

# Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus*

David J. Green<sup>a,b,\*</sup>, Adam D. Gordon<sup>a</sup>, Brian G. Richmond<sup>a</sup>

<sup>a</sup> Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, 2110 G St. NW, Washington, DC 20052, USA

<sup>b</sup> Hominid Paleobiology Doctoral Program, Department of Anthropology, The George Washington University, 2110 G St. NW, Washington, DC 20052, USA

Received 17 November 2005; accepted 4 September 2006

## Abstract

Previous analyses have suggested that *Australopithecus africanus* possessed more apelike limb proportions than *Australopithecus afarensis*. However, due to the errors involved in estimating limb length and body size, support for this conclusion has been limited. In this study, we use a new Monte Carlo method to (1) test the hypothesis that *A. africanus* had greater upper:lower limb-size proportions than *A. afarensis* and (2) assess the statistical significance of interspecific differences among these taxa, extant apes, and humans. Our Monte Carlo method imposes sampling constraints that reduce extant ape and human postcranial measurements to sample sizes comparable to the fossil samples. Next, composite ratios of fore- and hindlimb geometric means are calculated for resampled measurements from the fossils and comparative taxa. Mean composite ratios are statistically indistinguishable ( $\alpha = 0.05$ ) from the actual ratios of extant individuals, indicating that this method conserves each sample's central tendency. When applied to the fossil samples, upper:lower limb-size proportions in *A. afarensis* are similar to those of humans ( $p = 0.878$ ) and are significantly different from all great ape proportions ( $p \leq 0.034$ ), while *Australopithecus africanus* is more similar to the apes ( $p \geq 0.180$ ) and significantly different from humans and *A. afarensis* ( $p \leq 0.031$ ). These results strongly support the hypothesis that *A. africanus* possessed more apelike limb-size proportions than *A. afarensis*, suggesting that *A. africanus* either evolved from a more postcranially primitive ancestor than *A. afarensis* or that the more apelike limb-size proportions of *A. africanus* were secondarily derived from an *A. afarensis*-like ancestor. Among the extant taxa, limb-size proportions correspond with observed levels of forelimb- and hindlimb-dominated positional behaviors. In conjunction with detailed anatomical features linked to arboreality, these results suggest that arboreal posture and locomotion may have been more important components of the *A. africanus* behavioral repertoire relative to that of *A. afarensis*.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** Limb proportions; Postcrania; *Australopithecus*; Locomotion; Hominin evolution; Paleoanthropology

## Introduction

Previous studies of *Australopithecus afarensis* and *Australopithecus africanus* have suggested that *A. afarensis* possessed primitive craniodental characteristics and relatively modern

human-like limb proportions, whereas *A. africanus* combined derived craniodental anatomy with apelike limb proportions (McHenry and Berger, 1998a,b). This may represent one of several examples of a mosaic pattern in the evolution of hominin body proportions, including the possibility of homoplasy and/or convergent evolution (McHenry and Berger, 1998a; Wood and Collard, 1999; Wood and Richmond, 2000; Richmond et al., 2002). Richmond et al. (2002) and Dobson (2005) noted several potential examples: (1) the possibility that *Homo habilis* had relatively apelike humerofemoral length proportions compared to the earlier and generally more

\* Corresponding author. Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, 2110 G St. NW, Washington, DC 20052, USA. Tel.: +1 202 994 7475; fax: +1 202 994 6097.

E-mail address: [djgreen@gwu.edu](mailto:djgreen@gwu.edu) (D.J. Green).

primitive *A. afarensis* (Hartwig-Scherer and Martin, 1991; see also Johanson et al., 1987); (2) the unusually long forearms of the Bouri skeleton, BOU-VP 12/1 (Richmond et al., 2002), if published length estimates are correct (Asfaw et al., 1999, but see Reno et al., 2005a); and (3) relatively apelike upper:lower limb-size proportions in *A. africanus* (and possibly *H. habilis*) compared to *A. afarensis* (McHenry and Berger, 1998a,b).

Each of these suggested instances of homoplasy and/or convergent evolution in hominin body proportions have been challenged. The proposal that *H. habilis* had relatively apelike humerofemoral length proportions has been weakened on several grounds. First, Korey (1990) and Richmond et al. (2002) noted that the error involved in estimating fragmentary fossil limb lengths makes the current evidence too weak to support the claim that *H. habilis* had more apelike humerofemoral length proportions than *A. afarensis* (see also Reno et al., 2005a, and accompanying comments). Second, Richmond et al. (2002) and Haeusler and McHenry (2004) found that the differences between OH 62 and A.L. 288-1 in humerofemoral length and shaft proportions were not excessive compared to variation observed within ape species and modern humans (especially when the errors involved in estimating fossil limb lengths were taken into account), providing little support for the contention that *H. habilis* limb proportions were more apelike than those of *A. afarensis*. Third, the length estimates of the OH 62 femur are based on comparisons that use an *A. afarensis* femur (A.L. 288-1) as a model. Haeusler and McHenry (2004) challenged the appropriateness of the model because A.L. 288-1 and OH 62 represent different species. Furthermore, the A.L. 288-1 femur is known to be relatively short in comparison to femora of later *Homo* (Jungers, 1982), such that its use could bias estimates of the OH 62 femur towards a short length.

Haeusler and McHenry (2004) suggested that OH 34 is a better analog and used it to reconstruct a longer femur length for OH 62. However, there are several reasons to question whether OH 34 is an appropriate model. Like A.L. 288-1, OH 34 cannot be confidently attributed to the same species as OH 62. Specimen OH 34 comes from sediments dated to 1.15–0.8 million years ago (Ma) and could belong to *H. erectus* or *Paranthropus boisei*, whereas OH 62 (1.8 Ma) is attributed to *H. habilis* (Day and Molleson, 1976; Johanson et al., 1987; Haeusler and McHenry, 2004). Second, OH 34 is incomplete, so its length must first be estimated before it can be used to reconstruct the length of OH 62, further compounding estimation errors (Hartwig-Scherer, 1996; Smith, 1996a,b). Third, OH 34 shows evidence of taphonomic alteration by subaerial or other modes of weathering and erosion, probably after its fossilization, which likely contributed to its unusual gracility relative to contemporaneous hominin femora (Day and Molleson, 1976; Ruff, 1995; DJG and BGR, pers. obs.). As such, the facts that OH 34 is taphonomically altered, incomplete, and possibly from a different species suggest that it may not provide a reliable estimate of OH 62's femoral length. Thus far, no study has been able to compare the limb-length proportions of OH 62 and *H. habilis* with satisfactory precision (Korey, 1990; Richmond et al., 2002;

Collard and Lycett, 2005; Pearson and Peterson, 2005; Reno et al., 2005a). Therefore, the question of whether *H. habilis* had relatively apelike or humanlike limb-length proportions remains unanswered.

The second potential instance of homoplasy in the early hominin record involves the unusually long forearm lengths reconstructed for the Bouri skeleton (Asfaw et al., 1999). Richmond et al. (2002) noted that, given the published limb-length estimates (Asfaw et al., 1999), the Bouri skeleton would have had a brachial index (forearm length:humerus length) greater than those of African apes. Recently, Reno et al. (2005a) argued that the error surrounding the regression estimates of the radial and humeral lengths is too great to generate reliable brachial indices for BOU-VP 12/1. Instead, they used qualitative anatomical estimates and parsimony to conclude that the Bouri skeleton retained primitive, chimpanzee-like brachial proportions. Thus, the Bouri skeleton may serve as an example of mosaic evolution in limb proportions, combining a primitively long forearm with a derived, elongated femur (Asfaw et al., 1999). However, the errors involved in estimating the limb lengths of BOU-VP 12/1 (Collard and Lycett, 2005; Reno et al., 2005a) and A.L. 288-1 (Richmond et al., 2002; Reno et al., 2005a) preclude accurate characterizations of the brachial indices for either fossil.

As Dobson (2005) noted, this leaves *A. africanus* as potentially the only remaining published example of secondarily derived limb proportions. To test the hypothesis that *A. africanus* had more apelike limb-joint proportions than the earlier and craniodentally more primitive *A. afarensis*, McHenry and Berger (1998a) analyzed joint-size proportions in the two fossil taxa. Although McHenry and Berger (1998b) discussed differences in limb-length proportions, the focus of their analyses was on upper:lower limb-joint-size proportions. As with overall limb lengths, relatively large hindlimb joints in humans are an adaptation to bipedalism, while the opposite is true for climbing apes (e.g., *Pongo pygmaeus*), which have relatively large forelimb joints. Limb-size proportions, including articular joint surfaces, are not necessarily proxies of limb-length proportions. However, the relative sizes of the joints and shafts of the upper and lower limbs reflect functional demands and are a reliable indicator of the type and magnitude of loads transmitted through a limb during locomotion (Jungers, 1988; Godfrey et al., 1995; Currey, 2002).

McHenry and Berger (1998a) performed three analyses in their study. They first compared associated skeletons and found that Stw 431 (*A. africanus*) had larger upper:lower limb-joint proportions than did A.L. 288-1 (*A. afarensis*). More recently, Dobson (2005) used a resampling approach to show that some, but not all, of the differences between these two specimens were statistically significant. He showed that Stw 431 has a significantly smaller lumbosacral joint relative to the elbow, but that comparisons of the elbow and hip (acetabulum) were not statistically significant. Based on the limited number of limb-joint elements preserved, Dobson's (2005) reappraisal of the first of McHenry and Berger's (1998a) three analyses determined that the limb proportions of these two skeletons did not differ significantly.

In their second analysis, McHenry and Berger (1998a) sorted the upper- and lower-limb fossils of *A. afarensis* and *A. africanus* into size categories, and found *A. africanus* to have more small hindlimb elements. This methodology had the advantage of including more fossils, such as distorted or fragmentary fossils from which useful measurements were not available, but had the disadvantage of being qualitative and thus prone to interobserver error (Reno et al., 2005a).

In their third and final analysis, McHenry and Berger (1998a) estimated body mass from each upper and lower limb-joint measurement, using regression equations derived from both African apes and modern humans. They found that, when using the human regression, the joint measurements from the upper and lower limbs of *A. afarensis* produced similar body-mass estimates, whereas the joint measurements from the upper limb of *A. africanus* produced higher estimates than did those from the lower limb. This suggested that limb-joint-size proportions of *A. afarensis* were more modern-human-like, whereas those of *A. africanus* were more apelike. While this was a clever way to derive a common size measure from different anatomical regions, the analysis did not include an evaluation of the statistical significance of the results.

Given the importance of relative limb size in *A. africanus* for the discussion of the evolution of hominin body proportions, we build on McHenry and Berger's (1998a) analysis by using a newly developed resampling approach to evaluate the statistical significance of the differences in limb proportions between *A. afarensis*, *A. africanus*, great apes, and modern humans.

## Materials and methods

### Sample

Forelimb:hindlimb ratios of limb size were calculated for fossil samples of *A. afarensis*, *A. africanus*, and a comparative sample drawn from mixed-sex adult skeletal collections of *Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus* from the American Museum of Natural History (AMNH), the Cleveland Museum of Natural History (CMNH), and the National Museum of Natural History (NMNH) (Table 1).

Measurements included in this study were restricted to long-bone articular surfaces and cross-sectional dimensions of long-bone shafts. Because these types of measurements have been shown to be reliable indicators of the type and

magnitude of loads transmitted through a limb during locomotion (Jungers, 1988; Godfrey et al., 1995; Currey, 2002), forelimb and hindlimb sizes derived from these measurements should preserve a functional signal related to locomotion, although perhaps a different signal from that preserved by limb lengths.

Measurements were included if at least two different specimens preserving that element were available for both *A. afarensis* and *A. africanus*, as identified in McHenry (1992) and McHenry and Berger (1998a). A secondary analysis included all long-bone elements that are preserved in A.L. 288-1. On the basis of these criteria, three measurements were used for the forelimb: humeral head (HUMHEAD), distal humerus (ELBOW), and transverse radial head (RADTV). For the hindlimb, five measurements were used: femoral head (FEMHEAD), subtrochanteric femoral shaft (FEMSHAFT), distal femur (DISTFEM), proximal tibia (PROXTIB), and distal tibia (DISTTIB). All but one of these measurements are measures of joint size; the remaining one is subtrochanteric femoral shaft size (the results do not change when this measurement is removed; see below). Descriptions of these measurements, which follow the guidelines in McHenry and Corruccini (1978), McHenry (1992), and McHenry and Berger (1998a), are given below:

1. HUMHEAD is the maximum anteroposterior (AP) diameter of the humeral head taken perpendicular to the shaft axis.
2. ELBOW is the product of capitular height and articular width of the distal humerus. Capitular height was taken from the anteroproximal border of capitulum to the distoposterior border along the midline. Articular width was taken across the anterior aspect of the articular surface from the lateral border of the capitulum to the medial edge of the articular surface.
3. RADTV is the mediolateral (ML) diameter of the radial head.
4. FEMHEAD is the maximum superoinferior (SI) diameter of the femoral head.
5. FEMSHAFT is the product of the AP and transverse diameters of the femoral shaft, taken just inferior to the lesser trochanter.
6. DISTFEM is the product of the biepicondylar and shaft AP diameters of the distal femur.
7. PROXTIB is the product of the AP and transverse diameters of the proximal tibia. The AP diameter was taken with

Table 1  
Sample sizes for each variable

Species	HUMHEAD <sup>2</sup>	ELBOW	RADTV <sup>2</sup>	FEMHEAD <sup>2</sup>	FEMSHAFT	DISTFEM	PROXTIB	DISTTIB
<i>A. afarensis</i>	2	3	2	2	6	3	5	4
<i>A. africanus</i>	3	1	2	9	2	2	1	3
<i>H. sapiens</i>	50	50	50	50	50	50	50	50
<i>G. gorilla</i>	64	64	64	64	64	64	64	64
<i>P. troglodytes</i>	60	60	60	60	60	60	60	60
<i>P. pygmaeus</i>	30	30	30	30	30	30	30	30

Measurements included in this table are the long-bone measurements for which there is at least one representative specimen in the fossil samples of both *A. afarensis* and *A. africanus*. Specimen A.L. 288-1 has values for each measurement except DISTFEM.

one jaw of the calipers on the line connecting the posterior surfaces of the medial and lateral condyles and the other jaw on the most distant point on the medial condyle. Transverse diameter was the distance between the most lateral point on the lateral condyle to the most medial point on the medial condyle (perpendicular to the AP diameter).

8. DISTTIB is the product of the AP and transverse diameters of the distal tibia. The AP diameter is the distance between the most anterior and posterior points of the talar facet in the AP plane. Transverse diameter is the distance between the midline of the medial malleolus and the midline of the most medial point of the talar facet before the fibular facet begins.

While the primary analysis in this study used only those measurements for which two or more specimens were available for each fossil species (measurements 1, 3–6, and 8), a second analysis utilized all but one measurement (DISTFEM) for a comparison of A.L. 288-1 and the extant samples (Tables 1 and 2).

To ensure that measurements taken on the extant materials were collected in the same manner as was described in previous publications (McHenry, 1992; McHenry and Berger, 1998a), they were first replicated on a high-quality cast of A.L. 288-1 housed at NMNH. However, only published fossil measurements were used for the analyses in the present study (McHenry, 1992; McHenry and Berger, 1998a; Table 1).

#### Measuring relative limb-size proportions

For complete specimens, the overall sizes of the upper and lower limbs were calculated as geometric means (GM) of all of the measurements drawn from a particular limb. The GM has been shown to be effective in combining multiple

measurements into a single measure of size (Mosimann, 1970; Jungers et al., 1995). In this study, HUMHEAD, RADTV, and FEMHEAD are linear measurements, while the others are areal measurements. Because measurements must be of the same dimensionality to calculate the GM (i.e., all linear measurements or all areal measurements), the linear measurements were squared. For the primary analyses, forelimb and hindlimb geometric means (FLGM and HLG, respectively) were calculated as follows:

$$\text{FLGM} = [\text{HUMHEAD}^2 * \text{RADTV}^2]^{1/2} \quad (\text{Equation 1})$$

$$\text{HLGM} = [\text{FEMHEAD}^2 * \text{FEMSHAFT} * \text{DISTFEM} * \text{DISTTIB}]^{1/4} \quad (\text{Equation 2})$$

After FLGM and HLG were calculated, the ratio of forelimb to hindlimb size was calculated as a measure of relative size proportions between the two limbs as follows:

$$\text{Relative limb-size index (RLSI)} = \ln[\text{FLGM}/\text{HLGM}] \quad (\text{Equation 3})$$

Smith (1999) noted that distributions built from ratios of two positive values can be problematic in that they are bounded by zero on the low end and are unbounded at the high end; as such, the distributions cannot be symmetrical and thus cannot be normal. In the same study, Smith (1999) also showed that log-transforming the ratios—as has been done in this study—removes this constraint because ratios greater than one become positive, ratios less than one become negative, and therefore the logged-ratio values are unbounded at both the high and low ends. Additionally, our study used a randomization procedure for significance testing (see below); randomization methods of this sort

Table 2  
Fossil specimens included in the analysis

	HUMHEAD <sup>2</sup>	RADTV <sup>2</sup>	FEMHEAD <sup>2</sup>	FEMSHAFT	DISTFEM	DISTTIB
<i>A. afarensis</i>	A.L. 288-1r A.L. 333-107	A.L. 288-1p A.L. 333x-14	A.L. 288-1ap A.L. 333-3	A.L. 128-1 A.L. 211-1 A.L. 288-1ap A.L. 333-3 A.L. 333-95 A.L. 333w-40	A.L. 129-1a A.L. 333-4 A.L. 333w-56	A.L. 288-1ar A.L. 333-6 A.L. 333-7 A.L. 333-96
<i>A. africanus</i>	Sts 7 Stw 328 Stw 517	Stw 431 Stw 516	Sts 14 Stw 25 Stw 99 Stw 311 Stw 392 Stw 431* Stw 501 Stw 522 Stw 527	Sts 14 Stw 99	Sts 34 TM 1513	Stw 358 Stw 389 Stw 515

Fossil measurements were taken from McHenry (1992) and McHenry and Berger (1998a). Specimen A.L. 288-1m (ELBOW) and A.L. 288-1aq (PROXTIB) were also included in an additional analysis.

\*McHenry and Berger (1998a) noted that, while the only hindlimb element preserved in Stw 431 is a fragmentary pelvis, they were able to reconstruct femoral head size from the mostly intact acetabulum.

are useful because they do not make any assumptions regarding the distribution of data (Manly, 1997). In this study, we used the natural logarithm of forelimb:hindlimb ratios so that the magnitude of the difference between two ratios would be independent of whether FLGM or HGLM was in the numerator (Smith, 1999). Additionally, equal differences between log-transformed ratios are the same as equal proportional differences of the raw ratios (e.g.,  $\ln[2] - \ln[1] = \ln[1] - \ln[0.5]$ , just as  $2/1 = 1/0.5$ ); this allows comparison of proportional differences across the full range of observed logged ratios.

However, since the geometric means of forelimb and hindlimb measurements do not include the same number and type of measurements, the value of a single measure of RLSI is not easily interpreted. For example, although a positive value for a logged ratio (and thus a value greater than 1 for an unlogged ratio) indicates a larger number in the numerator than in the denominator, the implications of this relationship for relative limb size are unclear when the numerator and denominator are FLGM and HGLM.

More specifically, RLSI does not convey the same information that a ratio of lengths would because an individual RLSI value cannot be used to determine whether the forelimb is bigger than the hindlimb. However, when two RLSI values are compared for specimens A and B, if specimen A has the larger RLSI value, it has a larger forelimb *relative* to its hindlimb than specimen B does. In this manner, RLSI is a relative measure of limb size that can be used to determine whether specimens, or groups of specimens, differ in the size of their forelimbs relative to their hindlimbs. By comparing mean RLSI values among species, one can identify whether differences in these logged ratios are associated with differences in locomotor pattern among extant hominoids.

#### Pairwise taxon comparisons

It was not possible to calculate geometric means for the incomplete fossil specimens in the manner described above because of the lack of associated skeletons. However, it can be mathematically demonstrated that the arithmetic mean of RLSI values for a sample can be calculated by replacing individual measurements in Equations 1 and 2 with the geometric mean of each variable (Appendix). This equality can be written as follows:

$$\overline{\text{RLSI}} = \ln \left( \frac{[\text{GM}(\text{HUMHEAD}^2) * \text{GM}(\text{RADTV}^2)]^{\frac{1}{2}}}{[\text{GM}(\text{FEMHEAD}^2) * \text{GM}(\text{FEMSHAFT}) * \text{GM}(\text{DISTFEM}) * \text{GM}(\text{DISTTIB})]^{\frac{1}{4}}} \right) \quad (\text{Equation 4})$$

Note that geometric means are calculated independently for each variable, so that one need not know which specimen is associated with each measurement. An approach using a Monte Carlo method that takes advantage of this relationship was developed to calculate mean RLSI in order to allow comparison between fossil samples with missing data and extant samples.

For each comparative and fossil species, an iterative resampling procedure was repeated 5000 times (Fig. 1). First, each measurement was sampled *with replacement* a number of times equal to the smaller fossil sample size (Fig. 1, step 1). For example, the number of measurements sampled for HUMHEAD<sup>2</sup> was two—the sample size for *A. afarensis*—while the number sampled for DISTTIB was three—the sample size for *A. africanus* (Table 1). Once a particular measurement (e.g., HUMHEAD<sup>2</sup>) was sampled, the geometric mean of resampled values was calculated (Fig. 1, step 2). This process was repeated for the remaining five measurements and the mean RLSI was calculated following Equation 4 (Fig. 1, steps 3 and 4). The entire procedure was run 5000 times for each taxon to generate distributions of mean RLSI values (Fig. 1, step 5).

The resampling procedure produced mean RLSI values based on identical sample sizes for all taxa. This allowed for comparable distributions of mean RLSI to be calculated for both fossil and extant taxa, rather than single values for fossils and distributions for the extant material. Reducing the sample size of comparative taxa to that of fossil samples and drawing comparative samples separately for each measurement meant that the values drawn for each measurement in each iteration came from different subsets of specimens for a particular taxon; as such, this procedure produced distributions of mean RLSI with greater variance than would a procedure that resampled complete individuals a number of times equal to the comparative sample. Accordingly, the procedure used in this study is a more conservative test of differences in mean RLSI than a bootstrap analysis that does not account for differences in sample size and data structure.

Significance tests for pairwise comparisons of mean RLSI between taxa were conducted using a randomization procedure that calculated the difference between randomly paired RLSI values from each pair of taxon-specific distributions (such that the difference was always calculated as [*Species A* – *Species B*] and thus could take on positive or negative values). Proportions were calculated for differences greater than and less than zero, where a difference of zero indicated equal RLSI values in the two taxa under consideration. For a two-tailed test of significance for the difference in mean RLSI, the larger of the two proportions is equal to  $(1 - 2p)$ , where solving for  $p$  gives the  $p$ -value. As noted above, this randomization method makes no assumptions regarding the distribution of the data (i.e., it is a nonparametric test; Manly, 1997).

The advantage of the approach outlined above is that it allows direct comparison of mean RLSI values between samples without regard to missing data, thus permitting direct pairwise comparisons among *A. afarensis*, *A. africanus*, and the extant taxa under consideration. Despite the small sample sizes available for the fossil material, a resampling procedure of this sort

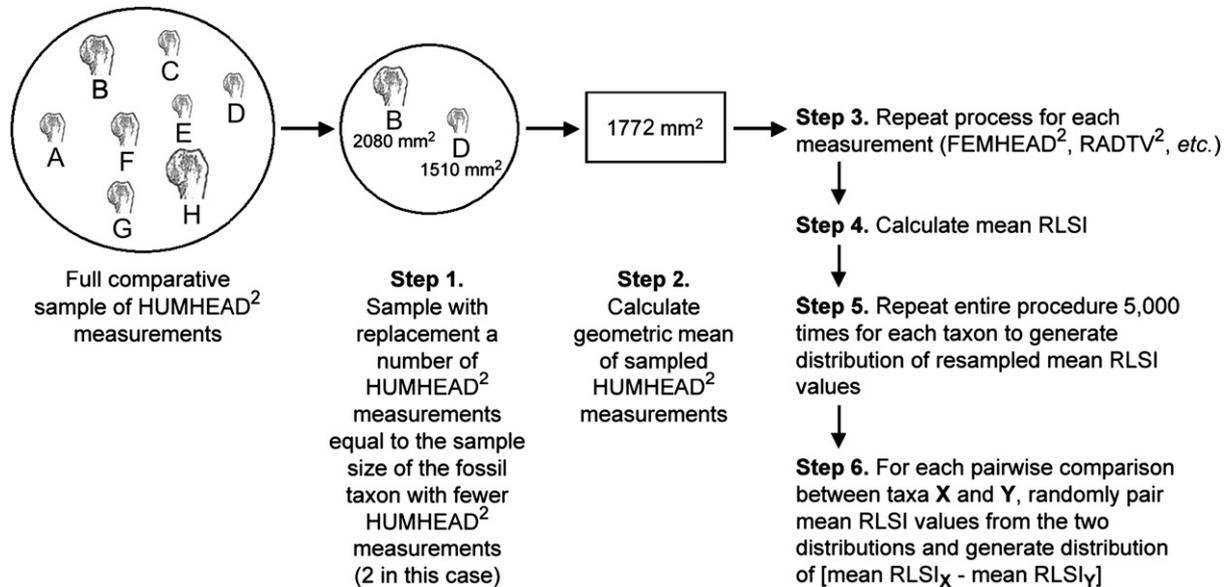


Fig. 1. A schematic diagram outlining the resampling procedure described in the text.

is legitimate because the number of unique values of mean RLSI for a given sample is the product of the number of possible ways to perform the sampling procedure for each measurement; if the fossil taxa were tested individually (in the absence of the other fossil taxon) there would be 4,365,900 possible resampled mean RLSI values for *A. afarensis* and 65,637,000 possible resampled mean RLSI values for *A. africanus*. When both taxa are considered together (and thus sample sizes are reduced in the first step of the sampling procedure as described above and in Fig. 1), there remain 1,327,104 unique values that could be calculated for *A. afarensis* and 1,259,712 for *A. africanus*. The number of unique values that can be calculated is sufficiently large that the resampling procedure with 5000 iterations is unlikely to sample many combinations more than once.

However, before using this randomization approach for pairwise tests of mean RLSI differences between taxa, the resampled mean RLSI distribution for each extant species was first compared to the distribution of actual individual RLSI values for each individual of that taxon to determine if both techniques tracked the same mean. Arithmetic means and standard deviations for both actual and resampled RLSI distributions were calculated and histograms are presented for visual comparison.

### Sampling bias

Another possibility that should be considered is that the fossil species may differ in relative limb size due to sampling bias. For example, if only large, male forelimb elements are preserved for *A. africanus* but a range of sizes from both sexes are preserved

for the hindlimb, then RLSI will be biased, producing a value greater than the actual population value for *A. africanus*. By basing RLSI on the geometric means of multiple measurements, the influence of individual size variables is greatly reduced, but to further investigate the effect of sampling, the pairwise-comparison procedure was performed on six modified measures of RLSI. In each case, one of the variables of the analysis was removed (i.e., a log-transformed forelimb:hindlimb ratio was calculated from five as opposed to six elements in each case). For example, rather than calculating forelimb size as the geometric mean of HUMHEAD<sup>2</sup> and RADTV<sup>2</sup>, in one case forelimb size was simply equal to RADTV<sup>2</sup>, and relative limb size was calculated as  $\ln(\text{RADTV}^2/\text{HLGM})$ . The process of systematically removing each variable from the data set lowers the statistical power by reducing the sample size and increases the probability that a single variable could sway the results. We then compared the results based on the reduced data sets to the results of the full data set. If all of these results show the same pattern, then it is unlikely that there is sex bias in the preservation of fore- or hindlimb elements for either fossil taxon.

### A.L. 288-1

Given the remarkable preservation of A.L. 288-1, it is worth comparing a measure of relative limb size in this fossil specimen, in which the elements are all known to be associated, to the same measure for the individual specimens of the extant taxa. All measurements except DISTFEM are available for A.L. 288-1, so a measure of relative limb size may be calculated as follows:

$$\text{RLSI}' = \ln \left( \frac{[\text{HUMHEAD}^2 * \text{ELBOW} * \text{RADTV}^2]^{\frac{1}{3}}}{[\text{FEMHEAD}^2 * \text{FEMSHAFT} * \text{PROXTIB} * \text{DISTTIB}]^{\frac{1}{4}}} \right) \quad (\text{Equation 5})$$

RLSI' was calculated for A.L. 288-1 and the extant specimens. Arithmetic means and standard deviations for extant RLSI' distributions were calculated and the observed value of RLSI' for A.L. 288-1 was considered in relation to the comparative extant sample.

## Results

### Individual RLSI versus resampled mean RLSI

The RLSI was calculated for each extant specimen; orangutans were shown to have the highest mean, followed by chimpanzees, gorillas, and humans (Table 3). This relationship reflects the large forelimb size relative to a given hindlimb size in *P. pygmaeus*, and the large hindlimb size relative to a given forelimb size in *H. sapiens* (Fig. 2). The ranking of RLSI values, with orangutans highest and humans lowest, corresponds with relative amounts of arboreality in extant hominoids. An analysis of variance of RLSI found a significant difference in means among the four extant species and no overlap in 95% confidence intervals for any of the species means ( $F = 820.43$ ; d.f. = 3, 200;  $p < 0.001$ ).

When compared to resampled mean RLSI distributions, actual species means were within 0.001 log units in all cases (i.e., ratios differ by 0.1% or less), and in all four extant species, the resampled mean is less than 0.02 standard deviations from the individual mean (Table 3). Furthermore, histograms of resampled and individual distributions show no discernible difference in means (Fig. 3). Although means differ significantly among species, the means of actual individual RLSI and resampled RLSI do not differ within species.

Note that, although standard deviations are roughly similar among species for the distributions of individual RLSI, the resampled distributions are more variable; for example, *G. gorilla* is nearly twice as variable as *P. troglodytes* (Table 3). This variability reflects the influence of sexual dimorphism on skeletal size. Because the resampling technique samples separately within each size variable, occasionally the procedure will sample only large individuals (i.e., males) for the forelimb and small individuals (i.e., females) for the hindlimb variables, and vice versa. These resampled measurements will result in unusually high and unusually low RLSI values, respectively. In the case of taxa with high skeletal

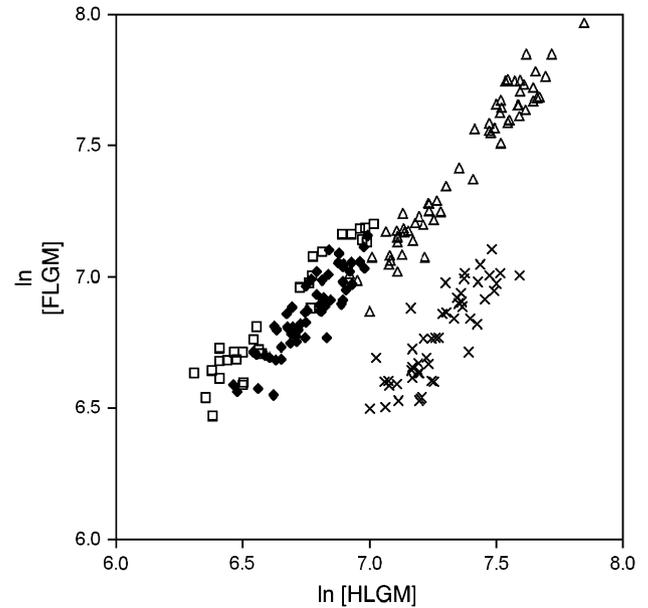


Fig. 2. Bivariate plot of logged forelimb and hindlimb size for extant species. Symbols:  $\square$ , *Pongo pygmaeus*;  $\blacklozenge$ , *Pan troglodytes*;  $\triangle$ , *Gorilla gorilla*;  $\times$ , *Homo sapiens*. Note that *P. pygmaeus* individuals tend to have larger forelimbs relative to their hindlimbs, while the reverse is true for *Homo*; *Pan* and *Gorilla* are intermediate.

dimorphism, the difference in size between the largest and smallest individuals will be greater than that in less dimorphic taxa. In this manner, the resampled mean RLSI distributions for more dimorphic taxa will have wider tails and higher standard deviations than distributions for less dimorphic taxa (Fig. 3). For example, the resampled distributions are relatively wide for the more dimorphic species in this study, *G. gorilla* and *P. pygmaeus*, but relatively narrow for the less dimorphic species, *H. sapiens* and *P. troglodytes* (Fig. 3). Consequently, one is less likely to find significant differences in mean RLSI between highly dimorphic taxa than between less dimorphic taxa.

### Pairwise taxon comparisons

The results in Table 3 and Fig. 4 show that mean RLSI is greater in *A. africanus* than in *A. afarensis*, indicating relatively larger forelimb size for a given hindlimb size in the former. Mean RLSI for both fossil species is between that observed in modern humans and the great apes (Table 3; Fig. 4).

A resampling analysis of pairwise species mean differences shows that mean RLSI is significantly greater in *A. africanus* than in both *A. afarensis* and *H. sapiens*, while *A. africanus* does not differ significantly from any of the great apes (Table 4). Mean RLSI for *A. afarensis* does not differ significantly from *H. sapiens*, but values are significantly lower in *A. afarensis* than in *G. gorilla*, *P. pygmaeus*, and *P. troglodytes*. Mean RLSI is significantly lower in *H. sapiens* than in all of the great ape species, while none of the resampled mean values differs significantly among the great apes (Table 4).

Table 3  
Comparison of individual and resampled mean RLSI values

Species	Individual ratios		Resampled ratios	
	Mean	SD	Mean	SD
<i>A. afarensis</i>	—	—	−0.471	0.189
<i>A. africanus</i>	—	—	−0.018	0.092
<i>Homo sapiens</i>	−0.501	0.092	−0.501	0.103
<i>Gorilla gorilla</i>	0.055	0.074	0.055	0.159
<i>Pan troglodytes</i>	0.106	0.068	0.107	0.090
<i>Pongo pygmaeus</i>	0.206	0.065	0.205	0.141

Higher values of RLSI are associated with higher levels of arboreality in extant hominoids. Note the similarity in means between resampled and individual ratios for extant species despite the differences in the two methods.

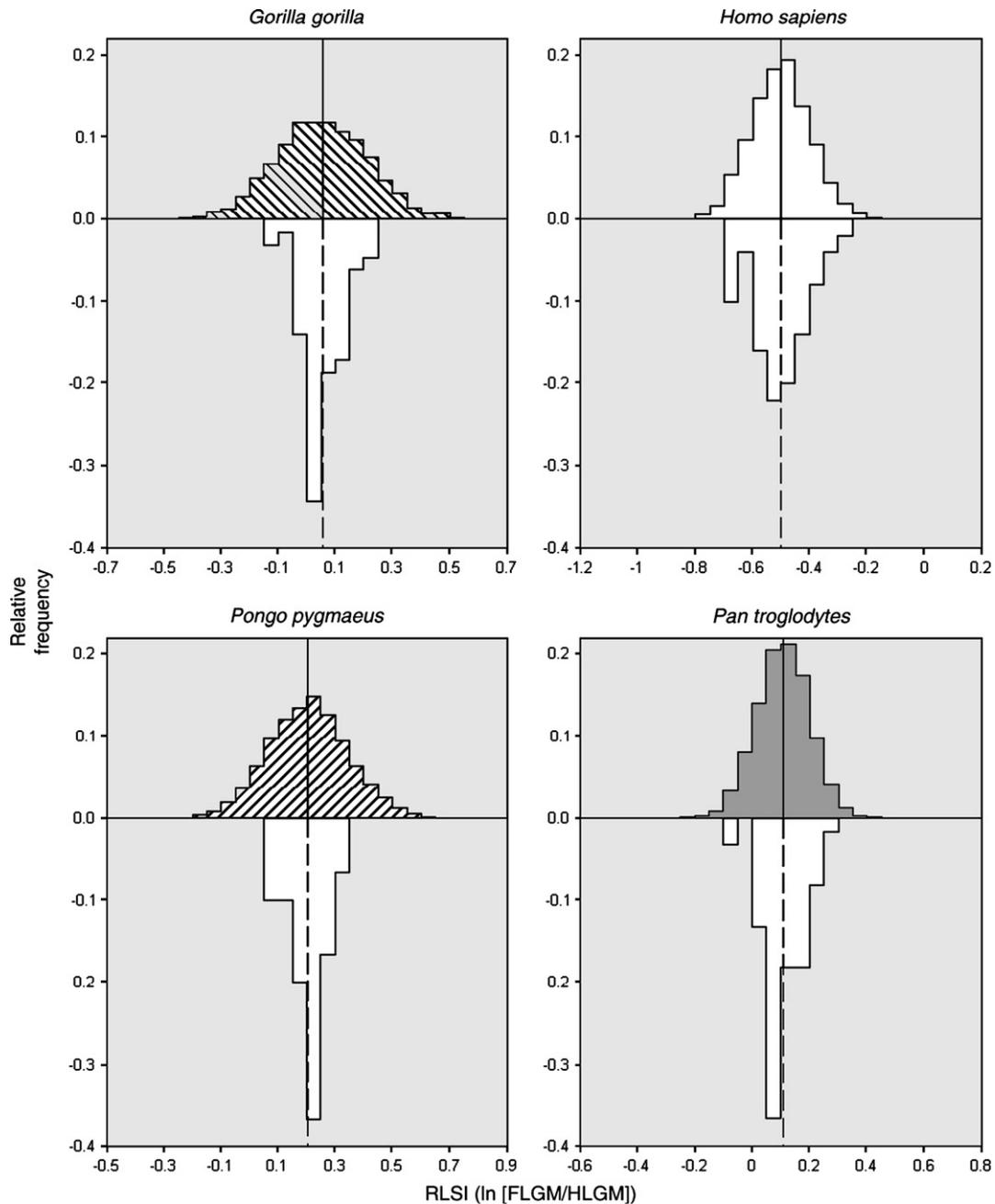


Fig. 3. Histograms of individual RLSI and resampled mean RLSI values for extant species. Upper histograms are resampled mean RLSI values; inverted histograms are individual RLSI values. Although standard deviations differ between the two methods, means are virtually identical within each species. Note that RLSI values on the X-axes differ for each species. Solid lines represent mean values for mean RLSI from the resampling procedure; dashed lines are RLSI means for the individual data—refer to Table 3.

### Sampling bias

Six reduced data sets were generated by removing one of the six variables from the primary data set before calculating geometric means of forelimb and hindlimb variables and their logged ratio. Resampled pairwise comparisons were calculated for each reduced data set. The  $p$ -values for the pairwise comparisons between the three hominin species are presented in Table 5. In all six reduced data sets, mean logged ratios were higher in *A. africanus* than in *A. afarensis* and *H. sapiens*,

as observed in the primary data set. Even with the removal of data from an already small data set, differences in mean logged ratios between *A. africanus* and the other two hominins are either significant or approach significance ( $p$ -values range from less than 0.001 to 0.110), differences between *A. afarensis* and *H. sapiens* are not significant in any of the cases ( $p$ -values range from 0.487 to 0.998), and logged ratios are always significantly greater in *A. africanus* than in *H. sapiens* ( $p$ -values range from less than 0.001 to 0.050; Table 5). The two cases in which the comparisons between *H. sapiens*, *A.*

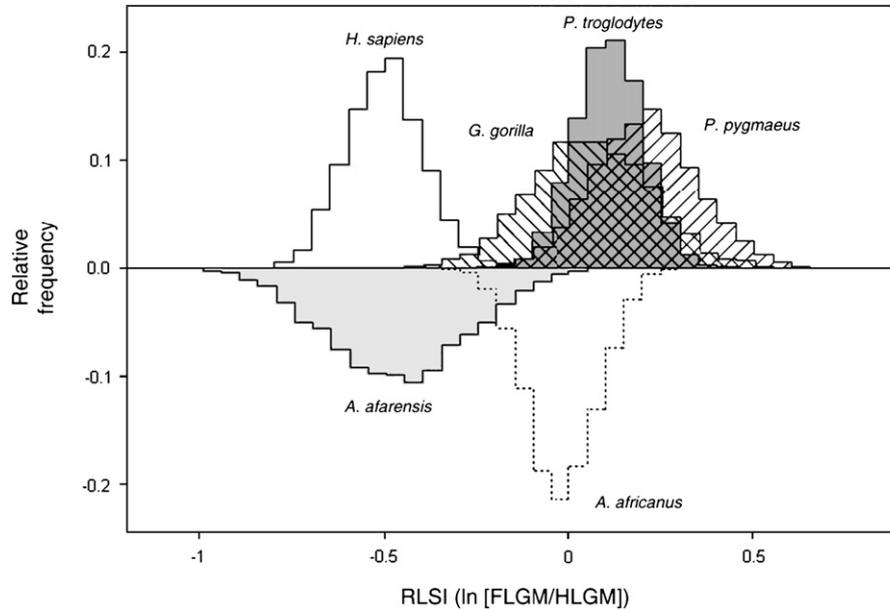


Fig. 4. Histograms of resampled mean RLSI values for extant and fossil species. Upper histograms are extant species; inverted histograms are fossil species. Extant species patterns: white area, *H. sapiens*; left to right downward diagonal, *G. gorilla*; left to right upward diagonal, *P. pygmaeus*; gray area, *P. troglodytes*. Fossil species: solid line, lightly shaded, *A. afarensis*; dotted line, unshaded, *A. africanus*. *Homo sapiens* and *A. afarensis* share similar relative limb-size relationships, while *A. africanus* resembles the great apes (i.e., larger forelimbs relative to the size of the hindlimbs).

*afarensis*, and *A. africanus* were not significant can also be attributed to the loss of statistical power by having forelimb represented by only one element, either HUMHEAD<sup>2</sup> or RADTV<sup>2</sup>. In addition, when FEMSHAFT is removed (and thus only articular dimensions are included in the analysis), the results do not differ from the first analysis: *A. africanus* and *H. sapiens* differ significantly in relative joint size ( $p < 0.001$ ), *A. afarensis* and *H. sapiens* do not differ significantly ( $p = 0.487$ ), and the two fossil taxa differ significantly from each other ( $p = 0.038$ ).

A.L. 288-1

As was observed with RLSI, RLSI' (Equation 5) values differed significantly among the four extant species, with no overlap in 95% confidence intervals for species means ( $F = 898.68$ ; d.f. = 3, 200;  $p < 0.001$ ). Higher values of RLSI' are also associated with a higher degree of arboreality in extant hominoids (Table 6). Distributions of RLSI' overlap for

all three great ape samples, but none of these distributions overlaps that of modern humans (Fig. 5). The value for A.L. 288-1 falls well within one standard deviation of the upper part of the human distribution and not within any of the distributions of the three great ape species (Table 6; Fig. 5).

Discussion

The results of this study strongly support the hypothesis that *A. africanus* had greater upper:lower limb-size (joint and shaft) proportions than *A. afarensis* (McHenry and Berger, 1998a). Furthermore, the present study's sampling approach, based on direct measurements, allowed us to assess the statistical significance of this pattern. The analysis of sampling bias shows that no single upper- or lower-limb measure had an overwhelming influence on our measures of the relative size of the respective limb as a whole (Table 5). The difference in relative limb size between these *Australopithecus* species was statistically significant, and whereas the upper:lower

Table 4  
Pairwise comparisons of mean RLSI values by species

	<i>A. afarensis</i>	<i>A. africanus</i>	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>
<i>A. afarensis</i>	—	<b>0.453</b>	-0.031	<b>0.525</b>	<b>0.578</b>	<b>0.676</b>
<i>A. africanus</i>	<b>0.031</b>	—	<b>-0.484</b>	0.072	0.125	0.223
<i>H. sapiens</i>	0.878	<b>&lt; 0.001</b>	—	<b>0.556</b>	<b>0.609</b>	<b>0.707</b>
<i>G. gorilla</i>	<b>0.034</b>	0.694	<b>0.002</b>	—	0.053	0.151
<i>P. troglodytes</i>	<b>0.004</b>	0.329	<b>&lt; 0.001</b>	0.782	—	0.098
<i>P. pygmaeus</i>	<b>0.003</b>	0.180	<b>&lt; 0.001</b>	0.480	0.562	—

Values above the diagonal are differences in mean RLSI (top species minus side species); values below the diagonal are the  $p$ -values for those differences. Differences significant at  $\alpha = 0.05$  are indicated in bold. Among the hominins, *A. afarensis* and *H. sapiens* both differ significantly from *A. africanus* in relative limb-size dimensions, but do not differ significantly from each other. Additionally, mean RLSI for *A. africanus* is not significantly different from any of the great apes.

Table 5

*P*-values for hominin pairwise comparisons of mean logged ratios of forelimb and hindlimb geometric means in the reduced data sets to test the possibility of sampling bias

Removed variable	<i>A. afarensis</i> vs. <i>A. africanus</i>	<i>A. afarensis</i> vs. <i>H. sapiens</i>	<i>A. africanus</i> vs. <i>H. sapiens</i>
HUMHEAD <sup>2</sup>	0.110	0.657	< <b>0.001</b>
RADTV <sup>2</sup>	0.086	0.767	<b>0.050</b>
FEMHEAD <sup>2</sup>	<b>0.026</b>	0.998	<b>0.001</b>
FEMSHAFT	<b>0.038</b>	0.487	< <b>0.001</b>
DISTFEM	<b>0.045</b>	0.925	< <b>0.001</b>
DISTTIB	<b>0.049</b>	0.826	<b>0.010</b>

Each row represents an analysis in which the specified variable was removed from the data set. In all cases, mean logged ratios for *A. africanus* are greater than those of *A. afarensis* and *H. sapiens*. Differences significant at  $\alpha = 0.05$  are indicated in bold.

limb-size proportions in *A. afarensis* resemble those seen in modern humans, the proportions in *A. africanus* resemble those of the great apes. These results have implications for our understanding of the evolution of limb proportions, locomotor behavior, and the phylogenetic history of these species.

Previous work by Dobson (2005) found that the upper:lower limb-size differences between A.L. 288-1 and Stw 431 were significant when first sacral centrum size represented the lower limb, but not when acetabular diameter was used as a proxy. These mixed results led Dobson (2005) to conclude that the sacral body is relatively small in Stw 431, and he suggested that the analysis of these two partial skeletons alone did not provide strong support for McHenry and Berger's (1998a,b) conclusion that *A. africanus* had greater upper:lower limb-joint proportions than *A. afarensis*. Since Dobson's (2005) study compared only one well-preserved skeleton for each species (Stw 431 and A.L. 288-1), it was a very conservative test of interspecific differences. Given that there are many more specimens known for both of these species, we built on the questions posed by Dobson (2005) and McHenry and Berger (1998a,b) and used the maximum number of available fossil specimens preserving the limb elements of interest (including elements from A.L. 288-1 and Stw 431; Table 2) to increase the statistical robusticity of our results. Our analysis shows that the upper:lower limb-size proportions are significantly different between these two *Australopithecus* species.

Table 6

Individual RLSI' values for extant species and A.L. 288-1

	Mean	SD
A.L. 288-1	-0.470*	—
<i>H. sapiens</i>	-0.525	0.090
<i>G. gorilla</i>	0.003	0.066
<i>P. troglodytes</i>	0.045	0.061
<i>P. pygmaeus</i>	0.185	0.058

As seen in the analysis of RLSI, higher values of RLSI' are associated with higher levels of arboreality in extant hominoids. The value of RLSI' for A.L. 288-1 is slightly greater than the mean value for *H. sapiens* and much lower than that of the great apes.

\*This value is the actual RLSI' for A.L. 288-1; all other values in this column display mean RLSI' for the extant individuals in each taxon.

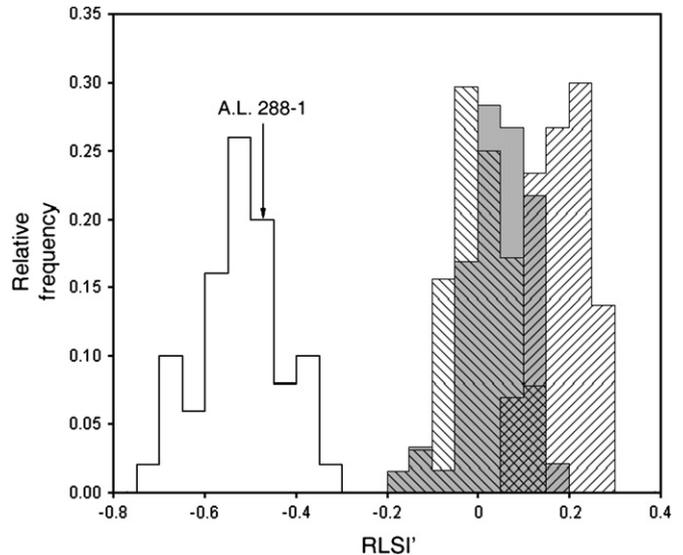


Fig. 5. Histograms of individual RLSI' values for extant species and A.L. 288-1 (see text for calculation of RLSI'). Extant species patterns: white area, *H. sapiens*; left to right downward diagonal, *G. gorilla*; left to right upward diagonal, *P. pygmaeus*; gray area, *P. troglodytes*. Arrow indicates the location of the RLSI' value for A.L. 288-1. Note the absence of overlap in the ape and human distributions and the position of A.L. 288-1 within the upper end of the human distribution.

In addition to the differences in mean value, *A. africanus* and *A. afarensis* also have noticeably different RLSI distributions (Fig. 4). The *A. afarensis* distribution is wider and shorter than that of *A. africanus*, resembling the distributions for the more sexually dimorphic ape species *G. gorilla* and *P. pygmaeus*. This is consistent with other evidence that *A. afarensis* displayed a relatively high level of sexual dimorphism (Johanson et al., 1982; McHenry, 1986a; Cole and Smith, 1987; McHenry, 1991a; Richmond and Jungers, 1995; Lockwood et al., 1996; Plavcan et al., 2005, but see Reno et al., 2003, 2005b). The differences in RLSI distributions (Fig. 4) also suggest that sexual dimorphism in *A. afarensis* was greater than that in *A. africanus*, a result that deserves further study (see also Lockwood, 1999; Gordon et al., 2006).

#### Primitive or secondarily derived?

As pointed out by McHenry and Berger (1998a), the ape-like limb-size proportions of *A. africanus* appear to contrast with the evidence that its craniodental characteristics are more derived. All published phylogenetic analyses (largely based on craniodental data) suggest that *A. africanus* is more closely related to *Paranthropus* and *Homo* than it is to *A. afarensis* (White et al., 1981; Skelton and McHenry, 1992; Strait et al., 1997; Wood and Collard, 1999; Strait and Grine, 2004). Given the evidence that the craniodentally primitive *A. afarensis* possessed limb-size proportions similar to later representatives of *Homo*, while *A. africanus* exhibited apelike proportions, what then were the primitive and derived conditions for limb-size proportions in these taxa? Two possibilities are apparent and are illustrated in Fig. 6. First, humanlike upper:lower limb-size proportions evolved early in human

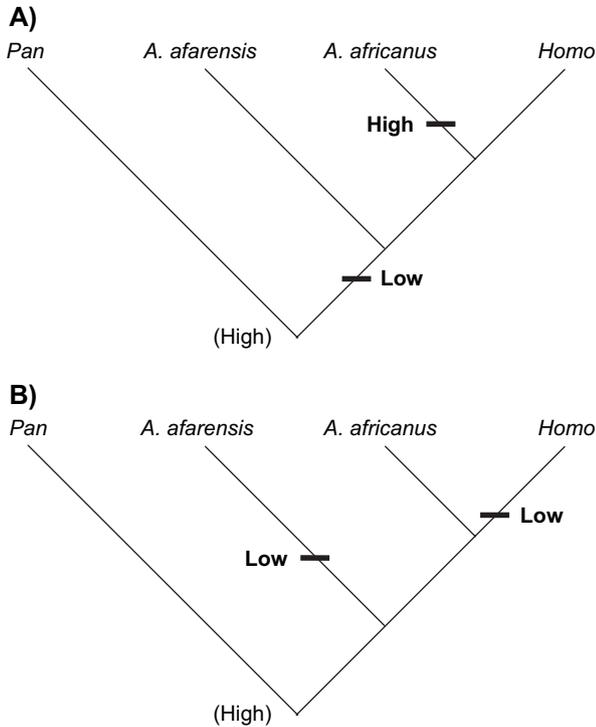


Fig. 6. Two scenarios concerning the evolution of upper:lower limb-size proportions, given this consensus cladogram and the likelihood that apelike, high upper:lower limb-size proportions are the primitive condition for the *Pan/Homo* clade. Either (A) humanlike upper:lower limb-size (joint and shaft) proportions were present in the common ancestor of *A. afarensis* and later hominins, and more apelike, high upper:lower limb-size proportions evolved secondarily in *A. africanus*, or (B) humanlike, low upper:lower limb-size proportions evolved independently in *A. afarensis* and *Homo*. Either possibility requires homoplasy in the evolution of limb size proportions.

evolution (by the time of the common ancestor of *A. afarensis* and later hominins), and more apelike, high upper:lower limb-size proportions evolved secondarily in *A. africanus*. The second possibility is that humanlike, low limb-size proportions evolved independently in *A. afarensis* and in *Homo*. Either interpretation indicates that homoplasy must have occurred in the evolution of hominin limb-size proportions (Fig. 6).

#### Locomotor implications

Studies of limb proportions have traditionally focused on relative limb lengths because of their well-documented and relatively well-understood links to posture and locomotion (e.g., Schultz, 1937; Jungers, 1985), but relative limb sizes also relate to function. Godfrey et al. (1995: 32) argued that “bone shaft rigidity or joint size” may be a better correlate of the “actual force transmission” through a given limb than bone length, and therefore a better measure of the different mechanical demands associated with various types of locomotion and posture (see also McHenry, 2005; Pearson and Peterson, 2005). The degree of limb-joint mobility also influences joint size (Rafferty and Ruff, 1994; Godfrey et al., 1995; Hamrick, 1996). Godfrey et al. (1995) noted that *P. pygmaeus* had the relatively largest humeral heads of the extant taxa they sampled, and that this

corresponded to the mobility and transarticular force transmission associated with orangutan locomotion.

Our measures of relative limb sizes also correspond to differences in locomotor and postural modes. Modern humans are committed bipeds and do not habitually use their upper limbs for locomotion. In this analysis, the *H. sapiens* mean RLSI was the lowest, reflecting their relatively large and bipedally adapted hindlimbs (Jungers, 1988; Ruff, 1988). Orangutans, the most arboreal of the four extant hominoids included in this study, had the highest mean RLSI, indicating the largest forelimb relative to overall hindlimb size. Among the African apes, the less arboreal gorillas had a slightly lower mean RLSI than chimpanzees (Tables 2, 5).

The limb-size proportions of *A. afarensis* and *A. africanus* have implications for the long-standing debate over whether or not arboreality was an important component of locomotor behavior in *Australopithecus* (McHenry, 1991b; Duncan et al., 1994; Stern, 2000; Ward, 2002). Both taxa display primitive anatomical features associated with arboreality, including curved manual proximal phalanges with well-developed flexor ridges (Stern and Susman, 1983; Susman et al., 1984; Ricklan, 1987; Susman, 1988), robust upper-limb bones (Robinson, 1972; Lovejoy et al., 1982; White et al., 1993; Drapeau et al., 2005), many features of the shoulder (Ciochon and Corruccini, 1976; Vrba, 1979; Stern and Susman, 1983; McHenry, 1986b), as well as other features related to posture (McHenry, 1991b; Spoor et al., 1994). The debate centers on how to interpret symplesiomorphic features, with some authors (Lovejoy, 1988; Latimer and Lovejoy, 1990; Latimer, 1991; Ward, 2002) basing locomotor reconstructions primarily on derived (i.e., bipedal) features, and others (Stern and Susman, 1983; Susman et al., 1984; Susman and Stern, 1991; Duncan et al., 1994; Sanders, 1998; Stern, 2000) interpreting both primitive and derived morphology as functionally significant. From either perspective, if the more apelike upper:lower limb-size proportions were secondarily derived in *A. africanus*, this suggests a morphological response to greater arboreality in this species relative to *A. afarensis*. Moreover, if *A. afarensis* and *Homo* evolved more humanlike limb-size proportions independently while *A. africanus* retained more apelike proportions, then it suggests that these australopith species were under different selection pressures regarding their postural and locomotor repertoire.

Among modern primates, there are many examples of closely related species that share a similar overall body design but differ in their emphasis on locomotor behaviors within their repertoire. For example, *Presbytis melalophos* has a greater leaping component in its locomotor repertoire compared to *P. obscura*, and these species differ significantly in muscular and osteological morphology related to leaping (Fleagle, 1977a,b). The differences in upper- and lower-limb sizes suggest that, in addition to bipedalism, *A. africanus* used postural and/or locomotor behaviors that involved relatively greater loading of the upper limb as part of its locomotor repertoire (Rose, 1991). This hypothesis predicts that other anatomical features should appear more adapted to arboreal behaviors in *A. africanus* than in *A. afarensis*.

## Conclusion

In this study, differences in the relative size of the upper and lower limbs—as measured by the RLSI—correspond with the observed levels of arboreality in the extant taxa. Additionally, our resampling analysis shows that *A. afarensis* was more similar to modern humans and *A. africanus* was more similar to the great apes. *Australopithecus afarensis* was significantly different from chimpanzees, gorillas, and orangutans, while *A. africanus* was significantly different from modern humans and *A. afarensis* (Table 3). This study corroborates McHenry and Berger's (1998a,b) conclusions that *A. africanus* possessed more apelike limb-size proportions that were distinct from those of *A. afarensis*, which more closely resembled the limb-size proportions of modern humans. In addition, this study used direct measurements of limb size and a new Monte Carlo method that allowed us to evaluate the statistical significance of species differences in body proportions.

The statistically significant differences in relative limb-size proportions between the eastern and southern African *Australopithecus* species suggests that they may have differed in their positional repertoires. A great deal of research has been devoted to the task of interpreting the locomotor anatomy of *A. afarensis*. Nonetheless, there is still disagreement over whether or not this group retained biologically meaningful arboreal retentions. The relatively forelimb-dominated limb-size proportions of *A. africanus*, if they were indeed derived with respect to *A. afarensis*, suggest that the former was under more intense selection for arboreal behaviors than *A. afarensis*.

The current consensus among published phylogenetic analyses consider *A. afarensis* to be a sister taxon of the clade containing *A. africanus* and early *Homo*. This would indicate that *A. africanus* either (1) secondarily derived apelike upper:lower limb proportions or that (2) *A. africanus* retained primitive limb-size proportions from a common ancestor shared with *A. afarensis*, and that *A. afarensis* and later *Homo* independently evolved their more humanlike upper:lower limb-size proportions (Fig. 6). Regardless of which scenario is supported by additional evidence, the results of this study strengthen the idea that hominin evolution progressed in a mosaic fashion (McHenry, 1975) and that *A. africanus* had significantly more apelike upper:lower limb-size proportions than did *A. afarensis*, possibly as a result of a greater emphasis on arboreal positional behaviors.

## Acknowledgements

We thank Eileen Westwig (AMNH), Jennifer Clark and Richard Potts (Human Origins Program at the Smithsonian Institution), Lyman Jellema and Yohannes Haile-Selassie (CMNH), and Linda Gordon and David Hunt (NMNH) for access to extant specimens and fossil casts under their care. We thank Phillip Williams for logistical help. We are grateful to Bill Kimbel, the associate editor, anonymous referees, Henry McHenry, Mike Plavcan, David Strait, and Bernard Wood for their useful and constructive comments on

earlier drafts of this manuscript. Finally, we acknowledge The George Washington University's Selective Excellence Initiative and the NSF Integrative Graduate Education and Research Traineeship (IGERT) program for support of this research.

## Appendix

Proof: Arithmetic mean of RLSI values for each individual skeleton is equal to RLSI calculated using geometric means of each variable across all individuals (Equation 4 in text).

For  $n$  individuals, mean RLSI can be expressed as

$$\overline{\text{RLSI}} = \sum_{i=1}^n \frac{1}{n} \text{RLSI}_i \quad (\text{A.1})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \frac{1}{n} \ln[\text{FLGM}_i/\text{HLGM}_i] \quad (\text{A.2})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \frac{1}{n} \ln[\text{GM}(F_i)/\text{GM}(H_i)] \quad (\text{A.3})$$

where  $\text{GM}(F_i)$  is the geometric mean of all forelimb measurements for the  $i$ th individual in the data set and  $\text{GM}(H_i)$  is the geometric mean of all hindlimb measurements for the  $i$ th individual. For  $p$  forelimb variables and  $m$  hindlimb variables, Equation A.3 can be restated as:

$$\overline{\text{RLSI}} = \sum_{i=1}^n \frac{1}{n} \ln \left[ \left( \prod_{j=1}^p F_{ji} \right)^{\frac{1}{p}} / \left( \prod_{k=1}^m H_{ki} \right)^{\frac{1}{m}} \right] \quad (\text{A.4})$$

This equation can be further reworked as follows:

$$\overline{\text{RLSI}} = \sum_{i=1}^n \left[ \frac{1}{n} \ln \left( \prod_{j=1}^p F_{ji} \right)^{\frac{1}{p}} - \frac{1}{n} \ln \left( \prod_{k=1}^m H_{ki} \right)^{\frac{1}{m}} \right] \quad (\text{A.5})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \left[ \frac{1}{n} \sum_{j=1}^p \ln(F_{ji})^{\frac{1}{p}} - \frac{1}{n} \sum_{k=1}^m \ln(H_{ki})^{\frac{1}{m}} \right] \quad (\text{A.6})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \left[ \sum_{j=1}^p \frac{1}{n} \ln(F_{ji})^{\frac{1}{p}} - \sum_{k=1}^m \frac{1}{n} \ln(H_{ki})^{\frac{1}{m}} \right] \quad (\text{A.7})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \sum_{j=1}^p \frac{1}{n} \ln(F_{ji})^{\frac{1}{p}} - \sum_{i=1}^n \sum_{k=1}^m \frac{1}{n} \ln(H_{ki})^{\frac{1}{m}} \quad (\text{A.8})$$

$$\overline{\text{RLSI}} = \sum_{i=1}^n \sum_{j=1}^p \frac{1}{n} \ln(F_{ji})^{\frac{1}{p}} - \sum_{i=1}^n \sum_{k=1}^m \frac{1}{m} \ln(H_{ki})^{\frac{1}{m}} \quad (\text{A.9})$$

$$\overline{\text{RLSI}} = \sum_{j=1}^p \sum_{i=1}^n \frac{1}{n} \ln(F_{ji})^{\frac{1}{p}} - \sum_{k=1}^m \sum_{i=1}^n \frac{1}{m} \ln(H_{ki})^{\frac{1}{m}} \quad (\text{A.10})$$

$$\overline{\text{RLSI}} = \sum_{j=1}^p \frac{1}{p} \sum_{i=1}^n \ln(F_{ji})^{\frac{1}{n}} - \sum_{k=1}^m \frac{1}{m} \sum_{i=1}^n \ln(H_{ki})^{\frac{1}{n}} \quad (\text{A.11})$$

$$\overline{\text{RLSI}} = \sum_{j=1}^p \frac{1}{p} \ln \left( \prod_{i=1}^n F_{ji} \right)^{\frac{1}{n}} - \sum_{k=1}^m \frac{1}{m} \ln \left( \prod_{i=1}^n H_{ki} \right)^{\frac{1}{n}} \quad (\text{A.12})$$

The logged quantities are the logged geometric means of each variable, as calculated for all individuals in the data set (e.g., geometric mean of all HUMHEAD<sup>2</sup> values, geometric mean of all RADTV<sup>2</sup> values, etc.), and can be restated as

$$\overline{\text{RLSI}} = \sum_{j=1}^p \frac{1}{p} \ln(\text{GM}[F_j]) - \sum_{k=1}^m \frac{1}{m} \ln(\text{GM}[H_k]) \quad (\text{A.13})$$

where GM[ $F_j$ ] is the geometric mean of the  $j$ th forelimb variable and GM[ $H_k$ ] is the geometric mean of the  $k$ th hindlimb variable. Equation A.13 can be further reworked as follows:

$$\overline{\text{RLSI}} = \sum_{j=1}^p \ln(\text{GM}[F_j])^{\frac{1}{p}} - \sum_{k=1}^m \ln(\text{GM}[H_k])^{\frac{1}{m}} \quad (\text{A.14})$$

$$\overline{\text{RLSI}} = \ln \left( \prod_{j=1}^p \text{GM}[F_j] \right)^{\frac{1}{p}} - \ln \left( \prod_{k=1}^m \text{GM}[H_k] \right)^{\frac{1}{m}} \quad (\text{A.15})$$

$$\overline{\text{RLSI}} = \ln \left[ \left( \prod_{j=1}^p \text{GM}[F_j] \right)^{\frac{1}{p}} / \left( \prod_{k=1}^m \text{GM}[H_k] \right)^{\frac{1}{m}} \right] \quad (\text{A.16})$$

Equation A.16 states that the arithmetic mean of RLSI is equal to the logged ratio of the geometric mean of geometric means of all forelimb variables divided by the geometric mean of geometric means of all hindlimb variables. In other words, arithmetic mean RLSI can be calculated by replacing individual measurements with geometric means for each variable in Equations 1 and 2 in the text, as shown by Equation 4 in the text.

## References

- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science* 284, 629–635.
- Cole, T.M., Smith, F.H., 1987. An odontometric assessment of variability in *Australopithecus afarensis*. *Hum. Evol.* 2, 221–234.
- Ciochon, R.L., Corruccini, R.S., 1976. Shoulder joint of Sterkfontein *Australopithecus*. *S. Afr. J. Sci.* 72, 80–82.
- Collard, M., Lycett, S.J., 2005. Plio-Pleistocene hominid limb proportions: Evolutionary reversals or estimation errors? *Curr. Anthropol.* 46, 581–582.
- Currey, J.D., 2002. *Bones: Structure and Mechanics*. Princeton University Press, Princeton, N.J.
- Day, M.H., Molleson, T.I., 1976. The puzzle from JK2—a femur and a tibial fragment (O.H. 34) from Olduvai Gorge, Tanzania. *J. Hum. Evol.* 5, 455–465.
- Dobson, S.D., 2005. Are the differences between Stw 431 (*Australopithecus africanus*) and A.L. 288-1 (*A. afarensis*) significant? *J. Hum. Evol.* 49, 143–154.

- Drapeau, M.S., Ward, C.V., Kimbel, W.H., Johanson, D.C., Rak, Y., 2005. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J. Hum. Evol.* 48, 593–642.
- Duncan, A.S., Kappelman, J., Shapiro, L.J., 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 93, 67–81.
- Fleagle, J.G., 1977a. Locomotor behavior and muscular anatomy of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *melalophos*). *Am. J. Phys. Anthropol.* 46, 297–308.
- Fleagle, J.G., 1977b. Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys. *Yearb. Phys. Anthropol.* 20, 440–453.
- Godfrey, L.R., Sutherland, M.R., Paine, R.R., Williams, F.L., Boy, D.S., Vuillaume-Randriamanantena, M., 1995. Limb joint surface areas and their ratios in Malagasy lemurs and other mammals. *Am. J. Phys. Anthropol.* 97, 11–36.
- Gordon, A.D., Green, D.J., Richmond, B.G., 2006. Size dimorphism in *Australopithecus afarensis*, modern humans, and the great apes: a non-temperate multivariate comparison. *Am. J. Phys. Anthropol.* 42 (Suppl.), 94.
- Haeusler, M., McHenry, H.M., 2004. Body proportions of *Homo habilis* reviewed. *J. Hum. Evol.* 46, 433–465.
- Hamrick, M.W., 1996. Articular size and curvature as determinants of carpal joint mobility and stability in strepsirrhine primates. *J. Morphol.* 230, 113–127.
- Hartwig-Scherer, S., 1996. On body-weight prediction in human evolution. *Curr. Anthropol.* 37, 661–663.
- Hartwig-Scherer, S., Martin, R.D., 1991. Was “Lucy” more human than her “child”? Observations on early hominid postcranial skeletons. *J. Hum. Evol.* 21, 439–449.
- Johanson, D.C., Taieb, M., Coppens, Y., 1982. Pliocene hominids from the Hadar formation, Ethiopia (1973–1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *Am. J. Phys. Anthropol.* 57, 373–402.
- Johanson, D.C., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* 327, 205–209.
- Jungers, W.L., 1982. Lucy’s limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297, 676–678.
- Jungers, W.L., 1985. Body size and scaling of limb proportions in primates. In: Jungers, W.L. (Ed.), *Size and Scaling in Primate Biology*. Plenum, New York, pp. 345–381.
- Jungers, W.L., 1988. Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. *J. Hum. Evol.* 17, 247–265.
- Jungers, W.L., Falsetti, A.B., Wall, C.E., 1995. Shape, relative size, and size-adjustments in morphometrics. *Yearb. Phys. Anthropol.* 38, 137–161.
- Korey, K.A., 1990. Deconstructing reconstruction: the OH 62 humerofemoral index. *Am. J. Phys. Anthropol.* 83, 25–33.
- Latimer, B., 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les hominidés*. CNRS, Paris, pp. 169–176.
- Latimer, B.M., Lovejoy, C.O., 1990. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 82, 125–133.
- Lockwood, C.A., 1999. Sexual dimorphism in the face of *Australopithecus africanus*. *Am. J. Phys. Anthropol.* 108, 97–127.
- Lockwood, C.A., Richmond, B.G., Jungers, W.L., Kimbel, W.H., 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 31, 537–548.
- Lovejoy, C.O., 1988. Evolution of human walking. *Sci. Am.* 259, 118–125.
- Lovejoy, C.O., Johanson, D.C., Coppens, Y., 1982. Hominid upper limb bones recovered from the Hadar formation: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57, 637–649.
- Manly, B.F.J., 1997. *Randomization, Bootstrap, and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- McHenry, H.M., 1975. Fossils and the mosaic nature of human evolution. *Science* 190, 425–431.
- McHenry, H.M., 1986a. Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *Hum. Evol.* 1, 149–156.

- McHenry, H.M., 1986b. The first bipeds: a comparison of the *A. afarensis* and *A. africanus* postcranium and implications for the evolution of bipedalism. *J. Hum. Evol.* 15, 177–191.
- McHenry, H.M., 1991a. Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 20, 21–32.
- McHenry, H.M., 1991b. First steps? Analysis of the postcranium of early hominids. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les hominidés*. CNRS, Paris, pp. 133–141.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407–431.
- McHenry, H.M., 2005. Plio-Pleistocene hominid limb proportions: Evolutionary reversals or estimation errors? *Curr. Anthropol.* 46, 583–584.
- McHenry, H.M., Berger, L.R., 1998a. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *J. Hum. Evol.* 35, 1–22.
- McHenry, H.M., Berger, L.R., 1998b. Limb lengths in *Australopithecus* and the origin of the genus *Homo*. *S. Afr. J. Sci.* 94, 447–450.
- McHenry, H.M., Corruccini, R.S., 1978. The femur in early human evolution. *Am. J. Phys. Anthropol.* 49, 473–488.
- Mosimann, J.E., 1970. Size allometry: size and shape variables with characteristics of the log normal and generalized gamma distributions. *J. Am. Stat. Assoc.* 65, 930–945.
- Pearson, O.M., Peterson, T.R., 2005. Plio-Pleistocene hominid limb proportions: Evolutionary reversals or estimation errors? *Curr. Anthropol.* 46, 584.
- Plavcan, J.M., Lockwood, C.A., Kimbel, W.H., Lague, M.R., Harmon, E.H., 2005. Sexual dimorphism in *Australopithecus afarensis* revisited: how strong is the case for a human-like pattern of dimorphism? *J. Hum. Evol.* 48, 313–320.
- Rafferty, K.L., Ruff, C.B., 1994. Articular structure and function in *Hylobates*, *Colobus*, and *Papio*. *Am. J. Phys. Anthropol.* 94, 395–408.
- Reno, P.L., Meindl, R.S., McCollum, M.A., Lovejoy, C.O., 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc. Natl. Acad. Sci. U.S.A.* 100, 9404–9409.
- Reno, P.L., DeGusta, D., Serrat, M.M., Meindl, R.S., White, T.D., Eckhardt, R.B., Kuperavage, A.J., Galik, K., Lovejoy, C.O., 2005a. Plio-Pleistocene hominid limb proportions: Evolutionary reversals or estimation errors? *Curr. Anthropol.* 64, 575–588.
- Reno, P.L., Meindl, R.S., McCollum, M.A., Lovejoy, C.O., 2005b. The case is unchanged and remains robust: *Australopithecus afarensis* exhibits only moderate skeletal dimorphism. A reply to Plavcan et al. (2005). *J. Hum. Evol.* 49, 279–288.
- Richmond, B.G., Aiello, L.C., Wood, B.A., 2002. Early hominin limb proportions. *J. Hum. Evol.* 43, 529–548.
- Richmond, B.G., Jungers, W.L., 1995. Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. *J. Hum. Evol.* 29, 229–245.
- Ricklan, D.E., 1987. Functional anatomy of the hand of *Australopithecus africanus*. *J. Hum. Evol.* 16, 643–664.
- Robinson, J.T., 1972. *Early Hominid Posture and Locomotion*. University of Chicago Press, Chicago.
- Rose, M.D., 1991. The process of bipedalization in hominids. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les hominidés*. CNRS, Paris, pp. 37–48.
- Ruff, C., 1988. Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparison to diaphyseal scaling. *J. Hum. Evol.* 17, 687–714.
- Ruff, C.B., 1995. Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthropol.* 98, 527–574.
- Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *J. Hum. Evol.* 34, 249–302.
- Schultz, A.H., 1937. Proportions, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum. Biol.* 9, 281–328.
- Skelton, R.R., McHenry, H.M., 1992. Evolutionary relationships among early hominids. *J. Hum. Evol.* 23, 309–349.
- Smith, R.J., 1996a. Biology and body size in human evolution. *Curr. Anthropol.* 37, 451–481.
- Smith, R.J., 1996b. Reply to Hartwig-Scherer. *Curr. Anthropol.* 37, 663–664.
- Smith, R.J., 1999. Statistics of sexual size dimorphism. *J. Hum. Evol.* 36, 423–459.
- Spoor, F., Wood, B.A., Zonneveld, F., 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369, 645–648.
- Stern, J.T., 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evol. Anthropol.* 9, 113–133.
- Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279–317.
- Strait, D.S., Grine, F.E., 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J. Hum. Evol.* 47, 399–452.
- Strait, D.S., Grine, F.E., Moniz, M.A., 1997. A reappraisal of early hominid phylogeny. *J. Hum. Evol.* 32, 17–82.
- Susman, R.L., 1988. New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus*. In: Grine, F.E. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 149–172.
- Susman, R.L., Stern, J.T., 1991. Locomotor behavior of early hominids: Epistemology and fossil evidence. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les hominidés*. CNRS, Paris, pp. 121–131.
- Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43, 113–156.
- Vrba, E.S., 1979. A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *Am. J. Phys. Anthropol.* 51, 117–130.
- Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yearb. Phys. Anthropol.* 35, 185–215.
- White, T.D., Johanson, D.C., Kimbel, W.H., 1981. *Australopithecus africanus*: its phyletic position reconsidered. *S. Afr. J. Sci.* 77, 445–470.
- White, T.D., Suwa, G., Hart, W.K., Walter, R.C., WoldeGabriel, G., de Heinzelin, J., Clark, J.D., Asfaw, B., Vrba, E., 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature* 366, 261–265.
- Wood, B.A., Collard, M., 1999. The human genus. *Science* 284, 65–71.
- Wood, B.A., Richmond, B.G., 2000. Human evolution: taxonomy and paleobiology. *J. Anat.* 196, 19–60.