are restricted to the basic observations of Kerley (1966) for three fusion sites. Such comparisons are made problematic by the lack of precision for age ranges of fusion events and growth rate distortions between *Pan* and *Homo*. It is evident that large sample sizes are necessary for refinement of understanding in skeletal fusion for *Pan*.

### Summary of dental development

Human dental emergence and mineralization have been well-established with many large-sample studies spanning multiple populations and covering healthy and stressed individuals. Sex differences in timing have been determined. Different populations have shown minor differences for mineralization pattern in some studies but not others. It is not entirely clear what the effect of population is but it is likely that any real differences are minor. Nutritional stress has also been shown to affect dental development. It has been documented that this system is less susceptible to systemic stress than skeletal development.

Emergence and mineralization timings are documented for chimpanzees. Sex differences are known to exist. Comparisons of different populations are lacking for mineralization and emergence. It should be noted that many of the studies of dental development agree with each other and these studies have often employed data from different populations. By inference it should be expected that deviations are not great, if present at all. Data comparing captive and wild as a proxy for stressed and unstressed populations have potentially shown some differences (Zihlman 2004), although the evidence for this effect has been challenged (Smith *et al.* 2010).

Bonobo dentition has been less extensively studied but emergence and mineralization timing is available. Nutritional stress effects have not been investigated. There are no sub-species to compare.

There are well-documented differences in both mineralization and emergence timing between chimpanzees and humans. Chimpanzees and bonobos have been compared by Boughner *et al*.(2012) with the conclusion that patterns of mineralization are not distinguishable between the species. Both species of *Pan* may be considered dentally analogous for the purposes of this study.

### Summary of long-bone growth in length

Metric changes in length of long-bones are well known for humans. Sex differences are known to exist both for timing and overall dimensions, with females smaller than males. Minor population differences have been documented. Some studies looking at these differences may suffer from acquiring data from using populations that are environmentally stressed. It should be noted that inconsistencies found between populations do not appear to relate to behavioural differences in terms of locomotion but rather, refer to differences of climate adaptation or potential genetic drift. Nutritionally stressed populations show notable delays in growth. Nutritionally stressed populations also show reduced stature. Data from large studies of healthy populations are available in reference texts such as Scheuer and Black (2004) and Schaefer *et al*. (2009).

Growth of chimpanzee long-bones has been observed in multiple studies. Sex differences are known, with females in advance of males. Wild samples have been found to be retarded in growth compared to captive samples, lending support to the presumption that wild samples are more stressed.

Information on bonobo long-bone growth is limited to the work of Shea in the 1980s. Long-bone growth rates were determined using a small sample across differing ages.

Shea’s (1981) work suggests that bonobos do not dramatically differ from chimpanzees, although his sample size was small. Comparisons of chimpanzees, bonobos, and humans have suggested that these species maintain static allometry for growth in length of long-bones (Shea 1981, 1983).

### Summary conclusion

Much data exist on chimpanzee growth and development but there are notable areas where information is lacking or is derived from small samples. No studies have integrated all three variables of epiphyseal fusion, dental mineralization, and long-bone length in a single study for either species of *Pan*.

# Materials and Methods

## Materials: The Collections

### Definition of species used

The skeletal collections used contained several sub-species of *Pan*. The species and sub-species of *Pan troglodytes* require some definition. The classifications of chimpanzee sub-species here are as defined by Groves (2001), and the differences have been described based largely on geographic separation (Ely *et al.* 2005). The sub-species of chimpanzees are *Pan troglodytes schweinfurthii*, *Pan troglodytes troglodytes*, *Pan troglodytes verus*,and *Pan troglodytes* vellerosus. Morphological differences including both soft tissue and the skeleton are not as clearly defined with only small amounts of comparative data available. It has been suggested that differences heavily overlap (Morbeck and Zihlman 1989). Based on mitochondrial DNA, the divergence between all of the different sub-species occurred around 900 000 years to 400 000 years before present (Hey 2010). These groups are not genetically isolated and have been observed to interbreed at the margins of their ranges (Yu *et al.* 2003). With regards to growth and development, no studies have focused on developmental differences between sub-species. Most studies of ontogeny have treated the individuals involved simply as members of *Pan troglodytes* without sub-species affiliations. Some studies have included mixed samples which have been treated without consideration for sub-species (e.g., Kuykendall *et al.* 1996). There has been effectively no research comparing different sub-species of chimpanzees using rigorous methodology.

Groves (2001) also defines *Pan paniscus* for the area south of the Congo River. There are no defined sub-species of bonobos.

### Species and sub-species

In total there were 219 specimens assessed in this study from which 214 were derived from three main collections: the Powell-Cotton Collection (Birchington, United Kingdom), the Adolph Schultz Collection at the University of Zurich (Zurich, Switzerland), and the Museum of Central Africa Collection (Tervuren, Belgium). Five additional specimens were obtained from the Weston Park Museum (Sheffield, United Kingdom). Table 3.1 indicates the number of specimens used at each location and the species/sub-species evaluated. The numbers for each individual sub-species of *Pan troglodytes* are partly derived from classification based on museum records and partly derived from re-assignment based on information provided by curatorial records at these collections. These re-assignments are justified in the discussion of provenance in section 3.1.2. It should be noted that the majority of *Pan troglodytes* sub-species were classified as either *Pan troglodytes schweinfurthii* or *Pan troglodytes troglodytes*.

**Table 3.1** Number of individuals for each species/sub-species listed by collection.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **species/sub-species** | **Powell-Cotton Museum** | **Adolph Schultz Collection** | **The Museum of Central Africa** | **Weston Park Museum** | **total** |
| *Pan paniscus* | 0 | 1 | 36 | 0 | 37 |
| *Pan troglodytes troglodytes* | 69 | 2 | 3 | 0 | 74 |
| *Pan troglodytes schweinfurthii* | 0 | 0 | 47 | 0 | 47 |
| *Pan troglodytes* | 0 | 46 | 5 | 5 | 53 |
| Unspecified *Pan* | 0 | 0 | 5 | 0 | 5 |
| total number of individuals | 69 | 49 | 96 | 5 | 219 |

The information provided for each specimen was variable both between and within collections. As indicated by Table 3.1, sub-species designation was reported for virtually all specimens at the Museum of Central Africa and the Powell-Cotton Museum. This was not true of the specimens from the University of Zurich where nearly all individuals were reported as being simply *Pan troglodytes*. How the determination of sub-species was made was never specified in any collection. It is likely that such information was deduced from records of geographic origin. Sub-species reports were accepted in this study for those specimens from the Museum of Central Africa due to collection location information agreeing with currently understood regions in which these sub-species reside. This was not the case for the Powell-Cotton Collection samples where there was a significant contradiction between the geographic area reported and the known range for the sub-species reported. All samples were reported there as being *Pan troglodytes schweinfurthii* (*Pan satryus schweinfurthii* on record cards) while the locations noted in museum records indicated that these samples all were derived from a region that can be confidently assigned to *Pan troglodytes troglodytes* (see section 3.1.2 regarding provenance of these collections for further analysis of geographic constraints). Geographic records at the Powell-Cotton Museum were both specific and consistently reported, providing the name of the location as well as longitude and latitude. The records that assigned these samples to *Pan troglodytes schweinfurthii* may have been using out-dated classification information. The use of the term ‘*satyrus*’ would suggest this. The dates in which these records were made were not provided. Given this information, it was decided to re-classify the *Pan troglodytes schweinfurthii* samples from the Powell-Cotton Museum as *Pan troglodytes troglodytes* for the purposes of this study.

### Provenance

The information provided regarding provenance for each specimen was variably reported. Table 3.2 provides the captivity status for each species. For most specimens it was possible to establish if the individual was captive or wild, although for a few specimens this information was not available. These were samples in which the collector’s name was given but no additional information was provided.

**Table 3.2** Captive vs. wild by species

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **species/sub-species** | **wild1** | **captive2** | **ambiguous3** | **not reported4** | **total** |
| *Pan paniscus* | 31 | 1 | 1 | 4 | 37 |
| Unspecified *Pan* | 2 | 0 | 0 | 3 | 5 |
| *Pan troglodytes* | 8 | 2 | 42 | 6 | 58 |
| *Pan troglodytes schweinfurthii* | 37 | 2 | 0 | 8 | 47 |
| *Pan troglodytes troglodytes* | 72 | 0 | 0 | 0 | 72 |
| entire sample | 150 | 21 | 5 | 43 | 219 |

1. Wild indicates that some descriptive term indication geographic origin was presented.
2. Captive indicates that there is a reference to a zoo or other captive circumstance.
3. Ambiguous indicates that in the description the origin simply refers to the individual collector such as ‘collected by Pilette.’
4. Not reported means that no information was given.

***3.1.2.a Provenance at the Museum of Central Africa***

At the Museum of Central Africa [MCA] the exact location or region where the individual was found was reported for many of the specimens. It should be noted that many of the MCA specimens which had been listed as being obtained from the Antwerp Zoo may have originally been wild animals. Their capture age and duration of time spent within the zoo was not specified. Due to the lack of records and the paucity of information regarding their origins, it shall be assumed for the purposes of this study that these had always remained captive animals. Table 8.1 in the appendix lists the reported locations for the wild specimens from the MCA.

***3.1.2.b Provenance at the Powell-Cotton Museum***

Virtually all of the specimens at the Powell-Cotton Museum had curation cards that provided species name, sex, locality, latitude and longitude, head and body measurements, span, height, girth, anatomical parts present and additional notes. A date was also provided, although it is not clear what this date represents. These dates were mostly from the 1930s. Virtually all individuals were listed as ‘*Pan satyrus* (*schweinfurthii*).’ As discussed below, it is unlikely that these specimens are members of this sub-species and they will be referred to here as members of *Pan troglodytes troglodytes*. Of these individuals, 45% were recorded as being collected from a single region of Cameroon, the Obala, Batouri District. The remainder of the specimens were also from various parts of Cameroon with the exception of one individual which had come from the Congo. Numbers of individuals from each location are available in Table 8.2 in the appendix.

Current classification indicates that *Pan troglodytes schweinfurthii* and *Pan troglodytes troglodytes* inhabit non-overlapping regions in central Africa. *Pan troglodytes schweinfurthii* resides north and east of the Congo river while *Pan troglodytes troglodytes* is located in the western margins of central Africa covering territories in Gabon, Congo and Cameroon (Stumpf 2007). These geographic subdivisions suggest that the entire sample from the Powell-Cotton Museum can be confidently re-assigned to the sub-species *Pan troglodytes troglodytes*.

***3.1.2.c Provenance at the Adolph Schultz Collection, University of Zurich***

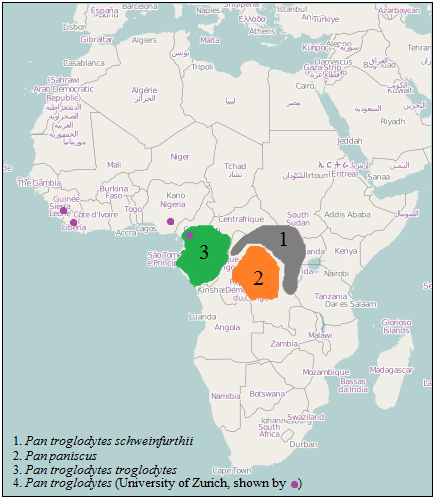
As indicated by Table 3.1, all of the specimens from the University of Zurich were ascribed *Pan troglodytes* without sub-species classification. A handful of individuals had geographic origins provided in curation records. These individuals were only specified to the country or region. The specimens from Liberia and Sierra Leone can be confidently ascribed to the sub-species *Pan troglodytes verus* as those two countries an entirely encapsulated by the range of this sub-species (Sugiyama 1989, 2004). The specimen from Equatorial Guinea may be assigned to *Pan troglodytes troglodytes* for the same reason. This country is entirely within the range of this sub-species (Stumpf 2007). This is also true for the Nigerian specimen, which can be classified as *Pan troglodytes vellerosus* (Sommer *et al*. 2004). Provenance for specimens at the Adolph Schultz Collection are listed in Table 8.3 in the appendix.

***3.1.2.d Provenance at Weston Park Museum***

There were five individuals from Weston Park Museum in Sheffield. Four of these had no provided information on provenance. One individual was reported to have come from Bostock’s Jungle, a local equivalent of a Zoo, and thus has been considered a captive animal for the purposes of this study. All of these individuals were reported as belonging to *Pan troglodytes*.

***3.1.2.e Summary of geographic origins***

Figure 3.1 provides a summary of the known geographic origins for the individuals in this sample. The samples of *Pan troglodytes* from the University of Zurich are identified by dots indicating the locations from which individuals were derived. The ranges for *Pan paniscus, Pan troglodytes schweinfurthii*, and *Pan troglodytes troglodytes* represent geographic regions where those species are found.



**Figure 3.1** Map showing the distribution of all major sub-species and the locations of individuals from the University of Zurich. (Image created using Open Street Map)

### Sex

Sex was not determined in this study by any means other than curation records. No osteological determinations were made for individuals that did not have reported sex. Sexually dimorphic features such as larger canines, more prominent brow ridges, differing facial morphology and overall greater robusticity in males (Cobb and O’Higgins 2007, Leutenegger and Kelly 1977) can be assessed in adults with relative ease but this is not necessarily the case for sub-adult individuals. Chimpanzees and bonobos show some similarity to humans with respect to the fact that these features are not as overtly visible if present at all during at earlier stages of development and thus make confident sex determinations difficult. The number of individuals present by sex for each species/sub-species is shown in Table 3.3. It is of particular note that females out-numbered males for both *Pan paniscus* and all the *Pan troglodytes* sub-species. This was a pattern that appeared at all institutions with the exception of Weston Park Museum where there was only one individual of confirmed sex.

**Table 3.3** Number of individuals listed for each sex by species and sub-species.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species** | **total no.** | **male**  **#** | **male**  **%** | **female**  **#** | **female**  **%** | **unknown**  **#** | **unknown**  **%** |
| *P. paniscus* | 37 | 17 | 46.0 | 13 | 35 | 7 | 19 |
| *P. troglodytes* | 54 | 19 | 35 | 27 | 50 | 7 | 13 |
| *P. troglodytes schweinfurthii* | 47 | 15 | 31 | 17 | 36 | 15 | 32 |
| *P. troglodytes troglodytes* | 74 | 29 | 39 | 45 | 61 | 0 | 0 |
| *P. troglodytes verus* | 2 | 0 | 0 | 2 | 100 | 0 | 0 |
| *P. troglodytes vellerosus* | 1 | 1 | 100 | 0 | 0 | 0 | 0 |
| *Pan species* (unspecified) | 5 | 0 | 0 | 0 | 0 | 5 | 100 |
| total | 219 | 81 | 36.99 | 104 | 47.49 | 34 | 15.53 |

Table 3.3 includes all individuals (wild, captive, ambiguous and unreported). To ensure that there was no significant sex bias by captivity status, analysis of the data Table 3.4 will be considered. These data indicate the number of individuals reported by sex for each provenance category. This includes all species and sub-species. The pattern whereby there are more females than males is also repeated in each sub-category of Table 3.4. When the wild specimens are sorted by sex and by species, the results can be seen in Table 3.5.

**Table 3.4** Number of individuals for each sex by captivity status.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **captivity status** | **male** | **female** | **unknown** | **all specimens** |
| captive | 7 | 9 | 14 | 30 |
| wild | 55 | 70 | 14 | 139 |
| ambiguous | 2 | 4 | 1 | 7 |
| not reported | 16 | 23 | 4 | 43 |
| total | 80 | 106 | 33 | 219 |

**Table 3.5** Wild specimen numbers by sex sorted by species and sub-species.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **species/sub-species** | **male** | **female** | **unknown** | **total** |
| *Pan paniscus* | 14 | 9 | 7 | 30 |
| *Pan troglodytes schweinfurthii* | 12 | 13 | 7 | 32 |
| *Pan troglodytes troglodytes* | 27 | 44 | 0 | 71 |
| *Pan troglodytes* | 2 | 4 | 0 | 6 |

There can be several observations made regarding these distribution patterns. With the exception of the *Pan paniscus* sample, the relative proportions of males, females, and unsexed individuals was consistent between species, sub-species, and within captive and wild categories. Overall the percentage of individuals with unknown sex was low at 15.5% for the entire sample. Males out-numbered females for all groupings of *Pan troglodytes* with 41% of sexed individuals of this species (excluding unknowns) being male and 59% female. Equivalent values for *Pan paniscus* were 57% male and 43% female. Despite these values not representing a perfectly even sex distribution, the do provide values that are quite acceptable for use in analysis of both sexes for both species.

### Completeness of the collections and condition: statement by collection

To further clarify which elements were required, bilateral assessments (both left and right sides) were taken for each individual and as such a complete skeleton was desirable. A statement simply quantifying presence or absence of skeletal elements at this juncture is not especially meaningful for understanding the feasibility of analysis. For example, the presence or absence of epiphyses has an impact on long-bone length and as such a list of numbers of each long bone would need to be qualified by the presence or absence of one of both of its epiphyses. Likewise with dentition, the presence or absence of teeth may or may not have an influence on the assessment of dental score (see section 3.4) and thus simply listing presence/absence values will not assist in understanding the effectiveness of data presence/absence for the analysis of results. Due to the complex nature of this, the completeness of elements used is described within each methodology section. The following provides the location of all completeness analyses within this chapter. Each of these analyses is completed for both species and both sexes independently.

Dentition:

1. Bilateral assessment of dentition by species including tooth presence and completion of quadrants: section 3.4.1 and 3.4.2.

Epiphyseal fusion:

1. Number of bilateral epiphyseal fusion site records: section 3.5.1
2. Number of complete epiphyseal fusion centre data points: section 3.5.1

Long-bone length:

1. Number of bilateral measurements for long bone length: section 3.6.1 and 3.6.2
2. Number of complete long bones: section 3.6.3

Cortical condition and state of preservation are important factors to consider as poor preservation may lead to difficulty in making assessments regarding epiphyseal fusion and ultimately with regards to error in measurement. For all of these collections the state of preservation was very good. Provided here is a brief statement for each collection regarding collection condition.

The condition of cortical bone for the Powell-Cotton Museum skeletal collection was extremely good. Some cut-marks were visible but this had no impact on the sites used for data collection in this study. Post-mortem fractures of long bones were not notably present and as such long-bone lengths could be obtained for virtually all long bones available. Epiphyses were often found glued to the ends of the bones.

In the Museum of Central Africa skeletal collection the cortical condition was generally good with most bones having no visible surface damage. Some specimens showed mild surface erosion. Some cut-marks remained due to disarticulation but these did not impede data collection. None of these specimens had decay severe enough to be considered a problem for evaluation of epiphyseal state or length measurements. Similarly to the Powell-Cotton Museum, epiphyses were often found glued. A few skeletons were articulated using wires, which created some difficulties for measurement and this was noted during data collection. Residual cartilage and liagmentous material made assessment difficult for hand and foot bones in some samples.

The skeletal collection at the University of Zurich demonstrated good cortical preservation with most bones having no visible surface damage. Some cut-marks remained due to disarticulation but these in no way impeded data collection. Many of the skulls had the top portion of the cranium removed, presumably for extraction of the brain for post-mortem examination or preparation. The piece of bone that was removed, which included parts of the frontal, parietal, and occipital, was not often present.

The individuals from Weston Park Museum were articulated on stands and intended for display. These skeletons retained a considerable amount of cartilage and ligamentous material making assessment difficult.

### Observation of pathological conditions

A variety of pathological conditions are known to affect skeletal development (Bogin 1999a, Scheuer and Black 2000). Many such conditions are not visible osteologically, but some may be symptomatic in the skeleton such as linear enamel hypoplastic defects in dentition which can be an indication of periods of nutritional stress among other things. The inclusion of only healthy individuals is desireable for the study of ontogeny. However, when using skeletonised collections with often limited information about the individual during life and cause of death, there is no means to conclusively demonstrate that all individuals were free of pathological conditions. In addition, many observed disturbances in skeletonised individuals may not represent an insult to normal development or the pattern of development. In humans there is evidence that nutritional stress may cause chronological delays in skeletal maturity (Bogin 1999a) but there is no evidence that the pattern of fusion events changes. It has been noted that dental development is less susceptible to systemic stress than is skeletal development and as a consequence, discrepancies may develop between expected skeletal and dental maturation (Cardoso 2007). Here the assumption is that chimpanzees and bonobos fundamentally operate on the same principles. Some evidence does suggest that this is true from comparisons of wild and captive chimpanzees (Zihlman *et al.* 2007).

As a matter of establishing criteria in which to accept a sample for data collection, only very overtly pathologically affected individuals were discounted. In other words, individuals excluded were those that appeared to have very obvious and severe systemic changes in bone structure such as substantial cortical remodelling and deformation of bones and teeth (Table 3.6). Only two individuals from the Museum of Central Africa fell into this category. Other potentially pathological conditions were subsequently observed during data collection and instead of immediately rejecting that individual, the condition was simply noted by verbal description. Analysis of variation potentially caused by pathological conditions can be found in sections 3.5.1 (Determining combined sample values for analysis of epiphyseal fusion). Evidence of fractures was also recorded. In the entire sample there were 9 individuals with clear evidence for fractures that were either healed or in a state of non-union and 3 which were suspected of having had a healed fracture with extensive remodelling.

**Table 3.6**  The three major categories of pathological conditions that were observed in the study populations.

|  |  |
| --- | --- |
| **condition** | ***N*** |
| suspected infection | 18 |
| linear enamel hypoplasia | 9 |
| other unidentified disturbance | 24 |
| total observed pathological individuals | 51 |

### Inclusion of species and sub-species for analysis

The numbers of each sub-species (Table 3.3; see section 3.1.3) show that the frequency of each sub-species divided by sex were typically in the range of 15 to 30 individuals. When considering that the number of individuals exhibiting unfused, mid-fusion, and complete fusion categories would be an even smaller sub-set of these groups, the available data would provide insufficient sample size. For *Pan paniscus* there were only 37 individuals in the entire sample. In the *Pan troglodytes* sample it was possible to group both at the species and sub-species level. In humans as well as other animals, variation in timing and pattern of growth is commonly observed and as such large sample sizes are desired to encompass as much of this variation as possible. This, coupled with the fact that sub-species comparisons would make the analysis impractically large for a single study, meant that it was decided from this point forward to only look at species-level comparisons. Information on sub-species and provenience will be retained for future analysis.

## Methodology: Data collection

### Overview of data categories

The study of skeletal growth and development is a significant area of research that encompasses many different types of information ranging from morphometrics to specific cellular processes. This particular study is concerned with tying together certain key variables of skeletal development in *Pan* and *Homo*. Selecting an appropriate and practical number of variables of study is necessary. There are three main types of information that are considered here: epiphyseal fusion, dental development, and long-bone length. The analysis of these variables in conjunction with each other will provide an important contribution to present literature.

These data were collected and compiled into a single database. Demographic data collection and developmental age range parameters are described in sections 3.2.2 and 3.2.3. The manner in which the data were collected for each major data type is outlined for dental recording (section 3.2.4), epiphyseal fusion (section 3.2.5), and long-bone length measurements (section 3.2.6).

### Demographic data

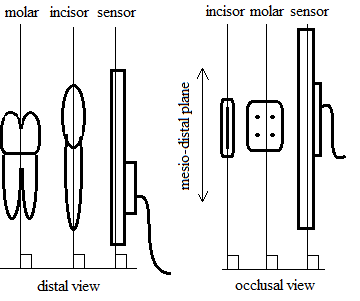
As indicated in section 3.1, as much data as possible were recorded for each specimen regarding provenance, sex, and species/sub-species affiliation. The original museum specimen numbers have been retained and any and all additional information was collected including such things as known mass (weight) and height of the individual at the time of death.

### Developmental age range

The specimens used for analysis included all age groups from the youngest individual available (neonates) to the point where there is full epiphyseal fusion of all bones with no residual fusion scarring for all but the last remaining epiphysis or epiphyses if there was more than one. This last remaining epiphysis had to be fused with only a residual scar line. This allowed for the collection of data purely from sub-adults and not requiring redundant data collection from fully mature adults. The last remaining epiphyses to fuse were found to be either the iliac crest or the medial clavicle for all species and sub-species used in this study. This was determined by surveying all older sub-adults and adults in each collection prior to commencing full-scale data collection.

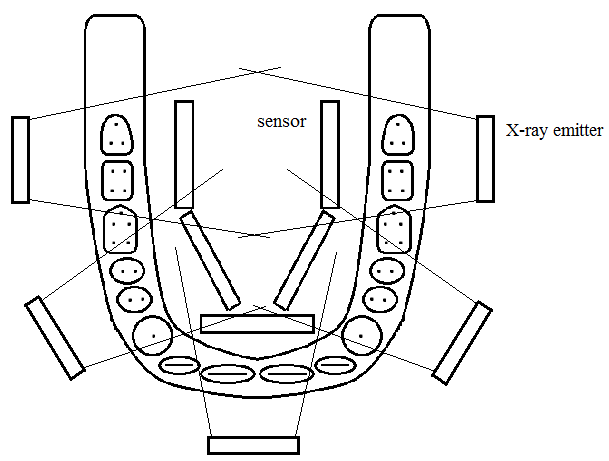
### Dental recording

Radiographs were taken for mandibular and maxillary teeth using a low-dosage, portable dental X-ray (Aribex NOMAD Pro®) provided by the Glover Laboratory at the University of Sheffield. The sensor used by this device obtained images 36.0 x 25.6 mm. This allowed for imaging of typically not more than three teeth per exposure. A system whereby the mandible was placed on foam mountings was devised and the sensor was put on the lingual side parallel with the plane of the tooth. Demirjian scores were used to assess dental maturity. This will be described below in section 3.2.4a. A fundamental requirement for the production of images used in assessment of Demirjian scores was to have a view of each tooth with the axis from the apex of the crown to the tip of the root positioned parallel with the sensor. It was also necessary to have each tooth oriented such that the mesio-distal plane was also parallel with the sensor. A demonstration of this is shown in Figure 3.2. It should be noted that the illustration in Figure 3.2 is only for showing the orientation of the teeth relative to the sensor and does not indicate distance from the sensor. In all cases the teeth were placed as close as possible to the sensor.

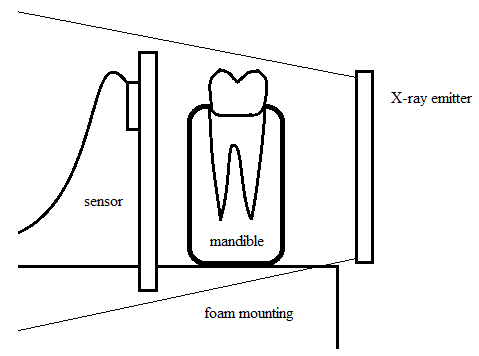


**Figure 3.2**  Demonstration of tooth orientation as shown from distal and occlusal views.

The standard mandibular imaging positions used are shown in Figures 3.3 and 3.4. These images demonstrate the positions of the sensor with all permanent dentition present under ideal conditions. In practice, there existed some variation between adults with respect to the morphology of the mandible with the lingual dimensions of the mandible sometimes making these standard positions impractical. In progressively younger individuals where interior dimensions of the mandible were smaller and more constricted, the sensor positions shown in Figure 3.3 had to be modified. In such cases, the sensor was placed in a position such that the plane of the sensor was parallel with the mesiodistal plane (Figures 3.4 and 3.5). This often involved taking additional X-rays in order to properly record all teeth. The distance between the teeth and the sensor was kept as close as possible in order to minimise distortion of the xray image. The assessment of dental maturity by Demirjian scores does not require direct measurements of teeth but it does require teeth to be parellel with the sensor or film as shown above in Figure 3.2. Increased distances raise the likelihood of distortions due to changes in angle of the tooth relative to the plane of the sensor being less obvious to the naked eye.



**Figure 3.3** Occlusal view of typical positions for mandibular X-ray imaging.



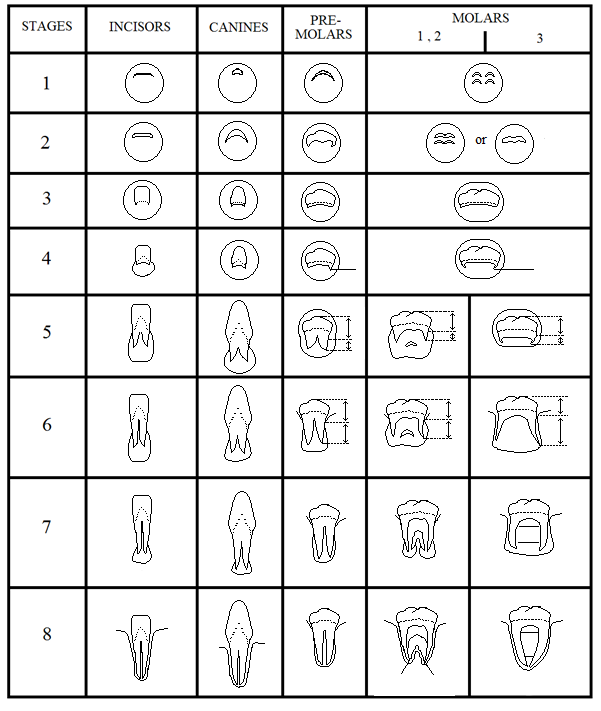
**Figure 3.4** Cross-sectional view of the mounting system for X-ray exposure of mandibular teeth.



**Figure 3.5**  Demonstration of the foam mounting system with a mandible in place (photo is author’s own)

***3.2.4a: Description and justification of the use of the Demirjian system***

To score the X-ray images the Demirjian method was used (Demirjian *et al.* 1973) which is a standard method for assessment of dental maturity in humans. The method was applied to 8 teeth. Prior studies of chimpanzee dental development such as Kuykendall (1996), Kuykendall *et al.* (1992), and Kuykendall and Conroy (1996) also used this method of dental scoring to assess maturity using known-age individuals. Kuykendall (1996) provided regression equations estimating chronological age of attainment from Demirjian score for both 7 and 8 teeth (third molar included or excluded). This is the most refined means for estimating age in skeletal collections of chimpanzees available without known ages being provided. The application of the method to bonobos requires some caution in the sense that Kuykendall’s work did not apply the method to this species. It could be argued that the application of the method is permissible provided that it is understood that this application is made on the basis of information derived from other studies. This information is as follows: Boughner *et al*. (2012) have indicated that patterning of bonobo mineralization likely does not differ from chimpanzees. Bonobo emergence timings also do not notably differ from chimpanzees as far as current research indicates (Bolter and Zihlman 2011). Assuming that Bolter and Zihlman’s (2011) comparatively small sample size predicted reliable ranges for emergence, it would seem likely that bonobos mineralization timings converge upon very similar values. Figure 3.6 demonstrates the Dermirjian developmental stages and Table 3.7 explains the criteria for each stage.

****

**Figure 3.6** Demirjian dental scoring stages redrawn from Demirjian (1973).

**Table 3.7** Definition of Demirjian scoring stages (Reproduced from Kuykendall 1996, Kuykendall *et al*. 1992, Kuykendall and Conroy 1996).

|  |  |
| --- | --- |
| Stage 1 | In both uniradicular and multiradicular teeth, the initial calcification is visible in the superior region of the tooth crypt as one or a series of inverted cones. There is no fusion of these calcified points. |
| Stage 2 | Fusion of the calcified points form one or several cusps which unite to give a regularly outlined occlusal surface. |
| Stage 3 | a) Enamel formation is complete at the occlusal surface. Its extension and convergence towards the cervical region is visible. |
| b) Beginning of a dentinal deposit is present below the enamel crown |
| c)The outline of the pulp chamber has a curved shape at the occlusal border. |
| Stage 4 | a) Crown formation is complete to the cementoenamel junction. |
| b) The superior border of the pulp chamber in uniradicular teeth has a definite curved form, being concave toward the cervical region. If the pulp horns are present, they give an outline like an umbrella top. In molars, the pulp chamber has a trapezoidal form. |
| c) Beginning of root formation is observable in the form of a spicule |
| Stage 5 | *Uniradicular teeth:* |
| a) The walls of the pulp chamber form straight lines, but may be interrupted but the presence of pulp horns |
| b) Root length is less than crown height. |
| *Premolars and Molars:* |
| a) Initial formation of the radicular bifurcation is visible as either a calcified point, or a semilunar mass. |
| b) Root length is still less than crown height |
| Stage 6 | *Uniradicular teeth:* |
| a) The walls of the pulp chamber approximate an isosceles triangle. The apex ends in a funnel shape |
| b) Root length is equal to or greater than the crown height. |
| *Molars:* |
| a) The calcified region of the bifurcation has developed further down from its semilunar stage to give more definition to the roots, which have funnel-shaped endings. |
| b) The root length is equal to or greater than the crown height. |
| Stage 7 | a) The walls of the root canals are parallel (distal root in molars). |
| b) The apical ends of the root canal are open, but NOT funnel-shaped. The periodontal membrane bulges around the root apices. |
| *c )* Proximal and distal roots of multiradicular teeth are parallel--root elongation is complete |
| Stage 8 | a) The apical end of the root canal is completely closed (distal root in molars). |
| b) The periodontal membrane has a uniform width around the roots and apices |

### Epiphyseal Fusion Recording

Epiphyseal fusion centres observed in this study were chosen with the specific objective of including sites that have been recorded in prior study as well as adding further elements that have yet to be observed in the literature. Tables 3.8 and 3.9 outline the fusion centres observed in this study.

**Table 3.8** Upper body epiphyseal fusion sites recorded.

|  |  |
| --- | --- |
| **bone** | **epiphysis** |
| humerus | proximal epiphysis fusion |
| distal capiptulum/trochlea/lateral epicondyle fusion |
| distal medial epipcondyle fusion |
| radius | proximal epiphysis fusion |
| distal epiphyses fusion |
| ulna | proximal epiphysis fusion |
| distal epiphyses fusion |
| hand | distal phalangeal epiphyses fusion |
| base of metacarpal 1 fusion |
| proximal and middle phalangeal epiphysis fusion |
| heads of metacarpals 2-5 fusion |
| clavicle | medial epiphysis fusion |
| lateral epiphysis fusion |
| scapula | coracoid process fusion |
| sub-coracoid centre and glenoid epiphysis fusion |
| acromial epiphysis fusion |
| medial border |

**Table 3.9** Lower body epiphyseal fusion sites recorded.

|  |  |
| --- | --- |
| **bone** | **epiphysis** |
| femur | femoral head fusion |
| greater trochanter fusion |
| lesser trochanter fusion |
| distal epiphysis fusion |
| tibia | proximal epiphysis fusion |
| distal epiphysis fusion |
| fibula | proximal epiphysis fusion |
| distal epiphysis fusion |
| foot | calcaneal epiphysis fusion |
| talar epiphysis fusion |
| distal phalanges, middle phalanges, metatarsal heads 2-5 fusion |
| proximal phalanges and base of metatarsal 1 fusion |
| pelvis | tri-radiate epiphysis fusion |
| anterior inferior iliac spine fusion |
| iliac crest fusion |
| ischial epiphysis fusion |

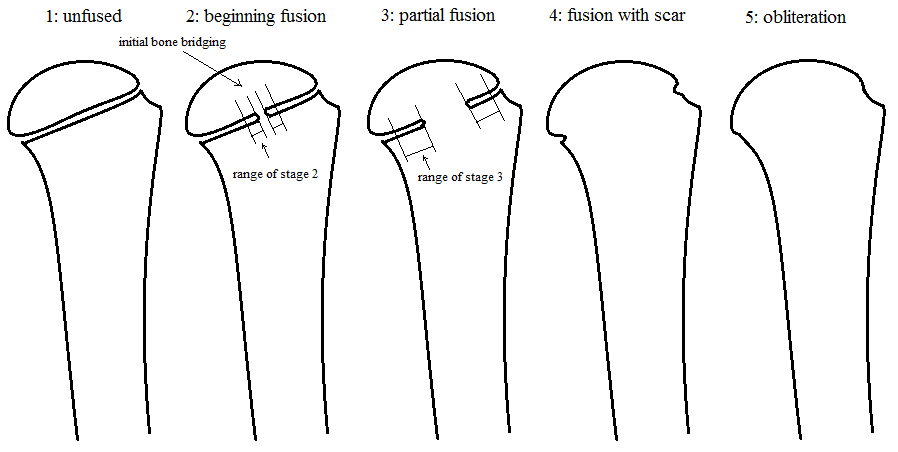
The selected sample is not an exhaustive list of all epiphyses present in the developing individual. There are other epiphyses present in the spinal column and on the ribs which were not evaluated because they are considerably more difficult to observe in osteological collections. Ribs are often broken or lost, and the epiphyses for these bones are very thin and easily broken. These sites were also not considered to be necesary for satisfying the core objectives of this study. The included epiphyses are exhaustive for all long bones, hand and feet. This study also observes all epiphyses of the pelvic and shoulder girdle with the exception of the pelvic ramus. The ramus was often encased in cartilage and difficult to observe. These regions are of particular interest for the study of changes in locomotory behaviour between bonobos, chimpanzees, and humans.

***3.2.5.a Epiphyseal Fusion Stages: scoring system***

As noted in Chapter 2 (section 2.2.1 and 2.2.2), there have been many studies of human epiphyseal closure and multiple scoring systems employed using both dry-bone and radiographic methods. Prior studies of chimpanzees have also employed both radiographic and dry-bones methodologies describing differing states of fusion with varying levels of detail. Some studies have simply reported ‘fused’ and ‘unfused,’ while others have recorded degrees of mid-fusion, such as ‘partially fused.’ This variation is the result of difficulties of observation encountered with two-dimensional images. The system used in this study was designed to permit comparison with prior and future studies, and describes ‘fused,’ ‘unfused,’ and three mid fusion stages. This information could always be reduced by assigning partially fused scores to a simpler ‘fused’ category for comparisons with studies where fewer stages have been recorded. It shall be shown in this study a similar reduction was required as a consequence of limited sample size of individuals fusing at each individual epiphysis (see sections 3.5.1 and 3.5.2). A description of the stages is presented in Table 3.10 and a graphic representation is provided in Figure 3.7.

**Table 3.10** Description of epiphyseal fusion stages observed.

|  |  |  |
| --- | --- | --- |
| **stage** | **basic description** | **detailed description** |
| 1 | unfused | The epiphysis is detached and may or may not yet be ossified. |
| 2 | beginning fusion | Bone bridging is visible at the earliest stage. Fusion does not appear to exceed more than 1/3 of the surface area of the hypertrophic zone. |
| 3 | partial fusion | Fusion of the epiphysis has completed between 1/3 of the surface area of the hypertrophic zone and a near completion state with a cartilage zone not less than 2 mm in depth. |
| 4 | complete fusion with scar | There is a scar or fusion line of no greater than 2mm in depth. Any visible remaining scar classifies the epiphysis at this stage even if there are areas of obliteration. |
| 5 | complete fusion with obliteration | There is complete obliteration of the fusion scar line. No fusion scar is visible at any point. |

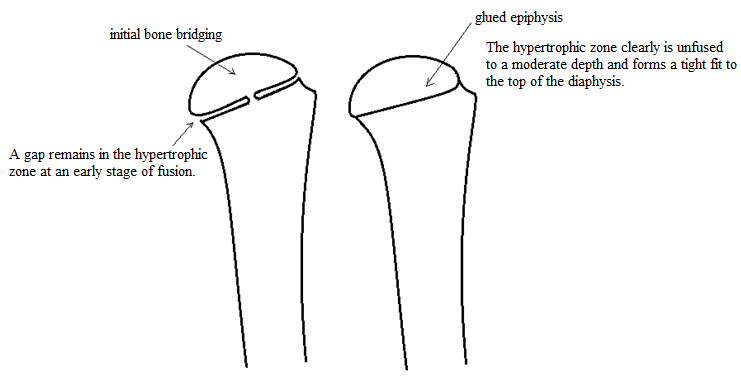


**Figure 3.7** Visual demonstration of epiphyseal fusion stages.

It should be noted that that the fused area was not directly measured for stages 2 and 3, where a fractional ratio of hypertrophic area is referred to. It would have been neither possible nor practical to find a means to exactly quantify this relationship for a large sample. Visual estimation was deemed sufficient. The error analysis in section 3.4.5 suggests that this type of assessment is consistent irrespective of the knowledge of exact areas. This is due to the fact that these ratios were chosen based on very visually distinct phases. Epiphyseal fusion is a continuous process, and these stages are meant to provide basic parameters used for the estimation of beginning fusion, partial fusion, and fusion with remaining scar.

There are two main problems encountered in the observation of epiphyseal closure. The first is a consequence of the curation process and this is the practice of gluing epiphyses to the diaphysis. Although this is not acceptable for modern collections, it was quite common in the early to mid-twentieth century when these collections were developed. This practice appeared frequently in the Adolph Schultz and the Museum of Central Africa collections. Confident detection of early fusion was assigned when a bone bridge was visible between the epiphysis and the diaphysis, but if an epiphysis was attached and no bone bridge was visible, a number of steps were taken to try and rule out the presence of glue. When glue was clearly extruded from the edge of the hypertrophic zone, a confident assessment of unfused could be made. This was the most common case observed. Occasionally glue was not obviously extruded and could only be detected by inspection of the hypertrophic zone.

In some instances glue was ‘suspected’ but could not be seen and no bone bridges were visible. This scenario happened typically with large long-bone epiphyses such as the proximal humerus and the distal femur. The reason the term ‘suspected’ is used in this case is due to the unusual nature of fusion, if fusion had actually occurred. When epiphyses are unfused there is a carilagenous complex that makes up the gap between the ends of the diaphysis and the epiphysis when bones are de-fleshed. This gap decreases in height with age and is typically 2-3mm in thickness for long-bones in humans just prior to fusion (see analysis by Byers *et al*. 2000). When fusion initiates, the closing of the gap begins in the centre and progresses outwards towards the sides (Scheuer and Black 2004), thus leaving a well-defined space at the sides. These gaps are present in all mammals. It was observed in data collection for this study that epiphyses in mid-fusion states for chimpanzees and bonobos appear to have gaps consistent with humans in terms of height. When bone bridges are beginning to appear between the epiphysis and the diaphysis at the point that the animal has died, the epiphysis is locked in place by the bone bridges and that gap of 2-3mm remains at the edges despite the dissapearance of the cartilage. When an unfused epiphysis is glued the gap is closed and the epiphysis forms an unusually ‘tight fit’ to the diaphysis. In the event that there was reasonable grounds to suggest that this was the case a designation of ‘unfused’ was assigned. This problem was also mitigated somewhat by the practice of taking bilateral measurements, although often if one side was fused then the other was also fused.



**Figure 3.8** Demonstration of glued epiphysis.

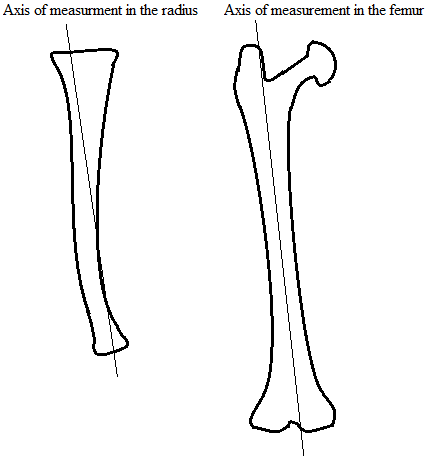
For some individuals, the bones had not been properly cleaned and a dried cartilage remained. This cartilage could have the effect of ‘glueing’ an epiphysis to the diaphysis, as it had in life. Dried cartilage is semi-transparent and an attempt was made to ‘see into’ the cartilage on these individuals to observe if bone briding was occuring. If an assessment could not be made, a score was not recorded and the site was reported as being obscured by cartilage. This issue was not as problematic for projecting fusion timing as might be expected due to the tendency for the individuals with remaining cartilage to be very young and not of an age when epiphyses begin fusing. It is quite possible that the cartilage was left as a means of keeping the epiphyses in place while in older individuals this was less of a concern. The issue affected not more than 10% of individuals, most of which were found at the Museum of Central Africa.

### Long-bone measurements

Similarly to the study of long-bone length in humans, the orientation of the bone had to be standardised. The description of the orientations used in this study are presented in Table 3.11. Measurements were taken for all long bones (humerus, radius, ulna, femur, tibia and fibula) using an osteometric board. The axis of all long bones was taken be a straight line directly through the main shaft of each bone. The radius and ulna in chimpanzees and bonobos are more curved than in humans due to more substantive forearm musculature and this had to be accounted for in measurements. An example of the axis of measure being projected through the radius is presented in Figure 3.9.

**Table 3.11**  Description of bone orientation for length measurements

|  |  |
| --- | --- |
| **bone** | **orientation** |
| humerus | bone is positioned with the posterior surface on the board. |
| radius | bone is positioned with the posterior surface on the board. The bone naturally tilts laterally |
| ulna | bone is positioned with the posterior surface on the board. The bone naturally tilts medially |
| femur | bone is positioned with the posterior surface on the board. The distal end lies flat causing lateral rotation of proximal end. |
| tibia | bone is positioned with the posterior surface on the board. The bone naturally tilts medially |
| fibula | the distal articular surface is placed facing the surface of the osteometric board |



**Figure 3.9** Demonstration of the axis of measure through the radius and femur.

Epiphyses present a problem for measurement of long-bone length in sub-adults. All long bones were measured regardless of whether epiphyses were present or not. An analysis of epiphysis presence and number of contributing long bones to complete long-bone length is provided in section 3.6. A coding variable was added for each bone that determined which epiphyses were present. This coding was as follows:

Code 1: no epiphyses present

Code 2: only the proximal epiphysis is present, the distal is missing

Code 3: only the distal epiphysis is present, the proximal is missing

Code 4: both epiphyses are present.

It should be noted that for some individuals falling within codes 2-4, one or both epiphyses were present but were not fused. As discussed previously with respect to glueing, epiphyses that are not fused actually form a tighter ‘fit’ to the diaphysis than fusing ones due to the gap present for the hypertrophic zone. This presented a slight challenge for measurement as there is a small difference between what the length would be with or without the hypertrophic cartilage. There was no means to correct for this at the measurement stage. It was determined that it was better to hold the epiphyses in place rather than simply taking the length of the bone without the epiphysis. The hypertrophic zone for a fusing epiphysis is is typically 2-3mm in thickness (Byers *et al*. 2000). This thickness constitutes little more than 1% of length for all long bones at stages measured and was likely of little statistical relevance.

## Methodology: Dental development

### Overview of data processing in dental development

It was desired in this project to produce comparable results with other studies using established techniques. Prior research of *Pan troglodytes* such as Kuykendall (1996), Kuykendall *et al*. (1992), and Kuykendall and Conroy (1996) used the Demirjian (1973) method to analyse a single quadrant of the mandibular dentition. In the present study this method was applied to produce a single summary dental score for each individual. In order to achieve this, several steps of analysis had to be first completed. As with most museum collections, missing teeth leading to missing data was a constant problem. Maximizing the number of individuals with dental scores was desireable as sample size was a limiting factor. The additional information provided by having two separate mandibular quadrants was useful for side substitution to make complete sets. For some individuals, mandibular scores were incomplete. In order to achieve the most complete set of scores the technique of multiple imputation was applied (Schafer 2000). This method was able to generate scores for 9 individuals that had incomplete dentition, bringing to the total number of individuals used in the epiphyseal fusion analysis to 177. Complete analysis is found in section 3.3.3.

### Assignment of dental scores

Dental scores were assigned with values from 1 to 8 using the Demirjian (1973) method for all adult mandibular dentition including both left and right quadrants. Additional codes (9 and 10) were added. The score of 9 represented missing tooth information whereby either the section of the mandible was missing or the socket was clearly present but the tooth was absent. The score of 10 represented no evidence for tooth presence. This was confirmed initially by visual observation of no socket presence or perforation of alveolar bone and subsequently by radiographic analysis.

The score of 10 requires some further clarification with respect to the analysis here. This score did not provide a reason for the absence of the tooth. There were a few potential causes of a tooth being absent and thus assigned a score of 10. The first was if an individual was too young to have a mineralized third molar. The second when a tooth was missing due to either agenesis or decay/trauma, either of which counts as missing data with respect to dental score. There are two ways of processing this type of missing data. Either the score represents a very young individual and counts as a ‘0’ when generating the summary score, or it represents a missing tooth category and is treated as missing data. Based on the analysis of Kuykendall (1996) and Kuykendall and Conroy (1996), if an individual had a first molar of at least stage 3 a third molar crown was very likely to have been present. Any individual with a first molar of this stage or higher was considered to be missing the tooth and thus was re-classified as having missing data. All individuals in the data set were recoded as either ‘0’ or ‘-’ with ‘0’ representing lack of development and ‘-’ representing missing data.

***3.3.2.a Recoding and completion of sets***

A composite score was calculated since only a single dental score for each individuals was required. All individuals had the potential to provide left and right quadrant scores. Not all individuals had complete dentition and many individuals were missing teeth. There were three conditions in which individuals in this study could be classified:

Condition 1: when both sets were complete for both quadrants of the mandible. In this case a summary score for both left and right was available for all 8 teeth.

Condition 2: when only one quadrant (left or right) mandibular score was complete.

Condition 3: when neither side was complete.

***3.3.2.b Comparison between sides for individuals in Condition 1***

Past research suggests that a statistically significant difference between sides for *Pan troglodytes* is not to be expected (Kuykendall *et al*. 1992) but a small amounts of individual variation and sample error would be entirely likely. To what extent this would hold true for *Pan paniscus* is not known but it is assumed this species would show a similar pattern. A trend towards directionality in deviations would also suggest the possiblity of inconsistency in the application of the Demirjian method. Table 3.12 summarises the variation found.

**Table 3.12** Number, direction and percentage of deviations between sides of the mandible

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **species** | **left minus right** | | **total number present1.** | **% of deviations2.** |
| *Pan paniscus* | minus3. | 5 | 98 | 6.1% |
| plus4. | 1 |
| *Pan troglodytes* | minus | 13 | 593 | 4.4% |
| plus | 13 |

1. The total number of pairs of teeth present for bilateral assessment. The total number of teeth is double this value.
2. The percentage of cases out of the total number of tooth pairs where there was an asymmetry between sides.
3. The deviations in which a negative number appeared as the difference.
4. The deviations in which a positive number appeared as the difference.

In chimpanzees it was found that the vast majority of individuals had no difference between sides (96.6%). Of the deviations between sides, there was a perfectly even split between positive and negative deviations, suggesting the variation was random. The percentage of cases which had identical scores for both sides in bonobos was also high with 94.9% showing the same value for both sides. The deviation appears biased towards the right side. By using a binomial probability equation it is possible to show that the two sides do not differ and the deviations are erroneous or random.

Binomial probability equation:

|  |  |  |  |
| --- | --- | --- | --- |
|  | P(k out of N) = | N!  k!(N-k)! | (pk)(qN-k) |

In this instance, k refers to the number successes (minuses), N refers to the total number of trials (both pluses and minuses), and p/q refer to the probability of success and failure (in this case both are equally probable). If it is assumed that the probability of positive or negative values would be p/q = 0.5, N = 6 and k = 5, then using the binomial probability equation our P(k out of N) = 0.09375. If the cut-off at P(k out of N) = 0.05 is set then we fail to reject the null hypothesis.

***3.3.2.c Conditions 2 and 3***

For Condition 2, where only one side (left or right) had a complete score, the only complete score present was simply placed in the final score variable. For some individuals with mandibles in Condition 3 where neither left nor right had complete dentition, there was the possibility of producing a ‘complete’quadrant by combining missing values from either left or right scores. Dental scores were thus possible for individuals with a number of missing teeth. Table 3.13 shows the number of complete scores for both left and right quadrants by species. Note that composites included all individuals with a complete quadrant plus those with assembled quadrants derived from individuals with Condition 3 where left and right teeth were combined to make a full quadrant.

**Table 3.13** Number of complete scores for both left and right quadrants by species.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **species/sub-species** | **total sample** | **complete right mandibles** | **complete left mandibles** | **complete composite mandibles** |
| *P. paniscus* | 37 | 14 | 13 | 22 |
| *P. troglodytes*1 | 177 | 116 | 130 | 145 |
| unidentified *Pan* | 5 | 4 | 4 | 4 |
| total | 219 | 134 | 147 | 171 |

1. combined *Pan troglodytes* includes all sub-species

Complete composite mandibles make up a large proportion of the total sample size with 78% (171 of 219) present but there still remained missing individuals. There were 15 individuals that had no skull present, these being a single bonobo and fourteen chimpanzees.

### Incomplete quadrants and imputed data

In the sample there were 47 individuals with mandibles that did not have complete composite dental scores. For 19 of these individuals there was no skull present and a score was not possible to calculate. However, for 28 of the individuals there were at least some teeth present. Of those 28 individuals, the mean number of teeth present was 11.63 ± 2.6 out of total possible sample of 16 (two quadrants of 8). This figure does not indicate the distribution of missing teeth but it is inferred that each of these individuals would be missing at least one tooth category. This amounts to at least 2 out of 16 missing with the highest completeness value for any individual of 87.5%. Provided that not all individuals were only missing one tooth and a small number of individuals were missing many, this would suggest that for most individuals the majority of teeth were present. Table 3.14 demonstrates number of teeth present by tooth category. The pattern of missing teeth is typical of tooth loss in osteological collections with incisors frequently missing and molars most often present.

**Table 3.14** Missing tooth frequency analysis for individuals with incomplete quadrants.

|  |  |  |  |
| --- | --- | --- | --- |
| **quadrant** | **tooth** | **number present** | **percentage present1.** |
| right mandible | incisor 1 | 10 | 33.3% |
| incisor 2 | 18 | 60.0% |
| canine | 23 | 76.7% |
| premolar 3 | 27 | 90.0% |
| premolar 4 | 26 | 86.7% |
| molar 1 | 23 | 76.7% |
| molar 2 | 25 | 83.3% |
| molar 3 | 21 | 70.0% |
| left mandible | incisor 1 | 11 | 36.7% |
| incisor 2 | 23 | 76.7% |
| canine | 23 | 76.7% |
| premolar 3 | 21 | 70.0% |
| premolar 4 | 23 | 76.7% |
| molar 1 | 25 | 83.3% |
| molar 2 | 27 | 90.0% |
| molar 3 | 23 | 76.7% |

1. This is the percentage present out of the total number of individuals with present skulls that have dentition (n=30).

With the majority of teeth present for most individuals, it is possible to confidently predict what the missing values should be based on patterns of the data available. The statistical methodology to be used here is multiple imputation (Schafer 2000). Multiple imputation is an algorithm-based method that determines patterning in the data set and then produces a most-likely value for a missing data entry based on the teeth that were present. With many incomplete quadrants missing only a small number of teeth and with the sample being relatively large (204 skulls with teeth present), it would be expected that the application of this method would be robust.

***3.3.3.a Preparation of tooth data for multiple imputation***

There existed the potential for developmental inter-specific differences as well as intra-specific differences between males and females. Males and females were analysed separately for *Pan troglodytes* while a mixed-sex sample was used for *Pan paniscus* due to sample sizes being too small for independent analysis of *Pan paniscus* males and females. For this species males, females, and unsexed individuals were pooled and imputation carried out using all 33 individuals (4 individuals did not have teeth). There is a risk of this method being unreliable if there existed significant differences in patterning (as opposed to timing) of dental maturation between sexes. Given the results of Boughner *et al.* (2012) showing high degrees of similarity, this seems unlikely. In chimpanzees and humans it is known that the overall pattern of maturation does not show major deviations between males and females. The assumption is made that this should be true for this sample as well.

Included in this analysis were also individuals with complete quadrants, those with teeth missing from one side or the other but having a complete composite score, and those individuals with incomplete composite scores. These data were loaded into SPSS Statistics 21. Variables were first analysed to look at the distribution and patterns of completeness. Both left and right quadrants were analysed in parallel within the same analysis. Based on the premise that there is no statistically significant difference between sides (Kuykendall *et al.* 1992), this approach made more sense than running each quadrant separately due to more complete data being present. Five iterations were run on each quadrant and these results were then compiled into an imputed data set. Imputed values were produced for all missing teeth from both left and right sides. Summary dental scores were taken for all individuals. Full imputation results are available in section 8.1 of the digital appendix. The resulting analysis of missing values are available in section 8.2 of the appendix for all three species. The total number of individuals with mandibular scores evaluated in the analysis is shown in Table 3.15. It is evident that all of the incomplete individuals that could be added for *Pan paniscus* and *Pan troglodytes* were added. It should be noted that the one bonobo that could not be added by imputation had only two teeth present, the left and the right I2, both of which were fully mature.

**Table 3.15** Number of individuals brought forward for analysis by the use of multiple imputation.

|  |  |  |
| --- | --- | --- |
| **data type** | ***P. paniscus***  ***N*** | ***P. troglodytes***  ***N*** |
| total individuals1. | 37 | 171 |
| missing skulls | 4 | 15 |
| individuals with at least one permanent tooth | 33 | 156 |
| composite or complete mandible scores | 19 | 131 |
| incomplete individuals (sexed and unsexed) | 12 | 25 |
| incomplete individuals for male and female *Pan troglodytes* 2. | - | 16 |
| individuals added by imputation2. | 11 | 16 |
| final no. individuals for analysis | 32 | 147 |

1. This is the total number of individuals in the study sample.
2. This excludes unsexed individuals.

### Distribution of dental scores

With the final dental scores now produced it is necessary to consider the distribution of scores as these will provide the range of development to be considered. It would be desirable to have an even spread of scores across a wide range of ages, although this may not be achievable. This study measured both long bone length and epiphyseal fusion and the distributions of data required for each are not analagous. Epiphyseal fusion requires a large group of individuals between the ages in which fusion begins to occur and completes. These events occur relatively later in development, often completing at the end of the growth. Conversely, long-bone length is continuous throughout the entire process of growth from birth to maturity. Prior studies of human epiphyseal closure have shown that this growth parameter can be quite variable. Whether it is more variable than long-bone growth rates is not a question that can be easily answered at this juncture. However, it is desired to have a large sample size for epiphyseal fusion ages as this variable is quite critical for this study. Table 3.16 provides numbers of individuals presented in dental score intervals of 10.

**Table 3.16** Distribution of dental scores sorted by intervals of 10 for both species and sexes.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Pan paniscus*** | | | | |
| **dental score** | **male** | **female** | **no sex** | **all individuals** |
| 0 to 10 | 0 | 0 | 0 | 0 |
| 10 to 20 | 2 | 0 | 0 | 2 |
| 21 to 30 | 2 | 0 | 3 | 5 |
| 31 to 40 | 2 | 2 | 0 | 4 |
| 41 to 50 | 3 | 0 | 0 | 3 |
| 51 to 60 | 4 | 4 | 1 | 9 |
| 61 + | 4 | 5 | 0 | 9 |
| sum | 17 | 11 | 4 | 32 |
| ***Pan troglodytes*** | | | | |
| **dental score** | **male** | **female** | **no sex** | **all individuals** |
| 0 to 10 | 0 | 0 | 2 | 2 |
| 11 to 20 | 4 | 6 | 3 | 13 |
| 21 to 30 | 9 | 9 | 2 | 20 |
| 31 to 40 | 9 | 6 | 0 | 15 |
| 41 to 50 | 11 | 13 | 5 | 29 |
| 51 to 60 | 14 | 15 | 2 | 31 |
| 61 + | 12 | 37 | 3 | 52 |
| sum | 59 | 86 | 17 | 162 |

The majority of individuals in the sample were at later stages of dental development for both species. The proportions of individuals at each stage was approximately equivalent for both bonobos and chimpanzees but the sample size was much larger for *Pan troglodytes*. Dental scores 0 to 10 corresponds to either newborn or fetal individuals (Kuykendall 1996). The lack of samples in this range was to be expected and was not of great concern. The sample size increased dramatically from dental score range 21 to 30 towards maturity. Kuykendall (1996) placed individuals in the range 21 to 30 at between 2 to 4 years of age. It seems unlikely that epiphyseal fusion for any epiphysis would be initiated by this young of an age due to the fact that a large amount of growth has yet to be achieved after this age. As a point of reference, Bolter and Zihlman (2012) estimated the intiation of fusion for the distal humerus at between 6-7 years for captive and 7-10 years for wild individuals of both species. In humans this is quite an early fusion event and although it presupposes that chimpanzees and humans do not differ by such an extreme amount as to overlap these ranges, it would seem unlikely that this is true purely from a developmental standpoint. It could be safely assumed that the higher dental score values encompass the majority if not all epiphyseal fusion events. The lack of individuals at lower stage ranges may result in more variation for analysis of *Pan paniscus* but would be sufficient for analysis of *Pan troglodytes* from stage 11 to 20 and higher as shall be shown in the analysis of epiphyseal fusion and long-bone length.

### Intra- and inter-observer error

Testing the consistency of measurement involved the re-evaluation of dental score for a randomised selection of 20 individuals. For intra-observer error, 15 individuals were re-evaluated by the primary researcher (Conrad Brimacombe, CB) and 12 different individuals were evaluated by a colleague (Isabelle Heyerdahl-King, IHK). Table 3.17 provides a list of the individuals used. It should be noted that prior to full-scale data collection, 10 individuals were completed by CB. These were discussed and compared with the results of Dr. Kuykendall such that variation could be reduced by having the observer being already accustomed to the system prior to data collection. In order to apply the same effect to the inter-observer error candidate (IHK), 5 preliminary trials were done before the 12 observed here and were not included in this analysis.

**Table 3.17** Individuals used for intra- and inter-observer error analysis.

|  |  |  |  |
| --- | --- | --- | --- |
| **inter-observer error** | | **intra-observer error** | |
| **sample** | **species** | **sample** | **species** |
| MCA 84036M03 | *Pan paniscus* | MCA 29057 | *Pan paniscus* |
| MCA 29060 | *Pan paniscus* | MCA 29040 | *Pan paniscus* |
| MCA 80046M02 | *Pan paniscus* | MCA 29043 | *Pan paniscus* |
| MCA 29055 | *Pan paniscus* | MCA 29047 | *Pan paniscus* |
| MCA 11293 | *Pan paniscus* | MCA 16380 | *Pan troglodytes* |
| MCA 29021 | *Pan paniscus* | UZ 7056 (K81 V-B) | *Pan troglodytes* |
| MCA 29056 | *Pan paniscus* | UZ PAL-190 (K81 VI-A) | *Pan troglodytes* |
| MCA 9931 | *Pan troglodytes* | UZ 7421 (K81 V-B) | *Pan troglodytes* |
| PCM M805 | *Pan troglodytes* | MCA 9584 | *Pan troglodytes* |
| PCM M967 | *Pan troglodytes* | PCM M274 | *Pan troglodytes* |
| PCM M299 | *Pan troglodytes* | MCA 30660 | *Pan troglodytes* |
| PCM M655 | *Pan troglodytes* | UZ AS-310 (K81 / 5-D) | *Pan troglodytes* |
|  |  | MCA 23511 | *Pan troglodytes* |
|  |  | UZ AS 778 (K81 VI-D) | *Pan troglodytes* |
|  |  | UZ 10742 (K81 V-D) | *Pan troglodytes* |

***3.3.4.a Intra-observer error***

The results for the 15 individuals that were re-evaluated by CB were compared to the original data set. This set of 15 individuals was re-evaluated some months after the original scoring of the teeth. Any anomalous individuals such as those with a particular pattern of tooth loss/damage or super-numery teeth were avoided. The total number of deviations were counted. With the exception of one outlier that differed by three stages, no teeth deviated by more than one stage. It is suspected that this outlier may have been due to mistaken tooth identity in the X-ray. There were 18 deviations reported from a total of 212 observations producing a deviation rate of 8.5%. If deviations were random it would be expected that the number of positive deviations would approximate equal numbers and this was indeed the case with 9 deviations higher and 9 lower. The deviations were evenly spread across all tooth types. Kuykendall (1992) found that greatest number of deviations were for stages 1,3 and 8. The pattern of deviations in this analysis were similar to these results with proportionately higher levels of variations found between stages 2 to 4 (few stage 1 teeth were present in this sample). Table 3.18 provides these values.

**Table 3.18** Number of deviations by tooth stage for intra-observer error.

|  |  |
| --- | --- |
| **stage change1.** | ***N*** |
| 5 to 32. | 1 |
| 2 to 3 | 5 |
| 3 to 4 | 5 |
| 4 to 5 | 2 |
| 5 to 6 | 1 |
| 6 to 7 | 2 |
| 7 to 8 | 2 |
| total | 18 |

1. Stage change refers to the deviation from one stage to the next. This includes all deviations from higher to lower comparing either second observation to original or vice versa.
2. This is the outlier mentioned in the above text.

The distribution in Table 3.18 is not even and the reason for this pattern is likely a consequence of varition in the difficulty of applying the classification criteria. The difference between stages 5 and 6, for example, requires the root to either be shorter than crown height (stage 5) or longer than crown height (stage 6), which is a feature that can be easily distinguished in an X-ray of even marginal quality. However, the difference between stage 3 and stage 4 is defined by the completion of the crown (stage 3) and initiation of cementum deposition (stage 4), which is a distinction that is much more difficult to observe. Similarly, it can be difficult to discern between the later stages of an incomplete crown (stage 2) and a recently complete one (stage 3). Variation in individual crown morphology could have an effect on the judgement of the observer as to whether the crown was complete or not. The difficulty in determining the distinction between these stages was more pronounced for canines where chimpanzee and bonobo teeth do not morphologically match the human teeth in the scoring system very well. A further complication for assessment of these criteria was the rotation of tooth crowns within the crypt. This tended to occur for stages below a Demirjian dental score of 5.

In order to test consistency over time, it was also important to rule out any trend towards higher or lower scores in the small number of deviations found. In other words, it was hoped that the observer did not have any positive or negative shift over time. There were 11 deviations that went down one stage and 7 deviations that went up one stage. The binomial probability equation was used and positive and negative values were considered. It was postulated that they were randomly distributed above and below 0 with equal probability. Here, *k* = 7, *N* = 19, and *p/q* = 0.5. It was found that P(k out of N) = 0.12 and the possibility that there was a trend of deviation towards lower or higher scores was rejected.

As a summary statement, intra-observer error comparisons suggest that the data are consistent with a small rate of insignificant error. This error was concentrated between certain stages and was demonstrably random.

***3.3.4.b Inter-observer error***

The results for the 12 individuals completed by IHK were compared to the assignments done by CB. There were 21 deviations from a total of 131 teeth, producing a deviation rate of 16.8%. This was a higher deviation rate than reported for intra-observer error. The distribution of deviations was again quite evenly spread through the dentition and deviations were never more than 1 stage apart. Of those 21 deviation, 11 were negative and 10 were positive. This also suggested that there was no tendency towards positive or negative values. Here, *k* = 10, *N* = 21, and *p*/*q* = 0.5. It was found that P(*k* out of *N*) = 0.17. Table 3.19 lists the number of deviations by stage type.

**Table 3.19** Number of deviations by tooth stage for inter-observer error.

|  |  |
| --- | --- |
| **stage change** | **number** |
| 3 to 2 | 2 |
| 4 to 5 | 8 |
| 5 to 6 | 5 |
| 7 to 8 | 6 |
| total | 21 |

More deviations were apparent between stages 4 to 5 when compared to intra-observer error. There were also a higher number of deviations between 5 to 6. These deviations were less consistent with the deviations found by CB, and also Kuykendall (1992), but they nonetheless represent an acceptable level of overall error.

To summarise inter-observer error, the values of deviation determined here were similar in nature to intra-observer error but with a slightly higher prevalence rate. There was no notable directionality of deviations towards positive or negative values. The patterning of these results was similar to that found by Kuykendall (1992), suggesting that there is sufficient consistency in application of the Demirjian (1973) method in this research.

***3.4.4.c Error analysis of the method from other studies***

With regards to further academic study of the reliability of the Demirjian method, analysis has been completed that has considered both accuracy and precision. There has been some variation with respect to the prediction of exact chronological age (Koshy and Tandon 1998, Nykänen *et al.* 1998) and a comparison using a more refined polynomial function (Chaillet and Demirjian 2004). There have been some modifications to refine the applicability of the method for different populations and to refine growth curves (Teivens and Mörnstad 2001a, 2001b). Since the chronological ages are unknown in this sample the level of accuracy of age estimation cannot be compared. However, the most important point to draw from these studies is that the overall precision of the method has not been challenged. For further discussion see Liversidge *et al.* (2006). The results found the current study stand comparatively well with other studies.

## Epiphyseal fusion

### Determining combined sample values for analysis of epiphyseal fusion

Bilateral assessment was taken for all epiphyses when possible. With the primary objective being to provide information on general state of fusion, a combined sample variable was created for each epiphysis. This variable provide a single value from each epiphysis for each individual. Humans have shown sight lateralisation with respect to upper limb length but there is no evidence for lateralisation of epiphyseal union. Based on this fact it is assumed that epiphyseal fusion is not lateralised and that there is no population-level difference between left and right side.

For all individuals where there was only one side present, this value was simply transferred to the combined sample variable. For those individuals that had both scores; if those scores were exactly the same then this value was again transferred directly to the combined sample variable. However, on some rare occasions there existed a difference between sides. Based on the principle of fluctuating asymmetry and developmental stability (Klingenberg and McIntyre 1998, Palmer and Strobeck 1986, 1992), small amounts of variation between sides would be expected. Small amounts of sampling error may also be expected, although with both bones being observed at the same time, deviations caused by wrongly classifying or inputting data for an epiphysis was considered highly unlikely. This was due to the fact that any observed difference between sides was immediately apparent to the observer. Whenever this situation arose during the data collection process the bones would be re-evaluated such that this difference could be confidently recorded. Developmental asymmetry has been correlated with environmental stress and in order to detect more extreme cases some analysis is warranted with respect to the distribution of asymmetry within this data set.

***3.4.1.a Analysis of frequency difference***

Table 3.20 provides the number of bilateral asymmetries for each epiphysis and the the total sample size of bilateral measurements. When values in the column ‘number of individuals with a difference between sides’ are considered, the variation is evidently small, typically between 2 and 4 percent. This variation is also quite evenly spread across all epiphyses. These values are sufficiently consistent that it may be asserted that there was no evidence for concentration of bilateral asymmetry towards any specific epiphysis.

In total, 67 individuals (30.8%) of the sample had at least one asymmetry. Pathological conditions observed in the sample were recorded and these included broken bones, unexplained lesions, and linear enamel hypoplastic defects (see analysis of pathology in section 3.1.6). The prevalence rate of reported pathological conditions excluding recently broken bones was determined both for individuals with asymmetries and for those without. Evidence for recent trauma such as recently broken bones was not considered potential evidence for insult to systemic health. The proximity to age at death likely had no longer-term implications for health status and thus would not impact on the individual as far as this study would be concerned. It was found that for the 67 individuals with asymmetries, 13 showed some possible sign of abnomormality (19%) while 27 of the remaining 152 individuals without asymmetries (18%) show signs of abnormalities. Application of a chi-squared statistic using these values provides an non-significant result (χ2 = 0.082953, p = 0.9593), suggesting that the population of suspected pathological individuals were not more likely to be asymmetric than the overall population.

**Table 3.20** Sample size and frequency of differences between sides for epiphyseal fusion.

|  |  |  |  |
| --- | --- | --- | --- |
| **bone** | **epiphysis** | **number of individuals contributing bilateral measurements** | **number of individuals with a difference between sides1.** |
| humerus | proximal epiphysis fusion | 198 | 4 (2.0%) |
| distal capiptulum/trochlea/lateral epicondyle fusion | 198 | 4 (2.0%) |
| distal medial epipcondyle fusion | 198 | 5 (2.5%) |
| radius | proximal epiphysis fusion | 195 | 7 (3.6%) |
| distal epiphyses fusion | 194 | 4 (2.1%) |
| ulna | proximal epiphysis fusion | 193 | 5 (2.6%) |
| distal epiphyses fusion | 195 | 8 (4.1%) |
| hand | distal phalangeal epiphyses fusion | 64 | 1 (1.6%) |
| base of metacarpal 1 fusion | 139 | 2 (1.4%) |
| proximal and middle phalangeal epiphysis fusion | 163 | 1 (0.6%) |
| heads of metacarpals 2-5 fusion | 181 | 0 (0.0%) |
| femur | femoral head fusion | 191 | 4 (2.1%) |
| greater trochanter fusion | 191 | 3 (1.6%) |
| lesser trochanter fusion | 190 | 3 (1.6%) |
| distal epiphysis fusion | 189 | 4 (2.1%) |
| tibia | proximal epiphysis fusion | 190 | 2 (1.1%) |
| distal epiphysis fusion | 190 | 4 (2.1%) |
| fibula | proximal epiphysis fusion | 190 | 6 (3.2%) |
| distal epiphysis fusion | 189 | 3 (1.6%) |
| foot | calcaneal epiphysis fusion | 171 | 0 (0.0%) |
| talar epiphysis fusion | 170 | 1 (0.6%) |
| distal phalanges, middle phalanges,  metatarsal heads 2-5 fusion | 170 | 7 (4.1%) |
| proximal phalanges and base of metatarsal 1 fusion | 166 | 4 (2.4%) |
| pelvis | triradiate epiphysis fusion | 210 | 5 (2.4%) |
| anterior inferior iliac spine fusion | 206 | 0 (0.0%) |
| iliac crest fusion | 202 | 4 (2.0%) |
| ischial epiphysis fusion | 206 | 5 (2.4%) |
| clavicle | medial epiphysis fusion | 180 | 3 (1.7%) |
| lateral epiphysis fusion | 170 | 0 (0.0%) |
| scapula | coracoid process fusion | 195 | 8 (4.1%) |
| sub-coracoid centre and glenoid epiphysis fusion | 193 | 4 (2.1%) |
| acromial epiphysis fusion | 190 | 4 (2.1%) |
| medial border | 190 | 4 (2.1%) |
| mean values | | 183.5 | 3.6 (1.9%) |

1. The number with a difference between sides refers to the number of individuals with bilateral asymmetry of epiphyseal union, regardless of the magnitude of difference. The percentage in brackets is this value as a percentage of the total number of bilateral measurements in the adjacent column.

When considering the net number of deviations by individual for the entire data set, the highest number came from a single individual with 6 asymmetries. It was noted that there were difficulties in measuring this individual due to gluing of epiphyses and this may have been a source of ambiguity for measurement. This individuals was not an extreme outlier and data from this individual was analysed. The remainder of individuals with asymmetric epiphyses ranged from having 1 to 4 deviations with a mean value of 1.68. Even if these values were considered as a percentage of data entries present for each individual, the numbers were not large enough for any difference from randomness to be found.

It is therefore possible to conclude that asymmetry of epiphyseal fusion in this data set is the result of very small amounts of variation caused either by measurement error or minor biological variation. Differences between sides did not concentrate within specific individuals which were either identified as potentially being pathological or otherwise.

The question remains as to how to deal with these asymmetries. It was decided to take the higher of the two scores for the epiphysis (more advanced stage). This arbitrary decision is equally as acceptable as staging down but has one advantage. For those epiphyses where one side had stage 2 fusion (beginning fusion) while the other was completely unfused (stage 1), selecting the lower score would mean that no fusion was recorded as having occured at all for the epiphysis, which is incorrect. It should also be noted that any obscuring effect of choosing the higher or lower value would likely be of little or no statistical relevance due the very lower prevalence rate of these asymmetries.

For all individuals where only one side was present, the value for that side was simply added to the final variable. For those individuals where both sides had exactly the same value, again that value was simply transferred to the final value. For the majority of epiphyses, 85-90% of individuals with dental scores were able to contribute values to the final fusion scores. There were some sites that deviated from this assertion and these were mostly hand and foot bones with the distal phalanges of the hand being the most prominent outlier. These deviations were expected as these bones are small and easily lost in the curation process.

### Ordering the sample and generated scores

*Pan paniscus* and *Pan troglodytes* individuals were sorted into individual data sets by sex and then ordered by dental score from lowest to highest. There were some instances where individuals had the same dental score, especially those with higher scores. This was of particular importance for the case of individuals with a dental score of 64 because this constituted fully mature dentition. For individuals with fully mature dentition (dental score 64), there there were 23 female and 5 male *Pan troglodytes* and 3 female and 2 male *Pan paniscus*. The presence of a large number of dental score 64 (DS64) individuals for both species and both sexes indicates that skeletal maturity proceeds dental maturity.

As opposed to the human pattern where the third molar erupts quite late in the developmental sequence, it is known from tooth emergence data that in catarrhine primates including studies of apes that full dentition is in place prior to full skeletal maturity (Bolter and Zihlman 2003, Schultz 1942, Zihlman *et al.* 2007). The timing of root completion, as opposed to emergence with respect to skeletal maturity has not been explored, although it would not be an unreasonable supposition to expect that the difference between the two would not be substantial. The relative timing of these events is what this study seeks to clarify. Chronological timing of third molar completion is available from Anemone *et al*. (1991, 1996), Kuykendall (1996) and Kuykendall and Conroy (1996) but there is no certainty as to how these age ranges relate to skeletal maturation. Past reported ranges for later epiphyses by Bolter and Zihlman (2012) and Kerley (1966) overlap third molar maturity. This was evidently a problem for analysis of this data set due to the maximal age indicator being reached for many individuals prior to the fusion of multiple epiphyses.

For DS64 individuals in female *Pan troglodytes* it was observed that unfused epiphyses for the distal radius, distal ulna, iliac crest, the acromium, the medial border of the scapula, and the medial clavicles were common. The number of individuals with unfused epiphyses for these bones ranged from 5 to 16 depending on the epiphysis. There were also 12 other epiphyses for which there were up to four individuals with unfused scores. This pattern was repeated for the male *Pan troglodytes* sample. For *Pan paniscus* individuals of both sexes these epiphyses were also unfused, although the numbers for each were inevitably smaller due to the difference in sample size. The criteria used to select individuals to be included in this sample was the presence of any remaining unfused epiphyses including individuals with only a remaining epiphyseal fusion scar line. When preliminary analysis of collections was completed prior to full-scale data collection for estimating the number of sub-adults available, it was observed that it was either the iliac crest or the medial clavicle were the last remaining unfused epiphyses. All other fusion centres were completely mature before these epiphyses. With the iliac crest and medial clavicle serving as an end-point and with unfused epiphyses present for the distal radius, distal ulna, the acromium and the medial border of the scapula, it would thus stand to reason that within this sample of DS64 individuals that there should be a range of fusion states observable.

***3.4.2.a Generated Scores: Theory***

A core objective of this study is to chart the sequence of epiphyseal fusion. With dental score being a limiting factor for later stage fusion events, a different approach was attempted. To solve this problem, a strategy was used based on the simple premise that all epiphyseal fusion plates will eventually fuse and that there is a general underlying pattern in which they fuse. Fundamentally this must be true given all past research. Dermirjian scores for dentition were a sum of a series of ordinal variables that increased in value with time. Epiphyseal fusion scores, which are also a series of increasing ordinal variables, behave likewise. If a summary or mean value of these epiphyseal fusion scores was taken for each individual, then it would be expected that as age increased that summary epiphyseal fusion score would increase in tandem. It shall be shown in section 3.4.2b that mean value is more appropriate in this study. These mean value scores could then be used to order individuals based on increasing levels of skeletal maturity. This would not provide any means to anchor epiphyseal fusion events with respect to the dental maturity but it would provide information regarding the order in which epiphyses fuse beyond dental maturity. The only potential challenge of doing this would be if fusion events substantially overlapped ranges of variation between epiphyses. This would mean that epiphyseal fusion scores would tend to cluster around similar values. In section 4.2.4 this will be shown to not be the case and distinct differences in position of fusion events will become apparent.

***3.4.2.b Producing mean epiphyseal fusion values for generated scores: Limitations and approach***

DS64 individuals from this point forward in the analysis of epiphyseal fusion will be considered a special subset of dental score. Ideally, producing a summary score for epiphyseal fusion centres would be the best method for assessing maturity and is a direct analogue of dental score. A sum of all scores could be taken and individuals ordered based on increasing score. However, in reality determining a generated score by simply adding all values for each fusion event and comparing scores in a similar fashion to dental scores would have been inadequate due to the problem of incomplete data. Missing data occurred no more frequently than it did with dental scores but the variables involved were more numerous. As opposed to 8 teeth, there were 33 epiphyses, and thus the likelihood that an individual would be missing at least one data entry was much higher.

Tables 3.21 and 3.22 show the distribution of missing data for epiphyseal fusion. The cumulative percentages show that that majority of individuals were missing data entries for small number of epiphyseal fusion sites. Individuals missing greater than 10 entries made up only 5.65% of individuals. These individuals were ones where only a small number of bones were present but their inclusion was still considered useful due to the provision of a complete dental score.

**Table 3.21**  Frequencies of missing values for epiphyseal fusion sites in *Pan paniscus* and *Pan troglodytes*.

|  |  |  |  |
| --- | --- | --- | --- |
| **no. missing entries** | **individuals** | **percentage of total** | **cumulative percentage** |
| 0 | 53 | 29.94 | 29.94 |
| 1 | 74 | 41.81 | 71.75 |
| 2 | 13 | 7.34 | 79.10 |
| 3 | 10 | 5.65 | 84.75 |
| 4 | 7 | 3.95 | 88.70 |
| 5 | 1 | 0.56 | 89.27 |
| 7 | 2 | 1.13 | 90.40 |
| 8 | 5 | 2.82 | 93.22 |
| 9 | 2 | 1.13 | 94.35 |
| 10+ | 10 | 5.65 | 100.00 |
| total | 177 | 100.00% | 100.00% |

1. The cumulative percentage is calculated as the sum of all individuals in the current stage and all stages with lower numbers of data points missing presented as a percentage of the total sample.

Apart from the distal phalanges of the hand, the number of missing entries was quite small per epiphysis. The number of missing entries for individuals showed an even spread of missing data throughout the sample set except for distal phalanges (Table 3.21). With the pattern of missing values evenly spread, simply removing variables with missing data points such that all sets would be complete would not be practical. For example, this would require the loss of the medial border of the scapula and all pelvic fusion sites except the tri-radiate. The removal of the affected individuals is also problematic due to the fact that individuals missing one of these entries for one bone were not necessarily the same individuals that were missing entries for another. This would cause the sample size to shrink to an unacceptably small size. However, what has been shown here is that the overall level of missing data for most individuals was quite small with typically only a few percent of entries missing. An approach was taken whereby a mean value for all epiphyseal fusion sites for each individual was produced as opposed to a summed score. This method would smooth out occasional missing data and approach the robusticity of summed scores due to the comparatively small level of incompleteness. A mean value is more appropriate than a median value in this circumstance because all epiphyses present contribute to a mean. If, for example, a very young individual begins fusion at two epiphyses, the median value for all epiphyses would remain 1, while the mean would encompass these fusion events and be slightly greater than 1. Mean epiphyseal fusion scores were calculated for all individuals with DS64 for both the *Pan paniscus* and *Pan troglodytes* sample. Mean values for epiphyseal fusion of DS64 individuals score ranged from 2.47 to 4.91 with the majority of the values falling between 4 and 4.91. It can be fairly confidently asserted that there was a considerable amount of fusion occuring after dental maturity.

**Table 3.22** Missing data by epiphysis showing number of individuals for the entire sample and for DS64 individuals

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **bone** | **epiphysis** | **data entries (whole sample)** | **number missing (whole sample)** | **data entries (dental score 64 individuals)** | **number missing (dental score 64 individuals)** |
| humerus | proximal epiphysis fusion | 173 | 4 | 30 | 0 |
| distal capiptulum/trochlea/lateral epicondyle fusion | 173 | 4 | 30 | 0 |
| distal medial epipcondyle fusion | 173 | 4 | 30 | 0 |
| radius | proximal epiphysis fusion | 171 | 6 | 30 | 0 |
| distal epiphyses fusion | 170 | 7 | 30 | 0 |
| ulna | proximal epiphysis fusion | 172 | 5 | 30 | 0 |
| distal epiphyses fusion | 171 | 6 | 30 | 0 |
| hand | distal phalangeal epiphyses fusion | 66 | 111 | 6 | 24 |
| base of metacarpal 1 fusion | 134 | 43 | 27 | 3 |
| proximal and middle phalangeal epiphysis fusion | 150 | 27 | 29 | 1 |
| heads of metacarpals 2-5 fusion | 162 | 15 | 29 | 1 |
| femur | femoral head fusion | 173 | 4 | 30 | 0 |
| greater trochanter fusion | 173 | 4 | 30 | 0 |
| lesser trochanter fusion | 173 | 4 | 30 | 0 |
| distal epiphysis fusion | 173 | 4 | 30 | 0 |
| tibia | proximal epiphysis fusion | 172 | 5 | 30 | 0 |
| distal epiphysis fusion | 171 | 6 | 30 | 0 |
| fibula | proximal epiphysis fusion | 170 | 7 | 29 | 1 |
| distal epiphysis fusion | 171 | 6 | 30 | 0 |
| foot | calcaneal epiphysis fusion | 163 | 14 | 29 | 1 |
| talar epiphysis fusion | 160 | 17 | 29 | 1 |
| distal phalanges, middle phalanges, metatarsal heads 2-5 fusion | 156 | 21 | 28 | 2 |
| proximal phalanges and base of metatarsal 1 fusion | 160 | 17 | 29 | 1 |
| pelvis | triradiate epiphysis fusion | 173 | 4 | 30 | 0 |
| anterior inferior iliac spine fusion | 170 | 7 | 29 | 1 |
| iliac crest fusion | 167 | 10 | 28 | 2 |
| ischial epiphysis fusion | 169 | 8 | 28 | 2 |
| clavicle | medial epiphysis fusion | 171 | 6 | 30 | 0 |
| lateral epiphysis fusion | 159 | 18 | 28 | 2 |
| scapula | coracoid process fusion | 173 | 4 | 30 | 0 |
| sub-coracoid centre and glenoid epiphysis fusion | 172 | 5 | 30 | 0 |
| acromial epiphysis fusion | 172 | 5 | 30 | 0 |
| medial border | 170 | 7 | 29 | 1 |
| **mean values** | | **164.42** | **12.58** | **28.70** | **1.30** |

***3.4.2.c Using mean values to produce generated extended dental scores***

These special subsets of DS64 individuals were analysed separately as four sub-sets, these being *Pan paniscus* females*, Pan* paniscus males, *Pan troglodytes* females and *Pan troglodytes* males. For un-sexed individuals, none of the *Pan paniscus* specimens had DS64 while there was a single *Pan troglodytes* individual in this category. As such, un-sexed individuals are not included here. Mean epiphyseal fusion values were used to order each of these sub-sets by their skeletal maturity, which resulted in two separate systems, dental score and skeletal score. Dental score allows for analysis of development up to the point of dental maturity while skeletal score allows for observation of fusion events after dental maturity.

A means by which to visualise fusion events after dental maturity but still using dental score would be to add increments to DS64 individuals such that the relative state of fusion past dental maturity may be observed. As an example, if there are *n* individuals with DS64, an incremental additional value would be added to 64 of x for the ith individual, generating a new score *Si*. In other words, *S*i = 64+*i*(*x*). If *x* = 0.3, then this will mean that for individuals *S*0, *S*1, *S*2 … *Sn* the values 64.0, 64.3, 64.6 … 64.0 + (*n* × 0.3) are achieved. The value of *x* is arbitrary. However, the choice of value does have an impact on scaling and should be proportionate to the number of individuals present. For *Pan troglodytes* females, for example, there were 23 individuals with DS64. If the incremental score of 0.3 is used, then there is a range from the youngest individuals of 64 to 70.6 for the oldest individuals. As will be shown in section 4.2.4, this scaling factor allows for the relative timing of fusion events to become clearly visible beyond the dental score of 64. With individuals sorted by dental score and additionally by mean epiphyseal fusion score it is possible to proceed to analyse epiphyseal fusion sequences.

***3.4.2d Consideration of other methods***

It is of note that dental wear has been used in prior studies of both humans and other animals to determine age at death (e.g., Lovejoy 1985). The use of this methodology has shown some reliability in humans for estimating age in larger samples. However, there are some critical limitations for the application of such an approach in this study. There are some studies of chimpanzee dental wear (e.g., Ungar and M’Kirera 2003) but equivalent studies predicting age by dental wear in chimpanzees do not exist as they do for humans. Additionally such methods rely on consistent dietary patterns within the population of study. With a mixed-sample of captive and wild, this cannot be assured and dental wear may prove much more variable. Futher complicating this approach is the fact that the ages of interest are all very young at which point there is little dental wear to observe. It is considered that generated dental score is a more reliable means for projecting extended maturational age in this study than attempting the use of dental wear.

### Application of mean epiphyseal fusion values for seriating epiphyses

The aforementioned addition of generated dental score values allows for observation of fusion events beyond dental maturity but due the system being an artificial combination of two systems, this makes any quantitative analysis of these differences invalid. It will be observed that there are several fusion events that occur after dental maturity. Any estimates of ages may not be calculated for these epiphyses but with their mean epiphyseal fusion scores they may be ordered. Mean epiphyseal fusion scores were determined for all individuals in the data set. Individuals could then be seriated based on increasing maturity irrespective of dental score.

### Estimation of age for fusion timing using dental score

As estimation of age is a critical component of this study, estimated ages for fusion events based on dental maturity will still be estimated for those epiphyses that had ranges below DS64. It will be shown in Chapter 4 that many mid-fusion ranges do fall below the cut-off of dental maturity and estimated ages of attainment may be determined.

### Evaluating number of individuals at each stage and recoding results into three stages

Table 3.23 provides sample sizes of mid-fusion (recorded stages 2-4) and complete fusion (recorded stage 5) for all epiphyses in *Pan troglodytes* females. Table 3.24 compares mid-fusion and complete fusion values in the upper limb for both species and sexes. It is important to note that the sample size for female *Pan paniscus* individuals was quite small once all dentally incomplete individuals were removed. There were two cases of fusion centres where no mid-fusion values were present and likewise two cases where no complete fusion was found. For *Pan troglodytes* the number of individuals for each epiphysis were much larger.

Mid-fusion values are of the greatest concern with respect to analysis as this state indicates when the process of fusion is occuring. Table 3.23 indicates that there were typically around 9 values for mid-fusion for each epiphysis in *Pan troglodytes* females. Proportionate values relative to sample size were found for *Pan troglodytes* males and *Pan paniscus* males and females. Table 3.24 indicates that the number of data entries for each epiphysis in the upper limb are greatest for females *Pan troglodytes*. This should be expected as *Pan troglodytes* females provided the largest sample for any of males or females of both species. With only 9 individuals being typical of mid-fusion events in *Pan troglodytes* females, most individual recorded stages (stages 2 - 4) would provide not more than 3 or 4 individuals for *Pan troglodytes* and single data points common for *Pan paniscus*. It was decided to consider mid-fusion as a single category from this point in the analysis. A case-by-case review may be possible in the future for some epiphyses, but certainly not for all.

**Table 3.23** Number of individuals in mid-fusion and complete fusion for *Pan troglodytes* females by epiphysis.

|  |  |  |  |
| --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N* mid-fusion1.** | ***N* complete fusion2.** |
|
| upper limb | proximal humerus | 19 | 12 |
| distal humerus | 8 | 48 |
| humeral medial epicondyle | 8 | 42 |
| proximal radius | 11 | 30 |
| distal radius | 16 | 9 |
| proximal ulna | 4 | 40 |
| distal ulna | 14 | 10 |
| hand | distal phalanges (hand) | 2 | 10 |
| base of metacarpal 1 | 7 | 29 |
| proximal and middle phalanges (hand) | 10 | 29 |
| metacarpal heads 2-5 | 7 | 25 |
| lower limb | femoral head | 10 | 29 |
| greater trochanter | 10 | 32 |
| lesser trochanter | 5 | 37 |
| distal femur | 19 | 12 |
| proximal tibia | 20 | 13 |
| distal tibia | 12 | 21 |
| proximal fibula | 14 | 16 |
| distal fibula | 9 | 24 |
| foot | calcaneus | 7 | 35 |
| talus | 2 | 46 |
| distal phalanges (foot) | 11 | 31 |
| middle phalanges (foot) | 10 | 29 |
| metatarsal heads (2-5) | 13 | 25 |
| base of metatarsal 1 | 8 | 32 |
| proximal phalanges (foot) | 8 | 27 |
| pelvis | triradiate | 8 | 39 |
| anterior inferior iliac spine | 1 | 40 |
| iliac crest | 18 | 0 |
| ischial epiphysis | 16 | 11 |
| clavicle | medial clavicle | 7 | 5 |
| lateral clavicle | 4 | 28 |
| scapula | coracoid | 9 | 39 |
| sub-coracoid and glenoid | 6 | 42 |
| acromium | 16 | 4 |
| medial border | 8 | 2 |
| mean | | 9.92 | 25.1 |
| median | | 9 | 28.5 |

1. Mid-fusion indicates the number of individuals with fusion score 2-4
2. Complete fusion indicates the number of individuals with fusion score 5

**Table 3.24** Number of unfused, mid-fusion, and complete fusion values for the upper limb in *Pan paniscus* and *Pan troglodytes*.

|  |  |  |
| --- | --- | --- |
| **male *Pan paniscus*** | **mid-fusion1.** | **complete fusion2.** |
| proximal humerus | 3 | 0 |
| distal humerus | 0 | 7 |
| humeral medial epicondyle | 5 | 2 |
| proximal radius | 5 | 2 |
| distal radius | 0 | 2 |
| proximal ulna | 1 | 7 |
| distal ulna | 0 | 2 |
| **female *Pan paniscus*** | **mid-fusion** | **complete fusion** |
| proximal humerus | 0 | 3 |
| distal humerus | 1 | 7 |
| humeral medial epicondyle | 3 | 4 |
| proximal radius | 1 | 3 |
| distal radius | 4 | 0 |
| proximal ulna | 2 | 5 |
| distal ulna | 3 | 1 |
| **female *Pan troglodytes*** | **mid-fusion** | **complete fusion** |
| proximal humerus | 19 | 12 |
| distal humerus | 8 | 48 |
| humeral medial epicondyle | 8 | 42 |
| proximal radius | 11 | 30 |
| distal radius | 16 | 9 |
| proximal ulna | 4 | 40 |
| distal ulna | 14 | 10 |
| **male *Pan troglodytes*** | **mid-fusion** | **complete fusion** |
| proximal humerus | 7 | 3 |
| distal humerus | 5 | 18 |
| humeral medial epicondyle | 7 | 13 |
| proximal radius | 3 | 10 |
| distal radius | 8 | 3 |
| proximal ulna | 6 | 12 |
| distal ulna | 6 | 4 |

1. Mid-fusion indicates the number of individuals with recorded score 2-4
2. Complete fusion indicates the number of individuals with recorded score 5

### Error analysis for epiphyseal fusion

Intra-observer error analysis was carried out using 13 individuals which were re-assessed at the University of Zurich. These data were acquired after a 6 month interval between the two sampling periods. Despite this period of time, familiarity with particular individuals remained possible. In order to reduce the likelihood of this all of the verbal descriptions made for each individual were evaluated. These 13 individuals were selected from those which had no notable features such as suspected pathological conditions or fractures. Data for inter-observer error was unfortunately not possible to collect due to time constraints on the data collection period.

For the 13 individuals there were 22 differences between the two data collection events out of a total of 775 data entries, producing a net deviation rate of 2.8%. There were nine deviations that were more than one stage apart. From these eight deviations, three were different by 2 stages, three were different by 4, and two were different by 3. Three deviations appeared in the talus, two in the sub-coracoid, and two in the lesser trochanter. Both the talar epiphysis and the lesser trochanter are often difficult to observe due to their small physeal area and this may have been a source of error. For the combined sample variable (combining left and right) no variable exceeded two deviations with the exception of the talus, which had four. This meant that the spread of deviations across all the variables was even and that apart from the talus, no particular epiphyses were more prone to error than others. The deviation rate for the talus is still quite low.

It was noted that with respect to difficulty of observation, the lesser trochanter, the talus, the medial and the lateral epiphysis of the clavicle were considered challenging. The clavicles were found to be difficult due to variation in morphology and lack of clear epiphyseal surfaces even when the epiphysis was not fused. The level of indentation of the medial end of the bone was used as an indicator but this trait sometimes appeared even in fused epiphyses. As opposed to the first two noted epiphyses where difficulties arose (the talus and lesser trochanter), the clavicles have no noted deviations, indicating that the observation system was at least internally consistent. Another area of potential concern was the iliac crest, which can be quite brittle and is subject to being broken when an individual in the early stages of fusion is skeletonised. This concern was met with a higher level of scrutiny when observations took place. There were no reported deviations for this epiphysis in the intra-observer error sample.

## Methodology: Long-bone length analysis

The purpose of collecting data for long-bone length was to provide a measure of dimensional growth that could be compared with dental score. Epiphyseal fusion events could also be considered as a function of changes in length. Length was recorded for all bones where a length measurement was possible, with or without epiphyses. It was preferrable to have long-bone length determined by bones with complete epiphyses but prior to data collection it was not known whether sufficient numbers of individuals with complete epiphyses could be obtained. There is a need to resolve a combined sample variable, similarly to epiphyseal fusion as measurements has been taken from both sides of the skeleton. This will involve assessing if lateralisation is present (section 3.5.2) as this is known to exist in humans and is a potential source of error. It shall be shown that this is not the case and a pooled sample will be produced.

### Presence or absence of epiphyses and distribution of data by bone type

Long-bone measures with both epiphyses present were desired as this represents the complete length of the bone. Due to uncertainty with respect to the completeness of the sample, the experimental design for this study provided for all bones to be measured irrespective of their epiphyseal plate presence/absence. The state of epiphyseal fusion plate presence was recorded (both present, proximal present only, distal present only, neither present). If a substantial proportion of bones were missing epiphyses, then a method of compensating for this problem could be devised. However, during data collection it became rapidly apparent that a large proportion of individuals had both epiphyses present for most long bones. This information is quantified here. A preliminary combined sample variable for filtering epiphysis presence/absence state was created. This variable allowed for the counting of the numbers of bones that had both epiphyses present, one from either left, right, or both sides. Table 3.25 provides the number of individuals contributing a complete measurement (both epiphyses present) for each long bone by species and sex.

**Table 3.25** Number of individuals contributing long-bone measurements both by species and sex.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species** | **humerus** | **radius** | **ulna** | **femur** | **tibia** | **fibula** | **max *N* 2.** |
| *P. paniscus* total1. | 28 | 27 | 19 | 32 | 29 | 17 | 37 |
| *P. troglodytes* total | 157 | 147 | 96 | 160 | 158 | 125 | 177 |
| *P. paniscus* females | 11 | 11 | 9 | 12 | 12 | 8 | 12 |
| *P. paniscus* males | 13 | 12 | 8 | 14 | 13 | 7 | 18 |
| *P. troglodytes* females | 85 | 80 | 58 | 86 | 86 | 69 | 91 |
| *P. troglodytes* males | 57 | 53 | 28 | 59 | 58 | 44 | 64 |

1. ‘total’ includes males, females, and unsexed individuals
2. ‘max n’ refers to the total number individuals present in each category from the original dataset. This would be the number of measurements present if all data were 100% complete.

For all long-bones the proportion of individuals with missing epiphyses decreased as length increased. This was an expected trend as older individuals are more likely to have fused epiphyses. There remained also the question of how many individuals had both long-bone measures with complete epiphyses as well as dental scores. Table 3.26 presents the number of individuals contributing at least one long bone length for each dental score interval of 10.

**Table 3.26** Number of individuals contributing long bone lengths with dental scores.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Pan troglodytes*** | | | | |
| **dental score** | **male** | **female** | **no sex** | **all individuals** |
| 0 to 10 | 0 | 2 | 2 | 4 |
| 11 to 20 | 4 | 4 | 3 | 8 |
| 21 to 30 | 9 | 9 | 2 | 18 |
| 31 to 40 | 9 | 6 | 0 | 15 |
| 41 to 50 | 11 | 13 | 5 | 24 |
| 51 to 60 | 13 | 15 | 2 | 29 |
| 61 + | 13 | 37 | 2 | 49 |
| sum | 59 | 86 | 14 | 159 |
| ***Pan paniscus*** | | | | |
| **dental score** | **male** | **female** | **no sex** | **all individuals** |
| 0 to 10 | 0 | 0 | 0 | 0 |
| 10 to 20 | 2 | 0 | 1 | 3 |
| 21 to 30 | 2 | 0 | 2 | 4 |
| 31 to 40 | 2 | 2 | 0 | 4 |
| 41 to 50 | 3 | 0 | 0 | 3 |
| 51 to 60 | 4 | 4 | 1 | 9 |
| 61 + | 4 | 5 | 0 | 9 |
| sum | 17 | 11 | 4 | 32 |

There was a paucity of individuals with lower dental scores in *Pan paniscus*. However, this problem would not be alleviated by the inclusion of individuals with incomplete epiphyses, as 32 individuals from the entire sample of 37 were accounted for (Table 3.24). The remaining 4 individuals lacked skulls and there was the single individual that had only two teeth as noted during imputation analysis (see section 3.3.3a). Even if a method for including incomplete bones was devised, it would be of no use here. The scores for *Pan troglodytes* follow a similar pattern to *Pan paniscus* but due to the much larger sample size, the lower dental scores are much better represented in this species. These values also follow a consistent pattern with the distribution of dental scores for the entire population (see section 3.3.4). The numbers of individuals do not substantially deviate from the numbers of individuals present for the entire sample. There were 159 chimpanzee specimens with complete long bones while the entire sample of dental scores for this species consisted of 162 individuals. Table 3.27 provides an assessment of the number of complete bones by bone type.

**Table 3.27** Number of complete bones by bone type.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Pan troglodytes* | | | | |
| **bone** | **entire sample** | **males** | **females** | **no sex** |
| humerus | 145 | 51 | 81 | 13 |
| radius | 135 | 49 | 74 | 12 |
| ulna | 88 | 25 | 54 | 9 |
| femur | 150 | 55 | 82 | 13 |
| tibia | 147 | 54 | 81 | 12 |
| fibula | 115 | 40 | 65 | 10 |
| *Pan paniscus* | | | | |
| **bone** | **entire sample** | **males** | **females** | **no sex** |
| humerus | 25 | 14 | 8 | 3 |
| radius | 24 | 12 | 9 | 3 |
| ulna | 17 | 8 | 7 | 2 |
| femur | 27 | 14 | 10 | 3 |
| tibia | 25 | 12 | 10 | 3 |
| fibula | 14 | 7 | 5 | 2 |

There is a distinct pattern in the frequencies of bone presence and this pattern directly correlates to the size of the epiphyseal plates. The ulna and the fibula, for example, have relatively smaller epiphyseal plates when compared to the femur and the tibia. For the humerus, the medial epicondyle is small but does not contribute to length, while the distal humerus fuses earlier than other long-bone epiphyses (see section 4.2). Small epiphyses are more frequently broken or lost and this was noted during data collection. As a consequence, bones such as the ulna were less frequently represented from younger individuals. Tables 3.28 and 3.29 provide the number of bones present by dental score for *Pan paniscus* and *Pan troglodytes*.

The values for *Pan paniscus* (Table 3.28) show the effects of single individuals within each dental score range and do not provide enough information to make a statement regarding the distribution of presence of bones. It does show that it was only males that had potentially sufficient numbers at each dental score range to produce a measure of growth over time/dental maturity. ‘Sufficient’numbers in this instance are the values acceptable for use in linear regression (see section 4.3.2).

**Table 3.28**  Number of present bones for each dental stage sorted by sex for *Pan panicus*.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species/sex** | **dental score** | **humerus** | **radius** | **ulna** | **femur** | **tibia** | **fibula** |
| *Pan paniscus*  no sex | 0 to 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 to 20 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 to 30 | 2 | 2 | 2 | 2 | 2 | 2 |
| 31 to 40 | 0 | 0 | 0 | 0 | 0 | 0 |
| 41 to 50 | 0 | 0 | 0 | 0 | 0 | 0 |
| 51 to 60 | 1 | 1 | 0 | 1 | 1 | 0 |
| 61+ | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pan paniscus*  females | 0 to 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 to 20 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 to 30 | 0 | 0 | 0 | 0 | 0 | 0 |
| 31 to 40 | 2 | 2 | 0 | 2 | 2 | 0 |
| 41 to 50 | 0 | 0 | 0 | 0 | 0 | 0 |
| 51 to 60 | 2 | 2 | 2 | 3 | 3 | 2 |
| 61+ | 4 | 5 | 5 | 5 | 5 | 3 |
| *Pan paniscus*  males | 0 to 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 to 20 | 2 | 1 | 0 | 1 | 0 | 0 |
| 21 to 30 | 1 | 1 | 1 | 1 | 1 | 1 |
| 31 to 40 | 2 | 2 | 0 | 1 | 2 | 0 |
| 41 to 50 | 2 | 1 | 1 | 3 | 1 | 0 |
| 51 to 60 | 4 | 4 | 3 | 4 | 4 | 3 |
| 61+ | 3 | 3 | 3 | 4 | 4 | 3 |

The presence of bones in the sample for *Pan troglodytes* over the full range of dental scores is more complete than that foud in the *Pan paniscus* sample. The data in Table 3.29 indicate that the numbers of bones for each bone type very closely follow each other as a proportion of the sample population and are consistent with the summary scores for all bones shown in Table 3.27. Female *Pan troglodytes* individuals in the category ‘61+’ are proportionately more numerous when compared to males in this category for all bones. Aside from this anomalous category where there clearly exists an excess of older females, males and females closely resemble each other in terms of bone presence by dental category for all bones. Even though they are substantially skewed towards older individuals, the numbers for all long bones cover a wide enough range of dental scores that it is likely that growth curves may be produced using regression techniques for males and females. The unsexed individuals are more problematic in terms of number. However, the only use for regression of unsexed individuals would be in the context of a pooled sample of males, females, and unsexed, representing both sexes.

**Table 3.29** Number of present bones for each dental stage sorted by sex for *Pan troglodytes*.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species/sex** | **dental score** | **humerus** | **radius** | **ulna** | **femur** | **tibia** | **fibula** |
| *Pan troglodytes*  no sex | 0 to 10 | 2 | 1 | 1 | 2 | 2 | 1 |
| 11 to 20 | 3 | 2 | 1 | 1 | 2 | 2 |
| 21 to 30 | 1 | 1 | 1 | 2 | 2 | 1 |
| 31 to 40 | 0 | 0 | 0 | 0 | 0 | 0 |
| 41 to 50 | 4 | 4 | 4 | 4 | 3 | 3 |
| 51 to 60 | 1 | 2 | 1 | 2 | 1 | 1 |
| 64+ | 1 | 1 | 1 | 1 | 1 | 1 |
| *Pan troglodytes*  females | 0 to 10 | 2 | 1 | 1 | 1 | 1 | 1 |
| 11 to 20 | 2 | 0 | 0 | 2 | 2 | 0 |
| 21 to 30 | 7 | 6 | 1 | 9 | 9 | 3 |
| 31 to 40 | 6 | 6 | 1 | 6 | 6 | 2 |
| 41 to 50 | 13 | 12 | 7 | 13 | 13 | 10 |
| 51 to 60 | 14 | 12 | 9 | 14 | 13 | 13 |
| 61+ | 37 | 37 | 35 | 37 | 37 | 36 |
|  | 0 to 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pan troglodytes*  males | 11 to 20 | 2 | 2 | 2 | 3 | 2 | 1 |
| 21 to 30 | 7 | 6 | 2 | 8 | 8 | 4 |
| 31 to 40 | 8 | 8 | 2 | 9 | 9 | 4 |
| 41 to 50 | 10 | 11 | 2 | 11 | 11 | 9 |
| 51 to 60 | 12 | 10 | 6 | 12 | 12 | 10 |
| 61+ | 12 | 12 | 11 | 12 | 12 | 12 |

### Investigating the possibility of lateralization

Humans show bone length asymmetry which is associated with handedness and there are consistent differences between sides (Auerbach and Ruff 2006). In chimpanzees and bonobos laterality is substantially less clear. Some reports suggest a slight tendency towards right-handedness in chimpanzees (Hopkins 2006, Hopkins and Pearson 2000) but with populations not necessarily tending towards one specific limb (Corp and Byrne 2003). In bonobos it has been suggested that there is no clear preference for hand use (Harrison and Nystrom 2008). With regards to osteological studies, some slight asymmetries have been reported with respect to sub-periosteal area of the humerus (Sarringhaus *et al.* 2005) but data specifically comparing left and right limb bone lengths appears to be lacking. Recent evidence based on humeral length in 40 chimpanzees suggested that there is no lateralisation (Barros and Soligo 2013). No data comparing humeral length in bonobos are available.

It would seem reasonable to postulate that if there does exist handedness in chimpanzees and bonobos, that this feature would be much less pronounced than it is for humans. This is because if distinct lateralisation were present then there would be much greater consensus regarding its presence given the amount of study already conducted considering the issue. As a consequence, the types of asymmetries seen in human limb dimensions are less likely to be present in the two *Pan* species.

In this study a combined sample variable would include some data from individuals that only have one side of the skeleton present. This could vary between left and right and also was found at a number of different dental score stages. In order to clarify if lateralization is a factor that may potentially reduce precision, differences between left and right are considered.

This procedure is commenced by first considering the humerus, which is the most lateralized bone in the human body. There were 19 left and 26 right humerii for *Pan paniscus* and 153 left and 149 right humerii for *Pan troglodytes* present. Of these, 16 *Pan paniscus* and 138 *Pan troglodytes* individuals had values for both sides. All values were inspected for extreme outliers (differences of more than 15 mm) as these were likely to be consequent of measurement error or a pathological condition. In humans, the deviation between sides is rarely greater than this value (Steele and Mays 1995). Two *Pan paniscus* and four *Pan troglodytes* individuals were removed due to greater than 30 mm difference between sides. The vast majority of individuals showed differences of less than 5 mm and these outlier individuals were likely the result of sampling error or some other unexplained effect. Figures 3.10 and 3.11 show individual points from humerii for *Pan paniscus* and *Pan troglodytes* respectively. A linear regression line is also plotted as well as a line of perfect isometry where left equals right.

**Figure 3.10**  Left and right humerii plotted again each other for *Pan paniscus* individuals.

**Figure 3.11** Left and right humerii plotted again each other for *Pan troglodytes* individuals.

The regression lines in Figures 3.14 and 3.15 almost perfectly overlap for both species, suggesting that there was no notable difference between right and left humerii with respect to length. Upon observation of the data points for individuals of *Pan troglodytes*, there appears not to be any significant trend of deviation above or below isometry for any point in development. If lateralization is a developed trait later in growth, then one might expect differences to appear more frequently at longer lengths, but this is clearly not the case. To compare these samples statistically, a non-parametric paired sample test was performed for the humerus in SPSS Statistics 21. Table 3.30 indicates *Z* scores and 2-tailed significance values for *Pan troglodytes* and *Pan paniscus* males and females.

**Table 3.30** Z scores and significance from 2-tailed paired sample test for the humerus in *Pan troglodytes* and *Pan pansicus*.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **test statistic** | ***Pan troglodytes*** | | ***Pan paniscus*** | |
| **females** | **males** | **females** | **males** |
| *Z* score | -0.938 | -0.65 | -1.063 | -1.378 |
| significance (2-tailed) | 0.348 | 0.516 | 0.288 | 0.168 |

**Table 3.31**  *Z* scores and 2-tailed significance for left-right comparisons of all long bones (excluding humerus) for male and female *Pan troglodytes* and *Pan paniscus*.

|  |  |  |
| --- | --- | --- |
| **species/sex/bone** | ***Z* score** | **significance (2-tailed)** |
| *P. paniscus* females radius | -1. | - |
| *P.paniscus* males radius | - | - |
| *P. troglodytes* female radius | -0.612 | 0.541 |
| *P. troglodytes* male radius | -1.131 | 0.258 |
| *P. paniscus* females ulna | -0.816 | 0.414 |
| *P.paniscus* males ulna | - | - |
| *P. troglodytes* female ulna | -0.163 | 0.870 |
| *P. troglodytes* male ulna | -0.634 | 0.526 |
| *P. paniscus* females femur | - | - |
| *P.paniscus* males femur | -0.141 | 0.888 |
| *P. troglodytes* female femur | -0.340 | 0.734 |
| *P. troglodytes* male femur | -0.524 | 0.600 |
| *P. paniscus* females tibia | -0.378 | 0.705 |
| *P.paniscus* males tibia | - | - |
| *P. troglodytes* female tibia | -0.641 | 0.521 |
| *P. troglodytes* male tibia | -1.342 | 0.180 |
| *P. paniscus* females fibula | -1.342 | 0.180 |
| *P.paniscus* males fibula | -0.447 | 0.655 |
| *P. troglodytes* female fibula | -0.519 | 0.604 |
| *P. troglodytes* male fibula | -0.169 | 0.866 |

1. ‘-’ means that all individuals had exactly the same score. This only occurred for *Pan paniscus* where small sample size contributed to this occurence. As such, no tests were performed.

It is clear that there is no statistically significant difference between left and right humeral measurements for either species. In humans this is the most asymmetric bone and it has been confirmed here that there is no significant difference for chimpanzees or bonobos. It may be inferred that it is very unlikely that the remaining bones of the body are asymmetric but to provide certainty this same statistical test was carried out for the remaining long bones and this was shown to be true. The results of these tests are shown in Table 3.31.

### Combined sample variable and dental score 64 individuals

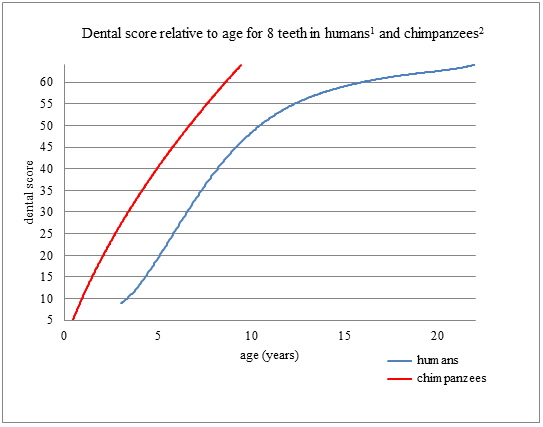
Given that there was no significant difference between sides with respect to length, a combined sample variable was created. A mean value for left and right was taken for individuals where there was a difference between sides. Long-bone lengths from the combined sample variable were sorted by species and by sex. The overall sample size present for individuals that also had corresponding dental scores is shown in Table 3.32.

**Table 3.32** Number of contributing measurements with dental scores for each long-bone in *Pan paniscus* and *Pan troglodytes*.

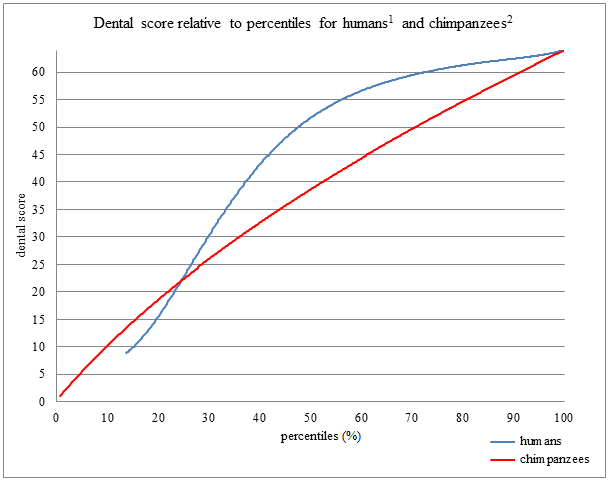
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Pan troglodytes*** | **males** | **females** | **unknown sex** | **total** |
| humerus | 51 | 81 | 0 | 132 |
| radius | 49 | 74 | 0 | 123 |
| ulna | 25 | 54 | 0 | 79 |
| femur | 55 | 82 | 0 | 137 |
| tibia | 54 | 81 | 0 | 135 |
| fibula | 40 | 65 | 0 | 105 |
| ***Pan paniscus*** | **males** | **females** | **unknown sex** | **total** |
| humerus | 14 | 8 | 3 | 25 |
| radius | 12 | 9 | 3 | 24 |
| ulna | 8 | 7 | 2 | 17 |
| femur | 14 | 10 | 3 | 27 |
| tibia | 12 | 10 | 3 | 25 |
| fibula | 7 | 5 | 2 | 14 |

## The problem of presenting data in a comparable framework

The presentation of long-bone growth data in past studies has mostly relied upon known-age samples. Those which have not (e.g., Shea 1981) have used emergence estimates for time and grouped individuals into age categories. Growth rate relative to time has been used to compare chimpanzees to humans. However, in the present study there are Demirjian scores from which lengths have been assigned as well as epiphyseal fusion data based on the same maturational indicator. The question remains as to which format is best for presenting growth patterns between chimpanzees and humans. Figure 3.12 presents regression curves for chimpanzee and human dental score plotted against chronological years as determined by prior studies. Figure 3.13 presents the same data but plotted as a percentage of growth in years.

1. Human data is based on Demirjian (1973), Demirjian and Levesque (1986) and Meinl *et al.* (2007)
2. Chimpanzee data is derived from regression by Kuykendall (1996)

**Figure 3.12** Chimpanzee and human Demirjian dental score relative to chronological age as determined by prior studies.

1. Human data is based on Demirjian (1973), Demirjian and Levesque (1986) and Meinl *et al.* (2007)
2. Chimpanzee data is derived from regression by Kuykendall (1996)

**Figure 3.13** Chimpanzee and human Demirjian dental score relative to percentiles of age as determined by prior studies.

While these data are well-known, it is important to observe in Figures 3.12 and 3.13 that the change in dental score as a function of age is not consistent between the two species. The increase in dental score with age reflects growth rate. Even when the duration of growth is scaled as a percentage of total growth period (birth to complete skeletal and dental maturation), the two species retain their distinctive patterns. One of the key factors behind this large difference is the human third molar. This tooth completes mineralization much later as a proportion of total growth period in humans than it does for chimpanzees. If the data for seven teeth (I1 to M2) were compared for both species as a percentage of the entire growth period the patterns become much more convergent. This may be hinted at by looking only at the earlier parts of the curve in Figure 3.13. However, in the present study there are data for 8 teeth and it is necessary to use third molar data in order to demonstrate the period of dental development relative to epiphyseal fusion. There are also other differences in terms of mineralization sequence from Kuykendall (1996) and others. These differences make the use of dental score as a direct means of comparison with humans technically inappropriate.

Two points can be drawn from this: 1) Dental score relative to years has no reliable direct translation between chimpanzees and humans, and 2) dental score relative to percentage of total growth period also mirrors growth rate. Comparing growth in these species must therefore rely on maturational indicators in both dental and skeletal systems. References to chronological time may only be made by aligning maturational events.

## Organisation of results

The main objective of this study was to measure the level of concordance in pattern and timing of skeletal systems in chimpanzees, bonobos and humans using dental mineralization, epiphyseal fusion, and growth in long-bone length. It is desireable to compare integrated data from *Pan* to *Homo* in order to better understand similarities and differences in skeletal developmental parameters between the two genera. As outlined in Chapter 2, some data already exist for chimpanzees and bonobos from each of these sub-systems, but integration is lacking from single-sample studies. Data collection methodology has now been presented for each of these sub-systems. The next step in this process is to consider how to integrate these systems using the data collected and compare them.

Within the context of growth theory, two major lines of inquiry have been highlighted that have theoretical significance, these being growth rate and sequences of developmental events. There is also theoretical discussion regarding allometric relationships and how sequences of events may relate to differences in morphology between species. The types of analyses performed on the data from this study seek to expand upon what is already known related to these topics and further integrate systems. Section 3.7.1 will describe how these topics will be addressed within the context of growth standard for chimpanzees (results presented in Chapter 4). Section 3.7.2 will address comparability of these results to studies of humans (results presented in Chapter 5). Not all types of analysis will be possible for both species due to the more limited sample size for *Pan paniscus*. Inclusion and exclusion of species in each analysis will be dealt with in each analysis.

### Standards of growth for chimpanzees and bonobos: Chapter 4

***3.7.1a: Growth rate***

Long-bone length is the only variable present in this study for evaluating growth rate. Age at death was not available for the individuals in these collections so growth in length may only be evaluated against other developmental parameters, which in this study shall be Demirjian summary dental score. Despite summary dental score being a sum of 8 categories of an ordinal variable for 8 teeth, this system provides the nearest approximation to a continuous variable of development. It has been shown that Demirjian summary dental score does not linearly relate to chronological age (section 3.6) and the increase in dental score with age approximates the curve determined in other studies for overall somatic growth with time. Long-bone length relative to dental score will be analysed using linear regression.

***3.7.1b Sequences of developmental events***

Epiphyseal fusion is the primary variable in which sequence shall be analysed. Analysis of dental developmental sequences could also be considered in this study. However, dental emergence and mineralization sequences are already well-known (e.g. Kuykendall 1996, Smith *et al*. 2007). Dental development will be limited to the production of summary Demirjian scores. Epiphyseal fusion events may be charted as a function of summary dental score. This provides information about the relationship between state of dental mineralization and skeletal fusion. Epiphyseal fusion may also be seriated independently as a sequence of events. This will be evaluated by considering mean epiphyseal fusion score and modular sequence derived from analysis of contingency tables.

***3.7.1c: Allometry***

The relationships of growth in length between different limb elements has in the past been analysed for *Pan troglodytes troglodytes* and *Pan paniscus* by Shea (1981) who found that the relative lengths of limb bones remain unchanged during growth. Shea (1981) also found that this consistency of limb-length is also found in humans. It is possible to confirm these patterns in the data set of the present study and extend these trends to further sub-species of *Pan troglodytes*. This will be done by employing linear regression analysis on Log10 transformed limb lengths.

***3.7.1d: Estimating chronological age for epiphyseal fusion events***

The estimation of chronological age for fusion events is possible using the regression equation for 8 teeth from Kuykendall (1996). The utility of pursuing a chronological reference is that it confirms the relationship between known-age studies and the present one. This allows for confident assessments of the relationship between maturation and chronological time.

### Comparisons of growth standards of Pan and Homo: Chapter 5

***3.7.2a: Comparison of epiphyseal fusion seriations of chimpanzees and humans***

With fusion sequence for chimpanzees and bonobos analysed by the use of modular sequence and mean epiphyseal fusion, comparisons with available human data is possible. Schaefer and Black (2007) provide a modular sequence for humans and comparison with this study will be made.

***3.7.2b: Comparison of dental sequences and epiphyseal fusion sequences between chimpanzees and humans***

Comparison of the sequence of epiphyseal fusion events and dental developmental events is limited by the fact that the dentition was analysed only using summary Demirjian dental score. As such discrete events such as molar emergence cannot be directly used as markers for grouping sequences of events. However, using standards from Kuykendall (1996) it is possible to estimate the timing of complete mineralization in certain teeth. This provides a means to group epiphyseal fusion events and count the number of events that occur in each grouping. This provides a basic measure as to how sequences of fusion and dental events compare in both humans and chimpanzees. This analysis will not be possible for bonobos given sample size limitations.

***3.7.2c: Relating sequences of fusion events to changes in allometry***

The relationship between fusion events are a proportion of growth in length is informative with respect to understanding how differences in dimensions are achieved between species. As such, this is a comparative analysis that will include humans and is found in Chapter 5. As outlined in Chapter 2, it is not known if changes in allometry between species affects the timing of epiphyseal fusion events as a proportion growth of length. Fusion events considered as a proportion of length will be compared between chimpanzees and humans.

# Results – Standards of growth for chimpanzees and bonobos

## Growth rate of long-bones as a function of dental score

### Analysis of growth rate as a function of dental score using regression analysis

This section will consider long-bone growth as a function of dental score. As outlined in Chapter 2, growth in length as a function of chronological years has been found to a be non-linear relationship for chimpanzees and bonobos (Leigh and Shea 1996). However, the nature of the relationship between growth in length for long-bones and dental score is not clear. This analysis begins by evaluating chimpanzee humeral length as a function of dental score and then expanding analysis to encompass all other long-bones. Figure 4.1 presents a scatterpot of humeral lengths for *Pan troglodytes* females plotted against dental score. There appear to be more individuals clustered around the higher dental score values of 62-64. This was a consequence of more individuals in this range having all epiphyses present for this bone. Fusion for the proximal epiphysis begins at these dental stages. The relationship appears linear. These data were analysed using linear regression analysis in SPSS Statistics 21. Regression results are presented in Table 4.1. Detailed results are available in section 8.3 of the appendix.

**Figure 4.1** Humeral length relative to dental score showing *Pan troglodytes* females.

**Table 4.1** Regression r-squared values for the humerus plotted against dental score for *Pan troglodytes* females.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  | **Change Statistics** | | | | |  |
| ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** | ***R*2 change** | ***F* change** | **df1** | **df2** | **sign. *F* change** | **Durbin-Watson** |
| .9301. | 0.866 | 0.864 | 5.5815 | 0.866 | 509.324 | 1 | 79 | 0 | 1.576 |

1. Predictors: (Constant), *Pan troglodytes* females humerus

With an *R*2 value of 0.866 and with residual analysis showing only very slight deviations, it may be accepted that chimpanzee humeral growth is linear as a function of dental score. DS64 individuals appear not to cause notable deviations, although the effect of the wider ranges at this score are visible in scatterplots for residuals. Results for *R*2 values for all long-bones in male and female *Pan troglodytes* are presented in Table 4.2. Growth in length as a function of dental score for these bones also behaves linearly with *R*2 values between 0.753 and 0.915. It is thus assumed that chimpanzee long-bone growth as a function of dental score may be plotted as a linear relationship for all long-bones. Full results for each bone are found in the appendix section 8.3. Figures 4.2 and 4.3 provide combined regression plots for all long-bones in male and female *Pan troglodytes*. Table 4.3 presents linear regression equations for the lines plotted in Figures 4.2 and 4.3.

**Table 4.2** Regression data for all 6 long bones in *Pan troglodytes* females and males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **species/sex** | **bone** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** |
|
| *Pan troglodytes* females | humerus | 0.930 | 0.866 | 0.864 | 19.2704 |
| radius | 0.917 | 0.840 | 0.838 | 16.7815 |
| ulna | 0.898 | 0.807 | 0.803 | 16.3876 |
| femur | 0.926 | 0.857 | 0.855 | 19.2221 |
| tibia | 0.926 | 0.857 | 0.855 | 16.7748 |
| fibula | 0.868 | 0.753 | 0.749 | 15.0836 |
| *Pan troglodytes* males | humerus | 0.875 | 0.766 | 0.761 | 22.8207 |
| radius | 0.933 | 0.870 | 0.867 | 16.0328 |
| ulna | 0.956 | 0.915 | 0.911 | 15.6222 |
| femur | 0.951 | 0.904 | 0.903 | 15.4383 |
| tibia | 0.941 | 0.886 | 0.884 | 14.3676 |
| fibula | 0.952 | 0.906 | 0.904 | 11.1698 |

**Figure 4.2** Multiple linear regressions for long-bone length in *Pan troglodytes* females.

**Figure 4.3** Multiple linear regressions for long-bone length in *Pan troglodytes* males.

**Table 4.3** Linear regression equations for *Pan troglodytes* males and females as plotted in Figure 4.2 and 4.3

|  |  |  |
| --- | --- | --- |
|  | regression equation for *Pan troglodytes* | |
| long-bone | females | males |
| humerus | *y* = 3.212 *x* + 87.869 | *y* = 3.1357*x* + 89.085 |
| radius | *y* = 2.8816*x* + 82.935 | *y* = 2.9265*x* + 79.682 |
| ulna | *y* = 3.1409*x* + 88.547 | *y* = 3.1135*x* + 84.563 |
| femur | *y* = 2.7238*x* + 70.272 | *y* = 3.2006*x* + 84.269 |
| tibia | *y* = 2.2443*x* + 77.612 | *y* = 2.7811*x* + 65.882 |
| fibula | *y* = 3.1357*x* + 89.085 | *y* = 2.443*x* + 64.541 |

Long bone length in *Pan paniscus*

Analysis of long-bone growth in *Pan paniscus* was more limited due to sample size being much smaller. Figure 4.4 shows humeral lengths for both male and female *Pan paniscus* plotted against dental score. Even though there appears to be a generally linear pattern observed for this bone, there were too few individuals present for regression analysis to reliably assess growth in length relative to dental score. Sex differences have been determined for *Pan paniscus* in the past (see Shea 1981) and as such combining sex for regression may not be valid. Shea (1981) also noted this limitation for his data set. This paucity of values is repeated for all other long bones.

**Figure 4.4** Male and female *Pan paniscus* humeral length plotted against dental score.

## Analysis of epiphyseal fusion sequences

Sequences will be evaluated by the following analyses:

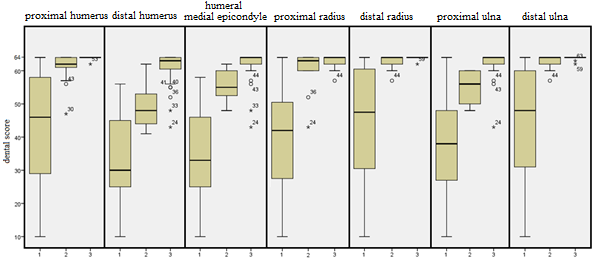
1. Epiphyseal fusion sequence will be compared to dental score (sections 4.2.1a-4.2.1c). This analysis will consider how these systems are related with dental score behaving as a continuous variable (justified in section). Descriptive statistics and analysis of limitations will be presented. A comparison between dental score and mean epiphyseal fusion score will be made (section 4.2.1d). This will assess the level of agreement between estimated maturity by dentition and epiphyseal fusion independently.

2. A seriation of fusion sequence will be produced by the use of two different methods. Epiphyseal fusion events will first be sorted by modular patterns as determined by contingency tables (section 4.2.2a). In the second approach, fusion events will be sorted by mean epiphyseal fusion score (sections 4.2.2b-4.2.2f).

### Comparing epiphyseal fusion sequences to dental score

***4.2.1a Evaluating limitations for analysis as a consequence of dental score 64 individuals***

As noted in Chapter 3, a limitation for this type of analysis is there are clearly individuals with multiple unfused epiphyses beyond DS64 in this data set. Another potential problem is that the range of dental scores for epiphyses that typically fuse below DS64 are derived from a sample that still often includes several individuals with DS64. Figure 4.5 illustrates this problem for the upper limb in *Pan troglodytes* females. This figure shows box plots for unfused, mid-fusion and complete fusion.



1: unfused

2: mid-fusion

3: complete fusion

**Figure 4.5** Mid-fusion and complete fusion for the epiphyses of the upper limb in *Pan troglodytes* females.

The effect of truncated ranges is evident for all mid-fusion and complete fusion events with the exception of the distal humerus and the humeral medial epicondyle. The proximal radius and proximal ulna have distributions with the majority of individuals below DS64 and this is true for many of the ranges of mid-fusion in other epiphyseal fusion sites. Determining mean values will not produce meaningful results for many later epiphyses as a result of the DS64 limitation. Median values are a more appropriate alternative. Table 4.4 provides median values and ranges of mid-fusion in each epiphysis for *Pan troglodytes* females. Median values above DS64 are highlighted in boldface. There were 8 epiphyses that had median value over DS64. This is in accordance with expectations set out in Chapter 3. Table 4.5 provides the same values for complete fusion from *Pan troglodytes* females.

Analysis of complete fusion ranges demonstrates that the majority of contributing fusion values have DS64. The remaining tables for *Pan troglodytes* males and *Pan paniscus* males and females are available in section 8.4 of the appendix (Tables 8.12-8.20). Full descriptive statistics are available for both *Pan troglodytes* and *Pan paniscus* males and females in the digital appendix section 8.2.1 (Tables 8.2.1.1-8.2.1.4).

**Table 4.4** Median values and ranges of fusion for all mid-fusion epiphyses in *Pan troglodytes* females.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median**  **dental score** | **minimum dental score** | **maximum dental score** |
| upper limb | proximal humerus | 19 | 62 | 47 | 64 |
| distal humerus | 8 | 48 | 41 | 62 |
| humeral medial epicondyle | 8 | 55 | 48 | 62 |
| proximal radius | 11 | 63 | 43 | 64 |
| distal radius | 16 | **64** | 57 | 64 |
| proximal ulna | 4 | 56 | 48 | 60 |
| distal ulna | 14 | **64** | 57 | 64 |
| hand | distal phalanges (hand) | 2 | 50 | 48 | 52 |
| base of metacarpal 1 | 7 | 61 | 43 | 64 |
| proximal and middle phalanges (hand) | 10 | 60.5 | 43 | 64 |
| metacarpal heads 2-5 | 7 | 62 | 60 | 64 |
| lower limb | femoral head | 10 | 62 | 56 | 64 |
| greater trochanter | 10 | 61.5 | 43 | 64 |
| lesser trochanter | 5 | 61 | 60 | 64 |
| distal femur | 19 | **64** | 60 | 64 |
| proximal tibia | 20 | 63.5 | 60 | 64 |
| distal tibia | 12 | 62.5 | 60 | 64 |
| proximal fibula | 14 | 63 | 60 | 64 |
| distal fibula | 9 | 63 | 60 | 64 |
| foot | calcaneus | 7 | 60 | 56 | 64 |
| talus | 2 | 57 | 52 | 62 |
| distal phalanges (foot) | 11 | 60 | 43 | 64 |
| middle phalanges (foot) | 10 | 62 | 43 | 64 |
| metatarsal heads (2-5) | 13 | 62 | 43 | 64 |
| base of metatarsal 1 | 8 | 62.5 | 56 | 64 |
| proximal phalanges (foot) | 8 | 61.5 | 43 | 64 |
| pelvis | triradiate | 8 | 56.5 | 10 | 62 |
| anterior inferior iliac spine | 1 | 55 | 55 | 55 |
| iliac crest | 18 | **64** | 62 | 64 |
| ischial epiphysis | 16 | **64** | 60 | 64 |
| clavicle | medial clavicle | 7 | **64** | 56 | 64 |
| lateral clavicle | 4 | 59 | 55 | 64 |
| scapula | coracoid | 9 | 58 | 45 | 64 |
| sub-coracoid and glenoid | 6 | 50 | 19 | 60 |
| acromium | 16 | **64** | 57 | 64 |
| medial border | 8 | **64** | 62 | 64 |

**Table 4.5** Median values and ranges of fusion for all complete fusion epiphyses in *Pan troglodytes* females.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median dental score** | **minimum dental score** | **maximum dental score** |
| upper limb | proximal humerus | 12 | **64** | 62 | 64 |
| distal humerus | 48 | 63 | 43 | 64 |
| humeral medial epicondyle | 42 | **64** | 43 | 64 |
| proximal radius | 30 | **64** | 57 | 64 |
| distal radius | 9 | **64** | 62 | 64 |
| proximal ulna | 40 | **64** | 43 | 64 |
| distal ulna | 10 | **64** | 62 | 64 |
| hand | distal phalanges (hand) | 10 | 62 | 56 | 64 |
| base of metacarpal 1 | 29 | **64** | 60 | 64 |
| proximal and middle phalanges (hand) | 29 | **64** | 60 | 64 |
| metacarpal heads 2-5 | 25 | **64** | 60 | 64 |
| lower limb | femoral head | 29 | **64** | 60 | 64 |
| greater trochanter | 32 | **64** | 60 | 64 |
| lesser trochanter | 37 | **64** | 43 | 64 |
| distal femur | 12 | **64** | 62 | 64 |
| proximal tibia | 13 | **64** | 62 | 64 |
| distal tibia | 21 | **64** | 62 | 64 |
| proximal fibula | 16 | **64** | 62 | 64 |
| distal fibula | 24 | **64** | 60 | 64 |
| foot | calcaneus | 35 | **64** | 43 | 64 |
| talus | 46 | 63 | 33 | 64 |
| distal phalanges (foot) | 31 | **64** | 56 | 64 |
| middle phalanges (foot) | 29 | **64** | 60 | 64 |
| metatarsal heads (2-5) | 25 | **64** | 60 | 64 |
| base of metatarsal 1 | 32 | **64** | 46 | 64 |
| proximal phalanges (foot) | 27 | **64** | 60 | 64 |
| pelvis | triradiate | 39 | **64** | 43 | 64 |
| anterior inferior iliac spine | 40 | **64** | 43 | 64 |
| iliac crest | 0 | - | - | - |
| ischial epiphysis | 11 | **64** | 62 | 64 |
| clavicle | medial clavicle | 5 | **64** | 64 | 64 |
| lateral clavicle | 28 | **64** | 43 | 64 |
| scapula | coracoid | 39 | **64** | 43 | 64 |
| sub-coracoid and glenoid | 42 | **64** | 43 | 64 |
| acromium | 4 | **64** | 64 | 64 |
| medial border | 2 | **64** | 64 | 64 |

***4.2.1b Projection of fusion using generated dental score***

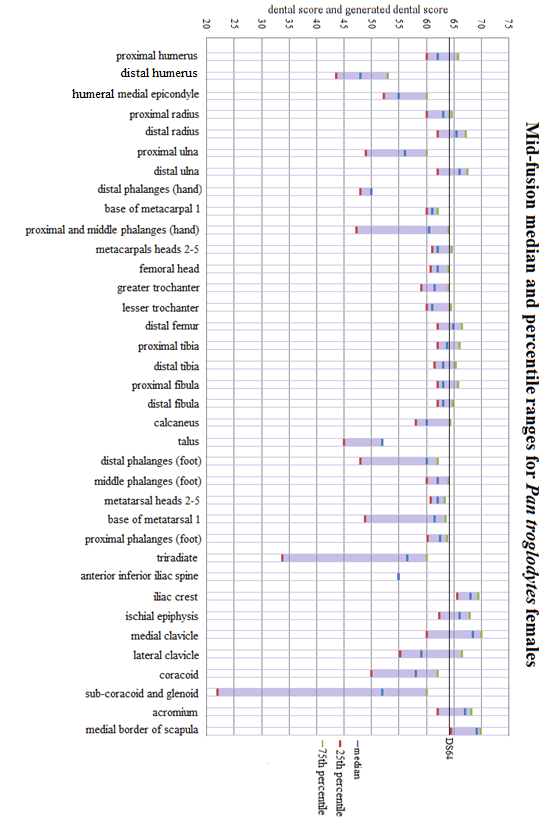
As outlined in Chapter 3, generated dental scores were produced for individuals with DS64 with additional increments added based on their mean epiphyseal fusion values (additional increment *x* = 0.3). To visualise these, median values were plotted. Plotted also were 25th and 75th percentiles. These values are listed for mid-fusion and complete fusion in Table 4.6 for *Pan troglodytes* females. Comparable data for *Pan troglodytes* males and *Pan paniscus* males and females are available in Tables 8.57 - 8.59 in the appendix.

Plots of mid-fusion and complete fusion data for *Pan troglodytes* males and females are shown below in Figures 4.6 - 4.9. Epiphyses with no range for percentiles lacked sufficient data. The majority of epiphyses had sufficient data. The grey regions between the 25th percentile, median, and 75th percentile are a visual aid and do not represent additional information. For *Pan paniscus* too few data entries were available for percentiles to be informative. It was common for many epiphyses to have only 2 - 5 data entries. For this species only median values for mid-fusion and complete fusion were plotted. Mid-fusion and complete fusion values were plotted on the same figure for females (Figure 4.10) and males (Figure 4.11).

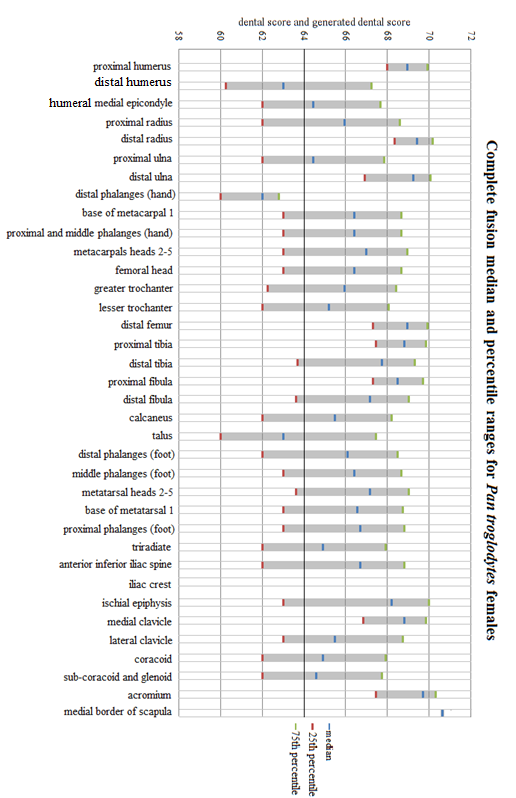
For *Pan troglodytes* individuals plotted against dental score in Figures 4.6 - 4.9 fusion events beyond DS64 are visible and are clearly patterned. It appears that *Pan paniscus* follow similar patterns, although the large amount of variation as a consequence of small sample size limits any further analysis.

**Table 4.6** Mid-fusion and complete fusion median, 25th and 75th percentiles values for generated dental score in *Pan troglodytes* females.

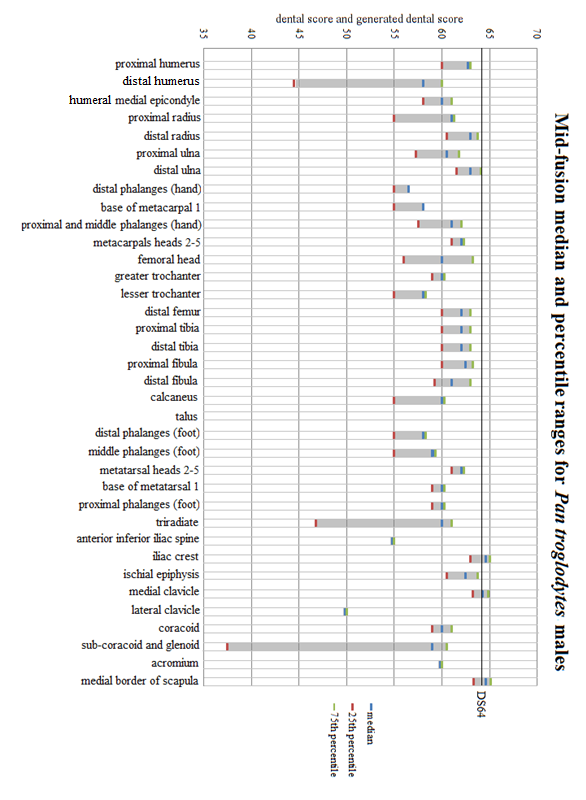
|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **mid-fusion** | | | **complete fusion** | | |
| **epiphysis** | **median** | **25th percentile** | **75th percentile** | **median** | **25th percentile** | **75th percentile** |
| proximal humerus | 62 | 60 | 65.8 | 68.95 | 67.975 | 69.925 |
| distal humerus | 48 | 43.5 | 53 | 63 | 60.25 | 67.225 |
| humeral medial epicondyle | 55 | 52.25 | 60 | 64.45 | 62 | 67.675 |
| proximal radius | 63 | 60 | 64.6 | 65.95 | 62 | 68.575 |
| distal radius | 65.5 | 62 | 67.15 | 69.4 | 68.35 | 70.15 |
| proximal ulna | 56 | 49 | 60 | 64.45 | 62 | 67.825 |
| distal ulna | 65.95 | 62 | 67.375 | 69.25 | 66.9 | 70.075 |
| distal phalanges (hand) | 50 | 48 | - | 62 | 60 | 62.8 |
| base of metacarpal 1 | 61 | 60 | 62 | 66.4 | 63 | 68.65 |
| proximal and middle phalanges (hand) | 60.5 | 47.25 | 64.075 | 66.4 | 63 | 68.65 |
| metacarpals heads 2-5 | 62 | 61 | 64.6 | 67 | 63 | 68.95 |
| femoral head | 62 | 60.75 | 64.075 | 66.4 | 63 | 68.65 |
| greater trochanter | 61.5 | 59 | 64.075 | 65.95 | 62.25 | 68.425 |
| lesser trochanter | 61 | 60 | 64.45 | 65.2 | 62 | 68.05 |
| distal femur | 64.9 | 62 | 66.4 | 68.95 | 67.3 | 69.925 |
| proximal tibia | 63.8 | 62 | 66.025 | 68.8 | 67.45 | 69.85 |
| distal tibia | 63 | 61.5 | 65.35 | 67.75 | 63.7 | 69.325 |
| proximal fibula | 63 | 62 | 65.8 | 68.5 | 67.3 | 69.7 |
| distal fibula | 63 | 62 | 64.75 | 67.15 | 63.625 | 69.025 |
| calcaneus | 60 | 58 | 64.3 | 65.5 | 62 | 68.2 |
| talus | 52 | 45 | - | 63 | 60 | 67.45 |
| distal phalanges (foot) | 60 | 48 | 62 | 66.1 | 62 | 68.5 |
| middle phalanges (foot) | 62 | 60 | 64.075 | 66.4 | 63 | 68.65 |
| metatarsal heads 2-5 | 62 | 60.75 | 63.25 | 67.15 | 63.625 | 69.025 |
| base of metatarsal 1 | 61.5 | 48.75 | 63.5 | 66.55 | 63 | 68.725 |
| proximal phalanges (foot) | 62.5 | 60.25 | 63.75 | 66.7 | 63 | 68.8 |
| triradiate | 56.5 | 33.75 | 60 | 64.9 | 62 | 67.9 |
| anterior inferior iliac spine | 55 | 55 | 55 | 66.7 | 62 | 68.8 |
| iliac crest | 68.05 | 65.55 | 69.475 | - | - | - |
| ischial epiphysis | 65.95 | 62.25 | 67.825 | 68.2 | 63 | 70 |
| medial clavicle | 68.5 | 60 | 70 | 68.8 | 66.85 | 69.85 |
| lateral clavicle | 59 | 55.25 | 66.425 | 65.5 | 63 | 68.725 |
| coracoid | 58 | 50 | 62 | 64.9 | 62 | 67.9 |
| sub-coracoid and glenoid | 52 | 22 | 60 | 64.6 | 62 | 67.75 |
| acromium | 67 | 62 | 68.2 | 69.7 | 67.45 | 70.3 |
| medial border of scapula | 69.1 | 64.5 | 69.85 | 70.6 | 70.6 | 70.6 |



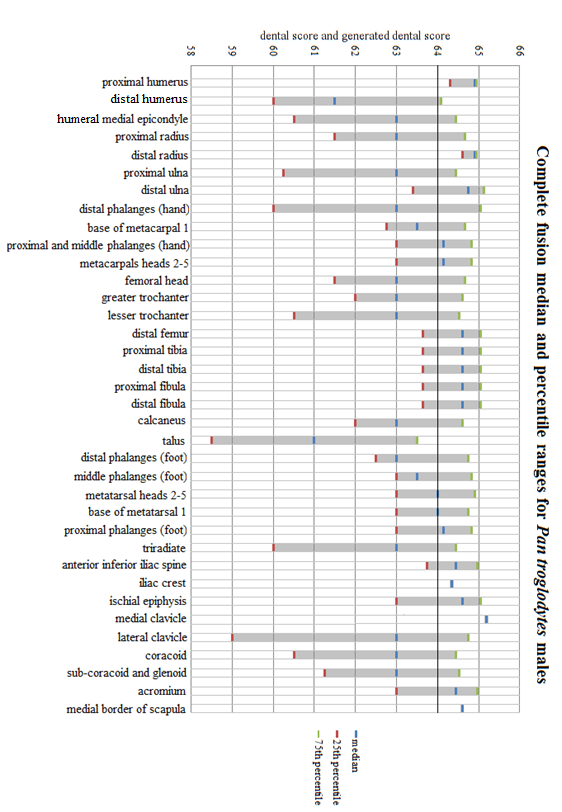
**Figure 4.6** Female *Pan troglodytes* mid-fusion with generated dental score.

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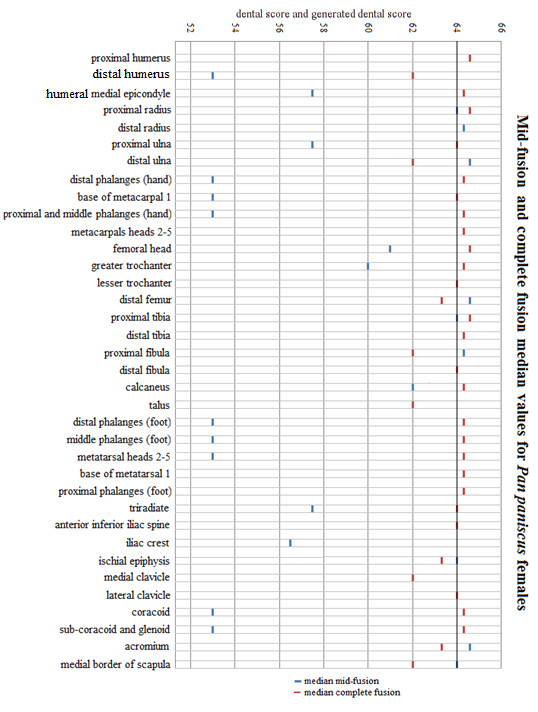
**Figure 4.7** Female *Pan troglodytes* complete-fusion with generated dental score.



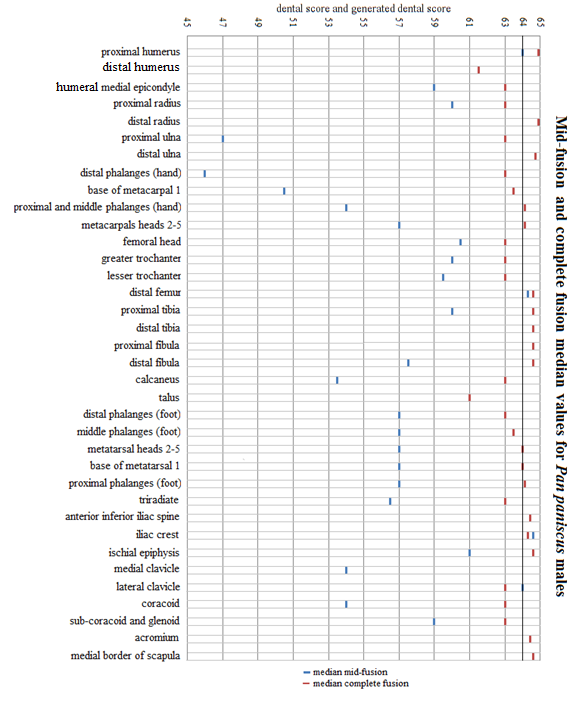
**Figure 4.8** Male *Pan troglodytes* mid-fusion with generated dental score.



**Figure 4.9** Male *Pan troglodytes* complete fusion with generated dental score.



**Figure 4.10** Female *Pan paniscus* mid-fusion and complete fusion median values plotted against dental score and generated dental score.



**Figure 4.11** Male *Pan paniscus* mid-fusion and complete fusion median values plotted against dental score and generated dental score.

***4.2.1c Analysis of sex differences when fusion events are compared to dental score for* Pan troglodytes**

As noted in Chapter 2, sex differences between males and females may be observed relative to chronological time with males delayed relative to females (Zihlman *et al*. 2007). It remains to be seen if this is the case for both dental and skeletal development, or if the delay only relates to skeletal development. This question may be considered for comparisons of fusion event timing with respect to dental score. Comparison are limited to epiphyses contributing values all below DS64 with acceptable sample sizes. An acceptable sample size may be defined as a minimum of 5 individuals. This limits the number of comparisons but there are a few epiphyses that meet this criteria, namely the distal humerus, humeral medial epicondyle, proximal ulna, femoral head, lesser trochanter, and middle phalanges of the foot. An independent t-test may be used to determine if there are differences between mid-fusion events. Using the central limit theorem the large number of ordinal categories presented by dental score approximates a normal distribution and the application of parametric tests to this distribution may be assumed to be robust (Norman 2010). The t-test test assumes normality of distributions. A Shapiro-Wilk test for normality was carried out for each epiphysis and the results are presented in Table 4.7. The lesser trochanter for female *Pan troglodytes* and the distal humerus for *Pan troglodytes* males violate this assumption but all others fail to reject the null hypothesis and normality is assumed. Independent sample t-tests were carried out for the humeral medial epicondyle, proximal ulna, femoral head, and middle phalanges of the foot. The results are shown in Table 4.8.

**Table 4.7** Shapiro-Wilk normality test for *Pan troglodytes* male and female epiphyses with dental scores below DS64.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  | **Shapiro-Wilk** | | |
| **sex** | **epiphysis** | **statistic** | **df** | **sig.** |
| *Pan troglodytes* females | distal humerus | 1.000 | 3 | 1.000 |
| humeral medial epicondyle | 0.893 | 3 | 0.363 |
| proximal ulna | 0.964 | 3 | 0.637 |
| femoral head | 0.893 | 3 | 0.363 |
| lesser trochanter | 0.750 | 3 | 0.000 |
| middle phalanges (foot) | 0.821 | 3 | 0.165 |
| *Pan troglodytes* males | distal humerus | 0.750 | 3 | 0.000 |
| humeral medial epicondyle | 0.987 | 3 | 0.780 |
| proximal ulna | 0.964 | 3 | 0.637 |
| femoral head | 0.964 | 3 | 0.637 |
| lesser trochanter | 1.000 | 3 | 1.000 |
| middle phalanges (foot) | 0.964 | 3 | 0.637 |

**Table 4.8** t-test comparison for male and female *Pan troglodytes* epiphyses that satisfy criteria for being below dental score 64.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | | **Levene's Test for Equality of Variances** | | **t-test for equality of means** | | | | | **95% confidence Interval of the Difference** | |
| **epiphysis** | | **F** | **sig.** | **t** | **df** | **Sig. (2-tailed)** | **mean differences** | **std. error differences** | **lower** | **upper** |
| humeral medial epicondyle | a1. | 4.072 | 0.07 | -1.7 | 13 | 0.108 | -3.38 | 1.957 | -8 | 0.85 |
| b2. |  |  | -1.8 | 10 | 0.101 | -3.38 | 1.8671 | -8 | 0.78 |
| proximal ulna | a | 5.878 | 0.04 | -1.7 | 8 | 0.127 | -4.83 | 2.8398 | -11 | 1.72 |
| b |  |  | -1.5 | 4.1 | 0.21 | -4.83 | 3.2498 | -14 | 4.14 |
| femoral head | a | 1.036 | 0.33 | 1.22 | 12 | 0.245 | 2.05 | 1.6764 | -2 | 5.7 |
| b |  |  | 1.01 | 4.1 | 0.371 | 2.05 | 2.0391 | -4 | 7.69 |
| middle phalanges (foot) | a | 0.268 | 0.62 | 0.61 | 11 | 0.558 | 2.5 | 4.1274 | -7 | 11.6 |
| b |  |  | 0.9 | 8.3 | 0.394 | 2.5 | 2.7764 | -4 | 8.86 |

1. Equal variances assumed
2. Equal variances are not assumed

None of the four epiphyses analysed showed differences between each other. This analysis is very limited in the sense that only four epiphyses satisfied the criteria necessary for this type of comparison. As such it cannot be unequivocally stated that fusion follows the same pattern in males and females with respect to dental score. However, the results from these epiphyses do lend support to the case that the relationship between skeletal and dental development is the same for both male and females irrespective of differences potentially observed in fusion timing relative to chronological years. It should be noted that a sex differences has been observed for chimpanzee dentition. This difference is in the completion of the canine (Kuykendall 1996). Regrettably this point of difference is near the end of completion of the dentition and would not affect the epiphyses listed here. It may be suggested that for earlier-fusing epiphyses that there are unlikely to be difference between the sexes. No epiphyses for complete fusion were available for this analysis. Producing a mixed-sex comparison of epiphyseal fusion events relative to chronological age is not necessarily justified with the limited amount of information at present.

***4.2.1d Assessing the difference between mean epiphyseal fusion value and dental score***

Having both a measure of skeletal maturation (mean epiphyseal fusion score) and dental maturation (dental score) for each individual permits comparison between the state of maturity for both systems. As noted in Chapter 3, it has been well-established that dental development is less susceptible to nutritional or environmental stress than skeletal development, resulting in an offset of the two systems (Chaillet and Demirjian 2004). Table 4.9 presents a comparison of dental score and mean epiphyseal fusion score for *Pan troglodytes* females. Dental scores for mean epiphyseal fusion value of 1 are not included here due to all epiphyses being unfused at this stage.

**Table 4.9** Mean epiphyseal fusion value compared to dental score for *Pan troglodytes* females by individual.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **mean epiphyseal fusion value** | **dental score** | **mean epiphyseal fusion value** | **dental score** | **mean epiphyseal fusion value** | **dental score** |
| 1.13 | 33 | 2.77 | 62 | 4.27 | 64 |
| 1.16 | 45 | 2.77 | 64 | 4.3 | 64 |
| 1.2 | 55 | 3.12 | 64 | 4.31 | 64 |
| 1.23 | 53 | 3.24 | 62 | 4.35 | 62 |
| 1.23 | 53 | 3.38 | 63 | 4.38 | 64 |
| 1.41 | 55 | 3.45 | 62 | 4.41 | 64 |
| 1.47 | 55 | 3.48 | 63 | 4.53 | 63 |
| 1.5 | 58 | 3.57 | 60 | 4.55 | 62 |
| 1.56 | 52 | 3.58 | 62 | 4.59 | 64 |
| 1.77 | 48 | 3.82 | 64 | 4.59 | 64 |
| 2.38 | 60 | 3.86 | 60 | 4.59 | 64 |
| 2.41 | 62 | 3.93 | 57 | 4.73 | 64 |
| 2.47 | 60 | 3.96 | 64 | 4.81 | 64 |
| 2.47 | 64 | 4.03 | 62 | 4.84 | 64 |
| 2.47 | 64 | 4.05 | 64 | 4.89 | 64 |
| 2.56 | 43 | 4.13 | 64 | 4.89 | 64 |
| 2.64 | 56 | 4.17 | 63 | 4.91 | 64 |
| 2.77 | 61 | 4.27 | 64 |  |  |

Mean epiphyseal fusion scores generally follow the same order as dental score score with a degree of fluctation depending on the individual. There were occasional outliers of higher dental score with lower mean epiphyseal fusion values. These outliers constitute large offsets between dental development and skeletal development. It should be noted that when the epiphyseal fusion values for these individuals are considered there is no consistent pattern of deviation of fusion events. None of the individuals presented in Table 4.9 had recorded pathological conditions. Table 4.10 demonstrates the same data for *Pan troglodytes* males and *Pan paniscus* males and females. Individuals with mean epiphyseal fusion value 1 were again not reported.

**Table 4.10** Mean epiphyseal fusion value compared to dental score for *Pan troglodytes* males and *Pan paniscus* males and females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| ***P. troglodytes* male** | | | | ***P. paniscus* female** | | ***P. paniscus* male** | |
| **mean epiphyseal fusion vale** | **dental score** | **mean epiphyseal fusion vale** | **dental score** | **mean epiphyseal fusion vale** | **dental score** | **mean epiphyseal fusion vale** | **dental score** |
| 13 | 1.03 | 60 | 1.80 | 1.30 | 53 | 1.10 | 45 |
| 20 | 1.03 | 61 | 1.81 | 1.76 | 53 | 1.82 | 47 |
| 50 | 1.03 | 55 | 1.91 | 1.83 | 62 | 1.88 | 61 |
| 31 | 1.05 | 59 | 2.66 | 2.15 | 51 | 2.10 | 59 |
| 43 | 1.06 | 61 | 2.73 | 3.50 | 60 | 2.25 | 60 |
| 46 | 1.06 | 60 | 3.48 | 4.14 | 64 | 2.88 | 54 |
| 55 | 1.10 | 64 | 3.88 | 4.45 | 64 | 2.95 | 60 |
| 43 | 1.12 | 63 | 3.92 | 4.48 | 64 | 3.28 | 61 |
| 44 | 1.17 | 62 | 3.98 | 4.92 | 62 | 4.34 | 64 |
| 53 | 1.24 | 60 | 4.05 |  |  | 4.79 | 64 |
| 59 | 1.25 | 63 | 4.14 |  |  |  |  |
| 60 | 1.31 | 63 | 4.70 |  |  |  |  |
| 60 | 1.38 | 64 | 4.72 |  |  |  |  |
| 58 | 1.44 | 64 | 4.88 |  |  |  |  |
| 58 | 1.60 | 64 | 4.89 |  |  |  |  |
| 61 | 1.71 | 64 | 4.94 |  |  |  |  |

***4.2.1e Summary of fusion event comparisons to dental score***

A pattern of fusion was visible when fusion events were compared to both dental score and generated dental score. Differences between the sexes were not found, although the data suitable for this comparison were limited. This comparison demonstrates clearly that at least several fusion events begin union beyond DS64.

### Producing a seriation of epiphyseal fusion sequences

***4.2.2a Seriation using contingency tables to produce a modular sequence for fusion***

Given the limitations for *Pan paniscus* epiphyseal fusion data observed in the previous section it was decided to begin this analysis by considering *Pan troglodytes* only. Contigency tables for mid-fusion values comparing each epiphysis were produced using SPSS 21 for both male and females. An example of such a table is provided in Table 4.11. Tables 4.12 and 4.13 below demonstrate the modular sequence order produced for male and female *Pan troglodytes*. Some sequence could not be established. These are highlighted by boldface lettering. The lateral clavicle and anterior inferior iliac spine were not included in this analysis due to suspected problems with reliability in measurement. The range of variation in fusion timing of these sites was too unpredictable.

**Table 4.11** Example of contingency table comparing the coracoid with the distal ulna in *Pan troglodytes* males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | | **distal ulna stage** | | | **total** |
| **1** | **2** | **3** |
| coracoid stage | 1 | 37 | 0 | 0 | 37 |
| 2 | 8 | 0 | 0 | 8 |
| 3 | 17 | 16 | 11 | 44 |
| total | | 62 | 16 | 11 | 89 |

Stage 1: unfused

Stage 2: mid-fusion

Stage 3: complete fusion

**Table 4.12** Modular sequence of fusion for *Pan troglodytes* females.

|  |  |
| --- | --- |
| **sequence number** | **epiphysis** |
| 1 | distal humerus |
| 2 | humeral medial epicondyle |
| 3 | sub-coracoid and glenoid |
| 4 | coracoid |
| 5 | triradiate |
| 6 | distal phalanges hand |
| 7 | proximal ulna |
| **8** | **talus** |
| **8** | **distal phalanges, middle phalanges, metatarsal heads 2-5** |
| 9 | calcaneus |
| 10 | proximal and middle phalanges of hand |
| **11** | **proximal radius** |
| **11** | **greater trochanter** |
| **11** | **proximal phalanges (foot) and base of metatarsal 1** |
| 12 | lesser trochanter |
| 13 | base of metacarpal 1 |
| 14 | femoral head |
| 15 | heads of metacarpals 2-5 |
| 16 | distal fibula |
| **17** | **proximal tibia** |
| **17** | **distal tibia** |
| **18** | **distal femur** |
| **18** | **proximal fibula** |
| 19 | proximal humerus |
| 20 | ischial epiphysis |
| 21 | distal radius |
| 22 | distal ulna |
| 23 | acromium |
| 24 | iliac crest |
| 25 | medial border of scapula |
| 26 | medial clavicle |

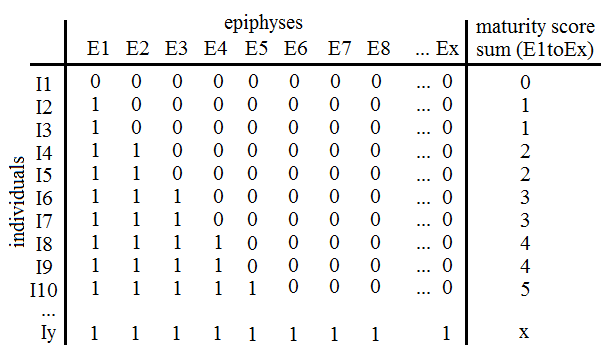
**Table 4.13** Modular sequence of fusion for *Pan troglodytes* males.

|  |  |
| --- | --- |
| **sequence number** | **epiphysis** |
| 1 | distal humerus |
| 2 | sub-coracoid and glenoid |
| 3 | **distal phalanges hand** |
| 3 | **triradiate** |
| 4 | talus |
| 5 | coracoid |
| 6 | base of metacarpal 1 |
| 7 | proximal ulna |
| 8 | distal phalanges, middle phalanges, metatarsal heads 2-5 |
| 9 | calcaneus |
| 10 | proximal and middle phalanges of hand |
| 11 | lesser trochanter |
| 12 | femoral head |
| **13** | **proximal radius** |
| **13** | **greater trochanter** |
| **13** | **proximal phalanges (foot) and base of metatarsal 1** |
| **14** | **heads of metacarpals 2-5** |
| **14** | **distal fibula** |
| 15 | distal tibia |
| 16 | distal femur |
| 17 | proximal tibia |
| 18 | distal radius |
| **19** | **proximal fibula** |
| **19** | **ischial epiphysis** |
| 20 | humeral medial epicondyle |
| 21 | distal ulna |
| 22 | proximal humerus |
| 23 | acromium |
| **24** | **iliac crest** |
| **24** | **medial clavicle** |
| **24** | **medial border of scapula** |

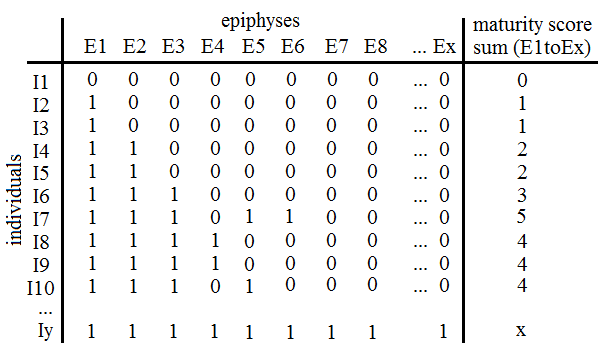
These sequences are similar but not identical. Differences found are the likely result of the smaller sample size for males. Contingency tables inherently require measurements from both epiphyses to be present for each individual. For many epiphyses in males this requirement meant that only a single fusion event was present. Order changes of closely fusing fusion events were frequent. For epiphyses where difficulty in observation due to cartilage was a frequent problem during data collection, such order changes were more common. Occasionally more large sequence changes occurred. For example, the proximal humerus is a later-fusing epiphyses but for a small number of individuals, fusion at this site deviates much earlier in sequence. It is likely these values were erroneus. This observation may also be made for the talus, the base of metacarpal 1 and the distal phalanges of both hands and feet. In theory, testing for significant difference in sequence between sexes would requires chi-squared tests for each shift in sequence order. Sample size for males was deemed too small for this analysis to reliably be conducted. Given the level of variability observed for modular sequence analysis in *Pan troglodytes,* it was decided not to conducted this analysis for *Pan paniscus*.

***4.2.2b: Seriating sequence order by assessing mean epiphyseal fusion score in males and females independently***

The use of mean epiphyseal fusion score for ordering fusion events is an alternative to the the application of contingency tables. The utility of this method will be assessed in this section. In theory, if all individuals underwent fusion in exactly the same order then simply ordering these individuals based on their mean epiphyseal fusion score would produce a clear pattern. Figure 4.12 demonstrates how an epiphyseal seriation would appear under ideal conditions. Figure 4.13 shows deviations more typically observed in the present study. ‘0’ is defined as unfused and ‘1’ as fused. Epiphyseal fusion events in Figure 4.7 follow a progression of E1, E2, E3 … Ex. In Figure 4.13 the order of these events is far less clear. Variations in sequence are to be expected. As outlined in Chapter 2, for humans sequences of fusion have been determined and reported by studies such as Schaefer and Black (2007). Specific polymorphic sites are highlighted in texts such as Scheuer and Black (2004). A more complete picture (e.g., Schaefer and Black 2007, Schaefer 2008) suggests that many different patterns occur for epiphyses that fuse closely in time and that there is simply a pattern that the majority of studies agree with. Larger samples have tended towards the most common patterns. There is no reason to believe that chimpanzees and bonobos show any differing levels of variation in sequence than humans.



**Figure 4.12** Hypothetical perfect seriation of epiphyseal fusion events.

**Figure 4.13** Typical types of order deviations.

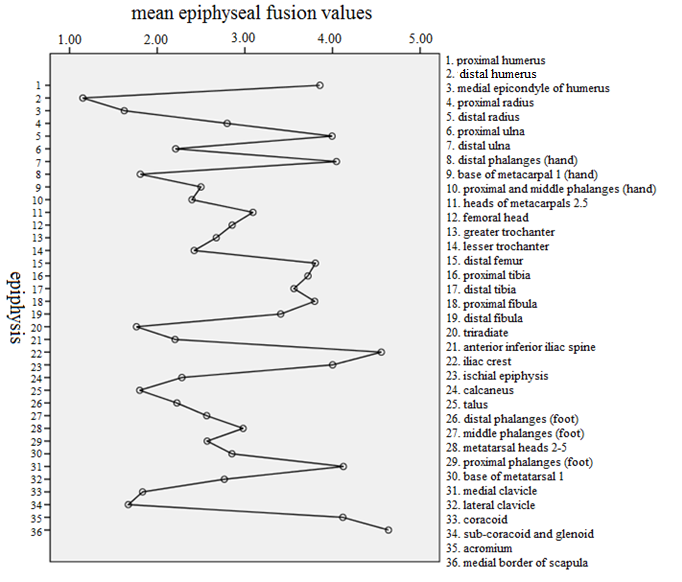
Due to the contraints previous mentioned only *Pan troglodytes* will be considered here. Mid-fusion and complete fusion were analysed separately. All data were analyzed using SPSS 21. Similar to dental score, mean epiphyseal fusion values are based on a series of many ordinal variables and by the central limit theorem behave as a continuous variable (Norman 2010). A one-way ANOVA was able to distinguish if any of the ranges of fusion for these epiphyses were significantly different. This test assumed that all variables were normally distributed. Shapiro-Wilk and Kolmogorov-Smirnov tests were applied to both males and female *Pan troglodytes* for both mid-fusion and complete fusion. Results are available in section 8.5 of the appendix (Tables 8.21-8.24). Complete fusion represents a permanent stable state after fusion has occurred. As such, ranges for complete fusion might be assumed that to be less likely to demonstrate normality due to the fact that these ranges will have no central tendency. This was not the case and the vast majority of epiphyses were normally distributed. Table 4.14 summarises epiphyses that were non-normal and those that were excluded from analysis due to limited sample size (3 or fewer individuals present).

**Table 4.14** Summary of non-normal ranges of mean epiphyseal fusion score for mid-fusion and complete fusion in *Pan troglodytes* males and females.

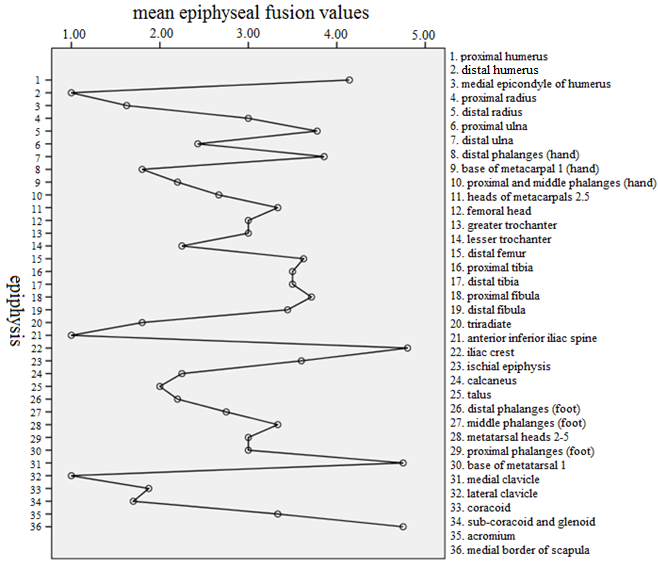
|  |  |  |  |
| --- | --- | --- | --- |
| **sex** | **fusion state** | **non-normal epiphyses** | **excluded epiphyses** |
| female | mid-fusion | distal humerus (p=0.03) | none |
| female | complete fusion | proximal humerus (p=0.002) | iliac crest |
| proximal fibula (p=0.034) | medial border of scapula |
| proximal phalanges (foot) (p=0.04) |  |
| sub-coracoid and glenoid (p=0.028) |  |
| male | mid-fusion | distal humerus (p=0.000) | anterior inferior iliac spine |
| sub-coracoid and glenoid (p=0.000) | lateral clavicle |
|  | talus |
| male | complete fusion | none | iliac crest |
| medial clavicle |
| medial border of scapula |

For epiphysis in mid-fusion for females, only the distal humerus was not normally distributed. For mid-fusion, in males the trochea and sub-coracoid and glenoid were not normally distributed. Tests of normality for complete fusion in females indicated that the proximal humerus, proximal fibula, proximal phalanges (foot) and the sub-coracoid and glenoid were not normally distributed. For complete fusion in males, all epiphyseal fusion ranges were normal. Of greater concern in this analysis is mid-fusion as this represents the process of fusion. For mid-fusion, there were 3 epiphyses out of a total of 69 that were not normally distributed. A one-way ANOVA was performed with, and without these epiphyses. Both returned p-values of 0.000, indicating that the presence of these epiphyses does not affect the difference in overlap of ranges and there is a significant difference for at least one range of fusion values. Subsequent post-hoc Bonferroni tests were used to distinguish which epiphyses differed from each other. Rather than excluding these from analysis, it was decided to continue analysis with these epiphyses present. Post-hoc Bonferroni comparisons with these epiphyses may simply be accepted as less robust. Non-parametric tests may subsequently be performed if necessary. Figures 4.14 and 4.15 show mean values for all mid-fusion epiphyses in male and female *Pan troglodytes*.

It may be observed in Figures 4.14 and 4.15 that the pattern of fusion events in males and females were generally the same with some exceptions. Differences between sex will be considered in section 4.2.2c. Post-hoc Bonferroni tests for determining which epiphyses significantly differed from each other produced a large number of comparisons. There were 36 epiphyses for each sex. All comparisons were too numerous to provide here but these are available in Table 8.2.2.1 of the digital appendix (section 8.2.2). A numbering legend for this table is presented in Table 8.2.2.2 in the digital appendix. Significant overlaps and differences were found for all epiphysis. To make sense of what these comparisons imply, an example will be considered. Table 4.15 provides post-hoc Bonferroni comparisons for the proximal humerus in *Pan troglodytes* females.



**Figure 4.14** Mean values for all epiphyses at mid-fusion states for *Pan troglodytes* females.

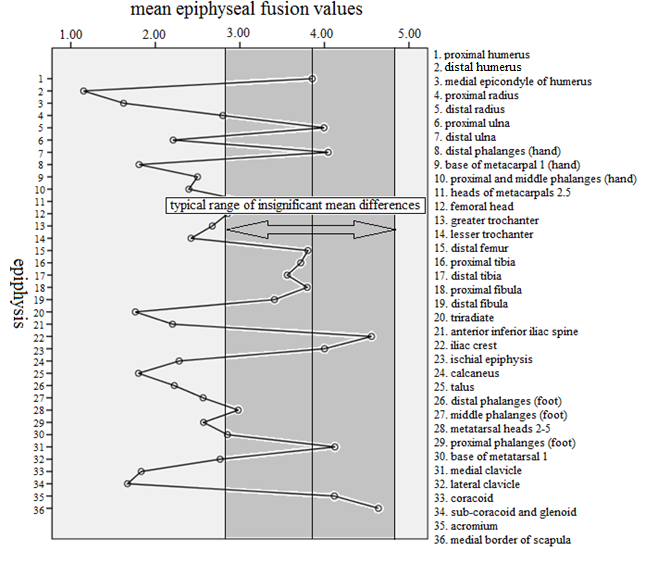


**Figure 4.15** Mean values for all epiphyses at mid-fusion states for *Pan troglodytes* females.

**Table 4.15** Post-hoc Bonferroni test of difference for the proximal humerus in *Pan troglodytes* females.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **(J) proximal humerus** | **mean difference (I-J)** | **std. error** | **sig.** | **95% confidence Interval** | |
| **lower Bound** | **upper Bound** |
| distal humerus | 2.66333\* | 0.22262 | 0.000 | 1.7747 | 3.552 |
| humeral medial epicondyle | 2.12667\* | 0.21347 | 0.000 | 1.2745 | 2.9788 |
| proximal radius | .97083\* | 0.1939 | 0.001 | 0.1968 | 1.7448 |
| distal radius | -0.38137 | 0.17481 | 1.000 | -1.0792 | 0.3164 |
| proximal ulna | 1.47667\* | 0.24803 | 0.000 | 0.4866 | 2.4668 |
| distal ulna | -0.37604 | 0.17781 | 1.000 | -1.0858 | 0.3337 |
| distal phalanges (hand) | 1.97667\* | 0.33071 | 0.000 | 0.6565 | 3.2968 |
| base of metacarpal 1 (hand) | .94833\* | 0.22262 | 0.016 | 0.0597 | 1.837 |
| proximal and middle phalanges (hand) | 1.42697\* | 0.19943 | 0.000 | 0.6309 | 2.223 |
| heads of metacarpals 2-5 | 0.71111 | 0.21347 | 0.601 | -0.141 | 1.5633 |
| femoral head | .87606\* | 0.19943 | 0.009 | 0.08 | 1.6721 |
| greater trochanter | 1.09970\* | 0.19943 | 0.000 | 0.3036 | 1.8958 |
| lesser trochanter | 1.18133\* | 0.26663 | 0.008 | 0.117 | 2.2457 |
| distal femur | -0.12143 | 0.16536 | 1.000 | -0.7815 | 0.5386 |
| proximal tibia | -0.04048 | 0.16536 | 1.000 | -0.7005 | 0.6196 |
| distal tibia | 0.17405 | 0.18487 | 1.000 | -0.5639 | 0.912 |
| proximal fibula | -0.05979 | 0.17781 | 1.000 | -0.7696 | 0.65 |
| distal fibula | 0.36433 | 0.20587 | 1.000 | -0.4574 | 1.1861 |
| triradiate | 1.97111\* | 0.21347 | 0.000 | 1.119 | 2.8233 |
| anterior inferior iliac spine | 0.99833 | 0.39651 | 1.000 | -0.5845 | 2.5811 |
| iliac crest | -.76567\* | 0.16741 | 0.004 | -1.4339 | -0.0974 |
| ischial epiphysis | -0.35333 | 0.17211 | 1.000 | -1.0404 | 0.3337 |
| calcaneus | 1.37833\* | 0.22262 | 0.000 | 0.4897 | 2.267 |
| talus | 1.86333\* | 0.33071 | 0.000 | 0.5432 | 3.1835 |
| distal phalanges (foot) | 1.47000\* | 0.1939 | 0.000 | 0.696 | 2.244 |
| middle phalanges (foot | 1.17970\* | 0.19943 | 0.000 | 0.3836 | 1.9758 |
| metatarsal heads 2-5 | .81067\* | 0.18114 | 0.006 | 0.0876 | 1.5337 |
| proximal phalanges (foot) | 1.25083\* | 0.22262 | 0.000 | 0.3622 | 2.1395 |
| base of metatarsal 1 | 0.86208 | 0.22262 | 0.08 | -0.0266 | 1.7507 |
| medial clavicle | -0.10667 | 0.23385 | 1.000 | -1.0401 | 0.8268 |
| lateral clavicle | 0.55333 | 0.29231 | 1.000 | -0.6135 | 1.7202 |
| coracoid | 1.83433\* | 0.20587 | 0.000 | 1.0126 | 2.6561 |
| sub-coracoid and glenoid | 2.03583\* | 0.22262 | 0.000 | 1.1472 | 2.9245 |
| acromium | -0.48078 | 0.17481 | 1.000 | -1.1786 | 0.217 |
| medial border | -.87267\* | 0.20587 | 0.018 | -1.6944 | -0.0509 |

As observed in Figures 4.14 and 4.15, the proximal humerus is a relatively late-fusing epiphysis in terms of mean epiphyseal fusion score but does not appear to be the last. When compared to this epiphysis, 14 of 35 other epiphyses (40%) were not significantly different while 21 did show differences (p-values shown above in Table 4.15). The most distant epiphysis that did not significantly differ was the anterior inferior iliac spine (mean difference of 0.99833). and the most proximate in terms of significant differences was the medial border of the scapula (mean difference of -0.87267, p=0.018). Essentially, epiphyses that had a mean epiphyseal fusion value distance greater than 1 would show significant differences and those nearer would not. This pattern is observed for all epiphyses. Figure 4.16 demonstrates how this ranges of no statistical differences may be visualised.



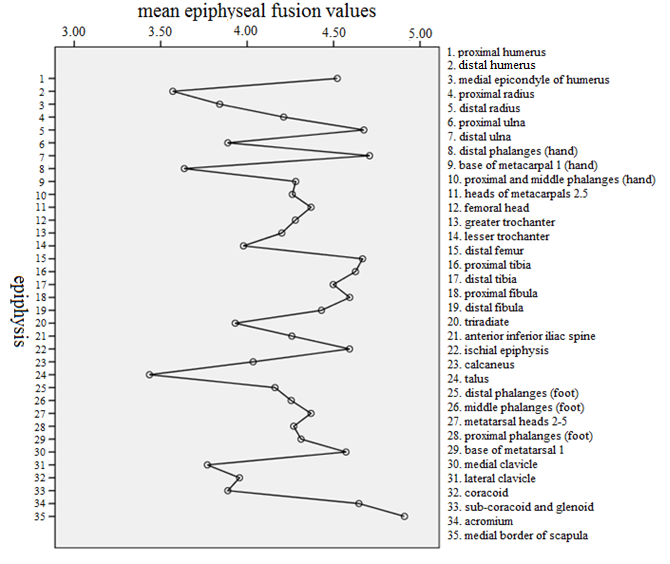
**Figure 4.16** Demonstration of range of no statistical significance for *Pan troglodytes* females.

This means that range of overlap for these epiphyses is too great for this type of statistical test to find differences for fusion events that occur close together. For epiphysis that are distant from each other in terms of mean epiphyseal fusion value such as the distal humerus and proximal humerus, there may be confidence in asserting that one is later than the other (p=0.000 in this case). A loose grouping of fusion events that statistically differ from each other are shown in Table 4.16 below. These same epiphyses are also significantly different for mid-fusion events in male *Pan troglodytes*.

**Table 4.16** Earlier and later epiphyses for mid-fusion *Pan troglodytes* females.

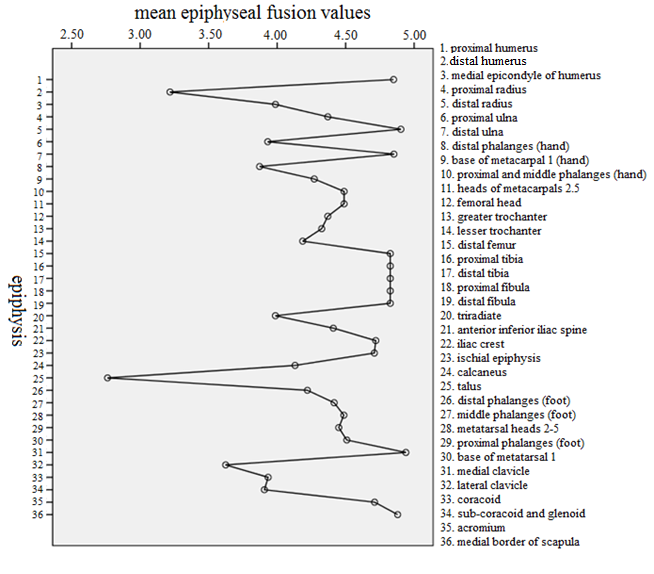
|  |  |
| --- | --- |
| **earlier epiphysis** | **later epiphyses** |
| distal humerus | proximal humerus |
| humeral medial epicondyle | distal radius |
| proximal radius | distal ulna |
| proximal ulna | iliac crest |
| epiphyses of hands and feet | ischial epiphysis |
| coracoid | medial clavicle |
| subcoracoid and glenoid | acromium |
|  | medial border of scapula |

The analysis completed above was done for complete fusion epiphyses. Figures 4.17 and 4.18 provide plots for mean values. Post-hoc Bonferroni tests are found in Table 8.2.3.1 of the digital appendix (section 8.2.3). Far fewer epiphyses showed significant differences. For example, the proximal humerus for females only showed a significant difference for the distal humerus (p=0.003) and the talus (p=0.000) with all other epiphyses showing non-significant differences. This was likely due to the much wider ranges of complete fusion.



Note: The iliac crest had no data.

**Figure 4.17** mean values for all epiphyses at complete fusion states for *Pan troglodytes* females.



**Figure 4.18** Mean values for all epiphyses at complete fusion states for *Pan troglodytes* males.

***4.2.2c Sex differences in modular sequence pattern for* Pan troglodytes**

The general patterns of mean epiphyseal fusion values presented in Figures 4.14, 4.15, 4.17, 4.18 appear very similar, suggesting that there may be no differences between males and females. Given that the distributions of these fusion events are virtually all normally distributed except for a few named epiphyses (see Table 4.14) an independent sample t-test could be applied. This was first performed for mid-fusion epiphyses. For both sexes was the distal humerus had a non-normal distribution (p = 0.002 females, p = 0.000 males). The the sub-coracoid and glenoid was non-normal for males (p = 0.000). Table 4.17 below provides results comparing male and female mid-fusion values using independent sample t-tests for each epiphysis. The anterior inferior iliac spine, the talus and the lateral clavicle were excluded from this analysis due to either the male or female sample having only one individual present. Instances where the test of equal variances indicate a statistically significant departure are highlighted in bold. Also highlighted are cases where there is a significant differences between the sexes by means of the 2-tailed t-test.

**Table 4.17** Independent sample t-test for comparing male and female mid-fusion mean epiphyseal fusion score ranges for all epiphyses in *Pan troglodytes*.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | | **levene's test for equality of variances** | | **t-test for equality of means** | | | | |
| ***F*** | **Sig.** | **t** | **df** | **Sig. (2-tailed)** | **Mean Difference** | **Std. Error Difference** |
|
| proximal humerus | a1. | .888 | .355 | -1.237 | 26 | .227 | -.41095 | .33232 |
| b2. |  |  | -1.608 | 18.427 | .125 | -.41095 | .25564 |
| distal humerus | a | 8.105 | **.016** | -2.177 | 11 | **.052** | -.16000 | .07349 |
| b |  |  | -1.859 | 5.221 | **.120** | -.16000 | .08605 |
| humeral medial epicondyle | a | 6.342 | **.024** | .027 | 15 | .979 | .00542 | .20370 |
| b |  |  | .028 | 10.907 | .978 | .00542 | .19486 |
| proximal radius | a | .004 | .953 | -.151 | 13 | .882 | -.06136 | .40652 |
| b |  |  | -.136 | 4.547 | .897 | -.06136 | .45025 |
| distal radius | a | 7.158 | **.013** | 1.682 | 24 | .106 | .40248 | .23927 |
| b |  |  | 1.309 | 9.182 | .222 | .40248 | .30740 |
| proximal ulna | a | .397 | .542 | .229 | 11 | .823 | .12238 | .53373 |
| b |  |  | .238 | 9.994 | .816 | .12238 | .51319 |
| distal ulna | a | 2.551 | .127 | 1.684 | 19 | .108 | .30357 | .18022 |
| b |  |  | 1.330 | 7.286 | .224 | .30357 | .22825 |
| distal phalanges (hand) | a | 1.877 | .220 | -.131 | 6 | .900 | -.04933 | .37710 |
| b |  |  | -.163 | 5.404 | .876 | -.04933 | .30214 |
| base of metacarpal 1 | a | 4.753 | **.052** | 2.485 | 11 | **.030** | .79500 | .31986 |
| b |  |  | 2.118 | 5.184 | **.086** | .79500 | .37544 |
| proximal and middle phalanges (hand) | a | 2.528 | 0.134 | -0.592 | 14 | 0.563 | -0.213 | 0.35974 |
| b |  |  | -0.514 | 6.937 | 0.623 | -0.213 | 0.4144 |
| heads of metacarpals 2-5 (hand) | a | .418 | .532 | -.484 | 10 | .639 | -.20111 | .41593 |
| b |  |  | -.411 | 2.779 | .711 | -.20111 | .48949 |
| femoral head | a | .136 | .718 | .241 | 14 | .813 | .06927 | .28713 |
| b |  |  | .202 | 5.510 | .847 | .06927 | .34253 |
| greater trochanter | a | 1.186 | .297 | -.515 | 12 | .616 | -.09636 | .18694 |
| b |  |  | -.871 | 10.973 | .402 | -.09636 | .11060 |
| lesser trochanter | a | 19.369 | **.003** | 1.082 | 7 | .315 | .33700 | .31150 |
| b |  |  | .968 | 3.358 | .398 | .33700 | .34820 |
| distal femur | a | .356 | .555 | 1.178 | 27 | .249 | .25351 | .21517 |
| b |  |  | 1.109 | 11.372 | .290 | .25351 | .22856 |

1. Equal variances assumed
2. Equal variances not assumed

(continued)

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | | **levene's test for equality of variances** | | **t-test for equality of means** | | | | |
| ***F*** | **Sig.** | **t** | **df** | **Sig. (2-tailed)** | **Mean Difference** | **Std. Error Difference** |
| proximal tibia | a1. | 2.395 | .133 | 1.151 | 27 | .260 | .26631 | .23130 |
| b2. |  |  | .914 | 8.925 | .385 | .26631 | .29129 |
| distal tibia | a | 3.421 | .079 | .208 | 20 | .837 | .05179 | .24904 |
| b |  |  | .176 | 9.225 | .864 | .05179 | .29421 |
| proximal fibula | a | .006 | .937 | .300 | 21 | .767 | .05455 | .18179 |
| b |  |  | .281 | 9.988 | .785 | .05455 | .19431 |
| distal fibula | a | 9.564 | **.007** | -.159 | 17 | .875 | -.04211 | .26412 |
| b |  |  | -.153 | 9.968 | .882 | -.04211 | .27555 |
| triradiate | a | .003 | .956 | .133 | 17 | .896 | .03622 | .27276 |
| b |  |  | .133 | 16.989 | .895 | .03622 | .27145 |
| iliac crest | a | .026 | .872 | -1.390 | 23 | .178 | -.19100 | .13741 |
| b |  |  | -1.199 | 5.314 | .281 | -.19100 | .15930 |
| ischial epiphysis | a | .059 | .811 | 2.273 | 21 | **.034** | .48267 | .21235 |
| b |  |  | 2.088 | 5.783 | **.084** | .48267 | .23116 |
| calcaneus | a | .180 | .681 | .999 | 10 | .341 | .28000 | .28024 |
| b |  |  | .939 | 5.229 | .389 | .28000 | .29828 |
| distal phalanges (foot) | a | .326 | .576 | .596 | 15 | .560 | .19933 | .33419 |
| b |  |  | .569 | 6.856 | .588 | .19933 | .35040 |
| middle phalanges (foot) | a | .508 | .489 | .168 | 13 | .869 | .03364 | .20065 |
| b |  |  | .144 | 4.239 | .892 | .03364 | .23404 |
| metatarsal heads 2-5 (foot) | a | .009 | .924 | -.581 | 16 | .569 | -.22733 | .39133 |
| b |  |  | -.556 | 2.757 | .620 | -.22733 | .40883 |
| proximal phalanges (foot) | a | 1.315 | .281 | -.646 | 9 | .534 | -.24750 | .38293 |
| b |  |  | -1.060 | 7.849 | .321 | -.24750 | .23341 |
| base of metatarsal 1 | a | 6.974 | **.027** | .558 | 9 | .591 | .14125 | .25322 |
| b |  |  | .884 | 8.615 | .401 | .14125 | .15984 |
| medial clavicle | a | 24.103 | **.001** | -1.147 | 9 | .281 | -.72750 | .63419 |
| b |  |  | -1.425 | 8.515 | .190 | -.72750 | .51036 |
| coracoid | a | 1.947 | .182 | .871 | 16 | .396 | .19400 | .22261 |
| b |  |  | .890 | 15.956 | .386 | .19400 | .21787 |
| sub-coracoid and glenoid | a | .418 | .527 | .354 | 16 | .728 | .08550 | .24167 |
| b |  |  | .348 | 14.039 | .733 | .08550 | .24566 |
| acromium | a | .192 | .666 | 2.770 | 18 | **.013** | .77078 | .27829 |
| b |  |  | 2.150 | 2.368 | **.144** | .77078 | .35853 |
| medial border of scapula | a | .576 | .462 | -.283 | 12 | .782 | -.04650 | .16416 |
| b |  |  | -.234 | 4.075 | .826 | -.04650 | .19873 |

1. Equal variances assumed
2. Equal variances not assumed

Two epiphyses with insufficient sample sizes were not analysed. These were the lateral clavicle and the anterior inferior iliac spine. The majority of epiphyses showed no significant difference between sexes with p values greater than 0.05. There were some exceptions. For mid-fusion, the distal humerus (p = 0.052), the base of metacarpal 1 (p = 0.03), the ischial epiphysis (p = 0.034), and the acromium (p = 0.013) differed significantly. Both sexes were found to have non-normal fusion distributions for the distal humerus. Variances were also unequal. When equal variances were not assumed, the p-value was not statistically significant (p = 0.120). For the base of metacarpal 1, the variances were only very slightly insignificant (p = 0.052) and with unequal variances there is no significant difference. For the acromium and the ischium, equal variances may be assumed. For the acromium there may be some limitation in terms of sample size for males (*N* = 3). For the ischium *N* = 5 for males and *N* = 19 for females. The sample size for males was small but was still deemed acceptable. As a general statement males and females do not differ with respect to mean mid-fusion epiphyseal fusion timing with some possible exceptions, most notable being the ischium. Ranges for complete fusion were also analysed. Table 4.18 shows independent sample t-tests for complete fusion comparing male and female *Pan troglodytes*. Significant values are highlighted in bold. The distal tibia and proximal fibula significantly differed with equal variances assumed (p = 0.014 for tibia, p = 0.045 for proximal fibula). The distal fibula differed with equal variances not assumed at p = 0.000. These were not the same epiphyses as differed for mid-fusion.

**Table 4.18** Independent sample t-test for comparing male and female complete fusion mean epiphyseal fusion score ranges for all epiphyses in *Pan troglodytes*.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | | **levene's test for equality of variances** | | **t-test for equality of means** | | | | |
| ***F*** | **sig.** | **t** | **df** | **sig. (2-tailed)** | **mean difference** | **std. error difference** |
|
| proximal humerus | a1. | 0.8486 | 0.3726 | -0.981 | 14 | 0.3432 | -0.3285 | 0.33477 |
| b2. |  |  | -1.936 | 13.986 | 0.0733 | -0.3285 | 0.16964 |
| distal humerus | a | 4.0439 | **0.048** | 1.2167 | 71 | 0.2277 | 0.3521 | 0.28938 |
| b |  |  | 1.109 | 30.988 | 0.2759 | 0.3521 | 0.31748 |
| humeral medial epicondyle | a | 0.16 | 0.69 | -0.586 | 57 | 0.56 | -0.1465 | 0.25003 |
| b |  |  | -0.591 | 22.003 | 0.561 | -0.1465 | 0.24803 |
| proximal radius | a | 0.1398 | 0.7104 | -0.835 | 40 | 0.4086 | -0.1588 | 0.19008 |
| b |  |  | -0.846 | 15.381 | 0.4107 | -0.1588 | 0.18771 |
| distal radius | a | 8.7742 | **0.012** | -1.888 | 12 | 0.0834 | -0.2279 | 0.12068 |
| b |  |  | -3.572 | 11.445 | **0.004** | -0.2279 | 0.0638 |
| proximal ulna | a | 0.0484 | 0.8267 | -0.173 | 53 | 0.8632 | -0.0432 | 0.24948 |
| b |  |  | -0.169 | 19.351 | 0.8673 | -0.0432 | 0.2551 |
| distal ulna | a | 4.4059 | 0.0559 | -1.589 | 13 | 0.136 | -0.1443 | 0.09081 |
| b |  |  | -1.98 | 8.8621 | 0.0796 | -0.1443 | 0.0729 |
| distal phalanges (hand) | a | 2.9503 | 0.1064 | -0.521 | 15 | 0.6101 | -0.2353 | 0.45188 |
| b |  |  | -0.433 | 5.4586 | 0.6814 | -0.2353 | 0.54309 |
| base of metacarpal 1 | a | 3.4915 | 0.0694 | 0.0528 | 38 | 0.9582 | 0.01 | 0.18942 |
| b |  |  | 0.0418 | 11.403 | 0.9674 | 0.01 | 0.23913 |
| proximal and middlephalanges (hand) | a | 0.4025 | 0.5296 | -1.261 | 38 | 0.215 | -0.2272 | 0.18018 |
| b |  |  | -1.225 | 10.428 | 0.2475 | -0.2272 | 0.18545 |
| heads of metacarpals 2-5 (hand) | a | 1.8729 | 0.1807 | -0.724 | 32 | 0.4744 | -0.1191 | 0.16458 |
| b |  |  | -0.648 | 10.047 | 0.5313 | -0.1191 | 0.18373 |
| femoral head | a | 1.2199 | 0.2761 | -0.532 | 39 | 0.5974 | -0.091 | 0.17085 |
| b |  |  | -0.499 | 13.842 | 0.6256 | -0.091 | 0.18229 |
| greater trochanter | a | 0.2403 | 0.6265 | -0.711 | 43 | 0.4809 | -0.1249 | 0.17561 |
| b |  |  | -0.707 | 16.82 | 0.4893 | -0.1249 | 0.17664 |
| lesser trochanter | a | 0.2129 | 0.6465 | -0.885 | 50 | 0.3805 | -0.2079 | 0.23501 |
| b |  |  | -0.911 | 18.983 | 0.3736 | -0.2079 | 0.22815 |
| distal femur | a | 3.0085 | 0.1021 | -1.723 | 16 | 0.1042 | -0.1583 | 0.09188 |
| b |  |  | -2.199 | 13.076 | **0.046** | -0.1583 | 0.07198 |

1. Equal variances assumed
2. Equal variances not assumed

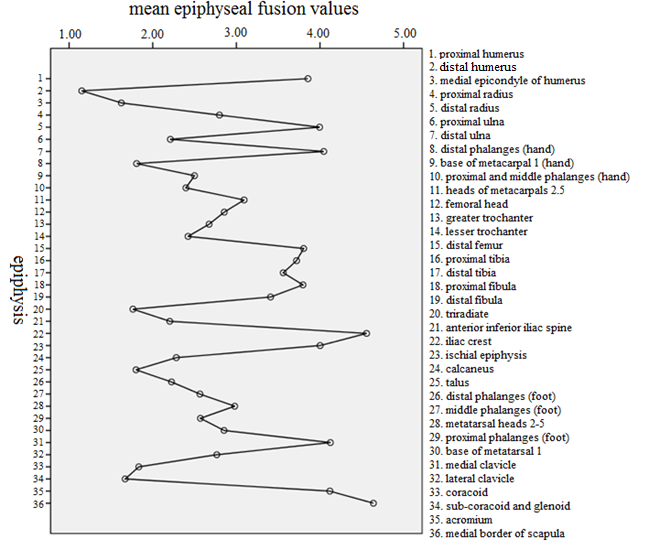
(continued)

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | | **levene's test for equality of variances** | | **t-test for equality of means** | | | | |
| ***F*** | **sig.** | **t** | **df** | **sig. (2-tailed)** | **mean difference** | **std. error difference** |
| proximal tibia | a1. |  |  |  |  |  |  | 0.09865 |
| b2. |  |  | -2.749 | 13.902 | **0.016** | -0.1993 | 0.07252 |
| distal tibia | a | 3.9417 | 0.0582 | -2.653 | 25 | **0.014** | -0.3278 | 0.12359 |
| b |  |  | -4.372 | 16.671 | **4E-04** | -0.3278 | 0.07497 |
| proximal fibula | a | 2.6979 | 0.1169 | -2.151 | 19 | **0.045** | -0.2191 | 0.10185 |
| b |  |  | -3.013 | 14.262 | **0.009** | -0.2191 | 0.07272 |
| distal fibula | a | 4.2837 | **0.047** | -2.868 | 29 | **0.008** | -0.396 | 0.1381 |
| b |  |  | -5.177 | 18.248 | **6E-05** | -0.396 | 0.0765 |
| triradiate | a | 0.1423 | 0.7075 | -0.222 | 53 | 0.8253 | -0.0565 | 0.25474 |
| b |  |  | -0.193 | 16.618 | 0.8494 | -0.0565 | 0.29301 |
| anterior inferior iliac spine | a | 1.1445 | 0.2925 | -0.578 | 33 | 0.5674 | -0.1511 | 0.26149 |
| b |  |  | -0.484 | 7.7595 | 0.642 | -0.1511 | 0.31237 |
| ischial epiphysis | a | 0.001 | 0.979 | -.741 | 15 | 0.47 | -0.1175 | 0.15854 |
| b |  |  | -.693 | 6.6111 | 0.5117 | -0.1175 | 0.16945 |
| calcaneus | a | 0.3482 | 0.558 | -0.387 | 46 | 0.7005 | -0.096 | 0.24814 |
| b |  |  | -0.353 | 14.522 | 0.7292 | -0.096 | 0.27216 |
| distal phalanges (foot) | a | 0.885 | 0.3514 | -1.138 | 49 | 0.2608 | -0.4206 | 0.36971 |
| b |  |  | -1.43 | 15.923 | 0.1721 | -0.4206 | 0.29417 |
| middle phalanges (foot) | a | 5.003 | **.037** | .571 | 19 | .574 | .10221 | .17889 |
|  | b |  |  | .527 | 11.494 | .608 | .10221 | .19380 |
| metatarsal heads 2-5 (foot) | a | 1.585 | .217 | -.684 | 31 | 0.499 | -0.1175 | 0.17182 |
| b |  |  | -.611 | 8.339 | 0.5576 | -0.1175 | 0.19239 |
| proximal phalanges (foot) | a | .373 | .545 | -1.036 | 37 | .307 | -.18033 | .17413 |
| b |  |  | -1.036 | 13.203 | .319 | -.18033 | .17404 |
| base of metatarsal 1 | a | 0.597 | 0.445 | -1.165 | 35 | 0.2519 | -0.1967 | 0.16881 |
| b |  |  | -1.109 | 10.5 | 0.2921 | -0.1967 | 0.17734 |
| medial clavicle | a | 2.9042 | 0.097 | 0.3362 | 36 | 0.7387 | 0.1456 | 0.43297 |
| b |  |  | 0.2752 | 10.424 | 0.7886 | 0.1456 | 0.52898 |
| coracoid | a | 0.5122 | 0.4773 | 0.0913 | 54 | 0.9276 | 0.0217 | 0.23741 |
| b |  |  | 0.0804 | 18.531 | 0.9368 | 0.0217 | 0.26939 |
| sub-coracoid and glenoid | a | 0.3009 | 0.5855 | -0.074 | 56 | 0.9411 | -0.0187 | 0.25226 |
| b |  |  | -0.065 | 18.247 | 0.9488 | -0.0187 | 0.28792 |
| acromium | a | 0.363 | 0.56 | -.355 | 10 | 0.7296 | -0.065 | 0.18285 |
| b |  |  | -.355 | 9.848 | 0.7297 | -0.065 | 0.18285 |

1. Equal variances assumed
2. Equal variances not assumed

***4.2.2.d Mixed sex samples for modular sequence pattern***

Given that males and females do not show significant differences for almost all epiphyses, it is worth exploring if a combined-sex sample produces a more distinct pattern due to increased sample size. Figures 4.19 and 4.20 demonstrate mid-fusion and complete fusion mean value plots. Post-hoc Bonferroni test results are available in Table 8.2.2.1 in the digital appendix (section 8.2.2).

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**Figure 4.19** Mean values for all epiphyses at mid-fusion states for combined sex *Pan troglodytes*.

****

**Figure 4.20** Mean values for all epiphyses at complete-fusion states for combined sex *Pan troglodytes*.

It was found that increasing sample size did not greatly affect the range of variation and the number of closely fusing epiphyses for a given epiphyses that did not show statistically significant differences did not necessarily change. In section 4.2.2b the proximal humerus that was analysed to demonstrate the range of significance. This analysis is repeated here for the combined-sex sample. Table 4.19 provides post-hoc Bonferroni test results for the proximal humerus in *Pan troglodytes* when looking at combined-sex mid-fusion values. Epiphyses where sex differences were unclear or not analysed due to sample size are not included in this analysis.

**Table 4.19** Post-hoc Bonferroni tests of the proximal humerus for mid-fusion combined-sex fusion events in *Pan troglodytes*.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **(J) proximal humerus** | **mean difference (I-J)** | **std. error** | **sig.** | **95% confidence interval** | |
| **lower bound** | **upper bound** |
| humeral medial epicondyle | 2.23195 | 0.180259 | 0.000 | 1.525182 | 2.938725 |
| proximal radius | 1.05795 | 0.183731 | 0.000 | 0.337563 | 1.77833 |
| distal radius | -0.139313187 | 0.159671 | 1.000 | -0.76536 | 0.486735 |
| proximal ulna | 1.64530 | 0.19676 | 0.000 | 0.873835 | 2.41677 |
| distal ulna | -0.189580745 | 0.164982 | 1.000 | -0.83645 | 0.457291 |
| distal phalanges (hand) | 2.04857 | 0.235029 | 0.000 | 1.127054 | 2.970089 |
| proximal and middle phalanges (hand) | 1.45960 | 0.180259 | 0.000 | 0.752829 | 2.166373 |
| heads of metacarpals 2-5 | 0.763571429 | 0.202281 | 0.089 | -0.02954 | 1.556687 |
| femoral head | 1.00045 | 0.183731 | 0.000 | 0.280063 | 1.72083 |
| greater trochanter | 1.18179 | 0.191901 | 0.000 | 0.42937 | 1.934202 |
| lesser trochanter | 1.43385 | 0.224644 | 0.000 | 0.55305 | 2.314648 |
| distal femur | 0.051243842 | 0.15533 | 1.000 | -0.55778 | 0.66027 |
| proximal tibia | 0.135726601 | 0.15533 | 1.000 | -0.4733 | 0.744753 |
| distal tibia | 0.295616883 | 0.167028 | 1.000 | -0.35928 | 0.950511 |
| proximal fibula | 0.059549689 | 0.164982 | 1.000 | -0.58732 | 0.706422 |
| distal fibula | 0.44712406 | 0.174256 | 1.000 | -0.23611 | 1.130358 |
| triradiate | 2.09291 | 0.174256 | 0.000 | 1.40968 | 2.776148 |
| anterior inferior iliac spine | 1.65274 | 0.356152 | 0.002 | 0.256313 | 3.049163 |
| iliac crest | -.70113 | 0.161318 | 0.008 | -1.33364 | -0.06862 |
| calcaneus | 1.57440 | 0.202281 | 0.000 | 0.781289 | 2.367521 |
| talus | 2.05607 | 0.313372 | 0.000 | 0.827381 | 3.284761 |
| distal phalanges (foot) | 1.63137 | 0.180259 | 0.000 | 0.924594 | 2.338137 |
| middle phalanges (foot | 1.29140 | 0.187588 | 0.000 | 0.555899 | 2.02691 |
| metatarsal heads 2-5 | .87552 | 0.177116 | 0.001 | 0.181067 | 1.569964 |
| proximal phalanges (foot) | 1.28607 | 0.208618 | 0.000 | 0.468109 | 2.104034 |
| base of metatarsal 1 | 1.00334 | 0.208618 | 0.001 | 0.185382 | 1.821306 |
| medial clavicle | -0.268474026 | 0.208618 | 1.000 | -1.08644 | 0.549488 |
| lateral clavicle | 1.090071429 | 0.284635 | 0.072 | -0.02594 | 2.206085 |
| coracoid | 2.02329 | 0.177116 | 0.000 | 1.328845 | 2.717742 |
| sub-coracoid and glenoid | 2.18607 | 0.177116 | 0.000 | 1.491623 | 2.88052 |
| medial border | -.78321 | 0.191901 | 0.026 | -1.53563 | -0.0308 |

When this is repeated for the proximal humerus in the combined sex-sample for mid-fusion events it was found that 11 of 21 events showed no statistically significant differences (52%). However, the distal humerus and ischial epiphysis were removed due to significant differences between sexes having been found. The furthest non-significant epiphyses in terms of mean value was the lateral clavicle (p = 0.068) which had a mean difference of 1.09077 from the proximal humerus. This epiphysis had an insufficient sample size for comparison by sex in the previous analysis so it may be discounted. The next closest significant difference was the heads of metacarpals 2 - 5 (p = 0.089) with a mean difference of 0.76357. The nearest epiphysis with a significant difference was the medial border of the scapula at a mean differences of 0.78321 (p = 0.026). These values are very similar to the values demonstrated for the proximal epiphysis when only females were considered. This pattern is repeated for all other epiphyses as may be observed in Table 8.2.2.1 in the digital appendix (section 8.2.2). Combining sex does not appear to make fusion event order clearer.

***4.2.2e Sequence of mean epiphyseal fusion values***

Despite seriation analysis demonstrating significant amounts of overlap in ranges, it is possible to order epiphyses based on their mean epiphyseal fusion value ranges. Table 4.20 presents mid-fusion sequence order for *Pan troglodytes* males and females. Table 4.21 provides values for complete fusion.

***4.2.2f Seriation fusion event for* Pan paniscus**

With substantially fewer data for *Pan paniscus* it would be unlikely that analysis of mean epiphyseal fusion value for ordering fusion events would be either useful or applicable. There were too few individuals present to provide sufficient data for ranges to be analysed.

**Table 4.20** Sequence order of mean values from lowest to highest for mid-fusion *Pan troglodytes* males and females.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **order number** | **mean epiphyseal fusion score** | **epiphysis (females)** | **mean epiphyseal fusion score** | **epiphysis (males)** |
| 1 | 1.09 | distal humerus | 1.25 | distal humerus |
| 2 | 1.63 | humeral medial epicondyle | 1.53 | talus |
| 3 | 1.72 | sub-coracoid and glenoid | 1.62 | humeral medial epicondyle |
| 4 | 1.78 | distal phalanges (hand) | 1.63 | sub-coracoid and glenoid |
| 5 | 1.78 | triradiate | 1.73 | coracoid |
| 6 | 1.89 | talus | 1.75 | triradiate |
| 7 | 1.92 | coracoid | 1.83 | distal phalanges (hand) |
| 8 | 2.28 | proximal ulna | 2.01 | base of metacarpal 1 |
| 9 | 2.28 | distal phalanges foot | 2.08 | distal phalanges foot |
| 10 | 2.33 | proximal and middle phalanges | 2.10 | calcaneal epiphysis fusion |
| 11 | 2.38 | calcaneal epiphysis fusion | 2.15 | proximal ulna |
| 12 | 2.50 | proximal phalanges foot | 2.24 | lesser trochanter |
| 13 | 2.57 | lesser trochanter | 2.53 | proximal and middle phalanges |
| 14 | 2.57 | middle phalanges foot | 2.54 | middle phalanges foot |
| 15 | 2.65 | greater trochanter | 2.75 | greater trochanter |
| 16 | 2.78 | proximal radius | 2.75 | proximal phalanges foot |
| 17 | 2.81 | base of metacarpal 1 | 2.75 | base of metatarsal 1 |
| 18 | 2.88 | femoral head | 2.81 | femoral head |
| 19 | 2.89 | base of metatarsal 1 | 2.85 | proximal radius |
| 20 | 2.94 | metatarsal heads 2-5 | 3.17 | metatarsal heads 2-5 |
| 21 | 3.04 | heads of metacarpals 2.5 | 3.24 | heads of metacarpals 2.5 |
| 22 | 3.39 | distal fibula | 3.43 | distal fibula |
| 23 | 3.58 | distal tibia | 3.46 | acromium |
| 24 | 3.75 | proximal humerus | 3.53 | proximal tibia |
| 25 | 3.79 | proximal tibia | 3.53 | distal tibia |
| 26 | 3.81 | proximal fibula | 3.62 | distal femur |
| 27 | 3.86 | medial clavicle | 3.62 | ischial epiphysis fusion |
| 28 | 3.87 | distal femur | 3.73 | distal radius |
| 29 | 4.11 | ischial epiphysis fusion | 3.76 | proximal fibula |
| 30 | 4.13 | distal ulna | 3.85 | distal ulna |
| 31 | 4.13 | distal radius | 4.16 | proximal humerus |
| 32 | 4.23 | acromium | 4.59 | medial clavicle |
| 33 | 4.52 | iliac crest fusion | 4.67 | medial border of scapula |
| 34 | 4.63 | medial border of scapula | 4.71 | iliac crest fusion |

Note: the lateral clavicle and the anterior inferior iliac spine have been omitted from this list.

**Table 4.21** Sequence order of mean from lowest to highest for complete fusion *Pan troglodytes* males and females.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **order number** | **mean epiphyseal fusion score** | **epiphysis (females)** | **mean epiphyseal fusion score** | **epiphysis (males)** |
| 1 | 4.52 | proximal humerus | 4.85 | proximal humerus |
| 2 | 3.57 | distal humerus | 3.22 | distal humerus |
| 3 | 3.84 | humeral medial epicondyle | 3.99 | humeral medial epicondyle |
| 4 | 4.21 | proximal radius | 4.37 | proximal radius |
| 5 | 4.68 | distal radius | 4.90 | distal radius |
| 6 | 3.89 | proximal ulna | 3.93 | proximal ulna |
| 7 | 4.71 | distal ulna | 4.85 | distal ulna |
| 8 | 3.64 | distal phalanges hand | 3.87 | distal phalanges hand |
| 9 | 4.28 | base of metacarpal 1 hand | 4.27 | base of metacarpal 1 hand |
| 10 | 4.26 | proximal and middle phalanges hand | 4.49 | proximal and middle phalanges hand |
| 11 | 4.37 | heads of metacarpals 2-5 hand | 4.49 | heads of metacarpals 2-5 hand |
| 12 | 4.28 | femoral head | 4.37 | femoral head |
| 13 | 4.20 | greater trochanter | 4.33 | greater trochanter |
| 14 | 3.98 | lesser trochanter | 4.19 | lesser trochanter |
| 15 | 4.67 | distal femur | 4.83 | distal femur |
| 16 | 4.63 | proximal tibia | 4.83 | proximal tibia |
| 17 | 4.50 | distal tibial | 4.83 | distal tibial |
| 18 | 4.59 | proximal fibula | 4.83 | proximal fibula |
| 19 | 4.43 | distal fibula | 4.83 | distal fibula |
| 20 | 3.93 | triradiate | 3.99 | triradiate |
| 21 | 4.26 | anterior inferior iliac spine | 4.41 | anterior inferior iliac spine |
| 22 | 4.59 | ischial epiphysis | 4.72 | iliac crest |
| 23 | 4.03 | calcaneus | 4.71 | ischial epiphysis |
| 24 | 3.44 | talus | 4.13 | calcaneus |
| 25 | 4.16 | distal phalanges foot | 2.76 | talus |
| 26 | 4.26 | middle phalanges foot | 4.22 | distal phalanges foot |
| 27 | 4.37 | metatarsal heads 2-5 foot | 4.42 | middle phalanges foot |
| 28 | 4.27 | proximal phalanges foot | 4.49 | metatarsal heads 2-5 foot |
| 29 | 4.31 | base of metatarsal 1 fusion foot | 4.45 | proximal phalanges foot |
| 30 | 4.57 | medial clavicle | 4.51 | base of metatarsal 1 fusion foot |
| 31 | 3.77 | lateral clavicle | 4.94 | medial clavicle |
| 32 | 3.96 | coracoid | 3.62 | lateral clavicle |
| 33 | 3.89 | sub-coracoid center and glenoid | 3.93 | coracoid |
| 34 | 4.65 | acromium | 3.91 | sub-coracoid center and glenoid |
| 35 | 4.91 | medial border | 4.71 | acromium |
| 36 |  |  | 4.88 | medial border |

Note: ischial epiphysis not included for females as there wer no individuals contributing complete fusion values.

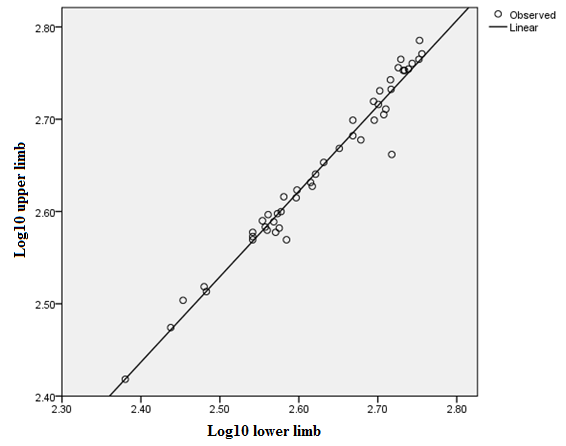
## Analysis of allometric relationships within Pan

### Confirming allometric relationships established in the past and adding new sub-species of Pan

This section will assess allometric relationships between long-bones in a similar manner to Shea (1981). This analysis will expand upon Shea’s (1981) work by including the sub-species *Pan troglodytes schweinfurthii*¸ which was not present in Shea’s original sample. It should be noted that Shea’s (1981) bonobo data was produced using the same individuals at the Museum of Central Africa as the bonobos in this study. As outlined in Chapter 2, Shea (1981) applied regression analysis to log10-scaled inter-membral indexes. He also evaluated variables not considered in the present study including trunk length, body weight and postural changes. Shea made two particularly important observations:

1. Growth in *Pan troglodytes* and *Pan paniscus* limbs is effectively isometric (the ratios of limb lengths are static throughout growth)
2. The average leg length is a little bit longer in *Pan paniscus* and this may be observable in growth trajectories.

All data were analysed using SPSS Statistics 21. Regression analysis is presented for a pooled sample using all *Pan troglodytes* individuals in the dataset including all sub-species. The results of regression applied at the species level demonstrated a high degree of linearity with an *R*2 value of 0.97. The high level of agreement for long-bone lengths in this analysis suggested that separate analysis determining linear regression results for individual sub-species of *Pan troglodytes* would not return meaningfully different results. Figure 4.21 presents a scatterplot for log10-scaled arm (humerus + radius) vs. leg (femur + tibia) data as well as a regression line for *Pan troglodytes* males. This includes individuals from all sub-species. Table 4.22 shows *R*2 values for linear regression analysis.

****

**Figure 4.21** log10 regression for male *Pan troglodytes* upper vs. lower limb.

**Table 4.22** Regression summary for male *Pan troglodytes* upper vs. lower limb.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **model** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** |
| 1 | 0.985a | 0.97 | 0.969 | 0.01557 |

1. Predictors: (Constant), *Pan troglodytes* male lower limb

Regression analysis was carried out for *Pan troglodytes* females and both male and female *Pan paniscus*. Detailed results are available in appendix section 8.6. Table 4.23 below presents *R*2 values from these analyses. All *R*2 results demonstrated a linear relationship for both species and sexes. Figure 4.22 shows *Pan troglodytes* and *Pan paniscus* male regression lines plotted together. Figure 4.23 presents the same information for *Pan troglodytes* and *Pan paniscus* females. Table 4.24 presents the regression equations for Figures 4.22 and 4.23.

**Table 4.23** Regression r-squared values for limb comparisons of *Pan troglodytes* females and *Pan paniscus* males and females

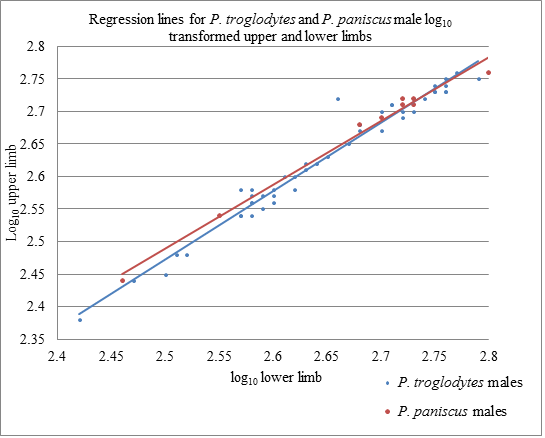
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **species/sex** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** |
| *Pan troglodytes* males | 0.9851. | 0.97 | 0.969 | 0.01557 |
| *Pan troglodytes* females | 0.9912. | 0.983 | 0.983 | 0.0113 |
| *Pan paniscus* males | 0.9953. | 0.991 | 0.99 | 0.01071 |
| *Pan paniscus* females | 0.9954. | 0.99 | 0.988 | 0.00977 |

1. Predictors: (Constant), *Pan troglodytes* males lower limb

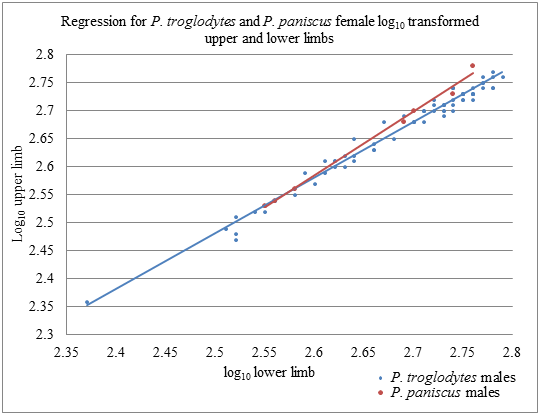
2. Predictors: (Constant), *Pan troglodytes* females lower limb

3. Predictors: (Constant), *Pan paniscus* males lower limb

4. Predictors: (Constant), *Pan paniscus* females lower limb



**Figure 4.22** Regression plot of log10 transformed intermembral indicies for *Pan troglodytes* and *Pan paniscus* males.



**Figure 4.23** Regression plot of log10 transformed intermembral indicies for *Pan troglodytes* and *Pan paniscus* females.

**Table 4.24** Linear regression equations of log10transformed limb data for *Pan troglodytes* and *Pan paniscus* males and females.

|  |  |  |
| --- | --- | --- |
| **sex** | ***P. troglodytes* linear regression equation** | ***P. paniscus* linear regression equation** |
| males | y = 1.0504x - 0.153 | y = 0.9819x + 0.0352 |
| females | y = 0.9856x + 0.0179 | y = 1.1348x - 0.3663 |

An isometric relationship between limb bones for males and females of both species found by Shea (1981) is reproduced here. *Pan troglodytes* results do not change despite the addition of *Pan troglodytes schweinfurthii* individuals from the Museum of Central Africa and the general *Pan troglodytes* individuals from the University of Zurich. Given the very high *R*2 values for all of these analyses, it would seem unlikely that when analysed separately that sub-species would produce differing results. This may be pursued in future analysis but is not considered here.

### Regression of serially homologous limb elements

In addition to regression for upper and lower limbs, correlations between individual long-bones were considered. Regression was again performed using log10 transformed length data. Results are presented in Table 4.25 for *Pan troglodytes* and Table 4.26 for *Pan paniscus*. Comparisons were made between serially homologous upper and lower limb units (e.g., humerus-femur) and within limbs (e.g., humerus-radius). Full regression results are available in appendix section 8.7. The individual limb elements analysis presented here provides further evidence that all long-bones scale isometrically. These results are in agreement with Shea’s (1981) data.

**Table 4.25** Regression values for analysis of serially homologous limb elements in *Pan troglodytes*.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **sex** | **bone-comparison** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** | **Durbin-Watson** |
| females | humerus-femur | 0.992a | 0.983 | 0.983 | 0.0123 | 1.565 |
| radius tibia | 0.986a | 0.971 | 0.971 | 0.01467 | 1.637 |
| humerus-radius | 0.987a | 0.975 | 0.975 | 0.0135 | 1.672 |
| tibia-femur | 0.990a | 0.981 | 0.981 | 0.0139 | 1.694 |
| males | humerus-femur | 0.856a | 0.734 | 0.728 | 0.0460 | 1.217 |
| radius tibia | 0.992a | 0.985 | 0.985 | 0.0113 | 1.631 |
| humerus-radius | 0.950a | 0.903 | 0.901 | 0.0280 | 1.477 |
| tibia-femur | 0.995a | 0.989 | 0.989 | 0.0103 | 1.623 |

**Table 4.26** Regression values for analysis of serially homologous limb elements in *Pan paniscus*.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **sex** | **bone-comparison** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** | **Durbin-Watson** |
| females | humerus-femur | 0.994 | 0.989 | 0.987 | 0.009 | 2.283 |
| radius tibia | 0.988 | 0.976 | 0.973 | 0.013 | 3.126 |
| humerus-radius | 0.999 | 0.998 | 0.998 | 0.004 | 2.287 |
| tibia-femur | 0.993 | 0.986 | 0.985 | 0.010 | 2.611 |
| males | humerus-femur | 0.981 | 0.962 | 0.958 | 0.022 | 2.708 |
| radius tibia | 0.996 | 0.992 | 0.991 | 0.010 | 1.507 |
| humerus-radius | 0.987 | 0.974 | 0.972 | 0.019 | 3.014 |
| tibia-femur | 0.996 | 0.992 | 0.991 | 0.009 | 2.318 |

## ***Calendar year estimation of epiphyseal fusion events for comparability to other studies.***

Estimated chronological ages were produced using Kuykendall’s (1996) regression for summary dental score using 8 teeth. It should be noted that Kuykendall’s (1996) estimation of third molar completion was only technically a projection beyond stage 6, as there were no teeth present with stages 7 or 8 in his analysis. Anemone *et al*. (1996) used a version of the Demirjian (1973) system in which complete third molar maturation was observed and their results agree with the projections of Kuykendall (1996) with maturation complete between 10-12 years. Kuykendall’s regression equation for 8 teeth will be used in this analysis as it is the only means available to predict age using summary dental score. Anemone’s (1996) study provided information for individual teeth but did not provide a regression equation. The concordance between Kuykendall’s (1996) regression estimate for third molar maturation timing and Anemone’s (1996) observation of real-world individuals provides support for the approach used here.

Estimated chronological ages using 8 teeth for both mid-fusion and complete fusion are shown in Table 4.27. Scores with median values of 64 are simply noted as greater than or equal to (≥) 9.453 years of age (>9.453). This is the value that is produce when DS64 is put into the regression equation. It should be noted that Kuykendall’s (1996) regression does not differentiate between males and females. Tables 4.28, 4.29 and 4.30 provide estimated age values for *Pan troglodytes* males and *Pan panicus* males and females.

Variation in chronological age estimates inevitably mirror the variation found when fusion timing relative to dental score was plotted (section 4.2.1). The limitations of sample size for *Pan paniscus* was problematic in that analysis. This problem is directly translated into this analysis for age estimations in terms of chronological years as the same data are used. It is worth noting the effect that these variations have for chronological age estimation. Given prior statements about the difficulty of collecting data for the lateral clavicle and the anterior inferior iliac spine, it is unsurprising that the values for these epiphyses vary much more than other epiphyses. Insufficient sample size for a given epiphysis was a recurrent problem for *Pan paniscus* and this is reflected in the inconsistency between male and female values as well as between *Pan paniscus* and *Pan troglodytes*. As brought forward from the results found for dental score, it is not possible to test differences between the two species.

**Table 4.27** Estimated chronological ages for fusion events based on median values of mid-fusion and complete fusion in *Pan troglodytes* females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N* mid-fusion** | ***N* complete fusion** | **mid-fusion median** | **complete fusion median** | **mid-fusion** | **complete fusion** |
| **dental score** | **dental score** | **years** | **years** |
| upper limb | proximal humerus | 19 | 12 | 62 | 64 | 9.033 | ≥9.453 |
| distal humerus | 8 | 48 | 48 | 63 | 6.317 | 9.242 |
| humeral medial epicondyle | 8 | 42 | 55 | 64 | 7.626 | ≥9.453 |
| proximal radius | 11 | 30 | 63 | 64 | 9.242 | ≥9.453 |
| distal radius | 16 | 9 | 64 | 64 | ≥9.453 | ≥9.453 |
| proximal ulna | 4 | 40 | 56 | 64 | 7.821 | ≥9.453 |
| distal ulna | 14 | 10 | 64 | 64 | ≥9.453 | ≥9.453 |
| hand | distal phalanges (hand) | 2 | 10 | 50 | 62 | 6.681 | 9.033 |
| base of metacarpal 1 | 7 | 29 | 61 | 64 | 8.826 | ≥9.453 |
| proximal and middle phalanges (hand) | 10 | 29 | 60.5 | 64 | 8.723 | ≥9.453 |
| metacarpal heads 2-5 | 7 | 25 | 62 | 64 | 9.033 | ≥9.453 |
| lower limb | femoral head | 10 | 29 | 62 | 64 | 9.033 | ≥9.453 |
| greater trochanter | 10 | 32 | 61.5 | 64 | 8.929 | ≥9.453 |
| lesser trochanter | 5 | 37 | 61 | 64 | 8.826 | ≥9.453 |
| distal femur | 19 | 12 | 64 | 64 | ≥9.453 | ≥9.453 |
| proximal tibia | 20 | 13 | 63.5 | 64 | 9.347 | ≥9.453 |
| distal tibia | 12 | 21 | 62.5 | 64 | 9.137 | ≥9.453 |
| proximal fibula | 14 | 16 | 63 | 64 | 9.242 | ≥9.453 |
| distal fibula | 9 | 24 | 63 | 64 | 9.242 | ≥9.453 |
| foot | calcaneus | 7 | 35 | 60 | 64 | 8.621 | ≥9.453 |
| talus | 2 | 46 | 57 | 63 | 8.018 | 9.242 |
| distal phalanges (foot) | 11 | 31 | 60 | 64 | 8.621 | ≥9.453 |
| middle phalanges (foot) | 10 | 29 | 62 | 64 | 9.033 | ≥9.453 |
| metatarsal heads (2-5) | 13 | 25 | 62 | 64 | 9.033 | ≥9.453 |
| base of metatarsal 1 | 8 | 32 | 62.5 | 64 | 9.137 | ≥9.453 |
| proximal phalanges (foot) | 8 | 27 | 61.5 | 64 | 8.929 | ≥9.453 |
| pelvis | triradiate | 8 | 39 | 56.5 | 64 | 7.919 | ≥9.453 |
| anterior inferior iliac spine | 1 | 40 | 55 | 64 | 7.626 | ≥9.453 |
| iliac crest | 18 | 0 | 64 | - | ≥9.453 | - |
| ischial epiphysis | 16 | 11 | 64 | 64 | ≥9.453 | ≥9.453 |
| clavicle | medial clavicle | 7 | 5 | 64 | 64 | ≥9.453 | ≥9.453 |
| lateral clavicle | 4 | 28 | 59 | 64 | 8.418 | ≥9.453 |
| scapula | coracoid | 9 | 39 | 58 | 64 | 8.217 | ≥9.453 |
| sub-coracoid and glenoid | 6 | 42 | 50 | 64 | 6.681 | ≥9.453 |
| acromium | 16 | 4 | 64 | 64 | ≥9.453 | ≥9.453 |
| medial border | 8 | 2 | 64 | 64 | ≥9.453 | ≥9.453 |

**Table 4.28** Estimated chronological ages for fusion events based on median values of mid-fusion and complete fusion in *Pan troglodytes* males.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N* mid-fusion** | ***N* complete fusion** | **mid-fusion median** | **complete fusion median** | **mid-fusion** | **complete fusion** |
| **dental score** | **dental score** | **years** | **years** |
| upper limb | proximal humerus | 7 | 3 | 62 | 64 | 9.242 | ≥9.453 |
| distal humerus | 5 | 18 | 48 | 63 | 8.217 | 8.929 |
| humeral medial epicondyle | 7 | 13 | 55 | 64 | 8.621 | 9.242 |
| proximal radius | 3 | 10 | 63 | 64 | 8.826 | 9.242 |
| distal radius | 8 | 3 | 64 | 64 | 9.242 | 9.453 |
| proximal ulna | 6 | 12 | 56 | 64 | 8.723 | 9.242 |
| distal ulna | 6 | 4 | 64 | 64 | 9.242 | ≥9.453 |
| hand | distal phalanges (hand) | 2 | 5 | 50 | 62 | 7.919 | 9.242 |
| base of metacarpal 1 | 2 | 10 | 61 | 64 | 8.217 | 9.347 |
| proximal and middle phalanges (hand) | 5 | 8 | 60.5 | 64 | 8.826 | ≥9.453 |
| metacarpal heads 2-5 | 2 | 8 | 62 | 64 | 9.033 | ≥9.453 |
| lower limb | femoral head | 4 | 10 | 62 | 64 | 8.621 | 9.242 |
| greater trochanter | 1 | 12 | 61.5 | 64 | 8.826 | 9.242 |
| lesser trochanter | 3 | 12 | 61 | 64 | 8.217 | 9.242 |
| distal femur | 7 | 5 | 64 | 64 | 9.033 | ≥9.453 |
| proximal tibia | 7 | 5 | 63.5 | 64 | 9.033 | ≥9.453 |
| distal tibia | 6 | 6 | 62.5 | 64 | 8.826 | ≥9.453 |
| proximal fibula | 5 | 6 | 63 | 64 | 9.242 | ≥9.453 |
| distal fibula | 7 | 6 | 63 | 64 | 8.621 | ≥9.453 |
| foot | calcaneus | 3 | 11 | 60 | 64 | 8.621 | 9.242 |
| talus | 0 | 21 | 57 | 63 | - | 8.826 |
| distal phalanges (foot) | 2 | 9 | 60 | 64 | 8.217 | 9.242 |
| middle phalanges (foot) | 3 | 8 | 62 | 64 | 8.418 | 9.347 |
| metatarsal heads (2-5) | 2 | 7 | 62 | 64 | 9.033 | ≥9.453 |
| base of metatarsal 1 | 2 | 9 | 62.5 | 64 | 8.621 | ≥9.453 |
| proximal phalanges (foot) | 2 | 8 | 61.5 | 64 | 8.621 | ≥9.453 |
| pelvis | triradiate | 8 | 13 | 56.5 | 64 | 8.621 | 9.242 |
| anterior inferior iliac spine | 1 | 6 | 55 | 64 | 7.626 | ≥9.453 |
| iliac crest | 5 | 1 | 64 | - | ≥9.453 | ≥9.453 |
| ischial epiphysis | 4 | 5 | 64 | 64 | 9.137 | ≥9.453 |
| clavicle | medial clavicle | 4 | 1 | 64 | 64 | ≥9.453 | ≥9.453 |
| lateral clavicle | 1 | 9 | 59 | 64 | 6.681 | 9.242 |
| scapula | coracoid | 6 | 14 | 58 | 64 | 8.621 | 9.242 |
| sub-coracoid and glenoid | 7 | 14 | 50 | 64 | 8.217 | 9.242 |
| acromium | 2 | 6 | 64 | 64 | 8.621 | ≥9.453 |
| medial border | 4 | 1 | 64 | 64 | ≥9.453 | ≥9.453 |

**Table 4.29** Estimated chronological ages for fusion events based on median values of mid-fusion and complete fusion in *Pan paniscus* females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N* mid-fusion** | ***N* complete fusion** | **mid-fusion median** | **complete fusion median** | **mid-fusion** | **complete fusion** |
| **dental score** | **dental score** | **years** | **years** |
| upper limb | proximal humerus | 0 | 3 | 62 | 64 | - | ≥9.453 |
| distal humerus | 1 | 7 | 48 | 63 | 7.242 | 9.033 |
| humeral medial epicondyle | 3 | 4 | 55 | 64 | 7.242 | ≥9.453 |
| proximal radius | 1 | 3 | 63 | 64 | ≥9.453 | ≥9.453 |
| distal radius | 4 | 0 | 64 | 64 | ≥9.453 | - |
| proximal ulna | 2 | 5 | 56 | 64 | 8.11725 | ≥9.453 |
| distal ulna | 3 | 1 | 64 | 64 | ≥9.453 | 9.033 |
| hand | distal phalanges (hand) | 2 | 4 | 50 | 62 | 7.242 | ≥9.453 |
| base of metacarpal 1 | 1 | 3 | 61 | 64 | 7.242 | ≥9.453 |
| proximal and middle phalanges (hand) | 2 | 4 | 60.5 | 64 | 7.242 | ≥9.453 |
| metacarpal heads 2-5 | 0 | 4 | 62 | 64 | - | ≥9.453 |
| lower limb | femoral head | 1 | 3 | 62 | 64 | 8.621 | ≥9.453 |
| greater trochanter | 1 | 3 | 61.5 | 64 | 8.621 | ≥9.453 |
| lesser trochanter | 0 | 4 | 61 | 64 | - | ≥9.453 |
| distal femur | 1 | 2 | 64 | 64 | ≥9.453 | ≥9.453 |
| proximal tibia | 1 | 2 | 63.5 | 64 | ≥9.453 | ≥9.453 |
| distal tibia | 0 | 3 | 62.5 | 64 | - | ≥9.453 |
| proximal fibula | 2 | 0 | 63 | 64 | ≥9.453 | - |
| distal fibula | 0 | 2 | 63 | 64 | - | ≥9.453 |
| foot | calcaneus | 1 | 3 | 60 | 64 | 9.033 | ≥9.453 |
| talus | 0 | 5 | 57 | 63 | - | ≥9.453 |
| distal phalanges (foot) | 2 | 3 | 60 | 64 | 7.053 | ≥9.453 |
| middle phalanges (foot) | 2 | 3 | 62 | 64 | 7.053 | ≥9.453 |
| metatarsal heads (2-5) | 2 | 3 | 62 | 64 | 7.053 | ≥9.453 |
| base of metatarsal 1 | 0 | 3 | 62.5 | 64 | - | ≥9.453 |
| proximal phalanges (foot) | 0 | 3 | 61.5 | 64 | - | ≥9.453 |
| pelvis | triradiate | 2 | 5 | 56.5 | 64 | 8.11725 | 8.826 |
| anterior inferior iliac spine | 0 | 3 | 55 | 64 | - | ≥9.453 |
| iliac crest | 3 | 0 | 64 | - | ≥9.453 | - |
| ischial epiphysis | 1 | 0 | 64 | 64 | ≥9.453 | - |
| clavicle | medial clavicle | 0 | 1 | 64 | 64 | - | 9.033 |
| lateral clavicle | 0 | 3 | 59 | 64 | - | ≥9.453 |
| scapula | coracoid | 3 | 4 | 58 | 64 | 7.242 | ≥9.453 |
| sub-coracoid and glenoid | 3 | 4 | 50 | 64 | 7.242 | ≥9.453 |
| acromium | 2 | 2 | 64 | 64 | ≥9.453 | 9.242 |
| medial border | 1 | 1 | 64 | 64 | ≥9.453 | 9.033 |

**Table 4.30** Estimated chronological ages for fusion events based on median values of mid-fusion and complete fusion in *Pan paniscus* males.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N* mid-fusion** | ***N* complete fusion** | **mid-fusion median** | **complete fusion median** | **mid-fusion** | **complete fusion** |
| **dental score** | **dental score** | **years** | **years** |
| upper limb | proximal humerus | 3 | 0 | 62 | 64 | ≥9.453 | 8.621 |
| distal humerus | 5 | 7 | 48 | 63 | 8.418 | 8.72325 |
| humeral medial epicondyle | 5 | 2 | 55 | 64 | 8.621 | ≥9.453 |
| proximal radius | 5 | 2 | 63 | 64 | 8.621 | ≥9.453 |
| distal radius | 0 | 2 | 64 | 64 | - | 8.621 |
| proximal ulna | 1 | 7 | 56 | 64 | 6.138 | ≥9.453 |
| distal ulna | 0 | 2 | 64 | 64 | - | 9.13725 |
| hand | distal phalanges (hand) | 2 | 4 | 50 | 62 | 5.961 | >9.453 |
| base of metacarpal 1 | 2 | 1 | 61 | 64 | 6.77325 | >9.453 |
| proximal and middle phalanges (hand) | 3 | 3 | 60.5 | 64 | 7.433 | >9.453 |
| metacarpal heads 2-5 | 5 | 2 | 62 | 64 | 8.621 | 8.826 |
| lower limb | femoral head | 6 | 1 | 62 | 64 | 8.72325 | ≥9.453 |
| greater trochanter | 3 | 3 | 61.5 | 64 | 8.621 | 8.826 |
| lesser trochanter | 2 | 5 | 61 | 64 | 8.51925 | ≥9.453 |
| distal femur | 1 | 1 | 64 | 64 | ≥9.453 | ≥9.453 |
| proximal tibia | 1 | 2 | 63.5 | 64 | 8.621 | ≥9.453 |
| distal tibia | 0 | 2 | 62.5 | 64 | - | ≥9.453 |
| proximal fibula | 0 | 2 | 63 | 64 | - | ≥9.453 |
| distal fibula | 2 | 2 | 63 | 64 | 8.11725 | 8.826 |
| foot | calcaneus | 2 | 5 | 60 | 64 | 7.33725 | 8.621 |
| talus | 0 | 9 | 57 | 63 | - | ≥9.453 |
| distal phalanges (foot) | 2 | 3 | 60 | 64 | 8.018 | ≥9.453 |
| middle phalanges (foot) | 2 | 3 | 62 | 64 | 8.018 | ≥9.453 |
| metatarsal heads (2-5) | 2 | 3 | 62 | 64 | 8.018 | ≥9.453 |
| base of metatarsal 1 | 4 | 2 | 62.5 | 64 | 8.018 | ≥9.453 |
| proximal phalanges (foot) | 4 | 2 | 61.5 | 64 | 8.018 | 8.826 |
| pelvis | triradiate | 4 | 5 | 56.5 | 64 | 7.91925 | 8.826 |
| anterior inferior iliac spine | 0 | 6 | 55 | 64 | - | - |
| iliac crest | 1 | 0 | 64 | - | ≥9.453 | - |
| ischial epiphysis | 4 | 0 | 64 | 64 | 8.826 | ≥9.453 |
| clavicle | medial clavicle | 1 | 2 | 64 | 64 | 7.433 | 8.418 |
| lateral clavicle | 0 | 2 | 59 | 64 | - | 8.72325 |
| scapula | coracoid | 1 | 6 | 58 | 64 | 7.433 | 9.13725 |
| sub-coracoid and glenoid | 3 | 4 | 50 | 64 | 8.418 | ≥9.453 |
| acromium | 0 | 2 | 64 | 64 | - | ≥9.453 |
| medial border | 1 | 1 | 64 | 64 | ≥9.453 | 9.033 |

Prior studies of epiphyseal fusion timing in chimpanzees and bonobos were outlined in Chapter 2. Bolter and Zihlman (2012) provided the most comprehensive data set for epiphyseal fusion in chimpanzees and bonobos and included data from Kerley (1966) and Zihlman *et al.* (2007). These data will be used form comparison here. Table 4.31 compares estimated chronological ages based on median dental score values from chimpanzees in the present study to data from Bolter and Zihlman (2012). Table 4.32 provides comparative data from Bolter and Zihlman (2012) for bonobos to data from the present study. All estimated ages based on dental score have an error range of +/- 0.92 (Kuykendall 1996).

**Table 4.31** Comparison of estimated mid-fusion and complete fusion ages in *Pan troglodytes* from the present study to data from Bolter and Zihlman (2012).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **prior studies** | | **data from the present study** | | | |
| **skeletal element** | **Captives from Yerkes, age in years, *N*=101.** | **Wild from Tai National Park, age in years, *N*=92.** | **female estimated age by median (years)** | | **male estimated age by median (years)** | |
| **mid-fusion** | **complete fusion** | **mid-fusion** | **complete fusion** |
| distal humerus | partial 6–7 | 7.96b< *x* <10 | 6.32 | 9.24 | 8.22 | 8.93 |
| acetabulum | partial 7 | 5.19< *x*<11.38 | 7.92 | ≥ 9.45 | 8.62 | 9.24 |
| proximal radius | partial 9 | 11.38< *x* <12 | 9.24 | ≥ 9.45 | 8.83 | 9.24 |
| coracoid | partial 9 | 10< *x* <11.38 | 8.22 | ≥ 9.45 | 8.62 | 9.24 |
| proximal femur | partial 9 | 11.38< *x* <12 | 9.03 | ≥ 9.45 | 8.62 | 9.24 |
| distal tibia | partial 9 | 11.38< *x* <12 | 9.14 | ≥ 9.45 | 8.83 | ≥ 9.45 |
| proximal tibia | partial 9-14 | >12 | 9.35 | ≥ 9.45 | 9.03 | ≥ 9.45 |
| humeral head | partial 9-14 | >12 | 9.03 | ≥ 9.45 | 9.24 | ≥ 9.45 |
| acromial process | <10 | >12 | ≥ 9.45 | ≥ 9.45 | 8.623. | ≥ 9.45 |
| iliac crest | partial 9-14 | >12 | ≥ 9.45 | - | ≥ 9.45 | ≥ 9.45 |

1. There were only two individuals present and both had the same dental score.
2. From Kerley (1966).
3. From Zihlman *et al.*(2007) and unpublished data.

**Table 4.32** Comparison of estimated mid-fusion and complete fusion ages in *Pan paniscus* from the present study to data from Bolter and Zihlman (2012).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **epiphysis** | **Bolter and Zihlman (2012) *N*=51.** | **data from the present study** | | | |
| **females estimated age by median (years)** | | **males estimated age by median (years)** | |
| **mid-fusion** | **complete fusion** | **mid-fusion** | **complete fusion** |
| distal humerus | <6.74 | 7.241. | 9.03 | 8.42 | 8.72 |
| acetabulum | <6.74 | 8.12 | 8.83 | 7.92 | 8.83 |
| proximal radius | 7.3 | ≥ 9.451. | ≥ 9.45 | 8.62 | ≥ 9.45 |
| coracoid | 7.3< *x* <8.54 | 7.24 | ≥ 9.45 | 7.43 | 9.12 |
| proximal femur | 7.3< *x* <8.54 | 8.621. | ≥ 9.45 | 8.72 | ≥ 9.451. |
| distal tibia | <8.54 | - | ≥ 9.45 | - | ≥ 9.45 |
| proximal tibia | partial 8.54 | ≥ 9.452. | ≥ 9.45 | 8.621. | ≥ 9.45 |
| humeral head | 8.54< *x* <11.68 | - | ≥ 9.45 | ≥ 9.45 | 8.62 |
| acromial process | 8.54< *x* <11.68 | ≥ 9.45 | 9.24 | - | ≥ 9.45 |
| iliac crest | partial 11.68 | ≥ 9.45 | - | ≥ 9.451. | - |

1. Sample of only 1 individuals

A few remarks should be made regarding chimpanzee comparisons. There exists a mixture of terms from the data provided by Bolter and Zihlman (2012) with a‘fused by’ classification for complete union and ‘partial fusion’ representing mid-fusion. ‘Fused by’ or ‘fused prior to’ (denoted as <) indicates that an individual observed had that epiphysis fused prior to observation. The large difference between ages reported for wild chimpanzees and captive specimens is also present. Comparison of captive past study results are more applicable to the data from the present study as Kuykendall’s (1996) sample for regression analysis was drawn only from captive individuals. There is general concordance between past studies and the present study within deviations of typically not more than a year for mid-fusion/partial fusion comparisons.

## Summary of standards of growth for chimpanzees and bonobos

### Growth Rate

Growth rate for long-bone length was plotted against dental score and linear regression analyses were peformed. It was found that the relationship between growth in long-bone length and dental score is significantly linear. Regression equations were presented for growth relative to dental score for each long-bone.

### Sequence of fusion events

Comparison of epiphyseal fusion events relative to dental score determined that some epiphyses fuse beyond complete dental maturity. DS64 was a limiting factor and this method was not suitable for ordering fusion events. Comparisons between sexes showed no significant differences, but the limitation of dental maturity prevented a rigorous analysis of this topic.

Fusion events sequences were determined using two different methods. The first was the application of contingency tables for producing a modular sequence of events and the second was the ordering of events using mean epiphyseal fusion score. A notable amount of variation was found and sequences varied somewhat between the application of the two methods. Sex differences were not apparent. Post-hoc Bonferroni tests were used to observe differences in mean epiphyseal fusion value and it was shown that there is a range of overlap for all sequences in which no statistically significant differences may be found. Consequently, precise order remains ambiguous but general patterns appear to be consistent both between sexes and between methodologies.

### Analysis of allometry

Shea’s (1981) results were confirmed for an expanded list of *Pan troglodytes* sub-species.

### Estimation of age for fusion in chronological years for comparability to prior studies

Estimations of fusion event timing in chronological years was produced using Kuykendall’s (1996) regression equation for 8 teeth. The data in this study were consistent with results from prior studies. An expanded list of estimated ages of fusion for given epiphyses was produced.

# Results – Comparisons of growth standards between *Pan* and *Homo*

## Comparison of human and chimpanzee epiphyseal fusion sequences

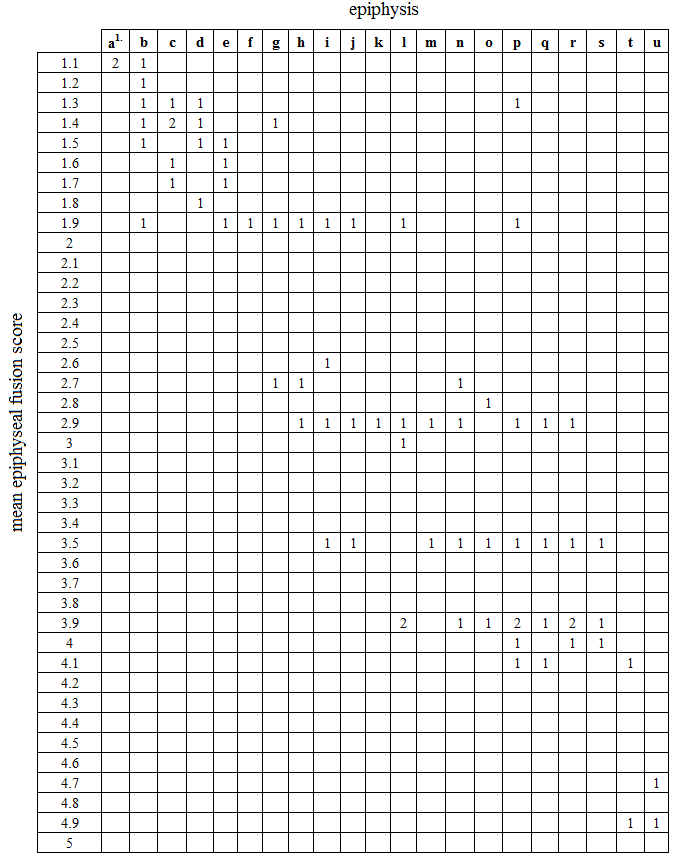
### Comparison of modular sequence patterns to Schaefer and Black (2007)

Schaefer and Black (2007) provided a modular sequence pattern using the stages of ‘beginning fusion’ and ‘complete fusion’ in human males for 21 epiphyses. They used contingency tables to establish an order of fusion events. The flow chart they produced provided a sequence for epiphyses with the fractional minority cases (those which changed sequence order) listed for each stage. Chimpanzee data presented in Chapter 4 showed a considerable amount of overlap and it appears that this was also true for the data in Schaefer and Black’s (2007) study.

A comparison of mid-fusion data as presented in Chapter 4 with the results provided by Schaefer and Black (2007) is problematic. The scoring method used in the Schaefer and Black’s (2007) study used three stages: unfused, partial fusion, and complete fusion. These appear superficially to be the same as the categories used in this study but they are not. Beginning fusion for Schaefer and Black (2007) included individuals with epiphyses up to but not including a fused epiphysis with a residual scar line. In the context of the system in which the data for this study was recorded, this meant that they used mid-fusion stages 2 and 3 for their mid-fusion category while placing 4 and 5 into complete fusion. In the present study fusion states 2, 3, and 4 were placed into mid-fusion (labelled as 2) and 5 into complete fusion (labelled as 3). This meant that mid-fusion stages from the present study would be potentially skewed due to the inclusion of epiphysis with a fusion scar line. Given that the duration of time that an epiphysis retains this scar line cannot be assumed to be constant between epiphyses, these data are not directly comparable. It is possible to re-calculate the order using Schaefer and Black’s (2007) system as this type of data are available in the original data set. As noted in Chapter 4, sample size for male *Pan troglodytes* mid-fusion events was a limiting factor. Removing individuals with residual scar lines reduced sample numbers even further. Table 5.1 provides sample size for mid-fusion events of *Pan troglodytes* males using Schaefer and Black’s (2007) criteria. Figure 5.1 demonstrates how these events are distributed for each epiphysis using a grid pattern. Epiphyses are represented by letters which are defined in Table 5.2.

**Table 5.1** Sample size for mid-fusion events in *Pan troglodytes* males using Schaefer and Black’s (2007) criteria.

|  |  |
| --- | --- |
| **epiphysis** | **sample size** |
| distal humerus | 2 |
| triradiate | 6 |
| medial | 5 |
| coracoid | 4 |
| proximal ulna | 4 |
| proximal radius | 1 |
| lesser trochanter | 3 |
| proximal femur | 3 |
| distal fibula | 4 |
| distal tibia | 3 |
| greater trochanter | 1 |
| proximal tibia | 5 |
| acromium | 2 |
| distal femur | 4 |
| proximal fibula | 3 |
| distal radius | 8 |
| distal ulna | 4 |
| ischial epiphysis | 5 |
| proximal humerus | 3 |
| iliac crest | 2 |
| medial clavicle | 2 |

****

1. These letters are defined in the table below

**Figure 5.1** Matrix showing fusion events for *Pan troglodytes* males using Schaefer and Black (2007) criteria.

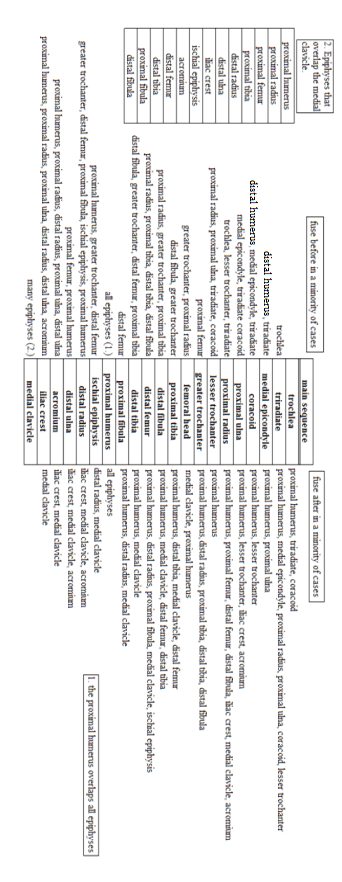
**Table 5.2** Legend of epiphyses for Figure 5.1.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| a | distal humerus | l | proximal tibia | |
| b | triradiate | m | acromium | |
| c | humeral medial epicondyle | n | distal femur | |
| d | coracoid | o | proximal fibula | |
| e | proximal ulna | p | distal radius | |
| f | proximal radius | q | distal ulna | |
| g | lesser trochanter | r | ischial epiphysis | |
| h | femoral head | s | proximal humerus | |
| i | distal fibula | t | iliac crest | |
| j | distal tibia | u | medial clavicle | |
| k | greater trochanter |  | |  |

Sample size was too small for application of Schaefer and Black’s (2007) criteria to male *Pan troglodytes*. Another approach was to consider combined sex data using Schaefer and Black’s (2007) criteria for epiphyses where differences were not found between sexes in Chapter 4. This also allowed for the inclusion of unsexed *Pan troglodytes* individuals. Table 5.3 presents sample sizes for each epiphysis when combined-sex data is considered. Contingency tables were produced comparing each epiphysis. A modular sequence chart is shown in Figure 5.2. Sequence order was determined by the net number of epiphyses that proceeded (fused prior to) or preceded (fused after) a given epiphysis.

**Table 5.3** Sample size for combined-sex *Pan troglodytes* mid-fusion epiphysis using Schaefer and Black’s (2007) criteria.

|  |  |  |  |
| --- | --- | --- | --- |
| **epiphysis** | ***N*** | **epiphysis** | ***N*** |
| proximal humerus | 18 | proximal tibia | 19 |
| distal humerus | 11 | distal tibia | 7 |
| humeral medial epicondyle | 12 | proximal fibula | 13 |
| proximal radius | 8 | distal fibula | 9 |
| distal radius | 16 | triradiate | 11 |
| proximal ulna | 9 | iliac crest | 17 |
| distal ulna | 14 | ischial epiphysis | 14 |
| proximal femur | 10 | medial clavicle | 9 |
| greater trochanter | 5 | coracoid | 12 |
| lesser trochanter | 7 | acromium | 18 |
| distal femur | 16 |  |  |



**Figure 5.2** Modular sequence for combined-sex *Pan troglodytes*.

There was a similar amount of overlap of fusion events as was observed in Chapter 4 for fusion sequences using the present study criteria. However, a general sequence remained discernable. Table 5.4 provides both the human sequence from Schaefer and Black (2007) and the chimpanzee sequence as shown above in Figure 5.2. Pairs or groups of epiphyses for which order could not be determined are highlighted in boldface. It should be noted that these particular epiphyses are separated in Figure 5.2 due to different epiphyses preceding and proceeding each. The order in this figure is arbitrary and this does not indicate a determination of sequence order.

**Table 5.4** Comparison of sequence differences between chimpanzees and humans using Schaefer and Black’s (2007) criteria.

|  |  |
| --- | --- |
| **combined-sex chimpanzees** | **Schaefer and Black (2007) humans** |
| distal humerus | triradiate |
| triradiate | **proximal ulna/ distal humerus** |
| humeral medial epicondyle | **proximal ulna/ distal humerus** |
| coracoid | coracoid |
| proximal ulna | proximal radius |
| **proximal radius/lesser trochanter** | femoral head |
| **proximal radius/lesser trochanter** | humeral medial epicondyle |
| greater trochanter | distal tibia |
| femoral head | lesser trochanter |
| **proximal tibia/distal fibula** | greater trochanter |
| **proximal tibia/distal fibula** | ischial epiphysis |
| **distal femur/distal tibia** | distal fibula |
| **distal femur/distal tibia** | proximal tibia |
| proximal fibula | distal femur |
| proximal humerus | acromium |
| ischial epiphysis | proximal fibula |
| distal radius | iliac creast |
| distal ulna | proximal humerus |
| acromium | distal radius |
| iliac crest | distal ulna |
| medial clavicle | medial clavicle |

The sequence order appears to be different between the two species. The level of overlap indicates that many of these sequence differences were based on very small differences in frequency and the removal of one or two individuals for a given epiphysis would shift sequence position several places. The appropriate test for this type of data would be a chi-squared or fisher exact test. However, for virtually all cases there would be insufficient sample size for statistical validity. Schaefer and Black (2007) had the luxury of a much larger sample size making the analysis of closely fusing epiphyses more distinctly resolved for their study. Even with this being the case the amount of overlap observed in their data also would have made this type of statistical analysis for frequency difference inconclusive for many epiphyses.

### Comparison of mean epiphyseal fusion sequence patterns to Schaefer and Black (2007)

In Chapter 4 mean epiphyseal fusion score was used as a maturational indicator for sequencing epiphyseal fusion events. It is worth investigating if this method produced different patterns than those found for modular sequence in the previous section when compared to Schaefer and Black (2007). Schaefer and Black’s (2007) criteria for epiphyseal fusion was applied to the combined-sex mid-fusion *Pan troglodytes* sample from this study. Results for post-hoc Bonferroni tests are available in Table 8.2.2.3 in the digital appendix (section 8.2.2). The sequence of fusion events was similar to that found using the present study criteria (including stages 2, 3 and 4). The level of overlap was also consistent with that observed for present-study criteria used in Chapter 4. The sequence of fusion events is shown in comparison with that of Schaefer and Black (2007) in Table 5.5.

**Table 5.5** Comparison of mid-fusion sequences between combined-sex chimpanzees using mean epiphyseal fusion value and humans from Schaefer and Black (2007).

|  |  |  |
| --- | --- | --- |
| **order number** | **chimpanzee epiphyses** | **Schaefer and Black (2007) human male epiphyses** |
| 1 | distal humerus | triradiate |
| 2 | humeral medial epicondyle | **proximal ulna/ distal humerus** |
| 3 | triradiate | **proximal ulna/ distal humerus** |
| 4 | coracoid | coracoid |
| 5 | proximal ulna | proximal radius |
| 6 | lesser trochanter | femoral head |
| 7 | proximal radius | humeral medial epicondyle |
| 8 | femoral head | distal tibia |
| 9 | greater trochanter | lesser trochanter |
| 10 | distal fibula | greater trochanter |
| 11 | distal tibia | ischial epiphysis |
| 12 | proximal humerus | distal fibula |
| 13 | distal femur | proximal tibia |
| 14 | proximal tibia | distal femur |
| 15 | proximal fibula | acromium |
| 16 | distal radius | proximal fibula |
| 17 | ischial epiphysis | iliac creast |
| 18 | distal ulna | proximal humerus |
| 19 | acromium | distal radius |
| 20 | medial clavicle | distal ulna |
| 21 | iliac crest | medial clavicle |

## Comparisons between epiphyseal fusion sequences and dental sequences

This section will consider comparisons of skeletal and dental sequences in chimpanzees and humans. This is contrasted with the comparison of dental score measured as a continuous variable to epiphyseal fusion events (section 4.2.1). In Chapter 4 it was found that sample size for *Pan paniscus* prohibited sequencing epiphyseal fusion based on mean epiphyseal fusion or contingency tables. Without these sequences, this species will not be analysed here and analysis will again only apply to *Pan troglodytes*.

Dental sequences may be evaluated using mineralization stages of individual teeth or tooth emergence. Molar emergence is often used as a reference as the timing between the emergence of each tooth can be a number of years. Comparing dental and epiphyseal fusion sequences would ideally use such landmarks to group epiphysis and then consider which epiphyses came before and after these events. However, this study is limited by the use of summary Demirjian dental score data. There are no distinct landmark points provided in summary dental score when using this system for assessing dental development. Emergence events may be associated with specific dental mineralization stages and it is possible to use the original Demirjian score for each tooth to re-classify the entire data set. However, due to the scale of this task, this would not be a practical approach and the process of doing so would also introduce further estimation error.

In this section the potential of Kuykendall’s (1996) age estimations for dental development will be investigated for use in observing the occurence of epiphyseal fusion events between the completion of individual teeth. The completion of dental maturity (apical closure of the third molar) is a critical landmark to consider in this application as well. Analysis of the number of epiphyses that fuse past DS64 may reveal that this event is occuring relatively earlier in chimpanzees. Comparisons of dental score to epiphyseal fusion in Chapter 4 have shown that several epiphyses fuse after this reference point. This does not occur in humans where only the medial clavicle typically fuses after third molar apical closure (Schaefer *et al*. 2009). Apical root closure of teeth was chosen as a reference for chimpanzees and humans and ages of attainment are shown in Table 5.6. For reference points other than complete third molar mineralization, the choice of completion of tooth mineralization is arbitrary. However, it is a feature that is measureable given the data available in this study. Age ranges for human epiphyseal fusion closure are provided in Table 5.7. This table provides ranges of fusion from a number of different studies. No single study of human epiphyseal fusion considers all of the epiphyses observed in the present study for chimpanzees and bonobos.

**Table 5.6** Human and chimpanzee dental apical closure ages and chimpanzee

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **tooth** | **apical closure in humans (years)1.** | | **apical closure in chimpanzees (years)2.** | | |
| **males** | **females** | **males** | **females** | **total sample** |
| M3 | 20.0 | 20.75 | -3. | - | - |
| M2 | 15.4 | 15.6 | 10.73 | - | 10.73 |
| M1 | 19.3 | 16.2 | 8.57 | 7.99 | 8.14 |
| P2 | 14.4 | 14.6 | 10.74 | 8.35 | 9.69 |
| P1 | 13.5 | 14.1 | 10.73 | 8.66 | 9.69 |
| C1 | 11.9 | 12.4 | 10.12 | no data | no data |
| I2 | 13.7 | 14.2 | 10.73 | 9.02 | 9.69 |
| I1 | 11.8 | 12.9 | 10.12 | 8.66 | 9.55 |

1. Data from Schaefer *et al*.(2009) except third molar which is from Moorrees *et al*.1963.
2. Data from Kuykendall (1996)
3. Kuykendall’s data had no third molar sub-adults with apical closure.

Age estimates of epiphyseal fusion timing for chimpanzees in this study were calculated using Kuykendall’s (1996) regression equation, which did not differentiate by sex. The estimated ages based on regression do not exactly match the estimated ages for apical closure as estimated for each individual tooth. Kuykendall’s (1996) estimated age for completion of the third molar (10.73 years) is older than the regression estimate based on 8 teeth (9.453 years). The ranges of error for these estimates overlap for both means of measurement and there is no immediate solution for this ambiguity. Using estimates for apical closures of individual teeth may shift categorization of epiphyses. To reduce the effect of this problem, only two reference points were used in this analysis. These were apical closure of the first and third molar. Apical closure of the first molar provides an early-stage reference point and third molar completion may be more confidently assessed as this represents dental maturity. The value for the first molar was derived from the median value of Kuykendall’s (1996) estimate for combined-sex Demirjian stage-8 teeth (8.14 years). Kuykendall’s (1996) regression equation estimate for age of completion of the third molar was 9.453 years. Epiphyses were grouped by these two apical closures. Table 5.8 provides a list of groups for epiphyses that correspond to each range of time between the complete mineralization of tooth apicies. These refer only to mid-fusion epiphyses that were observed in this study. The epiphyses in these groups are listed below in Table 5.9.

**Table 5.7** Epiphyseal fusion ranges in humans for both males and females derived from several different studies.

|  |  |  |  |
| --- | --- | --- | --- |
| **region** | **epiphysis** | **humans females (years)** | **humans males (years)** |
| feet | calcaneus | 10-16 (1) | 11-14 (1) |
| talus | not measured | not measured |
| distal phalanges | 11-13 (1) | 14-16 (1) |
| middle phalanges | 11-13 (1) | 14-16 (1) |
| metatarsal heads 2-5 fusion | 11-13 (1) | 14-16 (1) |
| hands | proximal phalanges | 13-15 (1) | 16-18 (1) |
| base of metatarsal 1 | 13-15 (1) | 16-18 (1) |
| distal phalanges | 13.5 (1) | 16 (1) |
| base of metacarpal 1 | 14-14.5 (1) | 16.5 (1) |
| proximal and middle phalanges | 14-14.5 (1) | 16.5 (1) |
| heads of metacarpals 2-5 | 14.5-15 (1) | 16.5 (1) |
| clavicle | medial clavicle | 17-33, closed after 21 (4) | 17-29, closed after 21(4) |
| scapula | coracoid | 11 to 17 (3) | 15-22 (3) |
| sub-coracoid and glenoid | 11-17 (3) | 15-18 (4) |
| acromium | 17-20 (4) | 17-21 (3) |
| medial border | - | 18-22 (4) |
| upper limb | proximal humerus | 17-23 (3) | 19-23 (3) |
| distal humerus | 15-18 (3) | approx 12 (3) |
| humeral medial epicondyle | 12-14 (5) | 16-18 (4) |
| proximal radius | 12-17 (3) | 15-18 (4) |
| distal radius | 17-22 (C&W) | 16-20 (4) |
| proximal ulna | 14-18 (5) | 15-18 (4) |
| distal ulna | 17-21 (3) | 17-20 (4) |
| lower limb | femoral head | 14-16 (2) | 16-20 (4) |
| greater trochanter | 13-16 (2) | 16-20 (4) |
| lesser trochanter | 13-16 (2) | 16-20 (4) |
| distal femur | 14-19 (2) | 16-20 (4) |
| proximal tibia | 14-19 (2) | 16-20 (4) |
| distal tibia | 14-16 (2) | 16-18 (4) |
| proximal fibula | 14-17 (2), 17-19 (3) | 16-20 (4) |
| distal fibula | 14-16 (2) 17-21 (3) | 16-20 (4) |
| pelvis | triradiate | 11-16 (2) | 11-18 (2) |
| anterior inferior iliac spine | 14-19 (3) | 16-18 (4) |
| iliac crest | 14-21 (2) | 17-21 (4) |
| ischium | 14-19 (2) | 16-20 (4) |

1. Schaefer *et al*.2009
2. Cardoso 2008
3. Coqueugniot and Weaver 2007
4. Schaefer 2008
5. Sahni and Jit 1995

**Table 5.8** Chimpanzee fusion events after apical closures estimated from Kuykendall (1996)

|  |  |  |  |
| --- | --- | --- | --- |
| **tooth** | **mid-fusion mean after age (years)1.** | **female groups** | **male groups** |
| before M1 | < 8.14 | A | D |
| between M1 and M3 | 8.14 < *x* < 9.453 | B | E |
| After M3 | > 9.453 | C | F |

**Table 5.9** Epiphysis groups for dental apical age ranges in chimpanzees.

|  |  |  |  |
| --- | --- | --- | --- |
| **group A** | distal humerus | talus | sub-coracoid and glenoid |
| proximal ulna | triradiate | humeral medial epicondyle |
| distal phalanges (hand) | anterior inferior iliac spine |  |
| **group B** | proximal radius | lesser trochanter | middle phalanges (foot) |
| base of metacarpal 1 | proximal tibia | metatarsal heads (2-5) |
| proximal and middle phalanges (hand) | distal tibia | base of metatarsal 1 |
| metacarpal heads 2-5 | proximal fibula | proximal phalanges (foot) |
| femoral head | distal fibula | lateral clavicle |
| greater trochanter | calcaneus | coracoid |
|  | distal phalanges (foot) |  |
| **group C** | acromium | ischia epiphysis | distal ulna |
| medial border | medial clavicle | distal radius |
| iliac crest | distal femur |  |
| **group D** | distal phalanges (hand) | anterior inferior iliac spine | lateral clavicle |
| **group E** | proximal humerus | greater trochanter | middle phalanges (foot) |
| distal humerus | lesser trochanter | metatarsal heads (2-5) |
| humeral medial epicondyle | distal femur | base of metatarsal 1 |
| proximal radius | proximal tibia | proximal phalanges (foot) |
| distal radius | distal tibia | triradiate |
| proximal ulna | proximal fibula | ischia epiphysis |
| base of metacarpal 1 | distal fibula | coracoid |
| proximal and middle phalanges (hand) | calcaneus | sub-coracoid and glenoid |
| metacarpal heads 2-5 | distal phalanges (foot) | acromium |
| femoral head |  |  |
| **group F** | iliac crest | medial clavicle | medial border |

Male and female chimpanzees differed somewhat in terms of which epiphyses were included into which groups. The majority of epiphyses fell into groups B and E. The smaller number of males in groups D and F when compared to female groups A and C implies that males undergo fusion more closely within the range of the developing dentition. However, certainty about exact number of epiphyses in each group is not assured for at least two reasons. First, male sample sizes were smaller leading to greater variability in estimated ages, although there is no reason to expect this would necessarily produce a trend towards moving fusion events closer together. In any case such variation could easily move epiphyses across boundaries. Second, the error range for Kuykendall’s regression equation (+/- 0.92 years) meant there was less certainty for epiphyses very near the cut-off points for groupings. There were 5 epiphyses for males that had a median dental score of 58, which represents 8.217 years. This is very close to the cutoff of 8.14 years and well within the error range of Kuykendall’s (1996) regression analysis. Several of the female estimated ages which were below this threshold were also equally close. As a general observation, the majority of epiphyses fused between apical root closure of the first and last adult tooth. There was a consistent pattern of a small number of epiphyses fusing before and after these teeth.

Humans epiphyseal fusion grouping are now considered. The definition of human mid-fusion varies from study to study. The ranges of fusion also vary markedly. It is possible to provide approximately equivalent data to that considered above for chimpanzees. Table 5.10 provides groupings of epiphyses for human females. It is notable that the first tooth to complete apical closure in humans is the first incisor as opposed to the first molar. For humans, there are also a small number of epiphyses that fuse before the apical root closure of the first tooth. The epiphyses that fuse before the apical closure of the first tooth are not necessarily the same set when comparing chimpanzees to humans. When considering the comparison of fusion sequences in the previous section, it would seem likely that these differences are consequent of small changes in order for heavily overlapping fusion centres. The earliest epiphyses in this grouping (e.g., the distal humerus and the humeral medial epicondyle) are always present, suggesting that at least at earlier stages the pattern is always the same. With respect to third molar maturation, unlike chimpanzees there is only one epiphysis that fuses after the completion of the third molar root in humans.

**Table 5.10** Groupings of mid-fusion epiphyses by dental apical closure for human females.

|  |  |  |
| --- | --- | --- |
| **teeth completing apical closure** | **epiphyses** | |
| Near completion of I1 and C  (up to ~13 years) | calcaneus | distal phalanges |
| distal phalanges | coracoid |
| middle phalanges | distal humerus |
| metatarsal heads 2-5 fusion | humeral medial epicondyle |
| Near completion of P1,I2, P2  (~14-15 years) | proximal phalanges | femoral head |
| base of metatarsal 1 | greater trochanter |
| base of metacarpal 1 | lesser trochanter |
| proximal and middle phalanges | distal tibia |
| heads of metacarpals 2-5 | triradiate |
| Near completion of M2 and M1  (~16-19 years) | sub-coracoid and glenoid | distal ulna |
| acromium | distal femur |
| medial border | proximal tibia |
| proximal humerus | proximal fibula |
| proximal radius | distal fibula |
| distal radius | anterior inferior iliac spine |
| proximal ulna | iliac crest |
| ischium |  |
| after completion of third molar  (~21-22 years) | medial clavicle |  |
|  |  |

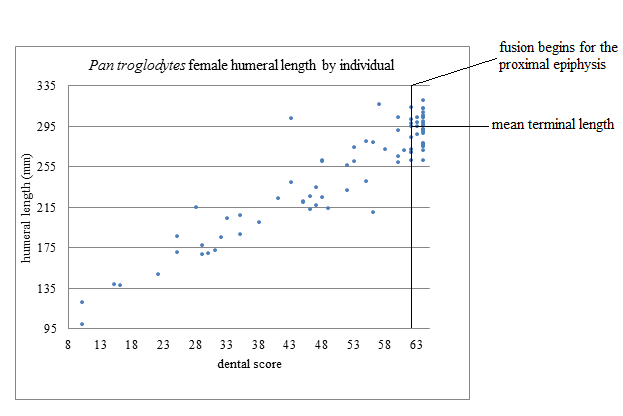
For humans, the third molar is a potential outlier even if the pattern is scaled to a longer period of maturity. The human second molar is complete at approximately age 16 according to Chaillet and Demirjian (2004). Kuykendall’s (1996) regression suggests that the third molar and second molar in chimpanzees likely mature within at most a year of each other. Anemone *et al*.’s (1991, 1996) data also confirm this. As a proportion of time spent during growth (the time prior to full skeletal maturity) the chimpanzee ratio of M2:M3 completion of approximately 10:11 years is a higher ratio than the human values for these teeth which are 16:20 years if the middle of the 18-22 range from Scheuer and Black (2004) is taken. A delay is observed in human dental maturation for the third molar. This delay is more pronounced relative to skeletal maturation in terms of the epiphyses that fuse after third molar completion.

The observations found for comparisons of dental and epiphyseal fusion sequences add to the general conclusions regarding comparisons of skeletal and dental development. It has been established by comparing dental score to epiphyseal fusion in Chapter 4 that many epiphyses may begin fusion after the completion of the third molar root. The analysis here suggests that the earlier stages of skeletal and dental maturity do not markedly differ between humans and chimpanzees. Kuykendall’s (1996) regression suggests that the third molar completes apical closure very close in time after the second molar. As stated previously, Anemone *et al*.’s (1991, 1996) data using complete mineralization data agrees with this observation. In humans third molar mineralization completes much later. This implies that there is a shift in dental developmental relative to skeletal development towards the end of maturation.

## Epiphyseal fusion as a proportion of long-bone length

It has been established that dental developmental sequence differs relative to skeletal fusion sequence between chimpanzees and humans. This means that this system is an inappropriate maturational reference from which to base comparisons of fusion timing as a function of long-bone growth in length between the two species. Another way in which growth and epiphyseal fusion can be considered is as percentage of growth in length. By doing this, neither rate of growth nor other maturational indicators influence comparisons. This permits the observation of the point of growth in length of a bone at which an epiphysis is no longer able to contribute to growth. This type of data is easily found for humans by using data on long-bone length and epiphyseal fusion from multiple studies. Long-bone length data from Maresh (1970) was used and epiphyseal fusion data derived from Cardoso (2007), Coqeuegnoit and Weaver (2007) and Shaefer (2008).

In order to use chimpanzee and bonobo data from the present study, final adult length needed to be determined. Complete fusion lengths provided this type of data and values were available for all long-bones. Mid-fusion values for bones in which the last epiphysis (terminal epiphysis) began to fuse were also acceptable for inclusion in calculating these values. This is because when the last epiphysis to fuse for a bone begins fusion that bone is no longer able to grow in length. Figure 5.3 demonstrates this principle for growth in humeral length relative to dental score.

**Figure 5.3** Demonstration of mean adult humeral length after fusion of the proximal epiphysis.

A mean value for all individuals with terminal epiphyses in either mid-fusion or complete fusion was taken. All bone lengths for each individual were then converted into a percentage of length. Individuals with mid-fusion epiphyses were identified then assessed with respect to percentage of growth in length. Tables 5.11 and 5.12 provide percentiles of epiphyseal mid-fusion events for growth in length for all 6 long-bones, comparing chimpanzee and humans. The ranges for epiphyseal fusion in chimpanzees often go over 100%. This is because the mean value for terminal length does not necessarily mean that fusing individuals were necessarily that close to the average. With cross-sectional data, there was no means to correct for this. In reality these values for terminal epiphyses will by definition be exactly 100% for each individual. The variation seen here is not substantial. It is important to observe the mid-fusion values for epiphyses that precede terminal epiphyses in these tables. These are the only epiphyses that may change between species relative to growth in length.

**Table 5.11** Comparison of mid-fusion timing relative to growth in long-bone length for female chimpanzees and humans.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis2.,3.** | **human females1.** | | **chimpanzee females** | | | |
| **(% length)** | **range of values (% length)** | ***N* (mid-fusion)** | **mean % mid-fusion** | **standard deviation mid-fusion (%)** | **mid-fusion range (%)** |
| proximal humerus | **100.0** | - | 21 | **99.9** | 7.0 | 92-110 |
| distal humerus | **91.0** | 914. | 10 | **85.6** | 7.5 | 76-97 |
| humeral medial epicondyle | **95.0** | 91-98 | 8 | **88.8** | 6.2 | 77-97 |
| proximal radius | **97.8** | 91-100 | 12 | **95.1** | 4.3 | 89-101 |
| distal radius | **100.0** | - | 17 | **102.2** | 4.7 | 93-108 |
| proximal ulna | **95.6** | 92-99 | 6 | **88.7** | 4.3 | 89-94 |
| distal ulna | **100.0** | - | 22 | **100.7** | 5.8 | 88-109 |
| femoral head | **100.0** | 92-100 | 11 | **98.8** | 4.3 | 93-107 |
| greater trochanter | **100.0** | - | 11 | **99.2** | 5.5 | 91-107 |
| lesser trochanter | **99.8** | 99-100 | 5 | **95.9** | 3.9 | 91-101 |
| distal femur | **100.0** | - | 21 | **101.1** | 5.0 | 93-110 |
| proximal tibia | **100.0** | - | 21 | **100.9** | 5.3 | 92-110 |
| distal tibia | **98.4** | 96-100 | 14 | **99.3** | 4.4 | 92-108 |
| proximal fibula | **100.0** | - | 16 | **101.6** | 5.3 | 92-112 |
| distal fibula | **100.0** | - | 10 | **99.3** | 4.2 | 92-107 |

1. Data for human length is from Maresh (1970)
2. Data for human female epiphyseal fusion is from Coqeuegnoit and Weaver (2007)
3. Data for female femur from Cardoso (2008)
4. For human distal humerus fusion one single age was given.

The normality of epiphyseal fusion distributions as a percentage of growth in length was considered using Shapiro-Wilk normality tests. These data are available in appendix section 8.8. No epiphyses significantly deviated from normality. It should also be observed that Schaefer’s (2008) data used for males provided numbers of individuals for each year of age. Mean values were achieved by mutiplying each age category by the percentage of individuals in each stage. The human female data from Coqeuegnoit and Weaver (2007) only provided ranges and the mean values were a midpoint of these ranges.

**Table 5.12** Comparison of mid-fusion timing relative to growth in long-bone length for male chimpanzees and humans.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis1.,2.** | **human males** | | **chimpanzee males** | | | |
| **males(% length)** | **range of values (% length)** | ***N* (mid-fusion)** | **mean % mid-fusion** | **standard deviation mid-fusion (%)** | **mid-fusion range (%)** |
| proximal humerus | **99.8** | 97-100 | 6 | **103.7** | 4.6 | 97-111 |
| distal humerus | **95.9** | 94-100 | 5 | **84.4** | 12.7 | 70-98 |
| humeral medial epicondyle | **98.5** | 97-100 | 8 | **93.56** | 5.8 | 83-98 |
| proximal radius | **97.1** | 94-100 | 8 | **97.7** | 7.6 | 88-103 |
| distal radius | **99.6** | 98-100 | 4 | **97.6** | 9.7 | 88-107 |
| proximal ulna | **95.7** | 94-100 | 6 | **94.6** | 4.1 | 89-97 |
| distal ulna | **99.9** | 99-100 | 6 | **98.1** | 7.7 | 89-108 |
| femoral head | **99** | 98-100 | 5 | **98.1** | 6.1 | 89-103 |
| greater trochanter | **99.2** | 98-100 | 3 | **102.1** | 2 | 100-103 |
| lesser trochanter | **99.2** | 98-100 | 4 | **96.1** | 6.5 | 89-103 |
| distal femur | **99.8** | 98-100 | 7 | **99.4** | 3.6 | 99-103 |
| proximal tibia | **100** | 100 | 7 | **98.8** | 7.3 | 88-108 |
| distal tibia | **100** | 100 | 7 | **98.8** | 7.3 | 88-108 |
| proximal fibula | **99.6** | 99-100 | 6 | **99.7** | 6.6 | 92-108 |
| distal fibula | **99.3** | 98-100 | 8 | **98.7** | 7.1 | 92-108 |

1. Data for human length is from Maresh (1970)
2. Data for human males from Schaefer (2008)

Ranges of fusion as a proportion of length in both chimpanzees and humans largely overlap. The range of variation in fusion as a percentage of length for chimpanzees was greater than it was for humans. This was likely due to the nature of smaller-sample cross-sectional data. Despite this, the patterns were essentially the same. The only exceptions may have been the distal humerus and humeral medial epicondyle, although these ranges still largely overlapped. It would be desireable to see if the values for these ranges could be put to a test for significance. However, there was no equivalent data for humans as exists for chimpanzees. Coqeuegnoit and Weaver (2007) only provided ranges of fusion times as opposed to raw data. Schaefer (2008) provided numbers for each age category, which were sufficient for establishment of central tendency but these data provided very skewed distributions. Other studies of humans provide the same type of data as the aforementioned studies. Future study including comparable human data may resolve these limitations in the future. At present it is assumed that the pattern of fusion relative to growth in length is effectively the same between the two species.

Bonobos

The number of available bone lengths from *Pan paniscus* were too few to be able to calculate terminal adult length with any confidence. Epiphyseal fusion values were likewise too few to provide reliable data. Given these limitations it would not be appropriate to attempt the same procedure here for this species.

## Summary of comparisons of growth standards between Pan and Homo

The modular sequence of epiphyseal fusion events determined for chimpanzees was compared to the human sequence determined by Schaefer and Black (2007). Sequence determined by mean epiphyseal fusion value was also compared to this study. Post-hoc Bonferroni tests were used to compare chimpanzee mean epiphyseal fusion value sequence to humans. It was found that sequences derived from this method varied for each epiphysis but no statistically significant differences in sequence order were discernable.

Furthering sequence comparisons a comparison of dental maturity to epiphyseal fusion was attempted using estimated chronological age for complete mineralization of the third molar and first adult tooth as a reference. It was shown that chimpanzees and humans both intiate fusion of a small number of epiphyses prior to the complete mineralization of the first adult tooth. Chimpanzees continue skeletal maturation for a greater number of epiphyses beyond dental maturity than do humans. Stated another way, human third molar maturity extends further into skeletal development than it does for chimpanzees.

Fusion events have never been considered in the context of long-bone growth as no studies previously have both types of data simultaneously. With dental score a problematic frame of reference for comparison between species, fusion events as a proportion of growth in length were analysed. This was done only for *Pan troglodytes* due to sample limitations for *Pan paniscus*. It was found that there were no differences between chimpanzees and humans.

# Discussion

## Introduction to discussion

This chapter will consider the implications that the data produced in this study will have for developmental theory and the study of fossil hominids. The chapter will be broken into two main sections. The applications within constructs of developmental theory will first be discussed (section 6.2). The applications of intergrated data for understanding growth rate, sequence, and allometry will be evaluated. This section will be followed by an analysis of the practical applications for the study of fossil hominids (section 6.3).

## Application of the results of this study to developmental theory

As presented in Chapter 2, there remains theoretical debate regarding the differences in developmental patterns between humans and other apes. This was framed within the context of the study of heterochrony. Debate has focused on the fundamental questions of whether humans demonstrate neoteny, hypermorphosis, or a mixture of both patterns when compared to other apes. There remains a lack consensus and a primary reason for differing perspectives relates to incomplete data required for an integrated analysis of skeletal sub-systems. Often one feature or aspect of development was analysed and used as evidence to support one theory while different evidence was used to support another. For example, Penin *et al*. (2002) and Bastir and Rosas (2004) analysed facial morphology and concluded that humans demonstrate neoteny. McKinney and McNamara (1991), Parker (1996), and Vrba (1996) measured overall somatic growth and came to the conclusion that humans were hypermorphic. Opposing arguments looking at the same region were essentially absent, either because only a single group of researchers considered that region or the data only supported that theory for lack of better evidence. For example, Vrba (1996) suggested that the longer period of human growth allowed for distortions in body shape between ancestor and descendant to occur. Given the information Vrba (1996) had at that time, this conclusion could be reached simply because it could not be refuted by skeletal evidence that did not yet exist.

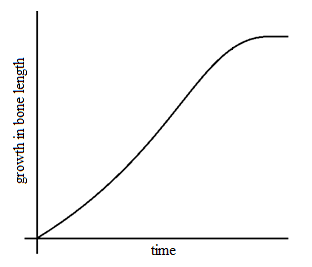
This section will attempt to bridge some of these contradictions by use of the integrated data from the present study by means of the addition of new data that had not existed during the formation of past models. This will be approached in the same manner in which these data have been analyses where growth rate and sequences of developmental events will be considered separately.

### Growth rate

***6.2.1a Growth rate with respect to time***

This study did not use individuals with known age and as such growth rate with respect to years was not measureable. As previously stated, estimated chronological ages from dental development would be possible using Kuykendall’s (1996) regression equation for dental age. However, with this information already well-established in the literature such data would add no new insights into such considerations and as estimates, such ‘ages’ would not represent real data points. The lack of chronological age data required that the assessment focus on aspects of relative growth between different skeletal sub-systems.

***6.2.1b Growth rate with respect to dental development in* Pan troglodytes**

The data produced in this study included both Demirjian dental score and long-bone length. This provided a unique opportunity for comparison of two types of data that have never been collected before in a single dataset. Summary Demirjian dental score behaved effectively as a continuous variable and as such provided an equivalent measure to a ‘maturational clock.’ Linear regression of long-bone length as a function of dental maturity score for *Pan troglodytes* found the relationship to be significantly linear for all long-bones. The question remains as to how this relationship compares to that observed for growth rate relative to chronological time. It has been observed that chimpanzee growth relative to time does not demonstrate the delayed period of growth associated in humans with childhood (Bogin 1997). However, this does not necessarily imply that chimpanzee growth relative to time is necessarily linear. Chimpanzee growth appears slightly geometric until near the end of growth when there is a slowing down just prior to adulthood (Kimura and Hamada 1996, Leigh and Shea 1996, Shea 1981). A representation of this growth curve is presented in Figure 6.1.

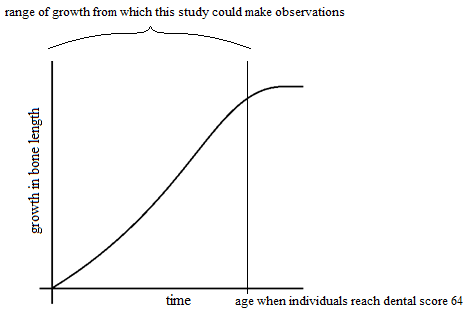
**Figure 6.1** Representation of a chimpanzee growth curve relative to time based on analysis in prior studies by Kimura and Hamada (1996), Leigh and Shea (1996).

There are two question raised in relation to this topic. First, the relationship between dental score and chronological time should be considered as this may go some way to explaining the linear relationships found when comparing long-bone length to dental score. Second, a consideration of what portion of the entire growth period was actually being measured by dental score must also be assessed as it has been found that growth relative to time in chimpanzees is non-linear for the entirety of the development. In this study it was found that growth continues after complete dental maturity (DS64) and this may include the tapering-off of growth observed in both chimpanzees and humans. In order to address this first question, the relationship between Kuykendall’s (1996) regression equation for 8 teeth and chronological time is considered. This relationship is demonstrated in Figure 6.2. The regression curve for Demirjian scores relative and chronological years has a slightly geometric slope.

**Figure 6.2** Reproduction of Kuykendall’s (1996) regression for dental score relative to chronological age.

Comparison of Figures 6.1 and 6.2 demonstrates that the shape of the curve for dental score relative to chronological time behaves with a slightly inverted curve compared to to that found for growth relative to chronological time. Leight and Shea (1996) provided parametric growth curves for chimpanzees but they did not provided a numeric regression equation for chimpanzee growth. No other studies have provided this information and it is likely that with the increasing segment early in growth and decreasing segment near the end of growth that a regression function for this curve would be a relatively complex polynomial. This makes direct comparison, certainly of the entire growth curve, unquantifiable. However, when considering the increasing segment early in growth, it may be suggested that the opposing effects of growth vs. time as opposed to dental score vs. time may counteract each other. This partially explains the much more linear relationship for comparisons of growth in long-bone length to dental score.

The second question that must be addressed is the effect of not having a dental reference for length data beyond DS64. It is possible that full dental maturity meant that observation ceased prior to the slow down in growth near complete maturation. The potential effect of this is demonstrated in Figure 6.3.



**Figure 6.3** Demonstration of the limitation of DS64 individuals for observing chimpanzee growth curves.

A number of long-bone epiphyses were observed to fuse beyond dental score and with this as evidence, it is likely that growth continued beyond the period observed by dental score in this study. There have been no studies of growth in long-bone length relative to chronological time that have also presented dental maturity data. Without age at death being known for the sample in the present study there are no means to determine how much of an effect the limitation of dental score has on the analysis of the data. However, it should be kept in mind that this later-stage slowing of growth only accounts for a small portion of the growth curve. Additionally, even if dental maturation did extend to or beyond the end of skeletal development there would be no means to assess if it would or would not slow in tandem with skeletal development, thereby maintaining a linear skeletal-dental relationship. Such an observation remains speculative and the present pattern of maturation must be accepted as it is. The result that dental score relative to growth in length of long-bones shows a high degree of linearity for the period of maturation observed is still very important. It implies that as a maturational ‘clock’ that dental mineralization provides a well-regulated reference. It may be questioned how well humans adhere to the principle that long-bone length is linearly related to dental score. It was noted in Chapter 3 that human and chimpanzee dental score regression curves relative to time demonstrated differences consistent with differences in growth pattern between the two species. This may imply that the same relationship between dental mineralization and skeletal development would be observed in humans. However, it has also been shown that there is an offset between skeletal and dental sequences in humans for the third molar, meaning that the period of total growth for human dental developmental is not directly analagous to chimpanzees. This makes direct comparison not technically valid as the same period of skeletal growth would not be observed.

***6.2.1c Growth rate with respect to dental development in* Pan paniscus**

As noted in Chapter 4, growth rate relative to dental development was not evaluated for *Pan paniscus* due to sample size limitations. However, with assumed consistency for dental development, as indicated by Boughner *et al*. (2012) and long-bone growth as indicated by Shea (1981), expectations should not have been different from the pattern observed in chimpanzees. To the extent possible given the limitations of the available data, the data for *Pan paniscus* appeared to confirm this trend. Thus, for comparisons of dental score to growth in length, this study has not expanded or brought forth any particularly new information relevant to developmental theory for this species. It has confirmed the results of past studies, notably Shea (1981) and found expected trends.

***6.2.1d Allometry and growth***

In Chapter 4, comparisons of log10-transformed intermembral indexes were made to results from Shea (1981). Some of the individuals were the same as those used by Shea including all of the *Pan paniscus* and *Pan troglodytes troglodytes* individuals, although his study did not include *Pan troglodytes schweinfurthii*. The analysis performed in the present study reproduced the log10-transform regression performed by Shea and determined that exactly the same trend was observed with the inclusion of a new sub-species (*Pan troglodytes schweinfurthii*). Limb length appears to remain isometrically scaled for all limbs during growth for both *Pan troglodytes* and *Pan paniscus*. Given that *Pan paniscus* has an older separation time from all sub-species of *Pan troglodytes* and Shea’s (1981) evidence suggested that *Pan paniscus* and *Pan troglodytes* shared the same pattern, it is not surprising that the sub-species of *Pan troglodytes* do not differ. All of Shea’s (1981) observations of limb segment growth have also held true for both species including the addition of *Pan troglodytes schweinfurthii*.

### Patterns of growth: analysis of sequences

The analysis of developmental sequence in this study focuses on epiphyseal fusion and the relationship between fusion events and dental development. This section will focus on *Pan troglodytes* as this is the *Pan* species from which the greater breadth of analysis was performed. Epiphyseal fusion sequence seriations will first be considered and the relevance of general trends discussed. Comparisons to humans as well as to general primate patterns will be made. For the second part of this analysis the relationship between skeletal and dental development in humans and chimpanzees will be compared and the implications of differences found discussed.

***6.2.2a Seriation of epiphyseal fusion events***

Analysis of chimpanzees

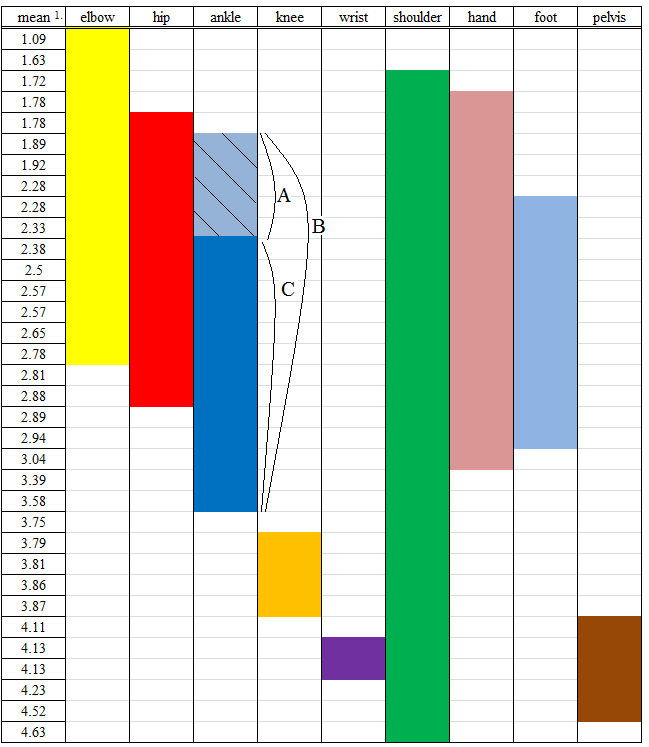
It Chapter 4 an attempt was made to distinguish sequence order in chimpanzees using both mean epiphyseal fusion score and contingency tables. The results of these procedures produced general patterns but there remained a high degree of overlap between epiphyses that fused closely in sequence. This pattern held true for both methods. Comparisons between males and females followed generally similar trends and comparison between the sexes did not determine any statistically significant differences overall.

With the present study being the first to attempt to seriate epiphyseal fusion events by any method, comparisons with past studies are not possible. It might be suggested that some general level of pattern comparison could be made with studies of epiphyseal fusion events done using known-age samples such as Bolter and Zihlman (2012), Kerley (1966) and Zihlman *et al*. (2007). Based on the estimated ages for fusion events produced in Chapter 4, it could be asserted that the results of this study agree with patterns found in these previous studies. However, with respect to confirming sequence of epiphyseal fusion, very little more can be said and this is because the ranges of estimated fusion timing from the known-age samples overlap with even less precision than do fusion events found in the present study. These studies also do not have as comprehensive of a list of epiphyses as those measured in the present study.

With this being said, a general consideration of pattern of epiphyseal fusion events may be considered with respect to fusion event groupings. Zihlman *et al.* (2007) noted that the pattern of fusion they observed in their Taï forest chimpanzees sample conforms to a previously observed pattern by Todd (1930), Schultz (1940, 1944), and Kerley (1966). The general sequence, from earliest to latest, was elbow, hip, ankle, knee, wrist, and shoulder. It was also noted that the upper limb has a common pattern of fusion for all primates: first, elbow then wrist followed by shoulder (Shigehara 1980). It was expected that the chimpanzees in the current study would demonstrate the same pattern. Not only were these regions evaluated in the present study but other fusion centres in the hands, feet, and the pelvis were considered. From either the sequence of mid-fusion mean epiphyseal fusion values or modular sequences observed in Chapter 5, it is possible to group these epiphyseal fusion events as shown in Figures 6.4 and 6.5 for males and females. The region between talar epiphyseal fusion and calcaneal epiphyseal fusion is distinguished in these figures due to inconsistencies in values that will be discussed. Modular sequence may also be used and are shown in Figures 6.6 and 6.7. Table 6.1 provides a classification of epiphysis groupings.

**Table 6.1** Epiphysis classification for regional comparison of epiphyses.

|  |  |
| --- | --- |
| **shoulder:** | **elbow:** |
| proximal humerus | distal humerus |
| coracoid | humeral medial epicondyle |
| sub-coracoid and glenoid | proximal radius |
| medial border of scapula | proximal ulna |
| **pelvis:** | **hip:** |
| iliac crest | geater/lesser trochanter |
| ischial epiphysis | femoral head |
|  | acetabulum |
| **hand:** | **ankle:** |
| base of metacarpal 1 | distal talus |
| heads of metacarpals 2-5 | distal fibula |
| distal phalanges | calcaneus |
| proximal and middle phalanges | talus |
| **foot:** | **knee:** |
| base of metatarsal 1 | proximal tibia |
| heads of metatarsals 2-5 | proximal fibula |
| distal phalanges | distal femur |
| proximal phalanges | **wrist:** |
| middle phalanges | distal radius |
|  | distal ulna |



1. Mean epiphyseal fusion value

\*The earliest mean mid-fusion event for a region forms the earliest mid-fusion point on each bar. The latest mid-fusion point indicates the end of each bar. Mean epiphyseal fusion values run down the left-hand column.

\*It should be noted that the acetabulum is included in hip epiphyseal fusion as opposed to the pelvis.

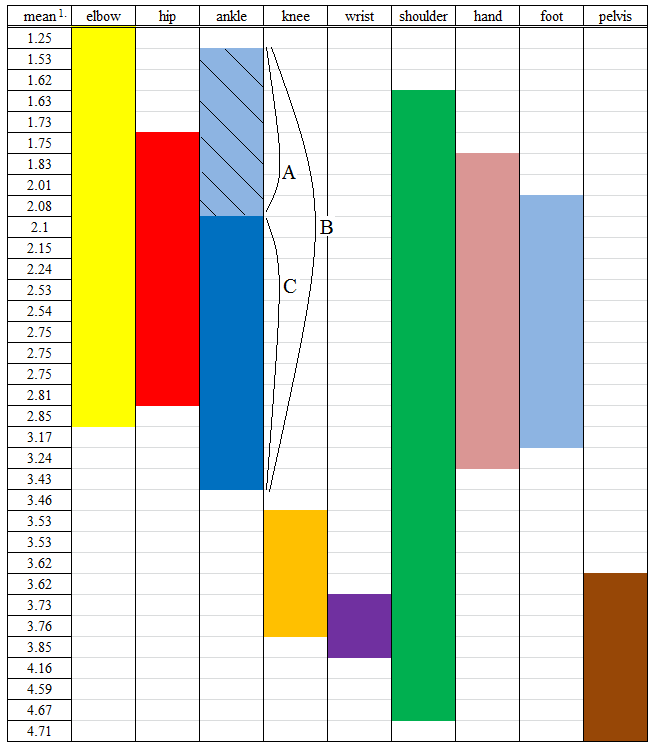
\*Colour blocks indicate at which mean epiphyseal fusion values epiphyses in these groups appear to be fusing.

A: range between talar epiphyseal fusion and calcaneal fusion value

B: the entire range of of ankle fusion including the talus

C: the range of ankle fusion excluding the talus

**Figure 6.4** Grouping of epiphyseal fusion events by region for *Pan troglodytes* females ordered by mean epiphyseal fusion values.



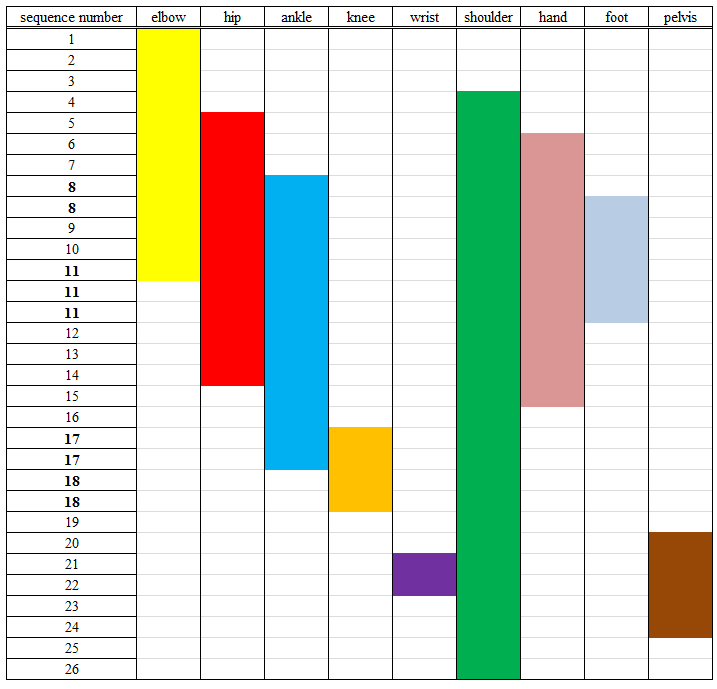
1. Mean epiphyseal fusion value

A: range between talar epiphyseal fusion and calcaneal fusion value

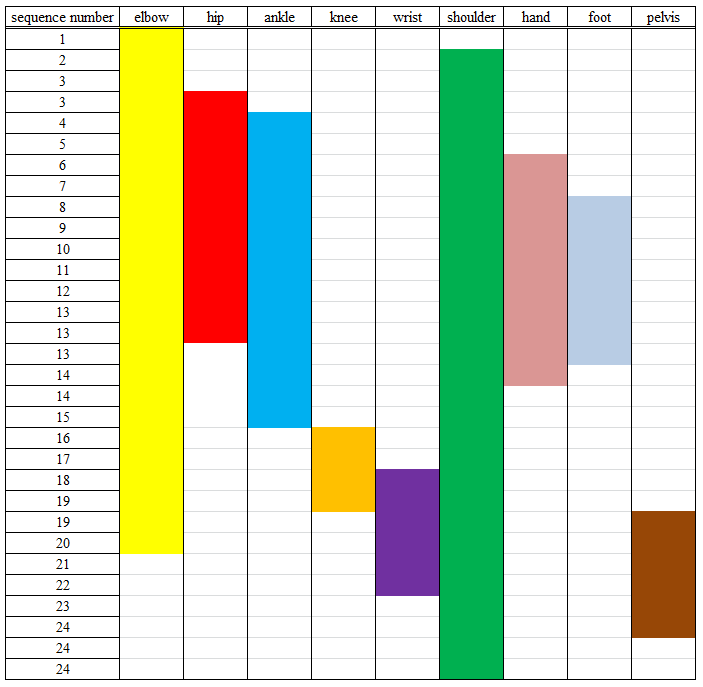
B: the entire range of of ankle fusion including the talus

C: the range of ankle fusion excluding the talus

**Figure 6.5** Grouping of epiphyseal fusion events by region for *Pan troglodytes* males ordered by mean epiphyseal fusion values.

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**Figure 6.6** Grouping of epiphyseal fusion events by region for *Pan troglodytes* females using modular sequence.

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**Figure 6.7** Grouping of epiphyseal fusion events by region for *Pan troglodytes* males using modular sequence.

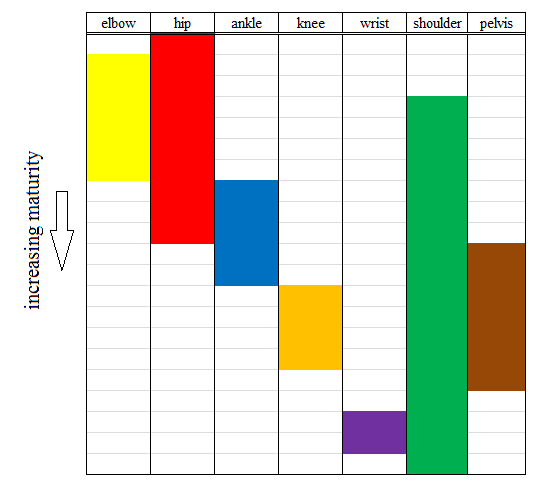
The ranges of fusion events based on mean epiphyseal fusion value (defined in section 4.2.2) followed the progression of elbow, hip, ankle, knee, and wrist for *Pan troglodytes* females, but not males. If the talus is excluded, males agree with the pattern only for the first fusion centres observed for the ankle. Previous studies (Bolter and Zihlman 2012, Kerley 1966, Zihlman *et al*. 2007) did not evaluate the talar epiphysis and based on present study there may be a difference between males and females. However, observations of mid-fusion events in this study were rare (there were only three observations for females and one for males) and this difference cannot therefore be shown to be statistically applicable for any testing. In addition, the difference between the last epiphysis of the elbow and the last epiphysis of the hip to fuse in males is not large (2.81 vs. 2.85 in mean epiphyseal fusion score). It could be suggested that the general patterns for both male and female *Pan troglodytes* agree with the general trend for primates discussed by Zihlman *et al*. (2007) with some minor exceptions. Shoulder epiphyses appear to fuse over a wide range of time but when considered by individual epiphyses, most fuse quite late in development and it is only the much earlier fusion of the coracoid that drives the initiation of the shoulder range quite early. Results from Zihlman *et al.* (2007) also placed the coracoid quite early in the fusion sequence and in doing so made their statement slightly confused without clarifying if the agreement was with the last elements to fuse or the overall range If the coracoid was removed, both their statement and results would agree with the present study. Kerley (1966) only recorded the coracoid as partially fused by age 9 due to limited data. Schutz’s (1940, 1944) and Todd’s (1930) data were equally limited. As such, these are likely general patterns of observation. In this context this study agrees with these patterns and is able to provide data for more epiphyses.

Modular fusion sequences confirm the patterning found using mean epiphyseal fusion value in this context. The only possibly exception was the elbow in males. This was caused by a deviated humeral medial epicondyle. It is entirely likely that this was the result of smaller sample size and does not represent a deviation in actual pattern. Both the patterns observed using mean epiphyseal fusion value and dental score would confirm this.

Comparing chimpanzees and humans

The general conclusion that may be brought forward from Chapter 5 where chimpanzee and human fusion sequences (as determined by Schaefer and Black 2007) were compared was that these species follow effectively the same pattern of maturation. This comes with the caveat that the level of overlap between closely fusing epiphyses may have obscured small differences. The approach taken in this comparison was that if the ranges could be distinguished statistically then it could be asserted without question that the sequences were different. The approach taken in this study was only able to determine broad trends of difference and was not able to distinguish closely-fusing epiphyses.

Epiphyses listed in Schaefer and Black’s (2007) modular sequence may be grouped using the same system (elbow, hip, ankle, knee, wrist, shoulder) referred to by Zihlman *et al*. (2007). This is demonstrated in Figure 6.8. It should be noted that Schaefer and Black (2007) did not include hand and foot fusion centres. Notably, the calcaneus and the talus were not included in their sequence. It is observed that the pattern of grouped epiphyses is essentially analgous to the pattern found for chimpanzees. Pelvis epiphyses appear to fuse somewhat earlier in chimpanzees than humans. This differences is caused mainly by a shift in position of the iliac crest. As was demonstrated in Chapter 5, this epiphysis showed a range of variation that heavily overlapped other late-fusing epiphyses. As such, it is not possible to prove that there exists an actual difference for this region. As a general statement, the regional pattern of fusion events is largely consistent between chimpanzees and humans.



**Figure 6.8** Regional pattern for humans derived from the modular pattern found in Schaefer and Black (2007).

***6.2.2b Sequence of dental development relative to skeletal development***

In Chapter 5 the relationship between epiphyseal fusion sequences and dental mineralization sequence was explored. There were two main conclusions from this analysis that are relevant for disussion. First, despite differences in mineralization sequence between humans and chimpanzees, the timing of first apical closure of any tooth happens after the mean epiphyseal fusion values of 8 mid-fusion events. Due to variation in sequence order as discussed in section 6.2.2a, these were not necessarily the same fusion events, although the very earliest ones such as the distal humerus and humeral medial epicondyle were always present. The second conclusion was that human third molar mineralization is delayed relative to late-fusing epiphyseal fusion events in humans. In chimpanzees complete third molar mineralization occurs close in time with the second molar and as a consequence many more epiphyseal fusion events happen after complete dental maturity. Prior studies have not addressed this type of comparison. This is likely consequent of the larger ranges of estimate times for fusion in chimpanzee skeletal maturity found in Bolter and Zihlman (2012), Kerley (1966) and Zihlman *et al*. (2007).

The next step in this analysis is to consider what the delay in third molar maturation in humans represents for developmental theory. It has been found that epiphyseal fusion patterning is effectively indistinguishable between humans and chimpanzees. Despite the rate at which these events mature relative to chronological time differing, the pattern in which they mature is consistent. On the other hand, dental development does not scale proportionately for the entire period of growth when comparing chimpanzees to humans with the third molar being the key contributor to this difference. A consideration of other primates is useful in this context. Smith *et al.* (1994) provided a list of first and last tooth emergence data for many different primate species. Tooth emergence is not a direct analogue for mineralization, but the two patterns are closely linked. Primates vary in the duration of growth in terms of chronological years, but the timing from first to last emergence stays proportionately constant. Humans dental development has long been known to be an exception to this rule. Shultz (1960) compared lemurs, macaques, gibbons, and chimpanzees to humans, finding humans to have and extended period of third molar maturation compared to all of these other species.

It may be concluded that human dental development is more deviant from a typical primate pattern than is skeletal development with the third molar shift appearing exclusively in humans. This differences does not fit neatly within the concepts of the neoteny-hypermorphosis debate. The relative delay of third molar maturity in humans is a temporary retention of a sub-adult feature but with full maturity eventually occuring, it may be better described as a more arbitrary difference in pattern.

***6.2.2c Separating growth rates and patterns***

At this point in discussion is it necessary to summarize what has presently been determined regarding growth rate and pattern. The following observations have been made for the chimpanzees in this study:

1. Growth rates are constant for all long bones relative to dental score for the period of growth observed in this study.
2. Growth rates relative to chronological time for humans and chimpanzees are not the same and as such sequences of events cannot be scaled by this measure.
3. Dental mineralization patterns are not the same between chimpanzees and humans and thus are not a valid means to directly compare other developmental parameters. In addition, the fact that dental maturity is reached before skeletal maturity is also limiting.
4. As a result of points 1.2. and 3. above, neither dental mineralization nor chronological time provide a compatible reference for integrating both growth and fusion events between chimpanzees and humans.
5. The sequence of epiphyseal fusion is not discernably different between humans and chimpanzees.
6. Fusion events occur at the same proportion of total growth in length of bone for both chimpanzees and humans.

In Chapter 5 epiphyseal fusion as a proportion of growth in length for long-bones was considered. It was found that there were no differences between humans and chimpanzees with respect to the timing of epiphyseal fusion events as a proportion of growth in length for each bone. This was a novel approach because it did not depend on time or dental score. The analysis suggests that when growth rates are removed from comparison by looking at the systems as percentages of growth that chimpanzees and humans demonstrate exactly the same general pattern. Fusion event scheduling as a proportion of final adult size is consistent between species. The implication of this is that skeletal development in humans and chimpanzees varies only in terms of the rate of growth relative to time. Chimpanzees and humans clearly differ in terms of allometry, but the proportionate amounts of time during which each bone grows is the same. The femur in humans, for example, is proportionately longer when compared to other bones than it is for chimpanzees. This bone does not achieve its greater length in humans by growing for a longer period of developmental time. That proportion of time remains constant. The bone simply gets longer at a faster rate by adding more material per unit of maturational time. This concept, coupled with the knowledge that sequence patterns are not distinguishable between *Pan* and *Homo* and that intermembral growth rates are consistent (Shea 1981) implies again that the morphological differences between these species cannot be defined by the simple concepts of neoteny-hypermorphosis debate.

A more abstract way of looking at this is to consider human and chimpanzee skeletal development as a standard ‘ape’ pattern for development. There is a maturational time clock that has maturational time units. Developmental events such as epiphyseal fusion are fixed relative to maturational time units. Maturational time units may or may not linearly relate to chronological time. Humans and chimpanzee had different ratios of long-bone lengths and these ratios are present from birth and simply scaled up to adult form. The only way that it is possible to achieve a difference in a length between two species is for more length to be added per unit time of the maturational clock. The rate of addition of length is contant. If a chimpanzee adds 5 units of length to the length of a femur a human may add 7, but the maturational time unit for the addition of those length units is the same. Initiation and fusion of epiphyseal events must remain on schedule in terms of maturational time units.

Bonobos

Without sufficient data from bonobos to complete the analysis of proportionate growth in length, conclusions with respect to bonobos are less certain. None of the data presented with respect to bonobos up to this point suggests that they differ markedly from chimpanzees but beyond this general assertion no firm conclusions can be made.

### Skeletal development relative to sexual maturity

In the analysis of developmental theory one remaining point must be considered. Two of the terms of heterochrony outlined in Chapter 2 pertained to sexual maturity. Specifically, progensis was the achievement of sexual maturity prior to attaining adult form and hypermorphsis was the achievement of adult form prior to sexual maturity (Rice 1997). Sexual maturity is defined as the age at which an individuals become able to reproduce (Harvey and Clutton-Brock 1985). This study did not directly measure sexual maturity in chimpanzees and bonobos. However, the age at which sexual maturity is attained is known relative to chronological age. With new information for the estimated timing of skeletal maturation relative to chronological years available in this study, the terms of progensis and hypermorphosis should be re-considered.

Female age at first birth is a limiting factor for reproduction and it is females which this section will focus on. When an individuals is able to reproduce and when they actually begin to bear offspring are not necessarily concurrent events. In humans the difference between the time of first birth and the age of sexual maturity varies between different societies and there are often non-biological cultural reasons for these shifts. Menarche in humans is well-document and it begins to occur somewhere between 12-14 years of age (Surbey 1990). It has been suggested that stress conditions may actually drive menarche earlier rather than later in humans (Chisholm 2005). However, the point at which human begin reproduction is much later in humans. Humans only reach completion of secondary sexual characteristics by the age of 17 (Cameron 2006). In hunter-gatherer societies it has been found that humans do not typically begin reproduction before 18-20 (Hill and Kaplan 1999). These societies appear to represent some of the earliest reproduction ages, with many human societies further delaying the event as a consequence of social and cultural pressures.

It has been reported that wild chimpanzees undergo menarche by 10 to 11 years (Boesche and Boesch-Achermann 2000, Nishida *et al.* 2003) while captives have been recorded as undergoing menarche as early as 8.5 years (Sugiyama 2004). These differences again invoke the debate as to whether wild animals are stressed relative to their captive counterparts. It is not clear if this is true with respect to attainment of sexual maturity. The captive data is much better controlled for observation of individuals and sample size. Menarche by 10 years of age will be used in this discussion as it is a value approximated by the majority of studies. Chimpanzees typically experience their first birth by 13-15 years (Hill and Kaplan 1999).

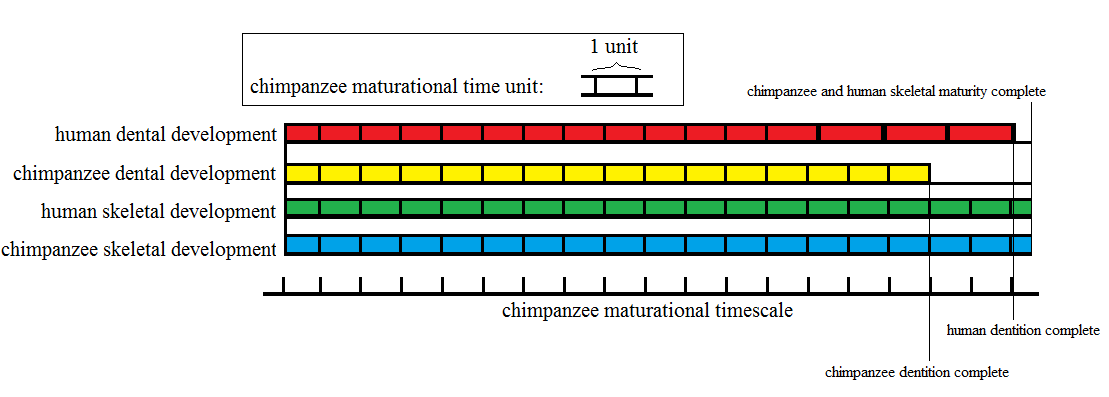
Given the estimates ages in this study, by the age of 10 in chimpanzees and by the ages of 12-14 in humans, the number of fusion events that have occurred and the state of dental maturity is effectively the same. This suggests that menarche is occuring at essentially the same point of a maturational sequence irrespective of time. When it comes to first birth, which in chimpanzees is between 13-15 and humans between 18-20, it appear that humans and chimpanzees both begin reproduction very near the end of skeletal maturation. The interval between these two events is particularly larger in humans, and is consistent with the observed extended period of growth known as adolecence (Bogin 1997). What is inferred from these data is that humans are following the same maturational pattern but are simply modifying the time at which these events occur. This means that humans are neither progenetic or hypermorphic as the timing of sexual maturation remains analagous between the two species in terms of skeletal maturation.

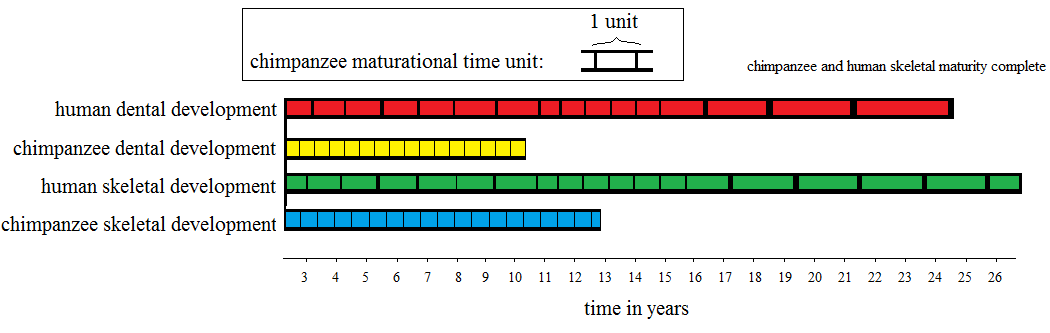
### General conclusions with respect to growth theory

Chimpanzees and humans appear to share the same sequence of fusion events. They do not share the same dental mineralization sequences. Comparing dental sequences with skeletal sequences suggests two things. Humans experience their first fully mature adult tooth at the same maturational time as chimpanzees relative to epiphyseal fusion events. However, the human third molar matures much later relative to epiphyseal fusion sequences. With respect to growth, humans and chimpanzees both appear to scale allometrically and experience fusion events at the same proportions of growth in length. Growth rates for chimpanzees relative to dental mineralization are effectively linear. This may not necessarily be true for humans given the complexity introduced by the extended period of dental mineralization. No human studies have directly compared long-bone length to dental score. A comparison between chimpanzees and humans would not use the same frame of reference due to the difference in duration of dental development relative to the entire period of growth.

For bonobos, far less may be directly concluded due to the limitation of sample size preventing many of the analyses that were used to develop these conclusions for chimpanzees. What has been demonstrated for *Pan paniscus* is that epiphyseal fusion sequences are generally analagous relative to dental development between *Pan paniscus* and *Pan troglodytes*. Growth rates are also in agreement between the two species. It is likely that bonobos share as very similar pattern of skeletal growth and development with chimpanzees.

Figures 6.9 and 6.10 provide a visualisation of developmental pattern differences between chimpanzees and humans using chimpanzees as a reference. Figure 6.9 illustrates how development in both of these species appear relative to the ‘maturational clock’ with chimpanzees setting the hypothetical units of this clock. Figure 6.10 shows how these species looks using chimpanzee maturational time units compared to chronological time. It is worth noting that the visible differences between the two species become more marked when looked at in terms of chronological years.

**Figure 6.9** Visualization of chimpanzees and humans using hypothetical chimpanzee maturational time units.

**Figure 6.10** Visualization of chimpanzees and humans development as compared to chronological years using chimpanzee maturational time units.

One final note regarding sequences should be considered within the context of figure 6.9. It should be recalled that King’s (2004) used discriminant function analysis to group different primates based on skeletal fusion and dental development. He noted that there was a distinct ape grouping for pattern of maturation but that chimpanzees appeared distinct from gorillas. It remains to be seen how the inclusion of human sequences into the same discriminant function analysis might also demonstrate grouping with offsets of sequences now known to exist.

## Application to fossil hominids

The study of sub-adult fossil hominids has been limited to few individuals. Those that have been found have ranged over large periods of geologic time and are often classified as different species. Examples include specimens such as *Australopithecus sediba* (Berger *et al.* 2010), the Dikika *Australopithecus afarensis* (Alemseged *et al.* 2006), the Nariokotome *Homo ergaster* (Clegg and Aiello 1999, Dean and Smith 2009, Smith 2004 among others), and more recent sub-adults neanderthals (Dean *et al.* 1986). Many of these specimens have been moderately to substantially incomplete with only a small number of epiphyses and/or teeth present. The Nariokotome *Homo ergaster* is an exception to this and has been intensively studied (Smith 2004, Walker and Leakey 1993). Even though the specimen is not fully complete it provides the most comprehensive sample of epiphyseal fusion sites from one individual compared with any other fossil specimen. A brief analysis of this individual is warranted and the information brought forth by this study placed in context of such analysis.

By virtue of the fact that epiphyseal fusion sequence is not discernably different between chimpanzees and humans, it would be reasonable to infer that this feature was likely the same for fossil human ancestors as well. Ruling out deviation and subsequent recoverging of developmental patterns at some point in evolutionary history will never be possible but given the level of concordance between chimpanzees, bonobos, and humans, such fluctuations would seem improbable. The consistency of basic sequences known for apes such as the elbow-hip-ankle sequence mentioned in section 6.2 also provides grounds to argue against deviation and reconverging of patterns. It suggests that fusion patterns may be generally shared among many primate genera.

The implication of this is that any prior study assessing epiphyseal fusion using human models was not misinformed about fusion sequence. Past studies such as Smith (2004) finding that this individual falls within the range of normal human variation in sequence were likely correct. It is when an assessment of chronological age has been attempted that problems have arisen (Graves *et al*. 2010). The two problematic variables are dental development and growth rate. Growth rate cannot be practically be measured in fossils and any assumption that epiphyseal fusion state relates directly to chronological years cannot be assumed to be correct. Dental development also does not produce the same chronological age estimation, as has been noted in the past (Dean and Smith 2009, Smith 2004). Additionally, there are sequence differences known for chimpanzee teeth when compared to humans (Kuykendall 1996). Therefore if chronological ages are sought, they must be found by other means such as from dental histology. For example, Dean and Lucas (2009) determined age for the Nariokotome specimen using incremental markings in dental enamel finding that the individual was younger than expected when human criteria were used. They suggested that the Nariokotome specimen fit closer with the expected ages for mineralization predicted by an ape model rather than human one.

The Nariokotome *Homo ergaster* specimen was described in detail by Walker and Leakey (1993) and Smith (1993). Unfused epiphyses included the triradiate and the proximal and distal ends of most long-bones. The distal humerus had commenced fusion. Dental emergence and radiographic data were available for the dentition. From these radiographs a Demirjian score could be assigned for I1 to M2 reading, in that order, 8,7,6,6,6,7,5. This means that the first and only tooth to have completed mineralization was the first incisor. The dental mineralization sequence for this individual was clearly more consistent with the human sequence and has been analysed in prior studies. As such this analysis simply considers epiphyseal fusion sequences in relation to mineralization of the first adult tooth, as described in Chapter 5. This study has shown that fusion sequences in humans and chimpanzees do not differ at this point of maturation. Only a couple phalanges from the hand were present and no foot or ankle bones were present at all, making counting the number of epiphyses prior to the completion of first complete tooth mineralization impossible. This limits any further direct application of the results of this study beyond any conclusions reached in prior studies.

The finding that humans and chimpanzees share the same epiphyseal fusion pattern allows for a re-evaluation of the conclusions of some previous studies. Clegg and Aiello (1999) suggested that the Nariokotome specimen did not deviate from a human pattern of development. This study supports this assertion by suggesting that the shared pattern between *Pan* and *Homo* has deeper ancestry than the split between the two genera and thus occurred prior to the appearance of *Homo ergaster*. Smith’s (2004) comparison of the Nariokotome specimen to a modern human sample concluded that it could be human but deviated from normal human development. This assertion of deviation was based more on estimation of body size for predicted age and enamel formation. Within the context of the skeletal data, the two studies actually agree and with the knowledge that ape sequences at this stage of growth converge with humans, this result would have been expected.

## Suggestions for future study/limitations of present research

The present study provides a great deal of new information about growth and development in *Pan*, However, there are clearly several limitations that future research may help to resolve. The most obvious limitation is DS64 and the problem this presented for estimation of chronological age for fusion of later epiphyses. Use of a known-age sample may be the only solution for this. Analysis of *Pan paniscus* was limited by sample size and a larger sample would permit many of the analyses performed in this study on *Pan troglodytes* to be done in tandem for *Pan paniscus*. Conducting similar research using more distantly-related species may also serve to compliment the assessment of developmental theory presented in this work.

# Concluding Remarks

Growth and development in *Pan* has been analysed by the study of epiphyseal fusion, dental development, and long-bone growth in a sample of 177 *Pan troglodytes* and 37 *Pan paniscus* specimens found in museum collections. The types of analyses performed in this study were done with the objectives of informing both a theoretical understanding of human growth and for refinement of growth standards applicable to the study of fossil hominids. The relationship between maturational events and growth rates was considered as was the relationship between dental and skeletal sequences. It was found that chimpanzees and humans share effectively the same pattern of skeletal fusion sequences. When groupings of epiphyses were considered, humans were found to follow a similar pattern to other primates of elbow-hip-ankle-knee, as outlined by Zihlman *et al*. (2007). Comparison of dental sequences to epiphyseal fusion sequences determined that humans are unusual among primates with third molar mineralization completing much closer to the terminal point of skeletal maturation. Comparisons of fusion events relative to long-bone growth have indicated that the differences in allometry between *Pan* and *Homo* are the result of different linear rates of individual long-bone growth and do not represent the effects of sequence changes. There are marked differences in both growth rate and duration of growth when *Pan* and *Homo* are compared. These differing growth curves may obscure comparisons of maturational event patterns and lead to determination of differences between species that may not actually exist. In terms of application to fossil hominids, the results of this study suggest that the sequence of epiphyseal fusion events should be expected to be the same. Differences in patterning between dental mineralization and skeletal fusion were identified between *Pan* and *Homo*. This has implications for the assessment of either fossil or extant species. Determining state of maturity through either dental or skeletal systems must take into account how species differ.

It was not possible to complete as many analyses for bonobo skeletal development as were done for chimpanzees due to the more limited sample size for this species. For the analyses that could be completed, it was found that bonobos did not differ from chimpanzees, suggesting a general *Pan* pattern of growth. Further study with larger sample sizes will help provide further clarity with respect to developmental parameters in this species.

***References***

Acheson, R.M. 1954. A method for assessing skeletal maturity from radiographs: A report from the Oxford Child Health Survey. *Journal of Anatomy* 88(4): 498-508.

Acheson, R.M. 1957. The Oxford method of assessing skeletal maturity. *Clinical Orthopaedics and Related Research* 10: 19-39.

Albert, A.M. Greene, D.L. 1999. Bilateral asymmetry in skeletal growth and maturation as an indicator of environmental stress. *American Journal of Physical Anthropology* 110(3): 341-349.

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

Almond, D. Edlund, L. 2007. Triver-Willard at birth and one year: evidence from US natality data 1983-2001. *Proceedings of the Royal Society B* 274(1624): 2491-2496.

Anemone, R.L. Mooney, M.P. Siegel, M.I. 1996. Longitudinal study of dental development in chimpanzees of known chronological age: implications for understanding the age at death for Plio-Pleistocene hominids. *American Journal of Physical Anthropology* 99(1): 119-133.

Anemone, R.L. Watts, E.S. Swindler, D.R. 1991. Dental development of known-age chimpanzees, Pan troglodytes (primates, pongidae). *American Journal of Physical Anthropology* 86(2): 229-241.

Ashizawa, K. Asami, T. Anzo, M. Matsuo, N. Matsuoka, H. Murata, M. Ohtsuki, F. Satoh, M. Tanaka, H. Tsukagoshi, K. Tsukagoshi, T. 1996. Standard RUS skeletal maturation of Tokyo children. *Annals of Human Biology* 23(6): 457-469.

Auerbach, B.M. Ruff, C.B. 2006. Limb bone bilateral asymmetry: variability and commonality among modern humans. *Journal of Human Evolution* 50(2): 203–218.

Barros, A. Soligo, C. 2013. Bilateral Asymmetry of Humeral Torsion andLength in African Apes and Humans. *Folia Primatologica* 84(3-5): 220-238.

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

Berger, L.R. de Ruiter, D.J. Churchill, S.E. Schmid, P. Carlson, K.J. Dirks, P.H.G.M. Kibii, J. 2010. *Australopithecus sediba*: A New Species of *Homo*-Like Australopith from South Africa. *Science* 5975(328): 195-204.

Bermúdez De Castro, J.M. Nicolas, M.E. 1995. Posterior dental size reduction in hominids: The Atapuerca evidence. *American Journal of Physical Anthropology* 96(4): 335–356.

Beunen. G, Lefevre. J, Ostyn. M, Renson. R, Simons. J, Van Gerven. D. 1990. Skeletal maturity in Belgian youths assessed by the Tanner-Whitehouse method (TW2). *Annals of Human Biology* 17(5): 355–376.

Beynon, A.D. Dean, M.C. Reid D.J. 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. *American Journal of Physical Anthropology* 86(2): 189-203.

Bininda-Emonds, O. R. P. Jeffery, J. E. Coates, M. I. Richardson, M. K. 2002. From Haeckel to event-pairing: the evolution of developmental sequences. *Theory Biosciences* 121: 297–320.

Bininda-Emonds, O.R.P. Jeffrey, J.E. Richardson, M.K. 2004. Is Sequence Heterochrony an Important Evolutionary Mechanism in Mammals? *Journal of Mammalian Evolution* 10(4): 335-361.

Bisgard, J.D. Bisgard, M.E. 1935. Longitudinal growth of long bones. *Archives of Surgery* 31(4): 568-578.

Blomquist, G.E. 2009. Brief Communication: Methods of Sequence Heterochrony for Describing Modular Developmental Changes in Human Evolution. *American Journal of Physical Anthropology* 138(2): 231-238.

Bock, R.D. Thissen, D. 1980. *Statistical problems of fitting individual growth curves*. In Johnston, F.E. Roche, A.F. Susanne, C. (eds.) Human Physical Growth and Maturation, Methodologies and Factors. Plenum: New York. pp. 265–290.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai Forest: behavioural ecology and evolution. New York: Oxford University Press. p.316.

Bogin, B.A. 1988. *Patterns of Human Growth*. Cambridge University Press: Cambridge.

Bogin, B.A. 1990. The evolution of human childhood. *BioScience* 40(1): 16–25.

Bogin, B.A. 1991. Measurement of growth variability and environmental quality in Guatemalan children. *Annals of Human Biology* 18(4): 285-294.

Bogin, B.A. 1997. Evolutionary hypotheses for human childhood. *American Journal of Physical Anthropology* 104(S25): 63-89.

Bogin, B.A. 1999a. *Patterns of Human Growth* 2nd Ed. Cambridge University Press, Cambridge.

Bogin, B.A. 1999b. Evolutionary Perspective on Human Growth. *Annual Review of Anthropology* 28: 109-153.

Bogin, B.A. MacVean, R.B. 1983. The relationship of socioeconomic status and sex to body size, skeletal maturation, and cognitive status of Guatemala City schoolchildren. *Child Development* 54(1): 115–128.

Bogin, B.A. Sullivan, T. Hauspie, R. MacVean, R.B. 1989. Longitudinal growth in height, weight, and bone age of Guatemala Latino and Indian schoolchildren. *American Journal of Human Biology* 1(1): 103–113.

Bogin, B.A. Smith, B.H. 1996. Evolution of the Human Life Cycle. American Journal of Human Biology 8(6): 703-716.

Bolter, D.R. 2011. A Comparative Study of Growth Patterns in Crested Langurs and Ververt Monkeys. *Anatomy Research International* Article ID 948671, 12 pages doi:10.1155/2011/948671.

Bolter, D.R. Zihlman, A.L. 2003. Morphometric analysis in wild-collected ververt monkeys (*Cercopithecus aethiops*) with implications for growth patterns in Old World monkeys, apes, and humans. *Journal of Zoology* 260(1): 99-110.

Bolter, D.R. Zihlman, A.L. 2011. Brief communication: Dental development timing in captive *Pan paniscus* with comparisons to *Pan troglodytes*. *American Journal of Physical Anthropology* 145(4) 647–652.

Bolter, D.R. Zihlman, A.L. 2012. Skeletal development in *Pan paniscus* with comparisons to *Pan troglodytes. American Journal of Physical Anthropology* 147(4): 629–636.

Boughner, J.C. Dean, M.C. 2004. Does space in the jaw inﬂuence the timing of molar crown initiation? A model using baboons (*Papio anubis*) and great apes (*Pan troglodytes*, *Pan paniscus*). *Journal of Human Evolution* 46(3): 253-277.

Boughner, J.C. & Dean, M.C. 2008. Mandibular Shape, Ontogeny and Dental Development in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*). *Evolutionary Biology* 35(4): 296 -308.

Boughner, J.C. Dean, M.C. Wilgenbusch, C.S. 2012. Permanent tooth mineralization in bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*). American Journal of Physical Anthropology 149(4): 560–571.

Braga, J. Heuze, Y. 2007. *Quantifying variation in human dental development sequences: An EVO-DEVO perspective*. Bailey, S.E. and Hublin J.J. (eds.) Dental Perspectives on Human Evolution. Springer, The Netherlands. pp.247-261.

Bramblett, C.A. 1969. Non-metric skeletal age changes in the Darajani baboon*. American Journal of Physical Anthropology* 30(2): 161-171.

Brodeur, A.E. Silberstein, M.J. and Graviss, E.R. 1981. *Radiology of the Pediatric Elbow.* G.K. Hall: Boston.

Bufill, E. Agustí, J. Blesa, R. 2011. Human neoteny revisited: The case of synaptic plasticity. *American Journal of Human Biology* 23(6): 729–739.

Byers, S. Moore, A.J. Byard, R.W. Fazzalari, N.L. 2000. Quantitative Histomorphometric Analysis of the Human Growth Plate From Birth to Adolescence. *Bone* 27(4): 495-501.

Calcagno, J.M. Gibson, K.R. 1988. Human dental reduction: Natural selection or the probable mutation effect. *American Journal of Physical Anthropology* 77(4): 505–517.

Cameron, N. 2006. *Assessment of Maturation*. In: Human Growth and Development. Cameron, N. ed. Academic Press, New York. pp. 363-382.

Cardoso, H.F.V. 2007. Environmental effects on skeletal versus dental development: Using a documented subadult skeletal sample to test a basic assumption in human osteological research. *American Journal of Physical Anthropology* 132(2): 223-233.

Cardoso, H.F.V. 2008. Epiphyseal union at the innominate and lower limb in a modern Portuguese skeletal sample, and age estimation in adolescent and young adult male and female skeletons. *American Journal of Physical Anthropology* 135(2): 161-170.

Chaillet, N. Demirjian A. 2004. Dental maturity in South France: A comparison between Demirjian's method and polynomial functions. *Journal of Forensic Sciences* 49(5): 1059-1066.

Chia, D.J. Ono, M. Woelfle, J. Schlesinger-Massart, M. Jiang, H. Rotwein, P. 2006. Characterization of Distinct Stat5b Binding Sites That Mediate Growth Hormone-stimulated IGF-I Gene Transcription. *The Journal of Biological Chemistry* 281: 3190-3197.

Chisholm, J.S. Quinlivan, J.A. Petersen, R.W. Coall, D.A. 2005. Early stress predicts age at menarche and first birth, adult attachment, and expected lifespan. *Human Nature* 16(3): 233-265.

Cheverud, J.M. 1981. Epiphyseal union and dental eruption in *Macaca mullata*. *The American Journal of Physical Anthropology* 56(2): 157-167.

Clegg, M. Aiello, L.C. 1999. A comparison of the Nariokotome *Homo erectus* with juveniles from a modern human population. *American Journal of Physical Anthropology* 110(1): 81–93.

Cobb, S. O’Higgins, P. 2007. The ontogeny of sexual dimorphism in the facial skeleton of the African apes. *Journal of Human Evolution* 53(2): 176-190.

Cockshott, W.P. Park, W,M, 1983. Observer variation in skeletal radiology. *Skeletal Radiology* 10: 86-90.

Coe, C.L. Connolly, A.C. Kraemer, H.C. Levine, S. 1979. Reproductive development of behavior of captive female chimpanzee. *Primates* 23(4): 393-405.

Colbert, M.W. Rowe, T. 2008. Ontogenetic Sequence Analysis: Using Parsimony to Characterize Developmental Sequences and Sequence Polymorphism. *Journal of Experimental Zoology* 310B(5): 398-416.

Conroy, G.C. Kuykendall, K. 1995. Paleopediatrics: Or when did human infants really become human? *American Journal of Physical Anthropology* 98(2): 121-131.

Conroy, G.C. Mahoney, C.J. 1991. Mixed longitudinal study of dental emergence in the chimpanzee, *Pan troglodytes* (primates, pongidae). *American Journal of Physical Anthropology* 86(2): 243–254.

Conroy, G.C. Vannier, M.W. 1987. Dental Development of the Taung skull from computerized tomography. *Nature* 329(6140): 625-627.

Coolidge, H.J. 1933. *Pan paniscus*: Pygmy chimpanzee from south of the Congo River. *American Journals of Physical Anthropology* 18(1): 1-59.

Coolidge, H.J. Shea, B.T. 1982. External Body Dimensions of *Pan paniscus* and *Pan troglodytes* Chimpanzees. *Primates* 23(2): 245-251.

Corp, N. Byrne, R.W. 2003. Sex difference in chimpanzee handedness. *American Journal of Physical Anthropology* 123(1): 62-68.

Coqueugniot, H. Weaver, T. 2007. Infracranial maturation in the skeletal collection from Coimbra, Portugal: New aging standards for epiphyseal union. *American Journal of Physical Anthropology* 134(3): 424-437.

Cundy, P, Patterson, D. Morris, L. And Foster, B. 1988. Skeletal age estimation in leg length discrepancy. *Journal of Pediatric Orthopaedics* 8: 513-515.

Dainton, M. & Macho, G. (1999). Heterochrony: somatic, skeletal, and dental development in Gorilla, Homo and Pan. In R.D. Hoppa & C.M. Fitzgerald (Eds.) *Human growth in the past: Studies from bones and teeth* (pp.32-64). Cambridge: Cambridge University Press, Cambridge.

Dean, C. Leakey, M.G. Reid, D. Friedemann, S. Schwartz, G.T. Stringer, C. Walker, A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414: 628-631.

Dean, M.C. Lucas, V.S. 2009. Dental and skeletal growth in early fossil hominins. *Annals of Human Biology* 36(5): 545-561.

Dean, M.C. Smith, B.H. 2009. *The First Humans – Origin and Early Evolution of the Genus Homo. Vertebrate Paleobiology and Paleoanthropology. In* Growth and Development of the Nariokotome Youth, KNM-WT 15000. Springer, The Netherlands. pp 101-120.

Dean, M.C. Stringer, C.B. Bromage, T.G. 1986. Age at death of the Neanderthal child from Devil's Tower, Gibraltar and the implications for studies of general growth and development in Neanderthals. *American Journal of Physical Anthropology* 70(3): 301–309.

Demirjian, A. Buschang, P.H. Tanguay, R. Kingnorth Patterson, D. 1985. Interrelationships among measures of somatic, skeletal, dental, and sexual maturity. *American Journal of Orthodontics* 88(5): 433-488.

Demirjian, A. 1986. *Dentition*. Human Growth: A Multidisciplinary Review. Taylor and Francis Ltd, London. pp. 269-295.

Demrijian, A. Goldstein, H. Tanner, J.M. 1973. A new system of dental age assessment. *Human Biology* 45(2): 211-227.

Demirjian, A. Levesque, G.Y. 1980. Sexual Differences in Dental Development and Prediction of Emergence. *Journal of Dental Research* 59(7): 1110-1122.

Diamanti, J. Townsend, G.C. 2003. New standards for permanent tooth emergence in

Australian children. Australian Dental Journal 48(1): 39-42.

Digby, K.H. 1916. The mesurement of diaphysial growth in proximal and distal directions. *Journal of Anatomy* 50 (Pt. 2): 187-188.

Dirks, W. Reid, D.J. Jolly, C.J. Phillips-Conroy, J.E. Brett, F.L. 2002. Out of the Mouths of Baboons: Stress, Life History, and Dental Development in the Awash National Park Hybrid Zone, Ethiopia. *American Journal of Physical Anthropology* 118(3): 239-252.

Dean, M.C. Wood, B.A. 1981. Developing pongid dentition and its use for aging individual crania in comparative cross-sectional growth studies. *Folia Primatologica* 36(1-2): 111-127.

Doran, D.M. 1993. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology* 91(1): 83–98.

Ely, J.J. Dye, B. Frels, W.I. Fritz, J. Gagneux, P. Khun, H.H. Switzer, W.M. Lee, D.R. 2005. Subspecies composition and founder contribution of the captive U.S. chimpanzee (*Pan troglodytes*) population. *American Journal of Primatology* 67(2): 223–241.

Fairbairn, D.J. 1997. Allometry for Sexual Size Dimorphism: Pattern and Process in the Coevolution of Body Size in Males and Females. *Annual Review of Ecology and Systematics* 28: 659-687.

Fazekas, I.Gy. Kósa, F. 1978. *Forensic Fetal Osteology* Akadémiai Kiado, Budapest.

Feuillan, P. Merke, D. Leschek, E.W. Cutler, G.B Jr. 1999. Use of aromatase inhibitors in precocious puberty. *Endocrine-Related Cancer* 6(2): 303 -306.

FitzGerald, C.M. 1998. Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. *Journal of Human Evolution* 35(4–5): 371–386.

Fleagle, J.G. 1998. *Primate Adaptation and Evolution.* 2ndEdition. Elsevier Academic Press. San Diego.

Fleagle, J.G. McGraw, W.S. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proceedings of the National Academy of Science of the United States of America* 96(3): 1157-1161.

Flecker, H. 1932. Roentgenographic observations of the times of appearance of epiphyses and their fusion with the diaphyses. *Journal of Anatomy* 67(Pt. 1): 118-164.

Flores-Mir, C. Nebbe, B. Major, P.W. 2004. Use of Skeletal Maturation Based on Hand-Wrist Radiographic Analysis as a Predictor of Facial Growth: A Systematic Review. *Angle Orthodontist* 74(1):118-124.

Frechkop, S. (1935). Notes sure les mammiferes. XVII; A propus du chimpanze de la rive gauche du Congo. *Musee Royale Histoire Naionale Belgique Bull.* 11: 1-41.

Galliari, C.A. 1988. A study of postnatal appendicular skeletal maturation in captive-born squirrel monkeys *(Saimiri boliuiensis). American Journal of Primatology* 16(1): 5-61

Garn, S.M. Blumethall, T. And Rohmann, C.G. 1965. On skewness in the ossification centers of the elbow. *American Journal of Physical Anthropology* 23(3): 303-304.

Garn, S.M. Rohmann, C.G. 1963. On the prevalence of skewness in incremental data. *American Journal of Physical Anthropology* 21(2): 235-236.

Garn, S.M. Rohmann, C.G. 1966. Interaction of nutrition and genetics in the timing of growth and

development*. Pediatric Clinics of North America* 13: 353-379.

Garn, S.M. Rohmann, C.G. Silverman, F.N. 1967. Radiographic standards for postnatal ossification and tooth calcification. *Medical Radiography and Photography* 43: 45-66.

Garn, S.M. Sandusky, S.T. Nagy, J.M. Trowbridge, F.L. 1973. Negro-Caucasoid differences in permanent tooth emergence at a constant income level. *Archives of Oral Biology* 18(5): 609-615.

Gavan, J.A. 1953. Growth and Development of the Chimpanzee; A Longitudinal and Comparative Study. *Human Biology* 25(2): 93-143.

Gavan, J.A. 1971. Longitudinal, postnatal growth in chimpanzee.In G.H. Bourne (Ed.) *The Chimpanzee. Volume 4, behaviour, growth, and pathology of chimpanzees* (pp.46-102). S. Karger: Basel.

Ghantus, M. 1951. Growth of the shaft of the human radius and ulna during the first two years of life. *American Journal of Roentgenology* 65: 784-786.

Gindhart, P. 1973. Growth standards for the tibia and the radius in children aged one month through eighteen years. *American Journal of Physical Anthropology* 39(1): 41-48.

Glassman, D.M. 1983. Growth and development in the saddle-back tamarin: the sequence and timing of dental eruption and epiphyseal union. *American Journal of Primatology* 5(1): 51-59.

Godfrey, L.R. Sutherland, M.R. 1995. Flawed inference: why size-based tests of heterochronic processes do not work. *Journal of Theoretical Biology* 172(1): 43-61.

Godfrey, L. Sutherland, M.R. 1996. Paradox of peramorphic paedomorphosis: Heterochrony and human evolution. *American Journal of Physical Anthropology* 99(1): 17-42.

Goswami, A. 2007. Cranial modularity and sequence heterochrony in mammals. *Evolution & Development* 9(3): 290–298.

Gould, S.J. 1977. *Ontogeny and Phylogeny*. Harvard University Press: Cambridge p.235.

Gould, S.J. 1981. *The Mismeasure of Man*. Norton: New York.

Graur, D. Higgins, D. G. 1994. Molecular Evidence for the Inclusion of Cetaceans

within the Order Artiodactyla. *Molecular Biology and Evolution* 11(3): 357-364.

Greulich, W.W. 1957. A comparison of the physical growth and development of American-born and native Japanese children. *American Joural of Physical Anthropology* 15(4):489-515.

Greulich, W.W. and Pyle, S.I. 1959. *Radiographic atlas of skeletal development of the hand and wrist*. 2nd edn. Stanford University Press, New York.

Graves, R.R. Lupo, A.C. McCarthy, R.C. Wescott, D.J. Cunningham, D.L. 2010. Just how strapping was KNM-WT 15000? *Journal of Human Evolution* 59(5): 542-554.

Groves, C. 2001. *Primate Taxonomy*. Smithsonian Institution Press: Washington.

Gunst, K. Mesotten, K. Carbonez, A. Willems, G. 2003. Third molar root development in relation to chronological age: a large sample sized retrospective study. *Forensic Science International* 136(1-3): 52–57.

Haavikko, K. 1970. The formation and the alveolar and clinical eruption of the permanent teeth. An orthopantographic study. *Proceedings of the Finnish Dental Society* 66(3): 101-170.

Hales, S. 1727 *Statistical essays. Volume 1. Vegetable statiks.* W. Innys.: London.

Hamada, Y. Udono, T. Teramoto, M. Sugawara, T. 1996. The Growth Pattern of Chimpanzees: Somatic Growth and Reproductive Maturation in *Pan troglodytes*. *Primates* 37(3): 279-295.

Hamada, Y. Udono, T. Teramoto, M. Hayasaka, I. 1998. Development of the Hand and Wrist Bones in Chimpanzees. *Primates* 39(2): 157-169.

Hamada,Y. Udono, T. 2002. Longitudinal analysis of length growth in the chimpanzee (*Pan troglodytes*). American Journal of Physical Anthropology 118 (3): 268–284.

Hamada, Y. and Chatani, K. 2003. A longitudinal study on hand and wrist skeletal maturation in chimpanzees (*Pan troglodytes*), with emphasis on growth in linear dimensions. *Primates* 44(3): 259-271.

Hansman, C.F. Maresh, M.M. 1961. A Longitudinal Study of Skeletal Maturation. *American Journal of Diseases of Children* 101(3):305-321.

Harvey, P.H. Clutton-Brock, T.H. 1985. Life-history variation in primates. *Evolution* 39(3): 559-581.

Hayama, S. 1965. Morphological studies of *Macaca* *fuscata* II. The sequence of epiphyseal union by roentgenographicestimation.  *Primates* 6(2):249-269.

Hewitt, D. Acheson, R.M. 1961. Some aspects of skeletal development through adolescence. II The inter-relationship between skeletal maturation and growth at puberty. *American Journal of Physical Anthropology* 19(4): 333.344.

Hey, J. 2010. The Divergence of Chimpanzee Species and Subspecies as Revealed in Multipopulation Isolation-with-Migration Analyses. *Molecular Biology and Evolution* 27(4): 921-933.

Hill, K. 1993. Life history theory and evolutionary anthropology. *Evolutionary Anthropology: Issues, News, and Reviews* 2(3): 78-88.

Hill, K. Kaplan, H. 1999. Life History Traits in Humans: Theory and Empirical Studies. Annual *Review of Anthropology* 28(1): 397-430.

Hoerr, N.L. Pyle, S.I. and Francis, C.C. 1962. *Radiographic Atlas of Skeletal Development of the Foot and Ankles: A Standard Reference*. Springfield IL: C.C. Thomas.

Holden, L. 1882. *Human Osteology*. 6th edition. Churchill: London.

Holliday, T.W. 1997. Body proportions in Late Pleistocene Europe and modern human origins. *Journal of Human Evolution* 32(5): 423–447.

Holliday, T.W. Ruff, C.B. 2001. Relative variation in human proximal and distal limb segment lengths. *American Journal of Physical Anthropology* 116(1): 26–33.

Holman, D.J. Jones, R.E. 1991. Longitudinal analysis of deciduous tooth emergence in Indonesian children. I. Life table methodology. *American Journal of Human Biology* 3(4): 389–403.

Hopkins, W.D. 2006. Comparative and familial analysis of handedness in great apes. *Psychological Bulletin* 132(4): 538-559.

Hopkins, W.D. Pearson, K. 2000. Chimpanzee (Pan troglodytes) handedness: Variability across multiple measures of hand use. *Journal of Comparative Psychology* 114(2): 126-135.

Hoppa, R.D. 1992. Evaluating human skeletal growth: An Anglo-Saxon example. *International Journal of Osteoarchaeology* 2(4): 275-288.

Huda, T.F.J. Bowman, J.E. 1995. Age determination from dental microstructure in juveniles. *American Journal of Physical Anthropology* 97(2): 135–150

Hussin, A.S. Mokhtar, N. Naing, L. Taylor, J.A. Mahmood, Z. 2007. The timing and sequence of emergence of permanent teeth in Malay schoolchildren in Kota Bharu, Malaysia. *Archives of Orofacial Sciences* 2: 36-40.

Jantz, R.L. Owsley, D.W. 1984. Long bone growth variation among Arikara skeletal populations. *American Journal of Physical Anthropology* 63(1): 3-20.

Jeanty, P. 1983. Fetal limb biometry. *Radiology* 147(2): 601-602.

Jeffery, J. E., Richardson, M. K., Coates, M. I. & Bininda-Emonds, O. R. P. 2002. Analyzing developmental sequences within a phylogenetic framework. *Systematic Biology*. 51(3): 478–491.

Jit, I. Kaur, H. 1989. Time of fusion of the human sternebrae with one another in Northwest India. American Journal of Physical Anthropology 80(2): 195-202.

Jit, I. Singh, B. 1971. A radiological study of the time of fusion of certain epiphyses in Punjabees. *Journal of Anatomical Society India* 20(1): 457-466.

Jungers, W.L. 1982. Lucy's limbs: skeletal allometry and locomotion in Australopithecus afarensis. *Nature* 297: 676 – 678.

Karlberg, J. 1985. *The human growth curve decomposed into three additive and partly superimposed components: The FBP model*. In Abstracts. Fourth International Congress of Auxology. Taylor and Francis: London p. 46.

Kaufman, M.J. 1992. *The atlas of mouse development*. Academic Press: London.

Kaul, S. Saini, S. Saxena, B. 1975. Emergence of permanent teeth in school-children in Chandigarh, India. *Archives of Oral Biology* 20(9): 587–593.

Katz, H.B. 1980. The influence of undernutrition on learning performance in rodents. *Nutrional Abstracts and. Reviews* 50(11): 767-784.

Keene, H.J. 1991. On heterochrony in heterodonty: A review of some problems in tooth morphogenesis and evolution. *American Journal of Physical Anthropology Supplement: Yearbook of Physical Anthropology* 34 (S13): 251–282.

Kelley, J. Schwartz, G.T. 2010. Dental development and life history in living African and Asian apes. *Proceedings of the National Academy of Sciences* *of the United States of America* 3: 1035-1040.

Kelley, J. Smith, T. 2003. Age at first molar emergence in early Miocene Afropithecus turkanensis and life-history evolution in the Hominoidea. *Journal of Human Evolution* 44(3): 307-329.

Kerley, E.R. 1966. Skeletal age changes in the chimpanzee. *Tulane Studies in Zoology* 13: 71-80.

Kilborn,S.H. Trudel,G. Uhthoff,H. 2002. Review of Growth Plate Closure Compared with Age at Sexual Maturity and Lifespan in Laboratory Animals. *Journal of the American Association for Laboratory Animal Science* 41(5): 21-26.

Kimura, T. Hamada, Y. 1996. Growth of wild and laboratory born chimpanzees. *Primates* 37(3): 237-251.

King, S.J. 2004. Relative timing of ontogenetic events in primates. *Journal of Zoology* 264:3: 267-280.

Kinzey, W.G. 1984. The dentition of the pygmy chimpanzee, *Pan paniscus*. In *The Pygmy* Chimpanzee Susman, R.L. ed. Plenum Press, New York pp. 65–88.

Kinzey, W.G. 1992. Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology* 88(4): 499–514.

Kinsey, W.G. 1997. *New World Primates: Ecology, Evolution, and Behaviour.* Kinsey, W.G. ed. Walter de Gruyter: New York.

Kirk, E.C. Simons, E.L. 2001. Diets of fossil primates from the Fayum Depression of Egypt: a quantitative analysis of molar shearing. ***Journal of Human Evolution* 40(3): 203-229.**

Klingenberg, C.P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews of the Cambridge Philosophical Society* 73(1): 79-123.

Klingenberg, C.P. McIntyre, G.S. 1998. Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution* 52(5): 1363-1375.

Knight, R.R. 1966. Bone characteristics associated with aging in elk. *Journal of Wildlife Management* 30(2): 369-374.

Koch, W. 1935. The age order of epiphyseal union in the skeleton of the European bison (bos bonasus L.) *The Anatomical Record* 61(3): 371-376.

Koshy, S. Tandon, S. 1998. Dental age assessment: the applicability of Demirjian's method in south Indian children. *Forensic Science International* 94(1-2): 73-85.

Kraemer, H.C. Horvat, J.R. Doering, C. McGinnis, P.R. 1982. Male chimpanzee development focusing on adolescence: integration of behavioral with physiological changes. *Primates* 23(3): 393-405.

Kumar, S. Filipski, A. Swarna, V. Walker, A. Hedges, S.B. 2005. Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proceedings of the National Academy of Sciences* 102(52): 18842-18847.

Kuykendall, K.L. Mahoney, C.J. Conroy, G.C. 1992. Probit and Survival Analysis of Tooth Emergence Ages in a Mixed-Longitudinal Sample of Chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* 89(3): 379-399.

Kuykendall, K. 1996. Dental Development in Chimpanzees (*Pan troglodytes*): The Timing of Tooth Calcification Stages. *American Journal of Physical Anthropology* 99(1):135-157.

Kuykendall, K. Conroy, G.C. 1996. Permanent Tooth Calcification in Chimpanzees (*Pan troglodytes*) Patterns and Polymorphisms. *American Journal of Physical Anthropology* 99(1): 159-174.

Laird, A.K. 1967. Evolution of the human growth curve. *Growth* 31: 345–355.

Lampl, M. Johnston, F.E. Malcolm, L.A. 1978. The effects of protein supplementation on the growth and skeletal maturation of New Guinean school children. *Annals of Human Biology* 5(3): 219-227.

Lasker, G.W. 1969. Human biological adaptability. *Science* 166(3912): 1480-1486.

Last, R.J. 1973. *Anatomy, Regional and Applied*. 5th edition. Churchill Livingstone: Edinburgh.

Leavens, D.A. Hopkins, W.D. Bard, K.A. 2005. Understanding the Point of Chimpanzee Pointing: Epigenesis and Ecological Validity. Current Directions in Psychological Science 14(4): 185-189.

Leigh, S.R. 2004. Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology Special Issue: Topic issue on Primate Cognitive Ecology* 62(3): 139–164.

Leigh, S.R. Shea, B.T. 1996. Ontogeny of Body Size Variation in African Apes. *American Journal of Physical Anthropology* 99(1): 43-45.

Leutenegger, W. Kelly, J.T. 1977. Relationship of Sexual Dimorphism in Canine Size and Body Size to Social, Behavioral, and Ecological Correlates in Anthropoid Primates. *Primates* 18(1): 117-136.

Sommer, V. Adanu, J. Faucher, I. Fowlera, A. 2004. Nigerian Chimpanzees (*Pan troglodytes vellerosus*) at Gashaka: two years of habituation efforts. *Folia Primatologica* 75: 295-316.

Lewall, E.G. Cowan, I.M. I963. Age determination in blacktail deer by degree of ossification of the epiphyseal plate in the long bones. *Canadian Journal of Zoology* 41(1): 629.

Lewis, A.B. Garn, S.M. 1960. The Relationship Between Tooth Formation and Other Maturational Factors. *The Angle Orthodontist* 30: 70-77.

Lieberman, D. E. Carlo, J. Ponce de Leon, M. & Zollikofer,C.P.E. (2007). A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos. *Journal of Human Evolution* 52(6): 647-662.

Liversidge, H. 2003. Variation in modern human dental development. *Patterns of Growth and Development in the Genus Homo.* Thompson, J.L. Krovitz, G.E. (eds.). Cambridge University Press. Cambridge. pp. 73-113.

Liversidge, H.M. Chaillet, N. Mörnstad, H. Nyström, M. Rowlings, K. Taylor, J. Willems, G. 2006. Timing of Demirjian's tooth formation stages. *Annals of Human Biology* 33(4): 454-470.

Liversidge, H.M. Herdeg, B. Rosing, F.W. 1998. Dental age estimation of non-adults. A review of methods and principles. In: *Dental Anthropology, Fundamentals, Limits and Prospects.* Rosing, K.W. and Teschler-Nicola, M. eds.. Springer: Vienna. pp. 419-442.

Liversidge, H.M. Speechly, T. 2001. Growth of permanent mandibular teeth of British children aged 4 to 9 years. *Annals of Human Biology* 28(3): 256-262.

Lovejoy, C.O. 1985. Dental wear in the Libben population: Its functional pattern and role in the determination of adult skeletal age at death. *American Journal of Physical Anthropology* 68(1): 47–56.

Lovejoy, C.O. Suwa, G. Simpson, S.W. Matternes, J.H. White, T.D. 2009. The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes. *Science* 326(5949): 73, 100-106.

Lucas, A. Morley, R. Cole, T. J. 1998. Randomised trial of early diet in preterm babies and later intelligence quotient. *British Medical Journal* 317: 1481-1487.

de Magalhães, J.P. Church, G.M. 2007. Analyses of human–chimpanzee orthologous gene pairs to explore evolutionary hypotheses of aging. *Mechanisms of Ageing and Development* 128(506): 355-364.

Mainland, D. 1953. Evaluation of the skeletal age method of estimation children’s development. I. Systematic errors in the assessment of roentgenograms. *Pediatrics*  12(2): 114-129.

Mainland, D. 1954. Evaluation of the skeletal age method of estimating children’s development. II. Variables errors in the assessment of roentgenograms. *Pediatrics* 13(2): 165-173.

Mainland, D. 1957. Evaluation of the skeletal age method of estimating children’s development. III. Comparison of methods and inspection in the assessment of roentgenograms. *Pediatrics* 20(6): 979-992.

Maresh, M.M. 1970. Measurement from roentgenograms. In: McCammon, R.W. ed. *Human Growth and Development*. Thomas: Springfield. pp. 157-200.

Martin, R.D. 1990. *Primate Origins and Evolution* Princeton University Press: Princeton.

Martin-de las Heras, S. García-Fortea, P. Ortega, A. Zodocovich, S. Valenzuela, A. 2008. Third molar development according to chronological age in populations from Spanish and Magrebian origin. *Forensic Science International* 174(1): 47-53.

Matsuzawa, T. Sakura, O. Kimura, Z. Hamada, Y. Sugiyama, Y. 1990. Case report on the death

of a wild chimpanzee (*Pan troglodytes verus*). *Primates* 31(4): 635-641.

McHenry, H.M. Coffing, K. 2000. *Australopithecus* to *Homo*: Transformations in Body and Mind. *Annual Review of Anthropology:* 125-146.

McKern, T.W. Stewart, T.D. 1957. Skeletal age changes in young American males, analysis from the standpoint of age identification. *Headquarters Quartermaster Research and Development Command,* Technical Report EP-45: Natick MA.

McNamara, K.J. 2002. *What is Hetereochrony*? Minugh-Purvis, N. McNamara, K.J. (eds.). Human Evolution through Developmental Change. John Hopkins University Press, Baltimore. pp.1-4.

Meindl, R.S. Lovejoy, C.O. 1985. Ectocranial suture closure: A revised method for the determination of skeletal age at death based on the lateral-anterior sutures. *American Journal of Physical Anthropology* 68(1): 57-66.

Meinl, A. Tangl, S. Huber, C. Maurer, B. Watzek, G. 2007. The chronology of third molar mineralization in the Austrian population—a contribution to forensic age estimation. *Forensic Science International* 169(2-3): 161–167.

Mensforth, R.P. 1985. Relative tibia long bone growth in the Libben and Bt-5 prehistoric skeletal populations. *American Journal of Physical Anthropology* 68(2): 247-262.

Michejda, M. 1987. Skeletal development of the wrist and hand in *Macaca mulatta* and man. *T Roentgenographic atlas*. Karger: Basel.

Miles, A. E. W. Bulman, J. S. 1994. Growth curves of immature bones from a Scottish island population of sixteenth to mid-nineteenth century: Limb-bone diaphyses and some bones of the hand and foot. *International Journal of Osteoarchaeology* 4(2):121-136.

Mitteroecker, P. Gunza, P. Bernhard, M. Schaefer, K. 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution* 46(6): 679–698.

Mitteroecker, P. Gunz, P. Bookstein, F.L. 2005. Heterochrony and geometric morphometrics: a comparison of cranial growth in Pan paniscus versus Pan troglodytes. Evolution and Development 7(3): 244-258.

Monge, J. Mann, A. Stout, A. Rogèr, J. Wadenya, R. 2007. *Dental calcification stages of the permanent M1 and M2 in U.S. children of African-American and European-American ancestry born in the 1990s*. In: Dental Perspectives on Human Evolution. Bailey, S.W. Hublin,m J.J. (eds). Spring: Netherlands. pp. 263-274.

Morbeck, M.E. Zihlman, A.L. 1989. Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates* 30(3): 369-382.

Moorrees, C. Fanning, E. Hunt, E. 1963. Age variation of formation stages for ten permanent teeth. *Dental Research* 42(6): 1490-1502.

Morriss-Kay, G.M. 2001. Derivation of the mammalian skull vault. *Journal of Anatomy* 199(1-2): 143-151.

Myatt, J.P. Crompton, R.H. Susannah K. S. Thorpe, S.K.S. 2011. Hindlimb muscle architecture in non-human great apes and a comparison of methods for analysing inter-species variation. *Journal of Anatomy* 219(2): 150–166.

Nass, G. 1977. Intra-group variations in dental eruption sequence of Macacu fuscata fuscata. *Folia Primatological* 28(4): 306-314.

Newell-Morris, L. Tarrant, L.H. 1978. Ossification in the hand and foot of the macaque (*Macaca nemestrina*). *American Journal of Physical Anthropology* 48(4): 441-454.

Newell-Morris, L. Tarrant, L.H. Farenbach, C.E. Sackett, G.P. 1980. Ossification in the hand of the pigtail macaque (*Macaca nemestrina*) 2. Order of appearance of centers and variability in sequence. *American Journal of Physical Anthropology* 53(3): 423-439.

Newman, M.T. 1953. The Application of Ecological Rules to the Racial Anthropology of the Aboriginal New World. *American Anthropologist* 55(3): 311–327.

Nilsson, O. Baron, J. 2004. Fundamental limits on longitudinal bone growth: growth plate senescence and epiphyseal fusion. *Trends in Endocrinology and Metabolism.* 15(8): 370-374.

Nishida, T. Corp, N. Hamai, M. Hasegawa, M. Hiraiwa-Hasegawa, H. Hosaka, K. Hunt, K.D. Itoh, N. Kawanaka, K. Matsumoto-Oda, A. Mitani, J.G. Nakamura, M. Norikoshi, K. Sakamaki, T. Turner, L. Uehara, S. Zamma, K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology* 59(3): 99–121.

Nissen, H.W. & Riesen, A.H. 1949a. Retardation in onset of ossification in chimpanzee related to various environmental and physiological factors. *The Anatomical Record* 105(4): 665-675.

Nissen, H.W. & Riesen, A.H. 1949b. Onset of ossification in the epiphyses and short bones of the extremities in chimpanzee. *Growth* 13: 45-70.

Nissen, H.W. Riesen, A.H. 1964. The eruption of the permanent dentition of chimpanzees. *American Journal of Physical Anthropology* 22(3): 285–294.

Noddle, B. 1974. Ages of epiphyseal closure in feral and domestic goats and ages of dental eruption. *Journal of Archaeological Science* 1(2): 195-204.

Nonaka, K. Ichiki, A. Muira, T. 1990. Changes in the eruption order of the first permanent tooth and their relation to season of birth in Japan. *American Journal of Physical Anthropology* 82(2): 191-198.

Norman, G. 2010. Likert scales, levels of measurement and the “laws” of statistics. *Advances in Health Sciences Education* 15(5): 625-632.

Nunn, C. L. & Smith, K. K. 1998. Statistical analyses of developmental sequences: the craniofacial region in marsupial and placental mammals. *The American Naturalist* 152(1): 82–101.

Nykänen, R. Espeland, L. Kvaal, S.I. Krogstad, O. 1998. Validity of the Demirjian method for dental age estimation when applied to Norwegian children. *Acta Odontologica Scandinavica* 56(4): 238-244.

Ogden, J.A. 1979. The development and growth of the musculo-skeletal system. In: *Scientific Basis of Orthopaedics* (J.A. Albright and R. Brands Eds.) Appleton-Century-Crofts: New York pp.41-103.

Ogden, J.A. Conlogue, G.J. Rhodin, A.G.J. 1981. Roentgenographic Indicators of Skeletal Maturity in Marine Mammals (*Cetacea*) Skeletal Radio1ogy 7(2): 119 123.

Olze, A. Taniguchi, M. Schmeling, A. Zhu, B.L. Yamada, Y. Maeda, M. Geserick, G. 2004. Studies on the chronology of third molar mineralization in a Japanese population. *Legal Medicine* 6(2): 73-79.

Palmer, A.R. Strobeck, C. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics* 17: 391-421.

Palmer, A.R. Strobeck, C. 1992. Fluctuating assymetry as a measure of developmental stability: Impications of non-normal distributions and power of statistical tests. *Acta Zoologica Fennica* 191: 57-72.

Parker, S.T. 1996. *Using cladistic analysis of comparative data to reconstruct the evolution of cognitive development in hominids*. In Martins, E. (ed.) Phylogenies and the Comparative Method in Animal Behavior. Oxford University Press: Oxford. pp. 433–448.

Pearson, O.M. 2000. Activity, climate, and postcranial robusticity. *Current Anthropology* 41(4): 569-607.

Penin, X. Berge, C. Baylac, M. 2002. Ontogenetic study of the skull in modern humans and the common chimpanzees: Neotenic hypothesis reconsidered with a tridimensional procrustes analysis. *American Journal of Physical Anthropology* 118(1): 50–62.

Persson, L. Kjell, L. De Roos, A. Gyllenberg, M. Christensen, B. 1998. Ontogenetic Scaling of Foraging Rates and the Dynamics of a Size-Structured Consumer-Resource Model. *Theoretical Population Biology* 54(3): 270-293.

Phillips-Conroy, J. Jolly, C.J. 1988. Dental eruption schedules of wild and captive baboons. *American Journal of Primatology* 15(1): 17-29.

Prakash, S. Cameron, N. 1981. Skeletal maturity of well-off children in Chandigarh, North India. *Annals of Human Biology* 8(2): 175-180.

Prakash, S. Pathamanathan, G. 1991. Tempo-unconditional 1-year bone score velocities in well-off north-west Indian children. *Annals of Human Biology* 18(4): 303-310.

Prendergast Moore, K. Thorp, S. Van Gerven, D.P. 1986. Pattern of dental eruption, skeletal maturation and stress in a Medieval Population from Sudanese Nubia. *Human Evolution* 1(4): 325-330.

Prieto, J.L. Barbería, E. Ortega, R. Magaña, C. 2005. Evaluation of chronological age based on third molar development in the Spanish population. *International Journal of Legal Medicine* 119(6): 349-354.

Pyle, S.I. and Hoerr, N.L. 1955. *Radiographic Atlas of Skeletal Development of the Knee*. C.C. Thomas: Springfield.

Pyle, I. Sontag, L.W. 1943. Variability in the onset of ossiﬁcation in the epiphyses and short bones of the extremities. *American Journal of Roentgenology, Radium Therapy, and Nuclear Medicine* 49: 795–798.

Raaum, R.L. Sterner, K.N. Noviello, C.M. Stewart, C.B. Disotell, T.R. 2005. Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. *Journal of Human Evolution* 48(3): 237-257.

Rae, T.C. Koppe, T. Spoor, F. Benefit, B. McCrossin, M. 2002. Ancestral loss of the maxillary sinus in Old World monkeys and independent acquisition in Macaca. *American Journal of Physical Anthropology* 117(4): 293–296.

Ramirez Rozzi, F. Lacruz, R.S. 2007. Histological study of an upper incisor and molar of a bonobo (Pan paniscus) individual. In *Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology*. Bailey, S.E. Hublin, J.J. (eds.) Spring: Netherlands pp. 163-176.

Ravosa, M.J. Daniel, A.N. 2010. Ontogeny and phyletic size change in living and fossil lemurs. *American Journal of Primatology* 72(2): 161-172.

Reid, D.J. Dean, M.C. 2006. Variation in modern human enamel formation times. *Journal of Human Evolution* 50(3): 329–346

Reid, D.J. Schwartz, G.T. Chandrasekera, M.S. 1998. A histological reconstruction of dental

development in the common chimpanzee, *Pan troglodytes*. *Journal of Human Evolution* 35(4–5): 427-448.

Rice, S.H. 1997. The analysis of ontogenetic trajectories: When a change in size or shape is not heterochrony. *Proceedings of the National Academic of Sciences* *of the United States of America* 94: 907-912.

Richardson, M. K., Jeffery, J. E., Coates, M. I. Bininda-Emonds, O. R. P. 2001. Comparative methods in developmental biology. *Zoology* 104(3-4): 278–283.

Richmond, B.G. Jungers, W.L. 1995. Size variation and sexual dimorphism in Australopithecus afarensis and living hominoids. *Journal of Human Evolution* 29(3): 229–245.

Roberts, D.F. 1981. Genetics of growth*. British Medical Bulletin* 37: 239-246.

Roche, A.F. 1992. Growth, Maturation and Body Composition The Fels Longitudinal Study (1929-1991) Cambridge University Press: Cambridge.

Roth, V.L. 1984. How Elephants Grow: Heterochrony and the calibration of developmental stages in some living and fossil species. *Journal of Vertebrate Paleontology* 4(1): 126-145.

Ruff, C.B. 1994. Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropolology* 37(S19): 65–107.

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

Sadler, T.W. 2004. Langman’s medical embryology. 9th Edition. Lippincott Williams and Wilkins: London.

Sahni, D. Jit, I. Sanjeev 1995. Time of fusion of epiphyses at the elbow and wrist joints in girls of Northwest India. *Forensic Science International* 74(1): 47-55.

Salter, R.B. Harris, W.R. 1963. Injuries involving the Epiphyseal Plate. An Instructional Course Lecture, The American Academy of Orthopaedic Surgeons. *The Journal of Bone and Joint Surgery* 45(3):587-622.

Sarringhaus, L.A. Stock, J.T. Marchant, L.F. McGrew, W.C. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). *American Journal of Physical Anthropology* 128(4): 840-845.

Scanes, C. G. 2011. Hormones and Growth in Domestic Animals. *Comprehensive Physiology*: 99–127.

Schafer, J.L. 2000. Analysis of Incomplete Multivariate Data*. Monographs on Statistics and Applied Probability* 72. Chapman and Hall/CRC. London.

Schaefer, M. 2008. A summary of epiphyseal union timings in Bosnian males. *International Journal of Osteoarchaeology* 18(5): 536-545.

Schaefer, M. Black, S. 2007. Epiphyseal Union Sequencing: Aiding in the Recognition and Sorting of Comingled Remains. *Journal of Forensic Sciences* 52(2): 277-285.

Schaefer, M. Black, S. Scheuer, L. 2009. *Juvenile Osteology: A Laboratory Field Manual*. Academic Press. Amsterdam.

Scheuer, L. Black, S.M. 2004. The Juvenile Skeleton. *Elsevier Academic Press.*

Schmeling, A. Reisinger, W. Loreck, D. Vendura, K. Markus, W. Geserick, G. 2000. Effects of ethnicity on skeletal maturation: consequences for forensic age estimations. *International Journal of Legal Medicine* 113(5): 253-258.

Schmeling, A. Schulz, R. Reisinger, W. Müher, M. Wernecke, K.D. 2004. Studies on the time frame for ossification of the medial clavicular epiphyseal cartilage in conventional radiography. *International Journal of Legal Medicine* 118(1):5-8.

Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge University Press: Cambridge.

Schultz, A. 1935. Eruption and decay of the permanent teeth in primates. *American Journal of Physical Anthropology* 19(4): 489-581.

Schultz, A.H. 1940. *Growth and development of the chimpanzee*. *Contributions to Embryology* 28: 1–6 Carnegie Institution of Washington publication ; no. 518.

Schultz, A.H. 1941. Growth and development of the orangutan. *Contributions to Embryology Carnegie Institution* 29: 57-110.

Schultz, A.H. 1942. Growth and development of the proboscis monkey. *Bulletin of the Museum Comparative Zoology* 89: 279-323.

Schultz, A.H. 1944. Age changes and variability in gibbons: a morphological study on a population sample of a manlike ape. *American Journal of Physical Anthropology* 2(1): 1-129.

Schultz, A.H. 1960. *Age changes in primates and their modiﬁcation in man*. In Tanner, J.M. (ed.): Human Growth. Pergamon, Oxford pp. 1–20.

Schwartz, G.T. Reid, D.J. Dean, C. Chandrasekera, M.S. 2000. Aspects of tooth crown development in common chimpanzees (*Pan troglodytes*) with a note on the possible role of sexual dimorphism in canine growth. *Proceedings of 11th International Symposium on Dental Morphology, Oulu, Finland*. pp. 323–337.

Sciulli, P.W. 2007. Relative dental maturity and associated skeletal maturity in prehistoric native Americans of the Ohio valley area. *American Journal of Physical Anthropology* 132(4): 545–557

Shea, B.T. 1981. Relative growth of the limbs and trunk in the African apes. *American Journal Physical Anthropology* 56(2): 179-201.

Shea, B.T. 1983. Allometry and heterochrony in the African apes. *American Journal of Physical Anthropology* 62(3): 275–289.

Shea, B.T. 1984. *An Allometric Perspective on the Morphological and Evolutionary Relationships between Pygmy (Pan Paniscus) and Common (Pan troglodytes) Chimpanzees.* *In* The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Randall L. Susman ed. Plenum Press: New York pp.98-130.

Shea, B.T. 1985. The ontogeny of sexual dimorphism in the African apes. *American Journal of Primatology* 8(2): 183–188.

Shea, B.T. 1989. Heterochrony in human evolution: The case for neoteny reconsidered. *Yearbook of Physical Anthropology* 32(S10): 69–101.

Shea, B.T. 1992. Developmental perspective on size change and allometry in evolution. *Evolutionary Anthropology* 1(4): 125–134.

Shigehara, N. 1980. Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew with reference to its systematic problem. *Primates* 21(1):1-19.

Simpson, S.W. Kunos, C.A. 1998. A radiographic study of the development of the human mandibular dentition. *Journal of Human Evolution* 35(4-5): 479-505.

Simpson, S.W. Lovejoy, C.O. Meindl, R.S. 1992. Further evidence on relative dental maturation and somatic developmental rate in hominoids. *American Journal of Physical Anthropology* 87(1): 29-38.

Small, C.G. 1996. *The Statistical Theory of Shape*. Springer: New York p.4.

Smart, J. L. 1977. Early life malnutrition and later learning ability: a critical analysis. In: *Genetics*, *Environment and* *Intelligence.* Oliviero, A. Ed. pp. 215-235. Elsevier: Amsterdam.

Smart, J. L. 1986. Undernutrition, learning and memory: review of experimental studies. In: *Proceedings of XIII* *International Congress of Nutrition.*  Taylor, T. G. and Jenkins, N. K. (eds.) John Libbey: London. pp. 74-78.

Smirthwaite, J.J. Rundle, S.D. Bininda-Emonds, O.R.P Spicer, J.I. 2007. An integrative approach identifies developmental sequence heterochronies in freshwater basommatophoran snails. *Evolution & Development* 9(2): 122–130.

Smith, A.R. Butler, T.M. Pace, N. 1975. Weight growth of colony-reared chimpanzees. *Folia Primatologica* 24(1): 29-59.

Smith, B.H. 1991. Standards of human tooth formation and dental age assessment. In: Kelley, M.A. Spencer Larsen, C. (eds.) *Advances in Dental Anthropology*. Wiley-Liss: New York, pp. 143-168.

Smith B.H. 1993. The physiological age of KNM-WT 15000. In: Walker A, Leakey R, editors. *The Nariokotome Homo erectus skeleton*. Cambridge, MA: Harvard University Press. pp 195–220.

Smith, B,H, Crummett, T.L. Brandt, K.L. 1994. Ages of eruption of primate teeth: A compendium for aging individuals and comparing life histories. *American Journal of Physical Anthropology*

*Supplement: The American Journal of Physical Anthropology Yearbook Series* 37(S19): 177–231.

Smith, B.H. Garn, S.M. 1987. Polymorphisms in eruption sequence of permanent teeth in American children. *American Journal of Physical Anthropology* 74(3): 289–303.

Smith, B.H. Boesch, C. 2011. Mortality and the magnitude of the‘‘wild effect’’ in chimpanzee tooth emergence. *Journal of Human Evolution* 60(1): 34–46.

Smith, C.B. Garn, S.M. 1987. Polymorphisms in eruption sequence of permanent teeth of American Children. *American Journal of Physical Anthropology* 74(3): 289-303.

Smith, K.K. 1997. Comparative patterns of craniofacial development in eutherian and metatherian mammals. *Evolution* 51(5): 1663–1678.

Smith, K. K. 2001. Heterochrony revisited: the evolution of developmental sequences. *Biological Journal of the Linnean Society* 73(2): 169–186.

Smith, K. K. 2002. Sequence heterochrony and the evolution of development. *Journal of Morphology* 252(1): 82–97.

Smith, S.L. 2004. Skeletal age, dental age, and the maturation of KNM-WT 15000. *American Journal of Physical Anthropology* 125(2): 105-120.

Smith, S.L. Buschang, P.H. 2005. Longitudinal models of long bone growth during adolescence. *American Journal of Human Biology* 17(6): 731–745.

Smith, T.M. Reid, D.J. Dean, M.C. Olejniczak, A.J. Martin, L.B. 2007. Molar development in common chimpanzees (*Pan troglodytes*). *Journal of Human Evolution* 52(2): 201–216.

Smith, T.M. Smith, B.H. Reid, D.J. Siedel, H. Vigilant, L. Hublin, J.J. Boesch, C. 2010. Dental development of the Tai Forest chimpanzees revisited. *Journal of Human Evolution* 58(5):363-373.

Smith, T.M. Machanda, Z. Bernard, A.B. Donovan, R.M. Papakyrikos, A.M. Muller, M.N. Wrangham, R. 2013. First molar eruption, weaning, and life history in living wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America* 110(8): 2787-2791.

Smith, R.N. 1969. Fusion of Ossification Centres in the Cat. *Journal of Small Animal Practice* 10(9): 523-530.

Stanford, C.B. 1999. *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton University Press: New Jersey.

Steele, J. Mays, S. 1995. Handedness and Directional Asymmetry in the Long Bones of the Human Upper Limb. *International Journal of Osteoarchaeology* 5(1): 39-49.

Stevens, D. Boyer, B. Bowen, C. Vaughan, A. 1999. Transplantation of Epiphyseal Plate Allografts Between Animals of Different Ages. *Journal of Pediatric Orthopeadics* 19(3): 398-403.

Stevenson, P.H. 1924. Age order of epiphyseal fusion in man. *American Journal of Physical Anthropology* 7(1): 53-93.

Stewart, T.D. 1934. Sequence of epiphyseal fusion, third molar eruption and suture closure in Eskimos and American Indians. *American Journal of Physical Anthropology* 19(3): 433-452.

Stini, W.A. 1969. Nutritional stress and growth: Sex differences in adaptive response. *American Journal of Physical Anthropology* 31(3): 417-426.

Stinson, S. 1985. Sex differences in Environmental Sensitivity During Growth. *Yearbook of Physical Anthropology* 28(S6): 123-147.

Stout, S.D. Lueck, R. 1995. Bone remodeling rates and skeletal maturation in three archaeological skeletal populations. *American Journal of Physical Anthropology* 98(2): 161-171.

Stumpf, R. 2007. Chimpanzees and Bonobos: Diversity within and Between Species. In Campbell, C. Fuentes, A. MacKinnon, K.L. Pagner, M. Bearder, S.K. (Eds.) *Primates in Perspective*. Oxford University Press: Oxford pp.132-344.

Sugiyama, Y. 1989. Population dynamics of chimpanzees at Bossou, Guinea. *In* Heltne, P.G. and Marquardt, L.G. eds. *Understanding Chimpanzees*. Harvard University Press: Cambridge pp.134-145.

Sugiyama, Y. 2004. Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology* 124(2): 154-165.

Sullivan, E.G. Haugen, A.O. 1976. Age determination of foxes by x-ray of forefeet. *Journal of Wildlife Management* 20(2): 210.

Sumner-Smith, G. 1966. Observations on Epiphyseal Fusion of the Canine Appendicular Skeleton. *Journal of Small Animal Practice* 7(4): 303-311.

Surbey, M.K. 1990. *Family composition, stress, and the timing of human menarche*. In Ziegler, T. E. Bercovitch, F. B. (eds.). Socioendocrinology of primate reproduction. Monographs in primatology, Volume. 13. Wiley-Liss: New York pp. 11-32.

Susman, R.L. 1979. Comparative and functional morphology of hominoid fingers. *American* *Journal of Physical Anthropology* 50(2): 215-236.

Swindler, D.R. Emel, L.M. Anemone, R.L. 1998. Dental Variability of the Liberian Chimpanzee, *Pan troglodytes verus*. *Human Evolution* 13(3-4):235-249.

Tanner, J.M. Whitehouse, R.H. Cameron, N. Marshall W.A. Healy, M.J.R. and Goldstein, H. 1983. *Assessment of Skeletal Maturity and Prediction of Adult Height (TW2 Method),* 2nd edition. Academic Press: London.

Tanner, J.M. Whitehouse, R.H. Cameron, N. Marshall, W.A. Healy, M.J.R. Goldstein, N.H. 2001. *Assessment of skeletal maturity and prediction of adult height (TW3 method).* 3rd ed. WB Saunders: London.

Tappan, N.C. Severson, A. 1971. Sequence of eruption of permanent teeth and epiphyseal union in new world monkeys. *Folia Primatologica* 15(3-4): 293-312.

Teivens A, Mörnstad H. 2001a. A modification of the Demirjian method for age estimation in children. *The Journal of Forensic Odonto-stomatology* 19(2): 26-30.

Teivens A, Mörnstad H. 2001b. A comparison between dental maturity rate in the Swedish and Korean populations using a modified Demirjian method. *The Journal of Forensic Odonto-stomatology*. 19(2): 31-35.

Todd, T.W. 1930. The anatomical features of epiphyseal union. *Child Development* 1(3): 186-194.

Toratora, G.J. and Anagnostakos, N.P. 1984. *Principles of Anatomy*. Fourth Edition. Harper and Row Publishers: New York. p. 127.

Trivers, R.L. Willard, D.E. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. *Science* 179(4068): 90-92.

Ubelaker, D.H. 1987. Estimating age at death from immature human skeletons: An overview. *Journal of Forensic Science* 32(5): 1254-1263.

Ubelaker, D.H. 1989. The estimation of age at death from immature human bone. In *Age Markers in the Human Skeleton*. Iscan, M.Y. (ed.) Charles C. Thomas: Springfield pp.55-70.

Ungar, P.S. M’Kirera, F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proceedings of the National Academy of Sciences of the United States of America* 100(7): 3874-3877.

Velhagen,W. A. 1997. Analyzing developmental sequences using sequence units. *Systematic Biology* 46:1: 204–210.

Vrba, E.S. 1996. Climate, heterochrony, and human evolution. *Journal of Anthropological Research* 52(1): 1–28.

Wagenen, G. van Asling, C.W. 1958. Roentgenographic estimation of bone age in the rhesus monkey (*Macaca* *mulatta*)*. American Journal of Anatomy* 103(2): 163-185.

Walker, D.N. 1987. Sequence of epiphyseal fusion in the Rocky Mountain Bighorn Sheep. *Western North American Naturalist* 47(1): 7-12.

Walker, A. Leakey, R. 1993. *The Nariokotome Homo Erectus Skeleton.* Springer-Verlag: Berlin. p. 235.

Wang, J. Zhou, J. Bondy, C.A. 1999. Igf1 promotes longitudinal bone growth by insulin-like actions augmenting chondrocyte hypertrophy. *Federation of American Societies for Experimental Biology* 13(14):1985-1990.

Watts, E.S. 1971. *A comparative study of skeletal maturation in the chimpanzee and rhesus monkey and its relationship to growth and sexual maturity.* Ph.D. thesis, University of Pennsylvania, Philadelphia PA.

Watts, E.S. 1982. Postnatal growth of nonhuman primates: the problem of adolescent spurt. *Human Biology* 54(1): 53-70.

Watts, E.S. 1985. *Adolescent growth and development of monkeys, apes and humans*. In: Watts, E.S. (ed.) Nonhuman primate models for human growth and development. Liss: New York. pp.41-65.

Watts, E.S. Gavan, J.A. 1982. Postnatal growth of nonhuman primates: The problem of the adolescent spurt. *Human Biology* 54(1): 53–70.

Webb, P.A.O. Suchey, J.M. 1985. Epiphyseal fusion of the anterior iliac crest and the medial clavicle in a modern sample of American males and females. *American Journal of Physical Anthropology* 68(4): 457-466.

Weaver, T.D. Steudel-Numbers, K. 2005. Does climate or mobility explain the differences in body proportions between Neandertals and their Upper Paleolithic successors? *Evolutionary Anthropology* 14(6): 218-223.

Weise, M. De-Levi, S. Barnes, K.M. Gafni, R.I. Abad, V. Baron, J. 2001. Effects of estrogen on growth plate senescence and epiphyseal fusion. *Proceedings of the National Academy of Sciences of the United States of America* 98(12): 6871–6876.

Wells, J.C.K. 2000. Natural Selection and Sex Differences in Morbidity and Mortality in Early Life. *Journal of Theoretical Biology* 202(1): 65-76.

White, T. 2000. Human Osteology, 2nd Edition. Academic Press: San Diego.

Winkler, L.A. 1996. Appearance of Ossification Centers of the Lower Arm, Wrist, Lower Leg, and Ankle in Immature Orangutans and Chimpanzees With an Assessment of the Relationship of Ossification to Dental Development. *American Journal of Physical Anthropology* 99(1): 191-203.

Wintheiser, J.G. Clauser, D.A. Tappen, N.C. 1977. Sequence of Eruption of Permanent Teeth and Epiphyseal Union in Three Species of African Monkeys. *Folia Primatologica* 27(3): 178-197.

Witschi, E. 1962. Development: rat. In: Altman PL, Dittmer DS, editors. *Growth Including Reproductive and Morphological Development*. Biological Handbooks of the Federation of American Societies for Experimental Biology: Washington. pp 302–314.

Ye, Y. Wang, C. Cao, L. 1992. Skeletal maturity of the hand and wrist in Chinese children in Changsha assessed by TW2 method. *Annals of Human Biology* 19(4): 427-430.

Yu, N. Jensen-Seaman, M.I. Chemnick, L. Kidd, J.R. Deinard, A.S. Ryder, O. Kidd, K.K. Li, W.H. 2003. Low nucleotide diversity in chimpanzees and bonobos. *Genetics* 164(4): 1511-1518.

Zihlman, A. 1984. *Body Build and Tissue Composition in Pan paniscus and Pan troglodytes, with Comparisons to Other Hominoids*. Susman, R.L. (ed.) The Pygmy Chimpanzee. Springer: Netherlands. pp. 179-200.

Zihlman, A. Bolter, D. & Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *Proceedings of the National Academy of Sciences of the United States of America* 101(29), 10541-10543.

Zihlman, A. Bolter, D. Boesch, C. 2007. Skeletal and dental growth and development in chimpanzees of the Tai National Park, Cote D’ivoire. *Journal of Zoology* 273(1): 63-73.

Zhilman A.L, & Cramer, D.L. 1978. Skeletal differences between pygmy (*Pan paniscus*) and common (*Pan troglodytes*) chimpanzees. *Folia Primatologica* 29(2): 86-94.

Zihlman, A.L. Morbeck, M.E. Goodall, J. 1990. Skeletal biology and individual life history of Gombe chimpanzees. *Journal of Zoology* 221(1): 37–61.

Zuck, T.T. 1938. The age order of epiphyseal union in the guinea pig. *The* *Anatomical Record* 70(4): 389–399.

**Appendix**

## 8.1 Demographic data

The following tables present location data for the specimens used in this study as discussed in Chapter 3, section 3.1.3.

: Reported locations for wild specimens at the Museum of Central Africa.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| ***Pan troglodytes schweinfurthii*** | | ***Pan paniscus*** | | |
| **location** | ***N*** | **location** | | ***N*** |
| ? Epulu | 1 | ? Ibembo | | 1 |
| ? Stanleyville | 1 | Basankusu | | 1 |
| Andudu (Uelé) | 1 | Batiakayandja, 18 km S.S.W. Ponthierville | | 2 |
| Bafwanaubo (Ituri bos) | 1 | Batiamoyowa, 35 km S.S.W. Ponthierville | | 4 |
| Bururi (Burundi) | 1 | Biondo, 30 km W. Ponthierville | | 2 |
| Buta | 4 | Bore, 13 km S.S.W. Ponthierville | | 1 |
| Congo | 1 | Coquilhatville | | 3 |
| Epulu | 1 | Djolu | | 5 |
| Epulu, terr. Mambasa | 1 | Dongo, 15 km S.E. Yahuma | | 3 |
| Kilo | 1 | Dongo, Oshwe 50 km S. Dekese (Kasai) | | 1 |
| Lugundu (Nyunzu) | 1 | Lingomo (Ikela), alt: 350 m | | 1 |
| Mawambi | 3 | Lulongo district (Mompono) | | 1 |
| Moba | 1 | Stanleyville left bank | | 1 |
| Muma (Prov. Uelé) terr. Abandia | 1 | Wamba (35 km E. Balangala, terr. Basankusu) | | 3 |
| Poko | 1 | **unspecified *Pan*** | | |
| region Bafwasende | 2 | **location** | ***N*** | |
| region Lubongola Chefferie Warega | 1 | Yahuma, terr. Yahuma | 1 | |
| Stanley Falls | 1 | ***Pan troglodytes troglodytes*** | | |
| Stanleyville | 1 | **location** | ***N*** | |
| Ubangi | 1 | Mayumbe | 2 | |
| Unaputi | 3 |  |  | |

: Locations from which *Pan troglodytes troglodytes* specimens were collected at the Powell-Cotton Museum.

|  |  |
| --- | --- |
| **location** | ***N*** |
| Batouri District/Cameroon | 4 |
| Beri/Batouri District/Cameroon | 1 |
| Between Batouri-Lomie/Cameroon | 3 |
| Bipindi District/Cameroon | 1 |
| Ebobonku/Nsang Melima/Cameroon | 2 |
| Kanyol/Batouri District/Cameroon | 1 |
| Kuambo/Bipindi-Kribi Rd/Cameroon | 1 |
| Lelo/Batouri District/Cameroon | 5 |
| Lolodorf-Mbalemajo Rd/Cameroon | 1 |
| Meyoss/Batouri District/Cameroon | 9 |
| Mifiaberg/Bipindi District/Cameroon | 1 |
| Ndinga/Batouri District/Cameroon | 2 |
| Ndokofass/NE of Yabassi/Cameroon | 1 |
| Obala/Batouri District/Cameroon | 31 |
| Olangina/Cameroon | 1 |
| River Sassa/SE L.Albert/Congo | 1 |
| S of Yaounde/Cameroon | 4 |

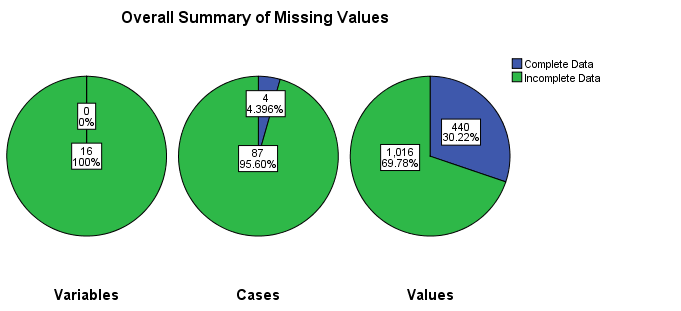
: Provenience for specimens from the University of Zurich and re-classification.

|  |  |  |
| --- | --- | --- |
| **location** | ***N*** | **sub-species re-classification** |
| unknown | 38 | none |
| captive | 1 | none |
| captive animal from Liberia | 1 | none |
| East Africa | 1 | none |
| Equatorial Guinea | 2 | *Pan troglodytes troglodytes* |
| Liberia | 1 | *Pan troglodytes verus* |
| Nigeria | 1 | *Pan troglodytes vellerosus* |
| Sierra Leone, West Africa | 1 | *Pan troglodytes verus* |

***8.2 Outputs from Imputation Analysis***

***8.2.1 Pan paniscus combined-sex analysis of patterns***

Presented here is an analysis of missing tooth data used for multiple imputation as discussed in Chapter 3, section 3.3.3. Imputation was calculated using logistic regression. Imputation iteration data available in section 8.1 of the digital appendix. Missing value summaries (Figures 8.1, 8.3, 8.5) provides data for the number of missing cases (individuals) and vales (teeth) used for imputation analysis. Figures 8.2, 8.4 and 8.6 are plots representing the most common patterns of missing tooth entries. The most common patterns are listed in descending order from top to bottom.

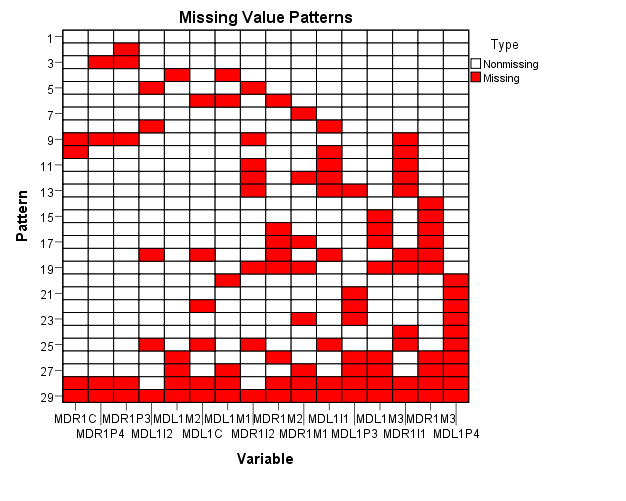


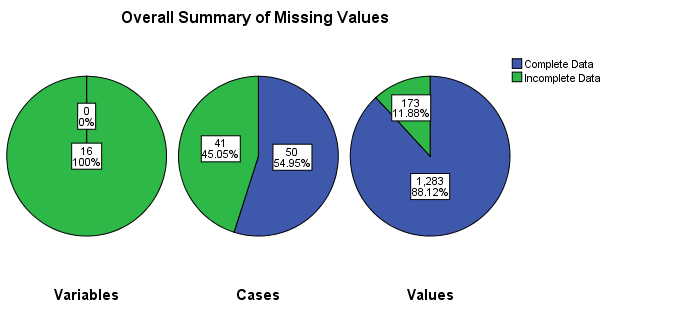
**Figure 8.1** Summary of missing values for *Pan paniscus* combined sex multiple imputation

**Table 8.4** Variable summary for missing tooth data in *Pan paniscus* combined sex multiple imputation.

|  |  |  |  |
| --- | --- | --- | --- |
| **tooth** | **missing** | | **valid *N*** |
| ***N*** | **percent** |
| MDL1P4 | 67 | 73.60% | 24 |
| MDR1M3 | 67 | 73.60% | 24 |
| MDR1I1 | 67 | 73.60% | 24 |
| MDL1M3 | 65 | 71.40% | 26 |
| MDL1P3 | 65 | 71.40% | 26 |
| MDL1I1 | 65 | 71.40% | 26 |
| MDR1M1 | 65 | 71.40% | 26 |
| MDR1M2 | 64 | 70.30% | 27 |
| MDR1I2 | 64 | 70.30% | 27 |
| MDL1M1 | 62 | 68.10% | 29 |
| MDL1C | 62 | 68.10% | 29 |
| MDL1M2 | 61 | 67.00% | 30 |
| MDL1I2 | 61 | 67.00% | 30 |
| MDR1P3 | 61 | 67.00% | 30 |
| MDR1P4 | 60 | 65.90% | 31 |
| MDR1C | 60 | 65.90% | 31 |

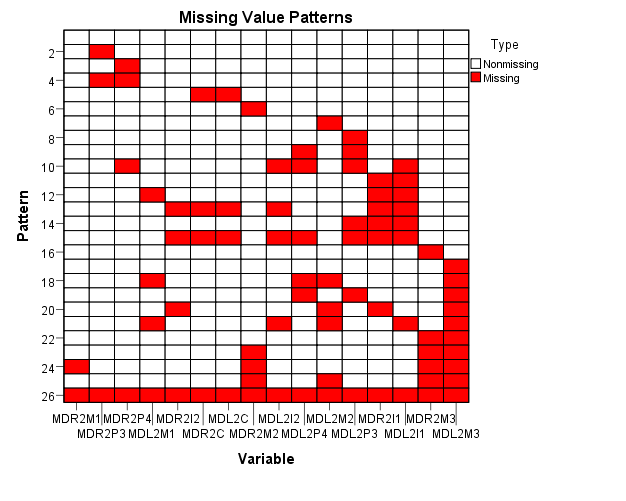
**Figure 8.2** Missing value patterns for *Pan paniscus* combined sex multiple imputation.

**8.2.2** ***Pan troglodytes* females analysis of patterns**

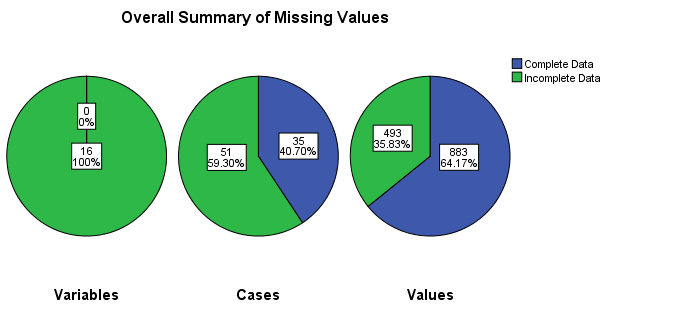
**Figure 8.3** Summary of missing values for *Pan troglodytes* females multiple imputation

**Table 8.5** Variable summary for missing tooth data in *Pan troglodytes* females multiple imputation.

|  |  |  |  |
| --- | --- | --- | --- |
| **tooth** | **missing** | | **valid *N*** |
| ***N*** | **percent** |
| MDL2M3 | 23 | 25.30% | 68 |
| MDR2M3 | 17 | 18.70% | 74 |
| MDL2I1 | 13 | 14.30% | 78 |
| MDR2I1 | 12 | 13.20% | 79 |
| MDL2P3 | 11 | 12.10% | 80 |
| MDL2M2 | 10 | 11.00% | 81 |
| MDL2P4 | 10 | 11.00% | 81 |
| MDL2I2 | 10 | 11.00% | 81 |
| MDR2M2 | 10 | 11.00% | 81 |
| a. Maximum number of variables shown: 25 | | | |
| b. Minimum percentage of missing values for variable to be included: 10.0% | | | |



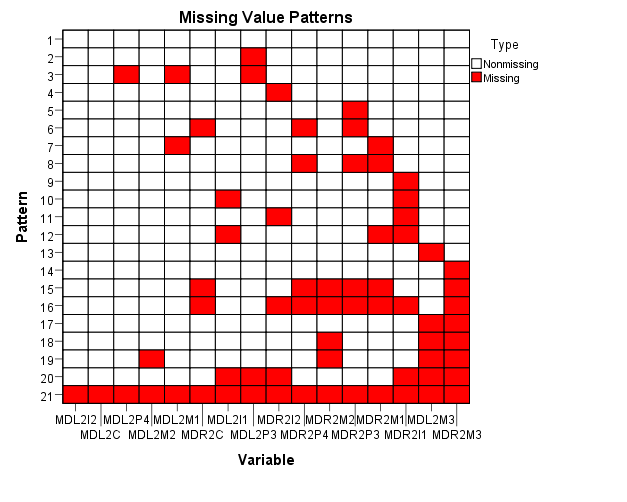
***8.2.3*** ***Pan troglodytes* males analysis of patterns**



**Figure 8.5** Summary of missing values for *Pan troglodytes* males multiple imputation

**Table 8.6** Variable summary for missing tooth data in *Pan troglodytes* males multiple imputation.

|  |  |  |  |
| --- | --- | --- | --- |
| **tooth** | **missing** | | **valid *N*** |
| ***N*** | **percent** |
| MDR2M3 | 38 | 44.20% | 48 |
| MDL2M3 | 35 | 40.70% | 51 |
| MDR2I1 | 34 | 39.50% | 52 |
| MDR2M1 | 32 | 37.20% | 54 |
| MDR2P3 | 32 | 37.20% | 54 |
| MDR2M2 | 31 | 36.00% | 55 |
| MDR2P4 | 31 | 36.00% | 55 |
| MDR2I2 | 31 | 36.00% | 55 |
| MDL2P3 | 30 | 34.90% | 56 |
| MDL2I1 | 30 | 34.90% | 56 |
| MDR2C | 30 | 34.90% | 56 |
| MDL2M1 | 29 | 33.70% | 57 |
| MDL2M2 | 28 | 32.60% | 58 |
| MDL2P4 | 28 | 32.60% | 58 |
| MDL2C | 27 | 31.40% | 59 |
| MDL2I2 | 27 | 31.40% | 59 |

**Figure 8.6** Missing value patterns for *Pan troglodytes* males multiple imputation

***8.3 Linear regression for long-bone length as plotted against dental score***

These data represent outputs from linear regression analysis considering the relationship between long-bone length and dental score as analysed in Chapter 4, section 4.1.1. Regression equations are presented in the text for section 4.1.1 These tables provide r-square values, ANOVA outputs and regression coefficients from the analysis.

**Table 8.7** Regression outputs for linear regression analysis of long-bone length plotted against dental score.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **species** | **bone** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** | **Durbin-Watson** |
| *Pan troglodytes* females | humerus | 0.93 | 0.866 | 0.864 | 5.5815 | 1.576 |
| radius | 0.917 | 0.84 | 0.838 | 16.7815 | 1.959 |
| ulna | 0.898 | 0.807 | 0.803 | 16.3876 | 2.441 |
| femur | 0.926 | 0.857 | 0.855 | 19.2221 | 1.674 |
| tibia | 0.926 | 0.857 | 0.855 | 16.7748 | 1.741 |
| fibula | 0.868 | 0.753 | 0.749 | 15.0836 | 1.922 |
| *Pan troglodytes* males | humerus | 0.875 | 0.766 | 0.761 | 22.8207 | 1.705 |
| radius | 0.933 | 0.87 | 0.867 | 16.0328 | 1.865 |
| ulna | 0.956 | 0.915 | 0.911 | 15.6222 | 1.811 |
| femur | 0.951 | 0.904 | 0.903 | 15.4383 | 1.962 |
| tibia | 0.941 | 0.886 | 0.884 | 14.3676 | 2.026 |
| fibula | 0.952 | 0.906 | 0.904 | 11.1698 | 2.082 |

**Table 8.8***Pan troglodytes* females linear regression ANOVA outputs for all long-bones as plotted against dental score.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **bone** | **model** | **sum of squares** | **df** | **mean square** | ***F*** | **sig.** |
| humerus | regression | 15867.07 | 1 | 15867.07 | 509.324 | 0.000 |
| residual | 2461.102 | 79 | 31.153 |  |  |
| total | 18328.173 | 80 |  |  |  |
| radius | regression | 106745.598 | 1 | 106745.598 | 379.043 | 0.000 |
| residual | 20276.527 | 72 | 281.618 |  |  |
| total | 127022.125 | 73 |  |  |  |
| ulna | regression | 58379.325 | 1 | 58379.325 | 217.386 | 0.000 |
| residual | 13964.698 | 52 | 268.552 |  |  |
| total | 72344.023 | 53 |  |  |  |
| femur | regression | 176650.194 | 1 | 176650.194 | 478.091 | 0.000 |
| residual | 29559.245 | 80 | 369.491 |  |  |
| total | 206209.439 | 81 |  |  |  |
| tibia | regression | 132829.062 | 1 | 132829.062 | 472.042 | 0.000 |
| residual | 22229.994 | 79 | 281.392 |  |  |
| total | 155059.056 | 80 |  |  |  |
| fibula | regression | 43670.026 | 1 | 43670.026 | 191.943 | 0.000 |
| residual | 14333.459 | 63 | 227.515 |  |  |
| total | 58003.485 | 64 |  |  |  |

**Table 8.9** *Pan troglodytes* males linear regression ANOVA outputs for all long-bones as plotted against dental score.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **bone** | **model** | **sum of squares** | **df** | **mean square** | ***F*** | **sig.** |
| humerus | regression | 83451.57 | 1 | 83451.57 | 160.243 | 0.000 |
| residual | 25518.36 | 49 | 520.783 |  |  |
| total | 108969.9 | 50 |  |  |  |
| radius | regression | 80946.75 | 1 | 80946.75 | 314.908 | 0.000 |
| residual | 12081.31 | 47 | 257.049 |  |  |
| total | 93028.06 | 48 |  |  |  |
| ulna | regression | 60063.74 | 1 | 60063.74 | 246.108 | 0.000 |
| residual | 5613.257 | 23 | 244.055 |  |  |
| total | 65677 | 24 |  |  |  |
| femur | regression | 119512.8 | 1 | 119512.8 | 501.436 | 0.000 |
| residual | 12632.08 | 53 | 238.341 |  |  |
| total | 132144.8 | 54 |  |  |  |
| tibia | regression | 83537.95 | 1 | 83537.95 | 404.683 | 0.000 |
| residual | 10734.26 | 52 | 206.428 |  |  |
| total | 94272.21 | 53 |  |  |  |
| fibula | regression | 45765.35 | 1 | 45765.35 | 366.814 | 0.000 |
| residual | 4741.05 | 38 | 124.764 |  |  |
| total | 50506.4 | 39 |  |  |  |

**Table 8.10** Coefficients of linear regression analysis of long-bones as plotted against dental score for *Pan troglodytes* females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **bone** | **model** | **unstandardized Coefficients** | | **standardized Coefficients** | **t** | **significance** |
| ***B*** | **std. error** | **Beta** |
| humerus | constant | -16.47(*B*1) | 3.624927 |  | -4.54623 | 0.000 |
| dental score | 0.2659 (*B*2) | 0.014876 | 0.921215 | 17.87679 | 0.000 |
| radius | constant | 82.935(*B*1) | 8.138 |  | 10.191 | 0.000 |
| dental score | 2.882(*B*2) | 0.148 | 0.917 | 19.469 | 0.000 |
| ulna | constant | 91.52(*B*1) | 11.971 |  | 7.646 | 0.000 |
| dental score | 3.007(*B*2) | 0.204 | 0.898 | 14.744 | 0.000 |
| femur | constant | 88.54(*B*1) | 7.676 |  | 11.535 | 0.000 |
| dental score | 3.141(*B*2) | 0.144 | 0.926 | 21.865 | 0.000 |
| tibia | constant | 70.27(*B*1) | 6.7 |  | 10.488 | 0.000 |
| dental score | 2.724(*B*2) | 0.125 | 0.926 | 21.727 | 0.000 |
| fibula | constant | 77.61(*B*1) | 9.241 |  | 8.399 | 0.000 |
| dental score | 2.244(*B*2) | 0.162 | 0.868 | 13.854 | 0.000 |

Note: *B*1 is the y intercept and *B*2 the slope for the regression equation.

**Table 8.11** Coefficients of linear regression analysis of long-bones as plotted against dental score for *Pan troglodytes* males.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **bone** | **model** | **unstandardized Coefficients** | | **standardized Coefficients** | **t** | **significance** |
| ***B*** | **std. error** | **Beta** |
| humerus | constant | 95.822(*B*1) | 11.308 |  | 8.474 | 0.000 |
| dental score | 2.901(*B*2) | 0.229 | 0.875 | 12.659 | 0.000 |
| radius | constant | 77.365(*B*1) | 8.209 |  | 9.425 | 0.000 |
| dental score | 2.948(*B*2) | 0.166 | 0.933 | 17.746 | 0.000 |
| ulna | constant | 79.1(*B*1) | 10.954 |  | 7.221 | 0.000 |
| dental score | 3.184(*B*2) | 0.203 | 0.956 | 15.688 | 0.000 |
| femur | constant | 80.171(*B*1) | 7.026 |  | 11.41 | 0.000 |
| dental score | 3.25(*B*2) | 0.145 | 0.951 | 22.393 | 0.000 |
| tibia | constant | 61.505(*B*1) | 6.861 |  | 8.964 | 0.000 |
| dental score | 2.828(*B*2) | 0.141 | 0.941 | 20.117 | 0.000 |
| fibula | constant | 53.522(*B*1) | 7.086 |  | 7.553 | 0.000 |
| dental score | 2.597(*B*2) | 0.136 | 0.952 | 19.152 | 0.000 |

Note: *B*1 is the y intercept and *B*2 the slope for the regression equation.

***8.4 Descriptive statistics for mid-fusion and complete fusion relative to dental score***

The following tables present descriptive statistics for ranges of dental scores at mid-fusion and complete fusion for all epiphyseal fusion sites as analysed in Chapter 4, section 4.2.1. The production of these was for the purposes of comparing dental development and skeletal fusion. These tables were those referred to but not presented in the text.

**Table 8.12** Median values and ranges of dental score for all mid-fusion epiphyses in *Pan troglodytes* males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median** | **minimum dental score** | **maximum dental score** |
| **dental score** |
| upper limb | proximal humerus | 7 | 63 | 60 | 64 |
| distal humerus | 5 | 58 | 43 | 60 |
| humeral medial epicondyle | 7 | 60 | 55 | 61 |
| proximal radius | 3 | 61 | 55 | 64 |
| distal radius | 8 | 63 | 55 | 64 |
| proximal ulna | 6 | 60.5 | 55 | 64 |
| distal ulna | 6 | 63 | 60 | 64 |
| hand | distal phalanges (hand) | 2 | 56.5 | 55 | 58 |
| base of metacarpal 1 | 2 | 58 | 55 | 61 |
| proximal and middle phalanges (hand) | 5 | 61 | 55 | 63 |
| metacarpal heads 2-5 | 2 | 62 | 61 | 63 |
| lower limb | femoral head | 4 | 60 | 55 | 64 |
| greater trochanter | 1 | 61 | 61 | 61 |
| lesser trochanter | 3 | 58 | 55 | 61 |
| distal femur | 7 | 62 | 59 | 64 |
| proximal tibia | 7 | 62 | 55 | 64 |
| distal tibia | 6 | 61 | 55 | 64 |
| proximal fibula | 5 | 63 | 60 | 64 |
| distal fibula | 7 | 60 | 55 | 64 |
| foot | calcaneus | 3 | 60 | 55 | 61 |
| talus | 0 |  |  |  |
| distal phalanges (foot) | 2 | 58 | 55 | 61 |
| middle phalanges (foot) | 3 | 59 | 55 | 61 |
| metatarsal heads (2-5) | 2 | 62 | 61 | 63 |
| base of metatarsal 1 | 2 | 60 | 59 | 61 |
| proximal phalanges (foot) | 2 | 60 | 59 | 61 |
| pelvis | triradiate | 8 | 60 | 31 | 61 |
| anterior inferior iliac spine | 1 | 55 | 55 | 55 |
| iliac crest | 5 | **64** | 63 | 64 |
| ischial epiphysis | 4 | 62.5 | 60 | 64 |
| clavicle | medial clavicle | 4 | **64** | 63 | 64 |
| lateral clavicle | 1 | 50 | 50 | 50 |
| scapula | coracoid | 6 | 60 | 58 | 61 |
| sub-coracoid and glenoid | 7 | 58 | 13 | 61 |
| acromium | 2 | 60 | 60 | 60 |
| medial border | 4 | **64** | 63 | 64 |

**Table 8.13** Median values and ranges of dental score for all complete fusion epiphyses in *Pan troglodytes* males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median** | **minimum dental score** | **maximum dental score** |
| **dental score** |
| upper limb | proximal humerus | 3 | **64** | 64 | 64 |
| distal humerus | 18 | 61.5 | 55 | 64 |
| humeral medial epicondyle | 13 | 63 | 59 | 64 |
| proximal radius | 10 | 63 | 60 | 64 |
| distal radius | 3 | **64** | 64 | 64 |
| proximal ulna | 12 | 63 | 59 | 64 |
| distal ulna | 4 | **64** | 63 | 64 |
| hand | distal phalanges (hand) | 5 | 63 | 59 | 64 |
| base of metacarpal 1 | 10 | 63.5 | 59 | 64 |
| proximal and middle phalanges (hand) | 8 | **64** | 62 | 64 |
| metacarpal heads 2-5 | 8 | **64** | 62 | 64 |
| lower limb | femoral head | 10 | 63 | 60 | 64 |
| greater trochanter | 12 | 63 | 59 | 64 |
| lesser trochanter | 12 | 63 | 59 | 64 |
| distal femur | 5 | **64** | 63 | 64 |
| proximal tibia | 5 | **64** | 63 | 64 |
| distal tibia | 6 | **64** | 63 | 64 |
| proximal fibula | 6 | **64** | 62 | 64 |
| distal fibula | 6 | **64** | 62 | 64 |
| foot | calcaneus | 11 | 63 | 59 | 64 |
| talus | 21 | 61 | 43 | 64 |
| distal phalanges (foot) | 9 | 63 | 59 | 64 |
| middle phalanges (foot) | 8 | 63.5 | 62 | 64 |
| metatarsal heads (2-5) | 7 | **64** | 62 | 64 |
| base of metatarsal 1 | 9 | **64** | 62 | 64 |
| proximal phalanges (foot) | 8 | **64** | 63 | 64 |
| pelvis | triradiate | 13 | 63 | 58 | 64 |
| anterior inferior iliac spine | 6 | **64** | 63 | 64 |
| iliac crest | 1 | **64** | 64 | 64 |
| ischial epiphysis | 5 | **64** | 63 | 64 |
| clavicle | medial clavicle | 1 | **64** | 64 | 64 |
| lateral clavicle | 9 | 63 | 58 | 64 |
| scapula | coracoid | 14 | 63 | 55 | 64 |
| sub-coracoid and glenoid | 14 | 63 | 59 | 64 |
| acromium | 6 | **64** | 63 | 64 |
| medial border | 1 | **64** | 64 | 64 |

**Table 8.14** Median values and ranges of dental score for all mid-fusion epiphyses in *Pan paniscus* females.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median** | **minimum dental score** | **maximum dental score** |
| **dental score** |
| upper limb | proximal humerus | 0 | - | - | - |
| distal humerus | 1 | 53 | 53 | 53 |
| humeral medial epicondyle | 3 | 53 | 51 | 62 |
| proximal radius | 1 | **64** | 64 | 64 |
| distal radius | 4 | **64** | 62 | 64 |
| proximal ulna | 2 | 57.5 | 53 | 62 |
| distal ulna | 3 | **64** | 64 | 64 |
| hand | distal phalanges (hand) | 2 | 53 | 53 | 53 |
| base of metacarpal 1 | 1 | 53 | 53 | 53 |
| proximal and middle phalanges (hand) | 2 | 53 | 53 | 53 |
| metacarpal heads 2-5 | 0 | - | - | - |
| lower limb | femoral head | 1 | 60 | 60 | 60 |
| greater trochanter | 1 | 60 | 60 | 60 |
| lesser trochanter | 0 | - | - | - |
| distal femur | 1 | **64** | 64 | 64 |
| proximal tibia | 1 | **64** | 64 | 64 |
| distal tibia | 0 | - | - | - |
| proximal fibula | 2 | **64** | 64 | 64 |
| distal fibula | 0 | - | - | - |
| foot | calcaneus | 1 | 62 | 62 | 62 |
| talus | 0 | - | - | - |
| distal phalanges (foot) | 2 | 52 | 51 | 53 |
| middle phalanges (foot) | 2 | 52 | 51 | 53 |
| metatarsal heads (2-5) | 2 | 52 | 51 | 53 |
| base of metatarsal 1 | 0 | - | - | - |
| proximal phalanges (foot) | 0 | - | - | - |
| pelvis | triradiate | 2 | 57.5 | 53 | 62 |
| anterior inferior iliac spine | 0 | - | - | - |
| iliac crest | 3 | **64** | 51 | 64 |
| ischial epiphysis | 1 | **64** | 64 | 64 |
| clavicle | medial clavicle | 0 | - | - | - |
| lateral clavicle | 0 | - | - | - |
| scapula | coracoid | 3 | 53 | 51 | 62 |
| sub-coracoid and glenoid | 3 | 53 | 51 | 62 |
| acromium | 2 | **64** | 64 | 64 |
| medial border | 1 | **64** | 64 | 64 |

**Table 8.15** Median values and ranges of dental score for all complete fusion epiphyses in *Pan paniscus* females.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median**  **dental score** | **minimum dental score** | **maximum dental score** |
| upper limb | proximal humerus | 3 | **64** | 62 | 64 |
| distal humerus | 7 | 62 | 51 | 64 |
| humeral medial epicondyle | 4 | **64** | 62 | 64 |
| proximal radius | 3 | **64** | 62 | 64 |
| distal radius | 0 | - | - | - |
| proximal ulna | 5 | **64** | 51 | 64 |
| distal ulna | 1 | 62 | 62 | 62 |
| hand | distal phalanges (hand) | 4 | **64** | 62 | 64 |
| base of metacarpal 1 | 3 | **64** | 62 | 64 |
| proximal and middle phalanges (hand) | 4 | **64** | 62 | 64 |
| metacarpal heads 2-5 | 4 | **64** | 62 | 64 |
| lower limb | femoral head | 3 | **64** | 64 | 64 |
| greater trochanter | 3 | **64** | 64 | 64 |
| lesser trochanter | 4 | **64** | 60 | 64 |
| distal femur | 2 | **64** | 64 | 64 |
| proximal tibia | 2 | **64** | 64 | 64 |
| distal tibia | 3 | **64** | 64 | 64 |
| proximal fibula | 0 | - | - | - |
| distal fibula | 2 | **64** | 64 | 64 |
| foot | calcaneus | 3 | **64** | 64 | 64 |
| talus | 5 | **64** | 53 | 64 |
| distal phalanges (foot) | 3 | **64** | 64 | 64 |
| middle phalanges (foot) | 3 | **64** | 64 | 64 |
| metatarsal heads (2-5) | 3 | **64** | 64 | 64 |
| base of metatarsal 1 | 3 | **64** | 64 | 64 |
| proximal phalanges (foot) | 3 | **64** | 64 | 64 |
| pelvis | triradiate | 5 | **61** | 60 | 64 |
| anterior inferior iliac spine | 3 | 64 | 51 | 64 |
| iliac crest | 0 | - | - | - |
| ischial epiphysis | 0 | - | - | - |
| clavicle | medial clavicle | 1 | 62 | 62 | 62 |
| lateral clavicle | 3 | **64** | 62 | 64 |
| scapula | coracoid | 4 | **64** | 62 | 64 |
| sub-coracoid and glenoid | 4 | **64** | 62 | 64 |
| acromium | 2 | 63 | 62 | 64 |
| medial border | 1 | 62 | 62 | 62 |

**Table 8.16** Median values and ranges of dental score for all mid-fusion epiphyses in *Pan paniscus* males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median** | **minimum dental score** | **maximum dental score** |
| **dental score** |
| upper limb | proximal humerus | 3 | **64** | 61 | 64 |
| distal humerus | 5 | 59 | 47 | 64 |
| humeral medial epicondyle | 5 | 60 | 54 | 61 |
| proximal radius | 5 | 60 | 54 | 61 |
| distal radius | 0 | - | - | - |
| proximal ulna | 1 | 47 | 47 | 47 |
| distal ulna | 0 | - | - | - |
| hand | distal phalanges (hand) | 2 | 46 | 45 | 47 |
| base of metacarpal 1 | 2 | 50.5 | 47 | 54 |
| proximal and middle phalanges (hand) | 3 | 54 | 47 | 60 |
| metacarpal heads 2-5 | 5 | 60 | 47 | 64 |
| lower limb | femoral head | 6 | 60.5 | 59 | 64 |
| greater trochanter | 3 | 60 | 54 | 60 |
| lesser trochanter | 2 | 59.5 | 59 | 60 |
| distal femur | 1 | **64** | 64 | 64 |
| proximal tibia | 1 | 60 | 60 | 60 |
| distal tibia | 0 | - | - | - |
| proximal fibula | 0 | - | - | - |
| distal fibula | 2 | 57.5 | 54 | 61 |
| foot | calcaneus | 2 | 53.5 | 47 | 60 |
| talus | 0 | - | - | - |
| distal phalanges (foot) | 2 | 57 | 54 | 60 |
| middle phalanges (foot) | 2 | 57 | 54 | 60 |
| metatarsal heads (2-5) | 2 | 57 | 54 | 60 |
| base of metatarsal 1 | 4 | 57 | 47 | 61 |
| proximal phalanges (foot) | 4 | 57 | 47 | 61 |
| pelvis | triradiate | 4 | 56.5 | 47 | 60 |
| anterior inferior iliac spine | 0 | - | - | - |
| iliac crest | 1 | **64** | 64 | 64 |
| ischial epiphysis | 4 | 61 | 60 | 64 |
| clavicle | medial clavicle | 1 | 54 | 54 | 54 |
| lateral clavicle | 0 | - | - | - |
| scapula | coracoid | 1 | 54 | 54 | 54 |
| sub-coracoid and glenoid | 3 | 59 | 54 | 60 |
| acromium | 0 | - | - | - |
| medial border | 1 | **64** | 64 | 64 |

**Table 8.17** Median values and ranges of dental score for all complete fusion epiphyses in *Pan paniscus* males.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **skeletal region** | **epiphyseal fusion site** | ***N*** | **median**  **dental score** | **minimum dental score** | **maximum dental score** |
| upper limb | proximal humerus | 0 | - | - | - |
| distal humerus | 7 | 60 | 47 | 64 |
| humeral medial epicondyle | 2 | 60.5 | 60 | 61 |
| proximal radius | 2 | **64** | 64 | 64 |
| distal radius | 2 | **64** | 64 | 64 |
| proximal ulna | 7 | 60 | 54 | 64 |
| distal ulna | 2 | **64** | 64 | 64 |
| hand | distal phalanges (hand) | 4 | 62.5 | 54 | 64 |
| base of metacarpal 1 | 1 | **64** | 64 | 64 |
| proximal and middle phalanges (hand) | 3 | **64** | 61 | 64 |
| metacarpal heads 2-5 | 2 | **64** | 64 | 64 |
| lower limb | femoral head | 1 | 61 | 61 | 61 |
| greater trochanter | 3 | **64** | 61 | 64 |
| lesser trochanter | 5 | 61 | 54 | 64 |
| distal femur | 1 | **64** | 64 | 64 |
| proximal tibia | 2 | **64** | 64 | 64 |
| distal tibia | 2 | **64** | 64 | 64 |
| proximal fibula | 2 | **64** | 64 | 64 |
| distal fibula | 2 | **64** | 64 | 64 |
| foot | calcaneus | 5 | 61 | 54 | 64 |
| talus | 9 | 60 | 47 | 64 |
| distal phalanges (foot) | 3 | **64** | 61 | 64 |
| middle phalanges (foot) | 3 | **64** | 61 | 64 |
| metatarsal heads (2-5) | 3 | **64** | 61 | 64 |
| base of metatarsal 1 | 2 | **64** | 64 | 64 |
| proximal phalanges (foot) | 2 | **64** | 64 | 64 |
| pelvis | triradiate | 5 | 61 | 60 | 64 |
| anterior inferior iliac spine | 6 | 61 | 59 | 64 |
| iliac crest | 0 | - | - | - |
| ischial epiphysis | 0 | - | - | - |
| clavicle | medial clavicle | 2 | **64** | 64 | 64 |
| lateral clavicle | 2 | 59 | 54 | 64 |
| scapula | coracoid | 6 | 60.5 | 59 | 64 |
| sub-coracoid and glenoid | 4 | 62.5 | 60 | 64 |
| acromium | 2 | **64** | 64 | 64 |
| medial border | 1 | **64** | 64 | 64 |

**Table 8.18** Mid-fusion and complete fusion median, 25th and 75th percentile dental score values for *Pan troglodytes* males.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **mid-fusion** | | | **complete fusion** | | |
| **median** | **25th percentile** | **75th percentile** | **median** | **25th percentile** | **75th percentile** |
| proximal humerus | 63 | 60 | 63 | 64.9 | 64.3 | - |
| distal humerus | 58 | 44.5 | 60 | 61.5 | 60 | 64.075 |
| humeral medial epicondyle | 60 | 58 | 61 | 63 | 60.5 | 64.45 |
| proximal radius | 61 | 55 | - | 63 | 61.5 | 64.675 |
| distal radius | 63 | 60.5 | 63.75 | 64.9 | 64.6 | - |
| proximal ulna | 60.5 | 57.25 | 61.825 | 63 | 60.25 | 64.45 |
| distal ulna | 63 | 61.5 | 64.075 | 64.75 | 63.4 | 65.125 |
| distal phalanges (hand) | 56.5 | 55 | - | 63 | 60 | 65.05 |
| base of metacarpal 1 | 58 | 55 | - | 63.5 | 62.75 | 64.675 |
| proximal and middle phalanges (hand) | 61 | 57.5 | 62 | 64.15 | 63 | 64.825 |
| metacarpals heads 2-5 | 62 | 61 | - | 64.15 | 63 | 64.825 |
| femoral head | 60 | 56 | 63.25 | 63 | 61.5 | 64.675 |
| greater trochanter | 60 | 59 | - | 63 | 62 | 64.6 |
| lesser trochanter | 58 | 55 | - | 63 | 60.5 | 64.525 |
| distal femur | 62 | 60 | 63 | 64.6 | 63.65 | 65.05 |
| proximal tibia | 62 | 60 | 63 | 64.6 | 63.65 | 65.05 |
| distal tibia | 62 | 60 | 63 | 64.6 | 63.65 | 65.05 |
| proximal fibula | 62.5 | 60 | 63.25 | 64.6 | 63.65 | 65.05 |
| distal fibula | 61 | 59.25 | 63 | 64.6 | 63.65 | 65.05 |
| calcaneus | 60 | 55 | - | 63 | 62 | 64.6 |
| talus | - | - | - | 61 | 58.5 | 63.5 |
| distal phalanges (foot) | 58 | 55 | - | 63 | 62.5 | 64.75 |
| middle phalanges (foot) | 59 | 55 | - | 63.5 | 63 | 64.825 |
| metatarsal heads 2-5 | 62 | 61 | - | 64 | 63 | 64.9 |
| base of metatarsal 1 | 60 | 59 | - | 64 | 63 | 64.75 |
| proximal phalanges (foot) | 60 | 59 | - | 64.15 | 63 | 64.825 |
| triradiate | 60 | 46.75 | 61 | 63 | 60 | 64.45 |
| anterior inferior iliac spine | 55 | 55 | 55 | 64.45 | 63.75 | 64.975 |
| iliac crest | 64.6 | 63 | 65.05 | 64.3 | 64.3 | 64.3 |
| ischial epiphysis | 62.5 | 60.5 | 63.75 | 64.6 | 63 | 65.05 |
| medial clavicle | 64.3 | 63.25 | 64.825 | 65.2 | 65.2 | 65.2 |
| lateral clavicle | 50 | 50 | 50 | 63 | 59 | 64.75 |
| coracoid | 60 | 59 | 61 | 63 | 60.5 | 64.45 |
| sub-coracoid and glenoid | 59 | 37.5 | 60.5 | 63 | 61.25 | 64.525 |
| acromium | 60 | 60 | 60 | 64.45 | 63 | 64.975 |
| medial border of scapula | 64.6 | 63.325 | 65.125 | 64.6 | 64.6 | 64.6 |

**Table 8.19** Mid-fusion and complete fusion median, 25th and 75th percentile dental score values for *Pan paniscus* females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **mid-fusion** | | | **complete fusion** | | |
| **median** | **25th percentile** | **75th percentile** | **median** | **25th percentile** | **75th percentile** |
| proximal humerus | - | - | - | 64.6 | 62 | - |
| distal humerus | 53 | 53 | 53 | 62 | 53 | 64.6 |
| humeral medial epicondyle | 57.5 | 53 | - | 64.3 | 62.5 | 65.05 |
| proximal radius | 64 | 64 | 64 | 64.6 | 62 | - |
| distal radius | 64.3 | 62.5 | 65.05 | - | - | - |
| proximal ulna | 57.5 | 53 | - | 64 | 56.5 | 64.9 |
| distal ulna | 64.6 | 64 | - | 62 | 62 | 62 |
| distal phalanges (hand) | 53 | 53 | 53 | 64.3 | 62.5 | 65.05 |
| base of metacarpal 1 | 53 | 53 | 53 | 64 | 62 | - |
| proximal and middle phalanges (hand) | 53 | 53 | 53 | 64.3 | 62.5 | 65.05 |
| metacarpals heads 2-5 | - | - | - | 64.3 | 62.5 | 65.05 |
| femoral head | 61 | 60 | - | 64.6 | 64 | - |
| greater trochanter | 60 | 60 | 60 | 64.3 | 62.5 | 65.05 |
| lesser trochanter | - | - | - | 64 | 61 | 64.9 |
| distal femur | 64.6 | 64 | - | 63.3 | 62 | - |
| proximal tibia | 64 | 64 | 64 | 64.6 | 62 | - |
| distal tibia | - | - | - | 64.3 | 62.5 | 65.05 |
| proximal fibula | 64.3 | 64 | - | 62 | 62 | 62 |
| distal fibula | - | - | - | 64 | 62 | - |
| calcaneus | 62 | 62 | 62 | 64.3 | 62.5 | 65.05 |
| talus | - | - | - | 62 | 53 | 64.6 |
| distal phalanges (foot) | 53 | 53 | 53 | 64.3 | 62.5 | 65.05 |
| middle phalanges (foot) | 53 | 53 | 53 | 64.3 | 62.5 | 65.05 |
| metatarsal heads 2-5 | 53 | 53 | 53 | 64.3 | 62.5 | 65.05 |
| base of metatarsal 1 | - | - | - | 64.3 | 62.5 | 65.05 |
| proximal phalanges (foot) | - | - | - | 64.3 | 62.5 | 65.05 |
| triradiate | 57.5 | 53 | - | 64 | 56.5 | 64.9 |
| anterior inferior iliac spine | - | - | - | 64 | 56.5 | 64.9 |
| iliac crest | 56.5 | 51 | - | - | - | - |
| ischial epiphysis | 64 | 64 | 64 | 63.3 | 53.75 | 65.05 |
| medial clavicle | - | - | - | 62 | 62 | 62 |
| lateral clavicle | - | - | - | 64 | 62 | - |
| coracoid | 53 | 51 | - | 64.3 | 62.5 | 65.05 |
| sub-coracoid and glenoid | 53 | 51 | - | 64.3 | 62.5 | 65.05 |
| acromium | 64.6 | 64 | - | 63.3 | 62 | - |
| medial border of scapula | 64 | 64 | 64 | 62 | 62 | 62 |

**Table 8.20** Mid-fusion and complete fusion median, 25th and 75th percentile dental score values for *Pan paniscus* males.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **mid-fusion** | | | **complete fusion** | | |
| **median** | **25th percentile** | **75th percentile** | **median** | **25th percentile** | **75th percentile** |
| proximal humerus | 64 | 61 | - | 64.9 | 64.3 | - |
| distal humerus | - | - | - | 61.5 | 60 | 64.075 |
| humeral medial epicondyle | 59 | 50.5 | 62.3 | 63 | 60.5 | 64.45 |
| proximal radius | 60 | 56.5 | 60.5 | 63 | 61.5 | 64.675 |
| distal radius | - | - | - | 64.9 | 64.6 | - |
| proximal ulna | 47 | 47 | 47 | 63 | 60.25 | 64.45 |
| distal ulna | - | - | - | 64.75 | 63.4 | 65.125 |
| distal phalanges (hand) | 46 | 45 | - | 63 | 60 | 65.05 |
| base of metacarpal 1 | 50.5 | 47 | - | 63.5 | 62.75 | 64.675 |
| proximal and middle phalanges (hand) | 54 | 47 | - | 64.15 | 63 | 64.825 |
| metacarpals heads 2-5 | 57 | 48.75 | 60.75 | 64.15 | 63 | 64.825 |
| femoral head | 60.5 | 59.75 | 64.15 | 63 | 61.5 | 64.675 |
| greater trochanter | 60 | 54 | - | 63 | 62 | 64.6 |
| lesser trochanter | 59.5 | 59 | - | 63 | 60.5 | 64.525 |
| distal femur | 64.3 | 64 | - | 64.6 | 63.65 | 65.05 |
| proximal tibia | 60 | 60 | 60 | 64.6 | 63.65 | 65.05 |
| distal tibia | - | - | - | 64.6 | 63.65 | 65.05 |
| proximal fibula | 64.6 | 64.6 | 64.6 | 64.6 | 63.65 | 65.05 |
| distal fibula | 57.5 | 54 | - | 64.6 | 63.65 | 65.05 |
| calcaneus | 53.5 | 47 | - | 63 | 62 | 64.6 |
| talus | - | - | - | 61 | 58.5 | 63.5 |
| distal phalanges (foot) | 57 | 54 | - | 63 | 62.5 | 64.75 |
| middle phalanges (foot) | 57 | 54 | - | 63.5 | 63 | 64.825 |
| metatarsal heads 2-5 | 57 | 54 | - | 64 | 63 | 64.9 |
| base of metatarsal 1 | 57 | 48.75 | 60.75 | 64 | 63 | 64.75 |
| proximal phalanges (foot) | 57 | 48.75 | 60.75 | 64.15 | 63 | 64.825 |
| triradiate | 56.5 | 48.75 | 59.75 | 63 | 60 | 64.45 |
| anterior inferior iliac spine | - | - | - | 64.45 | 63.75 | 64.975 |
| iliac crest | 64.6 | 64.6 | 64.6 | 64.3 | 64.3 | 64.3 |
| ischial epiphysis | 61 | 60.25 | 63.7 | 64.6 | 63 | 65.05 |
| medial clavicle | 54 | 54 | 54 | 65.2 | 65.2 | 65.2 |
| lateral clavicle | 64 | 64 | 64 | 63 | 59 | 64.75 |
| coracoid | 54 | 54 | 54 | 63 | 60.5 | 64.45 |
| sub-coracoid and glenoid | 59 | 54 | - | 63 | 61.25 | 64.525 |
| acromium | - | - | - | 64.45 | 63 | 64.975 |
| medial border of scapula | 64.6 | 64.6 | 64.6 | 64.6 | 64.6 | 64.6 |

***8.5*** ***Seriating epiphyseal fusion by mean epiphyseal fusion***

These tables represent normality tests for ranges of mean epiphyseal fusion values discussed in Chapter 4 (section 4.2.2b). This is in support of the one-way ANOVA and subsequent post-hoc Bonferroni where normality of the distribution of dental scores was assumed. The use of dental score as a continuous variable is justified in section 4.2.2b. Post-hoc Bonferroni test results are available in the digital appendix section 8.2.2.1.

**Table 8.21** Mean epiphyseal fusion normality tests for mid-fusion *Pan troglodytes* females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **Kolmogorov-Smirnov1.** | | | **Shapiro-Wilk** | | |
| **statistic** | **df** | **sig.** | **statistic** | **df** | **sig.** |
| proximal humerus | .324 | 8 | .013 | .755 | 8 | .009 |
| distal humerus | .384 | 8 | .001 | .708 | 8 | .003 |
| humeral medial epicondyle | .217 | 8 | .200\* | .897 | 8 | .269 |
| proximal radius | .226 | 8 | .200\* | .936 | 8 | .575 |
| distal radius | .175 | 3 | - | 1.000 | 3 | 1.000 |
| proximal ulna | .179 | 3 | - | .999 | 3 | .950 |
| distal ulna | .175 | 3 | - | 1.000 | 3 | 1.000 |
| distal phalanges (hand) | .179 | 3 | - | .999 | 3 | .950 |
| base of metacarpal 1 (hand) | .266 | 5 | .200\* | .824 | 5 | .126 |
| proximal and middle phalanges (hand) | .309 | 5 | .135 | .872 | 5 | .276 |
| heads of metacarpals 2-5 (hand) | .247 | 5 | .200\* | .961 | 5 | .812 |
| femoral head | .400 | 5 | .009 | .777 | 5 | .052 |
| greater trochanter | .210 | 5 | .200\* | .943 | 5 | .684 |
| lesser trochanter | .310 | 5 | .131 | .808 | 5 | .094 |
| distal femur | .282 | 5 | .200\* | .922 | 5 | .541 |
| proximal tibia | .153 | 10 | .200\* | .960 | 10 | .790 |
| distal tibial | .162 | 10 | .200\* | .931 | 10 | .453 |
| proximal fibula | .190 | 10 | .200\* | .946 | 10 | .620 |
| distal fibula | .188 | 10 | .200\* | .932 | 10 | .471 |
| triradiate | .188 | 9 | .200\* | .898 | 9 | .239 |
| anterior inferior iliac spine | - | - | - | - | - | - |
| iliac crest | .175 | 3 | - | 1.000 | 3 | 1.000 |
| ischial epiphysis | .272 | 3 | - | .947 | 3 | .554 |
| calcaneus | .203 | 3 | - | .994 | 3 | .850 |
| talus | .372 | 3 | - | .781 | 3 | .071 |
| distal phalanges (foot) | .179 | 3 | - | .999 | 3 | .950 |
| middle phalanges (foot) | .219 | 4 | - | .980 | 4 | .903 |
| metatarsal heads 2-5 (foot) | .219 | 4 | - | .980 | 4 | .903 |
| proximal phalanges (foot) | .316 | 4 | - | .779 | 4 | .070 |
| base of metatarsal 1 fusion (foot) | .207 | 4 | - | .966 | 4 | .816 |
| medial clavicle | .376 | 4 | - | .776 | 4 | .065 |
| lateral clavicle | .276 | 4 | - | .887 | 4 | .370 |
| coracoid | .249 | 8 | .153 | .842 | 8 | .080 |
| sub-coracoid and glenoid | .145 | 8 | .200\* | .928 | 8 | .498 |
| acromium | .249 | 8 | .153 | .876 | 8 | .171 |
| medial border | .200 | 8 | .200\* | .909 | 8 | .346 |

1. Lilliefors Significance Correction, \*. This is a lower bound of the true significance.

**Table 8.22** Mean epiphyseal fusion normality tests for mid-fusion *Pan troglodytes* males

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **Kolmogorov-Smirnov1.** | | | **Shapiro-Wilk** | | |
| **statistic** | **df** | **sig.** | **statistic** | **df** | **sig.** |
| proximal humerus | .344 | 3 | - | .841 | 3 | .215 |
| distal humerus | .385 | 3 | - | .750 | 3 | .000 |
| humeral medial epicondyle | .307 | 3 | - | .903 | 3 | .396 |
| proximal radius | .339 | 3 | - | .850 | 3 | .242 |
| distal radius | .177 | 3 | - | 1.000 | 3 | .961 |
| proximal ulna | .288 | 3 | - | .928 | 3 | .482 |
| distal ulna | .192 | 3 | - | .997 | 3 | .893 |
| distal phalanges (hand) | .317 | 3 | - | .887 | 3 | .346 |
| base of metacarpal 1 (hand) | .205 | 3 | - | .993 | 3 | .839 |
| proximal and middle phalanges (hand) | .325 | 3 | - | .876 | 3 | .312 |
| heads of metacarpals 2-5 (hand) | .355 | 3 | - | .819 | 3 | .159 |
| femoral head | .310 | 3 | - | .900 | 3 | .384 |
| greater trochanter | .245 | 3 | - | .971 | 3 | .672 |
| lesser trochanter | .254 | 3 | - | .963 | 3 | .632 |
| distal femur | .329 | 3 | - | .869 | 3 | .293 |
| proximal tibia | .177 | 3 | - | 1.000 | 3 | .961 |
| distal tibial | .177 | 3 | - | 1.000 | 3 | .961 |
| proximal fibula | .313 | 3 | - | .895 | 3 | .369 |
| distal fibula | .310 | 3 | - | .900 | 3 | .384 |
| triradiate | .238 | 3 | - | .976 | 3 | .702 |
| anterior inferior iliac spine | - | - | - | - | - | - |
| iliac crest | .365 | 3 | - | .797 | 3 | .107 |
| ischial epiphysis | .195 | 3 | - | .996 | 3 | .882 |
| calcaneus | .354 | 3 | - | .821 | 3 | .165 |
| talus | - | - | - | - | - | - |
| distal phalanges (foot) | .284 | 3 | - | .934 | 3 | .503 |
| middle phalanges (foot) | .339 | 3 | - | .850 | 3 | .242 |
| metatarsal heads 2-5 (foot) | .349 | 3 | - | .831 | 3 | .190 |
| proximal phalanges (foot) | .245 | 3 | - | .971 | 3 | .672 |
| base of metatarsal 1 fusion (foot) | .245 | 3 |  | .971 | 3 | .672 |
| medial clavicle | - | - | - | - | - | - |
| lateral clavicle | .319 | 3 | - | .885 | 3 | .340 |
| coracoid | .296 | 3 | - | .918 | 3 | .446 |
| sub-coracoid and glenoid | .385 | 3 | - | .750 | 3 | .000 |
| acromium | .178 | 3 | - | .999 | 3 | .954 |
| medial border | .365 | 3 | - | .797 | 3 | .107 |

1. Lilliefors Significance Correction

**Table 8.23** Mean epiphyseal fusion normality tests for complete fusion *Pan troglodytes* females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **Kolmogorov-Smirnov1.** | | | **Shapiro-Wilk** | | |
| **statistic** | **df** | **sig.** | **statistic** | **df** | **sig.** |
| proximal humerus | .423 | 5 | .004 | .640 | 5 | .002 |
| distal humerus | .269 | 5 | .200\* | .807 | 5 | .092 |
| humeral medial epicondyle | .315 | 5 | .118 | .870 | 5 | .268 |
| proximal radius | .289 | 5 | .200 | .928 | 5 | .582 |
| distal radius | .263 | 5 | .200\* | .839 | 5 | .161 |
| proximal ulna | .159 | 5 | .200\* | .975 | 5 | .905 |
| distal ulna | .229 | 5 | .200\* | .938 | 5 | .655 |
| distal phalanges (hand) | .264 | 5 | .200\* | .870 | 5 | .268 |
| base of metacarpal 1 (hand) | .222 | 5 | .200\* | .958 | 5 | .794 |
| proximal and middle phalanges (hand) | .253 | 5 | .200\* | .883 | 5 | .325 |
| heads of metacarpals 2-5 (hand) | .171 | 5 | .200\* | .984 | 5 | .954 |
| femoral head | .177 | 5 | .200\* | .980 | 5 | .933 |
| greater trochanter | .261 | 5 | .200\* | .936 | 5 | .638 |
| lesser trochanter | .159 | 5 | .200\* | .975 | 5 | .905 |
| distal femur | .274 | 5 | .200\* | .935 | 5 | .633 |
| proximal tibia | .222 | 5 | .200\* | .891 | 5 | .364 |
| distal tibial | .264 | 5 | .200\* | .894 | 5 | .376 |
| proximal fibula | .341 | 5 | .058 | .756 | 5 | .034 |
| distal fibula | .196 | 5 | .200\* | .968 | 5 | .865 |
| triradiate | .212 | 5 | .200\* | .899 | 5 | .406 |
| anterior inferior iliac spine | .258 | 5 | .200\* | .904 | 5 | .433 |
| iliac crest | - | - | - | - | - | - |
| ischial epiphysis | .218 | 5 | .200\* | .900 | 5 | .412 |
| calcaneus | .256 | 5 | .200\* | .826 | 5 | .131 |
| talus | .212 | 5 | .200\* | .950 | 5 | .735 |
| distal phalanges (foot) | .205 | 5 | .200\* | .921 | 5 | .535 |
| middle phalanges (foot) | .305 | 5 | .144 | .842 | 5 | .170 |
| metatarsal heads 2-5 (foot) | .245 | 5 | .200\* | .864 | 5 | .241 |
| proximal phalanges (foot) | .435 | 5 | .002 | .668 | 5 | .004 |
| base of metatarsal 1 fusion (foot) | .302 | 5 | .155 | .803 | 5 | .086 |
| medial clavicle | .231 | 5 | .200\* | .886 | 5 | .337 |
| lateral clavicle | .358 | 5 | .035 | .801 | 5 | .082 |
| coracoid | .268 | 5 | .200\* | .852 | 5 | .200 |
| sub-coracoid and glenoid | .337 | 5 | .065 | .746 | 5 | .028 |
| acromium | .253 | 5 | .200\* | .879 | 5 | .306 |
| medial border | - | - | - | - | - | - |

1. Lilliefors Significance Correction, \*. This is a lower bound of the true significance.

**Table 8.24** Mean epiphyseal fusion normality tests for complete fusion *Pan troglodytes* males.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **epiphysis** | **Kolmogorov-Smirnov1.** | | | **Shapiro-Wilk** | | |
| **Statistic** | **df** | **sig.** | **statistic** | **df** | **sig.** |
| proximal humerus | .302 | 3 | - | .910 | 3 | .417 |
| distal humerus | .328 | 3 | - | .870 | 3 | .296 |
| humeral medial epicondyle | .245 | 3 | - | .971 | 3 | .672 |
| proximal radius | .344 | 3 | - | .841 | 3 | .215 |
| distal radius | .328 | 3 | - | .871 | 3 | .298 |
| proximal ulna | .245 | 3 | - | .971 | 3 | .672 |
| distal ulna | .369 | 3 | - | .789 | 3 | .089 |
| distal phalanges (hand) | .370 | 3 | - | .785 | 3 | .080 |
| base of metacarpal 1 (hand) | .252 | 3 | - | .966 | 3 | .643 |
| proximal and middle phalanges (hand) | .302 | 3 | - | .910 | 3 | .417 |
| heads of metacarpals 2-5 (hand) | .302 | 3 | - | .910 | 3 | .417 |
| femoral head | .365 | 3 | - | .797 | 3 | .107 |
| greater trochanter | .289 | 3 | - | .927 | 3 | .478 |
| lesser trochanter | .324 | 3 | - | .877 | 3 | .316 |
| distal femur | .302 | 3 | - | .910 | 3 | .417 |
| proximal tibia | .302 | 3 | - | .910 | 3 | .417 |
| distal tibial | .302 | 3 | - | .910 | 3 | .417 |
| proximal fibula | .302 | 3 | - | .910 | 3 | .417 |
| distal fibula | .302 | 3 | - | .910 | 3 | .417 |
| triradiate | .185 | 3 | - | .998 | 3 | .923 |
| anterior inferior iliac spine | .175 | 3 | - | 1.000 | 3 | .995 |
| iliac crest | - | - | - | - | - | - |
| ischial epiphysis | .365 | 3 | - | .797 | 3 | .107 |
| calcaneus | .368 | 3 | - | .790 | 3 | .090 |
| talus | .178 | 3 | - | 1.000 | 3 | .959 |
| distal phalanges (foot) | .219 | 3 | - | .987 | 3 | .780 |
| middle phalanges (foot) | .219 | 3 | - | .987 | 3 | .780 |
| metatarsal heads 2-5 (foot) | .227 | 3 | - | .983 | 3 | .747 |
| proximal phalanges (foot) | .219 | 3 | - | .987 | 3 | .780 |
| base of metatarsal 1 fusion (foot) | .333 | 3 | - | .862 | 3 | .274 |
| medial clavicle | - | - | - | - | - | - |
| lateral clavicle | .363 | 3 | - | .802 | 3 | .119 |
| coracoid | .339 | 3 | - | .850 | 3 | .242 |
| sub-coracoid and glenoid | .353 | 3 | - | .823 | 3 | .170 |
| acromium | .291 | 3 | - | .925 | 3 | .470 |
| medial border | - | - | - | - | - | - |
| 1. Lilliefors Significance Correction | | | | | | |

***8.6 Linear regression comparisons with Shea (1981)***

The following data relate to linear regression of log10 transformed upper limb (humerus + radius) and lower limb (femur + tibia) intermembral indicies for comparison to Shea (1981). This is analysed in Chapter 4, section 4.3.1. Regression equations are found in text. Shea (1981) found a highly linear relationship between these indicies and this is reproduced in this study for an expanded number of *Pan troglodytes* sub-species.

**Table 8.25** Regression summary for comparison of upper vs. lower limb with Shea (1981) in *Pan paniscus* and *Pan troglodytes*.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **species** | **sex** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** |
| *Pan troglodytes* | males | 0.985 | 0.97 | 0.969 | 0.01557 |
| females | 0.991 | 0.983 | 0.983 | 0.0113 |
| *Pan paniscus* | males | 0.995 | 0.991 | 0.99 | 0.01071 |
| females | 0.995 | 0.99 | 0.988 | 0.00977 |

**Table 8.26** Linear regression ANOVA outputs for *Pan troglodytes* and *Pan paniscus* males and females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species** | **sex** | **model** | **sum of squares** | **df** | **mean square** | ***F*** | **sig.** |
| *Pan troglodytes* | males | regression | 0.353 | 1 | 0.353 | 1457.009 | 0.000 |
| residual | 0.011 | 45 | 0 |  |  |
| total | 0.364 | 46 |  |  |  |
| females | regression | 0.526 | 1 | 0.526 | 4120.634 | 0.000 |
| residual | 0.009 | 71 | 0 |  |  |
| total | 0.536 | 72 |  |  |  |
| *Pan paniscus* | males | regression | 0.087 | 1 | 0.087 | 757.571 | 0.000 |
| residual | 0.001 | 7 | 0 |  |  |
| total | 0.088 | 8 |  |  |  |
| females | regression | 0.048 | 1 | 0.048 | 499.006 | 0.000 |
| residual | 0 | 5 | 0 |  |  |
| total | 0.048 | 6 |  |  |  |

**Table 8.27** Coefficients for linear regression analysis comparison with Shea (1981) for *Pan troglodytes* and *Pan paniscus* males and females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **species** | **sex** | **unstandardized coefficients** | | **standardized coefficients** | **t** | **significance** |
| ***B*** | **std. error** | **Beta** |
| *Pan troglodytes* | males | 0.215(*B*1) | 0.064 |  | 3.38 | 0.002 |
| 0.926(*B*2) | 0.024 | 0.985 | 38.171 | 0.000 |
| females | 0.022(*B*1) | 0.042 |  | 0.524 | 0.602 |
| 1(*B*2) | 0.016 | 0.991 | 64.192 | 0.000 |
| *Pan paniscus* | males | 0.042(*B*1) | 0.096 |  | 0.436 | 0.676 |
| 0.988(*B*2) | 0.036 | 0.995 | 27.524 | 0.000 |
| females | 0.303(*B*1) | 0.105 |  | 2.881 | 0.035 |
| 0.889(*B*2) | 0.04 | 0.995 | 22.338 | 0.000 |

Note: B1 is the y intercept and B2 the slope for the regression equation.

***8.7 Regression of serially homologous limb elements in* Pan troglodytes*.***

The following tables relate to linear regression of serially homologous limb elements in *Pan troglodytes*. This is analysed in section 4.3.2. These tables provide r-square values, ANOVA results, and coefficients for regression.

**Table 8.28** Multiple limb element linear regression outputs for Pan troglodyes and Pan paniscus males and females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **species** | **sex** | **comparison** | ***R*** | ***R*2** | **adjusted *R*2** | **std. error of the estimate** | **Durbin-Watson** |
| *Pan troglodytes* | females | humerus-femur | 0.992 | 0.983 | 0.983 | 0.012276 | 1.565 |
| radius-tibia | 0.986 | 0.971 | 0.971 | 0.014687 | 1.637 |
| humerus-radius | 0.987 | 0.975 | 0.975 | 0.01351 | 1.672 |
| tibia-femur | 0.99 | 0.981 | 0.981 | 0.013891 | 1.694 |
| males | humerus-femur | 0.856 | 0.734 | 0.728 | 0.045988 | 1.217 |
| radius-tibia | 0.992 | 0.985 | 0.985 | 0.011326 | 1.631 |
| humerus-radius | 0.95 | 0.903 | 0.901 | 0.027957 | 1.477 |
| tibia-femur | 0.995 | 0.989 | 0.989 | 0.010299 | 1.623 |
| *Pan paniscus* | females | humerus-femur | 0.994 | 0.989 | 0.987 | 0.008689 | 2.283 |
| radius-tibia | 0.988 | 0.976 | 0.973 | 0.013074 | 3.126 |
| humerus-radius | 0.999 | 0.998 | 0.998 | 0.003825 | 2.287 |
| tibia-femur | 0.993 | 0.986 | 0.985 | 0.009504 | 2.611 |
| males | humerus-femur | 0.981 | 0.962 | 0.958 | 0.022096 | 2.708 |
| radius-tibia | 0.996 | 0.992 | 0.991 | 0.009931 | 1.507 |
| humerus-radius | 0.987 | 0.974 | 0.972 | 0.018772 | 3.014 |
| tibia-femur | 0.996 | 0.992 | 0.991 | 0.008924 | 2.318 |

**Table 8.29**Multiple limb-element linear regression ANOVA outputs for *Pan troglodytes* males and females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **sex** | **comparison** | **model** | **sum of squares** | **df** | **mean square** | ***F*** | **sig.** |
| females | humerus-femur | regression | 0.735 | 1 | 0.735 | 4878.193 | 0.000 |
| residual | 0.013 | 83 | 0 |  |  |
| total | 0.748 | 84 |  |  |  |
| radius-tibia | regression | 0.556 | 1 | 0.556 | 2579.793 | 0.000 |
| residual | 0.016 | 76 | 0 |  |  |
| total | 0.573 | 77 |  |  |  |
| humerus-radius | regression | 0.548 | 1 | 0.548 | 3002.04 | 0.000 |
| residual | 0.014 | 77 | 0 |  |  |
| total | 0.562 | 78 |  |  |  |
| tibia-femur | regression | 0.827 | 1 | 0.827 | 4283.421 | 0.000 |
| residual | 0.016 | 84 | 0 |  |  |
| total | 0.843 | 85 |  |  |  |
| males | humerus-femur | regression | 0.309 | 1 | 0.309 | 145.877 | 0.000 |
| residual | 0.112 | 53 | 0.002 |  |  |
| total | 0.421 | 54 |  |  |  |
| radius-tibia | regression | 0.417 | 1 | 0.417 | 3249.152 | 0.000 |
| residual | 0.006 | 50 | 0 |  |  |
| total | 0.423 | 51 |  |  |  |
| humerus-radius | regression | 0.348 | 1 | 0.348 | 445.029 | 0.000 |
| residual | 0.038 | 48 | 0.001 |  |  |
| total | 0.385 | 49 |  |  |  |
| tibia-femur | regression | 0.537 | 1 | 0.537 | 5066.315 | 0.000 |
| residual | 0.006 | 56 | 0 |  |  |
| total | 0.543 | 57 |  |  |  |

**Table 8.30** Multiple limb-element linear regression ANOVA outputs for Pan paniscus males and females.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **sex** | **comparison** | **model** | **sum of squares** | **df** | **mean square** | ***F*** | **sig.** |
| females | humerus-femur | regression | 0.053 | 1 | 0.053 | 697.348 | 0.000 |
| residual | 0.001 | 8 | 0 |  |  |
| total | 0.053 | 9 |  |  |  |
| radius-tibia | regression | 0.062 | 1 | 0.062 | 364.52 | 0.000 |
| residual | 0.002 | 9 | 0 |  |  |
| total | 0.064 | 10 |  |  |  |
| humerus-radius | regression | 0.053 | 1 | 0.053 | 3627.4 | 0.000 |
| residual | 0 | 7 | 0 |  |  |
| total | 0.053 | 8 |  |  |  |
| tibia-femur | regression | 0.065 | 1 | 0.065 | 717.866 | 0.000 |
| residual | 0.001 | 10 | 0 |  |  |
| total | 0.066 | 11 |  |  |  |
| males | humerus-femur | regression | 0.124 | 1 | 0.124 | 254.261 | 0.000 |
| residual | 0.005 | 10 | 0 |  |  |
| total | 0.129 | 11 |  |  |  |
| radius-tibia | regression | 0.095 | 1 | 0.095 | 964.013 | 0.000 |
| residual | 0.001 | 8 | 0 |  |  |
| total | 0.096 | 9 |  |  |  |
| humerus-radius | regression | 0.134 | 1 | 0.134 | 380.651 | 0.000 |
| residual | 0.004 | 10 | 0 |  |  |
| total | 0.138 | 11 |  |  |  |
| tibia-femur | regression | 0.088 | 1 | 0.088 | 1101.749 | 0.000 |
| residual | 0.001 | 9 | 0 |  |  |
| total | 0.088 | 10 |  |  |  |

**Table 8.31** Coefficients for linear regression in *Pan troglodytes* males and females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **sex** | **comparison** | **unstandardized coefficients** | | **standardized coefficients** | **t** | **significance** |
| ***B*** | **std. error** | **Beta** |
| females | humerus-femur | 0.02(*B*1) | 0.034 |  | 0.589 | 0.557 |
|  | 0.99(*B*2) | 0.014 | 0.992 | 69.844 | 0.000 |
| radius-tibia | -0.051(*B*1) | 0.047 |  | -1.096 | 0.277 |
|  | 1.005(*B*2) | 0.02 | 0.986 | 50.792 | 0.000 |
| humerus-radius | 0.046(*B*1) | 0.043 |  | 1.078 | 0.284 |
|  | 0.997(*B*2) | 0.018 | 0.987 | 54.791 | 0.000 |
| tibia-femur | 0.175(*B*1) | 0.034 |  | 5.178 | 0.000 |
|  | 0.957(*B*2) | 0.015 | 0.99 | 65.448 | 0.000 |
| males | humerus-femur | 0.558(*B*1) | 0.15 |  | 3.731 | 0.000 |
|  | 0.765(*B*2) | 0.063 | 0.856 | 12.078 | 0.000 |
| radius-tibia | 0.212(*B*1) | 0.037 |  | 5.684 | 0.000 |
|  | 0.927(*B*2) | 0.016 | 0.992 | 57.001 | 0.000 |
| humerus-radius | 0.217(*B*1) | 0.102 |  | 2.132 | 0.038 |
|  | 0.92(*B*2) | 0.044 | 0.95 | 21.096 | 0.000 |
| tibia-femur | 0.26(*B*1) | 0.029 |  | 8.817 | 0.000 |
|  | 0.921(*B*2) | 0.013 | 0.995 | 71.178 | 0.000 |

Note: B1 is the y intercept and B2 the slope for the regression equation.

**Table 8.32** Coefficients for linear regression in *Pan paniscus* males and females.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **sex** | **comparison** | **unstandardized coefficients** | | **standardized coefficients** | **t** | **significance** |
| ***B*** | **std. error** | **Beta** |
| females | humerus-femur | 0.122(*B*1) | 0.085 |  | 1.428 | 0.191 |
|  | 0.946(*B*2) | 0.036 | 0.994 | 26.407 | 0.000 |
| radius-tibia | 0.346(*B*1) | 0.105 |  | 3.293 | 0.009 |
|  | 0.865(*B*2) | 0.045 | 0.988 | 19.092 | 0.000 |
| humerus-radius | 0.084(*B*1) | 0.038 |  | 2.195 | 0.064 |
|  | 0.981(*B*2) | 0.016 | 0.999 | 60.228 | 0.000 |
| tibia-femur | 0.363(*B*1) | 0.076 |  | 4.79 | 0.001 |
|  | 0.877(*B*2) | 0.033 | 0.993 | 26.793 | 0.000 |
| males | humerus-femur | 0.118(*B*1) | 0.142 |  | 0.832 | 0.425 |
|  | 0.951(*B*2) | 0.06 | 0.981 | 15.946 | 0.000 |
| radius-tibia | 0.219(*B*1) | 0.068 |  | 3.199 | 0.013 |
|  | 0.919(*B*2) | 0.03 | 0.996 | 31.049 | 0.000 |
| humerus-radius | -0.022(*B*1) | 0.123 |  | -0.177 | 0.863 |
|  | 1.025(*B*2) | 0.053 | 0.987 | 19.51 | 0.000 |
| tibia-femur | 0.219(*B*1) | 0.066 |  | 3.344 | 0.009 |
|  | 0.937(*B*2) | 0.028 | 0.996 | 33.193 | 0.000 |

Note: B1 is the y intercept and B2 the slope for the regression equation.

***8.8*** ***Normality tests for fusion as a percentage of long-bone length in* Pan troglodytes**

Epiphyseal fusion events were evaluated as a function of growth in length of long-bones. Results are presented in Chapter 5, section 5.3. The normality of ranges of epiphyseal fusion as a function of percentage of growth in length was tested to see if data were skewed. The following results demonstrate that the data were normally distributed for all epiphyses.

**Table 8.33** Normality plots for fusion as a percentage of long-bone length in *Pan troglodytes*

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **sex** | **epiphysis** | **Kolmogorov-Smirnova** | | | **Shapiro-Wilk** | | |
| **statistic** | **df** | **sig.** | **statistic** | **df** | **sig.** |
| females | proximal humerus | .171 | 21 | .112 | .936 | 21 | .182 |
| distal humerus | .200 | 10 | .200 | .918 | 10 | .340 |
| humeral medial epicondyle | .221 | 8 | .200 | .942 | 8 | .628 |
| proximal radius | .143 | 12 | .200 | .939 | 12 | .490 |
| distal radius | .188 | 17 | .111 | .902 | 17 | .075 |
| proximal ulna | .234 | 6 | .200 | .916 | 6 | .476 |
| distal ulna | .135 | 22 | .200 | .950 | 22 | .322 |
| femoral head | .255 | 11 | .044 | .855 | 11 | .050 |
| greater trochanter | .187 | 11 | .200 | .907 | 11 | .225 |
| lesser trochanter | .166 | 5 | .200 | .970 | 5 | .873 |
| distal femur | .097 | 21 | .200 | .964 | 21 | .603 |
| proximal tibia | .143 | 21 | .200 | .949 | 21 | .327 |
| distal tibia | .143 | 14 | .200 | .975 | 14 | .938 |
| proximal fibula | .118 | 16 | .200 | .973 | 16 | .878 |
| distal fibula | .228 | 10 | .150 | .955 | 10 | .732 |
| males | proximal humerus | .178 | 6 | .200 | .977 | 6 | .935 |
| distal humerus | .290 | 5 | .198 | .866 | 5 | .249 |
| humeral medial epicondyle | .222 | 8 | .200 | .891 | 8 | .237 |
| proximal radius | .207 | 8 | .200 | .902 | 8 | .302 |
| distal radius | .273 | 4 | - | .860 | 4 | .260 |
| proximal ulna | .319 | 6 | .056 | .843 | 6 | .138 |
| distal ulna | .198 | 6 | .200 | .924 | 6 | .531 |
| femoral head | .211 | 5 | .200 | .890 | 5 | .358 |
| greater trochanter | .354 | 3 | - | .821 | 3 | .165 |
| lesser trochanter | .216 | 4 | - | .954 | 4 | .740 |
| distal femur | .167 | 7 | .200 | .921 | 7 | .477 |
| proximal tibia | .233 | 7 | .200 | .950 | 7 | .732 |
| distal tibia | .233 | 7 | .200 | .950 | 7 | .732 |
| proximal fibula | .259 | 6 | .200 | .877 | 6 | .255 |
| distal fibula | .269 | 8 | .092 | .888 | 8 | .225 |