



Contents lists available at ScienceDirect

Journal of Human Evolution

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

The effect of ontogeny on estimates of KNM-WT 15000's adult body size

Deborah L. Cunningham^{a,*}, Ronda R. Graves^b, Daniel J. Wescott^a, Robert C. McCarthy^c^a Texas State University, Department of Anthropology, San Marcos, TX 78666, USA^b Grunley Construction Company, Inc., Rockville, MD 20850, USA^c Benedictine University, Department of Biological Sciences, Lisle, IL 60532, USA

ARTICLE INFO

Article history:

Received 3 August 2017

Accepted 2 April 2018

Available online xxx

Keywords:

Homo erectus

Growth

Ontogeny

Nariokotome

Stature

Body mass

ABSTRACT

The *Homo erectus* specimen KNM-WT 15000 has played a critical role in our understanding of body size evolution. New interpretations suggest that KNM-WT 15000 had a younger age-at-death and a more rapid ontogenetic trajectory than previously suggested. Recent fossil discoveries and new interpretations suggest a wide range of body size and shape variation in *H. erectus*. Based on these new insights, we argue that KNM-WT 15000's adult stature and body mass could have been much smaller than has been traditionally presented in the literature. Using chimpanzee and modern human growth trajectories, we bracketed the range of possibilities for KNM-WT 15000's adult body size between 160.0 and 177.7 cm (5'3"–5'10") for stature and 60.0 and 82.7 kg (132–182 lbs.) for body mass. These estimates put KNM-WT 15000 near the mean rather than among the largest known *H. erectus* specimens.

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1. Introduction

"Once we stop trying to force Nariokotome into a human mold, we can explore a more evolutionary approach" (Dean and Smith, 2009: 116).

Because it is so complete, KNM-WT 15000 ("Nariokotome Boy"), a 1.53-million-year-old juvenile *Homo erectus* skeleton from West Lake Turkana, Kenya, is a key specimen for interpreting evolutionary changes in body size and shape in the genus *Homo* (Walker and Leakey, 1993a; Graves et al., 2010; Pontzer, 2012; Ruff and Burgess, 2015). However, estimates of its predicted adult stature and body mass have varied considerably over the past 25 years. Historically, this specimen has been reconstructed as a "strapping youth," with adult body mass and stature estimates making it one of the larger specimens of *H. erectus* (Ruff and Walker, 1993; Ruff and Burgess, 2015). Ruff and Walker (1993) originally estimated that, at death, the Nariokotome Boy was 160 cm (5'3") tall¹ and

weighed 48 kg (106 lbs). Starting with an age-at-death between 11 and 12 years (Smith, 1993) and assuming a modern human-like growth trajectory that includes an adolescent growth spurt, Ruff and Walker (1993) predicted that KNM-WT 15000 would have grown to be 185 cm (6'1") tall and weighed 68 kg (150 lbs) as an adult. Later, using hypothetical growth curves, Graves et al. (2010) predicted an adult stature of 163 cm (5'4") with taxon-specific cranial height adjustment (or 166 cm, ~5'5" without), assuming KNM-WT 15000 died between eight and 10 years of age (Dean and Smith, 2009). This estimate is substantially shorter than the previous estimate of 185 cm (Ruff and Walker, 1993), and partially reflects Graves et al.'s (2010) decision to use a growth model that did not include a modern human-like adolescent growth spurt.

Recently, Ruff and Burgess (2015) argued that KNM-WT 15000's adult stature would have ranged between 176.3 cm (5'9") and 180.4 cm (~5'11"), with a mean estimate of 178 cm (5'10") and a "best" estimate of ~180 cm (~5'11"). None of these estimates takes into account the fact that *H. erectus* differs from *Homo sapiens* in cranial height, as noted originally by Ruff and Walker (1993). Specifically, KNM-WT 15000's cranial height is 3 cm less than that of the mean cranial height of Howells's (1996) sub-Saharan human males, excluding the "Bushman" population (see Graves et al., 2010). Taking into account cranial height differences, Ruff and Burgess's (2015) adult estimates would range between 173 cm and 177 cm, still at least 10 cm taller than the adult estimate provided by Graves et al. (2010).

* Corresponding author.

E-mail address: dlc165@txstate.edu (D.L. Cunningham).

¹ This estimate assumes a modern human standard for *H. erectus*. Ruff and Walker (1993: 254) stated: "This [stature] should be viewed as a maximum estimate," pointing out that there is an argument to be made for reducing this figure by as much as 6 to 7 cm.

At the same time, new, larger estimates of bi-iliac breadth (Ruff, pers. comm.; Simpson et al., 2010, pers. comm.) and femoral head breadth (FHB) (Ruff, 2007, 2010) have changed estimates of KNM-WT 15000's body proportions. While estimates of KNM-WT 15000's adult stature have decreased by five to 19 cm since 1993, adult body mass estimates have increased from 68 kg (150 lbs; Ruff and Walker, 1993) to 77.8 kg (172 lbs; Ruff, 2010), and again to between 80.1 kg (177 lbs) and 82.6 kg (182 lbs; Ruff and Burgess, 2015). In other words, KNM-WT 15000 is reconstructed as being a little shorter on average but substantially heavier as an adult than originally thought (Ruff, 2010; Ruff and Burgess, 2015), aligning more closely with large specimens of *H. erectus sensu lato* (Ward et al., 2015; Boyle and DeSilva, 2015; Di Vincenzo et al., 2015).

Given the importance of body size for understanding the evolution and life history of *H. erectus* and early genus *Homo*, it is critical to obtain accurate estimates of adult stature and body mass for KNM-WT 15000. In this paper, we bracket the amount of growth remaining in this specimen's ontogeny using chimpanzee and modern human growth models, an approach similar to that used by Cameron et al. (2017) to estimate adult body size for the juvenile MH1 *Australopithecus sediba* specimen. Compared to modern humans, great apes have a rapid maturation rate, reaching final adult body size at an earlier chronological age. *Australopithecus*, *Paranthropus*, and members of early genus *Homo* exhibited a more precocious pattern of dental development than modern humans (Bromage and Dean, 1985; Smith, 1986; but see Smith et al., 2015), and likely followed a rapid somatic growth trajectory similar to extant African apes (Schwartz, 2012; Hublin et al., 2015). Therefore, it is not unreasonable to infer that the human growth pattern is derived and unique in the context of hominin life history, whereas the ape pattern is primitive and likely closer to the last common ancestor of the chimpanzee-human clade (Wrangham and Pilbeam, 2002; Robson and Wood, 2008). While KNM-WT 15000 grew like a member of *H. erectus*, and not like a chimpanzee or modern human, it makes sense to take advantage of the sister-species relationship between these two taxa to create an "extant phylogenetic bracket" (*sensu* Witmer, 1995) since chimpanzees and modern humans follow different ontogenetic patterns that yield varying body size estimates. Considering these observations, we provide a range of adult body size estimates for KNM-WT 15000.

2. Materials and methods

2.1. Chronological versus physiological age

Body size estimates for KNM-WT 15000 are dependent on both the starting age (i.e., chronological vs. physiological age) and the ontogenetic model used to project the amount of growth remaining to adulthood. The discrepancy between the stature estimates of Ruff (Ruff and Walker, 1993; Ruff, 2010; Ruff and Burgess, 2015) and Graves et al. (2010) is substantial, reflecting both of these considerations. Dean and Smith's (2009) microstructural analysis of long-period line periodicities in KNM-WT 15000 finds a "chronological" age-at-death between 7.6 and 8.8 years, but the fossil is far more advanced than modern human children in this age range, with a physiological age (based on tooth formation and skeletal ossification) more in line with modern human adolescents.

We argue that physiological age is more appropriate than chronological age when making interspecific comparisons, since species follow different ontogenetic patterns. Recognizing the imperfect fit of KNM-WT 15000 to a human or a chimpanzee model, we use physiological age estimates to set a "starting point" for chronological age, then estimate a range of adult body sizes by "growing up" the fossil using percent growth remaining from data obtained from chimpanzee and human growth curves.

2.2. Physiological age: human skeletal evidence

Skeletal evidence for KNM-WT 15000's physiological age comes from the distal humerus, clavicle, and distal femur. We argue that ossification data from these three bones point to this fossil being physiologically similar to humans with an age range of 14–16 years. Other long bones and the triradiate cartilage had not begun to fuse at the time-of-death (Walker and Leakey, 1993b).

Dean and Smith (2009) noted that ongoing ossification of the elbow joint and relatively broad shoulders indicate that KNM-WT 15000 is skeletally similar to a post-pubertal modern human adolescent because the distal humeral epiphyses (trochlea, capitulum, and lateral epicondyle) were fused into a composite, which had begun to fuse with the diaphysis, but the medial epicondyle had yet to fuse.

KNM-WT 15000's skeletal age can be bracketed between 14 and 18 years based on the timing of closure of the distal composite humeral epiphysis and the humeral shaft and 16–18 years based on timing of when the medial epicondyle joins the humeral shaft (Schaefer et al., 2009). Dean and Smith (2009), referencing Scheuer and Black's (2000) initial summary of modern human distal humeral development, settled on a "conservative" compromise of 13–13.5 chronological years for KNM-WT 15000. Dean and Smith (2009) pointed out that most of the studies in Scheuer and Black (2000) are based on children from the Northern Hemisphere, and that there is evidence of a hand-wrist ossification delay in modern African children from Benin relative to modern children from Europe, Asia and North America (Agossou-Voyame et al., 2005).² If a similar delay in growth also occurs in the distal humerus, this would push Dean and Smith's (2009) compromise age range of 13.0–13.5 to one even more advanced chronologically. Based on the above information, the physiological stage for KNM-WT 15000's distal humerus allows us to bracket this specimen into the human chronological age range of 14–16 years.

KNM-WT 15000 had broad shoulders (i.e., long clavicles), which also indicates a post-pubertal adolescent human developmental stage (Dean and Smith, 2009). While clavicle length varies in populations during growth, KNM-WT 15000's claviculo-humeral index is consistent with adolescent humans (Frelat et al., 2017). Likewise, each of KNM-WT 15000's clavicles are only slightly smaller than the clavicle of KNM-ER 1808 (Leakey and Walker, 1985; Walker and Leakey, 1993b), an adult *H. erectus* specimen. KNM-WT 15000's clavicle length (130.5 mm right; 130.4 mm left) is rarely observed in modern humans until 15–16 years of age and falls within the range of adult clavicle length based on mixed-sex nineteenth century English and twentieth century Portuguese samples (Black and Scheuer, 1996). However, it should be noted that McGraw et al. (2009) found this mean clavicle length in a well-nourished sample of Ohio males at 12–13 years of age (range ten to 16 years). Even so, we argue that the nineteenth century results may be more appropriate here because of a potential nutritional effect, and settle on a compromise chronological age range of 14–16 years for KNM-WT 15000 based on these studies.

² Agossou-Voyame et al. (2005) documented that the skeletal maturation of modern African boys is delayed relative to their European, North American, and Asian counterparts by 1.0–2.5 years based on hand bone development, and by as much as 3.5–3.8 years based on carpal development. If so, and if similar effects also occur in the distal humerus, this would push Dean and Smith's (2009) compromise age range of 13.0–13.5 to 14–16 based on hand bone development and 16.5–17.3 based on carpal development. The delay in the skeletal maturation of African children relative to the other samples may be due to a nutritional effect. It is unlikely that KNM-WT 15000 was as well-nourished as modern children from the Northern Hemisphere, and it is not improbable that the fossil's skeletal maturation was delayed similarly to that observed in the African children.

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