Journal of Human Evolution 57 (2009) 223–228

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Body size and its consequences: Allometry and the lower limb length of Liang Bua 1 (*Homo floresiensis*)

Trenton W. Holliday [a,*], Robert G. Franciscus [b]

[a] *Department of Anthropology, Tulane University, New Orleans, LA 70118, USA*
[b] *Department of Anthropology, Neuroscience Graduate Program, University of Iowa, Iowa City, IA 52242-1322, USA*

A R T I C L E I N F O

Article history:
Received 26 June 2008
Accepted 15 April 2009

Keywords:
Australopithecus
Femur length
Body mass
Homo floresiensis

A B S T R A C T

Bivariate femoral length allometry in recent humans, *Pan*, and *Gorilla* is investigated with special reference to the diminutive Liang Bua (LB) 1 specimen (the holotype of *Homo floresiensis*) and six early Pleistocene femora referred to the genus *Homo*. Relative to predicted body mass, *Pan* and *Gorilla* femora show strong negative length allometry while recent human femora evince isometry to positive allometry, depending on sample composition and line-fitting technique employed. The allometric trajectories of *Pan* and *Homo* show convergence near the small body size range of LB 1, such that LB 1 manifests a low percentage deviation (d_{yx} of Smith [1980]) from the *Pan* allometric trajectory and falls well within the 95% confidence limits around the *Pan* individuals (but also outside the 95% confidence limits for recent *Homo*). In contrast, the six early Pleistocene *Homo* femora, belonging to larger individuals, show much greater d_{yx} values from both *Pan* and *Gorilla* and fall well above the 95% confidence limits for these taxa. All but one of these Pleistocene *Homo* specimens falls within the 95% confidence limits of the recent human sample. Similar results are obtained when femoral length is regressed on femoral head diameter in unlogged bivariate space. Regardless of the ultimate taxonomic status of LB 1, these findings are consistent with a prediction made by us (Franciscus and Holliday, 1992) that hominins in the small body size range of A.L. 288-1 ("Lucy"), including members of the genus *Homo*, will tend to possess short, ape-like lower limbs as a function of body size scaling.

Introduction

Over a decade ago, we published a paper (Franciscus and Holliday, 1992) that outlined predictions deriving from lower limb length allometry in *Australopithecus* and *Homo*. The crux of our argument followed from two observations: 1) among the African apes, lower limb length (as indicated by the femur) exhibits negative allometry, such that at larger body mass lower limbs are relatively shorter, and 2) humans deviate from this African hominoid trend by maintaining relatively long lower limbs at larger sizes. We suggested that the bivariate relationship between femur length and body mass in humans may exhibit positive allometry, but we could not rule out an isometric relationship as the confidence limits for our human regression line spanned isometry.

From these observations, we made the following predictions: 1) very small-bodied hominins in both the genera *Australopithecus* and *Homo* will tend to fall among the smallest-bodied African apes for the femur length to body mass bivariate allometric relationship, and 2) larger-bodied members of the genus *Australopithecus* will possess longer lower limbs, similar to those of *Homo*, deviating positively from the African ape femur length to body mass allometric relationship. The recent discovery of a small-bodied hominin referred to the genus *Homo* (*H. floresiensis*; Brown et al., 2004; holotype Liang Bua [LB] 1) provides an independent test of the first of our predictions.

Background

In 1982, Jungers evaluated the position of the diminutive *Australopithecus afarensis* A.L. 288-1 "Lucy" specimen relative to those of the African apes for the bivariate femur length:body mass relationship using Smith's (1980) measure of percentage deviation from allometric expectation (or d_{yx}, calculated as [observed femoral length − predicted femoral length/predicted femoral length] × 100). He found that unlike modern humans, A.L. 288-1 exhibited no significant positive deviation from allometric expectation from the African ape femur length to body mass relationship, but rather, depending on the body mass estimate used, "Lucy" either had a femur that ranged from 2.1% *shorter* than expected for an African ape of her size to one that was a mere 0.1% longer than expected.

* Corresponding author.
E-mail address: thollid@tulane.edu (T.W. Holliday).

0047-2484/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jhevol.2009.04.007

In contrast, Jungers (1982) found that his sample of recent *H. sapiens* had much longer femora than those expected for African apes of their body mass, exhibiting an average percentage deviation from allometric expectation (d_{yx}) range of 38.1–44.9%. Even a single Mbuti "Pygmy" specimen in Jungers' (1982) sample had a femur that was 21.1–23.3% longer than expected for an African ape of her body mass. Jungers interpreted these results for "Lucy" as consistent with an ape-like (i.e., shorter) lower limb length characteristic of *Australopithecus afarensis*.

Wolpoff (1983) disputed Jungers' (1982) analysis. He found that relative to an indicator of "Lucy's" trunk height (the ventral body height of the specimen's isolated lumbar vertebra [A.L. 288-1ak], thought to be an L2 or L3), the diminutive *A. afarensis* specimen had a femur length:lumbar vertebral body height ratio (14.5) that fell within the range of recent human "Pygmies" (14.2–19.4), and just below the range (14.9–19.8) of a small sample of Native Americans. He concluded that, contra Jungers (1982), A.L. 288-1 had a femur length that, relative to a measure of the height of her trunk, was within the modern human range of variation, especially once her diminutive size was taken into account (Wolpoff, 1983).

In 1983, Jungers and Stern responded to Wolpoff's (1983) argument. They analyzed a sample of Mbuti "Pygmies" with an estimated body mass range that spanned "Lucy's" estimated body mass and pointed out that none of the "Pygmies" had a femur shorter than 326 mm, which is 16% longer than "Lucy's." They also noted that human children tend to reach "Lucy's" weight at age 9, at which point their mean femoral length of 345 mm is 20% longer than "Lucy's." Additionally, they argued that L2/L3 ventral height was not a sufficiently reliable measure of trunk height, opting instead to create an index of femoral length to total pelvic height. By this measure, "Lucy" lay 3.9 standard deviations beyond the modern human mean.

Subsequently, Jungers (1991b) used Fully's (1956) anatomical method to produce stature estimates for 19 "Pygmy" skeletons, and then he used a regression equation derived from the Ituri Project data to predict body mass from those stature estimates. He found that his sample likely weighed between 23.9 to 48.2 kg (a range that almost certainly spans "Lucy's" body mass), yet all of the humans possessed significantly longer femora than "Lucy," in both an absolute and relative (via femur length:body mass$^{1/3}$ ratios) sense (but see below).

In 1992, we argued that both Jungers (1982, 1991b; Jungers and Stern, 1983) and Wolpoff (1983) were correct—each had documented one-half of the scaling pattern exhibited by humans and apes with regard to the length of the femur (Franciscus and Holliday, 1992). Using both a better estimate of "Lucy's" trunk height (which we termed "skeletal trunk height" and defined as the summed dorsal body heights of her thoracic and lumbar vertebrae plus the ventral height of the sacrum), as well as estimates of body mass, we found two significant patterns. First, relative to the predicted height of her trunk, "Lucy's" femur was nearly as long as would be expected for a modern human of her diminutive size, just as Wolpoff (1983) had suggested. Second, and more importantly, relative to body mass, "Lucy's" femoral length appeared to fall at the confluence of the human and African ape allometric trajectories. This confluence is due, in part, to the fact that among African apes, the allometric relationship between femoral length and body mass is subisometric (i.e., exhibits negative allometry—a fact noted by Jungers and Stern [1983]). In other words, as African apes increase in size, their femora become disproportionately shorter. Note that the converse of this statement is also true—as African apes decrease in body mass, their femora get disproportionately longer. By way of contrast, as humans become larger, they retain longer femora. We suspected that the femoral length:body mass relationship among modern humans may have exhibited positive allometry, but given that the confidence limits for our allometric line spanned isometry, we could not reject the null hypothesis of isometry for that particular bivariate relationship (Franciscus and Holliday, 1992).

The more significant aspect of our second finding is that it explains the non-deviation of "Lucy" from the African ape femoral length:body mass allometric relationship. Specifically, because apes the size of "Lucy" would be expected to have relatively longer lower limbs than the large extant African apes, they fall in an area of overlap between the human and ape femoral length:body mass relationship. In other words, the human and ape femur length:body mass allometric lines appear to converge in "Lucy's" body mass range (Franciscus and Holliday, 1992). In contrast, most modern humans, who are much larger in size than "Lucy," will show greater positive deviations from African ape allometric expectation because as African apes get larger, their femora become shorter, a trend from which humans deviate.

From these observations we made two predictions. First, any hominin as small as "Lucy," including members of the genus *Homo*, would tend to have a femur as short as "Lucy's." Second, hominins much larger than "Lucy," including those referred to the genus *Australopithecus*, will evince much greater positive deviations from the ape allometric expectation for the femur length:body mass bivariate allometric relationship. We tested the second of these two predictions in 1992 and found that some femora assigned to the genus *Australopithecus* (or *Paranthropus*) did show significant positive deviation from African ape allometric expectation (Franciscus and Holliday, 1992), although these were based on fragmentary femora requiring length estimation (and as isolated postcranial elements, were also open to alternative taxonomic assignment). This result is not unexpected if one views *Australopithecus* as fundamentally bipedal (albeit with subtle anatomical differences likely due to retained arboreal competency), while the extant African apes are fundamentally quadrupedal.

The 2004 discovery of LB 1 provides an opportunity to: 1) independently test our first, as yet, untested prediction (and Wolpoff's [1983] contention), that an adult member of the genus *Homo* as small as "Lucy" (even adult "Pygmies" tend to be larger than she is; see below) will show a femoral length of near-equal length to that of "Lucy" and, 2) revisit the basic scaling argument put forth in our original paper with enhanced comparative data.

Table 1
Comparative samples.

	Female	Male	Total *n*
Recent Humans:			
African-American[a]	29	27	56
Andaman Islanders[b]	2	6	12
East Africa[c]	19	27	46
Egypt[d]	35	31	66
Kerma (Sudan)[e]	18	27	45
Nubia[e]	7	13	20
African "Pygmy"[f]	3	7	10
San[b]	5	3	8
West Africa[g]	5	16	21
African Apes:			
Pan troglodytes[h]	17	9	26
Gorilla gorilla[h]	7	20	27

[a] Terry Collection, Smithsonian Institution.
[b] Natural History Museum, London. The Andaman Island sample includes 4 individuals for whom sex could not be determined.
[c] Makere University, Kampala; Kenya National Museums; Nairobi.
[d] Peabody Museum, Harvard University.
[e] Duckworth Collection, University of Cambridge.
[f] Université de Genève, Geneva; Institute Royale des Science Naturelles, Brussels.
[g] Musée de L'Homme, Paris.
[h] Cleveland Museum of Natural History and the Smithsonian Institution.