Humeral Length Allometry in African Hominids (*sensu lato*) with Special Reference to A.L. 288-1 and Liang Bua 1

TRENTON W. HOLLIDAY
Department of Anthropology, 101 Dinwiddie Hall, 6823 St. Charles Avenue, Tulane University, New Orleans, LA 70118, USA;
thollid@tulane.edu

ROBERT G. FRANCISCUS
Department of Anthropology, University of Iowa, Iowa City, IA 52242-1322, USA; robert-franciscus@uiowa.edu

ABSTRACT

We have previously argued that the femora of A.L. 288-1 ("Lucy," referred to *Australopithecus afarensis*) and Liang Bua (LB) 1 (holotype of *Homo floresiensis*) have lengths near those expected for modern humans of their diminutive size. Jungers has argued that these same fossil hominins have humeri that are close in length to those expected for modern humans of their diminutive size. Yet the humero : femoral indices of these two fossil hominins are radically different (5 to 6 standard deviations) from the modern human mean. These findings are seemingly contradictory. We investigate bivariate humeral length allometry for A.L. 288-1, LB1, and the three extant African hominid (*sensu lato*) genera. Results show considerable overlap in bivariate space among *Homo*, *Pan*, and (female) *Gorilla* individuals in humeral length relative to body mass. However, despite this overlap, humeral length allometry varies greatly among the taxa, showing slight positive allometry to isometry in *Homo*, while showing strong negative allometry in *Pan* and *Gorilla*. Ordinary least-squares and reduced major axis regression lines of human humeral length on body mass$^{1/3}$ lie near, but more often fall below, the observed humeral lengths of A.L. 288-1 and LB1, indicating that these fossil hominins have slightly longer humeri than would be expected for humans of their small size. In terms of femoral length, A.L. 288-1 and LB1 had somewhat shorter femora than expected for a human of their small size. This combination of slightly longer humeri and somewhat shorter femora than modern humans accounts for these specimens' high humero : femoral indices.

INTRODUCTION

In terms of its length, the humerus is perhaps the most conservative of the limb bones among both humans and the African apes. Aiello (1981), for example, found that among the hominoids, only the highly suspensory Hylobatidae had significantly longer humeri relative to body mass; the other apes and humans showed considerable overlap in bivariate space. In addition, Jungers (1991a, 1994) has found that humeral length : body mass$^{1/3}$ ratios are not statistically significantly different across the African hominids (*sensu lato*), suggesting that the differences in humero-femoral indices between humans and African apes are due entirely, or nearly entirely, to the marked elongation of the lower limb in the former. Likewise, Drapeau and Ward (2007) found that humeral length did not discriminate among the large-bodied hominoids when compared to a multivariate surrogate for body size, nor did variation in humeral length correlate well with locomotor adaptation. Within recent human adults, Holliday and Ruff (2001) found that humeral length showed lower intrinsic (i.e., size-independent) variability than any other limb segment, with the possible exception of the femur.

In this analysis, we examine bivariate length allometry of the humerus in three extant hominid genera—*Homo*, *Pan*, and *Gorilla*—and the diminutive specimens A.L. 288-1 (the *Australopithecus afarensis* specimen popularly known as "Lucy") and Liang Bua (LB) 1 (the holotype of *Homo floresiensis*). We focus on these individuals because both have significantly higher humero-femoral indices than do modern humans (Brown et al. 2004; Johanson et al. 1982). In previous publications we have examined femoral length to body mass allometry of these two fossils, and determined that these specimens have femoral lengths close to those expected for hominins of their diminutive size (Franciscus and Holliday 1992; Holliday and Franciscus 2009). Thus, we investigate humeral length allometry to determine whether these two specimens' high humero-femoral index values reflect a relatively shorter femur (which would contradict our earlier analyses), a comparatively long upper limb (a hypothesis rejected by Jungers, 1982, 1994, 2009), or some combination of the two.

MATERIALS AND METHODS

The recent human skeletal comparative data used in this analysis include a large global sample of 1,308 recent humans (Table 1). The majority of these specimens (772) were measured by the first author (TWH), with the remainder provided courtesy of Drs. C.B. Ruff and C.E. Hilton, along with supplementary data culled from Münter (1936) and Slome (1929). Note that within the global sample not all

TABLE 1. COMPARATIVE SAMPLES.

	Female	Male	Total N
Recent Humans:			
African-American[1, 2]	29	31	60
Andaman Islanders[3]	2	6	13
"Anglo-Saxon"[4]	73	204	287
Australian Aborigines[5]	4	2	6
Bohemia[5]	17	22	39
Bosnia[5]	31	48	79
East Africa[6]	19	27	46
Egypt[5]	38	32	69
European-American[1, 7]	51	74	125
Kerma (Sudan)[8]	18	30	48
Koniag[1]	10	11	21
French (Early Medieval)[9]	12	14	32
German (Late Medieval)[10]	13	24	37
Norse[3]	9	14	23
Nubia[8]	7	13	20
Point Hope[11]	75	88	175
Puebloan[7]	48	60	108
"Pygmy" (Central Africa)[12]	3	7	10
Romano-British[3]	27	25	52
San[3, 13]	21	12	36
West Africa[14]	5	16	21
African Apes:			
Pan troglodytes[1, 7, 15]	21	14	35
Gorilla gorilla[1, 15]	11	25	36

[1]Smithsonian Institution
[2]C.A. Pound Human Identification Laboratory, University of Florida
[3]Natural History Museum, London
[4]Data from Münter (1936)
[5]Peabody Museum, Harvard University
[6]Makere University, Kampala; Kenya National Museums; Nairobi (data courtesy of C.B. Ruff)
[7]Department of Anthropology, University of New Mexico
[8]Duckworth Collection, University of Cambridge
[9]Laboratoire d'Anthropologie, Université de Bordeaux I
[10]Universität Tübingen
[11]American Museum of Natural History, New York (data courtesy of C.E. Hilton)
[12]Université de Genève, Geneva; Institute Royale des Science Naturelles, Brussels
[13]Data from Slome (1929)
[14]Musée de l'Homme, Paris
[15]Cleveland Museum of Natural History; University of the Witwatersrand

specimens preserve all measurements, and therefore sample size changes from analysis to analysis (minimum sample size=894). Note, too, that in light of the small body size of A.L. 288-1 and LB1, our sample includes several small adult (as determined via epiphyseal closure) individuals, including 10 Central African "Pygmies," 36 San, and 12 Andaman Islanders.

The African ape sample used in this study (see Table 1) includes 35 chimpanzees (*Pan troglodytes*) and 36 gorillas (*Gorilla gorilla*) from the Cleveland Museum of Natural History, the Smithsonian Institution, the University of New Mexico, Tulane University, and the University of the Witwatersrand, all measured by the authors, with supplemental data kindly provided by Dr. B. Latimer. As was the case with the human data, not all measurements are preserved in all individuals, and therefore sample size varies from

analysis to analysis (*Pan* minimum sample size=34; *Gorilla* minimum sample size=29).

For the hominin fossils, data for A.L. 288-1 were taken and/or modified from Johanson et al. (1982). Data for LB1 were taken and/or modified from Brown et al. (2004) and Larson et al. (2009).

The measurements used in our analyses are humeral maximum length, femoral bicondylar length, and body mass. Body mass for *Homo* was predicted from femoral head diameter, and was computed as the arithmetic average of results derived from two predictive formulae; the first is formula number 1 from Ruff et al. (1997) and the second is from Grine et al. (1995). Body mass for the African apes also was predicted from femoral head diameter, and was calculated as the mean of three predictive formulae—specifically, the mean of predictions derived from two non-human hominoid formulae from Jungers (1991b) was averaged with the result derived from an African ape predictive formula reported in Jungers and Susman (1984).

Because it is unlikely that femoral head diameter scales the same way to body mass in *Australopithecus* as it does in *Homo* (Harmon 2009; Lovejoy and Heiple 1972; Lovejoy et al. 2002; McHenry and Corruccini 1978; Richmond and Jungers 2008), two body mass predictions were calculated for A.L. 288-1 in these analyses, one following the protocol outlined above for recent *Homo*, and the second following the protocol used for the African apes. The human regression-predicted body mass for A.L. 288-1 is 26.3kg, while the nonhuman hominoid-derived prediction is 29.7kg. Both of these predictions fall within the A.L. 288-1 size range (23.5–30.0kg) proposed by Jungers (1982, 1994).

The femoral lengths reported in the literature for A.L. 288-1 and LB1 are both maximum lengths, while the comparative data used in the current analysis are bicondylar lengths. Therefore, we predicted bicondylar length for these two fossil specimens from their observed maximum femoral lengths (both=280mm) using the following formula:

$$Y=0.998X–2.692 \ (r=0.997).$$

This formula is calculated from the Anglo-Saxon sample of Münter (1936), and is based on 225 femora for which both maximum and bicondylar lengths were available. From this formula, the predicted bicondylar femoral length of both A.L. 288-1 and LB1 is 276.7mm, with a standard error of the estimate of 2.4mm. The 95% confidence limits for the (individual) prediction span from 272 to 280mm, equivalent to 2.1% of the observed maximum femoral length. Note that the difference between the observed maximum length and calculated bicondylar length for the two fossil specimens is 1.2%, within measurement error.

Analyses begin with the computation of two indices, the humero-femoral index (humerus length/femoral length x 100) and the humeral length : body mass index (humeral length/body mass$^{1/3}$). The former is evaluated using a special case of the Student's *t*-test (Sokal and Rohlf 1981) which tests for differences in index values between each fossil hominin individual and the extant sample means, while the latter is subjected to ANOVA among the extant samples and the special Student's *t*-test for the fossil individuals. Humeral length also was regressed on femoral length, and ordinary least-squares (OLS) and reduced major axis (RMA) lines were fit to the recent human, *Pan*, and *Gorilla* samples. Each of these line-fitting techniques has its proponents and detractors. Ordinary least-squares regression is argued to be more appropriate for prediction and d_{yx} (see below) computation (Hens et al. 2000; Jungers 1982; Martin et al. 2005; Smith 2009), but since both X (body mass) and Y (humeral length) are here measured with error, and since OLS assumes that X is measured without error (Hens et al. 2000; Martin et al. 2005), RMA may be more appropriate (but see Smith 2009). We therefore use both techniques and compare results.

For allometric analyses, all measurements were log-transformed. This serves to linearize the data for ease of computation of fitted lines. Log humeral length was then regressed on the cube root of log body mass, and OLS and RMA bivariate regression lines were fit to the recent human, *Pan*, and *Gorilla* samples. We are aware that some researchers argue that analyses of fossils should avoid predicting variables, rather focusing on analyses of homologous measurements shared between fossil and extant taxa (e.g., Haeusler and McHenry 2004; Haile-Selassie et al. 2010). However, we choose to use body mass for allometric analyses because it has long been considered the most appropriate standard by which to evaluate allometry (Darveau et al. 2002; Garcia and da Silva 2006; Jungers 1984; West et al. 1997).

Finally, in order to quantify the position of the humeral lengths of A.L. 288-1 and LB1 in allometric space relative to the recent human and African ape regression lines, we calculate Smith's (1980) measure of percentage deviation from allometric expectation (or d_{yx}, calculated as {[observed humeral length – predicted humeral length] / predicted humeral length} x 100) from the humeral length to predicted body mass regression lines for recent humans, chimpanzees, and gorillas. This percentage deviation measure is frequently used in assessments of fit to allometric expectation (cf., Biknevicius 1999; Holliday and Franciscus 2009; Jungers 1982; Kappelman 1996; Millien 2008; Millien and Bovy 2010; Niskanen and Junno 2009; Spocter and Manger 2007).

RESULTS

Summary statistics for the humero-femoral index (HL : FL) of the comparative samples and fossil hominins are found in Table 2. As has been demonstrated numerous times by previous workers (e.g., Jungers 1985; McHenry 1978; Richmond et al. 2002; Shea 1981), this index effectively discriminates *Homo*, *Pan*, and *Gorilla* from each other; the ranges of these genera do not overlap. Neither of the diminutive fossil hominins (A.L. 288-1, LB1) falls within the *Homo*, *Pan* or *Gorilla* ranges of variation.

Results of *t*-tests comparing the hominin fossils to recent humans are presented in Table 3. They show that both fossil hominins are significantly different from *Pan* and

**TABLE 2. SUMMARY STATISTICS FOR THE HL : FL INDEX:
COMPARATIVE SAMPLES AND FOSSIL HOMININS.**

Sample or Individual Specimen	Mean	S.D.	Range	N
Recent humans	71.5	2.3	63.3–80.6	1129
Pan troglodytes	102.3	3.3	94.4–107.3	34
Gorilla gorilla	116.4	3.1	110.3–121.9	29
A.L. 288-1	85.6			
LB1	87.8			

Gorilla for the HL : FL index, and are also statistically significantly different from the recent human sample. These results are not surprising given previous work on humero-femoral indices by the workers previously cited.

The humero-femoral index is problematic, however, in that with the possible exception of *Pan troglodytes*, hominid (*sensu lato*) humeral to femoral proportions do not show an isometric relationship with body mass (Haeusler and McHenry 2004). In light of this, a bivariate scatter plot of humerus length regressed on femur length is presented in Figure 1. This plot is similar to those generated by other workers (cf., Figure 2 in McHenry and Berger 1998, Figure 3 in Richmond et al. 2002, Figure 8 in Haeusler and McHenry 2004, Figure 6 in Morwood et al. 2005, and Figure 3b in Lordkipanidze et al. 2007). In the current plot it is apparent that gorillas have the longest humeri relative to their femora, humans the shortest, with chimpanzees intermediate between the other two hominid genera. A.L. 288-1 and LB1 lie well beyond the 95% confidence limits about both the recent human and the chimpanzee individuals—a result consistent with that of other workers (Haeusler and McHenry 2004; McHenry and Berger 1998; Morwood et al. 2005; Richmond et al. 2002).

Summary statistics for the humeral length : body mass$^{1/3}$ indices are presented in Table 4. Jungers (1991a, 1994) found these indices to be similar across *Pan*, *Gorilla*, and *Homo*. Our index values differ marginally from those reported in Jungers (1994); our mean index for *Homo* is ca. 3.3% smaller, our mean index for *Pan troglodytes* is ca. 3.6% larger, and our *Gorilla* mean index is ca. 3.2% smaller. This could be a sampling issue, because Jungers' (1994) samples are extremely small, or it could be a result of the fact that his individuals (with the exception of his "Pygmy" sample) were of known body mass, whereas body mass has been predicted for the current sample (it is also possible that some combination of both these factors is at work). Nonetheless, like Jungers (1991a, 1994), we find marked overlap in index values among the three extant African hominid genera (all means are within approximately 1.0 standard deviation of each other). As for A.L. 288-1 and LB1, their HL : body mass$^{1/3}$ index values are all closer to the human mean than to either of the African ape means.

Our ANOVA results of a test for differences in HL : body mass$^{1/3}$ indices among the extant hominid genera are reported in Table 5. They indicate that (contra Jungers [1991a, 1994]), there is a significant difference ($p<0.05$) in the HL : body mass$^{1/3}$ index among the extant hominid genera. The exact nature of that difference is revealed via Scheffé's post-hoc test, the results of which are also reported in Table 5. Similar to what was found by Jungers (1991a, 1994), in our analysis, *Homo* and *Gorilla* are not significantly different from each other for the HL : body mass$^{1/3}$ index. However, unlike Jungers' results, here we find that *Pan* differs from both *Gorilla* and *Homo* in that it (*Pan*) has a signifi-

TABLE 3. FOSSIL HOMININ VS. EXTANT SAMPLES HL : FL INDEX *T*-TEST RESULTS*.

Fossil hominins HL : FL index *t*-test results:

	t$_s$	*p*	Reject null hypothesis of similarity?
Recent humans vs:			
A.L. 288-1	6.1250	<0.0001	Yes
LB1	7.0807	<0.0001	Yes
Chimpanzees vs:			
A.L. 288-1	−4.9160	<0.0001	Yes
LB1	−4.2684	<0.0001	Yes
Gorillas vs:			
A.L. 288-1	−9.6043	<0.0001	Yes
LB1	−8.9183	<0.0001	Yes

*special computation of Student's *t*-statistic for comparison of a single individual to a sample mean; Sokal and Rohlf (1981)
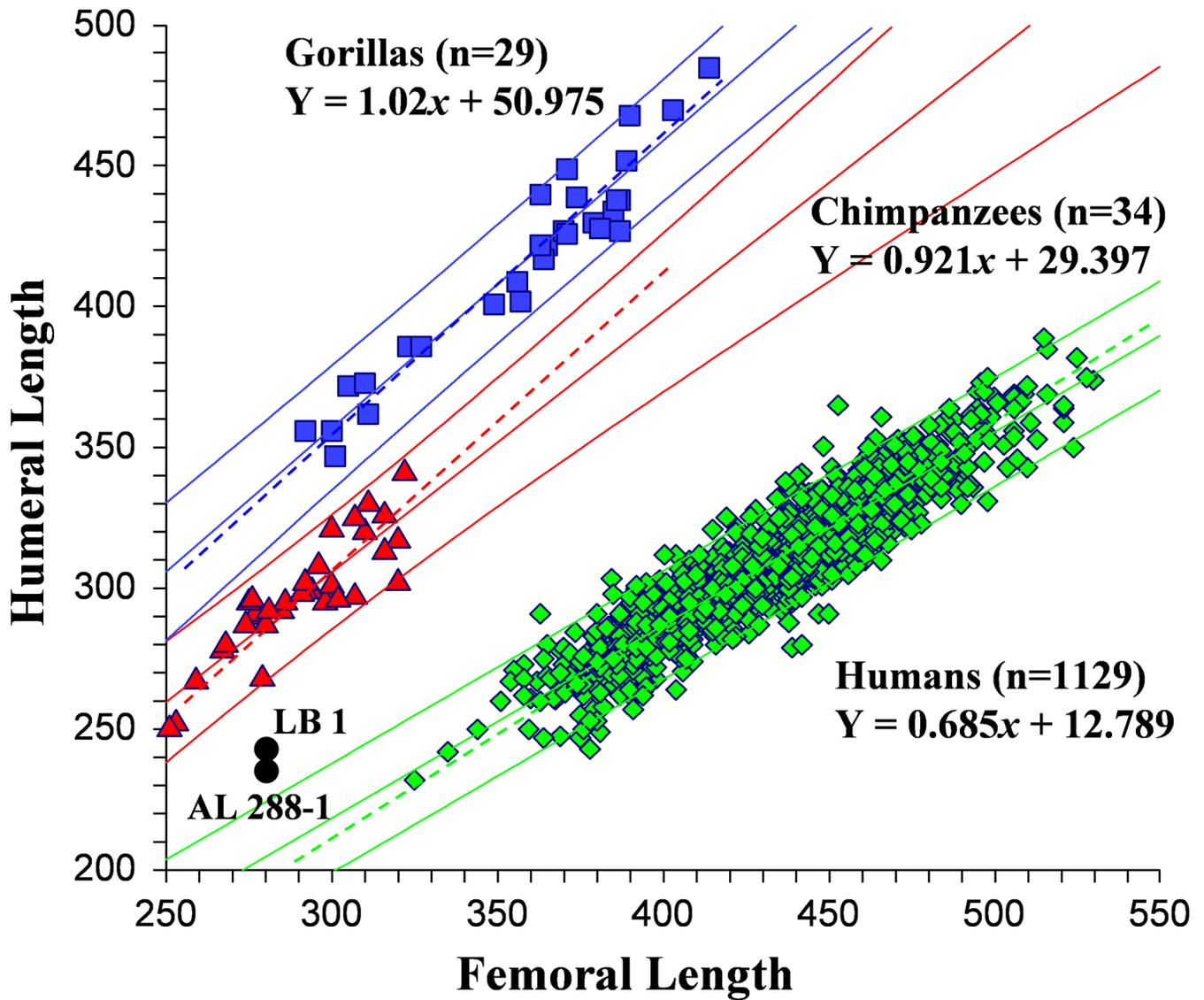
Figure 1. Scatter plot of humeral length (in mm) regressed on femoral length (in mm) for recent humans, Gorilla, Pan, *A.L. 288-1, and LB1. Recent humans are indicated by green diamonds;* Pan *by red triangles;* Gorilla *by blue squares, and fossil hominins by black circles. The OLS regression line for the recent humans is shown in green, as are the 95% confidence limits for the individuals about that line. The* Pan *and* Gorilla *OLS regression lines are shown in red (*Pan*) and blue (*Gorilla*), as are the corresponding 95% confidence limits for the individuals about those lines. The RMA lines for* Homo, Pan, *and* Gorilla *are indicated by dashed lines the same color as their respective OLS lines. Human RMA formula: Y=0.7454X–13.215;* Pan *RMA formula: Y=1.0479X–7.367;* Gorilla *RMA formula: Y=1.0608X+36.4938.*

TABLE 4. SUMMARY STATISTICS FOR THE HL : Body Mass$^{1/3}$ INDEX: COMPARATIVE SAMPLES AND FOSSIL HOMININS.

Sample or Individual Specimen	Mean	S.D.	Range	N
Recent humans	7.85	0.45	6.54-9.27	894
Pan troglodytes	8.33	0.55	7.45-9.67	34
Gorilla gorilla	8.04	0.55	6.72-8.99	30
A.L. 288-1	7.65–7.97			
LB1	7.60			

TABLE 5. ANOVA TABLE AND SCHEFFÉ'S POST-HOC TEST RESULTS, EXTANT HOMINID SAMPLES, HL : Body Mass$^{1/3}$ INDICES.

ANOVA Table	DF	Sum of Squares	Mean Square	Fs	*p*
Among Groups	2	860.4648	430.2324	20.77	<0.000001*
Within Groups	955	19782.65	20.71482		
Total	957	20643.12			

Scheffé's Test

	Homo	*Pan*	*Gorilla*
Homo		*	n.s.†
Pan			*

*Significantly different at family-wide α level of 0.05
†Not significantly different at $p<0.05$

cantly higher HL : body mass$^{1/3}$ index than the other two hominid genera.

The fossil hominin HL : body mass$^{1/3}$ indices are compared to those of the extant hominids via the computation of the same specialized Student's *t*-statistic that was used for the HL : FL indices, the results of which are presented in Table 6. Results reveal that neither A.L. 288-1 or LB1 can be distinguished from any of the extant hominid samples at the 0.05 level.

The bivariate allometric humeral length : body mass patterning in recent *Homo*, fossil hominins, and the two African ape genera is presented in Figure 2. What is perhaps the most interesting phenomenon observable in the scatter plot is that despite having very different allometric trajectories, there remains nonetheless significant overlap among individual humans, chimpanzees, and female gorillas in bivariate space. Due to their large size, the male gorillas fall beyond the scatter of the other hominids, but even still, they fall about an extension of the *Homo* OLS allometric line—only two male gorillas fall outside of the 95% confidence limits calculated about the recent *Homo* individuals. Likewise, a majority (27 of 34, or ca. 79%) of the chimpanzees fall within the 95% confidence limits about the recent *Homo* individuals. This overlap mirrors the similarity in HL : body mass$^{1/3}$ indices among the three extant hominid genera reported by Jungers (1991a, 1994), and found (albeit to a lesser extent) by us. However, despite this overlap in bivariate space, the humerus is behaving in a different allometric manner in *Homo* vs. in *Pan* and *Gorilla*. In *Homo*, the OLS line shows slight positive allometry (slope of 1.046).

TABLE 6. FOSSIL HOMININ VS. EXTANT SAMPLES HL : Body Mass$^{1/3}$ INDEX *T*-TEST RESULTS*.

Fossil hominins HL : Body Mass$^{1/3}$ index *t*-test results:

	t_s	*p*	Reject null hypothesis of similarity?
Recent humans vs:			
A.L. 288-1 (human regression)	0.2694	0.788	No
A.L. 288-1 (hominoid regression)	−0.4434	0.658	No
LB1	−0.7964	0.426	No
Chimpanzees vs:			
A.L. 288-1 (human regression)	−0.6514	0.519	No
A.L. 288-1 (hominoid regression)	−1.2213	0.231	No
LB1	−1.3165	0.197	No
Gorillas vs:			
A.L. 288-1 (human regression)	−0.1274	0.900	No
A.L. 288-1 (hominoid regression)	−0.7007	0.489	No
LB1	−0.7964	0.432	No

*special computation of Student's *t*-statistic for comparison of a single individual to a sample mean; Sokal and Rohlf (1981)
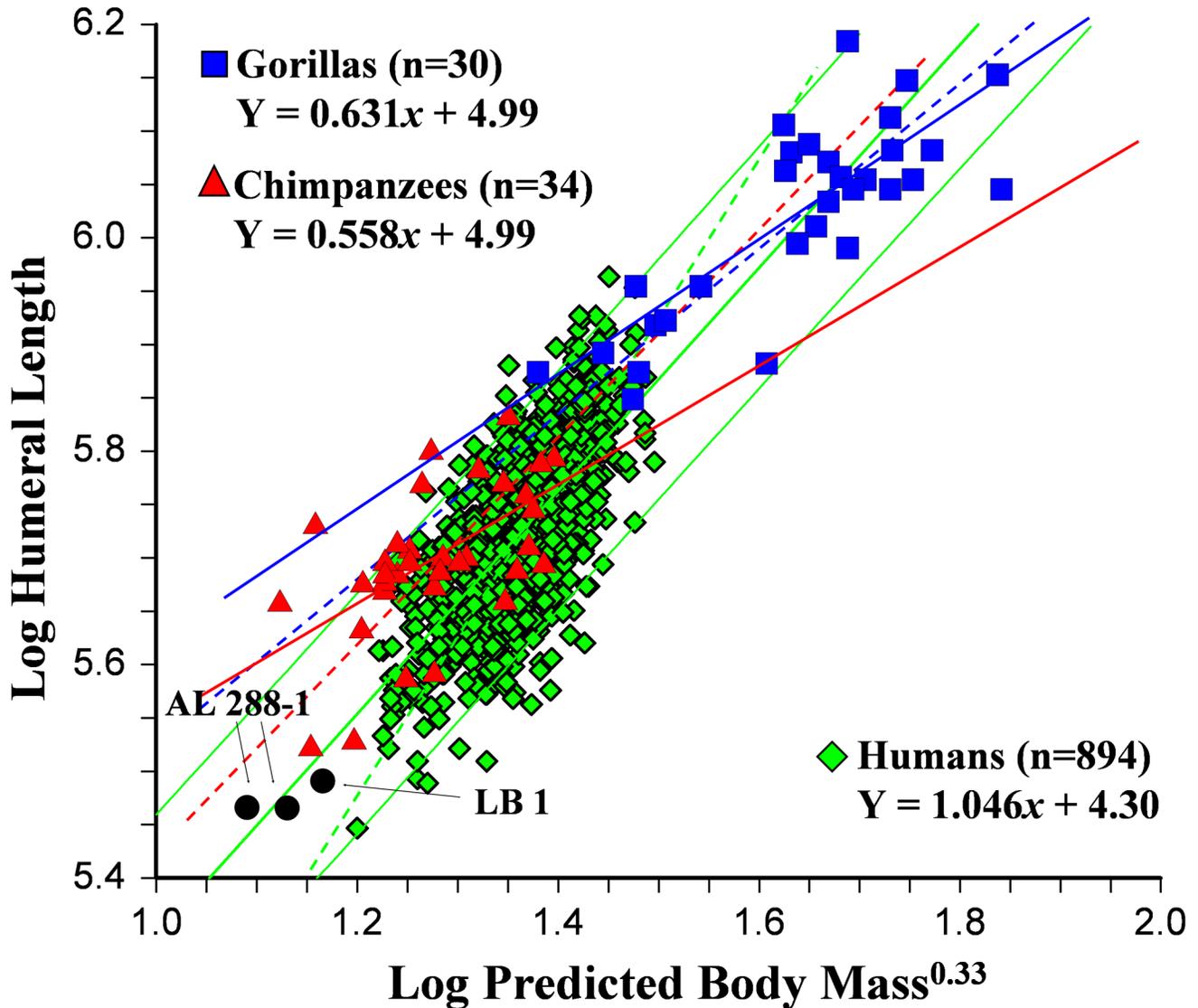
Figure 2. Scatter plot of log humeral length (in mm) regressed on log predicted body mass[1/3] (in kg) for recent humans, Gorilla, Pan, *A.L. 288-1, and LB1. Recent humans are indicated by green diamonds;* Pan *by red triangles;* Gorilla *by blue squares, and fossil hominins (including two body mass estimates for A.L. 288-1) by black circles. The OLS regression line for the recent humans is shown in green, as are the 95% confidence limits for the individuals about that line. The African ape OLS regression lines are shown in red (*Pan*) and blue (*Gorilla*). The RMA slopes for the recent humans and the African apes are indicated by dashed lines the same color as their respective OLS lines. Human RMA formula: Y=1.5022X+3.677;* Pan *RMA formula: Y=0.9757X+4.4517;* Gorilla *RMA formula: Y=0.7799X+4.745.*

However, since the 95% confidence limits (0.975–1.117) for the OLS slope span 1.0, we cannot rule out an isometric relationship between humerus length and body mass, a result corroborating that of Sylvester et al. (2008). The steeper human RMA slope, however, exhibits strong positive allometry (slope of 1.502). By way of contrast, in the two African ape genera, humeral length shows strong negative allometry—a finding consistent with those of Jungers (1982, 1985) and Drapeau and Ward (2007). The chimpanzee OLS slope, for example, is 0.558, with 95% confidence limits (0.269–0.846) that do not span 1.0. The chimpanzee RMA line is, as expected, steeper (its slope is 0.976), but still subisometric. Likewise, the gorilla OLS slope of 0.631 also has 95% confidence limits (0.453–0.808) that do not span

isometry, and the gorilla RMA line also has a subisometric slope of 0.78.

The diminutive and high humero-femoral index-bearing A.L. 288-1 and LB1 individuals tend to fall near the human OLS regression line. Quantification of the distance from the allometric trajectory is most easily accomplished via computation of the fossil hominins' percentage deviation from allometric expectation (Smith's [1980] d_{yx}); these data are reported in Table 7. A.L. 288-1, for whom we used two body mass predictions (one derived from three nonhuman hominoid regressions, the other based on two recent human regressions), falls almost directly upon the recent human OLS regression line, no matter which predicted body mass is used. Her d_{yx} values are −1.4% (nonhuman

TABLE 7. COMPARISON OF OLS- AND RMA-PREDICTED HL AND FL FOR A RECENT HUMAN THE SAME BODY SIZE AS A.L. 288-1 ("LUCY") AND LIANG BUA (LB) 1 TO THE OBSERVED LIMB LENGTHS OF THOSE FOSSIL HOMININS[1].

A.L. 288-1: Nonhuman hominoid regression predicted body mass of 29.7 kg:

	Predicted Humerus Length (mm)	Observed Humerus Length (mm)	Percentage Difference (observed to predicted)
OLS:	240.0	236.8	−1.4%
RMA:	215.9	"	+8.8%

	Predicted Femur Length (mm)	Observed Femur Length (mm)	Percentage Difference (observed to predicted)
OLS:	340.4	276.7	−23.0%
RMA:	313.0	"	−13.1%

A.L. 288-1: Recent human regression predicted body mass of 26.3 kg:

	Predicted Humerus Length (mm)	Observed Humerus Length (mm)	Percentage Difference (observed to predicted)
OLS:	230.0	236.8	+2.9%
RMA:	203.0	"	+14.3%

	Predicted Femur Length (mm)	Observed Femur Length (mm)	Percentage Difference (observed to predicted)
OLS:	320.0	276.7	−15.6%
RMA:	293.8	"	−6.2%

LB1: Recent human regression predicted body mass of 32.8 kg:

	Predicted Humerus Length (mm)	Observed Humerus Length (mm)	Percentage Difference (observed to predicted)
OLS:	248.8	243.0	−2.4%
RMA:	226.8	"	+6.7%

	Predicted Femur Length (mm)	Observed Femur Length (mm)	Percentage Difference (observed to predicted)
OLS:	352.3	276.7	−27.3%
RMA:	326.5	"	−18.0%

[1]The OLS and RMA slopes for log femoral length regressed on the cube root of log body mass$^{1/3}$ used in calculation of values in this table are based on the "global" sample of 731 recent humans reported in Holliday and Franciscus (2009: 226), and not just the 284 "heat-adapted" individuals used in Figure 1 of that paper. The recent human RMA formula for the femur length-body mass relationship is not reported in Holliday and Franciscus (2009); it is $Y=1.424X+4.132$.

hominoid prediction) and +2.9%, meaning that based on the OLS model, her humerus is only 1% shorter to 3% longer than would be expected for a human of her diminutive size—a result consistent with that of Jungers (1982, 2009). Likewise, Liang Bua 1 (*H. floresiensis*), who has nearly identical humerus and femur lengths to that of A.L. 288-1 but

who was in all likelihood heavier, deviates only –2.2% in humerus length from what would be expected for a recent human of her small body size following an OLS regression model. Note, however, that relative to the steeper slope of the human RMA regression, both A.L. 288-1 and LB1 have longer humeri than would be expected for a modern human of their diminutive size (and see below).

In contrast, despite falling near some chimpanzees in bivariate space, A.L. 288-1 and LB1 show markedly negative d_{yx} values from the chimpanzee OLS regression line (A.L. 288-1 nonhuman hominoid-predicted body mass d_{yx}= -13.8%; human-predicted body mass d_{yx}= -11.8%; LB1 d_{yx}= -13.1%), meaning these small hominins have shorter humeri than would be expected for a chimpanzee of their size. In spite of this finding, the fossils do lie closer to the (steeper) chimpanzee RMA line. Both these fossil individuals show a much more pronounced negative deviation (ca. –20.0%) from the gorilla OLS regression line, but given the marked difference in size between these diminutive specimens and even the smallest female gorilla, the extrapolation of the gorilla line to these fossil hominins is unwarranted.

DISCUSSION

The humero-femoral index of A.L. 288-1 has long begged an explanation, given that it lies so far beyond the human range of variation (in the current study its index value [85.6] falls over 6 standard deviations above the recent human mean), while at the same time falling far short of African ape ranges of variation (here, for example, its value lies 5 standard deviations below the chimpanzee mean). The more recent discovery of the holotype of *Homo floresiensis* (LB1) with a nearly identical index value (87.8, which in this study falls 7 standard deviations above the modern human mean, and some 4 standard deviations below the chimpanzee mean) has been of even greater importance because while LB1's exact taxonomic assignation is uncertain (Argue et al., 2006; Conroy and Smith, 2007; Falk et al., 2007; Gordon et al., 2008; Hershkovitz et al., 2007; Jacob et al., 2006; Martin et al., 2006; Morwood et al., 2005; Obendorf et al., 2008; Oxnard et al., 2010; Tocheri et al., 2007; Vannucci et al., 2011), whatever the specimen's ultimate taxonomic "fate," it clearly belongs within the genus *Homo*. This indicates that not only do high humero-femoral indices have great antiquity among the Hominini in general, but were also very likely plesiomorphic for the genus *Homo* as well (Hartwig-Scherer and Martin, 1991; Holliday, n.d.).

The major hypotheses generated to explain these humero-femoral indices have been related almost exclusively to locomotion. Specifically, if the high humero-femoral indices of these two specimens reflect shorter femora, and by extension, shorter lower limbs, then this would by default make A.L. 288-1 and LB1 less efficient at striding bipedal locomotion than hominins with longer lower limbs (Jungers 1982; Pontzer 2007; Steudel-Numbers 2006; Steudel-Numbers and Tilkens 2004). If, in contrast, their high humero-femoral indices are due to long humeri, then this, when (perhaps) coupled with elongated antebrachial segments, could reflect a continued selective pressure for arbo-

real competency (Senut 1978; Susman et al. 1984).

Over the past 20+ years, much of the field has accepted the position argued by Jungers (1982, 1991a, 1994) that the humero-femoral index of A.L. 288-1 (and by extension that of LB1; Jungers 2009; Morwood and Jungers 2009) is due to a much shorter femur than would be expected for a hominin of such diminutive size, coupled with a humerus of the expected length for a small-sized hominin. Yet our own analyses (Franciscus and Holliday 1992; Holliday and Franciscus 2009) suggested that the femoral lengths of both A.L. 288-1 and LB1 were about what would be expected for such small-sized hominins. We therefore set out to investigate humeral allometry across hominins and the African apes to verify if long humeri were the root of the high humero-femoral indices of these two fossil hominins.

Our allometric results for the humerus mirror those of Jungers (1991a, 1994, 2009) and Drapeau and Ward (2007) in that A.L. 288-1 (and LB1) appear to be characterized by humeri that are as long, but likely slightly longer than, those that would be expected for a human of their same diminutive size. Given the dearth of variability in relative humeral length among the African hominids (Aiello 1981; Drapeau and Ward 2007; Jungers 1991a, 1994; the current study), this result is perhaps not surprising. What is confirmed by the current analyses is that, despite the marked overlap in bivariate space among humans, chimpanzees, and gorillas for the humeral length to body mass relationship (and even though male gorillas tend to fall about an extension of the human OLS regression), these three genera do *not* share a common humeral length allometric trajectory. On the contrary, humans tend to show slight positive allometry to isometry in humeral length (as was found by Jungers [1982] and Sylvester et al. [2008]), whereas both chimpanzees and gorillas show strong negative allometry (consistent with the results of Drapeau and Ward [2007] and Jungers [1982, 1985]). In previous studies we have found that the femur shows much the same pattern of positive allometry (or perhaps isometry) with increasing size in recent humans (Franciscus and Holliday 1992; Holliday and Franciscus 2009).

These two separate observations (i.e., positive allometry to isometry in both humeral and femoral length among recent humans), make it unlikely that human HL : FL indices would be negatively correlated with body mass, since humeri do not become relatively longer with decreasing body size. This means that small size alone cannot explain the high humero-femoral indices of A.L. 288-1 and LB1. Indeed, using the nonparametric Spearman's rho statistic, Jungers (2009) has shown that HL : FL indices are *not* significantly correlated with body size among recent humans. In the current analyses, both the OLS and RMA regressions of human humeral length on body mass$^{1/3}$ fall close to the observed length of the humerus in A.L. 288-1 and LB1. We have previously demonstrated that the same pattern is found for the femur; i.e., A.L. 288-1 and LB1 fall near the human OLS and/or RMA slopes for femoral length on body mass$^{1/3}$ (Franciscus and Holliday 1992; Holliday and Franciscus 2009; and see Figure 3a in Pontzer et al. 2010). This

then begs the question as to why these diminutive fossil specimens have high HL : FL indices falling well beyond the range of recent humans.

It appears that the answer is that while both the humerus and femur of A.L. 288-1 and LB1 fall within the expected range for a human of their small size, if we consider both OLS and RMA regression lines, their humeri tend to be slightly longer than expected while their femora are shorter than expected. Specifically, the percentage deviations of A.L. 288-1 and LB1 from the human OLS and RMA humeral and femoral length to body mass$^{1/3}$ relationships show the following pattern. For the humerus, A.L. 288-1 has a humerus that ranges from 1.4% shorter to 14.3% longer than that expected for a human of her body size (see Table 7), yielding an average deviation from allometric expectation of +6.2%. Similarly, LB1 has a humerus 2.4% shorter to 6.7% longer than that expected for a modern human of her size, for a mean deviation of +2.2%. In terms of the femur, A.L. 288-1 has a femur that falls between 6.2% to 23% shorter than expected for a modern human of her body size (mean deviation= -14.5%); LB1 has a femur that falls between 18% to 27.3% shorter (mean deviation= -22.7%) than that expected for a human of her size. This suggests that one need not invoke strong selection for arboreal competency in either *Au. afarensis* (or *H. floresiensis*), neither in the form of (greatly) elongated upper limbs nor (radically) foreshortened lower limbs, but rather it is simply a combination of slightly longer humeri and somewhat shorter femora (both of which individually fall within the expected range of variation for modern humans of such diminutive size) that is responsible for the high humero-femoral indices that characterize these two specimens.

CONCLUSIONS

In summary, the conclusions drawn from the present analysis are:

1. Among the African hominids (*sensu lato*), humeral length is more phylogenetically conservative than femoral length, as reflected in humeral length : body mass ratios and analysis of bivariate humeral length allometry.
2. While there is much overlap among *Homo*, *Pan*, and (at least female) *Gorilla* individuals in bivariate space for the humeral length to body mass relationship, humeral length and body mass show very different allometric trajectories with slight positive allometry to isometry in humans and strongly negative allometry in *Pan* and *Gorilla* (as found previously by Jungers [1982, 1985] and Drapeau and Ward [2007]).
3. The high HL : FL indices of A.L. 288-1 and LB1 are due to a humerus that was slightly longer than that expected of diminutive modern humans and a femur that was somewhat shorter than expected for a similarly small-sized recent human.

REFERENCES

Aiello, L.C. 1981. The allometry of primate body proportions. In Day, M.H. (ed.), *Vertebrate Locomotion*. Academic Press, London, pp. 331–358.

Argue, D., Donlon, D., Groves, C., and Wright, R. 2006. *Homo floresiensis*: microcephalic, pygmoid, *Australopithecus* or *Homo*? *Journal of Human Evolution* 51, 360–374.

Biknevicius, A.R. 1999. Body mass estimation in armoured mammals: cautions and encouragements for the use of parameters from the appendicular skeleton. *Journal of Zoology, London* 248, 179–187.

Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., JatmikoWayhu Saptomo, E., and Rokus Awe Due. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431, 1055–1061.

Conroy, G.C. and Smith, R.J. 2007. The size of scalable brain components in the human evolutionary lineage: with a comment on the paradox of *Homo floresiensis*. *Homo* 58, 1–12.

Darveau, C.-A., Suarez, R.K., Andrews, R.D., and Hochachka, P.W. 2002. Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* 417, 166–170.

Drapeau, M.S.M and Ward, C.V. 2007. Forelimb segment length proportions in extant hominoids and *Australopithecus afarensis*. *American Journal of Physical Anthropology* 132, 327–343.

Falk, D., Hildebolt, C., Smith, K., Morwood, M.J., Sutikna, T., JatmikoSaptomo, E.W., Imhof, H., Seidler, H., and Prior, F. 2007. Brain shape in human microcephalics and *Homo floresiensis*. *Proceedings of the National Academy of Sciences, USA* 104, 2513–2518.

Franciscus R.G. and Holliday T.W., 1992. Hindlimb skeletal allometry in Plio-Pleistocene hominids with special reference to AL-288-1 (''Lucy''). *Bulletin et Mémoires de la Societé d'Anthropologie de Paris* 22, 1–16.

Garcia, G.L.M. and da Silva, J.K.L. 2006. Interspecific allometry of bone dimensions: a review of the theoretical models. *Physics of Life Reviews* 3, 188–209.

Gordon, A.D., Nevell, L., and Wood, B. 2008. The *Homo floresiensis* cranium (LB1): size, scaling, and early *Homo* affinities. *Proceedings of the National Academy of Sciences, USA* 105, 4650–4655.

Grine, F.E., Jungers, W.L., Tobias, P.V., and Pearson, O.M. 1995. Fossil *Homo* femur from Berg Aukas, Northern Namibia. *American Journal of Physical Anthropology* 97, 151–185.

Haeusler, M. and McHenry, H.M. 2004. Body proportions of *Homo habilis* reviewed. *Journal of Human Evolution* 46, 433–465.

Haile-Selassie, Y., Latimer, B.M., Alene, M., Deino, A.L., Gibert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., and Lovejoy, C.O. 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences, USA* 107, 12121–12126.

Harmon, E.H. 2009. The shape of the early hominin femur. *American Journal of Physical Anthropology* 139, 154–171.

Hartwig-Scherer, S. and Martin, R.D. 1991. Was "Lucy" more human than her "child"? Observations on early hominid postcranial skeletons. *Journal of Human Evolution* 21, 439–449.

Hens, S.M., Konigsberg, L.W., and Jungers, W.L. 2000. Estimating stature in fossil hominids: which regression model and reference sample to use? *Journal of Human Evolution* 38, 767–784.

Hershkovitz, I., Kornreich, L., and Laron, Z. 2007. Comparative skeletal features between *Homo floresiensis* and patients with primary growth hormone insensitivity (Laron Syndrome). *American Journal of Physical Anthropology* 134, 198–206.

Holliday, T.W. n.d. Body size, body shape, and the circumscription of the genus *Homo*. *Current Anthropology* (under review).

Holliday, T.W. and Franciscus, R.G. 2009. Body size and its consequences: Allometry and the lower limb length of Liang Bua 1 (*Homo floresiensis*). *Journal of Human Evolution* 57, 253–257.

Holliday, T.W. and Ruff, C.B. 2001. Relative variation in human proximal and distal limb segment lengths. *American Journal of Physical Anthropology* 116, 26–33.

Jacob, T., Indriati, E., Soejono, R.P., Hsu, K., Frayer, D.W., Eckhardt, R.B., Kuperavage, A.J., Thorne, A., and Henneberg, M. 2006. Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. *Proceedings of the National Academy of Sciences, USA* 103, 13421–13426.

Johanson, D.C., Lovejoy, O.C., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., and Coppens, Y. 1982. Morphology of the Pliocene partial skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. *American Journal of Physical Anthropology* 57, 403–451.

Jungers, W.L. 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297, 676–678.

Jungers, W.L. 1984. Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. *Yearbook of Physical Anthropology* 27, 73–97.

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 Press, New York, pp. 345–381.

Jungers, W.L. 1991a. A pygmy perspective on body size and shape in *Australopithecus afarensis* (AL 288-1, "Lucy").

In Senut, B. and Coppens, Y. (eds.), *Origine(s) de la bipédie chez les hominidés*. Cahiers de Paléoanthropologie, Paris, pp. 215–224.

Jungers, W.L. 1991b. Scaling of postcranial joint size in hominoid primates. *Human Evolution* 6, 391–399.

Jungers, W.L. 1994. Ape and hominid limb length. *Nature* 369, 194.

Jungers, W.L. 2009. Interlimb proportions in humans and fossil hominins: variability and scaling. In Grine, F.E., Leakey, R.E., and Fleagle, J.G. (eds.), *The First Humans: Origins of the Genus Homo*. Springer, Dordrecht, pp. 93–98.

Jungers, W.L. and Susman, R.L. 1984. Body size and skeletal allometry in African apes. In Susman, R.L. (ed.), *The Pygmy Chimpanzee: Evolutionary Morphology and Behavior*. Plenum Press, New York, pp. 131–178.

Kappelman, J. 1996. The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution* 30, 243–276.

Larson, S.G., Jungers, W.L., Tocheri, M.W., Orr, C.M., Morwood, M.J., Sutikna, T., Rokhus Due Awe, and Djubiantono, T. 2009. Descriptions of the upper limb skeleton of *Homo floresiensis*. *Journal of Human Evolution* 57, 555–570.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., and Rook, L. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.

Lovejoy, C.O. and Heiple, K.G. 1972. Proximal femoral anatomy of *Australopithecus*. *Nature* 235, 175–176.

Lovejoy, C.O., Meindl, R.S., Ohman, J.C., Heiple, K.G., and White, T.D. 2002. The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of morphogenesis to the human fossil record. *American Journal of Physical Anthropology* 119, 97–133.

Martin, R.D., Genoud, M., and Hemelrijk, C.K. 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. *Journal of Experimental Biology* 208, 1731–1747.

Martin, R.D., MacLarnon, A.M., Phillips, J.L., and Dobyns, W.B. 2006. Flores hominid: new species or microcephalic dwarf? *The Anatomical Record A. Discoveries in Molecular, Cellular, and Evolutionary Biology* 288, 1123–1145.

McHenry, H.M. 1978. Fore- and hindlimb proportions in Plio-Pleistocene hominids. *American Journal of Physical Anthropology* 49, 15–22.

McHenry, H.M. and Berger, L.R. 1998. Limb lengths in *Australopithecus* and the origin of the genus *Homo*. *South African Journal of Science* 94, 447–450.

McHenry, H.M. and Corruccini, R.S. 1978. The femur in early human evolution. *American Journal of Physical Anthropology* 49, 473–488.

Millien, V. 2008. The largest among the smallest: the body

mass of the giant rodent *Josephoartigasia monesi*. *Proceedings of the Royal Society B: Biological Sciences* 275, 1953–1955.

Millien, V. and Bovy, H. 2010. When teeth and bones disagree: body mass estimation of a giant extinct rodent. *Journal of Mammalology* 91, 11–18.

Morwood, M.J. and Jungers, W.L. 2009. Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography. *Journal of Human Evolution* 57, 640–648.

Morwood, M.J., Brown, P., Jatmiko, Sutikna, T., Wahyu Saptomo, E., Westaway, K.E., Rokus Awe Due, Roberts, R.G., Maeda, T., Wasisto, S., and Djubiantono, T. 2005. Further evidence for small-bodied hominins from the late Pleistocene of Flores, Indonesia. *Nature* 437, 1012–1017.

Münter, A.H. 1936. A study of the lengths of the long bones of the arms and legs in man, with special reference to Anglo-Saxon skeletons. *Biometrika* 28, 258–294.

Niskanen, M. and Junno, A.-L. 2009. Estimation of African apes' body size from postcranial dimensions. *Primates* 50, 211–220.

Obendorf, P.J., Oxnard, C.E., and Kefford, B.J. 2008. Are the small human-like fossils found on Flores human endemic cretins? *Proceedings of the Royal Society B: Biological Sciences* 275, 1287–1296.

Oxnard, C., Obendorf, P.J., and Kefford, B.J. 2010. Postcranial skeletons of hypothyroid cretins show a similar anatomical mosaic as *Homo floresiensis*. *PLOS One* 5:e13018.

Pontzer, H. 2007. Effective limb length and the scaling of locomotor cost in terrestrial animals. *Journal of Experimental Biolology* 210, 1752–1761.

Pontzer, H., Rolian, C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D., and Zollikofer, C.P.E. 2010. Locomotor anatomy and biomechanics of the Dmanisi hominins. *Journal of Human Evolution* 58, 492–504.

Richmond, B.G. and Jungers, W.L. 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* 319, 1662–1665.

Richmond, B.G., Aiello, L.C., and Wood, B.A. 2002. Early hominin limb proportions. *Journal of Human Evolution* 43, 529–548.

Ruff, C.B., Trinkaus, E., and Holliday, T.W. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387, 173–176.

Senut, B. 1978. *Contribution à l'étude de l'humérus et des articulations chez les Hominidés du Plio-Pléistocène*. Thèse Doctorat 3ème cycle, Paris: Université Pierre et Marie Curie.

Shea, B.T. 1981. Relative growth of the limbs and trunk in the African apes. *American Journal of Physical Anthropology* 56, 179–201.

Slome, D. 1929. The osteology of a Bushman tribe. *Annals of the South African Museum* 24, 33–60.

Smith, R.J. 1980. Rethinking allometry. *Journal of Theoretical Biology* 87, 97–111.

Smith, R.J. 2009. Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology* 140, 476–486.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. 2nd edition. Freeman, San Francisco.

Spocter, M.A. and Manger, P.R. 2007. The use of cranial variables for the estimation of hominin body mass. *American Journal of Physical Anthropology* 134, 92–105.

Steudel-Numbers, K.L. 2006. Energetics in *Homo erectus* and other early hominins: the consequences of increased lower limb length. *Journal of Human Evolution* 51, 445–453.

Steudel-Numbers, K.L. and Tilkens, M.J. 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *Journal of Human Evolution* 47, 95–109.

Susman, R.L., Stern, J.T., and Jungers, W.L. 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatologica* 43, 113–156.

Sylvester, A.D., Kramer, P.A., and Jungers, W.L. 2008. Modern humans are not (quite) isometric. *American Journal of Physical Anthropology* 137, 371–383.

Tocheri, M.W., Orr, C.M., Larson, S.G., Sutikna, T., Jatmiko Saptomo, E.W., Awe Due, R., Djubiantono, T., Morwood, M.J., and Jungers, W.L. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317, 1743–1745.

Vannucci, R.C., Barron, T.F., and Holloway, R.L. 2011. Craniometric ratios of microcephaly and LB1, *Homo floresiensis*, using MRI and endocasts. *Proceedings of the National Academy of Sciences, USA* 108:14043–14048

West, G.B., Brown, J.H., and Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276, 122–126.