



## Just how strapping was KNM-WT 15000?

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### ABSTRACT

For over twenty years, the young, male *Homo erectus* specimen KNM-WT 15000 has been the focus of studies on growth and development, locomotion, size, sexual dimorphism, skeletal morphology, and encephalization, often serving as the standard for his species. Prior research on KNM-WT 15000 operates under the assumption that *H. erectus* experienced a modern human life history, including an adolescent growth spurt. However, recent fossil discoveries, improvements in research methods, and new insights into modern human ontogeny suggest that this may not have been the case. In this study, we examine alternative life history trajectories in *H. erectus* to re-evaluate adult stature estimates for KNM-WT 15000. We constructed a series of hypothetical growth curves by modifying known human and chimpanzee curves, calculating intermediate growth velocities, and shifting the age of onset and completion of growth in stature. We recalculated adult stature for KNM-WT 15000 by increasing stature at death by the percentage of growth remaining in each curve. The curve that most closely matches the life history events experienced by KNM-WT 15000 prior to death indicates that growth in this specimen would have been completed by 12.3 years of age. These results suggest that KNM-WT 15000 would have experienced a growth spurt that had a lower peak velocity and shorter duration than the adolescent growth spurt in modern humans. As a result, it is likely that KNM-WT 15000 would have only attained an adult stature of 163 cm (~5'4"), not 185 cm (~6'1") as previously reported. KNM-WT 15000's smaller stature has important implications for evolutionary scenarios involving early genus *Homo*.

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### Introduction

The 1984 discovery of a ~1.5 million-year-old partial skeleton of African *Homo erectus/ergaster* provided a unique view into the biology, morphology, and evolution of early *Homo* (Walker and Leakey, 1993). This specimen, KNM-WT 15000, is particularly informative due to its relative completeness and young age at death. Often referred to as Nariokotome Boy, KNM-WT 15000 has served as the standard for *H. erectus* in studies on growth and development, encephalization, and locomotion (e.g., McHenry, 1991, 1992; Tardieu, 1994, 1998; Leigh, 1996, 2006; McHenry and Coffing, 2000; Pearson, 2000; Dean et al., 2001; Ohman et al., 2002; Richmond et al., 2002; Steudel-Numbers, 2006; Lordkipanidze et al., 2007; Robson and Wood, 2008; Dean and Smith, 2009). Early descriptions portrayed KNM-WT 15000 as a tall, thin, male *H. erectus* with tropical body proportions adapted for life in sub-Saharan Africa (Holliday and Ruff, 1997). Using

modern human comparative samples, Smith (1993) initially estimated an age of 11 to 12 years at death for KNM-WT 15000 but cautioned that the ontogenetic sequence of molar eruption and epiphyseal closure did not comfortably match modern human standards. If Nariokotome Boy had followed a modern human-like pattern of growth and development, he would have been on the cusp of an adolescent growth spurt that would have resulted in an adult stature of 185 cm (~6'1") and a body mass of 68 kg (~150 lbs; see Ruff and Walker, 1993).

While this early work incorporated state-of-the-art methods, recent discoveries and new methods for estimating age at death support a re-evaluation of the evidence for an adolescent growth spurt and extended, modern human-like ontogeny in KNM-WT 15000. These new developments suggest that KNM-WT 15000 was younger than originally estimated (Dean et al., 2001; Dean and Smith, 2009), with a life history intermediate between chimpanzees and modern humans (Tardieu, 1998; Dean et al., 2001; Simpson et al., 2008; Dean and Smith, 2009), and a brain size at birth larger than previously projected (Coqueugniot et al., 2004; Simpson et al., 2008). Together, these factors support a life history trajectory unlike that exhibited by modern humans, with

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a growth spurt of lesser magnitude and shorter duration. This study investigates the impact of these new lines of evidence on KNM-WT 15000's adult stature. To estimate adult stature for KNM-WT 15000, we developed 18 intermediate growth trajectories using modern human and chimpanzee growth curves as baselines, for a total of 20 curves. We then calculated 500 adult stature estimates using five statures at death and five ages at death. Adult stature estimates range between 144 cm and 225 cm. The two growth curves that most closely match the pattern and timing of life history events in KNM-WT 15000 produce estimates ranging between 159 cm and 168 cm, with an average "best" estimate of 163 cm ( $\sim 5'4''$ ).

## Background

### Age at death

Table 1 lists different age at death estimates for KNM-WT 15000. During her initial analysis of Nariokotome Boy, Smith (1993) used modern human and chimpanzee models to develop a series of age estimates based on dental eruption, dental formation, and epiphyseal closure. Age at death estimates calculated from modern human dental and skeletal models ranged between 10.4 and 15.0 years (Table 1). Age at death estimates cluster around 11 years based on dental development and eruption and 13 years based on epiphyseal closure of long bones. A two to three year difference is not uncommon in modern human populations, although it is atypical for skeletal age to exceed dental age (Clegg and Aiello, 1999; Smith, 2004). Among other things, the disjunction between dental and skeletal age produced by the modern human models led Smith (1993: 219) to conclude that KNM-WT 15000's growth and development were a "somewhat uneasy fit" to modern human growth standards. Chimpanzee models, on the other hand, placed Nariokotome Boy at 7.0 to 9.0 years of age at death, with a degree of difference between dental and skeletal age estimates that is "about as expected by chimpanzee standards" (Smith, 1993: 219).

In addition to estimating age at death using modern human and chimpanzee models, Smith (1993) constructed an "intermediate" conceptual model for KNM-WT 15000. In earlier work, Smith (1989, 1991) predicted that the timing of tooth emergence and overall pace of life history in *H. erectus* would be intermediate between extant great ape and human models. Later, Smith (1993) averaged the timing of events in modern human and extant chimpanzee life history to produce an intermediate model of *H. erectus* life history, adjusting the model to account for the pattern of events in KNM-WT 15000 at death. According to this conceptual model, early *H. erectus* matured more slowly than a chimpanzee but did not experience a human-like adolescent growth spurt. Smith (1993: 215) noted that the lack of an adolescent growth spurt was

"perhaps the most speculative aspect" of this model, concluding that a better understanding of adolescent growth was required to more accurately evaluate life history in *H. erectus*.

In total, Smith (1993) provided three models of growth and development for KNM-WT 15000. The chimpanzee model suggested a 7.0 to 9.0 year age at death but did not match the pattern of dental eruption observed in KNM-WT 15000. The modern human model produced a discrepancy between dental and skeletal age estimates that is within the range of variation of modern human adolescents. The conceptual model, based on an intermediate growth trajectory, indicated a nine to ten year age at death. According to this conceptual model, Nariokotome Boy would not have experienced a growth spurt of the same intensity and duration as the fully modern human adolescent growth spurt. Ruff and Walker (1993) estimated adult stature and body mass using the modern human model, assuming that stature and body mass would increase markedly in KNM-WT 15000 during a prolonged adolescent growth spurt. Stature and body mass estimates calculated using either of Smith's (1993) other two models would have produced shorter adult stature estimates for KNM-WT 15000.

### Stature at death

Ruff and Walker (1993) estimated a stature at death of 160 cm (range 156 cm to 163 cm) for KNM-WT 15000 using regression equations based on the relationship between stature and the lengths of the femur, tibia, and ulna. They derived the regression equations from analyses of modern human populations demonstrating appendicular skeletal proportions that were similar to those exhibited by KNM-WT 15000 (Ruff and Walker, 1993). These authors cautioned that a stature at death of 160 cm ( $5'3''$ ) was probably slightly elevated, as it did not account for differences in cranial height between *H. erectus* and *Homo sapiens* (Ruff and Walker, 1993). Since this initial analysis, a number of researchers have used a variety of methods and comparative samples to calculate stature for KNM-WT 15000 (Table 2), with estimates of stature at death ranging between 144.0 cm and 165.8 cm. Ruff (2007) recently used regression equations developed from modern human children in the Denver growth study to estimate a stature at death of 157 cm (range 150.5 cm to 169.1 cm).

### Adult stature and body mass

In their initial analysis, Ruff and Walker (1993) estimated that KNM-WT 15000's stature would have increased from 160 cm at death to 185 cm ( $6'1''$ ) in adulthood, with confidence intervals yielding a range of 177 cm ( $5'10''$ ) to 193 cm ( $6'4''$ ). To obtain adult stature, Ruff and Walker (1993) increased the measured lengths of KNM-WT 15000's femur, tibia, and ulna by the percent of growth remaining between 11 and 12 years and adulthood in U.S. whites,

**Table 1**  
Different age at death estimates for KNM-WT 15000

Age (years)	Method	Reference sample	Reference
7.5–8.0	Epiphyseal union	Chimpanzee	Smith (1993)
7.5–9.0	Dental eruption and formation	Chimpanzee	Smith (1993)
7.6–8.8	Microanatomy of dentine and enamel	Fossil hominin	Dean and Smith (2009)
~8.0	Dental enamel, perikymata formation	Great ape and modern human	Dean et al. (2001)
10.4–10.7	Dental formation	Modern European	Smith (1993)
10.5–11.7	Dental eruption and formation	Modern human	Smith (1993)
11.0–15.0	Epiphyseal union, individual elements	Modern human	Smith (1993)
11.1	Dental eruption	Modern African	Smith (1993)
12.0	Dental eruption, ignoring canines	Modern African	Smith (1993)
13.0–13.5	Epiphyseal union, combining minima and maxima for all elements	Modern human	Smith (1993)
15.0	Distal femoral morphology	Modern human	Tardieu (1998)

**Table 2**  
Stature at death estimates for KNM-WT 15000 based on 11 to 12 years age at death. Statures used to calculate adult stature in this study are in bold

Mean (cm)	Range	Reference
<b>144.0</b>	141.0–147.0	Ohman et al. (2002)
<b>157.0</b>	155.0–160.0	Feldesman and Lundy (1988)
<b>157.0</b>	150.5–169.1	Ruff (2007)
157.4	None provided	Feldesman (1992)
<b>160.0</b>	156.0–163.0	Ruff and Walker (1993)
161.2	151.1–169.3	Hens et al. (2000)
161.8	158.0–164.0	Feldesman et al. (1990)
162.0	None provided	McHenry (1991)
164.0	160.0–168.0	Brown et al. (1985)
<b>165.8</b>	None provided	Feldesman et al. (1990)

Pecos Pueblo Amerindians, and Kodiak Island Eskimos and Aleuts. Ruff and Walker (1993) then calculated adult stature using these estimated adult long bone lengths in regression formulae derived from Ugandan Nilohamite and Nilote tribesmen. These populations exhibit body proportions and adult long bone dimensions that closely match those extrapolated for Nariokotome Boy. The final adult stature estimate of 185 cm was derived using an estimate of adult long bone lengths, thereby requiring two estimates. Single-step estimates of adult stature from stature at death are much higher, ranging between 189.5 cm and 197 cm. As observed by Dean and Smith (2009: 104), it was apparent that Ruff and Walker had difficulty determining a “sensible prediction” from the data that were available at the time.

Ruff and Walker (1993) then used KNM-WT 15000’s adult stature prediction in conjunction with projected adult bi-iliac breadth to estimate adult body mass. Using a variety of reference populations, they estimated that KNM-WT 15000 would have weighed approximately 68 kg (150 lbs) as an adult.

Ruff and Walker’s (1993) stature and body mass estimates are often used as standards in hominin studies. However, as the authors originally cautioned, it is important to acknowledge that these estimates are predicted on several assumptions about growth, development, and life history (see Ruff and Walker, 1993). Although these assumptions were justified at the time of the original analyses, new data and interpretations provide a solid foundation for their reconsideration. A number of key insights are important in this regard. First, new dental analyses (Dean et al., 2001; Dean and Smith, 2009) indicate that KNM-WT 15000’s age at death was closer to Smith’s (1993) original estimate of 7.0 to 9.0 years of age based on great ape models than to the widely-accepted estimate of 11 to 12 years of age used by Ruff and Walker (1993). Second, analysis of femoral morphology (Tardieu, 1998) suggests that KNM-WT 15000 was approaching adulthood. Additionally, recent studies show that some non-human primates experience growth spurts that differ in duration, magnitude, and timing from the modern human adolescent growth spurt (Tanner et al., 1990; Bogin, 1993, 1995, 1996; Bogin and Smith, 1996; Leigh, 1996; Hamada et al., 1999; Hamada and Udono, 2002). Finally, the discovery of a female hominin pelvis from Gona, Ethiopia suggests that previous ideas about brain size at birth and encephalization in early *Homo* warrant reconsideration (Simpson et al., 2008, but see Ruff, 2010). These new findings support the hypothesis that *H. erectus* had a different growth trajectory and schedule of life history events than either modern humans or chimpanzees, as originally proposed in Smith’s (1993) conceptual model. This in turn raises questions about KNM-WT 15000’s adult stature and body mass. In this study, we examine a number of theoretical growth trajectories and life history sequences to determine the combination that most closely fits the known pattern of dental eruption and epiphyseal closure in Nariokotome Boy. We then use these growth trajectories to calculate new adult stature estimates for KNM-WT 15000.

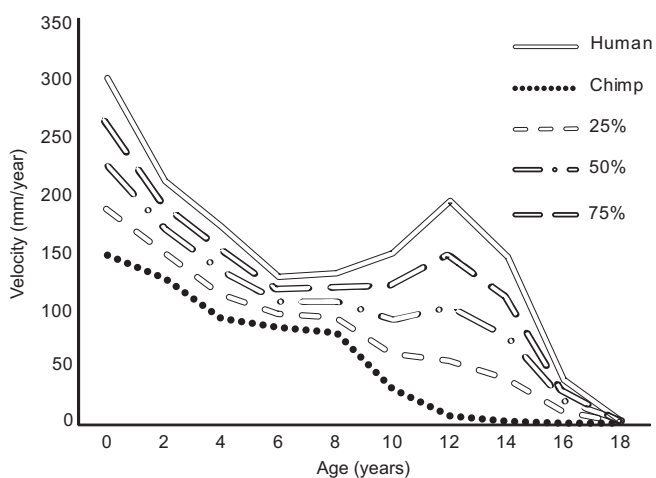
## Materials and methods

Individual growth can be predicted most accurately by assessing trajectories developed from growth studies of individuals from the same population (Ruff and Walker, 1993; Ruff, 2007). Since this is not possible for *H. erectus*, the next-best option is to consider growth in populations with similar body proportions living under comparable environmental conditions (Ruff and Walker, 1993). Since *H. erectus* may have experienced an intermediate growth trajectory, we used chimpanzee (*Pan troglodytes verus*) and modern human growth velocity curves to set upper and lower limits on the rate of growth in KNM-WT 15000.

We chose a growth curve for rural male pastoralists from South Africa (Cameron et al., 1992) to represent growth in stature in modern humans. Cameron et al. evaluated growth bi-annually in a longitudinal five-year study, with subjects ranging in age from six to 19 years. This population is characterized by tropically-adapted body and limb proportions, similar to KNM-WT 15000. We considered the high levels of daily activity in these rural South African pastoralists to be a reasonable match for KNM-WT 15000 (see also Aiello and Key, 2002). A longitudinal study of an East African hunter–gatherer population would have been preferable, but we were unable to locate a published growth curve matching these criteria.

To represent growth in chimpanzees, we used data from Hamada and Udono’s (2002) analysis of length growth in male chimpanzees. This study compared longitudinal data for growth in crown-rump, thigh, and leg length (total body length) to cross-sectional data for the same measurements. While total body length is not an exact proxy for erect stature in humans, it does account for variation in the timing of growth in body segments. Hamada and Udono (2002) constructed separate male and female velocity curves for growth in total body length from measurements recorded for 105 chimpanzees. In addition, Hamada and Udono (2002) constructed growth curves for “fast-,” “average-,” and “slow”-growing chimpanzees from longitudinal growth curves of five male and seven female chimpanzees. They found that the growth trajectory for the “average” groups was comparable to the trajectory for the cross-sectional velocity curves (Hamada and Udono, 2002). While the trajectory of growth is similar in the “average” curve and the curve produced using cross-sectional data, it should be noted that we chose to use the cross-sectional velocity curve (Hamada and Udono, 2002: Fig. 3b), since the “average” curve was created by combining the distance curves for two “average”-growing male chimpanzees. In other words, Hamada and Udono’s (2002) “average” curve does not actually represent the growth trajectory of a single chimpanzee but instead combines data for two individuals. In addition, we preferred to use data directly from the male chimpanzee velocity curve rather than potentially compounding errors by creating a velocity curve using data extracted from the distance curve. Finally, the cross-sectional velocity curve developed by Hamada and Udono (2002) for naturally-reared captive chimpanzees may provide a more accurate representation of growth in wild chimpanzees than other studies of captive chimpanzees. Based on the timing of long bone epiphyseal fusion, Zihlman et al. (2007) suggested that wild chimpanzees attain adult length one to three years later than captive chimpanzees. The naturally-reared captive chimpanzees in Hamada and Udono’s (2002) study attained adult total body length at approximately 13 years of age, which is two years later than indicated by previously-published data for captive chimpanzees (Grether and Yerkes, 1940; Schultz, 1940; Gavan, 1953). The timing of growth completion in captivity suggests that natural conditions in captivity may not substantially affect the age at which adult body size is attained, in effect closely approximating wild conditions.

We generated data for the baseline velocity curves from the published human and chimpanzee curves using the program Engauge™ (Mitchell, 2002). Engauge™ converts image files into numerical data for analysis when the original data are unavailable (Mitchell, 2002). The program reduces operator error by automating axes matching, point matching, and curve tracing. After scanning the published image, the user defines the axis points and specifies the scale. The software estimates  $x$  and  $y$  coordinates along the best-fit line (in this case, the published curves), outputting a data file that can be utilized by other software applications including Microsoft Excel™ and Statistica™. We scanned the modern human male distance curve from Cameron et al. (1992) to obtain the  $x$  and  $y$  coordinates. We generated a velocity curve for modern humans by dividing the difference in stature at a given age by the change in age, and graphing the age on the  $x$ -axis and the velocity on the  $y$ -axis. We then scanned Hamada and Udono's (2002) velocity curve. We used the  $x$  and  $y$  coordinates calculated for the Cameron et al. (1992) velocity curve and those provided by Engauge™ for the Hamada and Udono (2002) velocity curve to determine the total area under the curve and the percentage of that area remaining at each age of interest. It is important to note that the area remaining under the curve does not equal the amount of growth remaining that could be calculated by dividing an age-specific stature by the final adult stature. Instead, we calculated the growth remaining at each year of age by adding all the percentages for each increment of time between a given year of age and attainment of adult stature, and dividing by the total area under the curve. Therefore, our stature estimates for a given year represent all ages between the first and last day of the year, providing an average growth velocity for that year. To construct growth curves for KNM-WT 15000, we developed intermediate growth curves at magnitudes of 25%, 50%, and 75% between the modern human and chimpanzee baselines (Fig. 1). We refer to these curves as intermediate magnitude (IM) growth curves. The 50% growth curve ("IM 50%") was calculated by averaging the velocities of the human and chimpanzee curves at each year of life, the "IM 75%" curve by averaging the "IM 50%" and human curves, and the "IM 25%" curve by averaging the "IM 50%" and chimpanzee curves. The IM curves represent growth trajectories employing modern human,



**Fig. 1.** Modern human, chimpanzee, and intermediate growth curves used to estimate stature in KNM-WT 15000. The 50% growth curve (IM 50%) was calculated by averaging the velocities of the human and chimpanzee curves at each year of life, the IM 75% curve by averaging the IM 50% curve and human curve, and the IM 25% curve by averaging the IM 50% curve and the curve for chimpanzees.

chimpanzee, and intermediate velocities but do not account for shifts in the ages at which life history events (LHEs) occur (Fig. 1).

To account for these shifts, we accelerated the schedule of LHEs (including 95% completion of brain growth, eruption of the permanent incisors, canines, and molars, and epiphyseal union) in the IM growth curves. Chimpanzee total body length growth velocities are consistently lower than stature growth velocities in modern humans (Fig. 1). For the first four years, growth decelerates in both species but decreases more rapidly in humans. Between four and six years of age, the growth trajectories begin to converge, with humans continuing to experience a rapid decrease in growth velocity while chimpanzee growth velocities level off. From four to eight years of age, chimpanzees experience a short period of slight growth retardation, followed by a rapid deceleration in growth velocity from eight to 12 years and attainment of total body length before 14 years of age. Modern humans, on the other hand, experience a slight increase in growth rate at the end of the juvenile period (approximately eight years of age), followed by an increase in growth rate at approximately ten to 12 years of age. Therefore, we accelerated life history events in the IM growth curves to generate growth curves with life history schedules intermediate between human and chimpanzee schedules. In these altered life history curves (which we refer to as ALH curves), LHEs occur earlier than in modern humans but later than in chimpanzees. For example, the molars erupt in the same sequence as in modern humans, but earlier in ontogeny. We referred to prior studies to determine the target age for completion of growth in our ALH curves. Hamada and Udono's (2002) study shows that growth in length in naturally-reared captive chimpanzees is completed between 12 and 13 years of age. Smith's (1993) conceptual model suggested that the maturation in a 14.5-year-old *H. erectus* was approximately equivalent to that of an 18-year-old modern human (which is the average age at which South African males in Cameron et al.'s [1992] study achieve adult stature). In addition, Zihlman et al. (2007) documented complete fusion of the long bones, including the distal femur, in wild chimpanzees at the same age. To achieve completion of growth at approximately 12 and 14.5 years of age, we multiplied the ages along the curve by 0.7 and 0.8. In addition, to narrow the gap between 14.5 and 18 years of age, we multiplied each age by 0.9, resulting in growth completion at 16.2 years. These calculations shifted take-off velocity from ten years of age (the age of onset in modern humans) to approximately seven, eight, and nine years, so that growth is complete by 12.3, 14.3, and 16.2 years of age, respectively. These curves are referred to as "ALH 12.3," "ALH 14.3," and "ALH 16.2" curves. We created a total of 18 growth curves from the original modern human and chimpanzee growth curves by varying the rate of growth and the timing of life history events.

We estimated adult stature by increasing each stature at death by the percentage of growth remaining (had Nariokotome Boy survived to adulthood). The percentage of growth remaining was derived by calculating the area under the growth curve between each age at death (8–9, 9–10, 10–11, and 11–12 years) and cessation of growth. We predicted adult statures for four previously estimated statures at death (see Table 2), including the extreme high (165.8 cm, Feldesman et al., 1990) and low (144.0 cm, Ohman et al., 2002) values, the stature most often used in comparative studies, 157 cm (Feldesman and Lundy, 1988; Ruff, 2007), and the original stature at death estimate, 160 cm (Ruff and Walker, 1993). We also included an adjusted stature of 154 cm, which we derived by reducing Ruff's (2007) estimate of 157 cm by 3 cm to account for differences in cranial height between *H. sapiens* and *H. erectus* (Delson, 1995). This 3-cm difference was calculated by subtracting 10.2 cm (the cranial height reported for KNM-WT 15000 by Gabunia et al. [2000]) from 13.2 cm (the average basion-bregma height for modern sub-Saharan African males, excluding the



“Bushman” population, from Howells’s [1996] cranial data set). We then estimated KNM-WT 15000’s adult stature by increasing each of the five baseline statures by the percentage of growth remaining.

To evaluate whether our results increase the known range of variation in *H. erectus*, we conducted a set of bootstrap analyses on the coefficient of variation (CV) of femoral bicondylar length (FOL). We used FOL instead of stature to eliminate additional error caused by estimating stature from long bone lengths. We compared CVs calculated for Ruff and Walker’s (1993) initial estimates (adult FOL average = 517 mm, KNM-WT 15000 at 11 to 12 years of age) to those calculated using our new estimates (adult FOL average = 466.5 mm, KNM-WT 15000 at eight to nine and nine to ten years of age). We conducted two sets of analyses: one set included *H. erectus* femora contemporaneous with KNM-WT 15000 (KNM-ER 736, KNM-ER 1808, and KNM-ER 737); the other included all African *H. erectus* for which we were able to obtain FOL measures (OH 28, OH 34, KNM-ER 737, KNM-ER 1808, KNM-ER 736, KNM-ER 1481, KNM-ER 3728, and KNM-ER 1472; see Table 3). There are two estimates for KNM-ER 736 femur length. The two estimates, 482 mm and 500 mm, were derived using KNM-ER 999 and KNM-WT 15000 as models, respectively. We conducted separate analyses for the two previous estimates of femoral bicondylar length for KNM-ER 736. Modern human ( $n = 53$ ) and chimpanzee ( $n = 58$ ) comparative samples from the American Museum of Natural History (New York, NY), Smithsonian National Museum of Natural History (Washington, DC), Museum of Comparative Zoology (Cambridge, MA), Chicago Field Museum (Chicago, IL), and University of the Witwatersrand (Johannesburg, South Africa) were used as comparative samples (see Cunningham [2005] for further details). All apes were either wild-shot or collected after death in the wild. The modern human samples consist of skeletons from Africa (Egypt and South Africa) and North America (Utah cliff dwellers). To model variation in the *H. erectus* samples, we selected 1,000 random samples of either four or nine individuals, with replacement, from each comparative population for contemporaneous *H. erectus* and African *H. erectus*. Additional details about this bootstrapping procedure can be found in Lockwood et al. (1996).

## Results

We developed 18 hypothetical growth trajectories in addition to the modern human and chimpanzee growth trajectories. Using these 20 growth curves, we predicted adult statures using five ages at death and five statures at death, for a total of 500 individual estimates (Fig. 2). These 500 adult stature estimates for KNM-WT 15000 range between 144.0 cm and 225.5 cm,

depending on the age at death, stature at death, and growth trajectory used (Fig. 2). Our final estimate, 163 cm (5’4”), was calculated by averaging estimates produced by the “ALH 12.3/25%” and “ALH 12.3/50%” curves, assuming an age at death between eight and ten years and a stature at death of 154 cm (details follow). Not surprisingly, estimates using the earliest age at death (eight years) produced the greatest range of adult statures, while estimates calculated using an age at death of 12 years produced the smallest range. A stature at death of 144.0 cm resulted in the shortest adult stature estimates and 165.8 cm resulted in the tallest. As expected, the combination of the shortest stature (144.0 cm) and the oldest age at death (12 years) yielded the shortest adult stature, 144.0 cm. The combination of the youngest age at death (8 years) and the tallest stature at death (165.8 cm) yielded the highest estimate, 225.5 cm (Fig. 2).

Modern human growth curves produced adult stature estimates ranging between 162.4 cm (KNM-WT 15000 12 years old and 144.0 cm at death) and 225.5 cm (eight years old and 165.8 cm at death). It is important to note that our methods produce estimates consistent with previous research. When modeled at 11 to 12 years of age at death and 160 cm in stature, the South African male growth curve resulted in an adult stature prediction of 185.7 cm (range 180.4 cm–191 cm). This estimate is almost identical to the estimate originally calculated by Ruff and Walker (1993; 185 cm, range 177 cm–193 cm). The chimpanzee growth curve produced a minimum adult stature of 144.4 cm and a maximum of 177.1 cm. Figure 2a illustrates the statures estimated from these curves, as well as stature estimates calculated using the IM 25% curve (minimum 152.8 cm, maximum 199.6 cm), the IM 50% curve (minimum 157.4 cm, maximum 212.4 cm), and the IM 75% curve (minimum 160.4 cm, maximum 220.0 cm).

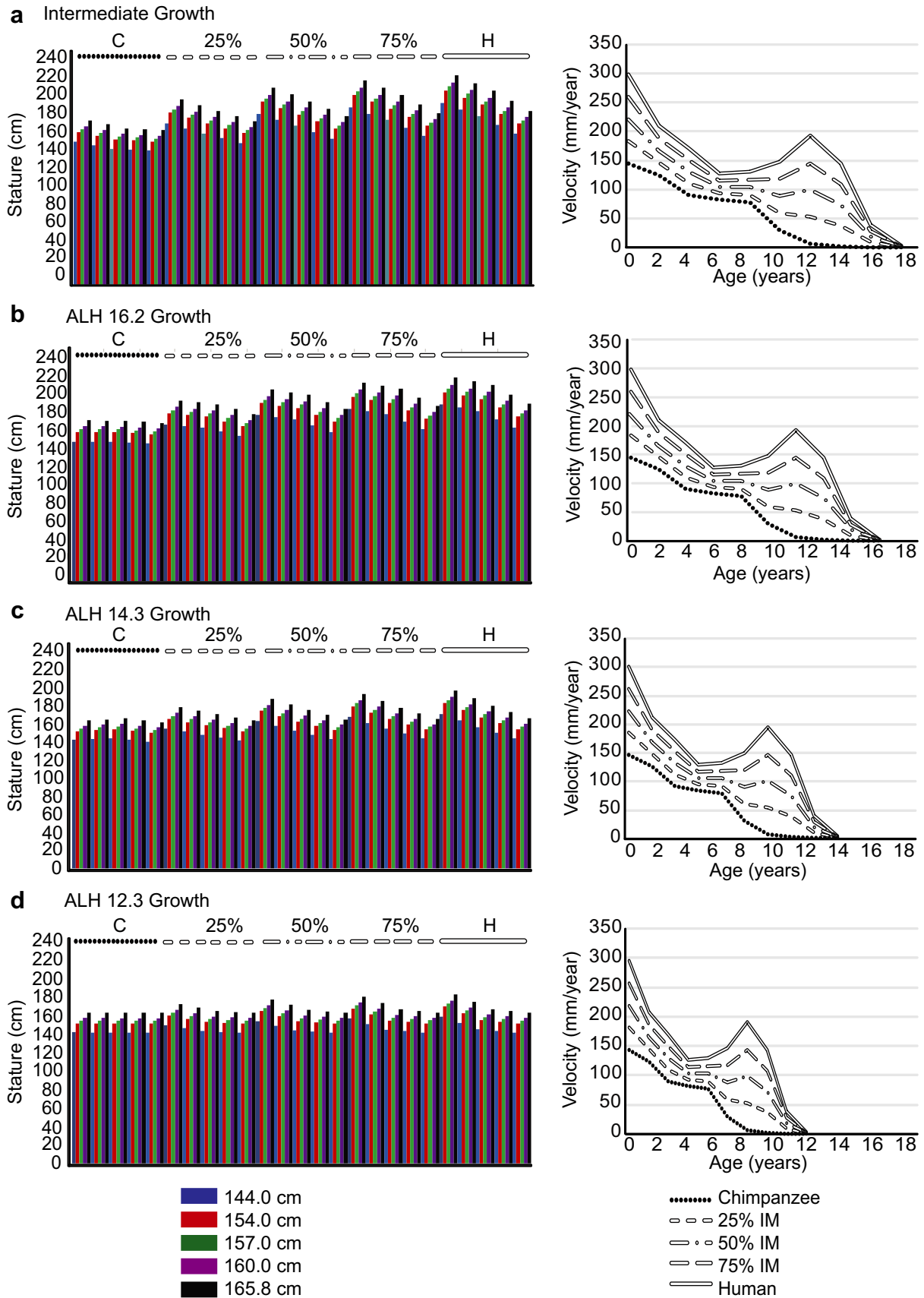
Altered life history growth curves produced adult statures ranging between 144.0 cm and 213.6 cm (Fig. 2b–d). The “ALH 16.2” curves, which accelerate life history events slightly relative to the modern human curve, produce adult stature estimates for KNM-WT 15000 that range between 144.4 cm and 213.6 cm (Fig. 2b). “ALH 14.3,” which moderately accelerates life history events, produces stature estimates ranging between 144.0 cm and 202.0 cm (Fig. 2c). Finally, “ALH 12.3,” which substantially accelerates life history events, yields adult stature estimates ranging between 144.0 cm and 186.0 cm (Fig. 2d).

We eliminated curves from consideration that relied on improbable assumptions. For example, it is unlikely that KNM-WT 15000 grew like a chimpanzee but experienced LHEs even earlier during ontogeny, completing growth at 8.4 years of age (“ALH 12.3/Chimpanzee”). Likewise, it is doubtful that KNM-WT 15000 grew slowly, like a modern human, but with an extremely accelerated

**Table 3**  
Homo erectus samples used to calculate coefficients of variation (CVs) for bootstrapping analyses

Specimen	Age (Ma)	FOL (mm)	<i>H. erectus</i> sample		Reference
			Contemporaneous	African	
OH 28	0.70	450		X	Ruff and Walker (1993)
OH 34	1.00	430		X	Day and Molleson (1976)
KNM-WT 15000	1.53	466.5	X	X	This study
KNM-WT 15000	1.53	517 <sup>a</sup>	X	X	Ruff and Walker (1993)
KNM-ER 737	1.60	440	X	X	Ruff and Walker (1993)
KNM-ER 1808	1.69	480	X	X	Ruff and Walker (1993)
KNM-ER 736	1.70	482	X	X	Geissman (1986)
KNM-ER 736	1.70	500	X	X	Ruff and Walker (1993)
KNM-ER 1481	1.89	395		X	Ruff and Walker (1993)
KNM-ER 3728	1.89	390		X	Ruff and Walker (1993)
KNM-ER 1472	1.89	400		X	Ruff and Walker (1993)

<sup>a</sup> For adult bicondylar femoral length in KNM-WT 15000, we averaged Ruff and Walker’s (1993) estimates of 504 mm (12 years of age at death) and 530 mm (11 years of age at death).



**Fig. 2.** Intermediate growth curves used to predict stature in KNM-WT 15000. Adult stature estimates (left) for each set of growth curves (right) demonstrate the range and variability of potential adult statures derived from intermediate magnitudes of growth and life history schedules. A summary of the minimum and maximum statures produced by each growth curve is included in the text.

schedule of LHEs (“ALH 12.3/Human”). Our final estimate of 163 cm is an average of the statures calculated from the “ALH 12.3/25%” and “ALH 12.3/50%” curves, and is based on the supposition that KNM-WT 15000 was approximately 8 years of age and 154 cm at death. This curve would have allowed Nariokotome Boy an additional 4.3 years of growth.

We suggest that new evidence for an earlier age at death (7.6 years–8.8 years, see Dean et al., 2001; Dean and Smith, 2009), a more advanced skeletal maturity at death (Tardieu, 1998), and a reduced likelihood of secondary altriciality (Coqueugniot et al., 2004; Simpson et al., 2008) make the “ALH 12.3” curves the most parsimonious. Additionally, the timing of life history events in the “ALH 12.3” curves matches the reconstructed sequence of LHEs in KNM-WT 15000 more closely than any other curves. As noted above, a number of studies suggest that growth and development in *H. erectus* differed from growth and development in both modern humans and extant apes (Smith, 1993; Dean et al., 2001; Coqueugniot et al., 2004; Simpson et al., 2008; Dean and Smith, 2009; Zollikofer and Ponce de León, 2010). Therefore, we eliminated curves that required KNM-WT 15000 to grow exactly like a modern human or an extant chimpanzee. We eliminated the “ALH 12.3/75%” and “ALH 12.3/Human” velocity curves based on Coqueugniot et al.’s (2004) determination that the pattern of brain development in *H. erectus* more closely resembled that of apes than modern humans. We eliminated the “ALH 12.3/Chimpanzee” curve based on Smith’s (1993) conclusion that the pattern of dental eruption in KNM-WT 15000 differs from chimpanzees in a human-like direction. We were left with the “ALH 12.3/25%” and “ALH 12.3/50%” curves. Using these two preferred curves, Nariokotome Boy grows at velocities intermediate between modern humans and chimpanzees but is growing faster than a chimpanzee early in life, thus allowing him to obtain a larger stature (total body length) at 8 years of age than could be obtained by a chimpanzee at the same age. It is important to note that the average adult stature produced by all “ALH 12.3” curves with an age at death between eight and ten years is 163.3 cm, only 0.3 cm higher than the average of the “ALH 12.3/25%” and “ALH 12.3/50%” growth curves that form the basis for our final estimate.

Our new estimate reduces the range of variation in FOL (and by extension, stature) in contemporary and early African *H. erectus*. Coefficients of variation calculated using our new estimate for FOL in KNM-WT 15000 are lower than those calculated using Ruff and Walker’s (1993) FOL estimate, regardless of which estimate of KNM-ER 736 is used (Table 4). Bootstrapping results indicate that CVs for contemporaneous *H. erectus* specimens fit comfortably into the CV distribution for *P. troglodytes* and *H. sapiens*, as do CVs for African *H. erectus* when modern *H. sapiens* are used as the reference sample. Coefficients of variation for all available African *H. erectus*

femora, however, exceed the range of variation exhibited by *P. troglodytes* in three out of four analyses (see Table 5). While bootstrapping results do not differ significantly from each other using the new and old estimates of femur length (and, by extrapolation, stature), the new FOL estimates do produce lower CVs for all analyses.

In summary, KNM-WT 15000 would have grown an additional five to 14 cm before reaching adulthood if, at death, he was eight to ten years of age, 154 cm tall, and growing faster than a modern human but slower than a chimpanzee. According to this scenario, KNM-WT 15000 would have attained an adult stature ranging between 159 cm (5’2”) and 168 cm (5’6”). When 95% confidence intervals are used to calculate Nariokotome Boy’s stature at death, the range of adult stature estimates increases, to between 152 cm (5’0”) and 179 cm (5’10”). According to our preferred models of growth and development, growth in stature will be completed by 12 years of age (~4 years after death), so that the majority of growth has already occurred, and point estimates (163 cm, 5’4”) and adult stature estimates calculated using 95% confidence intervals (164 cm, 5’4.6”) differ by less than 1 cm.

## Discussion

Recent fossil discoveries and new methods for evaluating age at death and skeletal maturity support the rationale that a reassessment of KNM-WT 15000’s adult size is due. Analysis of enamel formation and dental development suggests that KNM-WT 15000 was younger at death than originally estimated (Dean et al., 2001; Dean and Smith, 2009). Distal femoral morphology indicates that KNM-WT 15000 was nearing skeletal maturity at death (Tardieu, 1998). Current views of growth in primates (including modern humans) suggest that the adolescent growth spurt evolved only recently, after the origin of *H. erectus* (Bogin, 1993, 1996; Leigh, 1996). Finally, a female *Homo* pelvis from Gona described by Simpson et al. (2008) provides additional support for relatively larger newborn brain size in *H. erectus*, suggesting that *H. erectus* infants were unlikely to be secondarily altricial (Coqueugniot et al., 2004). These new developments strongly suggest that the pattern of growth, development, and life history was different in early *Homo* than it is in *H. sapiens*.

### Age and maturity estimation

The emergence of permanent teeth is a stable marker of life history events (Smith, 1993; Bogin, 1996; Dean et al., 2001). Dean et al. (2001) showed that enamel development in the anterior teeth of KNM-WT 15000 more closely resembled the pattern exhibited by australopiths, and that crown and root formation

**Table 4**  
Summary statistics for coefficient of variation (CV) analyses of bicondylar length of the femur (FOL)<sup>a</sup>

FOL estimate (mm)	FOL estimate (mm)		CV analysis					
	KNM-ER 736	KNM-WT 15000 <sup>b</sup>	<i>n</i>	Mean	Range Min	Max	Std Dev	CV <sup>c</sup>
Contemporaneous <i>H. erectus</i>	482.0	466.5	4	471.6	440	482	19.3	4.1
Contemporaneous <i>H. erectus</i>	500.0	466.5	4	471.6	440	500	25.2	5.3
Contemporaneous <i>H. erectus</i>	482.0	517.0	4	479.8	440	517	31.5	6.6
Contemporaneous <i>H. erectus</i>	500.0	517.0	4	484.3	440	517	33.1	6.8
African <i>H. erectus</i>	482.0	466.5	9	437.0	390	482	35.9	8.2
African <i>H. erectus</i>	500.0	466.5	9	439.0	390	500	39.1	8.9
African <i>H. erectus</i>	482.0	517.0	9	442.7	390	517	44.1	10.0
African <i>H. erectus</i>	500.0	517.0	9	444.7	390	517	46.4	10.4

<sup>a</sup> See text for explanation of the differing estimates used for bicondylar femoral length (FOL).

<sup>b</sup> 466.5 cm is the estimate for femoral length generated in this study; 517 cm is the estimate derived from Ruff and Walker (1993) – see note for Table 3.

<sup>c</sup> CV =  $(\sigma/\bar{x}) \times 100$ .

**Table 5**Probabilities (%) of sampling coefficients of variation in bicondylar femoral length (FOL) in *P. troglodytes* and *H. sapiens* samples greater than those in *H. erectus* ( $\alpha = 0.025$ )

FOL estimate (mm)			CV analysis		
	KNM-ER 736	KNM-WT 15000 <sup>a</sup>	<i>n</i>	Chimpanzee	Modern human
Contemporaneous <i>H. erectus</i>	482.0	466.5	4	70.8	81.0
Contemporaneous <i>H. erectus</i>	500.0	466.5	4	50.5	71.6
Contemporaneous <i>H. erectus</i>	482.0	517.0	4	30.9	60.7
Contemporaneous <i>H. erectus</i>	500.0	517.0	4	26.4	57.7
African <i>H. erectus</i>	482.0	466.5	9	2.5	52.6
African <i>H. erectus</i>	500.0	466.5	9	0.6	42.1
African <i>H. erectus</i>	482.0	517.0	9	0.1	28.6
African <i>H. erectus</i>	500.0	517.0	9	0.0	24.5

<sup>a</sup> 466.5 cm is the estimate for femoral length generated in this study; 517 cm is the estimate derived from Ruff and Walker (1993)—see note for Table 3.

times were consistently shorter than those of modern humans. Based on this evidence, Dean et al. (2001) suggested that, at death, KNM-WT 15000 was closer to eight than to 11 or 12 years of age. More recently, Dean and Smith (2009) calculated a refined estimate of 7.6 to 8.8 years of age for Nariokotome Boy based on the timing of enamel and dentine formation in the upper canine and M2. Overall, their conclusions supported the original model suggested by Smith (1993: 215, Fig. 9.7) in which KNM-WT 15000 erupted his second molars before nine years of age and was less than ten years of age at death (Dean and Smith, 2009).

Skeletal morphology also supports a rapid life history in KNM-WT 15000. Tardieu et al. (Tardieu, 1994, 1997, 1998; Tardieu and Trinkaus, 1994; Tardieu and Damsin, 1997) evaluated shape changes during ontogeny in the modern human femur. Despite postmortem damage to the distal condyles of both femora, Tardieu (1998) determined that the morphology of KNM-WT 15000's distal femur clearly indicated shape changes typically observed during human adolescence. She suggested that the extreme protuberance of the external trochlea, the deep trochlear groove, and the elliptical profile of the external condyle indicated an age of approximately 15 years if Nariokotome Boy matured like a modern human. Based on this evidence, Tardieu (1998) suggested that Nariokotome Boy had most likely already experienced adolescent peak velocity and that *H. erectus*, as a species, exhibited a pattern of life history that included a growth spurt of lesser intensity and shorter duration than that of modern humans.

The discrepancy between a 7.6- and 8.8-year dental age (Dean and Smith, 2009) and a 13-year-old skeletal age (Smith, 1993) presents a dilemma. As previously noted, it is not uncommon for there to be a two to three year difference between dental and skeletal age in modern humans, but generally skeletal age lags behind dental age (Clegg and Aiello, 1999; Smith, 2004). These new age estimates increase the dental and skeletal age disjunction to approximately five years (seven years if Tardieu's [1998] estimate of 15 years at death is accurate), with skeletal age exceeding dental age. While it is possible for excessive disjunctions in skeletal and dental age to occur in individuals with endocrine disorders (Dean and Smith, 2009), it is unlikely to occur in a normal individual. In the words of Dean and Smith (2009: 108), "...it is clear that for a child like Nariokotome, with skeletal age advanced by 34+ months over the dentition, a pediatrician would be justified in sending the case to an endocrinologist." On the other hand, if KNM-WT 15000 experienced a chimpanzee-like pattern of growth and life history, a dental age of 7.5 to 9.0 years (Smith, 1993) or 7.6 to 8.8 years (Dean and Smith, 2009) and a skeletal age of 7.5 to 8.0 years (Smith, 1993) are in agreement (Table 1). Finally, a compilation of studies assembled by Dean and Smith (2009) strongly supports the position that dental age is a more accurate predictor of chronological age than is skeletal age. Together, these lines of evidence support a much younger age at death for Nariokotome Boy than suggested in previous studies.

### Pathology

Not only does KNM-WT 15000 demonstrate growth and development inconsistent with modern human standards, but it is also likely that he experienced pathological conditions that would have affected the timing of epiphyseal fusion. It has been suggested that KNM-WT 15000 may have suffered from scoliosis, spina bifida, spondyloepiphyseal dysplasia tarda, axial dysplasia, and/or some other-as-yet unidentified pathological condition (Latimer and Ohman, 2001; Ohman et al., 2002; Meyer, 2005). Since these pathological conditions affect the timing of growth in general and epiphyseal union in particular, it becomes increasingly important to rely on dental age to predict KNM-WT 15000's age at death. This may also explain why KNM-WT 15000's distal femur was incompletely fused, despite its mature appearance. It is also important, in this case, to acknowledge that pathological conditions affecting the axial skeleton undoubtedly have some effect on growth in stature. In this case, it is likely that these conditions would result in a shorter, not taller, adult stature. Therefore, we caution that any study using this specimen should only be undertaken with a clear acknowledgment of the potential influence of pathological conditions on adult stature.

### Adolescent growth

Smith (1993) considered an adolescent growth spurt the most speculative part of the theoretical growth trajectory for *H. erectus*, suggesting that a better understanding of the significance of adolescent growth was needed (Smith, 1993). Antón and Leigh (2003: 241), in their comparison of *H. sapiens* and *H. erectus* cranial ontogeny, were unable to find unequivocal evidence for an adolescent growth spurt in *H. erectus*, although they warned that sufficient data were available to "urge caution in dismissing the idea of an adolescent growth spurt in early *H. erectus*." The modern human adolescent growth spurt is thought to have evolved as a somatic growth "catch-up" mechanism (Lehninger, 1982; Bogin, 1993, 1996; Allman and Hasenstaub, 1999). During the early years of life, energy is focused on growing the metabolically expensive brain (Aiello and Wheeler, 1995), and somatic growth and sexual maturation are delayed until brain growth is completed. After cessation of brain growth, energy is refocused into somatic growth, and growth velocities rebound. The period between cessation of brain growth and the onset of adolescence allows humans to learn skills required for survival (Watts, 1985, 1990). Non-human primates do not demonstrate similar delays between life history events (Bogin, 1996). Since the adolescent growth spurt is so energetically expensive, it has been hypothesized that there must be a "trade-off" benefit to delaying somatic growth until late in ontogeny. Gurven and Walker (2006) suggested that modern humans experience an adolescent growth spurt because smaller somatic size during childhood is beneficial. Modern humans are



unique among primates in that they are able to support several dependent offspring at the same time (Hawkes et al., 1998; Blurton Jones et al., 1999; Hawkes, 2003; Hrdy, 2005; Kramer, 2005; Gurven and Walker, 2006). Weanlings consume an adult-type diet and are placed into direct competition with mature individuals (Gurven and Walker, 2006). By remaining small, these dependent juveniles reduce feeding competition with adults (Janson and Van Schaik, 1993) and are therefore able to devote a substantial amount of time during childhood to social learning. Thus, an adolescent growth spurt allows the individual to remain small early in life and then achieve final adult size after critical social skills have been learned. Nariokotome Boy, on the other hand, had likely already reached a ~154 cm stature by 8 years of age and was growing substantially faster than expected for a modern human.

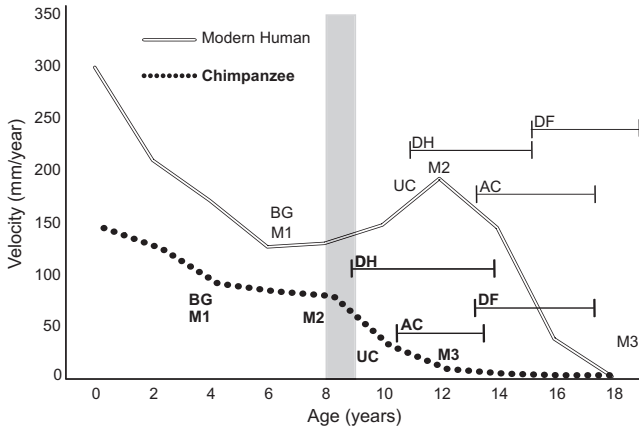
The velocity growth curves for human stature and chimpanzee total body length (summed length of crown-rump, femur, and tibia) highlight the difference between modern human and chimpanzee growth and development (Fig. 1). Both species exhibit growth spurts, but these spurts differ in rate, timing, and duration (Leigh, 1996). Pre-pubertal growth spurts in mass have been documented in many primates (Tanner, 1962; Laird, 1967; Timiras and Valcana, 1972; Leigh, 1996; Leigh and Shea, 1996; Hamada et al., 1996), but to date only slight increases in crown-rump length and total body length have been observed in chimpanzees (Hamada and Udono, 2002). Male chimpanzees (and possibly macaques) undergo a small growth spurt in length during the period between emergence of the first and third molars (Watts and Gavan, 1982; Tanner et al., 1990), but peak velocity is not as high and the growth spurt not as extended as in modern human adolescence. The velocity of chimpanzee growth decreases slightly between the ages of four and eight, and then begins to decline rapidly until adult total body length is reached at between 12 and 13 years of age. Chimpanzee growth spurts therefore differ in their onset, offset, and intensity compared to the modern human adolescent growth spurt (see Fig. 1; Bogin, 1993, 1996). The growth spurts in the “ALH 12.3/25%” and “ALH 12.3/50%” curves approximate the juvenile pre-pubertal growth spurt exhibited by chimpanzees, which is of shorter duration and lesser magnitude than the full-blown modern human adolescent growth spurt. We contend that these curves most closely match what is currently known about growth and development in *H. erectus* but acknowledge that the data currently available limit our ability to choose a single curve. It is also possible that future studies documenting growth in wild chimpanzee length may provide evidence to support a different set of growth curves.

#### Neonatal brain size

In modern humans, the size of the adult female pelvic outlet and neonatal head are nearly identical (Simpson et al., 2008), and modern humans deliver altricial neonates with relatively small brains (Zaveloff and Boyce, 1982). Modern human infants are born with brains approximately 25% of adult size and therefore require an extended period of brain growth postnatally to make up the difference (Herndon et al., 1999; Holloway et al., 2004). Parents must invest significant energy in offspring, providing most of the necessary requirements for survival until brain growth is completed. Walker and Ruff (1993) argued that *H. erectus* was born with a relatively small brain, thereby requiring an extended period of postnatal brain growth like modern *H. sapiens*. To calculate *H. erectus* neonatal brain size, Walker and Ruff (1993) extrapolated pelvic dimensions for a female *H. erectus* by applying a modern human level of sexual dimorphism to their reconstruction of KNM-WT 15000's estimated adult pelvic dimensions. Walker and Ruff (1993) then used their extrapolated dimensions for a female *H. erectus* pelvis to predict a brain size at birth of 200 to 240 g,

which is approximately 25% of adult size (mean 915 g, range 624 g to 1109 g—see Holloway et al., 2004). Walker and Ruff's (1993) small neonatal brain size estimate is consistent with the hypothesis that *H. erectus*, like *H. sapiens*, delivered an altricial neonate requiring an extended and/or rapid period of brain growth (see also Begun and Walker, 1993; Leigh, 2006). Begun and Walker (1993) estimated that the infant *H. erectus* brain would have gained an additional 500 g during the first year, subsequently adding 200 g prior to adulthood. This method for predicting neonatal brain size in *H. erectus* was reasonable given the lack of female *H. erectus* pelvic remains in 1993, but the discovery of new fossils has prompted some researchers to encourage a reconsideration of the original Nariokotome pelvic reconstruction (Arsuaga et al., 1999; Ruff, 2010). In addition, the discovery of a female *H. cf. erectus* pelvis, BSN49/P27 (Simpson et al., 2008), suggests that pelvic sexual dimorphism may have been greater in early *H. erectus* than it is in modern humans. The BSN49/P27 female pelvis has widely flaring ilia, an anteroposteriorly-broadened birth canal, and a larger pelvic inlet and outlet than expected from the original predictions based on Walker and Ruff's (1993) reconstruction of KNM-WT 15000. Ruff (2010) recently suggested that the BSN49/P27 pelvis may have been misidentified as *H. erectus*, but in his assessment of this fossil pelvis, he also determined that all pre-modern hominins, including *H. erectus*, had mediolaterally wide pelvises with a wider birth canal. He concluded that non-rotational birth would have been possible in archaic *Homo* and all earlier fossil hominins (see Ruff, 2010). Assuming that the anteroposterior diameter of the pelvic inlet and midplane breadth limit parturition in *H. erectus* as they do in *H. sapiens* (Tague, 1989; Walrath, 1997; Correia et al., 2005), these new lines of evidence suggest that the initial estimates of neonatal brain size (Walker and Ruff, 1993) and growth (Begun and Walker, 1993) in *H. erectus* were likely based on estimated measurements that were too restrictive. Simpson et al. (2008) estimated brain volume at birth in *H. erectus* to be closer to 330 g, over 30% greater than previous predictions. Intriguingly, 330 g is 34%–36% of adult brain size in *H. erectus*, a value intermediate between modern humans (fetal brains 25% of adult size) and chimpanzees (fetal brains 36%–40% of adult size; Herndon et al., 1999; Holloway et al., 2004). If *H. erectus* followed a modern human-like brain growth trajectory, a 330 g brain size at birth would have produced a 1300 g adult brain, a figure well outside the range of even the largest-brained middle Pleistocene *H. erectus*. Simply put, a 330 g brain size at birth rules out secondary altriciality in *H. erectus*, a point also made by Coqueugniot et al. (2004). Conversely, if KNM-WT 15000 followed a chimpanzee-like pattern of brain growth, a 330 g brain size at birth would produce an 850 g adult brain, a value well within the established range for early *H. erectus*, and only slightly smaller than the adult estimate for KNM-WT 15000.

The picture of a young, fast-growing, early-maturing KNM-WT 15000 born with a relatively large, non-altricial brain is inconsistent with a modern human-like life history. Since there is a strong correlation in mammals between eruption of the first permanent molars and the asymptotic conclusion of brain growth (Smith, 1989; Smith and Tompkins, 1995), it is likely that KNM-WT 15000 would have completed the majority of brain growth by four to five years of age, the time at which his first permanent molars erupted (Dean et al., 2001). In chimpanzee males, a growth spurt in body length occurs between four and eight years of age (Hamada and Udono, 2002), beginning with eruption of the first molar and ending shortly before the second molar erupts. In KNM-WT 15000, the second molars are fully erupted. Therefore, if KNM-WT 15000 grew according to a chimpanzee-like growth trajectory, he had already completed the majority of somatic growth at the time of death. A combination of dental and skeletal data can be used to



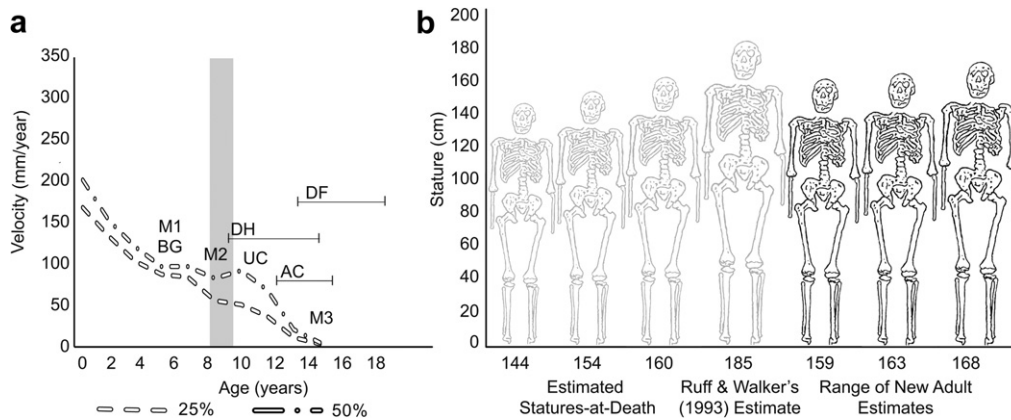
**Fig. 3.** Chimpanzee and modern human stature velocity growth curves with major life history events plotted at their age of occurrence. The shaded region outlines the approximate age of KNM-WT 15000. Life history events include: AC = fusion of the ischium, ilium, and pubis at the acetabulum; BG = brain growth 95% complete; DF = distal femur epiphyseal union; DH = distal humerus epiphyseal fusion; M1 = eruption of first molars; M2 = eruption of second molars; M3 = eruption of third molars; UC = eruption of upper canines.

hone this estimate even further. In KNM-WT 15000, the distal humerus is partially fused, other long bones are not yet fused, and the permanent upper canines have yet to erupt, suggesting an age of no more than 10.5 years compared to wild chimpanzee standards (Zihlman et al., 2007). Complete eruption of the second molars in KNM-WT 15000 suggests an age at death ranging between eight and 10.5 years (Zihlman et al., 2007). Unfortunately, there are currently no known studies documenting the age at which wild chimpanzees attain adult total body length, but Zihlman et al. (2007) suggest that skeletal maturation may occur as much as one to three years later than has been documented for captive chimpanzees (Schultz, 1940; Gavan, 1953). The growth curve from Hamada and Udono (2002) used in this study demonstrates attainment of adult total body length at 12 to 13 years of age, and may therefore provide a valid proxy for growth and development in wild chimpanzees.

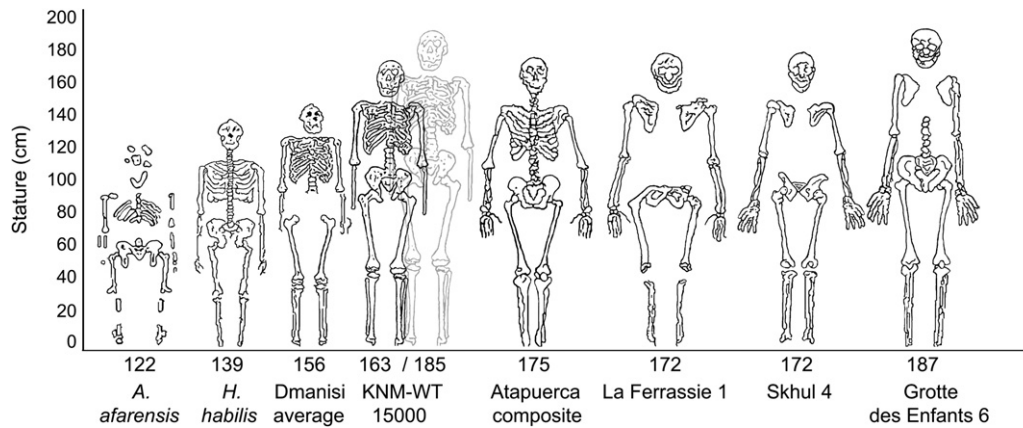
To determine age at death, we plotted life history events (including 95% completion of brain growth, eruption of the permanent molars [M1, M2, and M3] and upper canines, and fusion of the primary elements of the hip bone and distal epiphyses of the humerus and femur) for KNM-WT 15000 on the growth trajectories

of chimpanzees and modern humans (Smith, 1993; Simpson et al., 1996; Winkler, 1996; Zihlman et al., 2007; Fig. 3). In KNM-WT 15000, the first and second molars have erupted, the distal humeral epiphyses have partially fused (Smith, 1993; Ruff and Walker, 1993), the upper canines and third molars have not erupted (Smith, 1993), the distal femur has not fused (Ruff and Walker, 1993), and the primary elements of the hip have not begun to fuse at the acetabulum (Ruff and Walker, 1993). This sequence of events constrains KNM-WT 15000 to approximately eight to nine years of age using a chimpanzee model (vertical gray bar on Fig. 3) without having to make exceptions for non-sequential events. KNM-WT 15000 does not fit the modern human curve with the same precision. For example, eruption of the second molars before the upper canines occurs in only 11%–13% of modern humans (Barrett et al., 1964; Smith and Garn, 1987; Smith, 1993) but is common in chimpanzees. A skeletal age of eight to ten years is also concordant with Smith's (1993) initial assessment of dental and skeletal age in KNM-WT 15000, and the earlier age of approximately eight years aligns well with the dental age of 7.6 to 8.8 years predicted by Dean and Smith (2009).

The "ALH 12.3" growth curves fit most closely with the pattern and timing of LHEs in KNM-WT 15000. In modern humans and chimpanzees, growth velocities decrease following M1 eruption, level out immediately, and then later increase after eruption of M2. In the "ALH 14.3" and "ALH 16.2" growth curves, the timing of eruption of M1 and M2 eruption is offset, with LHEs occurring before associated fluctuations in growth velocities. The "ALH 12.3/IM 50%" growth curve is accelerated in comparison to modern human models, with life history events occurring at a rate 33% slower than in chimpanzees. We consider this number meaningful because it represents the difference in size between modern human and chimpanzee brains at birth. At birth, modern human brains are 25% of adult size, while chimpanzee brains are ~40%. Chimpanzees and modern humans vary by 15%. Coqueugniot et al. (2004) and Simpson et al. (2008) suggest that *H. erectus* may have been born with a brain 35% of adult size (range 34% to 36%). The difference in the 35% predicted for *H. erectus* and the 40% suggested for chimpanzees is equivalent to 5% difference at birth, or 33% of the difference between chimpanzees and modern humans. Curve "ALH 12.3/IM 50%" demonstrates a stable growth velocity between four and 5.5 years of age, immediately following completion of M1 eruption and brain growth (Fig. 4). A slight drop in velocity occurs before a minor growth spurt at seven years of age, which lasts until 9.8 years, with peak velocity occurring at 8.5 years. It should be



**Fig. 4.** The "ALH 12.3/50%" and "ALH 12.3/25%" growth curves illustrating congruence with life history events. In the "ALH 12.3" curves, life history events have been shifted to occur earlier in ontogeny, but their schedule and relative positions along the growth curve have been maintained (a). Adult stature estimates calculated from the "ALH 12.3" curves (159 cm–168 cm) are illustrated next to estimated statures at death (144 cm, 154 cm, and 160 cm) and Ruff and Walker's (1993) adult stature of 185 cm (b). This figure represents the difference between Ruff and Walker's (1993) adult estimate and our new estimates but is not intended to represent changes in shape that would have occurred when KNM-WT 15000 reached adulthood.



**Fig. 5.** Increase in stature from early hominins to anatomically modern humans incorporating our revised stature estimate of 163 cm (dark KNM-WT 15000). Stature estimates are from McHenry (1991), Arsuaga et al. (1999), Ruff et al. (1997), Formicola (2003), Trinkaus (2006), and Lordkipanidze et al. (2007). Data used to calculate cranial height reductions are from Gabunia et al. (2000), Martin et al. (2006), Trinkaus (2006), Gordon et al. (2008), and Rightmire (2008).

noted that this growth spurt is of lesser magnitude and shorter duration than the modern human adolescent growth spurt. Cessation of growth occurs around 12.3 years of age, approximately 3.3–4.3 years after KNM-WT 15000's estimated age at death. However, with the current information that is available, we are unable to rule out the "ALH 12.3/25%" curve which demonstrates growth more closely resembling a chimpanzee than the "ALH 12.3/50%" curve. In lieu of finding female *H. erectus* pelvis and associated infant crania, it may be impossible to rule out secondary altriciality in this species.

Adult stature estimates for KNM-WT 15000 derived from the "ALH 12.3/IM 50%" and the "ALH 12.3/25%" growth curve (assuming an initial age at death of eight to ten years of age, and a stature at death of 154 cm) range between 159 cm and 168 cm (Fig. 4). This estimate is consistent with the average stature (163 cm, or 160 cm adjusting for difference in cranial height) for East African adult male *H. erectus* specimens (Table 3), although it is important to note that at least two early East African *H. erectus* specimens (KNM-ER 736 and KNM-ER 1808) are larger, and, at 180 cm and 173 cm, respectively, possess statures approaching the original estimate for KNM-WT 15000. In addition, 1.51–1.53-million-year-old footprints from Ileret are hypothesized to be associated with a hominin whose reconstructed stature is 175 cm, although it should be noted that this stature estimate is back-calculated from footprint length (Bennett et al., 2009). Based on this stature reconstruction, Bennett et al. (2009) have suggested that these footprints belong to *H. erectus*. Our revised stature for KNM-WT 15000 is consistent with a gradual increase in stature from early hominins to anatomically modern humans (Fig. 5).

#### Alternate considerations

All of the current data suggest that KNM-WT 15000 would have completed growth in stature between 12 and 13 years of age. However, it is important to note that the timing of growth and development is delayed in wild chimpanzees relative to their captive counterparts (Leigh and Shea, 1996; Hamada and Udono, 2002; Zihlman et al., 2007). Eruption of permanent teeth and fusion of long bones occur one to three years later in wild chimpanzees than in captive chimpanzees (Zihlman et al., 2007). There are currently no studies that document growth in length in wild chimpanzees, so we have had to rely on data from captive chimpanzees for this study. Zihlman et al. (2007) suggested that wild chimpanzees do not reach skeletal maturity until approximately

one to three years after captive chimpanzees. Since long bones in captive chimpanzees are completely fused at ten to 11 years of age (Schultz, 1940; Gavan, 1953), Zihlman et al.'s (2007) suggestion pushes skeletal maturity in wild chimpanzees to approximately 11–14 years of age. Captive chimpanzees raised in natural conditions attain adult total body length at 12 to 13 years of age (Hamada and Udono, 2002) yet demonstrate extended growth in the radius, ulna, and wrist (Hamada et al., 2003). These captive chimpanzees may therefore provide a reasonable proxy in the absence of data for wild chimpanzees since they demonstrate both extended growth in total body length and delayed ossification in the upper limbs. At present, there is no direct evidence that the timing of growth in total body length differs between wild and captive chimpanzees. If future studies confirm that total body length in wild chimpanzees continues to increase markedly beyond 14 years of age, then statures estimated from the hypothetical growth curves in this study would need to be revisited. If, in fact, KNM-WT 15000 grew until he was 14 years of age, he would have attained an adult stature ranging between 165 cm and 178 cm. However, the timing of LHEs in these curves do not match the timing of LHEs that KNM-WT 15000 had experienced at death to the same precision that the ALH 12.3 curves match his LHEs. Additionally, current evidence suggests that KNM-WT 15000 was approximately 154 cm and eight years of age at death, but other evidence suggests he may have been as short 144 cm (Ohman et al., 2002) and as old as 10 years (Dean et al., 2001). If Nariokotome Boy was eight years old and shorter at death (144 cm), then he would have only attained an adult stature of 154 cm (between 152 cm and 156 cm) using our preferred curves. If he was 10 years of age at death, his adult stature would have been shorter as well, reaching only 146 cm if he was 144 cm at death or 159 cm if he was 154 cm at death. There are a number of alternative statures and ages at death suggested for KNM-WT 15000. Our hypothetical growth curves for *H. erectus* allow us to predict adult stature from any number of alternative ages and virtually all statures at death, whereas previous methods based on growth regressions for specific populations at specific ages limit the range of predictions to the ages that were considered.

#### Conclusions

In this study, we suggest that the pace of *H. erectus* life history was unique—fast, like chimpanzee life history, but with a small growth spurt that allowed KNM-WT 15000 to achieve statures exceeding chimpanzee total body lengths at earlier ages. The



weight of the available evidence suggests that, at death, Nariokotome Boy was closer to eight years of age, 154 cm tall, and had already experienced a large portion of growth in stature, although his long bone epiphyses had not yet fully fused. Based on these parameters, we estimated an adult stature of 163 cm (range 152 cm to 179 cm). These results are consistent with the pattern of dental eruption (Smith, 1993) and recent studies re-evaluating dental enamel formation (Dean et al., 2001; Dean and Smith, 2009) and skeletal maturation (Smith, 1993; Tardieu, 1998). In addition, one of our growth velocity curves (“ALH 12.3/IM 50%”) is consistent with the pace of brain growth inferred from new estimates of *H. erectus* neonatal brain size (Coqueugniot et al., 2004; Simpson et al., 2008). Finally, our estimates are consistent with stature estimates for other early African *H. erectus* specimens.

Previous interpretations of body size evolution in early *Homo* suggest that there was a transition from an *Australopithecus*-like body build, which has been reconstructed for *Homo habilis* (Johanson et al., 1987; Leakey et al., 1989; Hartwig-Scherer and Martin, 1991; McHenry and Coffing, 2000), to a “hot-adapted,” linear body build, reconstructed for *H. erectus* and KNM-WT 15000 in particular. Our new estimates of body size in KNM-WT 15000 suggest that *H. erectus* may not be the “great leap forward” previously envisioned. *H. erectus* lies at a crucial point in time when changes in encephalization, locomotion, energetics, sexual dimorphism, and many other derived characteristics of the genus *Homo* appeared. Future studies incorporating new estimates of KNM-WT 15000’s stature and body mass have the potential to alter our view of this transition.

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