

Relative Limb Strength and Locomotion in *Homo habilis*

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ABSTRACT The *Homo habilis* OH 62 partial skeleton has played an important, although controversial role in interpretations of early *Homo* locomotor behavior. Past interpretive problems stemmed from uncertain bone length estimates and comparisons using external bone breadth proportions, which do not clearly distinguish between modern humans and apes. Here, true cross-sectional bone strength measurements of the OH 62 femur and humerus are compared with those of modern humans and chimpanzees, as well as two early *H. erectus* specimens—KNM-WT 15000 and KNM-ER 1808. The comparative sections include two locations in the femur and two in the humerus in order to encompass the range of possible section positions in the OH 62 specimens. For each combination of section locations, femoral to humeral strength proportions of OH 62 fall below the

95% confidence interval of modern humans, and for most comparisons, within the 95% confidence interval of chimpanzees. In contrast, the two *H. erectus* specimens both fall within or even above the modern human distributions. This indicates that load distribution between the limbs, and by implication, locomotor behavior, was significantly different in *H. habilis* from that of *H. erectus* and modern humans. When considered with other postcranial evidence, the most likely interpretation is that *H. habilis*, although bipedal when terrestrial, still engaged in frequent arboreal behavior, while *H. erectus* was a completely committed terrestrial biped. This adds to the evidence that *H. habilis* (*sensu stricto*) and *H. erectus* represent ecologically distinct, parallel lineages during the early Pleistocene. *Am J Phys Anthropol* 138:90–100, 2009. © 2008 Wiley-Liss, Inc.

Obligate terrestrial bipedalism is one of the key characteristics defining modern humans and distinguishing them from other primates. Although evidence for some form of terrestrial bipedal locomotion appears in the hominin fossil record perhaps as far back as 6–7 million years (Ma) ago (Senut et al., 2001; Zollikofer et al., 2005; Richmond and Jungers, 2008), there is also evidence for significant variation in the locomotor repertoires of early hominins and the extent to which they retained (or evolved) adaptations for arboreal locomotion (Johanson et al., 1987; Leakey et al., 1989, 1998; Hartwig-Scherer and Martin, 1991; Heinrich et al., 1993; Spoor et al., 1994; McHenry and Berger, 1998; Asfaw et al., 1999; Stern, 2000; Ward et al., 2001; Harcourt-Smith and Aiello, 2004; Green et al., 2007; Haeusler and McHenry, 2007). However, interpretations have been hampered by a paucity of fossil specimens with associated crania and postcrania (and thus, uncertainty regarding the taxonomic attribution of available postcrania), large error ranges in reconstructions of incomplete specimens, and disagreements regarding the functional significance of particular morphological traits (e.g., Korey, 1990; Stern, 2000; Ward et al., 2001; Richmond et al., 2002; Haeusler and McHenry, 2004; Reno et al., 2005; Wood and Constantino, 2007).

The OH 62 partial skeleton has figured prominently in such debates. It is the only definitive *Homo habilis* (*sensu stricto*) (Wood, 1992) specimen with securely associated and relatively well-preserved cranial and postcranial material, the latter including both forelimb and hind limb elements. OH 62 was discovered in 1986 in Olduvai Gorge, Tanzania, and is dated to about 1.8 Ma (Johanson et al., 1987). It consists of portions of the skull, the proximal half of the left femoral shaft and neck, a small proximal portion of the right tibia, almost all of the right humeral shaft, part of the right radial shaft, and much of the right ulna. On the basis of simi-

larities in cranial morphology to other specimens ascribed to *H. habilis* (*sensu stricto*), particularly Stw 53, it was attributed to this taxon.

Locomotor affinities of OH 62 have been assessed primarily on the basis of its forelimb to hind limb proportions, which are known to be associated with locomotor behavior among living primates (Schultz, 1937; Aiello, 1981; Jungers, 1985) and have played a key role in interpreting early hominin fossils (McHenry, 1978; Johanson et al., 1982; Jungers, 1982; Wolpoff, 1983; Asfaw et al., 1999, and see references above). Initial analyses (Johanson et al., 1987) concentrated on comparisons to the *Australopithecus afarensis* A.L. 288-1 (“Lucy”) (Johanson et al., 1982), the best-preserved small-bodied early hominin specimen. In most dimensions—measured or estimated—the OH 62 upper limb remains equaled or exceeded those of A.L. 288-1, while its lower limb remains (principally the femur) appeared to be smaller. In particular, using a length estimate for the humerus of 264 mm, and a length estimate for the less complete femur of “no greater than that of A.L. 288-1 (280 mm),” the authors derived a possible humerofemoral length index of “close to 95%,” which is more like that of

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modern chimpanzees (averaging about 1.00) than modern humans (averaging about 0.72) (Shea 1981; Ruff, 2003). In this sense, it was more “primitive” than A.L. 288-1, with a length index of 0.85. Hartwig-Scherer and Martin (1991) carried out more extensive metric comparisons between upper (fore-) to lower (hind) limb proportions of OH 62, A.L. 288-1, and modern humans and African apes, and again concluded that in most respects OH 62 fell closer to apes than to humans, while A.L. 288-1 was more human in proportions. This result was surprising, given that *H. habilis* is more craniodentally derived toward modern humans than is *A. afarensis*.

These conclusions were strongly questioned by Korey (1990), however, who demonstrated that length estimations for the less complete OH 62 femur were subject to so much error that its humerofemoral length proportion could not be clearly distinguished from that of A.L. 288-1, although OH 62 did fall closest to *Pan* when compared among modern humans and African apes. Richmond et al. (2002) found the difference in humerofemoral length proportions between OH 62 and A.L. 288-1 to be greater than that usually encountered within modern hominoid species, although they cautioned that length estimates for OH 62 were too insecure to arrive at any firm conclusions in this regard. They also noted that humerofemoral shaft circumference proportions showed much more overlap between modern humans and great apes and thus had “far less power in discriminating species-level differences in skeletal form” than did length proportions. Haeusler and McHenry (2004) also found overlap between modern human and African ape distributions for upper (fore-) to lower (hind) limb diaphyseal breadth and circumference proportions, with OH 62 almost invariably falling within the regions of overlap. Using a different reconstruction method than previous researchers, they concluded that OH 62’s humerofemoral length proportion may have been similar to that of modern humans. Other researchers find the various proposed femoral length reconstructions for OH 62 to be unconvincing, and thus its humerofemoral length proportions to be “ultimately unknowable” (Reno et al., 2005).

The general approach of all of these studies was to estimate the range of error involved in determining the size of unpreserved portions of fossils, for example, the missing distal portion of the OH 62 femur, and then to incorporate this error range into comparisons with dimensions measured on other fossils and modern samples. However, because fossil reconstruction error is often difficult to estimate accurately, this leaves any conclusions reached from such comparisons open to question. An alternative method employed here, is to use actual, nonreconstructed dimensions of a fossil to calculate its proportions, and then “bracket” those proportions within possible ranges of proportions of the comparative specimens/samples. This approach requires collection of more comparative data, but has the advantage that no dimensions are estimated.

The present study also includes comparisons of true cross-sectional dimensions of long bones rather than external breadths or circumferences. As noted earlier, interlimb proportions constructed from long bone external breadths and circumferences often show overlap between modern humans and African apes, decreasing their effectiveness for inferring locomotor behavior (Richmond et al., 2002; Haeusler and McHenry, 2004, 2007). However, true cross-sectional measures of diaphyseal strength are more effective than simple linear external measurements for discriminating between locomotor

groups among modern nonhuman primates (Ruff, 2002), and between humans and other primates (Ruff, 2003, 2008). This is likely due in part to their incorporation of variation in medullary cavity size, which is substantial among both living and fossil primates (Ruff et al., 1993; Ruff, 2002, 2008), as well as variation in details of external morphology that contribute to bone strength.

Also, although in part genetically determined and/or phylogenetically constrained (Ruff et al., 2006; O’Neill and Dobson, 2008), long bone cross-sectional properties are also developmentally plastic and responsive to changes in mechanical loadings (Jones et al., 1977; Woo et al., 1981; Nakatsukasa et al., 1995; Robling et al., 2002; Ruff et al., 2006), more so than other morphological characteristics such as bone length (Lanyon, 1980; Trinkaus et al., 1994; Ruff, 2003). As noted by Ward et al. (2001: p 362): “The adaptive significance of primitive retentions is not readily testable, as it is difficult to refute either the hypothesis that plesiomorphic characters were retained by stabilizing selection or that they merely had not been selected against. . . . Finding characters with a strong epigenetic component, and thus influenced by an individual’s actual activity patterns over its lifetime, could possibly demonstrate that an animal may have engaged in a particular behavior.” Interlimb bone strength proportions do in fact change during life in direct response to altered locomotor patterns (Carrier and Leon, 1990; Ruff, 2003). Analysis of such proportions thus avoids or minimizes some of the interpretive problems associated with more evolutionarily conservative traits.

In this study, femoral to humeral strength proportions of OH 62 are compared with those of modern humans and chimpanzees in order to shed further light on the locomotor behavior of *H. habilis*. Comparisons are also carried out between OH 62 and two other early (1.7–1.5 Ma) *Homo* specimens—KNM-WT 15000 and KNM-ER 1808—craniodentally attributed to *Homo erectus* (Walker et al., 1982; Leakey and Walker, 1985; Feibel et al., 1989; Walker and Leakey, 1993). Variation in strength proportions between these specimens are interpreted in the context of proposed locomotor and phylogenetic diversity among early *Homo*.

MATERIALS AND METHODS

Section contours of the OH 62 femoral and humeral diaphyses were obtained from casts of naturally broken sections made prior to reconstruction of the fossils (provided to the author courtesy of C.O. Lovejoy). External breadths and circumferences measured on the casts are indistinguishable from those measured on the original fossils at corresponding locations (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991; Haeusler and McHenry, 2004, and M. Haeusler, pers. comm.). Figure 1 shows the locations of the sections. The femoral section is the most distal complete section (except for a missing chip anteromedially), proximal to a 20- to 30-mm posteromedial shaft fragment, and ~130-mm distal to the proximal end of the fossil. The humeral section is at the junction of the two largest shaft pieces, almost exactly at the midpoint of the entire reconstructed fossil.

The distal surface of the femur and the proximal surface of the humeral segment just distal to the section of interest were used for recording section contours. Scaled, digital photographs of the casts were taken and

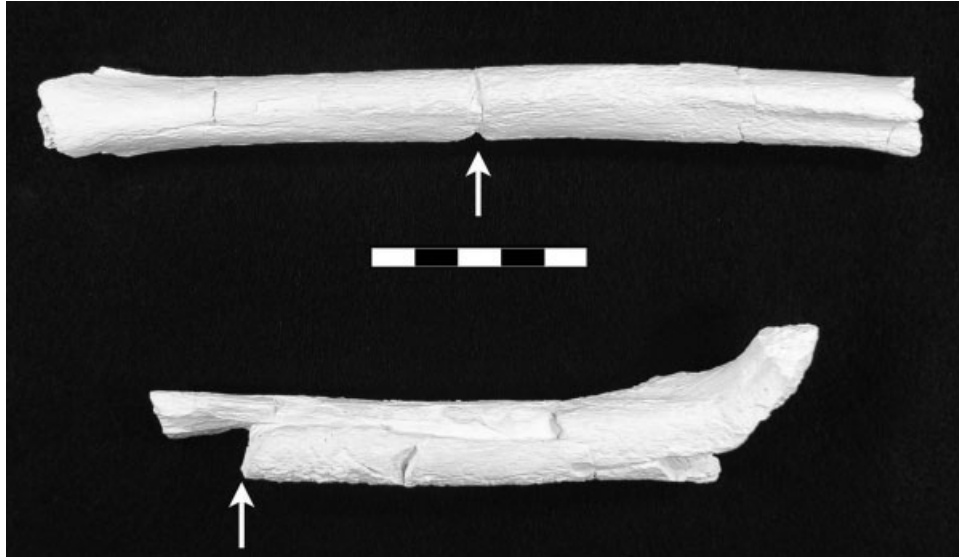


Fig. 1. Anterior view of casts of the OH 62 right humerus (top) and left femur (bottom), arranged with proximal to the right. Arrows show locations of cross sections analyzed in this study. Scale bar = 5 cm.

corrected for obliquity and defects in section contours. Endosteal boundaries are clearly visible in both sections. There is a 2- to 5-mm wide defect (wider periosteally) in the anteromedial cortex of the femur, the end of a long, longitudinally running crack (see Fig. 1), with an additional shallow (maximum 3-mm deep) 6-mm wide chip missing medial to the crack at the section location. However, the original periosteal and endosteal contours here can be easily reconstructed using adjacent contours of both the existing proximal as well partial distal piece of the femur. The posterior cortex of the humeral section is beveled distally, extending through a portion of the posteromedial surface (see Fig. 1). The contour of the shaft just distal to this beveling and of the adjoining more proximal humeral segment were used to establish the original surface position. Other small defects (<0.5 mm in depth) in the external contours of the femur and humerus were corrected by filling in to match adjacent preserved surfaces. The anterolateral external surface of the femur has small (~0.5-mm thick) nodules of adherent matrix observable on the cast (Fig. 1, also on the original specimen, M. Haeusler, pers. comm.), which were not included in the contour. All corrections to contours were made digitally after photographing, with reference to external dimensions measured on both the casts as well as the original specimens (Hartwig-Scherer and Martin, 1991; Haeusler and McHenry, 2004, and M. Haeusler, pers. comm.). The sections used for analysis are shown in Figure 2.

The external surface of the OH 62 femur has been interpreted as being sufficiently exfoliated to prevent “any calculation of reliable robusticity measures such as shaft geometric indices” (Reno et al., 2005). However, the original describers of the fossil (Johanson et al., 1987) referred to only “slight exfoliation” of the femur. It is apparent from observation of both the cast as well as the original specimen (M. Haeusler, pers. comm.) that much of the original surface is preserved, and that original contours can be accurately reconstructed. Indeed, most surface alterations of the femur, that is, the longitudinal cracks and postdepositional accretions, would be expected to increase rather than decrease its cross-



Fig. 2. Femoral (left) and humeral (right) cross sections from OH 62. Reconstructed area in femur represented in gray. Lateral is to the right, anterior above. Scale bar = 1 cm.

sectional dimensions. This would tend to make comparisons between OH 62 and other *Homo* samples or specimens more conservative, by increasing femoral/humeral strength proportions in OH 62.

Corrected cross section photographs of OH 62 were imported into ImageJ (rsb.info.nih.gov/ij/), and analyzed using a custom macro (Momentmacro.J; www.hopkinsmedicine.org/fae/mmacro.htm), which calculates mechanical section properties: areas, second moments of area, and section moduli. Although a number of section properties are reported here for general descriptive purposes, comparisons of femoral to humeral strength proportions focus on the polar section modulus, Z_p , a property related to both torsional and average bending strength (Ruff, 2000). From a mechanical standpoint, Z_p is the most appropriate parameter for comparing overall strength of the femur and humerus (Ruff, 2008). The polar section modulus is also less dependent on precise orientation of a section relative to mediolateral (M-L) and anteroposterior (A-P) axes, an advantage when specimens are missing one or both ends (normally used in orienting long bones), as is the case with OH 62. Here, for consistency with earlier studies (Ruff, 1995, 2000, 2002, 2008), section moduli were derived as second moments of area divided by the appropriate radius (half diameter). The polar section modulus was calculated as the polar

TABLE 1. Cross-sectional properties of OH 62 femoral and humeral sections

	TA	CA	%CA	I_x	I_y	Z_x	Z_y	J	Z_p
Femur	264.9	220.3	83.2	5,294	5,700	566	588	10,995	1,154
Humerus	204.6	163.1	79.7	3,232	3,249	389	401	6,482	790

TA, total subperiosteal area (mm^2); CA, cortical area (mm^2); %CA, percent cortical area (CA/TA 100); I_x , I_y , second moments of area about M-L and A-P axes (mm^4); J , polar second moment of area (mm^4); Z_x , Z_y , section moduli about M-L and A-P axes (mm^3); Z_p , polar section modulus (mm^3).

second moment of area (J) divided by the average radius of the section (half the average of A-P and M-L diameters).

Approximate locations of the OH 62 sections were determined relative to femoral and humeral lengths, as defined previously (Ruff, 2002, 2008). Femoral length is the distance from the average distal projection of the femoral condyles to the superior surface of the femoral neck, and humeral length is the distance from the lateral lip of the trochlea to the superior surface of the humeral head, measured parallel to the longitudinal axis of the diaphysis.

The femoral section is clearly distal to the formation of the linea aspera (see Fig. 2, also Haeusler and McHenry, 2004; Fig. 2). Although variable, the linea aspera generally forms in human femora about 2/3's of bone length from the distal end. If the section were at 65% of bone length (as defined above), the maximum length of the entire femur (as traditionally defined) would be at least 385-mm long, much longer than most estimates and about equivalent to the longest estimate yet proposed (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991; Richmond et al., 2002; Haeusler and McHenry, 2004). If the section were as far distal as 50% of bone length, maximum femur length would be about 280 mm, equivalent to that of A.L. 288-1 and similar to that used by most authors. As noted by previous researchers (Haeusler and McHenry, 2004), on anatomical grounds the most distal femoral section is very unlikely to be located further distally than this. Thus, it is very probable that the available femoral section is between 50 and 65% of bone length from the distal end.

The humeral section is located about 15-mm distal to the deltoid tuberosity, which in humans normally extends distal to 50% of bone length. If it were as far distal as 40% of bone length from the distal end, maximum bone length would need to be well over 280 mm, considerably longer than any previous estimate of its length (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991; Haeusler and McHenry, 2004), to accommodate the preserved anatomy of the proximal and distal ends of the specimen. Thus, it is very likely that the available humeral section falls between 40 and 50% of bone length from the distal end.

Comparisons between OH 62 and the modern comparative samples and fossil specimens were carried out for all four possible combinations of the femoral 50 and 65%, and humeral 40 and 50% section locations. Considered together, these comparisons must include equivalent locations along the femoral and humeral diaphyses, regardless of the exact reconstructed lengths of the OH 62 specimens.

The two other fossil specimens with associated femora and humeri included here are KNM-WT 15000, an ~12-year-old male (Walker and Leakey, 1993; Ruff, 2007), and KNM-ER 1808, an adult probable female (Leakey and Walker, 1985; although see McHenry, 1991), both

attributed to *H. erectus*. Corrections for the pathological periosteal deposits on the KNM-ER 1808 femur and humerus (Walker et al., 1982; Leakey and Walker, 1985) were made as described previously (Ruff, 2008). The modern human sample includes Pecos Pueblo Native Americans ($n = 60$) and East Africans ($n = 40$) (Ruff, 1995). Chimpanzees include 20 *Pan troglodytes* and 3 *Pan paniscus* (Ruff, 2002). Data were obtained at 50 and 65% of femoral length, and 40 and 50% of humeral length from the distal end, for all specimens, except the East African sample, where data were only available for the femoral 50% and humeral 40% sections. Section properties for the comparative samples and specimens were obtained as described previously (Ruff, 1995, 2000, 2002, 2008).

Femoral-to-humeral strength proportions of the fossil specimens relative to the modern comparative samples were assessed through bivariate analyses of log-transformed data. Reduced major axis (RMA) regressions were calculated through the two modern samples, and standard errors of estimate (SEE) and 95% confidence limits used to evaluate the proportions of the fossil specimens. RMA analysis has been argued to be the most appropriate bivariate regression technique when both variables are measured with error and the goal is to examine relative proportions, as is the case here (Rayner, 1985; Hofman, 1988; Aiello, 1992). RMA minimizes the sum of triangular areas bounded by the regression line and horizontal and vertical lines drawn to the data points (Hofman, 1988); thus, the residual mean square of these areas was used to calculate SEE's and 95% prediction intervals for individual data points (Zar, 1984). The positions of fossil specimens relative to the modern human and chimpanzee regression lines were quantified as their (triangular) residuals relative to the SEE's of the two lines (for a more detailed description of the general procedure, see Organ and Ward, 2006).

RESULTS

Section properties of the OH 62 femur and humerus are listed in Table 1. In terms of relative cortical thickness (percent cortical area, %CA), the OH 62 femur (83.2%) is similar to other early *Homo* femora near mid-diaphysis (about 80–85%, see Ruff et al., 1993) and is elevated relative to modern humans [$71.5\% \pm 7.3\%$ (SD) in the combined Pecos and East African sample at femoral midshaft]. The OH 62 humerus also has relatively thick cortices (%CA = 79.7%), similar to the KNM-ER 1808 mid-distal humerus (81.7%, Ruff, 2008) and again elevated relative to modern humans ($59.8\% \pm 9.9\%$ in the Pecos/East African sample). The KNM-WT 15000 femur and humerus have relatively thinner cortices, consistent with his juvenile age status (Ruff et al., 1994; Ruff, 2008) (also see Fig. 4 below).

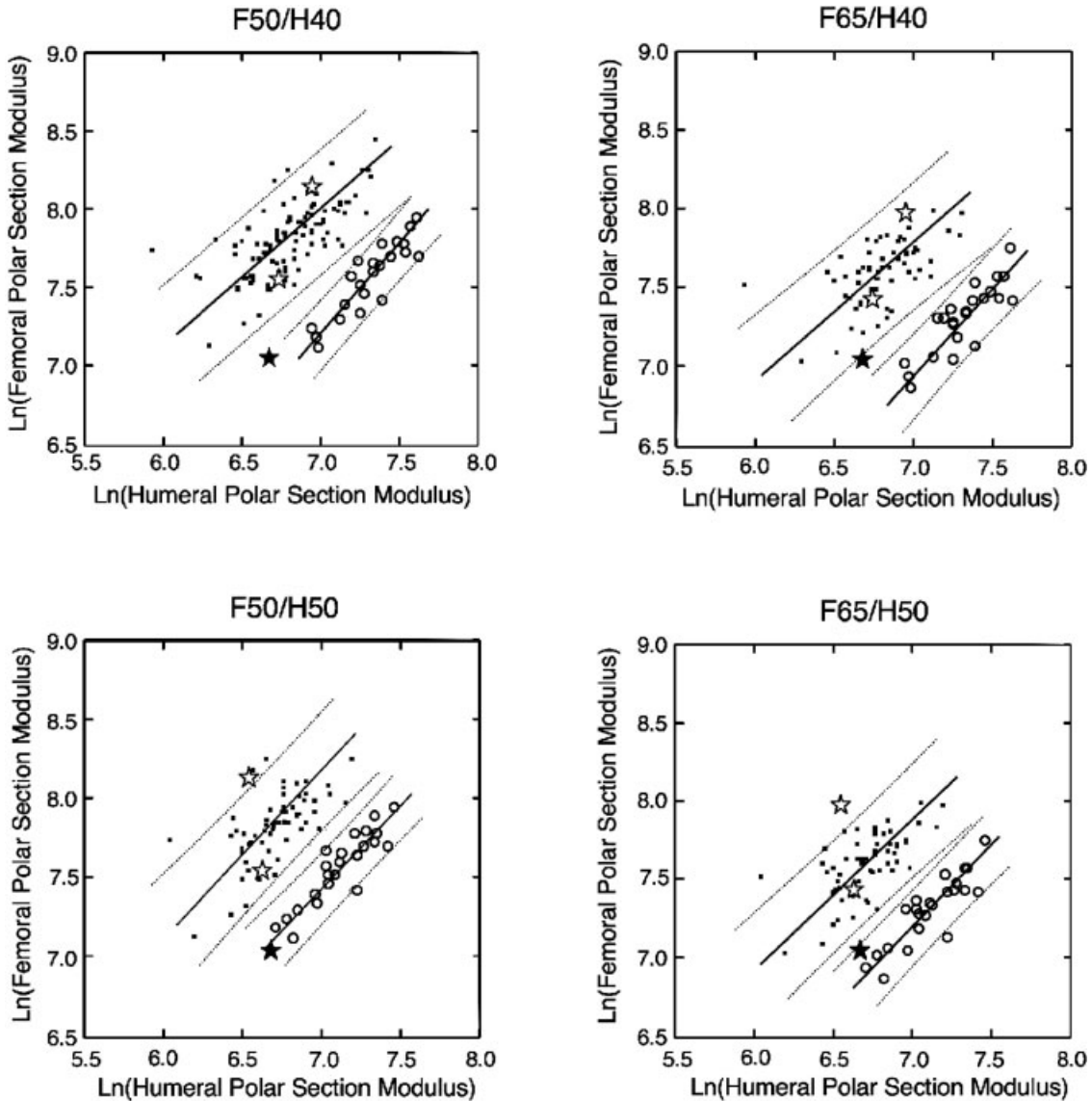


Fig. 3. Femoral to humeral strength distributions for four possible combinations of section locations in modern humans, chimpanzees, OH 62, KNM-WT 15000, and KNM-ER 1808. F50, F65: femoral 50 and 65% locations; H40, H50: humeral 40 and 50% locations; measured as percentages of bone length from the distal end. Small filled symbols: modern humans; circles: modern chimpanzees; filled star: OH 62; open stars: KNM-ER 1808 (higher position), KNM-WT 15000. Reduced major axis regression lines (solid) and 95% prediction intervals (dotted) drawn for modern samples.

Figure 3 shows the bivariate distributions of femoral to humeral strength of the two modern samples and the positions of the three fossil specimens, for each possible combination of the four section locations. Table 2 gives the relevant RMA regression statistics for the modern human and chimpanzee samples. Relative deviations of the fossils from the human and chimpanzee RMA regressions are given in Table 3.

Data distributions and 95% prediction intervals for modern humans and chimpanzees do not overlap for any of the comparisons. All slopes are nonsignificantly different ($P > 0.05$) from isometry (1.0). OH 62 falls below the 95% prediction interval of modern humans for all four section combinations. OH 62 falls near the lower edge or slightly below the observed size range for the modern chimpanzee sample, but is within the 95% prediction interval (or extrapolated prediction interval) for chim-

panzees in three of the four comparisons. In contrast, KNM-WT 15000 and KNM-ER 1808 fall well within or even above the modern human data distribution, and very far from chimpanzees in all comparisons. As discussed previously (Ruff, 2008) and also below, the slightly low position of KNM-WT 15000 within modern humans can be explained on the basis of his immaturity and sex, and the relatively high position of KNM-ER 1808 may be due in part to her sex (if the female attribution of this specimen is correct), as well as some error associated with correction for pathology in this specimen. But in any event, both of these specimens are clearly much more closely aligned with modern humans than is OH 62.

Figure 4 shows cross-sectional outlines of a typical modern chimpanzee and human (all within 0.7 SD of sample means for Z_p), and the three fossil specimens at

TABLE 2. Reduced major axis regression statistics for femoral to humeral polar section modulus (Z_p , log-transformed) in modern samples

Taxon	<i>n</i>	Sections ^a	Slope	SE slope	Intercept	<i>r</i>	SEE ^b
<i>Homo</i>	100	F50/H40	0.884	0.066	1.807	0.675	0.197
	60	F50/H50	1.074	0.111	0.622	0.620	0.189
	60	F65/H40	0.877	0.094	1.636	0.576	0.201
	60	F65/H50	0.975	0.099	1.059	0.634	0.177
<i>Pan</i>	23	F50/H40	1.148	0.113	-0.932	0.891	0.101
	23	F50/H50	1.084	0.104	-0.143	0.898	0.101
	23	F65/H40	1.120	0.127	-0.885	0.855	0.116
	23	F65/H50	1.060	0.112	-0.227	0.873	0.111

^a F, femur; H, humerus; 40, 50, and 65, section locations as percentages of bone length from the distal end.

^b Standard error of estimate of triangular areas bounded by RMA regression line and horizontal and vertical lines drawn to data points (see text).

TABLE 3. Relative deviation of fossil limb proportions from modern human and chimpanzee samples^a

	F50/H40		F65/H40		F50/H50		F65/H50	
	<i>Homo</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
OH 62	-3.54	2.05	-2.48	3.78	-3.76	0.38	-2.94	1.79
KNM-WT 15000	-1.12	6.04	-0.73	6.34	-0.95	4.88	-0.49	5.58
KNM-ER 1808	1.04	9.21	1.10	8.81	2.53	11.39	3.09	11.13

^a Fossil residual/sample standard error of estimate (see Table 2), reduced major axis regression of log-transformed femoral (F) on humeral (H) polar section modulus. 40, 50, and 65, section locations as percentages of bone length from the distal end. Underlined values within 95% prediction interval of modern sample.

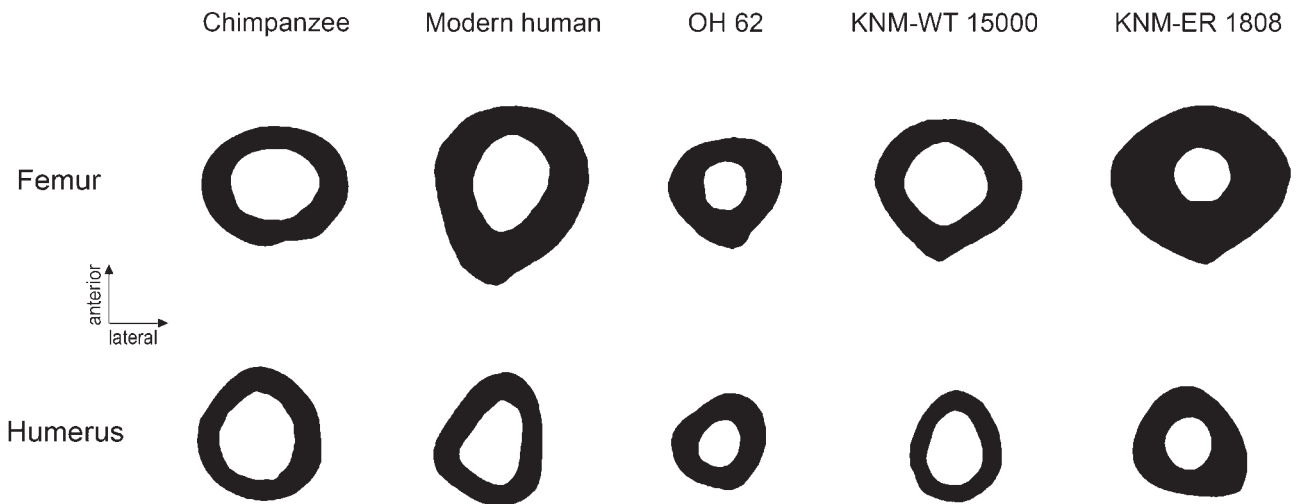


Fig. 4. Representative femoral and humeral cross sections for modern chimpanzees and humans, and three fossil specimens. Comparative sections taken at 50% of bone length in the femur and 40% of bone length in the humerus. Modern human and chimpanzee (both males) are within 0.7 SD of modern sample means for femoral to humeral polar section modulus. Arrows are 1-cm long.

the femoral 50% and humeral 40% locations, visually illustrating the degree of variability in proportions between them. In modern humans, femora are much stronger than humeri, with a ratio of femoral to humeral strength (Z_p) averaging 2.82 (SD 0.63). The same is true in KNM-WT 15000, with a ratio of 2.26, and in KNM-ER 1808, with a ratio of 3.30. In contrast, in modern chimpanzees femora and humeri are almost equal in strength (ratio of 1.29 ± 0.13). OH 62, with a femoral/humeral strength ratio of 1.46, is intermediate between humans and chimpanzees, but clearly much more similar to chimpanzees.

DISCUSSION

Because of its temporal position, and rare combination of upper and lower limb bones together with diagnostic cranial elements, the limb bone remains of OH 62 have figured prominently, although controversially, in various evolutionary scenarios regarding the acquisition of bipedal locomotion among early hominins (Leakey et al., 1989; Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Wood and Collard, 1999; Richmond et al., 2002; Haeusler and McHenry, 2004, 2007). The approach taken here avoids many of the problems in past analyses

of OH 62, by comparing only nonestimated dimensions and including structural proportions known to be directly associated with locomotor behavior, and that clearly distinguish modern humans from other primates.

Comparisons of interlimb proportions using long bone external breadths or circumferences have almost invariably placed OH 62 in a region of overlap between modern humans and chimpanzees (Richmond et al., 2002; Haeussler and McHenry, 2004, 2007).¹ External linear dimensions, however, only partially characterize long bone subperiosteal contours (Stock and Shaw, 2007) (and see Fig. 4). Furthermore, because of systematic differences in the relative cortical thickness of the femur and humerus in modern humans and chimpanzees (Ruff, 2008, and see Fig. 4), use of even true subperiosteal areas will underestimate the difference in femoral to humeral strength between them. Interestingly, in the only previous comment on internal dimensions of the OH 62 specimens (determined using computed tomography), it was noted that “The cortex of the arm bones appeared to be amazingly thick—more robust even than that of many chimpanzees” (Johanson and Shreeve, 1989: p 287). In fact, both the humerus and femur of OH 62 have relatively thick cortices compared to both modern humans and modern chimpanzees, although they are not unusually thick when compared to other early *Homo* adult specimens (see above and Ruff, 2008). Thus, incorporation of both actual subperiosteal contours and the medullary cavity is critical to reconstruction and interpretation of long bone diaphyseal strength in early hominins.

In every comparison of relative femoral to humeral strength bracketing possible section locations along the diaphysis, OH 62 falls below the limits of a modern human sample incorporating a diverse range of body sizes and shapes (Ruff, 1995, 2000). It should be noted that femoral to humeral strength proportions of these modern humans, like those of anthropoid primates in general (Ruff, 2003) (including the modern chimpanzees analyzed here), are isometric. Thus, there is no indication that interlimb strength proportions, within species, vary as a function of body size. As a further test of this, the femoral to humeral strength proportions of two African Pygmy skeletons were calculated (data provided by L. Shackelford); these were found to fall well within the data scatter for the combined Pecos-East African sample. Therefore, the very small body size of OH 62 does not in itself explain its nonhuman-like strength proportions.

In all but one comparison, OH 62 falls within the 95% prediction interval of modern chimpanzees, although in some comparisons this involves slight downward extrapolation of the modern sample limits. The one comparison where OH 62 falls outside the chimpanzee 95% prediction interval is the femoral 65% to humeral 40% proportion. This represents, in fact, the most extreme potential positioning of the OH 62 sections, requiring both femoral and humeral length estimates well beyond those of most observers. The most probable longitudinal position of the two sections is somewhere between the extreme values considered here, which, given the patterns shown above, suggests that OH 62 would fall within the chimpanzee distribution, although most likely near its upper edge, that is, toward humans. Thus, OH 62 has femoral/hum-

eral strength proportions that are more like those of a modern chimpanzee than a modern human, but that are still likely somewhat intermediate between the two.

In contrast, the two early *Homo* specimens craniodentally assigned to *H. erectus* (or *ergaster*)—KNM-ER 1808 and KNM-WT 15000—both fall within or even above the modern human distributions for femoral to humeral strength. KNM-WT 15000 is within the lower part of these distributions. However, it has been shown (Ruff, 2003) that femoral/humeral strength proportions do not reach adult values until late adolescence among modern humans, and also that males have slightly lower proportions than females. When plotted against a modern human growth trajectory, KNM-WT 15000 falls exactly where expected for a male of his approximate age (Ruff, 2008). Modern human females have somewhat higher femoral/humeral strength proportions, which could explain, in part, the relatively high position of KNM-ER 1808, if that specimen is female and if modern sex differences in upper and lower body strength proportions also characterized early *Homo*. It is also possible that there was some error in the corrections for the pathological deposits on this specimen; however, since a much thicker layer was subtracted from the femur than from the humerus (Walker et al., 1982; Leakey and Walker, 1985; Ruff, 2008), it would appear more likely that true femoral rather than humeral strength was underestimated by this procedure. It is also possible that (adult) *H. erectus* were actually characterized by particularly strong lower limb bones, or that KNM-ER 1808 had a less robust than usual upper limb (the humeral shaft was originally described as “lightly built,” Leakey and Walker, 1985: 140). Regardless, it is apparent that both *H. erectus* specimens are very unlike either chimpanzees or OH 62 in strength proportions.

The degree to which possible bilateral asymmetry in limb bone strength could have affected these comparisons is difficult to assess. The modern samples were side-balanced, including an approximately equal number of right and left humeri and femora. Among the fossil specimens, both femora were available for KNM-WT 15000, with properties taken as an average between them (Ruff, 2008), the KNM-ER 1808 femur is from the right side, and the OH 62 femur is from the left side. Bilateral asymmetry in transverse diaphyseal dimensions of lower/hind limb bones is small in both modern humans and chimpanzees (Trinkaus et al., 1994; Sarringhaus et al., 2005; Auerbach and Ruff, 2006), so these differences are unlikely to have affected any comparisons. However, systematic bilateral asymmetry is significant in the modern human upper limb, favoring the right side (Trinkaus et al., 1994; Auerbach and Ruff, 2006), and asymmetry in upper limb bone strength is more pronounced in Late Pleistocene humans (Trinkaus et al., 1994; Churchill and Formicola, 1997). All three fossils are represented by right humeri, so any comparisons between them should be equally affected by this factor (unless one individual was left-dominant rather than right-dominant in upper limb use). However, since the modern comparative samples were side-balanced, this could have decreased relative femoral/humeral strength proportions in all three of the fossil specimens (by increasing humeral strength). This assumes that early *Homo*, including *H. habilis*, was characterized by side dominance in upper limb use, which is not clearly established (Lazenby, 2002). Comparison of external breadths of the right and left ulnae of KNM-WT 15000 indicates some right dominance (3–4%), equivalent to that found in modern

¹Hartwig-Scherer and Martin (1991) found OH 62 to group more closely with African apes than with modern humans in most interlimb comparisons, but presented no data on overlap between the two modern groups for breadth or circumference proportions.

humans, although such comparisons are to some degree confounded by his age (Ruff, 2008). No directional asymmetry is evident in the paired early *Homo* adolescent humeri D2715 and D2680 from Dmanisi (Lordkipanidze et al., 2007). Modern chimpanzees show only slight directional asymmetry (favoring the left side) in total subperiosteal area of the humeral diaphysis—about 0.5% (Sarringhaus et al., 2005, my calculation from their Table 1), which suggests less than a 1% directional difference in Z_p (Stock and Shaw, 2007). Thus, any consideration of possible side bias in fossil humeri will be affected by the particular model chosen for analogy. However, given the greater similarity in interlimb strength proportions of OH 62 and chimpanzees; it seems highly unlikely that OH 62 was more bilaterally asymmetric in humeral strength than KNM-WT 15000 and KNM-ER 1808. Thus, observed differences in proportions between OH 62 and the other two fossils should be valid, if not conservative.

The present findings strongly argue for fundamental differences in use of the limbs in *H. habilis* and *H. erectus*, with *H. habilis* characterized by relatively greater upper limb mechanical loading. There are other indications for increased mechanical loading of the upper limb in *H. habilis*, in particular, the powerful grasping capabilities of the OH 7 juvenile hand (Napier, 1962; Susman and Creel, 1979; Susman and Stern, 1979), which has been interpreted as evidence for frequent climbing behavior (Susman and Creel, 1979; Susman and Stern, 1979, 1982) (although see Moyá-Solá et al., 2008 for an alternative taxonomic attribution of this specimen). Following a similar rationale to that presented here, Susman and Stern (1982) argued that “The phenotypic plasticity of bone suggests that the thick-walled, robust, and heavily muscled character of the O.H. 7 hand is not simply a vestige of a suspensory (hominoid) heritage” (p. 933), but rather reflects actual arboreal behavior. However, in other respects the OH 7 hand shows clear affinities to modern humans (Napier, 1962; Susman and Creel, 1979). Other lower limb remains attributed to *H. habilis*, including the OH 8 foot and OH 35 leg bones, also show a combination of primitive and derived characteristics, although with clear hallmarks of bipedality (Davis, 1964; Day and Napier, 1964; Archibald et al., 1972; Susman and Stern, 1982; Kidd et al., 1996). It should be noted that the taxonomic attribution of these specimens to *H. habilis* has been questioned (Gebo and Schwartz, 2006; Wood and Constantino, 2007, and references therein), although also defended (Susman, 2008). KNM-ER 3735, a partial associated but very fragmentary skeleton dated to about 1.9 Ma, may also represent *H. habilis* (*sensu stricto*) (Leakey et al., 1989), and several features of its forelimb remains also suggest enhanced climbing abilities (Leakey et al., 1989; Haeusler and McHenry, 2007). Direct forelimb to hind limb comparisons have yielded somewhat contradictory results (Leakey et al., 1989; Haeusler and McHenry, 2007), although such comparisons are hampered by the incomplete and weathered state of the remains.

Haeusler and McHenry (2004, 2007) noted that the general cross-sectional geometry of the KNM-ER 3735 and OH 62 femoral diaphyses, including a “well-developed pilaster,” is “human-like,” and this can be confirmed here for OH 62 (see Fig. 4 above). This could be an indication of human-like mechanical loading of the femur in *H. habilis*. However, the proximal femoral diaphysis of OH 62 shows a rather “nonhuman-like” cross-sectional shape, being nearly circular (Johanson et al., 1987, and pers. obs.) and in this respect very unlike that of *H. erectus*

femora, which are strongly mediolaterally buttressed (Ruff, 1995; Haeusler and McHenry, 2004). Furthermore, the distinctness of the linea aspera, or posterior “pilaster” in human femora is dependent to some extent on the degree of mediolateral expansion of the diaphysis (Ruff, 1995); thus, it is difficult to interpret in isolation.

If the OH 7 hand, OH 8 foot, and OH 35 tibia and fibula do actually belong to *H. habilis*, then, together with the evidence presented here, this indicates a locomotor repertoire in *H. habilis* that included terrestrial bipedality but that also incorporated a significant arboreal (climbing, forelimb suspensory) component. It is even possible that adaptations for terrestrial bipedality in the lower limb created greater mechanical loads on the upper limb because climbing was more inefficient (Aiello, 1994; Wolpoff, 1996), thus accounting for the more chimpanzee-like limb strength proportions in *H. habilis* despite its terrestrial bipedality. Arboreal capabilities may well have been selectively advantageous for escape from predators and sleeping, as well as foraging, in such a small-bodied hominin (Susman and Stern, 1982). No such adaptation is apparent in early African *H. erectus*, who had fully modern limb proportions, and, by implication, fully modern locomotor behavior.²

The early *Homo* specimens from Dmanisi, dated to about 1.77 Ma, are approximately contemporaneous with OH 62 (Rightmire et al., 2006; Lordkipanidze et al., 2007). In terms of cranial morphology, they are most closely linked to early African *H. erectus* (or *ergaster*) (Lordkipanidze et al., 2006; Rightmire et al., 2006). Although certain “primitive” features of the postcranial remains have been noted, humerofemoral length proportions are completely modern (Lordkipanidze et al., 2007). Interlimb diaphyseal breadth proportions also appear to be similar to those of modern humans. There is a typographical error in the humeral midshaft breadths of the adult specimen, D4507, reported in Lordkipanidze et al., 2007, Table 1, as is clearly apparent from visual inspection of Figure 2 of the same publication. Correct maximum and minimum external breadths of the humeral midshaft are 18.0 and 16.5 mm, respectively (Rightmire, pers. comm.), which are considerably smaller than the midshaft A-P and M-L breadths of the associated femur, D4167: 26.5 and 22.2 mm, respectively. Using formulae derived by Stock and Shaw (2007) from modern human long bones, approximate values for femoral and humeral Z_p in these specimens can be calculated as 2390 and 988 mm³, respectively. These values give a femoral/humeral strength ratio of 2.42, and fall within the 95% prediction interval of modern humans (Fig. 3 above), although in the lower part of the distribution. However, as discussed above, external breadths may not accurately reflect overall cross-sectional morphology. In fact, Lordkipanidze et al. report that the D4167 femur has a “narrow medullary canal in comparison to modern humans” (2007: p 307), which would increase femoral Z_p (although humeral strength may also be greater if humeral cortical

²Larson et al. (2007) have recently documented a difference in humeral head torsion and possibly relative clavicular length between modern humans and KNM-WT 15000 (although there is overlap between the two for both characteristics, particularly relative clavicular length), which they suggest may indicate a difference in shoulder positioning. However, with respect to key characteristics distinguishing humans from the arboreal apes—orientation of the scapular spine and glenoid fossa—KNM-WT 15000 clearly groups with modern humans.

thickness was increased). In any event, despite being of smaller body size than most (but perhaps not all—see Spoor et al., 2007) early African *H. erectus*, in terms of relative limb loadings and inferred locomotor behavior, the Dmanisi individual is clearly more similar to *H. erectus* (KNM-WT 15000 and KNM-ER 1808) than to *H. habilis* (OH 62).

The results reported here support recent craniofacial evidence for long-term sympatry and “some form of niche differentiation between *H. erectus* and *H. habilis* [*sensu stricto*], one that may have included foraging or dietary differences” in the Early Pleistocene of East Africa (Spoor et al., 2007). They are also consistent with a relatively early separation between *H. erectus* and *H. habilis* (*sensu stricto*) lineages, with earliest (pre-1.8 Ma) *H. erectus* possibly represented by specimens such as the KNM-ER 3228 innominate and the KNM-ER 1472 and 1481a femora (1.89–1.95 Ma), all of which closely resemble later *H. erectus* (Leakey et al., 1989). Fully developed terrestrial bipedalism in early *H. erectus*, including the Dmanisi specimens, may have facilitated colonization of regions outside of Africa, with the more arboreally dependent *H. habilis* lineage remaining more geographically restricted (although see Dennell and Roebroeks, 2005 for a contrasting view). In any event, the present results are consistent with the view that early hominins, including early *Homo*, were characterized by varying combinations of arboreality and terrestrial bipedality, resulting in the mosaic of postcranial morphological features observed among various lineages (Harcourt-Smith and Aiello, 2004).

CONCLUSIONS

Femoral to humeral strength proportions of the *H. habilis* OH 62 specimen fall outside the range of modern humans, regardless of which bone length estimates for OH 62 are used to locate sections along the diaphysis. In most comparisons, OH 62 also falls within the femoral/humeral strength distributions for modern chimpanzees, which do not overlap with those for modern humans. In contrast, two early *H. erectus* specimens, KNM-WT 15000 and KNM-ER 1808, both fall far from chimpanzees and well within (or even above) modern human distributions. Because cross-sectional diaphyseal properties are developmentally plastic and responsive to applied mechanical loadings during life, this indicates that distribution of mechanical loads through the upper and lower limbs of *H. habilis* differed from that of modern humans and *H. erectus*. Results are consistent with locomotor differentiation between the two early *Homo* lineages, with *H. habilis* more reliant on arboreal climbing while *H. erectus* was a fully committed terrestrial biped.

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