

THE TIMING OF GROWTH SPURTS IN NEANDERTHALS

by

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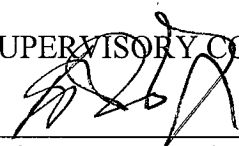
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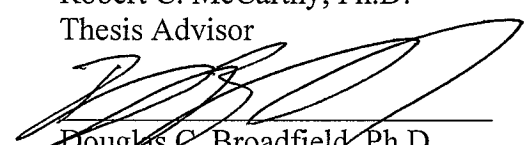
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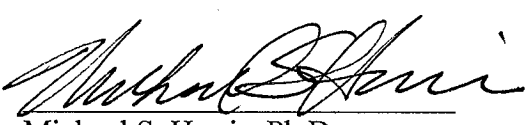
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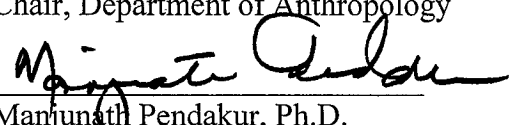
  
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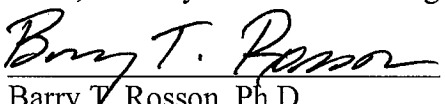
  
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## Abstract

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The timing of skeletal growth spurts in modern humans is unique among mammals. In modern humans, peak growth occurs after puberty during the adolescent period, whereas large-bodied non-human primates exhibit an earlier juvenile growth spurt. Based on limited data, previous researchers have suggested that Neanderthals experienced a late, modern human-like adolescent growth spurt. In this study, I examined the timing of stature and facial growth spurts in Neanderthals to test the hypothesis that Neanderthals grew like modern humans. In order to assess the timing of Neanderthal growth spurts, I plotted a non-human primate regression estimate of age at puberty onto Neanderthal stature and mandibular velocity growth curves. The mandibular growth curve exhibits a discernible growth spurt after puberty, reminiscent of the modern human adolescent growth spurt. Future research on additional regions of the skeleton is necessary to further refine this estimate for the timing of Neanderthal growth spurts.

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## Chapter 1: Introduction

Modern human growth, development and life history are unique compared to all other primates. We grow slowly, reproduce at late ages and have extended lifespans. One unique aspect of modern human growth and development is the adolescent growth spurt. It has been hypothesized that this pattern of growth is exhibited by both sexes of virtually every population of normally developing modern humans (Bogin, 1993, 1994, 1999, 2002, 2003, 2006). Compared to non-human primates, the timing of the modern human adolescent growth spurt is unique. Modern humans experience the greatest peak in growth after the onset of puberty. Non-human primate growth spurts, on the other hand, occur before puberty (Bogin, 2003). Additionally, while most modern humans experience a similar spurt during adolescence, the non-human primate spurt is varied among species, with large-bodied primates experiencing greater growth velocities than small-bodied primates (Leigh, 1996).

Differences in modern human and non-human primate growth have led researchers to question the origins of the adolescent growth spurt. Many researchers argue that *Homo erectus* was the first hominin species to exhibit a modern human-like pattern of growth (Ruff and Walker, 1993; Tardieu, 1998; Clegg and Aiello, 1999; Antón and Leigh, 2003). Studies on growth and development in *H. erectus* have primarily

focused on KNM-WT 15000, a ~1.55 m.y.a. juvenile erectine from Lake Turkana, Kenya (Ruff and Walker, 1993; Smith, 1993).

When this specimen was originally described, Ruff and Walker (1993) reconstructed KNM-WT 15000's body proportions using modern human growth standards. They assumed that KNM-WT 15000 was 11 to 12 years of age, which in modern humans would place him on the cusp of an adolescent growth spurt. This spurt would have theoretically increased KNM-WT 15000's stature- and body mass-at death from 160 cm and 48 kg to 185 cm and 68 kg in adulthood. Other researchers (Tardieu, 1998; Clegg and Aiello, 1999; Antón and Leigh, 2003) have also suggested that KNM-WT 15000 and other erectines might have experienced an adolescent growth spurt. Tardieu (1998) and Clegg and Aiello (1999) examined stature growth spurts, while Antón and Leigh (2003) examined facial growth. The results of these three studies weakly support the presence of an erectine adolescent growth spurt. Antón and Leigh (2003), in particular, argue that while the results of their study are equivocal, the presence of an adolescent growth spurt in *H. erectus* cannot be completely ruled out.

More recently, researchers have found KNM-WT 15000 had an intermediate pattern of growth. While early reconstructions suggested that KNM-WT 15000 was 11 to 12 years old at the time of his death, improved aging methods have shifted these estimates to ~8 years of age. New age estimates, an expanded knowledge of primate ontogeny, and new fossil discoveries have led researchers to question original body size estimations. Graves and colleagues (n.d) used distance and velocity growth curves from modern humans and chimpanzees to create a number of hypothetical growth curves for KNM-WT 15000. The researchers matched the best-fit curve to the sequence of life

history events already completed in KNM-WT 15000. This curve exhibits a small spurt of lesser intensity and shorter duration than the modern human adolescent spurt. With this new information, Graves and colleagues (n.d.) reconstructed KNM-WT 15000's hypothetical adult stature and body mass at 163 cm and 55.7 kg.

Since emerging evidence seems to support the contention that *H. erectus* did not have an adolescent growth spurt, it is of interest to examine growth in later hominins. Neanderthals offer one avenue for these investigations. *H. neanderthalensis* was a hominin species that lived for ~170,000 years (Mellars, 2004) throughout the Old World (Zubrow, 1989). While many aspects of Neanderthals lives are preserved in the fossil record, the pace of growth and development in Neanderthals is unclear. Did Neanderthals experience a fast, chimpanzee-like or slow, modern human-like life history? There is evidence in support of both patterns. Studies of Neanderthal teeth seem to indicate that dental development in Neanderthals fell in the range of modern human variation (see Guatelli-Steinberg, 2009). Growth and developmental research also seems to suggest that Neanderthals experienced a modern human-like pattern of growth (Nelson and Thompson, 1999, 2002; Thompson and Nelson, 2000). While the results of these studies were consistent with the presence of an adolescent growth spurt, the researchers were unable to confidently predict the duration, magnitude and age-of-onset of this spurt.

The presence of an adolescent growth spurt in Neanderthals has important implications for modern humans. While Bogin (1993, 1994, 1999, 2002, 2003, 2006) suggested that adolescent growth is unique to modern humans, a Neanderthal adolescent growth spurt contradicts this contention. In this thesis, I examined the timing of stature and facial growth spurts in Neanderthals to test the hypothesis that Neanderthals

experienced modern human growth and development. In order to assess the timing of growth spurts in Neanderthals, I plotted a regression estimate of age at puberty onto velocity growth curves generated using Neanderthal stature and mandibular data. The results of this study may shed light onto growth, development and life history in Neanderthals.

## **Chapter 2: Background Information**

Compared to other mammals, primates have a uniquely slow life history strategy (Hennemann, 1983; Miller and Zammuto, 1983; Harvey and Clutton-Brock, 1985; Prothero and Jurgens, 1987; Wooten, 1987; Charnov, 1991, 1993; Harvey and Nee, 1991; Ross, 1992; Charnov and Berrigan, 1993), with big brains, a late age-at-weaning, a long juvenile period, and a delayed age-at-first reproduction. In addition to prolonged developmental periods, primates live extended lives.

While growth, development, and life history in primates are unique among mammals, modern humans are unique among primates. These differences can be seen in both the timing of life history stages and in patterns of growth. Within primates, great apes live longer and reproduce later than smaller-bodied monkeys and prosimians (Charnov and Berrigan, 1993; Joffe, 1997). Modern humans and orangutans exhibit the slowest life history strategy of all. This point is shown in Figure 1, adapted from Shultz (1960). According to this view, human life history is the extension of a pattern common in primates. Modern humans have extended life histories compared to “early humans,” early humans have extended life histories relative to chimpanzees, chimpanzees to monkeys, monkeys to lemurs, and on and on. Therefore, there is a fast-slow continuum in primates that mirrors the fast-slow continuum in mammals. Hominins,

including Neanderthals, would then represent a sort of midpoint between fast-growing, short-lived lemurs and slow-growing, long-lived modern humans. At the time that Schultz (1960) summarized his views about growth and development in the figure below, very little was known about growth and development in fossil hominins. Since then, improved methods and an expanded fossil record have allowed researchers to broaden their knowledge of life history in fossil hominins.

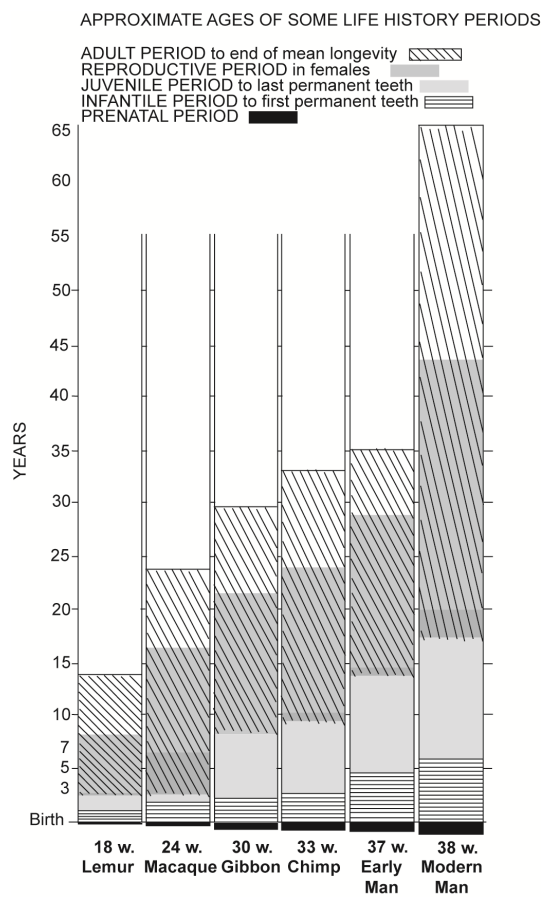


Figure 1: Life history differences in lemurs, gibbons, macaques, chimpanzees, early humans and modern humans (adapted from Schultz, 1960)

The shift from infancy to childhood occurs with weaning. This is a stressful, transitional event where the individual habitually consumes adult foods, but is still dependent on adults for their procurement (Dettwyler, 1995). This period of dependency lasts from approximately ages three to seven, ending when the first molar erupts (Bogin, 1999). Primates do not follow this pattern of development, instead weaning their offspring to independence (Clark, 1977; Galdikas and Wood, 1990; Charnov and Berrigan, 1993; Dettwyler, 1995; Kennedy, 2005). During this period of dependence, somatic growth is stalled, while brain growth is accelerated. For this reason, childhood has been hypothesized to be functionally related to adolescence and the adolescent growth spurt (Lehninger 1982; Bogin 1993, 1994, 1999; Allman and Hasenstaub 1999).

### *Growth in primates*

Growth in primates is characterized by two marked increases in size. The first is a spurt shortly after birth that is characteristic of all mammals, and the second is a juvenile growth spurt. In the non-human primate juvenile growth spurt, the greatest peak in growth occurs before the onset of puberty. This biological marker indicates that the individual is capable of reproducing, although reproduction may be delayed until later in life. In modern humans, the greatest peak in growth occurs after the onset of puberty. This difference has important energetic implications. In primates, the onset of puberty indicates an energetic shift, where energy from growth is now placed towards reproduction. This life history shift allows non-human primates to devote large amounts of energy to reproduction, thus ensuring the survival of their offspring. Modern humans do not experience this shift. Modern humans begin devoting a portion of their energy



budgets to reproduction while a large portion of their energetic requirements are still focused on growth. This theoretically places modern humans at an energetic disadvantage. However, reproduction in modern humans is typically delayed until after all growth has been completed (Bogin, 1999).

It has been hypothesized that the adolescent growth spurt is a uniquely derived trait of modern human growth that is displayed by virtually every modern human population (according to Bogin, 1993, 1994, 1999, 2002, 2003, 2006). This growth spurt can be found in many measurements of the body, including stature and mandibular height. These spurts occur simultaneously (Bambha and Natta, 1963; Mitani and Sato, 1992), with the greatest peak in growth occurring during adolescence, around 14.5 years of age (see figure 2) (Eveleth and Tanner, 1990; Bogin, 1999; Antón and Leigh, 2003). While certain non-human primates, such as chimpanzees, baboons, and macaques, experience a body mass spurt before the end of puberty, this pubertal spurt is not a universal characteristic of growth in all primate species (Leigh, 1996; Leigh and Shea, 1996; Hamada and Uono, 2002).

Leigh (1996) examined the timing of growth spurts in thirty-five primate species using cross-sectional data collected zoos and primate research facilities. Although cross-sectional data is typically not used to investigate growth spurts (since growth spurts may be depressed or masked completely [Eveleth and Tanner, 1990]), Leigh (1996) was able to archive body mass growths spurts in several anthropoid primates (e.g. chimpanzees, gorillas, bonobos and orangutans) and Old World monkeys (e.g. macaques, mandrills and baboons). Leigh (1996) argues that cross-sectional data is acceptable in his study since he was able to find growth spurts, although the spurts are likely less-marked than they

would be in wild, longitudinal data. Leigh (1996) found marked spurts in a number of male primates and some females, although the timing and pattern of growth spurts was inconsistent among primate groups, suggesting that juvenile growth spurts are not universal among primates.

Although Leigh (1996) investigated cross-sectional growth in primates, Hamado and Usono (2002) provided one non-human primate growth study to use longitudinal data. These researchers examined body length growth among twelve chimpanzee specimens. All the individuals used in this study were captive chimpanzees and were all housed in different environments. Hamado and Usono (2002) constructed examples of “average-,” “slow-” and “fast-growing” chimpanzees and 25%, 50% and 75% summary curves. The “slow-growing” chimpanzees exhibited a modern human-like adolescent growth spurt while the “fast-growing” chimpanzees did not experience any growth spurt. These growth curves were constructed by adding the growth of two chimpanzees together. For example, the “average-growing” male curve was constructed using data from two individuals, Nicky and Tick. To construct the curve, early growth data from Nicky was added to later growth data from Tick. This piecemeal approach assumes that later growth from Nicky would have continued on an “average” trajectory and that early growth in Tick followed a similar pattern. The results of the study showed that chimpanzees living in favorable environmental conditions did not exhibit an adolescent growth spurt. The individuals in deleterious environments experienced a pattern of catch-up growth in the juvenile period similar to a modern human-like adolescent growth spurt. This study suggests that some chimpanzees may experience a juvenile growth spurt, but that the samples used in Hamado and Usono (2002) may not represent growth

in wild chimpanzees. Zilhman et al. (2004), for example, found that wild chimpanzees grow slower than captive chimpanzees. It is unknown if these differences would have affected length growth.

### *Hominin growth and development: australopiths*

Australopiths were the first group of hominins hypothesized to experience a prolonged, modern human-like life history strategy. In 1925, Dart described the first australopith, the Taung child, a 2.8 m.y.a. juvenile from Taung, Republic of South Africa. When Dart (1925) first described the specimen, he aged the juvenile at 6 years using modern human growth standards. Since Taung was estimated to have erupted his first molar at 6 years, researchers argued that this juvenile, as well as other australopiths, had a prolonged life history. This view on growth and development in australopiths continued for several decades. For example, Mann (1975) estimated rates of dental development, eruption and tooth wear in *Australopithecus africanus*. Mann (1975) noted that *A. africanus* had similar rates of dental development and eruption to modern humans, leading him to suggest that australopiths experienced a prolonged childhood and juvenile periods.

Later studies of australopith growth and development relied heavily on the microscopic structure of tooth enamel (Bromage and Dean, 1985; Bromage, 1987; Dean, 1987). When a histological section was taken from the tooth, underlying growth lines, or Straie of Retzius, were found to correlate to these external markers, or perikymata. Benyon and colleagues (1991) found that these lines are put down every eight to ten days. This range of value can be used to predict the rate of dental development in extinct

hominins, including australopiths. These investigations into the underlying structure of australopith teeth found that growth and development in early hominins was a mosaic of “ape-like” and “human-like” developmental features, with fast dental development. This fast rate of dental development would then translate into a fast, chimpanzee-like life history strategy (see Dean, 2006).

*Hominin growth and development: Homo erectus*

Early hominins like australopiths likely experienced a fast life history strategy. However, the pace of growth and development in later hominins, such as *Homo erectus* is still unclear. Early studies of growth in *H. erectus* focused on KNM-WT 15000, a ~1.55 m.y.a., nearly complete juvenile from Lake Turkana. When this specimen was originally described in 1993, Ruff and Walker argued that KNM-WT 15000 was 11 to 12 years old at the time of his death. They also assumed that KNM-WT 15000 would have experienced a fully modern human-like pattern of prolonged growth and development, complete with an adolescent growth spurt. Since KNM-WT 15000 was 11 to 12 years old at death, Ruff and Walker (1993) assumed that he was on the cusp of his adolescent growth spurt. This marked increase would have allowed the Nariokotome youth to gain an additional 25 cm (160-185 cm) and 20 kg (48-68 kg) had he survived to adulthood. These reconstructed body proportions have since been used in a number of studies on *H. erectus* (e.g., Leonard and Robertson, 1997; Aiello and Key, 2002; Bramble and Lieberman, 2004; Steudel-Numbers, 2006).

Smith (1993) also examined growth and development in KNM-WT 15000. In contrast to Ruff and Walker (1993), Smith (1993) argued that the overall pattern of dental

development, eruption and ephiphyseal closure in KNM-WT 15000 might not fit modern human growth standards. Although Smith (1993) noted that modern human growth standards were a “somewhat uneasy fit,” she argues for a short adolescent period in KNM-WT 15000. This contention is supported in later studies, such as Tardieu (1998), who argues that KNM-WT 15000 experienced an adolescent growth spurt, although it was likely less pronounced and of shorter duration than modern humans.

While the majority of research on *H. erectus* growth and development has focused on the postcranial skeleton of KNM-WT 15000, Antón and Leigh (2003) provided an experimental study of craniofacial growth in *H. erectus*. Antón and Leigh (2003) used a small, aged sample of African *H. erectus* to investigate changes in growth velocity in facial and mandibular height. These researchers created arithmetic-velocities between age classes (“infant”, “child”, “late child”, “juvenile”, “adolescent”, “mid-adolescent”, and “mature”) by dividing the difference in size by the change in age groups for their *H. erectus* samples and two cross-sectional samples of modern humans. Antón and Leigh (2003) found that the greatest peak in growth in both facial height and mandibular height in their *H. erectus* samples matched that of the modern human samples. While the results of this study are somewhat equivocal as to the presence of an adolescent growth spurt in the erectine face, Antón and Leigh (2003) argued against outright rejection of adolescence in *H. erectus*. Larger sample sizes in future analyses may lend support to the hypothesis that *H. erectus* experienced an adolescent growth spurt.

More recently, there is an increasing abundance of evidence suggesting growth and development in *H. erectus* did not follow a modern human-like trajectory. Dean and colleagues (Dean et al., 2001; Dean, 2006; Dean and Smith, 2009) examined the

histological composition of the anterior teeth in a large sample of fossil hominins, including KNM-WT 15000, to determine if fossil hominins experienced a prolonged, modern human-like development, or an accelerated, non-human primate-like life history. These researchers found little evidence for rapid dental development in all early hominins, including australopiths and *H. erectus*. Additionally, Dean and Smith (2009) found that KNM-WT 15000 and other erectines developed their teeth more quickly than do modern humans, suggesting that *H. erectus* did not experience a modern human-like growth and development. Recent research by Graves et al. (n.d.) supports this viewpoint. Graves et al. (n.d.) created a number of hypothetical growth curves for KNM-WT 15000 by modifying distance and velocity curves for modern humans and chimpanzees. The intermediate curves that best match the sequence of life history events known to have occurred in KNM-WT 15000 archives a small growth spurt during the juvenile period. This small spurt would have allowed the Nariokotome youth to achieve an additional 9 cm (154-163cm) and 8 kg (48-56 kg), much less than predicted from an adolescent growth spurt. Graves et al. (n.d.) argue that adolescence was not a component of growth in *H. erectus*, suggesting that this pattern of growth and development appeared sometime later in the hominin fossil record.

#### *Hominin growth and development: Neanderthals*

There has been a long-held belief that growth, development and life history in Neanderthals was faster than that of modern humans. These studies relied on juvenile

specimens. Luckily, there are several nearly complete juvenile crania, some with associated postcrania. One juvenile specimen is Gibraltar 2, a ~57.5 k.y.a juvenile from Forbe's Quarry. This specimen had been previously estimated to be ~5.9 years old based on the degree of molar root completion (Skinner and Sperber, 1982). Dean et al. (1986) argued that the standards used by Skinner and Sperber (1982) are inappropriate, because the data only predict a median root age for males. Using updated modern human data and perikymata counts, Dean et al. (1986) estimated age-at-death in Gibraltar 2 at 4.45 years. More recently, Stringer and Dean (1997) estimated age-at-death to be closer to 4.13 years of age, suggesting that dental development in Neanderthals may be faster than previously thought.

Recent research also supports the idea that Neanderthals experienced fast dental development. Ramirez Rozzi and Bermúdez de Castro (2004) and Smith et al. (2007) examined rates of Neanderthal dental formation. Ramirez Rozzi and Bermúdez de Castro (2004) examined perikymata counts in anterior teeth, while Smith et al. (2007) looked at both anterior and molar teeth. These researchers found lower perikymata counts in their Neanderthal samples, indicating that dental formation and eruption in Neanderthals was 15% faster than in modern humans. This fast growth and development would have allowed Neanderthals to reach adulthood quickly. Additionally, Smith et al. (2007) found fast rates of dental formation in both anterior and molar teeth, suggesting that dental formation and eruption in Neanderthals was faster than in modern humans. An adolescent growth spurt may not have been necessary with such a fast rate of development.

Recently, it has become clear that Neanderthal growth and development may not have been as fast as previously thought. Guatelli-Steinberg and colleagues (Guatelli-Steinberg et al., 2005; Guatelli-Steinberg et al., 2007; Guatelli-Steinberg, 2009) argued that Neanderthals experienced delayed, modern human-like dental development. Homologous patterns of dental development between Neanderthals and modern humans lead Guatelli-Steinberg et al. (2005) to suggest that all other aspects of Neanderthal and modern human life history were the same as well. To examine the rate of Neanderthal dental development, Guatelli-Steinberg et al. (2005) examined perikymata counts in anterior Neanderthal teeth. Previous research (Ramirez Rozzi and Bermúdez de Castro, 2004) found lower rates of perikymata counts in their sample. Guatelli-Steinberg and colleagues (2005), on the other hand, found the number of perikymata counts in their Neanderthal sample to fall within the range of modern human variation.

The differences in these studies may be related to different assumptions about perikymata counts among modern humans. Ramirez Rozzi and Bermúdez de Castro (2004) argue that perikymata counts are similar among all modern human populations, regardless of differences in dental eruption. Guatelli-Steinberg and colleagues (2005), on the other hand, find significant differences in perikymata counts among modern humans, indicating that there may be a wide range of variation in formation times.

While Guatelli-Steinberg et al. (2005) argue that similar perikymata counts in anterior teeth among Neanderthals and modern humans indicate homologous dental development (and by extension homologous somatic growth), it is still unknown how differences in enamel thickness would have affected the overall rate of dental formation and eruption. Additionally, as noted by Smith et al. (2007) formation times in anterior



teeth are not a reliable predictor of life history (see also Ramirez Rozzi and Bermúdez de Castro, 2004).

In addition to prolonged dental development, there is emerging evidence to support a slow, modern human-like life history strategy in Neanderthals. Recent research on neonatal brain size in Neanderthals suggests that Neanderthals had a similar rate of brain growth to that of modern humans (Ponce de Leon et al., 2008). Ponce de Leon et al. (2008) used 3-D modeling to reconstruct brain size in a number of young Neanderthals (Mezmiskaya, Dederiyeh 1 and Dederiyeh 2). The researchers then used these specimens to construct a distance brain growth curve. This curve followed a rapid, modern human-like growth trajectory. However, it may have taken Neanderthals a longer time to complete brain growth. A fast (but extended) rate of brain growth would have been energetically costly for Neanderthals and would have required slow rates of somatic growth. An adolescent growth spurt may have been necessary to reach final adult body size. However, the timing of this growth spurt is still unknown. As discussed above, childhood may be functionally related to adolescence. McCarthy et al. (n.d.) recently examined the evidence for childhood in Neanderthals. McCarthy et al. (n.d.) created a number of weaning age estimates. These estimates were then subtracted from estimates of M1 eruption to predict the duration of childhood in Neanderthals. The results of this study indicated that Neanderthals experienced a short childhood period. If, as it has been suggested, childhood is related to adolescence, the presence of a childhood period in Neanderthals suggests that an adolescent period may be present as well.

Several researchers have investigated the adolescent period in Neanderthals. Nelson and Thompson (1999, 2002) and Thompson and Nelson (2000) examined the

Neanderthal growth and development with Teshik-Tash 1 and Le Moustier 1, aged at 9.9 and 15.5 years respectively. In a number of studies, Thompson and Nelson compared femoral length in a number of juvenile specimens, and a sample of adult Neanderthals. Additionally, Thompson and Nelson (2000) calculated proportional femoral lengths to determine how much growth was needed to achieve mean adult size. Thompson and Nelson (2000) also calculated proportional femoral lengths in an Inuit sample. They found that the Neanderthal trajectory lies just below the modern human trajectory.

There are a number of factors that could have depressed the Neanderthal trajectory (e.g. dietary deficiencies, environmental effects, etc.), Thompson and Nelson (2000) suggest that compared to modern humans, Neanderthals may have had faster rates of dental development or delayed postcranial maturation. Le Moustier 1, for example, was calculated to have achieved 85.1% of mean adult stature by his estimated age of 15.5. In modern humans, 96.9% of mean height is achieved by this age (Nelson and Thompson, 1999). If Le Moustier 1 was to reach mean adult size, he would have required an extremely late growth spurt (Thompson and Nelson, 2000). While Nelson and Thompson (1999) and Thompson and Nelson (2000) argued that Neanderthals exhibited slow, linear growth, consistent with growth in modern humans, they are unable to confirm the presence of a Neanderthal adolescent growth spurt. The researchers argue that an expanded knowledge of growth in earlier hominins, modern humans, and non-human primates may allow future investigations into Neanderthal growth spurts.

### **Chapter 3: Hypothesis Testing**

In this thesis, I tested three hypotheses about the timing of growth spurts in Neanderthals. I used stature and mandibular data to examine the timing of growth spurts in Neanderthals. I used two measurements to examining Neanderthal growth spurts for several important reasons. First, in growth studies, longitudinal data is preferred when examining adolescent growth spurts (Evelith and Tanner, 1990). However, longitudinal data is unavailable for fossil hominins and cross-sectional data must be used. Evelith and Tanner (1990) have noted that cross-sectional data may depress the magnitude of growth spurts and occasionally mask a spurt completely (see also Leigh, 1996). While it is possible to archive skeletal growth spurts in cross-sectional samples (e.g. Leigh, 1996), it is unknown how cross-sectional would bias a hominin sample. Antón and Leigh (2003) showed that it is possible to visualize facial growth spurts using small cross-sectional samples. For this reason I examined growth in Neanderthals with multiple measurements.

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**Hypotheses to be tested in this research:**

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H0: Neanderthals do not exhibit a growth spurt in any part of the body.

H1: Neanderthals experienced a juvenile growth spurt.

H2: Neanderthals experienced an adolescent growth spurt.

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To test the timing of growth spurts in Neanderthals, I am using several comparative modern human samples. I used cross-sectional Inuit data as a comparative stature sample. To examine mandibular growth, I used published Alaskan and Australian facial growth curves from Antón and Leigh (2003). I used cross-sectional data because it matches both Neanderthal samples.

As discussed above, chimpanzees, like other large-bodied non-human primates, experience the greatest peak in growth after the onset of puberty, while modern humans experience the greatest peak before (see figure 2). I will use this contrast to analyze both Neanderthal growth curves (see figure 3). In this context, I am using “sexual maturity” as a proxy for the onset of puberty. In modern humans, puberty occurs at ~11.3 years of age while chimpanzees reach puberty at ~8.4 years. If the greatest peak in growth occurs before the onset of puberty, Neanderthals would have experienced an adolescent growth spurt. In contrast, if the greatest peak in growth occurs after puberty, Neanderthals would have experienced a juvenile growth spurt.

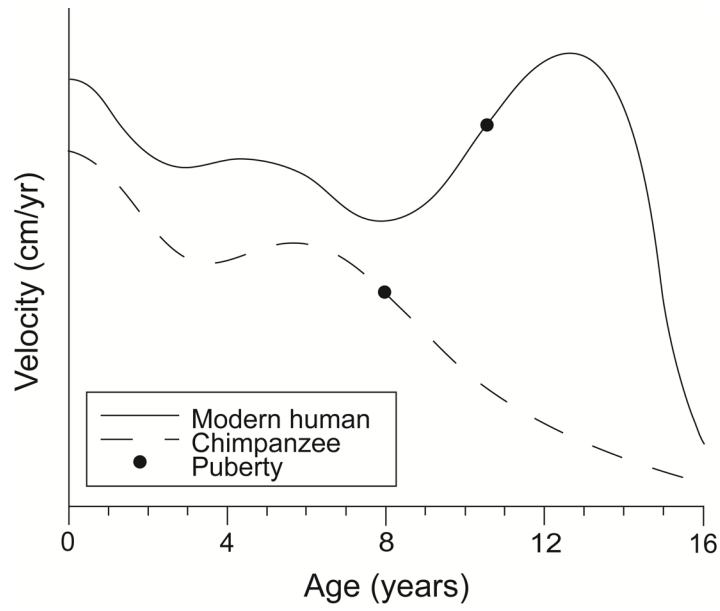


Figure 2: The timing of peak growth velocity relative to puberty in chimpanzees and modern humans.

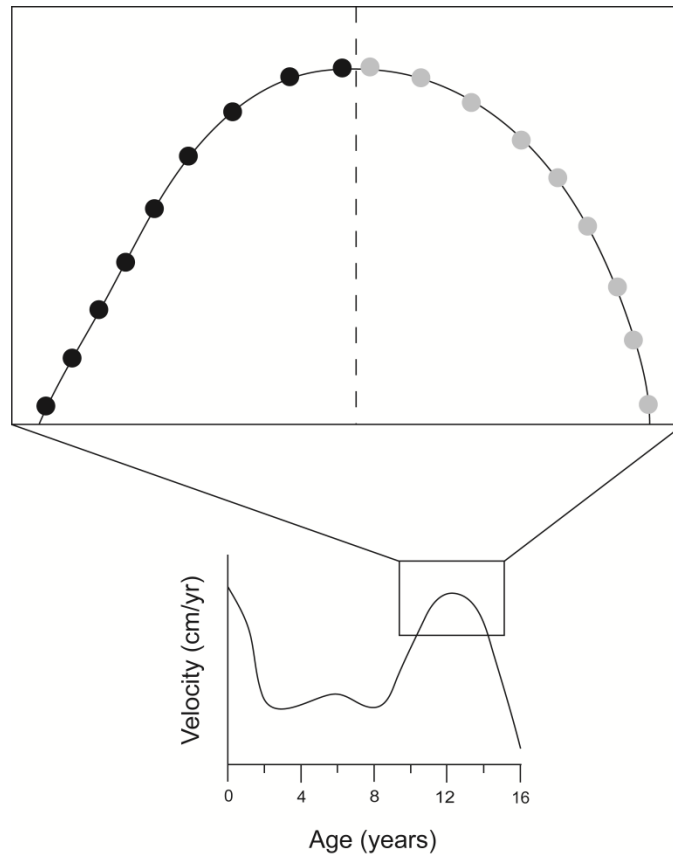


Figure 3: Magnified peak growth velocity: black points occur before the onset of puberty, indicating an adolescent growth spurt, while grey points occur after puberty, indicating a non-human primate juvenile growth spurt.

The null hypothesis of this research tests the possibility that Neanderthals did not experience a growth spurt of any kind. If the Neanderthal growth , curves exhibit acceleration of any kind, the null hypothesis would be rejected. This pattern of growth is seen in figure 4 (H0). The absence of both an adolescent and juvenile growth spurt in the Neanderthal samples has two implications. The lack of an adolescent growth spurt suggests that this pattern of growth is a recently evolved characteristic of growth in *H. sapiens*, and the lack of a juvenile growth spurt suggests that Neanderthals grew

differently from all other large-bodied primates. In this scenario, age at puberty is ignored, since there is no marked increase in size in either growth spurt.

While it is possible that Neanderthals will show no marked growth spurt in size, it is likely that Neanderthals will exhibit one of two growth spurts. The first, a juvenile growth spurt, would imply that Neanderthals grew more like a non-human primate. If Neanderthals had a juvenile growth spurt, I would expect to see the greatest peak in growth occurring before the onset of puberty (see graph H1 in Figure 4). However, Neanderthals might have experienced an adolescent, rather than a juvenile, growth spurt. In this scenario, the greatest peak in growth would occur after the onset of puberty (see graph H2 in Figure 4).

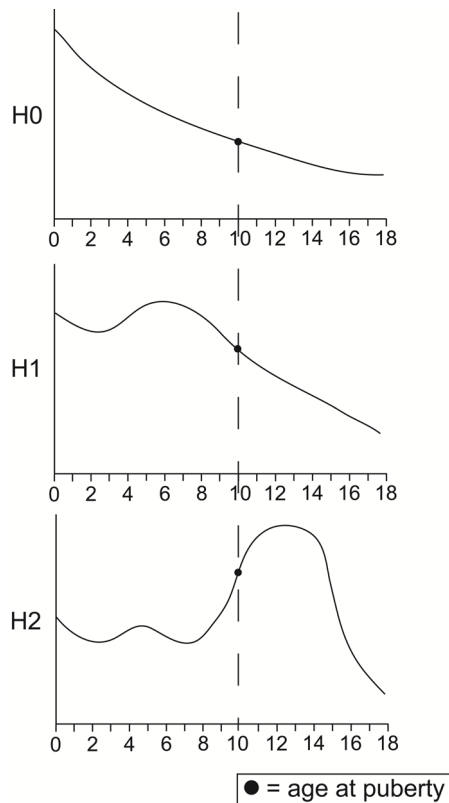


Figure 4: Hypothesized results for Neanderthal growth spurt analyses showing age at puberty relative to peak velocity

## Chapter 4: Materials and Methods

In this thesis, I used two lines of evidence to test the timing of growth spurts in Neanderthals. I used estimates of stature to examine somatic growth, and mandibular height data to examine patterns of facial growth. I used these growth curves and an estimate of the duration of the juvenile period in Neanderthals to determine if the timing of Neanderthal growth spurts is consistent with non-human primate-like juvenile growth or a modern human-like adolescent growth spurt instead.

### **Materials**

#### *Stature growth spurt*

For the first analysis, I used published and unpublished data on immature and mature Neanderthals to investigate skeletal growth. Previous investigations of Neanderthal skeletal growth relied on two individual specimens, and in this study I was able to assemble an expanded sample in this thesis (n=15) (see table 1).



Table 1: Specimens used to construct stature growth curve

<b>SPECIMEN</b>	<b>AGE (YRS)</b>	<b>STATURE (CM)</b>	<b>REFERENCE</b>
La Ferrassie 5	0.00	52.80	Cowgill (pers. com.)
La Ferrassie 4b	0.30	56.84	Heim (1982)
Amud 7	0.34	67.88	Cowgill (pers. com.)
Kiik-Koba 2	0.45	62.93	Vlêck (1973)
Shanidar 10	1.71	79.10	Cowgill et al. (2007)
Dederiyeh 1	2.05	81.68	Kondo et al. (2000)
Dederiyeh 2	2.15	74.92	Kondo et al. (2000)
Roc de Marsal 1	3.25	84.16	Madre-Dupouy (1992)
Cova Negra Femur 1	3.70	98.18	Arsuaga et al. (2007)
La Ferrassie 6	4.00	85.46	Heim (1982)
Cova Negra 42165	5.50	87.17	Arsuaga et al. (2007)
Spy III	6.50	115.05	Cowgill (pers. com.)
Teshik-Tash 1	9.90	112.9	Nelson & Thompson (1999)
Ehringsdorf G	12.20	136.73	Cowgill (pers. com.)
Le Moustier 1	15.50	138.5	Nelson & Thompson (1999)

For the juvenile specimens, stature was estimated using age-specific regression equations from Ruff (2007). Ruff (2007) published age-specific equations from the Denver Growth Study that can be used to predict stature (in cm) from long bone length (in mm) in juvenile fossil hominins. Intermetaphyseal length was measured in younger specimens (0-11) since the epiphyses have not yet fused. I also used Ruff's (2007)

equations to predict stature in a sample of Inuits (n=53) (Wescott, pers. comm.). This cold-adapted population is frequently used as a comparative sample in Neanderthal studies.

*Facial growth spurt*

To investigate facial growth in Neanderthals, I used published mandibular data from Minugh-Purvis (1988). I chose to investigate the timing of growth in condylar height following Antón and Leigh (2003). Minugh-Purvis (1988) measured condylar height as the distance between the first molar and the superior border of the condyle. Specimens used to construct the facial growth curve are listed in table 2 (n=7).

Table 2: Specimens used to construct mandibular growth curve from Minugh-Purvis (1988)

<b>SPECIMEN</b>	<b>AGE (YRS)</b>	<b>MANDIBULAR HT (MM)</b>
Pech de l'Azé 1	2.75	28.4
Roc de Marsal 1	3.25	32.4
Zaskalnaya VI	9.50	49.0
Teshik-Tash 1	9.90	56.0
Krapina Mandible C	11.25	54.4
Ehringsdorf 7/8	12.00	51.0
Le Moustier 1	15.50	49.5

I used data from Antón and Leigh (2003) as a comparative modern human sample. These researchers measured mandibular height (the distance from M1 to the superior border of the mandibular condyle) in two samples: a dolichocephalic Australian sample (n=26) and a brachycephalic Alaskan sample (n=32). It is known that females exhibit smaller facial dimensions than males. For this reason, Antón and Leigh (2003) only included females in their analyses. I digitized the velocity growth curves for both samples using Engage v. 2.15 (Mitchell, 2002). This digitizing software program converts image files into numerical data that can be used for analysis in a variety of statistical programs (Mitchell, 2002). After scanning the images, I defined the axis points and specified a scale. The software then estimates x and y coordinates along the best-fit line, outputting a data file that can be then be manipulated in other statistical software. I used Minitab v. 15 to manipulate the data from Antón and Leigh (2003).

#### *Duration of the juvenile period*

To estimate the duration of the juvenile period (DJ) in Neanderthals, I used the known relationship between adult female body mass and DJ in primates (see appendix A for raw data used in PIC analysis). I used primate body masses from Smith and Jungers (1997), primate DJ data from Lee and Kappeler (2003), and Neanderthal body mass data from Ruff et al. (1997) (see table 3).

Table 3: Estimated adult female body masses in Neanderthals from Ruff et al. (1997)

SPECIMEN	BODY MASS (g)
Grotte du Prince	74800
La Ferrassie 2	67000
Krapina 208	68400
Krapina 209	63700
Krapina 214	62200
La Quina 5	71200
Shanidar 6	59400
Spy 1	67500
Tabun C1	63200

## Methods

### *Phylogenetically independent contrasts analysis*

To estimate DJ in Neanderthals, I used phylogenetically independent contrasts (PIC) analysis. It is well-known that species do not represent independent units, and that phylogenetic correlation can play a significant role in biasing comparative analyses (Felsenstein, 1985). This phylogenetic non-independence reduces the number of degrees of freedom, lowers statistical power, and affects parameter estimation (Grafen, 1989; Harvey and Pagel, 1991; Martins and Garland, 1991). For this reason, linear regression is not an appropriate statistical method for the examination of the correlated evolution of a trait, or traits.

In PIC, contrasts are calculated as weighted averages between the character values of sister species, sister species and nodes, and nodes throughout the phylogeny, working down from the tips to the interior nodes (Felsenstein, 1985; Nunn and Barton, 2002). To estimate DJ, I generated a primate phylogeny with appropriate branch lengths using 10kTrees (Arnold et al., 2009; Matthews et al., 2009). This phylogenetic website allows users to construct a phylogeny sampled from a Bayesian tree inference. The constructed tree was uploaded into Mesquite v. 2.71 (Maddison and Maddison, 2008). I modified branch lengths and calculated independent contrasts in the PDAP add-on (Midford et al., 2008). Next, I standardized branch lengths to correct for known error associated with the misinterpretation of rates of evolutionary change along branches when some branches are long (Garland et al., 1999; Nunn and Barton, 2002). I used a natural log transformation. I checked the accuracy of this transformation by examining the correlations between the absolute values of the independent contrasts and their standard deviations (after Diaz-Uriarte and Garland, 1996, 1998).

To estimate DJ in Neanderthals, I transformed the scaled contrasts back into log-transformed data space by plotting the log-transformed character values against adult female body mass (following Garland et al., 1992; Garland et al., 1999) and used least-squares regression to predict a Neanderthal value for DJ. To correct for log detransformation bias, I adjusted the natural log estimate by the average of two quasi-maximum likelihood estimator (QMLE) correction factors (calculated using the error of the estimate and error variance, respectively), following Smith (1993).

### *Growth curve modeling*

To model stature in Neanderthals, I used generalized logistic regression. Since the growth of any given organism is not exponential, a special s-shaped curve accurately visualizes the parameters of growth. Generalized logistic regression is one of the most widely used methods to visualize this trend. This method is favored over other non-parametric statistical tests, such as LOWESS regression, since generalized logistic regression outputs growth parameters that can be used to predict size at different ages. LOWESS regression, on the other hand, is more useful for visualizing the shape of the curve, rather than making predictions from the curve.

I used GenStat v. 12 (Payne et al., 2009ab) to run to generalized logistic regression. I then used the growth parameters output by GenStat v.12 to estimate fitted values in Excel 2007. I plotted these fitted values on a scatterplot to visualize the distance growth curve. I then created velocity growth curves for each distance curve by dividing the difference in size at a given age by the change in age.

To model mandibular growth in Neanderthals, I followed Antón and Leigh's (2003) methodology for examining facial growth in cross-sectional hominin samples. Antón and Leigh (2003) used a small *H. erectus* sample (n=5) to examine facial growth spurts. The researchers placed their samples into age classes (child, adolescent, mature) and calculated velocity values for each of the age classes. I separated the Neanderthal sample into four age classes (child, early adolescent, mid-adolescent and late adolescent) and took the average for each. I then calculated arithmetic-velocities for each of the groups by dividing the difference in size at a given age by the change in age or age class.

## Chapter 5: Results

The regression equation and statistics for the comparison between logged values of adult female body mass and DJ are presented, along with bivariate scatterplots of species contrast values, in Figure 5. The estimated point value for Neanderthal DJ is 7.57 years (95% confidence interval 5.21-9.93).

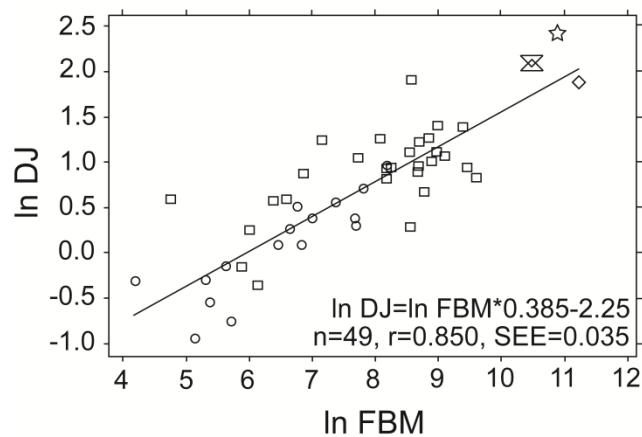


Figure 5: Bivariate scatterplot for the duration of the juvenile period (DJ) versus adult female body mass (FBM) in primates. Circles represent strepsirrhines, squares catarhines, inverted triangle *Pongo*, diamond *Gorilla*, triangle *Pan*, and star *H. sapiens*

The stature velocity growth curve is presented in figure 6 and the mandibular growth curve in figure 7. The Neanderthal stature velocity growth curve exhibits deceleration in growth without any acceleration. The mandibular velocity growth curve exhibits a spurt at 9.7 years. The greatest peak in growth in this analysis occurs after the onset of “puberty.” The lower limit of the 95% confidence interval falls before the

greatest peak in growth velocity, but the upper limit of the 95% confidence interval falls just after the greatest peak in growth velocity. This range is represented by the shaded grey region in both curves.

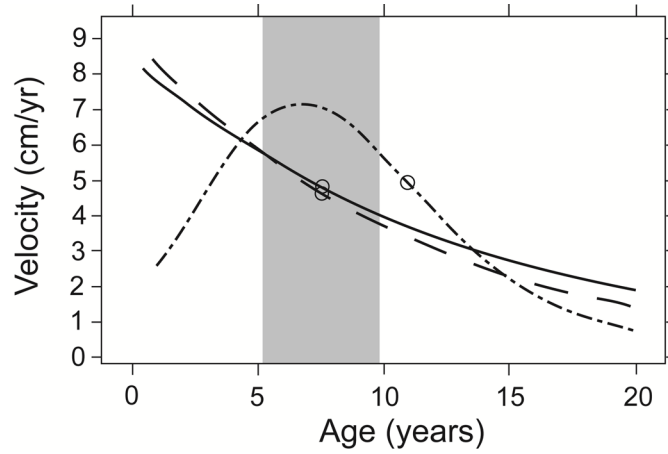


Figure 6: Velocity stature growth curve for Inuits (---), male Neanderthals (—) and female Neanderthals (-.-): open circle shows age at puberty and grey bar shows 95% confidence intervals for PIC estimate.

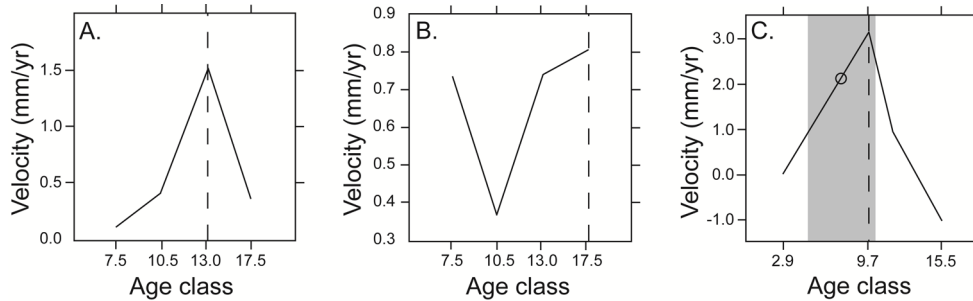


Figure 7: Velocity growth curves for Australians (A), Alaskans (B) and Neanderthals (C). Dashed line marks age at peak velocity, open circle shows estimated age at puberty, and grey shaded bar shows 95% confidence intervals for PIC estimate.



## Chapter 6: Discussion

### Stature growth curve

My analysis of stature growth in Neanderthals did not show a growth spurt (see figure 6). The growth curve exhibits a deceleration in growth throughout ontogeny without any acceleration during either the juvenile or adolescent periods. This pattern of growth suggests that stature growth in Neanderthals was different than other large-bodied primates. However, it is unknown if this curve represents the actual stature growth pattern of Neanderthals, or if the growth spurt is masked by the cross-sectional nature of the sample. As discussed above, cross-sectional data is not ideal when investigating growth spurts. In particular, Eveleth and Tanner (1990) note that a mixed cross-sectional/longitudinal sample should be used when investigating adolescent growth spurts. This type of sample would allow the actual magnitude, duration, and timing of any possible adolescent growth spurts to be properly visualized. While it is possible to use cross-sectional data to investigate growth spurts (e.g. Leigh, 1996), samples need to be robust and include numerous individuals at each age group. Since the Neanderthal sample is so small, it likely affected my chance of archiving a growth spurt. Additionally, most samples do not fall within the “adolescent” age category, thus potentially masking the timing of any growth spurt.

Problems with cross-sectional data are also evident in the Inuit sample. Many studies have shown that Inuits experience an adolescent growth spurt (e.g. Rode and Shepard, 1984; Condon, 1988). However, my cross-sectional sample of 53 Inuits shows a peak velocity at ~7 years of age. While this spurt may be related to the juvenile spurt experienced by most modern humans (Bogin, 1999), there is no acceleration of growth during adolescence. The lack of an expected Inuit adolescent stature growth spurt highlights the issues with cross-sectional data in this study.

### **Facial growth curve**

While the stature growth curve is equivocal as to the presence of an adolescent growth spurt, results from the facial growth curve analysis are consistent with the presence of a modern human-like adolescence growth spurt (see Figure 7). In my analysis of growth in mandibular condylar height, Neanderthals experience peak velocity at 9.7 years of age. This value is earlier than peak velocity for both modern human samples, which occurs at ~13 years of age in the Australian sample and ~17.5 years of age in the Alaskan sample. When the PIC estimate for DJ is plotted on the Neanderthal facial curve, the greatest peak in growth occurs before the point estimate and lower confidence interval and just after the upper confidence limit. In this analysis, I am only able to predict the timing of the Neanderthal growth spurt and am unable to confidently predict the duration or magnitude of this spurt. While there is a 0.23 year difference between the age at peak velocity and the upper confidence limit, it should be noted that this difference is small, suggesting that Neanderthals likely experienced a modern human-like adolescent growth spurt in the face. However, I am unable to confidently

reject the hypothesis that Neanderthals experienced a non-human primate-like juvenile growth spurt in the face.

Although these results support the idea that Neanderthals may have experienced an adolescent growth spurt in the face, it is important to note that the timing of this developmental period in Neanderthals may be accelerated relative to puberty in modern humans. Modern humans reach puberty ~11 years of age (data from Lee and Kappeler, 2003), and, on average, experience the greatest peak in mandibular growth velocity around 14.5 years of age (Antón and Leigh, 2003). My estimate of age at puberty in Neanderthals is 7.57 years, a value ~3.4 years earlier than modern humans.

### **Life history implications**

As discussed above, there is some evidence suggesting that Neanderthals developed more quickly than modern humans. This fast rate of development is supported by the PIC analysis. In addition to accelerating life history variables, Neanderthals may have experienced fast facial growth, thus experiencing “adolescence,” but at a different time than do modern humans. Previous research on Neanderthals, and other hominins, has assumed that the timing of developmental events occurred at the same time as in modern humans (e.g. Ruff and Walker, 1993; Antón and Leigh, 2003; Caspari and Lee, 2004). Adolescence, for example, is typically viewed at a marked increase in growth, with peak velocity occurring sometime after puberty (Bogin, 1999), usually around 14.5 years of age (Antón and Leigh, 2003). This value was used by Antón and Leigh (2003) to diagnose the growth of *H. erectus*. Since their sample did not show peak velocity occurring at this age, Antón and Leigh (2003) were unable to confidently confirm the

presence of an adolescent growth spurt in the erectine face. However, as suggested in this study, the presence of adolescence is not constrained by a modern human-like age at peak velocity.

If Neanderthals experienced adolescence earlier than modern humans, it is of interest to examine the timing of all other life history events. While previous researchers have suggested that Neanderthals experienced an accelerated life history, there is emerging evidence to suggest that Neanderthals experienced a prolonged life history. As discussed above, Ponce de León et al. (2008) has argued that that life history in Neanderthals was as slow as, or slower, than that of modern humans. This slow life history strategy is hypothesized to be related to the energetic requirements of growing a large brain. It is possible that Neanderthals combined fast somatic growth with delayed life history. This strategy would likely have been energetically expensive. Future investigations into the energetic constraints of Neanderthal growth, development and life history are necessary to address issues of Neanderthal energetic budgets (e.g., Snodgrass and Leonard, 2009).

### **Limitations of this study**

Previous investigations into Neanderthal growth and development were unable to confidently predict the age of onset, duration and magnitude of Neanderthal growth spurts. My study is limited in a similar regard, although I am able to predict the age of onset of the Neanderthal growth spurt. In my analyses, Neanderthals experienced peak velocity in mandibular growth at 9.7 years. When I plot the puberty estimate onto the velocity curve, both the lower confidence limit and the point estimate are consistent with

an adolescent growth spurt, while the upper confidence limit falls just after peak velocity, suggesting that Neanderthals may have experienced a non-human primate-like juvenile growth spurt in the face. However, the difference between age at peak velocity and the puberty estimate generated in this study is relatively small (0.23 years). While I am unable to overtly confirm the presence of an adolescent growth spurt in the Neanderthal face, the results of these analyses are consistent with modern human-like growth. Future research and an expanded fossil record may create more confidence in the hypothesis that Neanderthals experienced an adolescent growth spurt.

In addition to limiting confidence intervals, there are some issues with my regression technique. In PIC, average species values are used to predict another average species value. These average values do not take into consideration the range of variation among primates in the same species. It is also possible that mixed samples (e.g., wild and captive) may affect the average value used in the PIC analysis. Additionally, the modern human value for DJ falls well above the non-human primate regression line (see figure 5), suggesting that the length of the juvenile period in modern humans is longer than expected. If Neanderthals experienced a modern human-like DJ, it is possible that the actual Neanderthal value would also fall above the line. A longer Neanderthal DJ period would suggest that peak velocity would occur before the onset of puberty, indicating that Neanderthals likely experienced a juvenile growth spurt.

## Chapter 7: Conclusions

The adolescent growth spurt is hypothesized to be a unique aspect of modern human growth and development. If this pattern of growth was truly unique to our species, we would expect to find different patterns of growth in all other hominoids, including our extinct hominin relatives. While there is conflicting evidence on the presence of an erectine adolescent growth spurt, the majority of Neanderthal growth studies suggest that our growth pattern was shared with our most recent hominin ancestor. The results of this research support this contention, at least for the presence of an adolescent growth spurt in the face. However there are limitations to my method and I am only able to predict the timing of this growth spurt. The duration and magnitude of the facial growth spurt remain somewhat unclear.

As discussed above, there are several reasons why the stature growth curve may have been diminished or masked. Cross-sectional data is not ideal when constructing growth curves. It is possible to uncover growth spurts using cross-sectional data (e.g. Leigh, 1996). Since I did not find a stature growth spurt, I am unable to determine if the lack of a growth spurt is due to the nature of cross-sectional data or if Neanderthals did not have a growth spurt in stature. Although my analysis of stature growth in Neanderthals did not show evidence of a growth spurt, the mandibular growth spurt analysis did exhibit a growth spurt. This growth spurt is likely an adolescent growth

spurt, but I cannot rule out the possibility that Neanderthals experienced a non-human primate-like juvenile growth spurt in the face.

There is emerging evidence that life history in Neanderthals may have been as slow as or slower than that of modern humans (e.g. Ponce de León et al., 2008). If early stages of Neanderthal life history were prolonged (such as prolonged brain growth, late dental development, and an extended childhood period), it is likely that somatic growth would have been delayed until some other point during their development. My analyses suggest that Neanderthals experienced a growth spurt in mandibular height. However, with my limited number of measurements, I am not able to confidently determine if this spurt is a non-human primate-like juvenile growth spurt, or a modern human-like adolescent growth spurt. Future research will investigate the timing of growth spurts in other areas of the Neanderthal face. These analyses may add support to the hypothesis that Neanderthals experienced an adolescent growth spurt in the face.

*Appendix A: Raw data used in PIC analysis: adult female body mass (FBM) data from Smith and Jungers (1997) and duration of the juvenile period (DJ) data from Lee and Kappeler (2003)*

<b>SPECIES</b>	<b>FBM (KG)</b>	<b>DJ (YRS)</b>
<i>Cheirogaleus medius</i>	0.282	0.86
<i>Microcebus murinus</i>	0.067	0.73
<i>Daubentonia madagascariensis</i>	2.490	2.04
<i>Lepilemur mustelinus</i>	0.777	1.30
<i>Eulemur fulvus</i>	2.180	1.46
<i>Eulemur mongoz</i>	1.600	1.75
<i>Hapalemur griseus</i>	0.870	1.67
<i>Lemur catta</i>	2.210	1.35
<i>Propithecus verreauxi</i>	3.690	2.62
<i>Arctocebus calabarensis</i>	0.306	0.47
<i>Loris tardigradus</i>	0.218	0.58
<i>Nycticebus coucang</i>	0.643	1.09
<i>Perodicticus potto</i>	0.930	1.09
<i>Galago moholi</i>	0.173	0.039



<i>Galago senegalensis</i>	0.205	0.74
<i>Otolemur crassicaudatus</i>	1.110	1.47
<i>Tarsius banacus</i>	0.117	1.82
<i>Aotus trivirgatus</i>	0.736	1.81
<i>Cebus albifrons</i>	2.290	2.85
<i>Callimico goeldii</i>	0.468	0.70
<i>Callithrix geoffroyi</i>	0.395	0.85
<i>Leontopithecus rosalia</i>	0.598	1.78
<i>Sagunius oedipus</i>	0.404	1.29
<i>Callicebus moloch</i>	0.956	2.39
<i>Allouatta palliata</i>	5.193	1.35
<i>Alouatta seniculus</i>	5.227	3.03
<i>Ateles fusiceps</i>	9.160	2.91
<i>Ateles geoffroyi</i>	7.290	2.76
<i>Lagothrix lagothricha</i>	7.055	3.53
<i>Miopithecus talapoin</i>	1.280	3.44
<i>Erythrocebus patas</i>	6.500	1.96
<i>Cercopithecus aethiops</i>	3.273	3.55
<i>Cercopithecus neglectus</i>	3.601	3.22
<i>Macaca fascicularis</i>	3.590	2.27
<i>Macaca fuscata</i>	8.030	4.07
<i>Macaca mulatta</i>	7.966	3.05

<i>Macaca nemestrina</i>	5.841	2.46
<i>Macaca radiata</i>	3.850	2.56
<i>Macaca silenus</i>	6.100	3.41
<i>Mandrillus sphinx</i>	12.900	2.56
<i>Cercocebus albigena</i>	6.020	2.61
<i>Papio cynocephalus</i>	12.184	4.03
<i>Theropithecus gelada</i>	14.800	2.30
<i>Hylobates lar</i>	5.340	6.73
<i>Pongo pygmaeus</i>	35.753	7.88
<i>Gorilla gorilla</i>	75.667	6.58
<i>Pan troglodytes</i>	35.885	8.36
<i>Homo sapiens</i>	53.614	11.27

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## References

- Aiello, L.C., Key, C.A., 2002. The energetic consequences of being a *Homo erectus* female. *Am. J. Hum. Biol.* 14: 551-565.
- Allman, J., Hasenstaub, A., 1999. Brains, maturation times, and parenting. *Neurobio. Aging* 20: 447-454.
- Antón, S.C., Leigh, S.R., 2003. Growth and life history in *Homo erectus*. In *Patterns of Growth and Development in the Genus Homo*, J.L. Thompson, G.E. Krovitz, A.J. Nelson (eds.), pp. 219-245. Cambridge: Cambridge University Press.
- Arnold, C., Matthews, L.J., Nunn, C.L., 2009. The 10kTrees Website: A New Online Resource for Primate Phylogeny. In review.
- Arsuaga, J.L., Villaverde, V., Quam, R., Martinez, I., Carretero, J.M., Lorenzo, C., Garcia, A., 2007. New Neandertal remains from Cova Negra (Valencia, Spain). *J. Hum. Evol.* 52: 31-58.
- Bambha, J.K., van Natta, P., 1963. Longitudinal study of facial growth in relation to skeletal maturation during adolescence. *Am. J. Ortho.* 49: 481-493.
- Benyon, A.D., Dean, M.C., Reid, D.J., 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. *Am. J. Phys. Anthropol.* 86: 189-203.
- Bogin, B., 1993. Why must I be a teenager at all? *New Sci.* 137: 34-38.
- Bogin, B., 1994. Adolescence in evolutionary perspective. *Acta Paed. Suppl.* 406: 29-35.
- Bogin, B., 1999. *Patterns of Human Growth*. New York: Cambridge University Press.
- Bogin, B., 2002. The Evolution of Human Growth. In *Human Growth and Development*, N. Cameron (ed.), pp. 295-320. Orlando: Elsevier Science.
- Bogin, B., 2003. The human pattern of growth and development in paleontological perspective. In *Patterns of Growth and Development in the Genus Homo*, J.L. Thompson, G.E. Krovitz, A.J. Nelson (eds.), pp. 15-44. Cambridge: Cambridge University Press.

- Bogin, B., 2006. Modern human life history: The evolution of human childhood and fertility. In *The Evolution of Human Life History*, K. Hawkes, R.R. Paine (eds.), pp. 197-230. Santa Fe: School of American Research Press.
- Bromage, T.G., 1987. The biological and chronological maturation of early hominids. *J. Hum. Evol.* 16: 257-272.
- Bromage, T.G., Dean, M.C., 1985. Re-evaluation of the age at death of immature fossil hominids. *Nature* 317: 525-527.
- Caspari, R., Lee, S.H., 2004. Older age becomes common late in human evolution. *Proc. Natl. Acad. Sci.* 101: 10895-10900.
- Charnov, E.L., 1991. Evolution of life history variation among female mammals. *Proc. Natl. Acad. Sci.* 88: 1134-1137.
- Charnov, E.L., 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford University Press, New York.
- Charnov, E.L., Berrigan, D., 1993. Why do female primates have such long lifespans and so few babies? *or* life in the slow lane. *Evol. Anthropol.* 1: 191-194.
- Clark, C.B., 1977. A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In *Primate Bio-Social Development*, S. Chevalier-Skolnikoff, F. Poirer (eds.), pp. 235-260. London: Garland Publishing Inc.
- Clegg, M., Aiello, L. C., 1999. A comparison of the Nariokotome *Homo erectus* with juveniles from a modern human population. *Am. J. of Phys. Anthropol.* 110: 81-93.
- Condon, R.G., 1988. *Inuit Youth: Growth and Change in the Canadian Arctic*. Ann Arbor: UMI Research Press.
- Cowgill, L.W., Trinkaus, E., Zeder, M.A., 2007. Shanidar 10: a Middle Paleolithic immature distal lower limb from Shanidar Cave, Iraqi Kurdistan. *J. Hum. Evol.* 53: 213-223.
- Dart, R.A., 1925. *Australopithecus africanus*: the ape man of South Africa. *Nature* 115: 195-199.
- Dean, M.C., 1987. The dental developmental status of six East African juvenile fossil hominids. *J. Hum. Evol.* 16: 197-213.
- Dean, M.C., 2006. Tooth microstructure tracks the pace of human life-history evolution. *Proc. R. Soc. B* 273: 2799-2808.

- 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. *Am. J. Phys. Anthropol.* 70: 301-309.
- Dean, M.C., Leakey, M.G., Reid, D.J., Schrenk, F., Schwartz, G.T., Stringer, C.B., Walker, A., 2001. Growth processes in the teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414: 628-631.
- Dean, M.C., Smith, B.H., 2009. Growth and development of the Nariokotome youth, KNM-WT 15000. In *The First Humans – Origin and Early Evolution of the Genus Homo*, F.E. Grine, J.G. Fleagle, R.E. Leakey (eds.), pp. 101-120. Dorchester: Springer.
- Detwyler, K.A., 1995. A time to wean: The hominid blueprint for the natural age of weaning in modern human populations. In *Breastfeeding: Biocultural Perspectives*, P. Stuart-Macadam, K.A. Detwyler (eds.), pp. 39-74. New York: Aldine de Gruyter.
- Díaz-Uriarte, R., Garland, T., 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. *Syst. Biol.* 45: 27-47.
- Díaz-Uriarte, R., Garland, T., 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* 47: 654-672.
- Eveleth, P.B., Tanner, J.M., 1990. *Worldwide Variation in Human Growth*. New York: Press Syndicate of the University of Cambridge.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125: 1-15.
- Galdikas, B.F.M., Wood, J.M., 1990. Birth spacing patterns in humans and apes. *Am. J. Phys. Anthropol.* 83: 185-191.
- Garland, T., Harvey, P.H., Ives, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41: 18-32.
- Garland, T., Midford, P., Ives, A.R., 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am Zool.* 39: 374-388
- Grafen, A., 1989. The phylogenetic regression. *Philo. Proc. Roy. Soc. B* 326: 119-157.
- Graves, R.R., Lupo, A.C., McCarthy, R.C., Wescott, D.J., Cunningham, D.L., n.d. Just how strapping was KNM-WT 15000? Submitted to *J. Hum. Evol.*

- Guatelli-Steinberg, D., Reid, D.J., Bishop, T.A., Larsen, C.S., 2005. Anterior tooth growth periods in Neandertals were comparable to those of modern humans. *Proc. Natl. Acad. Sci.* 102: 13197-14202.
- Guatelli-Steinberg, D., Reid, D.J., Bishop, T.A., 2007. Did the lateral enamel of Neandertal anterior teeth grow differently from that of modern humans? *J. Hum. Evol.* 52: 72-84.
- Guatelli-Steinberg, D., 2009. Recent studies of dental development in Neanderthals: implications for Neanderthal life histories. *Evol. Anthropol.* 18: 9-20.
- Hamada Y., Usono T., 2002. Longitudinal analysis of length growth in the chimpanzee (*Pan troglodytes*). *Am. J. Phys Anthropol.* 118: 268-284.
- Harvey, P.H. and Clutton-Brock, T.H., 1985. Life history variation in primates. *Evol.* 39, 559-581.
- Harvey, P.H. and Nee, S., 1991. How to live like a mammal. *Nature* 350: 23-24.
- Harvey, P.H., Pagel, M.D., 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hennemann, W.W., 1983. Relationship among body mass, metabolic rate, and the intrinsic rate of natural increase in mammals. *Oecologia* 56: 104-108.
- Heim, J.L., 1982. *Les enfants Néandertaliens de La Ferrassie*. Paris : Masson.
- Joffe, T.H., 1997. Social pressures have selected for an extended juvenile period in primates. *J. Hum. Evol.* 32: 593-605.
- Kennedy, G., 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. *J. Hum. Evol.* 48, 123-145.
- Kondo, O., Dodo, Y., Akazawa, T., Muhesen, S., 2000. Estimation of stature from the skeletal reconstruction of an immature Neandertal from Dederiyeh Cave, Syria. *J. Hum. Evol.* 38: 467-473.
- Lee, P.C., Kappeler, P.M., 2003. Socioecological correlates of phenotypic plasticity of primate life histories. In *Primate Life Histories and Socioecology*, P.M. Kappeler, M.E. Pereira (eds.), pp. 41-65. Chicago: The University of Chicago Press.
- Lehninger, A.L., 1982. *Principles of Biochemistry*. New York:Worth.
- Leigh, S.R., 1996. Evolution of human growth spurts. *Am. J. Phys. Anthropol.* 101: 455-474.

- Leigh, S.R., Shea, B.T., 1998. Ontogeny of body size variation in African apes. *Am. J. Phys. Anthrop.* 99: 43-65.
- Leonard, W.R., Robertson, M.L., 1997. Comparative primate energetics and hominid evolution. *Am. J. Phys. Anthrop.* 102: 265-281.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432: 345-352.
- Maddison, W.P., Maddison, D.R., 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5 <http://mesquiteproject.org>.
- Madre-Dupouy, M., 1992. *L'Enfant du Roc de Marsal: Cahiers de Paléanthropologie*. Paris: Éditions du Centre National de la Recherche Scientifique.
- Mann, A.E., 1975. Paleodemographic aspects of the South African Australopithecinae. Ph.D. dissertation, University of Pennsylvania, Philadelphia.
- Martins, E.P., Garland, T., 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulated study. *Evol.* 45: 534-557.
- Matthews, L., Arnold, J.C., Machanda, Z., Nunn, C.L., 2009. Body size effects on speciation and extinction rates in primates. In prep.
- McCarthy, R.C., Lupo, A.C., Cowgill, L.W., (n.d.). Neanderthal weaning, brain growth, and the evolution of human childhood. Submitted to *J. Hum. Evol.*
- Mellars, P., 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432: 461-465.
- Midford, P.E., Garland Jr., T., Maddison, W., 2008. PDAP:PDTREE package for Mesquite, version 1.12. [http://mesquiteproject.org/pdap\\_mesquite/](http://mesquiteproject.org/pdap_mesquite/).
- Millar, J.S., Zammuto, R.M., 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64: 631-635.
- Minitab Inc. (2006). Minitab Statistical Software, Release 15 for Windows, State College, Pennsylvania. Minitab® is a registered trademark of Minitab Inc.
- Minugh-Purvis, N., 1988. Patterns of craniofacial growth and development in Upper Pleistocene hominids. Ph.D. dissertation, University of Pennsylvania, Philadelphia.
- Mitani, H., Sato, K., 1992. Comparison of mandibular growth with other variables during puberty. *Ang. Ortho.* 62: 217-222.
- Mitchell, M., 2002. Engauge® software. Source Forge, Inc.

- Nelson, A.J., Thompson, J.L., 1999. Growth and Development in Neandertals and other fossil hominids: implications for the evolution of hominid ontogeny. In *Human Growth in the Past*, R.D. Hoppa, C.M. FitzGerald (eds.), pp. 88-110. Cambridge: Cambridge University Press.
- Nelson, A.J., Thompson, J.L., 2002. Adolescent postcranial growth in *Homo neanderthalensis*. In *Human Evolution Through Developmental Change*, N. Minugh-Purvis, K.J. McNamara (eds.), pp. 442-478. Baltimore: The Johns Hopkins University Press.
- Nunn, C.L., Barton, R.A., 2001. Comparative methods for studying primate adaptation and allometry. *Evol. Anthropol.* 10: 81-98.
- Payne, R.W., Harding, S.A., Murray, D.A., Soutar, D.M., Baird, D.B., Glaser, A.I., Channing, I.C., Welham, S.J., Gilmour, A.R., Thompson, R., Webster, R., 2009. *GenStat Release 12 Reference Manual, Part 1 Summary*. VSN International, Hemel Hempstead.
- Payne, R.W., Harding, S.A., Murray, D.A., Soutar, D.M., Baird, D.B., Glaser, A.I., Channing, I.C., Welham, S.J., Gilmour, A.R., Thompson, R., Webster, R., 2009. *GenStat Release 12 Reference Manual, Part 2 Directives*. VSN International, Hemel Hempstead.
- Ponce de León, M.S., Golovanova, L., Doronichev, V., Romanova, G., Akazawa, T., Kondo, O., Ishida, H., Zollikofer, C.P.E., 2008. Neanderthal brain size at birth provides insights into the evolution of human life history. *Proc. Natl. Acad. Sci.* 105: 13764-13768.
- Prothero, J., Jurgens, K.D., 1987. Scaling of maximum lifespan in mammals: a review. *Basic Life Sci.* 42: 49-74.
- Ramirez Rozzi, F.V. and Bermúdez de Castro, J.M., 2004. Surprisingly rapid growth in Neanderthals. *Nature* 428: 936-939.
- Rode, A., Shepard, R.J., 1984. Ten years of "civilization": fitness of Canadian Inuit. *J. Appl. Physiol.* 56: 1472-1477.
- Ross, C., 1992. Environmental correlates of the intrinsic rate of natural increase in primates. *Oecologia* 90: 383-390.
- Ruff, C.B., 2007. Body size prediction from juvenile skeletal remains. *Am. J. Phys. Anthropol.* 133: 698-716.
- Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387: 173-176.



- Ruff, C., and Walker, A., 1993. Body size and body shape. In *The Nariokotome Homo erectus Skeleton*, A. Walker, R. Leakey (eds.), pp. 234-265. Cambridge: Harvard University Press.
- Schultz, A.H., 1960. Age changes in primates and their modification in man. In *Human Growth*, J.M. Tanner (ed.), pp. 1-20). Oxford: Pergamon Press.
- Skinner, M.F., Sperber, G.H., 1982. *Atlas of Radiographs of Early Man*. New York: Liss.
- Smith, B.H., 1993. The physiological age of KNM-WT 15000. In *The Nariokotome Homo erectus Skeleton*, A. Walker, R. Leakey (eds.), pp. 195-220. Cambridge: Harvard University Press.
- Smith, R.J., 1993. Logarithmic transformation bias in allometry. *Am. J. Phys. Anthrop.* 90, 215-228.
- Smith, R.J., Jungers, W.L., 1997. Body mass in comparative primatology. *J. Hum. Evol.* 32: 523-559.
- Smith, T.M., Toussaint, M., Reid, D.J., Olejniczak, A.J., Hublin, J.J., 2007. Rapid dental development in a Middle Paleolithic Belgian Neanderthal. *Proc. Nat. Acad. Sci.* 104: 20220-20225.
- Snodgrass, J.J., Leonard, W.R., 2009. Neanderthal energetics revisited: insights into population dynamics and life history evolution. *PaleoAnthropology* 2009, 220-237.
- Studel-Numbers, K.L., 2006. Energetics in *Homo erectus* and other early hominins: the consequences of increased lower-limb length. *J. Hum. Evol.* 51: 445-453.
- Stringer, C.B., Dean, M.C., 1997. Age at death of Gibraltar 2 – a reply. *J. Hum. Evol.* 32: 471-472.
- Tardieu, C., 1998. Short adolescence in early hominids: Infantile and adolescent growth spurt of the human femur. *Am. J. Phys. Anthrop.* 107: 163-178.
- Thompson, J.L., Nelson, A.J., 2000. The place of Neandertals in the evolution of hominid patterns of growth and development. *J. Hum. Evol.* 38: 475-495.
- Vlêck, E., 1973. Postcranial skeleton of a Neanderthal child from Kiik-Koba, U.S.S.R. *J. Hum. Evol.* 2: 537-544.
- Wooten, J.T., 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. *Evolution* 41: 732-749.

Zihlman, A., Bolter, D., Boesch, C., 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *Proc. Natl. Acad. Sci.* 101: 10541-10543.

Zubrow, E., 1989. The demographic modeling of Neanderthal extinction. In *The Human Revolution*, P. Mellars, C.B. Stringer (eds.), pp. 212-231. Princeton: Edinburgh University Press.