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Early hominin limb proportions

Recent analyses and new fossil discoveries suggest that the evolution of hominin limb length proportions is complex, with evolutionary reversals and a decoupling of proportions within and between limbs. This study takes into account intraspecific variation to test whether or not the limb proportions of four early hominin associated skeletons (AL 288-1, OH 62, BOU-VP-12/1, and KNM-WT 15000) can be considered to be significantly different from one another. Exact randomization methods were used to compare the differences between pairs of fossil skeletons to the differences observed between all possible pairs of individuals within large samples of *Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens*. Although the difference in humerofemoral proportions between OH 62 and AL 288-1 does not exceed variation in the extant samples, it is rare. When humerofemoral midshaft circumferences are compared, the difference between OH 62 and AL 288-1 is fairly common in extant species. This, in combination with error associated with the limb lengths estimates, suggests that it may be premature to consider *H.* (or *Australopithecus*) *habilis* as having more apelike limb proportions than those in *A. afarensis*. The humerofemoral index of BOU-VP-12/1 differs significantly from both OH 62 and AL 288-1, but not from KNM-WT 15000. Published length estimates, if correct, suggest that the relative forearm length of BOU-VP-12/1 is unique among hominins, exceeding those of the African apes and resembling the proportions in *Pongo*.

Evidence that *A. afarensis* exhibited a less apelike upper:lower limb design than *A. africanus* (and possibly *H. habilis*) suggests that, if *A. afarensis* is broadly ancestral to *A. africanus*, the latter did not simply inherit primitive morphology associated with arboreality, but is derived in this regard. The fact that the limb proportions of OH 62 (and possibly KNM-ER 3735) are no more humanlike than those of AL 288-1 underscores the primitive body design of *H. habilis*.

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Introduction

Variations in fore and hindlimb proportions in living primates are correlated with significant differences in positional behavior (Jungers, 1985; Fleagle, 1999). As a result, limb proportions are important in efforts to reconstruct locomotion in fossil taxa, including hominins. They also have relevance for those interested in recovering phylogenetic relationships. Many primate clades show considerable diversity in limb proportions. For example, sympatric cali-

trichines differ in intermembral proportions in ways that relate to significant differences in substrate use within their arboreal environments (Garber & Leigh, 2001). Large-bodied papionins apparently independently evolved high intermembral indices, probably as a result of parallel increased commitments to terrestrial locomotion (Lockwood, 1999). Extant and subfossil lemur clades are among the most diverse in terms of limb designs (Jungers *et al.*, 2001).

Like other primate clades, the picture emerging from the hominin fossil record and

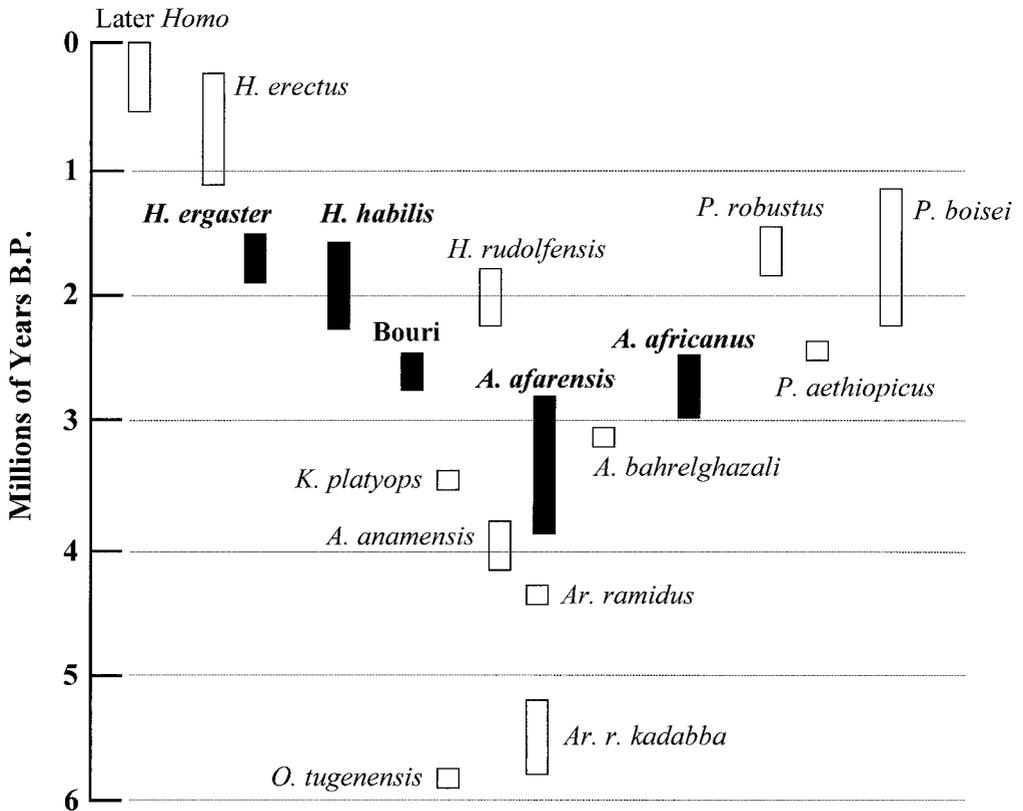


Figure 1. Hominin phylogram. Evidence for limb proportions is considered for the taxa (and the Bouri remains) shown in bold.

analytical advances is one of complexity in the evolution of limb design. A simple model of hominin evolution, with fossil hominins with primitive (i.e., apelike) limb proportions being succeeded by those with more modern humanlike limb proportions, is no longer tenable. The 1974 discovery (Johanson & Taieb, 1976) of the *Australopithecus afarensis* (or *Praeanthropus afarensis*) partial skeleton AL 288-1 led to the realization that the humerofemoral proportions of *A. afarensis* are intermediate between those of modern humans and extant African apes. Specifically, compared to modern humans, AL 288-1 has a short femur relative to body mass (Jungers, 1982) but apparently not relative to stature (Hens *et al.*, 2000). Debates continue over whether, or how,

short legs relative to body mass would influence locomotor kinematics and efficiency (Jungers, 1982; Rak, 1991; Steudel, 1996; Kramer, 1999).

The earliest unambiguous evidence of more modern humanlike limb proportions in the fossil record comes from the remarkably complete skeleton KNM-WT 15000, attributed to *Homo ergaster* (Figure 1), or early African *H. erectus* (Brown *et al.*, 1985; Wood, 1992; Walker & Leakey, 1993b). Like modern humans, this skeleton has relatively long femora and short forearms (Ruff & Walker, 1993).

The discovery of a fragmentary partial skeleton, OH 62, attributed to *H. habilis* (Figure 1), complicated the picture (Johanson *et al.*, 1987). The femur of this

skeleton is comparable in size to, or smaller than, that of AL 288-1, while the humerus appears to be substantially longer than that of AL 288-1. In other words, if the limb length estimates are correct, OH 62 has more apelike upper-to-lower limb proportions compared to AL 288-1. This suggests an evolutionary reversal in limb proportions from the earlier (Figure 1) and generally more primitive taxon *A. afarensis*, to the more recent and in some ways more derived *H.* [or *Australopithecus* (Wood & Collard, 1999)] *habilis* (Hartwig-Scherer & Martin, 1991). However, the error associated with estimating the OH 62 humerus length unfortunately stands in the way of making secure conclusions about the skeleton's humerofemoral length proportions (Korey, 1990).

There is an unfortunate lack of associated skeletal remains of *A. africanus* from which relative limb bone lengths can be determined. However, there are enough unassociated upper and lower limb fossil fragments to ascertain that in *A. africanus* various joints of the upper limb are larger relative to lower limb joints than is the case in either modern humans or *A. afarensis* (McHenry & Berger, 1998a). Thus, unless the joint:limb length relations differ between these taxa, indirect evidence suggests that *A. africanus* (Figure 1) has more apelike upper to lower limb length proportions than those of the earlier, and craniodentally more primitive, taxon *A. afarensis* (McHenry & Berger, 1998b).

The most recent factor complicating the pattern of the evolution of the hominin postcranial skeleton is the partial skeleton from the Bouri deposits, possibly representing *A. garhi*. The Bouri skeleton (Figure 1) reportedly combines modern human-like humerofemoral proportions with a relatively long, apelike forearm (Asfaw *et al.*, 1999). The large, isolated Omo L40-19 ulna (Howell & Wood, 1974; Aiello *et al.*, 1999) from the Shungura Formation (ca. 2.3 Ma;

Feibel *et al.*, 1989) also suggests the presence of a hominin with substantial body size or forearm length.

Therefore, if the limb length estimates are correct for these various associated skeletons, they suggest that the evolution of limb proportions within the hominin clade is more complex than previously anticipated. Specifically, a purely temporal sequence (Figure 1) suggests that intermediate humerofemoral, and possibly brachial, proportions are seen by at least 3.2 Ma in AL 288-1. This would be followed by more apelike humerofemoral proportions in *A. africanus* (McHenry & Berger, 1998a), then by humanlike humerofemoral but apelike upper limb proportions in the Bouri skeleton. More apelike humerofemoral proportions would follow in *Homo* (or *A.*) *habilis*. Finally, modern humanlike humerofemoral and upper limb proportions occur in *Homo ergaster* and persist with relatively minor changes in subsequent taxa.

Because of their rarity, the known associated skeletons have been treated as representative for their respective taxa. However, as with other morphological features, limb proportions vary within species. Are the differences in limb proportions among the associated skeletons reviewed above so substantial that they are unlikely to have occurred in two members of the same species? In other words, could the differences between these associated skeletons be merely a product of random sampling from species with essentially the same limb proportions?

Eckhardt (2000) has recently argued that the differences in the humerofemoral proportions of OH 62 and AL 288-1 might not be excessive when compared to the variation seen between, and possibly within, modern human populations. Specifically, he found the difference in humerofemoral index between OH 62 and AL 288-1 to match the difference between a Japanese sample reported by Shapiro (1939) and a rough

average from an unspecified modern human sample referred to in Leakey & Lewin (1992). However, the data on the Japanese sample were collected as external measurements on living subjects rather than osteological measurements. Thus, these data are not directly comparable and additional analyses are warranted.

The goal of this study is to consider hominin limb proportions in the context of quantitative information about variation within relevant comparative taxa. This study tests the null hypothesis that the differences observed among these associated skeletons are not significantly different from one another. Specifically, it examines both the possibilities and probabilities that the differences between pairs of these hominin specimens could be found within extant hominoid species.

Methods

Length and midshaft circumference were measured on the humerus, radius, femur, and tibia of comparative samples of great apes and humans. The comparative data consist of mixed subspecies samples of *Gorilla gorilla* (30 males, 23 females), *Pan troglodytes* (19 males, 16 females), *Pongo pygmaeus* (16 males, 16 females), a species sample of *Pan paniscus* (nine males, eight females), and a sample of deliberately mixed populations of *H. sapiens* (46 males, 42 females, 14 unknown). Measurements were collected on specimens housed at the following institutions: the Natural History Museum (London), the Smithsonian Institution's National Museum of Natural History (Washington, D.C.), the Powell Cotton Museum (Birchington), the Musée Royal de l'Afrique Centrale (Tervuren), and the Raymond Dart Collection of The University of Witwatersrand. The fossil associated skeletons examined in this study include AL 288-1 (*A. afarensis*), OH 62 (*H. habilis*), the Nariokotome skeleton

KNM-WT 15000 (*H. ergaster*, or early African *H. erectus*), and the Bouri skeleton BOU-VP-12/1 (possibly *A. garhi*). Two of the original fossils (OH 62 and KNM-WT 15000) were examined by BW and LA. However, length estimates and measurements for the fossils were taken from the literature in most cases (Table 1). The midshaft circumference measurements of KNM-WT 15000 were measurements taken by BR on a cast (housed at the Smithsonian Institution's National Museum of Natural History). Published measurements (Walker & Leakey, 1993a) of the original were compared with measurements made by BR on a cast, and the differences were less than 5% between the two sets of measurements. Although there appears to be slight age-related variation in limb proportions between the ages of 10 and 18 years, Ruff & Walker (1993) concluded that limb proportions of 11–12-year-old boys are very similar to those of 18-year-old boys. Given the similarity in proportions at these ages, and the evidence that the growth pattern of KNM-WT 15000 may be similar to that of modern humans (Clegg & Aiello, 1999), we do not attempt to make adjustments for the age of KNM-WT 15000 (see Ruff & Walker, 1993).

Four limb proportion indices were examined, the humerofemoral index ($100 \times$ humerus length/femur length), the brachial index ($100 \times$ radius length/humerus length), the crural index ($100 \times$ tibia length/femur length), and the humerofemoral circumference index ($100 \times$ humerus midshaft circumference/femur midshaft circumference) (Aiello & Dean, 1990). Two humerofemoral and brachial index estimates were calculated for BOU-VP-12/1, one using limb length estimates based on "anatomical grounds" and preferred by Asfaw *et al.* (1999), and a second using the limb length estimates derived from regressions (Asfaw *et al.*, 1999). Two brachial indices were also computed for AL 288-1 and OH 62,

Table 1 Long bone dimensions (mm) of early hominin associated skeletons

Measurement	AL 288-1	OH 62	BOU-VP-12/1	KNM-WT 15000
Humerus length	237, 239*	264	226†, 236‡	319
Humerus midshaft circumference	55.5	52.5 (52.0–55.5)§		55
Radius length	174¶, 215**	210††, 246‡‡	231	255
Radius midshaft circumference	34	38		
Femur length	280.5	280	335‡, 348†	432
Femur midshaft circumference	67	60 (60–62)§		71
Tibia length				380

Dimensions of AL 288-1 and OH 62 taken from [Hartwig-Scherer & Martin \(1991\)](#), those of BOU-VP-12/1 from [Asfaw *et al.* \(1999\)](#), and KNM-WT 15000 from [Walker & Leakey \(1993a\)](#), unless indicated otherwise.

*From [Jungers \(1982\)](#). Used in computation of lowest Brachial Index estimate for AL 288-1.

†Based on regression of African apes and humans ([Asfaw *et al.* \(1999\)](#)).

‡Based on “anatomical grounds”, and preferred by [Asfaw *et al.* \(1999\)](#).

§Value taken from [Hartwig-Scherer & Martin \(1991\)](#), values in parentheses represent ranges of the combined values from [Hartwig-Scherer & Martin \(1991\)](#) and from measurements taken at, above and below midshaft ([Lockwood](#), personal communication).

||Collected by BR on a cast.

¶Based on the humanlike estimate from [Schmid \(1983\)](#).

**Based on regression limited to chimpanzees and bonobos ([Asfaw *et al.* \(1999\)](#)).

††Conservatively low estimate by [Hartwig-Scherer & Martin \(1991\)](#).

‡‡Maximum estimate of [Hartwig-Scherer & Martin \(1991\)](#).

based on the highest and lowest published estimates of the radius lengths of each specimen ([Table 1](#); [Schmid, 1983](#); [Hartwig-Scherer & Martin, 1991](#); [Asfaw *et al.*, 1999](#)).

Because of the problems involved in estimating limb lengths from fragmentary remains, we also compared measures of humerus and femur size that could be directly taken on the fossils, namely midshaft circumferences. These are not proxies for length, but provide an independent and more direct assessment of limb bone size. As noted, published midshaft circumferences were employed for AL 288-1 and OH 62 ([Hartwig-Scherer & Martin, 1991](#)), and those for KNM-WT 15000 were taken on the NMNH cast. Because of the uncertainty in identifying the precise location of midshaft without knowing the exact lengths of the OH 62 femur and humerus, circumference measurements were collected on a cast (courtesy of C. Lockwood, Institute for Human Origins, Arizona State University) at 1 and 2 cm above and below the location identified as midshaft. The highest, and thus most apelike, humerofemoral circumference

index was computed by combining the largest humeral circa-midshaft circumference (55.5 mm, taken 2 cm above “midshaft”, C. Lockwood, personal communication) with the smallest in the range of values for femoral circa-midshaft circumference (60 mm, from [Hartwig-Scherer & Martin, 1991](#)). The lowest, most humanlike humerofemoral circumference index was calculated by combining the smallest humeral circa-midshaft circumference (52.0 mm, [Hartwig-Scherer & Martin, 1991](#)) with the largest femoral circa-midshaft circumference (62 mm, 2 cm above “midshaft”, C. Lockwood, personal communication). In this manner, we assessed the potential effect on humerofemoral circumference proportions of measuring circumference above or below the true location of the midshafts of OH 62.

Exact randomization was used to compare the differences between pairs of fossil skeletons with the differences among all possible pairings of individuals in the reference samples ([Grine *et al.*, 1993](#); [Richmond & Jungers, 1995](#); [Lockwood *et al.*, 1996](#)). The human and gorilla samples were limited to

fifty individuals for the exact randomization calculations. This balanced-sex human sample comprises individuals of known sex, randomly selected from a larger dataset, from the following museum collections: Dart, University of the Witwatersrand, southern African blacks ($n=12$); Canadian Museum of Civilization, Inuit ($n=12$); Terry, Smithsonian Institution, North American blacks ($n=12$); and the Natural History Museum (London), various British ($n=14$). The limited availability of the *Pan paniscus* sample precluded the use of this species in the exact randomization computations.

The difference in limb proportions between individuals was calculated as the arithmetic difference in limb proportions between the two fossils in question. Arithmetic difference was employed because the limb proportion indices are ratios and thus reflect shape (Jungers *et al.*, 1995). The same computation was performed for each extant species, with differences computed for every possible pair of individuals. Thus, the sample of 50 gorillas generated 1225 unique pairwise comparisons. The final step was a comparison with the fossil pair differences in order to assess the probability of sampling such a difference within a single species.

Results

The differences in limb proportions between the great apes and modern humans found here are consistent with those reported in previous studies (e.g. Schultz, 1930; Shea, 1981; Jungers, 1985; Aiello & Dean, 1990; Lovejoy, 1993). Orang-utans exhibit the highest humerofemoral index, followed by gorillas, common chimpanzees, bonobos, and finally modern humans (Figure 2). The bivariate relationship between humerus and femur lengths shows that intertaxonomic differences are not due to size alone (Figure 3; Jungers, 1985). Both the Nariokotome

and Bouri skeletons resemble the modern human sample in their humerofemoral proportions, and AL 288-1 is intermediate between *Pan* and *Homo*. If the published length estimates are correct, OH 62 has a relatively longer humerus than AL 288-1 and the other associated fossil hominin skeleton considered here.

The difference in humerofemoral proportions between the Nariokotome and Bouri skeletons is small when compared to the differences observed between pairs of individuals within any of the reference taxa (Figure 4; Table 2). The "anatomical grounds" length estimates (those preferred by Asfaw *et al.*, 1999, as opposed to their regression-based estimates; see above) for Bouri result in humerofemoral proportions that are very similar to those of the Nariokotome skeleton (Figure 2; Table 2). Limb length estimates for the Bouri skeleton based on an African ape/human regression yield a humerofemoral index less similar to the Nariokotome skeleton (Figure 2; Table 2). The difference between Nariokotome and this estimate of Bouri is observed in less than 5% of human (0.1%) and chimpanzee (3.6%) samples, and is rare in orang-utan (5.0%) and gorillas (7.1%) (Table 2). The degree of difference between OH 62 and the Bouri skeleton is never observed within any of the comparative taxa, regardless of which Bouri length estimates are used (Table 2). The differences between AL 288-1 and the Nariokotome skeleton are significant ($P<0.05$), but more extreme differences can be found in samples of each of the living apes (Figure 4; Table 2). The humerofemoral proportions of AL 288-1 are significantly more humanlike than those of OH 62; a comparable level of difference is almost never observed in the human sample, and only rarely (2.5% to 4.6%) in extant great ape samples (Figure 4; Table 2). However, a change of only 0.25 mm in any of the limb length estimates for either fossil makes the difference in humerofemoral proportions

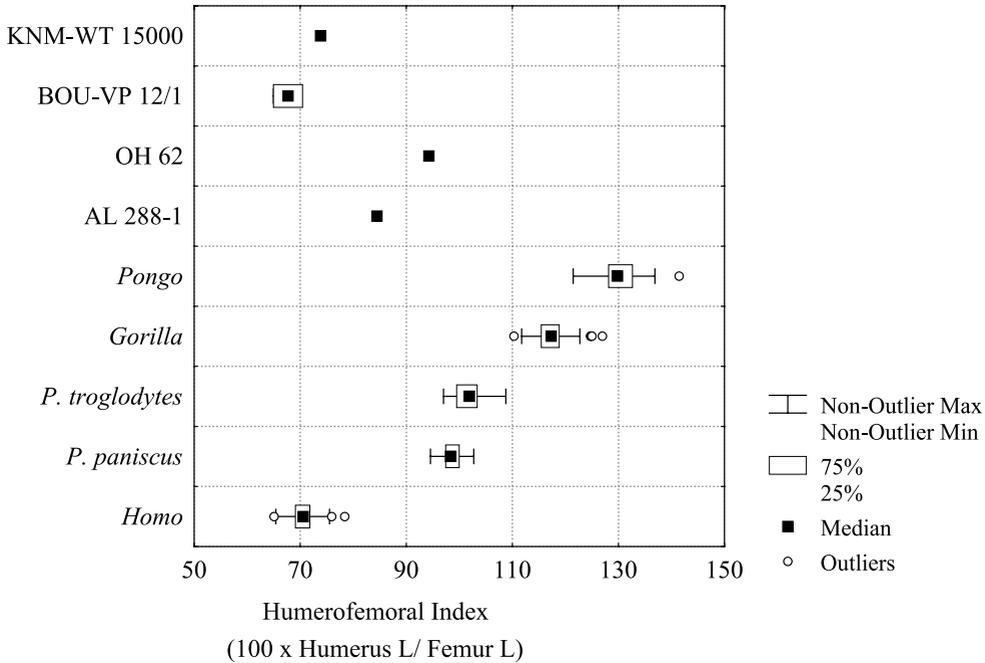


Figure 2. Box plot of humerofemoral (HF) index ($100 \times \text{humerus length}/\text{femur length}$) in extant great apes and fossil hominins. Of the fossil hominin partial skeletons, OH 62 has the highest and most apelike HF proportions, followed by lower HF proportions in AL 288-1, KNM-WT 15000 and BOU-VP 12/1. The range of values for BOU-VP 12/1 results from the lowest and highest estimates of the humerus and femur lengths (see Table 1) provided by Asfaw *et al.* (1999); the lowest HF index is obtained from length estimates derived from African ape and human regressions, the highest HF index is a product of their preferred estimates, based on “anatomical grounds”. In each box plot, the small square represents the median value, the box represents the interquartile range (central 50% of the data), the bars indicate the nonoutlier range, and open circles denote outliers.

between AL 288-1 and OH 62 become nonsignificant compared with the gorilla sample. Thus, if the length of the AL 288-1m (right humerus) is 239 mm (Jungers, 1982), as opposed to 237 mm (Johanson *et al.*, 1982; Hartwig-Scherer & Martin, 1991), the humerofemoral index difference between these specimens are not significant compared to the variation in orang-utan ($P > 0.05$) and gorilla ($P > 0.06$) samples (human, $P < 0.001$; chimpanzee, $P = 0.03$). Furthermore, Korey (1990) has shown that when the error involved in the humerus length estimate for OH 62 is taken into account, a standard deviation of about 7.7 for the humerofemoral index is estimated for this specimen.

Because both AL 288-1 and OH 62 are thought to represent female individuals (Johanson *et al.*, 1982; Johanson *et al.*, 1987; Wood & Quinney, 1996; Tague & Lovejoy, 1998; but see Häusler & Schmid, 1995, 1997), we also compared the differences between AL 288-1 and OH 62 to the pairwise differences in female-only samples of each of the comparative species. The analyses yielded similar results. The difference between the fossils was never observed in the female-only human or orang-utan samples, and was rare in gorillas (ca. 3.0%) and chimpanzees (ca. 6.5%).

Humerus to femur ratios based on mid-shaft circumference (Figure 5) are similar, but not identical, to those based on length

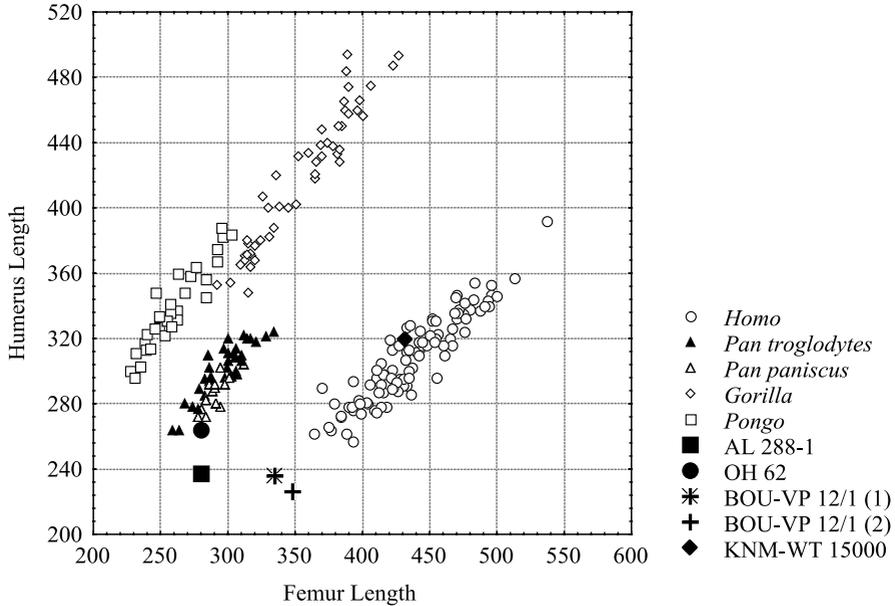


Figure 3. Bivariate plot of humerus length and femur length in extant great apes and fossil hominins. Extant genera are fairly distinct from one another in humerofemoral proportions. The humerofemoral proportions of OH 62, if correct, closely resemble those of *Pan*. AL 288-1 is intermediate between *Pan* and *Homo*, and KNM-WT 15000 and BOU-VP 12/1 most closely resemble modern humans. The two values shown for BOU-VP 12/1 represent the combination of humerus and femur length estimates (Asfaw *et al.* 1999) resulting in high and low WF indices. Size alone does not account for the differences in hominid limb proportions.

(Figure 2) in terms of their interspecific distributions. Note also that intraspecific variation in circumference proportions (Figure 5) is greater than the variation in length-based proportions (Figure 2). As with the humerofemoral length proportions, orang-utans have the largest humerofemoral circumference ratios, humans have the lowest ratios, and the African apes are intermediate (Figure 5). However, while gorillas have relatively longer humeri than chimpanzees and bonobos, they do not have relatively larger humeral circumferences. In this measure, too, OH 62 is more apelike than AL 288-1 (Figure 5). However, unlike the results based on limb length estimates, the difference in humerofemoral shaft circumference between OH 62 and AL 288-1 is easily matched in extant species (Figure 6; Table 3). This pattern holds when maximum and minimum circumferences taken

near midshaft are combined to produce extreme ranges of humerofemoral circumference indices for OH 62 (Figure 5). It is somewhat surprising that the differences between the Nariokotome skeleton and AL 288-1 are also not significant (Figure 6; Table 3). Thus, individuals with humerofemoral circumferences as different as that observed between AL 288-1 and KNM-WT 15000 could readily be drawn from any of the extant species. Even the differences between OH 62 and KNM-WT 15000 can be accommodated in 7–14% of pairwise comparisons within the great ape and human samples (Figure 6; Table 3).

The discrepancy between results in limb length proportions and limb shaft circumference proportions due to the greater intraspecific variability and interspecific overlap in circumference proportions (compare Figures 2 and 5). The greater

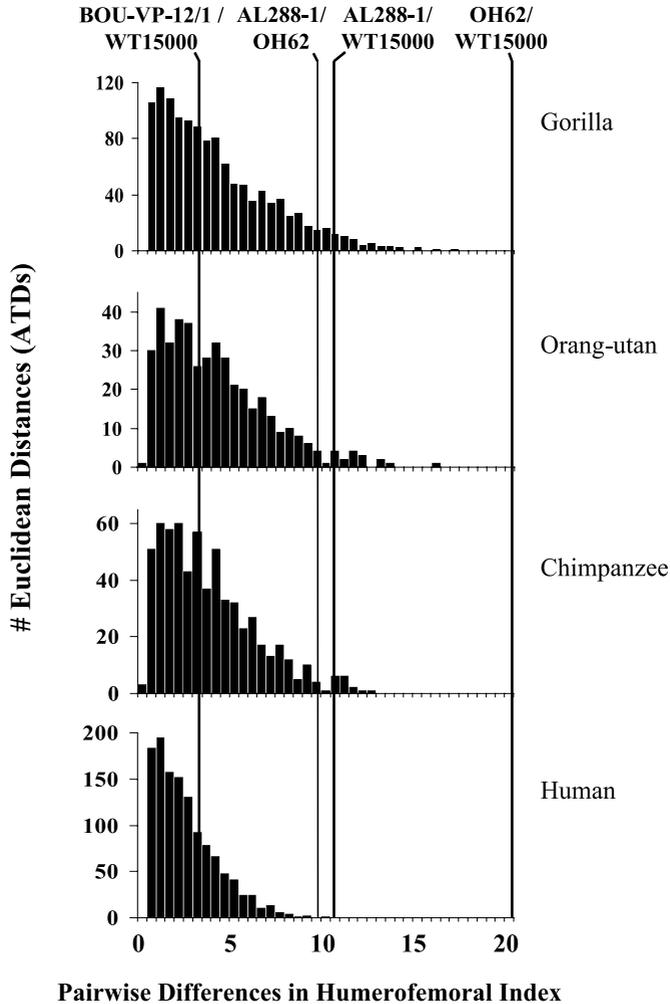


Figure 4. Differences in humerofemoral (HF) index between fossil pairs and between all possible pairs in each extant taxon. Note that difference in HF proportions between OH 62 (estimate) and KNM-WT 15000 is never observed in any extant sample, whereas the difference between BOU-VP 12/1 (estimate) and KNM-WT 15000 is comparable to intraspecific differences. The differences between AL 288-1 and OH 62 (estimate), and between AL 288-1 and KNM-WT 15000, are rare but possible in most extant samples. Given the uncertainties in the limb length estimates of OH 62, the HF index may or may not be significantly different from that of AL 288-1.

variability is undoubtedly a product of cortical modeling and remodeling sensitivity to activity that does not appear to influence length (Lanyon, 1980; Trinkaus *et al.*, 1994; Sumner & Andriacchi, 1996). Humeral and femoral cross-sectional properties also vary with length during growth as a result of the different loading demands on the upper and

lower limbs (Ruff *et al.*, 1994; Sumner & Andriacchi, 1996). Periosteal surface modeling is most sensitive to mechanical activity prior to mid-adolescence, after which the endosteal surface becomes more sensitive (Ruff *et al.*, 1994). The femur:humerus ratio of cross-sectional properties reaches adult levels after about 10 years of age (Sumner &

Table 2 Probabilities (%) of sampling pairwise differences in humerofemoral length indices

Fossil pairs	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>
AL 288-1/OH 62	0·0†	2·5*	4·6*	4·1*
AL 288-1/BOU-VP-12/1 ¹	0·0†	0·0†	0·3†	0·2†
AL 288-1/BOU-VP-12/1 ²	0·0†	0·0†	0·0†	0·0†
AL 288-1/WT 15000	0·0†	1·4*	2·9*	1·4*
OH 62/BOU-VP-12/1 ¹	0·0†	0·0†	0·0†	0·0†
OH 62/BOU-VP-12/1 ²	0·0†	0·0†	0·0†	0·0†
OH 62/WT 15000	0·0†	0·0†	0·0†	0·0†
WT 15000/BOU-VP-12/1 ¹	20·9	42·6	45·2	47·0
WT 15000/BOU-VP-12/1 ²	0·1†	3·6*	7·1	5·0

Probabilities (%) of sampling, from extant hominoid groups, differences in humerofemoral indices as great as those observed between pairs of fossils (i.e., probability that differences between fossil pairs could be drawn from extant samples). * Denotes a probability of $\leq 5\%$, and † indicates a probability of $\leq 1\%$.

¹Humerofemoral index (70) based on "anatomical grounds" estimates, preferred by *Asfaw et al. (1999)*.

²Humerofemoral index (65) based on estimates of African ape and human regression (*Asfaw et al., 1999*).

Andriacchi, 1996), suggesting that these age-related changes do not interfere with comparisons between the adult hominin skeletons and KNM-WT 15000, who was about 11–14 years old at death (*Ruff & Walker, 1993*). However, as a result of greater variability in diaphyseal dimensions, circumference proportions have far less power in discriminating species-level differences in skeletal form.

The problems of working with estimated limb lengths from associated skeletons are even more pronounced when investigating variation in length proportions within the upper limb. Depending on the method chosen to reconstruct length, or the reference sample used in a regression analysis, the limb length estimates for AL 288-1 (*Table 1*) yield brachial indices that range between values that are low for modern humans to those typical of chimpanzees (*Figure 7*). In fact, the range of estimates for AL 288-1 is greater than the ranges of actual values for each of the extant taxa (*Figure 7*). The range in estimates for OH 62 is also very wide (*Figure 7*). The relative forearm length of KNM-WT 15000 resembles that of gorillas and humans, and *Ruff & Walker (1993)*

show that the brachial index of the Nariokotome skeleton most closely resembles people from warm climates. Interestingly, if the length estimates for the Bouri skeleton are correct, then this skeleton is unique among hominins in having a relative forearm length that can only reasonably be matched in extant orang-utans (*Figure 7*). The degree of difference in brachial proportions between KNM-WT 15000 and the Bouri skeleton is never observed in any of the extant samples.

Length proportions within the lower limb can only be computed for the Nariokotome skeleton. The crural index of KNM-WT 15000 is high. It is greater than that observed in gorillas and bonobos, falls at the upper range of the human and chimpanzee samples, and best approximates the orang-utan values (*Figure 8*). However, *Ruff & Walker (1993)* point out that the elongated distal limb segments of the Nariokotome skeleton resembles those seen in modern humans from low latitudes. Apart from slightly lower values in gorillas, there is very little difference among the African apes and humans in crural indices (*Schultz, 1930*).

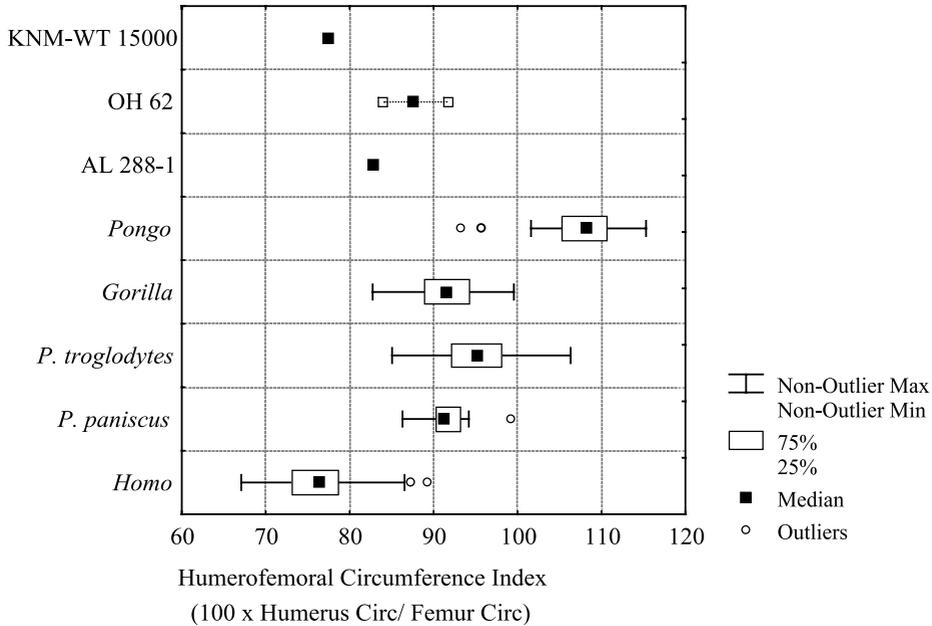


Figure 5. Box plot of humerofemoral circumference (HFC) index ($100 \times$ humerus midshaft circumference/femur midshaft circumference) in extant great apes and fossil hominins. With the exception of the relatively low HFC index of gorillas, the intertaxonomic pattern mimics the pattern in humerofemoral (length) index. Note, however, that variation is greater within taxa, and greater overlap exists between taxa. Of the fossil hominin partial skeletons, OH 62 has the highest and most apelike HF proportions, followed by lower HF proportions in AL 288-1, and KNM-WT 15000. In each box plot, the small square represents the median value, the box represents the inter-quartile range (central 50% of the data), the bars indicate the non-outlier range, and open circles denote outliers.

Discussion

Current data on associated skeletons suggest that the evolution of hominin limb proportions is far from parsimonious. Despite disagreements on hominin phylogeny, most published phylogenies (based on craniodental evidence) agree that *H. ergaster* is more closely related to modern humans than are either *A. afarensis* or *H. habilis*, and that *H. habilis* is more closely related to the *H. ergaster*–*H. sapiens* clade than is *A. afarensis* (e.g., Chamberlain & Wood, 1987; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Strait *et al.*, 1997; Wood & Collard, 1999). If these phylogenetic hypotheses are correct, then the presumably apelike humerofemoral proportions of the *Pan/Homo* common ancestor are followed by intermediate proportions in *A. afarensis*, followed by more

apelike proportions in *A. africanus* (depending on its phylogenetic position) and possibly in *H. habilis*, and finally by humanlike limb proportions in *H. ergaster* (Figure 9). Unless the Bouri skeleton samples the sister taxon of the *H. ergaster*–*H. sapiens* clade (Asfaw *et al.*, 1999), then this skeleton serves as yet another example of potential homoplasy in hominin evolution. Only if current limb length estimates are grossly in error could the differences between OH 62 and BOU-VP 12/1 be encompassed by intraspecific variation. The only phylogenetic scenario involving no humerofemoral proportion reversals is one in which *A. afarensis* is more closely related to a Bouri skeleton–*H. ergaster*–*H. sapiens* clade than it is to *A. africanus*. The position of *H. habilis* in this scenario depends on whether its limb

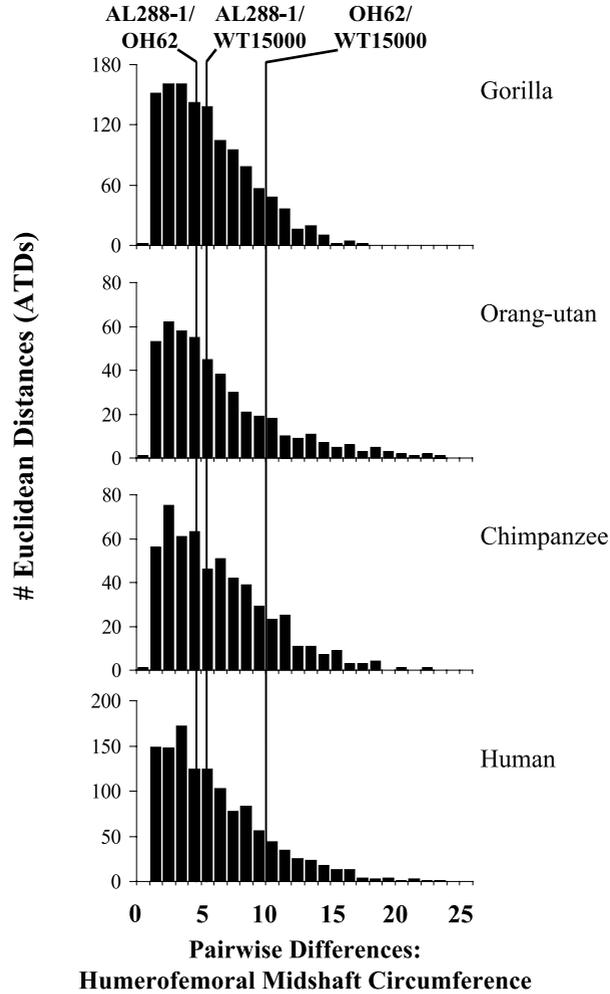


Figure 6. Differences in humerofemoral circumference (HFC) index between fossil pairs and between all possible pairs in each extant taxon. Note that, while not common, the difference in HFC proportions between OH 62 (estimate) and KNM-WT 15000 is matched in more than 5% of every extant sample. Pairs as different in HFC proportions as AL 288-1/KNM-WT 15000 and AL 288-1/OH 62 are easily found in each extant sample.

proportions more closely resemble those of *A. afarensis* or *A. africanus*. The scenario becomes even more complex when intra-limb proportions are considered because the brachial index of the Bouri skeleton does not follow the humerofemoral index in being modern humanlike, and may represent a reversal from a less extreme brachial index.

The results presented here support conclusions by [Korey \(1990\)](#) and [Eckhardt](#)

[\(2000\)](#) that it may be premature to consider that the species represented by OH 62 has substantially more apelike humerofemoral proportions than does *A. afarensis*. If limb length estimates are correct for these associated fossil skeletons, then their differences are very close to what we would accept as “significant”. When compared to the variation in our skeletally-derived mixed-population human sample, humerofemoral

Table 3 Probabilities (%) of sampling pairwise differences in humerofemoral midshaft circumference indices

Fossil pairs	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>
AL 288-1/OH 62	45.4	48.3	42.1	44.5
AL 288-1/WT 15000	38.2	41.7	34.7	37.4
OH 62/WT 15000	11.8	13.4	7.3	14.0
OH 62-A/AL 288-1	13.2	8.3	15.0	15.0
OH 62-A/WT 15000	2.4*	0.5†	2.0*	5.0*
OH 62-B/AL 288-1	87.6	87.2	89.1	87.7
OH 62-B/WT 15000	29.8	26.5	34.2	30.3

Probabilities (%) of sampling, from extant hominoid groups, differences in humerofemoral midshaft circumference indices as great as those observed between pairs of fossils (i.e., probability that differences between fossil pairs could be drawn from extant samples). Circumference values for OH 62 are taken from Hartwig-Scherer & Martin (1991). The largest and smallest circumference values at "midshaft" and 1 cm and 2 cm above and below "midshaft" were used to construct maximum (OH 62-A; most apelike) and minimum (OH 62-B; most humanlike) humerofemoral circumference indices. Only in the contrast between OH 62-A and KNM-WT 15000 is the difference so great that there is less than a 5% probability of being randomly drawn from an extant great ape or human sample. * Denotes a probability of $\leq 5\%$, and † indicates a probability of $\leq 1\%$.

differences between OH 62 and AL 288-1 are highly unusual (Figure 4; Table 2). This result contrasts with Eckhardt's (2000) conclusion that the difference between OH 62 and AL 288-1 is most likely less than the variation within a single modern human sample. Therefore, if estimates are correct for the humeri and femora of OH 62 and AL 288-1, then there is a low probability that these individuals could be drawn from the same species. However, very small alterations (mm or less) in limb length estimates result in profoundly different interpretations. Korey (1990) has shown that the degree of error involved in these length estimates substantially exceeds that needed to conclude that OH 62 has a humerofemoral index that is no more apelike than that of AL 288-1. Our results based on measurements of humerofemoral circumference, although far more conservative, support the notion that AL 288-1 and OH 62 may not be significantly different in humerofemoral proportions. Therefore, with the evidence currently at hand, it is premature to conclude that AL 288-1 and OH 62 have significantly different limb proportions (Figure

9). Additional remains of *A. afarensis* and *H. habilis* are needed to gain a better assessment about intraspecific variation in these taxa and to test the hypothesis that *H. habilis* had relatively apelike limb proportions.

It has been suggested that another partial skeleton, KNM-ER 3735, may be attributable to *H. habilis* (Leakey *et al.*, 1989). It is unfortunately too fragmentary to estimate limb lengths with confidence. However, Leakey *et al.* (1989) compared the sizes of the upper and lower limb elements (e.g., joint surfaces) of KNM-ER 3735 with those of AL 288-1 and *H. sapiens* and *P. troglodytes*. In this comparison, the lower limb elements of KNM-ER 3735 were only slightly larger than those of AL 288-1, but the upper limb elements of KNM-ER 3735 were much larger than those of AL 288-1. In other words, KNM-ER 3735 exhibits a higher ratio of upper to lower limb element sizes than that of AL 288-1 and therefore appears more like chimpanzees in this respect (Leakey *et al.*, 1989). Further research is needed to determine how much more apelike this skeleton is compared to AL 288-1, and thus to assess precisely how

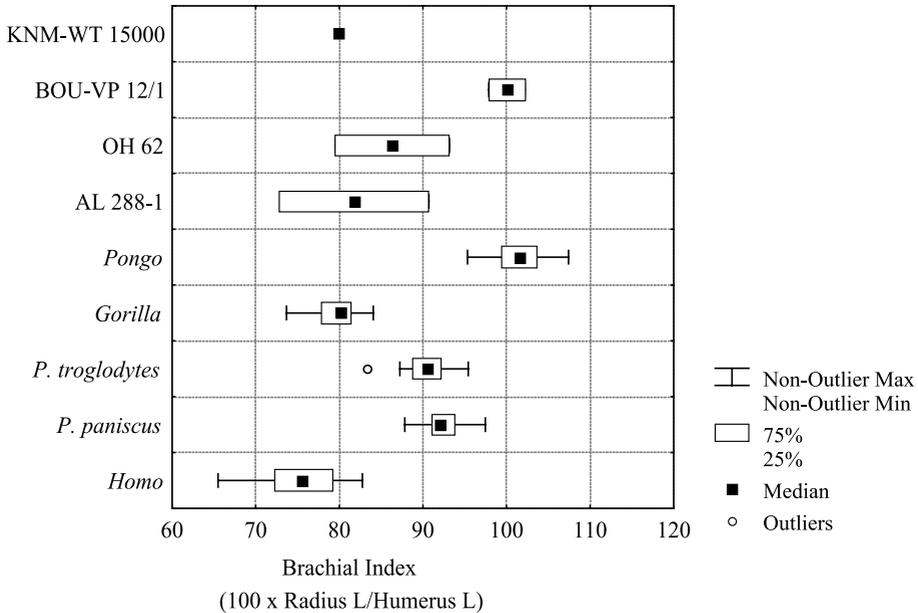


Figure 7. Box plot of brachial index ($100 \times \text{radius length/humerus length}$) in extant great apes and fossil hominins. Of the fossil hominin partial skeletons, BOU-VP-12/1 has the highest brachial proportions, followed by a lower index in the other three partial skeletons. The range of values for BOU-VP-12/1 results from the lowest and highest estimates of humerus lengths (see Table 1) provided by Asfaw *et al.* (1999). Both, including the lower brachial index obtained from their preferred “anatomical grounds” estimates, exceed brachial proportions typical of *Pan* and resembles *Pongo*. In each box plot, the small square represents the median value, the box represents the interquartile range (central 50% of the data), the bars indicate the nonoutlier range, and open circles denote outliers.

KNM-ER 3735 affects the claim that *H. habilis* had significantly more apelike limb proportions than *A. afarensis*.

Lovejoy (1993) raises the possibility that the AL 333-109 humerus and AL 333-3 femur fragments might belong to the same individual. If so, it would provide a second individual to compare with AL 288-1 and allow researchers to gain a better idea of the humerofemoral proportions typical of *A. afarensis*. Aside from deriving from the same fossil-rich locality, there is no clear evidence that AL 333-109 and AL 333-3 belong to the same individual (Lovejoy *et al.*, 1982a,b). These two specimens are unfortunately much more fragmentary than the humeri and femora of OH 62 and AL 288-1, making length estimates of both bones even less reliable. At present, then, these AL 333 fossils do not offer sound evidence regarding

limb length proportions. Lovejoy (1993) also makes the provocative argument (not contingent on the AL 333 fossils representing one individual) that AL 288-1's intermediate humerofemoral index is more humanlike than it appears due to negative allometry in human humerofemoral proportions (i.e., a relatively high humerofemoral index might be expected for smaller humans). This suggestion was tentatively supported by the appearance of slight negative allometry in the humerofemoral index of a large sample of Caucasian males. However, the significance (i.e., whether the line differs significantly from isometry) of the relation was not reported and, unfortunately, AL 288-1 is so much smaller than the human sample that a great deal of extrapolation was necessary. Furthermore, it would be appropriate to include females in a

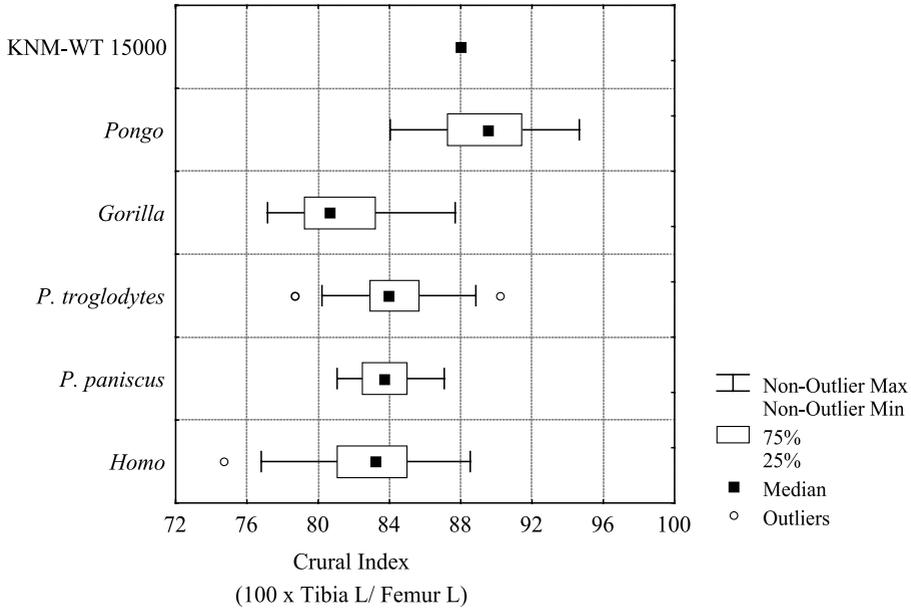


Figure 8. Box plot of crural index ($100 \times$ tibia length/femur length) in extant hominoids and KNM-WT 15000. The crural index of KNM-WT 15000 is at the upper range of the modern humans sampled here, and overlaps with *Pan* and *Pongo*. However, the high crural proportions in KNM-WT 15000 may be influenced by climatic adaptations and possibly pathology. Note the overall similarity in extant hominoid crural proportions compared to humerofemoral and brachial proportions. In each box plot, the small square represents the median value, the box represents the interquartile range (central 50% of the data), the bars indicate the nonoutlier range, and open circles denote outliers.

regression analysis given the likelihood that AL 288-1's gender was female (Johanson *et al.*, 1982; Wood & Quinney, 1996; Tague & Lovejoy, 1998). Jungers (1982) found nearly isometric relations for femur and humerus lengths relative to body mass in a limited sample that included small- and large-bodied humans. The conclusion that Lucy's femur is relatively short holds when compared to a greater sample of pygmy humans of comparable body mass (Jungers, 1991).

The associated skeletons AL 288-1 and OH 62 are unfortunately too fragmentary to make reliable length estimates for the radius (Asfaw *et al.*, 1999), thus rendering any estimates of the brachial indices equally unreliable for these fossils. However, even with the most generous radius length estimates, no one has proposed that the brachial

indices of these skeletons would have exceeded those of African apes (Figure 7). On the other hand, if the radius length estimates are correct for the Bouri skeleton, this individual has a brachial index substantially higher than any proposed for AL 288-1 and OH 62. The long ulna Omo L40-19, dated to ca. 2.3 Ma (Feibel *et al.*, 1989), may be further evidence of a hominin with either high brachial proportions, or large body mass, around this time (Aiello *et al.*, 1999). If their chronological sequence reflects a simple ancestor-descendant relationship, this would suggest a reversal in brachial proportions in the Bouri skeleton (more apelike) from the *A. afarensis* condition, followed by a second reversal in *H. ergaster* (more humanlike). As noted in the original description (Asfaw *et al.*, 1999), the Bouri skeleton is especially intriguing

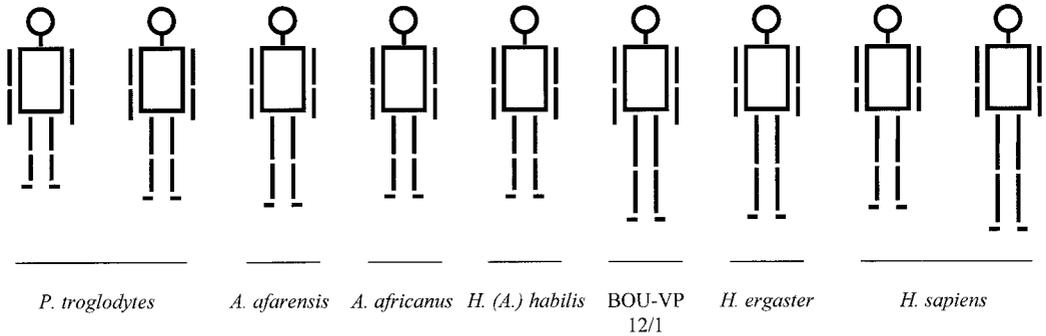


Figure 9. Schematic diagram of limb proportions in extant taxa (*P. troglodytes*, far left; *H. sapiens*, far right) and fossil taxa. Two schematic individuals, representing extremes in air sample, are shown for each extant taxon. Each fossil taxon (and Bouri) is represented by an individual skeleton (it remains to be determined whether or not these specimens are truly representative of their respective taxa): *A. afarensis* (AL 288-1), *H. (A.) habilis* (OH 62), Bouri (BOU-VP 12/1), and *H. ergaster* (KNM-WT 15000). Data on associated limbs are not currently available for *A. africanus*; in light of studies by [McHenry & Berger \(1998a,b\)](#), *A. africanus* is provisionally given limb proportions equivalent to those of *H. (A.) habilis*. Since humerus length, relative to body mass, does not differ among African apes and humans ([Jungers, 1994](#)), the schematic representations were given equal humerus lengths. Intermembral and brachial proportions are shown relative to this standardized humerus length. African apes and humans also show little interspecific differences in crural proportions ([Aiello & Dean, 1990](#)), so all schematics were given equivalent crural indices, with the exception of *H. ergaster*, for which crural proportions are known. Trunks and heads are shown for illustrative purposes only and are not drawn to scale. Lines are shown in grey where little or no direct evidence is available.

because, if present length estimates are correct, the skeleton uniquely combines humanlike humerofemoral and apelike (*Pongo*-like) brachial proportions, demonstrating that intra- and interlimb proportions can be dissociated, and in fossil forms can assume combinations not seen in extant hominids ([Wood & Richmond, 2000](#)).

Determining whether limb proportions are significantly different between hominin species is of obvious importance to our understanding of the evolutionary history of hominin skeletal design. It also influences our interpretations of locomotor adaptations within the hominin clade. To those who view australopiths as partly arboreal, evidence of a higher humerofemoral index in *H. habilis* would suggest that this taxon was even more committed than *A. afarensis* to arboreal postures and behaviors. Researchers that reconstruct early hominin locomotion without a significant arboreal component generally argue that primitively-retained arboreal characteristics are not

informative, and instead base locomotor reconstruction on derived morphology ([Latimer & Lovejoy, 1990](#)). [Latimer \(1991\)](#) has offered the most explicit rationale. He argued that, because derived, functionally relevant features are the product of natural selection, they provide unambiguous evidence for functional behavior (see also [Ward et al., 1997](#)). Few would disagree with this statement. Within this framework, evidence that *H. habilis* had more apelike limb proportions than that seen in *A. afarensis* would provide what most researchers would consider as unambiguous evidence of arboreal behavior in the former because the derived limb proportions of *H. habilis* would be thought to be the product of natural selection. This would be consistent with primitive arboreal features retained in the skeleton of *H. habilis* ([Susman & Stern, 1982](#)). The relatively larger upper limbs of *A. africanus* compared to those of *A. afarensis* ([McHenry & Berger, 1998a](#)) suggest that larger upper limbs are derived. Therefore,

regardless of one's philosophy on the importance of primitive retentions in reconstructing function, relatively (compared to *A. afarensis*) large upper limbs in *A. africanus* (or *H. habilis*) provide strong evidence that arboreal positional behaviors were important components of the positional repertoire.

The approach of interpreting behavior from derived morphology is, however, dependent upon a reliable phylogeny because it is necessary to determine—for every functional trait—whether the features are derived or primitive. For example, the relatively apelike limb size proportions of *A. africanus* would not be considered secondarily derived in alternative phylogenetic scenarios, including one in which *A. africanus* did not evolve from an *A. afarensis*-like ancestor, or if *A. africanus* retains the primitive condition from which *A. afarensis* is derived. Only in these phylogenetic scenarios would the relatively apelike limb size proportions of *A. africanus* be considered primitive and thus ambiguous to some in their relevance to functional reconstructions. The approach of using only derived traits to interpret function is only as reliable as the phylogeny upon which it is based.

The limb proportions of *H. habilis* also bear on the issue of its taxonomy. No matter whether this taxon had limb proportions like that of *A. afarensis*, or was more apelike, *H. habilis* differed from later members of the genus *Homo* in this fundamental measure of skeletal design. Furthermore, if the Bouri skeleton represents an ancestor of *Homo*, then OH 62 either represents a reversal to a more apelike skeletal design, or OH 62 is not as closely related to later *Homo* as is the older Bouri material. If *H. habilis* is a sister taxon to a clade comprising Bouri and later *Homo*, and Bouri postcrania belong to *A. garhi*, then *Homo* would be paraphyletic. The primitive nature of the OH 62 limb proportions, and the large upper:lower limb sizes of KNM-ER 3735, support the hypothesis that *H. habilis* was more similar

to the australopiths in limb design than to the derived skeletal proportions and committed bipedal locomotor pattern of later *Homo* (i.e., members of the *H. ergaster*–*H. sapiens* clade) (Wood & Collard, 1999; McHenry & Coffing, 2000).

Conclusion

In comparison with intraspecific variation in extant great apes and humans, the humanlike humerofemoral indices of KNM-WT 15000 and the Bouri skeleton (BOU-VP-12/1) are significantly different from both OH 62 and AL 288-1, but not from one another. Differences in humerofemoral indices as great as that between AL 288-1 and OH 62 are almost never observed in humans, and are rare in extant great apes. Differences in humerofemoral midshaft circumferences between the two fossils are commonly matched within extant species. However, intraspecific variation in midshaft dimensions is very high, and therefore very conservative. In all but one fossil pair contrast (KNM-WT 15000 *vs.* most apelike estimate of OH 62), the degree of differences in humerofemoral circumference index are fairly commonly observed within extant species.

Estimates of the brachial indices of AL 288-1 and OH 62 are too variable to contribute much to our understanding of hominin limb evolution. The brachial index of KNM-WT 15000 resembles those of modern humans and gorillas, while that of BOU-VP-12/1 (if estimates are correct) is comparable to the high brachial index of modern orang-utans. The difference in brachial index between these skeletons is never observed in the extant samples. The extremely long forearm of the Bouri skeleton greatly exceeds estimates for AL 288-1 and appears to be derived relative to a more African apelike forearm.

Very small changes in estimated limb lengths (e.g., the 2 mm difference in lengths

of the AL 288-1m humerus estimated by Jungers, 1982, and Johanson *et al.*, 1982) make the difference in humerofemoral index between AL 288-1 and OH 62 insignificant compared to the variation within extant great apes and humans. The error associated with estimating the length of the OH 62 humerus alone (Korey, 1990) is much greater than that needed to make the differences between these fossils insignificant. Therefore, given current evidence, it is premature to consider OH 62's humerofemoral length proportions as significantly different, or more apelike, than that of AL 288-1.

If the upper:lower limb joint size comparisons of fossils attributed to *H. habilis* (Leakey *et al.*, 1989) and *A. africanus* (McHenry & Berger, 1998a) prove to be significantly more apelike than those of *A. afarensis*, it would indicate a reversal (in most phylogenetic models) in the evolution of limb joint size. Having derived traits functionally related to arboreal locomotion would lend strong support to the hypotheses that *A. africanus* and *H. habilis* practiced arboreal positional behaviors in conjunction with bipedalism. The primitive limb length, circumference, and joint size proportions of *H. habilis* (OH 62 and KNM-ER 3735) support the hypothesis that this taxon is more similar in body design to the australopithecines than to later members of the genus *Homo* (and to the older Bouri skeleton), which may be relevant to decisions over whether or not *H. habilis* belongs in the genus *Homo* (Wood & Collard, 1999).

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