Journal of Human Evolution 80 (2015) 74–82

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

How much more would KNM-WT 15000 have grown?

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A R T I C L E I N F O

Article history:
Received 7 May 2014
Accepted 22 September 2014
Available online 14 November 2014

Keywords:
Stature
Body mass
Homo erectus
Nariokotome boy
Chimpanzee
Gorilla

A B S T R A C T

Because of its completeness, the juvenile *Homo ergaster/erectus* KNM-WT 15000 has played an important role in studies of the evolution of body form in *Homo*. Early attempts to estimate his adult body size used modern human growth models. However, more recent evidence, particularly from the dentition, suggests that he may have had a more chimpanzee-like growth trajectory. Here we re-estimate his adult stature and body mass using ontogenetic data derived from four African ape taxa: *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii*, *Pan paniscus*, and *Gorilla gorilla gorilla*. The average percentage change in femoral and tibial lengths and femoral head breadth between individuals at the same stage of dental development as KNM-WT 15000 – eruption of M2s but not M3s – and adult individuals with fully fused long bone epiphyses, was determined. Results were then applied to KNM-WT 15000, and his adult size estimated from skeletal dimensions using modern human prediction formulae. Using this approach, adult stature best estimates of 176–180 cm and body mass best estimates of 80–83 kg were obtained. These estimates are close to those estimated directly from longitudinal changes in body length and body mass between 8 and 12 years of age in chimpanzees, the suggested chronological equivalent to KNM-WT 15000's remaining growth period. Thus, even using an African ape growth model, it is likely that KNM-WT 15000 would have attained close to 180 cm in stature (without a slight reduction for his lower cranial height) and 80 kg in body mass as an adult. Other evidence from the East African Early Pleistocene indicates that KNM-WT 15000 was not unusually large-bodied for his time period.

Introduction

KNM-WT 15000, or the "Nariokotome Boy", a 1.47 Ma *Homo ergaster/erectus* from West Turkana, Kenya (Walker and Leakey, 1993a; McDougall et al., 2012), is the most complete early hominin skeleton ever discovered. As such, it has played a prominent role in assessments of body size and shape, encephalization, locomotor kinematics, and life history in early *Homo* (Ruff and Walker, 1993; Smith, 1993; Ruff et al., 1997; Tardieu, 1998; Clegg and Aiello, 1999; Dean et al., 2001; Smith, 2004; Wang et al., 2004; Dean and Smith, 2009; Graves et al., 2010; Ruff, 2010; Dingwall et al., 2013; Uhl et al., 2013). However, many of these analyses are complicated by the juvenile status of KNM-WT 15000. Comparisons to other fossil hominins or modern humans must take into account his developmental status, either by comparing him to individuals of a similar developmental stage, or by extrapolating his growth to adulthood so that he can be compared with adult specimens. Because juvenile comparative specimens or samples are more rare, the latter option is more feasible in most cases. Either option, however, involves judgments regarding the most appropriate reference sample to use, i.e., modern humans, modern great apes, or some compromise between the two (Ruff and Walker, 1993; Smith, 1993; Dean and Smith, 2009; Graves et al., 2010). Which reference sample is chosen can have potentially large effects on how his body size is reconstructed, with corresponding implications for early *Homo* as a whole.

Previous studies

Ruff and Walker (1993) originally estimated KNM-WT 15000's adult stature by first estimating the remaining growth in length of his long bones, using modern human reference samples, and then estimating adult stature using ecogeographically matched modern human adults, i.e., those with high limb length to stature proportions similar to those of the fossil (Holliday and Ruff, 1997). Based on a modern human dental age of about 11 years (Smith, 1993) and a skeletal age of about 13 years (Ruff and Walker, 1993; Smith, 1993), age-at-death was taken as 11 or 12 years of age. Stature estimates at his time of death of 160 cm (using modern

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http://dx.doi.org/10.1016/j.jhevol.2014.09.005

adult equations) and as an adult of 185 cm were derived, neither of which factored in a reduction of several centimeters for his lower cranial height. Body mass was estimated from stature and bi-iliac (maximum pelvic) breadth, again using modern human reference samples (Ruff, 1994), with bi-iliac breadth measured from the reconstructed pelvis (Walker and Ruff, 1993), scaled up in adults by assuming a constant bi-iliac/stature ratio (supported by analyses of modern human growth; Ruff and Walker, 1993). Estimates of 48 kg at time of death and 68 kg extrapolated to an adult were obtained.

These results were subsequently modified somewhat, mainly because of the availability of new data for modern juveniles. Using new equations generated from the Denver Growth Study sample (Ruff, 2007), KNM-WT 15000 was estimated to be slightly shorter (at most 157 cm, again not including the reduced cranial height) and heavier (50–53 kg) at death than originally estimated (Uhl et al., 2013, using a very different technique but also based on modern humans, recently obtained a similar 50th percentile estimate of 51.7 kg). The same modern growth sample was used to estimate remaining growth in femoral head breadth of KNM-WT 15000, from which an adult body mass of 77.8 kg was derived using modern human adult equations (Ruff, 2010). In all of these calculations, an age-at-death of 11–13 years was employed.

However, from the outset, questions were raised about the appropriateness of using only modern humans as reference samples for estimating KNM-WT 15000's chronological age and growth trajectory to adulthood. His pattern of tooth formation, disjunction between dental and skeletal maturity, and very tall stature (for a modern human 11–12-year-old) suggested to Smith (1993) some similarities to chimpanzee growth patterns. Clegg and Aiello (1999) found that, due in part to uncertainties in applying developmental standards to humans in general, KNM-WT 15000 fell within the observed range of variation for dental and skeletal maturity of a modern human population, although he was still tall for his age. S.L. Smith (2004) made a similar point, although she noted that his growth pattern would have been unusual for a modern human.

Based on dental microstructural analyses, Dean et al. (2001) estimated that chronological age-at-death of KNM-WT 15000 might have been closer to 8 rather than 12 years. Dean and Smith (2009) reiterated how unusual his combination of dental and skeletal maturities would be for a modern human and gave further evidence that his chronological age was close to 8 years, which would make his very large body size even more extreme (for a modern human). They concluded that “To us, the most parsimonious explanation for this combination of facts is that the growth curve of early *Homo erectus* was *more* like that in modern chimpanzees. More specifically, whereas the precise growth curve of *H. erectus* was likely unique, it apparently differed from ours in the direction of chimpanzees” (Dean and Smith, 2009: 117; emphasis original). This is consistent with more general findings for hominins prior to *Homo sapiens* (for a recent review, see Smith, 2013). Tardieu (1998) described a relatively square distal femoral epiphysis with a higher lateral than medial trochlear ridge in KNM-WT 15000, which suggested a chronological age of about 15 years when compared to modern humans. This implies a relatively mature stage of development, with relatively less growth remaining than was assumed in the original analyses of KNM-WT 15000.

Building on these new assessments, Graves et al. (2010) reanalyzed the growth trajectory and adult stature of KNM-WT 15000 using a combination of modern human and chimpanzee growth curves. Their favored model used a starting height of 154 cm at death (equivalent to the 157 cm estimated by Ruff, 2007; with a subtraction of 3 cm for lower cranial height), a chronological age-at-death of 8 years, 4.3 years of remaining growth, and the average of two growth velocity curves intermediate between those of modern humans and chimpanzees – one directly intermediate (“50% curve”) between humans and chimpanzees, and one halfway between this and chimpanzees (“25% curve”). The resulting best estimate of adult stature (again with a lower cranial height) was 163 cm, which represents an increase of only 9 cm, or 5.8%, over his estimated stature at death.

Several questions can be raised concerning these new analyses and their underlying assumptions, however. First, the assumption that growth was almost complete in KNM-WT 15000, i.e., that “he was approaching adulthood” or “was nearing skeletal maturity at death” (Graves et al., 2010: 544, 548) is based heavily on the aforementioned study of distal femoral epiphyseal shape by Tardieu (1998). However, as noted by Tardieu, the distal femoral epiphyses of KNM-WT 15000 are distorted through post-depositional cracking and crushing (also see Walker and Leakey, 1993b). The better-preserved left epiphysis (KNM-WT 15000G) is shown in Figure 1. There is a crack running through the middle of the patellar trochlear surface (just visible in Fig. 1) and indications of compression between the medial and lateral condyles, artificially reducing the mediolateral breadth of the epiphysis and narrowing the trochlear notch (and thus increasing its apparent relative depth). Another crack distorts the lateral condyle itself, and much of the medial surface of the medial condyle is heavily abraded. Walker and Leakey estimated its original bi-epicondylar breadth to be about 80 mm, which, even with some reconstruction of missing surfaces, is still much wider than could be achieved without mediolateral decompression of the epiphysis (Fig. 1). The ratio used by Tardieu (1998) was based on the preserved M-L articular, rather than bi-epicondylar breadth (Tardieu, pers. comm.). However, given the distortion of the entire epiphysis, any shape ratios based on M-L and A-P linear breadths of the preserved specimen are unreliable. Tardieu (1998:172) also claimed that “The higher protuberance of the external lip of the femoral trochlea, in relation to the internal one, is distinct” in KNM-WT 15000. However, as shown in Fig. 1, the two ridges are about equal in height above the posterior condylar plane. As noted above, the trochlear groove itself is artificially narrowed and deepened through general crushing of the epiphysis. Thus, femoral trochlear morphology also cannot be used to argue for a late adolescent developmental stage for KNM-WT 15000.

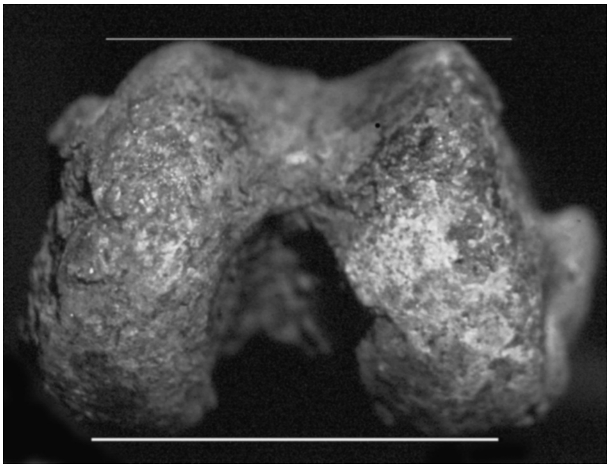

Figure 1. Distal view of left femoral epiphysis of KNM-WT 15000. Lateral is to the right. Horizontal lines are 50 mm long and parallel; the thicker inferior line intersects the posterior edge of the condyles while the thinner superior line intersects the anterior-most extent of the medial and lateral lips of the trochlea. The large projection visible laterally is a piece of displaced bone resulting from cracking of the lateral epiphysis. The smaller apparent projection on the antero-medial contour is a remnant produced by severe abrasion of most of the medial surface of the medial condyle.