

# Femoral/humeral strength in early African *Homo erectus*

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## Abstract

Lower-to-upper limb-bone proportions give valuable clues to locomotor behavior in fossil taxa. However, to date only external linear dimensions have been included in such analyses of early hominins. In this study, cross-sectional measures of femoral and humeral diaphyseal strength are determined for the two most complete early *Homo erectus* (or *ergaster*) associated skeletons—the juvenile KNM-WT 15000 and the adult KNM-ER 1808. Modern comparative samples include an adult human skeletal sample representative of diverse body shapes, a human longitudinal growth series, and an adult chimpanzee sample. When compared to appropriately age-matched samples, both *H. erectus* specimens fall very close to modern human mean proportions and far from chimpanzee proportions (which do not overlap with those of humans). This implies very similar mechanical load-sharing between the lower and upper limbs, and by implication, similar locomotor behavior in early *H. erectus* and modern humans. Thus, by the earliest Pleistocene (1.7 Ma), completely modern patterns of bipedal behavior were fully established in at least one early hominin taxon.

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## Introduction

Comparisons between lower and upper limb-bone size have played a key role in attempts to reconstruct locomotor patterns and determine phylogenetic relationships among early hominins (McHenry, 1978; Johanson et al., 1982; Jungers, 1982; Wolpoff, 1983; Johanson et al., 1987; Grausz et al., 1988; Leakey and Walker, 1989; Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Asfaw et al., 1999; Haeusler and McHenry, 2004; Green et al., 2007). To date, these analyses have been limited to external dimensions of limb bones (i.e., lengths, circumferences, breadths, or products of breadths). While such comparisons provide valuable insights into locomotor behavior (e.g., Schultz, 1937; Aiello, 1981; Jungers, 1985), inclusion of bone internal dimensions can increase discriminatory power, particularly in analyses of bone-strength proportions (Schaffler et al., 1985; Ruff, 1987; Demes and Jungers, 1993; Jungers et al., 1998; Connour et al., 2000;

Ruff, 2002). Bone-strength comparisons may be especially informative in testing locomotor hypotheses, because there is evidence that changes in locomotion directly influence relative limb-bone strengths (Carrier and Leon, 1990; Nakatsukasa et al., 1995; Ruff, 2003b). Lower-to-upper limb-bone strength proportions clearly distinguish modern humans from other anthropoid primates (Ruff, 2003b).

Well-preserved, associated upper and lower limb-bone remains are extremely rare in the early hominin fossil record. Among the fossils attributed to early *Homo*,<sup>1</sup> the most complete specimen is KNM-WT 15000, a male juvenile *H. erectus* dated to about 1.53 Ma (Brown et al., 1985; Walker and Leakey, 1993a). Limb-length proportions, and by extension, locomotor

<sup>1</sup> “Early *Homo*” here includes *H. habilis* (sensu stricto and sensu lato), *H. rudolfensis*, *H. ergaster*, and *H. erectus*. However, as pointed out by others (Wood, 1992; McHenry, 1994; Wood and Collard, 1999), it is often difficult to assign postcranial fossils within this group to particular taxa, and there is disagreement over the morphological traits characteristic of specific taxa (e.g., see Haeusler and McHenry, 2004). Here I follow Walker and coworkers (Walker et al., 1982; Walker and Leakey, 1993a) in assigning KNM-WT 15000 and KNM-ER 1808 to early African *H. erectus*.

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behavior, of KNM-WT 15000 have been considered to be essentially similar to those of modern humans (Ruff and Walker, 1993; Asfaw et al., 1999). However, limb-breadth proportions of this specimen may be more ambiguous. Haeusler and McHenry (2004) noted that, while most upper-to-lower limb-bone breadth proportions of KNM-WT 15000 fall close to the mean of their modern adult human sample, “size of its distal humerus shaft relative to femur mid-shaft size ... lies in the upper range of the modern human variation and thus resembles the proportion of OH 62 and A.L. 288-1” (p. 446); that is, towards African apes. Actually, in Haeusler and McHenry’s (2004; Fig. 4b) plot of distal humeral anteroposterior (AP) breadth/femoral midshaft circumference, A.L. 288-1 is directly on the modern human regression line, and OH 62 and KNM-WT 15000 are well above it and overlap with great apes; thus, KNM-WT 15000 appears *less* “modern” in this respect than A.L. 288-1. In terms of humeral *midshaft* circumference to femoral midshaft AP  $\times$  mediolateral (ML) breadth proportions, both A.L. 288-1 and OH 62 are near the upper edge of Haeusler and McHenry’s (2004; Fig. 4a) modern human distribution, while KNM-WT 15000 is somewhat high but well within the overall distribution. Thus, there may be evidence in KNM-WT 15000 for some deviation from modern humans in limb-breadth proportions. However, these analyses did not include true cross-sectional properties incorporating internal dimensions, or an age-matched comparative sample for KNM-WT 15000. This latter issue is significant, since there is evidence that, among modern humans, relative lower-to-upper limb-bone strength continues to change during growth until mid–late adolescence (Ruff, 2003b).

Another early *Homo* specimen with well-preserved (although partially pathological) upper- and lower-limb elements is KNM-ER 1808, an adult *H. erectus* dated to approximately 1.69 Ma (Walker et al., 1982; Leakey and Walker, 1985; Feibel et al., 1989). On the basis of preserved pelvic elements, it was considered to be female by its original describers (Leakey and Walker, 1985), although this has been disputed (McHenry, 1991). Most surfaces of its long bones are covered with a variable thickness of coarse-woven periosteal bone that is a result of some pathology, possibly hypervitaminosis A (Walker et al., 1982). However, the pathological deposits and original subperiosteal surfaces are clearly distinguishable on broken sections in the diaphyses (Walker et al., 1982). This characteristic allowed a corrected cast of the largely intact right femur to be made (Leakey and Walker, 1985), which was used previously to derive cross sections of this bone (Ruff, 1995). Periosteal deposits on the humeri are much thinner (1–2 mm) than those on the femur, and are also clearly visible at broken sections, again allowing corrections to periosteal contours, as described below.

Femora and humeri of these two specimens—KNM-WT 15000 and KNM-ER 1808—are used here to examine the lower-to-upper limb-bone strength proportions in early African *Homo erectus* and to compare these proportions to those of appropriately matched modern humans and chimpanzees. The null hypothesis is that bone-strength proportions and, by inference, locomotor behavior in this early *Homo* taxon were indistinguishable from those in modern humans.

## Materials and methods

The right and left femora and right humerus of KNM-WT 15000, and the right femur and right humerus of KNM-ER 1808 were used in this study. Properties of the right and left femora of KNM-WT 15000 were averaged for all analyses. Except for the characteristic pathological deposits on KNM-ER 1808, bone surfaces are generally well preserved.

The methods used to derive cross-sectional properties for the KNM-WT 15000 and KNM-ER 1808 femora have been described previously (Ruff, 1995). Briefly, multiple-plane radiography was used to obtain cortical thicknesses of the original specimens at eight locations around the cortex. Plaster casts of the femora (in the case of KNM-ER 1808, the corrected cast produced by Alan Walker [Leakey and Walker, 1985]) were sectioned and the cortical breadths were used to reconstruct the endosteal perimeter. The section surfaces were then photographed and manually digitized, with section properties determined using a version of the SLICE program (Nagurka and Hayes, 1980). Humeral cross-sectional contours were obtained using computed tomographic (CT) scanning (Siemens Somatom CR, Aga Khan Hospital, Nairobi, Kenya). Appropriateness of CT display settings were verified by comparison of images to known dimensions measured on the specimens. Hard copies of the images were then scanned and analyzed using ImageJ and a custom macro (MomentMacro, available at: [www.hopkinsmedicine.org/fae/mmacro.htm](http://www.hopkinsmedicine.org/fae/mmacro.htm)). The thickness of pathological periosteal deposits on the KNM-ER humerus, similar to those demonstrated on the femur (Walker et al., 1982), could be directly measured at a partially open section on the original specimen, just distal to the section of interest (see below); these varied from 1.2 mm (anterior) to 1.6 mm (posterior) in depth around the cortex. The equivalent thicknesses were manually subtracted from the outer bone contour obtained from CT images prior to analysis.

Modern human comparative samples were obtained from skeletal samples of adults from Pecos Pueblo, New Mexico ( $n = 60$ ), and eastern Africa ( $n = 40$ ) (Ruff, 1995, 2000), and a longitudinal growth series of U.S. whites from Denver ( $n = 20$ ) (Ruff, 2003b), each equally divided between males and females. The adult samples represent a very wide range of body morphologies (Ruff, 1995). Cross-sectional properties for adults were determined through direct sectioning, CT scanning, or multiplane radiography combined with external molding of periosteal surfaces, followed by analysis with SLICE or an equivalent image-analysis program (NIH Image 1.52moi-b5) (Ruff, 1995, 2000). Cross-sectional properties for the growth series were obtained from radiographs taken at 6-month intervals from age 6 months through 14 years, annually from 14 to 17 years, and at 19 years (Ruff, 2003b).

In addition, a comparative sample of adult chimpanzees ( $n = 20$  *Pan troglodytes* and  $n = 3$  *P. paniscus*) was used as a non-bipedal contrast within a similar size range as the human samples. Specimens were all wild-shot and included an equal number of males and females (except for two male and one female *P. paniscus*). Cross-sectional properties were derived using CT, SLICE, and NIH Image as described previously (Ruff, 2002).

Cross-sectional data were obtained at 50% of femoral length (i.e., midshaft) and 40% of humeral length from the distal end. “Length” here corresponds to the lengths defined in Ruff (2002)—from the average distal projection of the femoral condyles to the superior surface of the femoral neck, and from the lateral lip of the trochlea to the humeral head, both measured parallel to the longitudinal axis of the diaphysis. Equivalent cross section locations among younger juveniles in the human growth series with undeveloped epiphyses were determined as previously described (Ruff, 2003b). Lengths of the femora and humerus in KNM-WT 15000 can be determined with minimal reconstruction (Walker and Leakey, 1993b), as can length of the right femur of KNM-ER 1808 (Walker et al., 1982; Leakey and Walker, 1985). Length of the less complete right humerus of KNM-ER 1808 can be reconstructed by analogy with modern and fossil specimens of similar size, and in any event, slight misplacement of section location has little impact on cross-sectional properties in the mid-distal humeral diaphysis (for example, the average differences between properties measured at 35% and 40% of humeral length are 0.7% and 2.6% for cortical area and polar section modulus, respectively, in the Pecos sample).

The adult comparative samples included an equal number of right and left femora and humeri, while the Denver growth series sample were all measured on the left side. Bilateral asymmetry is minimal in lower-limb bones, but asymmetry in human upper limb-bone cross-sectional diaphyseal breadths can be substantial (Trinkaus et al., 1994; Churchill and Formicola, 1997; Auerbach and Ruff, 2006). However, bilateral asymmetry in upper-limb bones is considerably reduced in modern human juveniles compared to adults (see Ruff, 2007), so any potential bias introduced by this factor in the Denver sample should be relatively small. External breadth measurements at midshaft on the right and left ulnae of KNM-WT 15000 are 12.4 and 12.0 mm (AP), respectively, and 9.9 and 9.5 mm (ML), respectively, indicating a 3–4% right-biased asymmetry, similar to that found in modern adult male upper-limb bones (Auerbach and Ruff, 2006) (although with differences this small, measurement error must also be considered). Because both fossil humeri are from the right side, they actually constitute a conservative test of the hypothesis here: since right humeri would usually be expected to be stronger than left humeri, their inclusion creates a potentially more “primitive” proportion (larger upper limb relative to lower limb) compared to the side-balanced (adult) or left-biased (juvenile) modern human samples.

The primary cross-sectional geometric property compared was the polar section modulus, an index of average bending/torsional strength (Ruff, 2000). Given the location of muscle insertions on the humerus and its variable positions during use (locomotor and nonlocomotor), it is very likely that the humeral shaft undergoes both AP and ML bending loads *in vivo*; the same is true for the hominin femoral midshaft (Ruff, 1995). Thus, a measure that combines bending strengths in all planes (as well as torsional strength) is most appropriate for assessing overall mechanical loading of the two limbs. The polar section modulus was derived as the polar second

moment of area (J) divided by the average radius of the section (half the average of AP and ML diameters) following Ruff (2002). Although the more recently available Momentmacro software (see Web site above) calculates true AP and ML section moduli (second moment of area divided by maximum distance from neutral axis), some of the comparative data were collected using older methods that did not. Since this difference in calculation has a small but significant effect on results (true section moduli will always be less than or equal to section moduli derived using a radius), and because even the currently available software does not calculate a true polar section modulus, the method using the average radius was used here for consistency (for further justification, see Ruff, 2002). It should be noted that estimates of torsional rigidity or strength using the polar second moment of area or section modulus will be inaccurate when sections depart significantly from circularity (greater than about a 1.5 ratio of maximum to minimum bending rigidity; see Daegling, 2002). However, all of the sections considered here are relatively circular (see below), so this factor should not be a significant issue. It should also be noted that section moduli represent only an approximation of true *in vivo* strength, which will also depend on the actual mechanical loading environments of the bones (Lieberman et al., 2004). However, as argued elsewhere (Ruff et al., 2006), when mechanical loading conditions are unknown, as is the case here, section moduli are the best available estimates of bending/torsional strength. Other section properties for the two fossils—subperiosteal and cortical areas (TA and CA) and percent cortical areas (CA/TA)—are also listed here for general descriptive purposes.

Following previous studies (Ruff, 2002, 2003b) femoral-to-humeral strength proportions were assessed using a log-log bivariate plot for adults and a plot of log femoral/humeral ratios by age group for the longitudinal growth series. All analyses were carried out using SYSTAT (SYSTAT: Statistics, 1990).

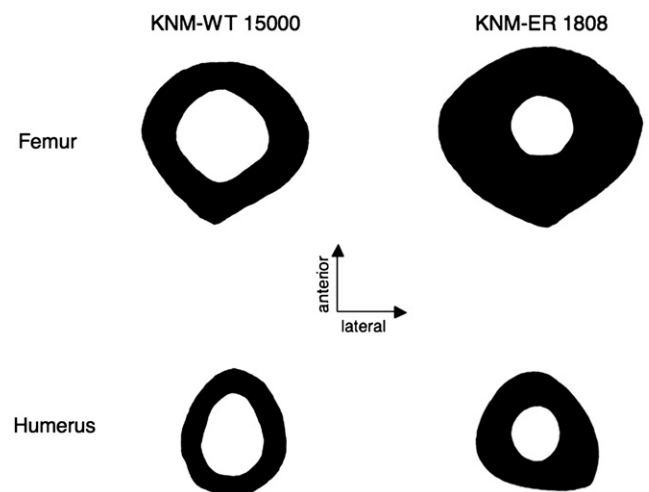


Fig. 1. Cross-sectional outlines for the femoral 50% (midshaft) and humeral 40% (mid-distal shaft) sections of KNM-WT 15000 and KNM-ER 1808 (left femur for KNM-WT 15000; all other bones are from the right side). Arrow lengths = 1 cm.

Table 1  
Cross-sectional properties of femoral 50% and humeral 40% sections in KNM-WT 15000 and KNM-ER 1808<sup>1</sup>

		TA	CA	%CA	I <sub>x</sub>	I <sub>y</sub>	Z <sub>x</sub>	Z <sub>y</sub>	J	Z <sub>p</sub>
KNM-WT 15000	Femur <sup>2</sup>	402	262	65.2	11128	11612	922	978	22740	1900
	Humerus	243	132	54.3	4327	3165	541	384	7492	839
KNM-ER 1808	Femur	551	478	86.8	20813	27251	1542	1879	48064	3433
	Humerus	240	196	81.7	4380	4679	521	520	9059	1041

<sup>1</sup> Abbreviations are as follows: TA = total subperiosteal area (mm<sup>2</sup>); CA = cortical area (mm<sup>2</sup>); %CA = percent cortical area (CA/TA · 100); I<sub>x</sub>, I<sub>y</sub> = second moments of area about ML and AP axes (mm<sup>4</sup>); J = polar second moment of area (mm<sup>4</sup>); Z<sub>x</sub>, Z<sub>y</sub> = section moduli about ML and AP axes (mm<sup>3</sup>); Z<sub>p</sub> = polar section modulus (mm<sup>3</sup>).

<sup>2</sup> Average of right and left sides.

## Results

Cross-sectional outlines for the KNM-WT 15000 and KNM-ER 1808 femora and humeri are shown in Fig. 1, and section properties are given in Table 1. The femoral section for KNM-WT 15000 shown in Fig. 1 is from the more complete left femur (15000G), although section properties listed in Table 1 are averages of the right and left femora (bilateral asymmetry is less than 5% for all properties).

The extreme cortical thickness of the adult KNM-ER 1808 is apparent in Fig. 1: percent cortical area (cortical area/subperiosteal area; %CA) in the femur (86.8) is above the range of the entire modern comparative sample (mean ± SD: 69.8 ± 8.4), and %CA in the humerus (81.7) is above all but one modern individual (62.7 ± 10.3). Relative cortical thickness in KNM-WT 15000 is much lower, falling somewhat below the modern adult means. This aspect of KNM-WT 15000 has been noted previously (Ruff et al., 1994) and was shown to be a characteristic of juvenile long bones in general. The KNM-ER 1808 femur also demonstrates well the “typical” *Homo erectus* or “erectus-like” increase in relative ML dimensions, with ratios of ML/AP rigidities (second moments of area) and strengths (section moduli) almost outside the range of the modern comparative sample (both >1.8 SD from the modern mean) (Ruff, 1995). Specimen KNM-WT 15000 is also above (≥0.7 S.D.) the modern mean in femoral midshaft ML/AP rigidity and strength, but much less extreme in this regard, perhaps as a consequence of his age and still developing lower limb (including pelvis) (Ruff, 1995). Humeral cross-sectional shape is more variable between the two fossil specimens.

Figure 2 is a log-log plot of humeral-to-femoral polar section modulus in the modern adult comparative samples and the two fossils. Reduced major axis (RMA) lines are plotted through the modern human and chimpanzee samples for reference. Neither RMA line is significantly different from 1.0 ( $p \geq 0.10$ ,  $t$ -tests) (Hofman, 1988); thus, femoral and humeral strengths are approximately isometrically scaled within both modern human and chimpanzee adults, similar to the pattern found within all anthropoid species (Ruff, 2003b). There is no overlap between species. Specimen KNM-ER 1808 falls somewhat above the modern human regression line, while KNM-WT 15000 is well below it, although still within the modern human distribution and well above the chimpanzee distribution.

Figure 3 shows age changes in the log ratio of femoral-to-humeral polar section modulus in the Denver human growth series

by sex. As described previously (Ruff, 2003b), there is a sharp increase in the ratio after the initiation of full weight-bearing on the lower limb at 1 year of age, followed by a slower increase through childhood and adolescence until about 14 years in females and 16 years in males. Skeletal age for KNM-WT 15000 is estimated at 12 years (for justification, see Ruff, 2007). His femoral/humeral strength proportion falls directly on the estimated trend line for modern adolescent males and is virtually identical to the means for 10.5–12.5-year-old males. Specimen KNM-ER 1808's proportion is higher, as expected given the results in Fig. 2, and falls somewhat above the female means for older adolescents. The mean log-ratios for Denver older adolescents (≥15 years, pooled or separate sex) and the combined Pecos and eastern African adult sample fall between 0.91 and 1.06, which, in raw space, corresponds to femoral-to-humeral strength ratios of about 2.5–2.9. Specimen KNM-ER 1808's ratio is about 3.3, while that for KNM-WT 15000 is about 2.3 (Table 1). The mean femoral-to-humeral strength ratio for adult chimpanzees is about 1.3.

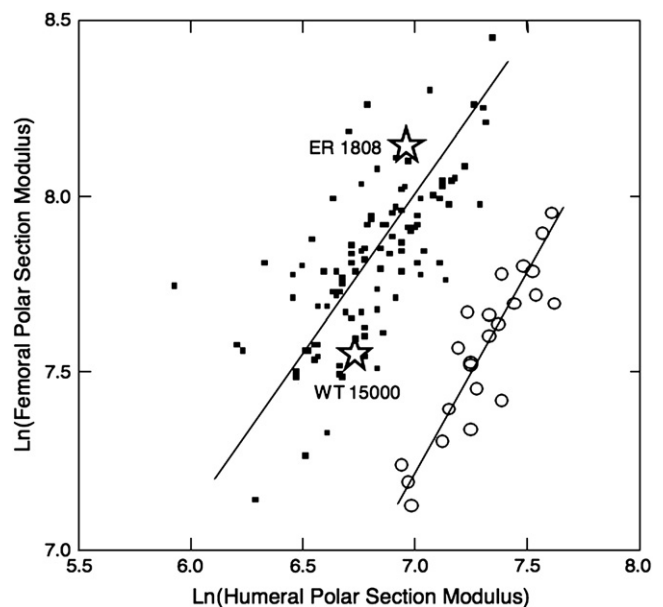


Fig. 2. Femoral midshaft strength versus humeral mid-distal shaft strength (polar section modulus) in the adult modern human and chimpanzee comparative samples, KNM-WT 15000, and KNM-ER 1808. Filled symbols: modern humans; open symbols: chimpanzees. All data are natural-log-transformed. RMA lines are plotted through modern samples.

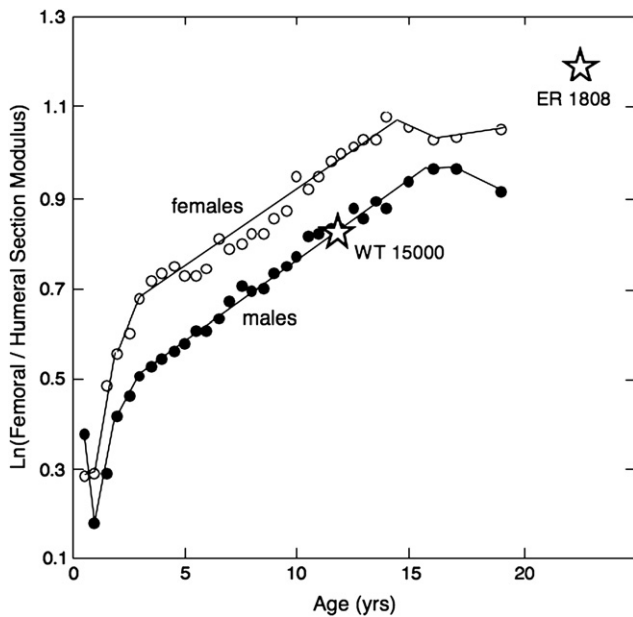


Fig. 3. Age changes in the natural-log ratio of femoral midshaft versus humeral mid-distal shaft strength (polar section modulus) in the Denver longitudinal growth series, KNM-WT 15000, and KNM-ER 1808. Age of KNM-WT 15000 estimated at 12 years (Ruff, 2007); age of KNM-ER 1808 is arbitrary. Each modern data point is the mean of 10 individuals, measured sequentially. Open symbols: females; filled symbols: males. Linear trend lines drawn through data points by eye (see Ruff, 2003b).

## Discussion

When compared with appropriately matched modern human samples, KNM-WT 15000 and KNM-ER 1808 both exhibit femoral-to-humeral diaphyseal strength proportions indistinguishable from those of modern humans. Because cortical-bone geometry is developmentally plastic, responding to changes in its mechanical environment during life (Jones et al., 1977; Woo et al., 1981; Ruff, 2003b; Ruff et al., 2006), this result implies that relative mechanical loadings of the lower and upper limbs were also very similar to those of modern humans. This, in turn, indicates that modern bipedal locomotion was fully developed among early African *Homo erectus* in terms of both mechanical mechanisms of weight support (and nonsupport in the upper limb) and behavioral patterns (i.e., frequent bipedal terrestrial travel and a complete release from dependence on arboreal substrates). Although this general conclusion has been reached on the basis of other skeletal features and specimens (McHenry, 1978; Walker and Leakey, 1993a; Asfaw et al., 1999; Wood and Collard, 1999), it is important to confirm it using traits known to be associated with actual behavior, avoiding possible complications arising from “phylogenetic inertia” (Ward, 2002).<sup>2</sup>

The current study does not address the issue of specific components of bipedalism that may have characterized early

*H. erectus* (e.g., the importance of long-distance running versus walking; Bramble and Lieberman, 2004). Both of the modern adult comparative samples included here were likely relatively physically active throughout life (Ruff, 2000), and long-distance travel (including running) was probably common among at least Pecos Pueblo males (Nabokov, 1981; Ruff and Hayes, 1983). Pecos Pueblo males have slightly but nonsignificantly greater femoral-to-humeral strength ratios (mean  $\pm$  SE:  $2.88 \pm 0.11$ ), than East African males ( $2.65 \pm 0.10$ ) ( $p = 0.12$ ,  $t$ -test), while females from the two samples are closer in proportions ( $2.84 \pm 0.14$  and  $2.90 \pm 0.14$  in Pecos and East Africans, respectively;  $p > 0.75$ ,  $t$ -test), which may support a subtle effect of long-distance travel on lower-to-upper limb proportions. Other behavioral differences, such as reliance on water versus terrestrial transport, have been shown to produce significant effects on lower-to-upper limb-bone strength proportions among modern humans (Stock and Pfeiffer, 2001). Regardless, it is apparent from other evidence that, by the early Pleistocene, *H. erectus* was capable of very long-distance terrestrial travel (Anton, 2003), and the present results are concordant with this idea.

Sexual dimorphism in lower-to-upper limb-bone strength is influenced by both behavior and more systemic, genetic/hormonal factors (i.e., increased upper-body strength among males in general) (Ruff, 2003a; and see Denver growth series results above). Both KNM-WT 15000 and KNM-ER 1808 fall closest to age-matched modern human counterparts of the same sex (assuming that the original female sex designation for KNM-ER 1808 is correct). This could indicate that the general lower-to-upper body strength distinction between the sexes characteristic of modern humans was already present among early *H. erectus*. This hypothesis must remain very tentative, however, given the overlap in proportions between modern human males and females (see above) and the sample sizes for the fossils ( $n = 1$  per sex!). The correction for pathological deposits on the KNM-ER 1808 specimens is also by necessity approximate, and it likely contributes some error to reconstruction of their geometric section properties. An estimate of the possible magnitude of this error was derived by adding and subtracting 1 mm and 0.5 mm to the corrected periosteal contours of the femoral and humeral sections, respectively (the femoral deposits are much thicker; see Walker et al., 1982; Leakey and Walker, 1985). Effects on individual log-transformed  $Z_p$  values were relatively minor (less than  $\pm 1.5\%$ ) but ranged up to  $\pm 15\%$  for log-transformed femoral/humeral  $Z_p$  at the extreme values for the two sections. However, even at these extremes, KNM-ER 1808 always fell within the distribution and above the regression line for modern human adults, and closer to Denver late adolescent females than to late adolescent males.

One other specimen commonly attributed to early *Homo erectus*—KNM-ER 803—also preserves portions of the lower- and upper-limb bones (Day and Leakey, 1974; McHenry, 1978, 1994). The specimen as a whole is much less complete than KNM-WT 15000 or KNM-ER 1808, however, and does not preserve any parts of the humeri. On the basis of external breadth measurements of fragments of the ulnar and femoral shafts, as well as other dimensions, McHenry (1978)

<sup>2</sup> This is not meant to imply that there is no genetic component to long-bone cross-sectional morphology, but rather that genetic contributions to morphology will be modified by actual mechanical loadings during life (see Ruff et al., 2006).

concluded that its limb proportions were very similar to those of modern humans and unlike those of great apes. The specimen is dated to the same time period as KNM-WT 15000, and thus is consistent with the interpretations of early *H. erectus* morphology and behavior presented here.

These interpretations are not meant to imply that mechanical loadings of the limbs were identical in early *H. erectus* and modern humans, however. The ML reinforcement of the femoral diaphysis, well developed in KNM-ER 1808 and apparently incipient in the still-growing-at-death KNM-WT 15000, is indicative of relatively increased ML bending loads. This is likely attributable to an increase in femoral neck length—known to characterize KNM-WT 15000—and a hypothesized increase in pelvic biacetabular distance relative to that in modern humans (Ruff, 1995). There are indications from the preserved portion of the linea terminalis of KNM-WT 15000 that the inferred ML broadening of the lower pelvis characteristic of adult *H. erectus* had not yet developed, although this is difficult to assess accurately because of the incompleteness and immaturity of the specimen (Walker and Ruff, 1993). In any event, the cross-sectional morphology of his femur is consistent with the general complex of lower-limb traits described for adult *H. erectus* and their biomechanical implications regarding weight transfer around the hip (Ruff, 1995).

Variation in humeral cross-sectional shape is more difficult to interpret, in part because of the less well-defined, “multi-functional” role of the upper limb in humans, and because of the variable influences of muscular insertion areas (supracondylar, deltoid) on humeral morphology, despite attempts to avoid them by choosing a mid-distal location on the shaft (e.g., see Ruff and Larsen, 2001). Part of the difference in morphology between KNM-WT 15000 and KNM-ER 1808 could be attributable to such factors, possibly age-related, although data are currently lacking to test this possibility.

The analysis of the Denver longitudinal growth series shows how important it is to consider developmental status when evaluating skeletal structural features. As shown here, and elsewhere (Ruff et al., 1994; Ruff, 2003b, 2007), skeletal proportions vary continuously throughout growth as a result of varying growth velocities for different dimensions (Ruff, 2003a). In terms of lower and upper limb-bone strengths, the lower limb tracks changes in body size (chiefly body mass) more closely than does the upper limb (Ruff, 2003a), which gradually declines in strength relative to body size until mid-late adolescence, when body size also stabilizes (Ruff, 2003b). Specimen KNM-WT 15000 fits this general pattern well, and his deviation from the adult KNM-WT 1808 can thus be explained on a developmental rather than locomotor or other behavioral basis (all Denver subjects were obviously fully bipedal within his age range). The position of KNM-WT 15000 here within modern human adults is very similar to that shown by Haeusler and McHenry (2004: Fig. 4b) in their comparison of humeral distal shaft AP breadth with femoral midshaft circumference, which is thus also likely to be simply a consequence of his developmental status.

Interestingly, bivariate distributions of upper-to-lower (or forelimb-to-hindlimb) limb-bone dimensions in the same paper

by Haeusler and McHenry (2004) usually show some overlap between human and chimpanzee data scatters, while the two species did not come close to overlapping in the present comparison of true bone strengths. This difference may in part be attributable to the larger sample sizes in the Haeusler and McHenry study, particularly for *Pan*. Their *Pan* sample also included captive animals, although they noted that these generally had larger forelimb-to-hindlimb proportions than wild specimens and thus would tend not to overlap with modern humans. (Their modern human sample also included some very small-bodied humans—pygmies, not represented here—but there is no evidence for convergence of human and chimpanzee femoral-to-humeral strength proportions with smaller size in the present study.) The inclusion of internal as well as external dimensions, and calculation of true section properties rather than linear dimensions, improves discrimination between locomotor groups in general among anthropoid primates (Ruff, 2002). As shown above, relative cortical thickness (%CA) is greater in the femur than in the humerus in both modern and early *Homo* ( $p < 0.001$ , paired *t*-test in the modern sample). This is not true of chimpanzees, in which humeral and femoral relative cortical thicknesses are nonsignificantly different, and even tend to be greater in the humerus (mean %CA = 68.9) than in the femur (66.5) ( $p = 0.14$ , paired *t*-test). Thus, external dimensions alone will underestimate the difference in femoral-to-humeral strength proportions between humans and chimpanzees.

This fact also argues for caution in mechanical interpretations based on external dimensions alone in comparisons involving other early hominin specimens. Results of comparisons involving a variety of external breadth measurements suggest considerable variation in lower-to-upper limb proportions among early hominins, including specimens attributed to *Homo* (McHenry, 1978; Johanson et al., 1982; Johanson et al., 1987; Grausz et al., 1988; Leakey et al., 1989; Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Haeusler and McHenry, 2004; Green et al., 2007). However, until these dimensions can be placed into a more secure mechanical context, their functional significance will remain obscure. For example, articular and cross-sectional diaphyseal dimensions of long bones have different growth trajectories, different mechanical consequences, and appear to respond in different ways to mechanical stimuli (Godfrey et al., 1991; Lieberman et al., 2001; Ruff, 2002; Ruff, 2007), yet they are frequently combined in statistical comparisons of lower- and upper-limb size, confounding precise functional interpretations.

At least two critical specimens—A.L. 288-1 and OH 62—have sufficiently well-preserved femoral and humeral diaphyses to allow analyses similar to those carried out in the present study (Johanson et al., 1982; Johanson et al., 1987).<sup>3</sup>

<sup>3</sup> New postcranial remains of early *Homo* from Dmanisi, Georgia (1.77 Ma), including some matched lower- and upper-limb elements, were very recently described (Lordkipanidze et al., 2007). While certain “primitive” morphological features of the postcranium were noted, most characteristics of the lower limb were similar to those of modern humans, as were humeral/femoral length proportions. Humeral/femoral diaphyseal breadth proportions also appear more similar to those of modern humans than to nonhuman hominoids, although specific comparisons were not carried out.

Both specimens show apparent differences from modern humans and early *H. erectus* in femoral structural characteristics that may indicate altered bipedal locomotor behavior (Ruff, 1995, 1998). Comparisons of femoral and humeral strengths in these specimens, when available, will provide important evidence regarding whether fully modern bipedalism was characteristic of all early hominins, or only developed with the evolution of *H. erectus*.

## Conclusions

The two most complete early *Homo erectus* specimens available—KNM-WT 15000 and KNM-ER 1808—both show femoral-to-humeral diaphyseal-strength proportions indicative of fully modern bipedalism, demonstrating that, by 1.7 Ma at the latest, this form of locomotor behavior was completely established within at least this taxon. Recognition of developmental changes in limb-strength proportions is critical for interpretation of juvenile fossil specimens such as KNM-WT 15000. External bone-breadth measurements give clues to behavioral differences among past species, but are not a substitute for true structural analyses.

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