Special Issue: *Australopithecus sediba*

Body Size and Proportions of *Australopithecus sediba*

TRENTON W. HOLLIDAY
Department of Anthropology, Tulane University, New Orleans, LA 70118, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; thollid@tulane.edu

STEVEN E. CHURCHILL
Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; churchy@duke.edu

KRISTIAN J. CARLSON
Department of Integrative Anatomical Sciences, Keck School of Medicine of the University of Southern California, Los Angeles, CA 90033, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; kristian.carlson@usc.edu

JEREMY M. DESILVA
Department of Anthropology, Dartmouth College, Hanover, NH 03755, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; jeremy.m.desilva@dartmouth.edu

PETER SCHMID
Anthropological Institute and Museum, University of Zurich, Winterthurerstr. 190, CH-8057 Zurich; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; smidi@aim.uzh.ch

CHRISTOPHER S. WALKER
Department of Molecular Biomedical Sciences, College of Veterinary Medicine, North Carolina State University, Raleigh, NC 27607; Department of Evolutionary Anthropology, Box 90383, Duke University, Durham, NC 27708, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; Christopher_walker@ncsu.edu

LEE R. BERGER
Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, SOUTH AFRICA; profleeberger@yahoo.com

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ABSTRACT

While the timing, duration, and nature of the shift is debated, human evolution ultimately involved an increase in body size relative to our Miocene ancestors, and a transition from a more arboreal to a more terrestrial way of life. This is reflected not only in the articular and muscular attachment morphology of the upper and lower limbs, but also in the relative proportions of the limb segments, in particular the relative lengths of the bones of the forearm (and to a lesser extent, those of the arm) contrasted with those of the lower limb. Specifically, from both fossil and extant hominoid morphology, it is evident that hominin evolution was characterized by an increase in lower limb length and joint size and a decrease in upper limb (particularly forearm) length and articular size. These shifts appear to have been non-concurrent, with at least some of the increase in lower limb length antedating the decrease in antebrachium length. Well-preserved skeletal elements from the upper and lower limb of 1.98 Ma *Australopithecus sediba* from Malapa, South Africa, contribute to our understanding of this adaptive shift, as well as facilitating an investigation of the species' body size. In terms of body size, *Au. sediba* appears to have been small for a Plio-Pleistocene hominin, with body mass estimates ranging from ca. 30–36kg. Morphology consistent with climbing and/or suspensory behavior has been documented in the upper limb and foot of *Au. sediba*. In addition, the lower limb does not appear to be as elongated as that of early *Homo*, suggesting that long-distance terrestrial bipedality was not a regular part of the species' behavioral repertoire.

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INTRODUCTION

The limb and body proportions of *Homo sapiens* are unusual among the living hominoids in that the upper limb, especially the antebrachium (forearm), is greatly foreshortened, while both segments of the lower limb are markedly elongated (Drapeau and Ward 2007; Jungers 2009; Schultz 1937; White et al. 2015). Longer lower limbs are an adaptation to terrestrial bipedality, making this mode of locomotion more efficient, while shorter forearms likely reflect the lack of upper limb use during terrestrial bipedality, coupled with a decreased involvement in arboreal locomotor activities (Jungers 1982; Pontzer 2007; Sylvester 2006). Humans also show different allometric trends than do the great apes, in that human limb lengths are isometric to slightly positively allometric with body size, while in the great apes, limb lengths tend to show negative allometry with body size (Holliday and Franciscus 2009, 2012; Jungers 1982; Sylvester et al. 2008). The shift in limb proportions within the hominin lineage may have been mosaic in nature. For example, it has been argued that *Australopithecus afarensis* had shorter lower limbs than (at least some) members of the genus *Homo* (Jungers 1982, 2009; Stern 2000), or, alternatively, that their lower limbs were nearly as long as those of *H. sapiens*, once their smaller body mass is taken into account (Holliday 2012; Pontzer 2012; Lovejoy et al. 2016; Ward 2002; Wolpoff 1983). It is also possible that the antebrachia of *Au. afarensis* were as foreshortened as would be expected for a human of their body size (Drapeau and Ward 2007; Holliday 2012; Ward 2002). In contrast, the later South African species *Au. africanus* may have been characterized by shorter lower limbs and longer upper limbs than its East African cousin, perhaps reflecting a greater degree of arboreality for this paleospecies (McHenry and Berger 1998), although the limb proportion evidence available for this species remains limited and fragmentary. It has also been argued that *H. habilis* had a similarly long-armed and short-legged body shape (Hartwig-Scherer and Martin 1991; Stern 2000; but see Haeusler and McHenry 2004; Richmond et al. 2002); however, the fragmentary state of the associated skeletons referred to this taxon precludes an accurate assessment of their overall body proportions (Holliday 2012), and the taxonomic attribution of key postcranial specimens to this taxon is questionable (Berger et al. 2010). Also, at Bouri, Ethiopia, a 2.5 Ma specimen (perhaps representing *Au. garhi*) has been said to evince modern human-like humero-femoral length proportions in the context of elongated antebrachia (Asfaw et al. 1999), but its estimated humeral length has recently been called into question (Churchill et al. 2013; Holliday 2012). In contrast to the scant data present for other early hominin taxa, it is widely recognized that *H. erectus* (*sensu lato*) evinces limb proportions that fall within the range of people today (Antón 2003), although there are some data suggestive of a somewhat elongated upper limb among the earlier members of this taxon (Holliday 2012).

Body size, and in particular, body mass, is itself a key morphological feature with energetic, behavioral, and ecological correlates (Damuth and MacFadden 1990), and hominin evolution clearly involved an overall increase in body size from the *Pan*/*Homo* LCA to that found in modern humans. Since the 1980s, when analyses of the *Au. afarensis* specimen A.L. 288-1 ("Lucy") and KNM-WT 15000 *H. erectus* ("Nariokotome Boy") were the field's cutting edge, the most-commonly held view was that this size increase was first manifest with the emergence of *H. erectus*. The more recent discovery and analysis of larger-sized *Au. afarensis* specimens (Haile-Selassie et al. 2010; Ward et al. 2012), along with new assessments of early hominin body size (Grabowski et al. 2015) demonstrating clear overlap in size between *Australopithecus* and *Homo*, have led some researchers to argue that this long-held view of a simplistic dichotomy between small-bodied australopiths and large-bodied *Homo* is no longer tenable (Grabowski et al. 2015; Jungers et al. 2016).

There is continuing controversy surrounding the estimation of body mass in fossil hominins, ranging from issues as varied as which line-fitting technique one should use (Aiello 1992; Grabowski et al. 2015; Ruff et al. 2012; Smith 2009) to which variable(s) are more likely to yield accurate results (Elliot et al. 2016; Jungers et al. 2016; McHenry 1992; Ruff et al. 2000; Walker et al. 2018), to whether multivariate measures should be used (Grabowski et al. 2015; Jungers et al. 2016), to issues surrounding the use of recent industrialized / less active / more obese populations to estimate the body mass of prehistoric humans (Niskanen et al. 2018; Squyres and Ruff 2015), to workers who suggest all methods are likely to lead to unreliable results (Jeanson et al. 2017).

An additional problem with using data from *H. sapiens* to estimate body mass of australopiths concerns scaling of the femoral head, the skeletal variable most frequently used in estimating hominin body mass (Jungers et al. 2016; McHenry 1992; Ruff et al. 2018; Squyres and Ruff 2015). Specifically, members of the genus *Homo* tend to have larger femoral heads than australopiths (Harmon 2005, 2009; Holliday et al. 2010; Jungers 1988; Lovejoy et al. 1973), and Ruff et al. (2018) find that australopiths tend to have much smaller femoral head/shaft breadth proportions than modern humans, as revealed in Figure 4 in Grabowski et al. (2015).

Grabowski and colleagues (2015) use a multivariate estimation technique that tends to minimize the impact of femoral head size on body mass estimation and should therefore circumvent this problem. Their results suggest that the published body masses of many early hominins are overestimates. For example, while White et al. (2009)

estimate the body mass of *Ardipithecus ramidus* at ca. 50kg, Grabowski et al. (2015) calculate its mass at 32.1kg. Similarly, while previous estimates (Antón 2012; Antón et al. 2014; Holliday 2012; McHenry 1988, 1992; Steudel 1980; Wolpoff 1973) of *Au. africanus* body mass range from 34–45.5kg, Grabowski et al. (2015) estimate the mean mass of this taxon at 30.5kg.

Ruff et al. (2018) point out that the Grabowski et al. (2015) data are cadaveric body weights from the Terry and Hamann-Todd skeletal collections, and note that both Terry and Todd state how unreliable their recorded body masses are, given wasting and variable dehydration of the bodies in question, as well as variability in how much time transpired between death and the cadavers' arrival for processing. It is perhaps unsurprising, then, that the Grabowski et al. (2015) equations yield much lower body mass estimates than other previous studies, and their estimates should be taken with caution.

Despite the above, the majority of data still suggest that the first significant body size increase in the Hominini was manifest among members of the genus *Homo*, rather than in *Australopithecus* (Antón et al. 2014; Grabowski et al. 2015; Holliday 2012; Jungers et al. 2016; McHenry 1992, 1994; Pontzer 2012; Ruff 2002), and in light of this fact, the body size and proportions of the 1.98 Ma paleospecies *Au. sediba*, from the site of Malapa, South Africa, are of particular interest because of the species' temporal position and its possible phylogenetic links to the genus *Homo* (Berger et al. 2010; Dembo et al. 2016; Irish et al. 2013). As has been discussed elsewhere (Berger 2013; Berger et al. 2010), in much of its postcranial anatomy, *Au. sediba* shares apomorphies with the genus *Homo*, while other aspects of its morphology retain the more plesiomorphic (i.e., australopith-like) condition. Assessment of the limb and body proportions of Malapa Hominin 1 (MH1) has been somewhat difficult due to the fragmentary nature and juvenile status of the individual. In contrast, Malapa Hominin 2 (MH2), an adult female, has thus far yielded a nearly complete upper limb and pectoral girdle skeleton, along with a fairly complete pelvis and partial femur, permitting detailed evaluation of that individual's limb and body proportions. In addition, the complete left femoral diaphysis of MH1 has recently been discovered encased within a large breccia block. This bone and a distal tibia originally assigned to MH1 but now assigned to another (likely) adult individual (MH4) allow for the investigation of relative lower limb length in *Au. sediba*. In terms of body size, dimensions of lower limb weight-bearing articular surfaces (see below) suggest that all three *Au. sediba* individuals had body masses between ca. 30–36 kg, placing them in the size range of smaller individuals of *Au. afarensis* and *Au. africanus*, and well below the size range of specimens attributed to early *Homo* (Holliday 2012; Jungers 1982; McHenry 1992). Grabowski et al. (2015) calculate an even smaller body mass estimate for *Au. sediba* at 25.8kg (but see above). In this study, we evaluate body proportions in *Au. sediba* to assess if they differ from those of *Au. africanus* via the use of regression (ordinary least-squares [OLS]) analyses.

MATERIALS

Data for *Au. sediba* were taken by the authors and their colleagues on either the original specimens, or from virtual reconstructions (Tables 1 and 2). Most *Au. sediba* osteometric data have been reported previously (Berger et al. 2010; Churchill et al. 2013; DeSilva et al. 2013; Kibii et al. 2011); however there are some new *Au. sediba* data analyzed here not reported in previous analyses. First, the distal four-fifths of a tibia with a preserved length of 233.8mm was originally assigned to MH1, but has since been provisionally assigned to a second (presumed) adult individual, MH4. Using the preserved distal end of the bone and positioning it within a natural mold of the specimen evident in the calcified matrix, the mean length estimate derived by three of us (TWH, SEC, and LRB) is between 267–275.5mm, depending on whether the top of the mold represents the metaphyseal or epiphyseal surface. This measurement corroborates the estimate reported in DeSilva et al. (2013) of 271mm, with a range of 267–275mm. Here we also calculate the articular area of this tibia's trochlear facet, modeling its surface as a trapezoid using the following measurements: tibial talar trochlear surface mediolateral diameter: 17.2mm, tibial talar trochlear surface anteroposterior diameter (medial): 18mm, tibial talar trochlear surface anteroposterior diameter (lateral): 18.3mm.

Given similarities in crural indices (tibial length / femur length) across the African apes and humans, femur length was also estimated for MH4 from the tibial length estimate cited above. Here we use the mean crural index of 83.6 of our human sample (Table 3) to yield two MH4 femur length estimates: 319.4 and 329.5mm (see Table 1). This conservative crural index method is preferable to OLS prediction of femoral length from tibial length in that the MH4 tibia lies at the extreme upper end of the *P. troglodytes* sample and the extreme lower end of the *H. sapiens* sample. For this reason, OLS regressions give widely divergent femur length estimates with large 95% confidence intervals (Table 4). Note, too, that tibial length for the A.L. 288-1 specimen was also estimated at 234.1mm from femur length using the same crural index value (see Table 1).

The juvenile status of MH1 necessitated estimation of three important parameters. First, the right humerus of this individual lacks the proximal epiphysis, but is otherwise intact. To estimate maximum length of the bone, we virtually fit the right humeral head of the similarly-sized individual MH2 onto the MH1 humerus, producing a length estimate of 248mm. Second, the left femoral diaphysis of the MH1 juvenile was discovered via medical CT scanning of a block of calcified clastic matrix. Subsequent estimation of its length *in situ* was made from a rendering of the specimen, yielding a preserved maximum length of 262mm (sans epiphyses). In order to estimate what its bicondylar length would be with attached epiphyses, a measurement of the diaphysis in its anatomical orientation (259mm) was combined with the similarly-sized MH2 epiphyses, yielding a femoral length estimate of 287mm, the length we use in these analyses. This estimation method was checked against that of Ruff (2007), who measured diaphyseal and

TABLE 1. *AUSTRALOPITHECUS SEDIBA* AND COMPARATIVE FOSSIL LOWER LIMB DATA (mm).

Specimen/Taxon	AP femoral head diameter	Femoral Length	Tibial Length	Bi-iliac Breadth	Source
MH1	32.5	287	-	-	see text
MH2	32.7	-	-	250	Berger et al. (2010); Kibii et al. (2011); see text
MH4	-	(319.4–329.5)	(267–275.5)	-	see text
ARA-VP-6/500 (*Ar. ramidus*)	-	312–323	262	-	Lovejoy et al. (2009)
A.L. 152-2 (*Au. afarensis*)	33.1	327	-	-	Harmon (2005)
A.L. 288-1 (*Au. afarensis*)	28.3	280	234.1	258	Johanson et al. (1982); Ruff (1991); see text
A.L. 827-1 (*Au. afarensis*)	38.1	368–382	-	-	Harmon (2005)
KSD-VP-1/1 (*Au. afarensis*)	38	418–438	-	-	Haile-Selassie et al. (2010)
KNM-ER 1472 (*Homo* sp.)	38.6	401	-	-	DeSilva measurements
KNM-ER 1481 (*Homo* sp.)	42.1	396	332.6	-	DeSilva measurements
KNM-WT 15000 (*H. erectus*)	(46) from SI diameter	432	380	292	Ruff and Walker (1993)
Dmanisi 3901/4507 (*H. erectus*)	40	386	306	-	Lordkipanidze et al. (2007)
OH 35 (*Homo* sp.)	-	-	259	-	Susman and Stern (1982); see text
Liang Bua 1 (*H. floresiensis*)	31	280	237.5	-	Brown et al. (2004); Jungers et al. (2009)
Kabwe E.691 (*Homo rhodesiensis* or *H. heidelbergensis*)	-	-	416	-	Churchill measurement

TABLE 2. *AUSTRALOPITHECUS SEDIBA* AND COMPARATIVE FOSSIL UPPER LIMB DATA (mm).

Specimen/Taxon	Clavicle Length	Humerus Length	Humerus AP Head Diameter	Humerus Distal Articular Breadth	Radius Length	Radius AP Head Diameter	Source
MH1	-	248	-	37.7	-	-	see text
MH2	107.5	269	32.3	32.4	226	18.8	see text
ARA-VP-6/500 (*Ar. ramidus*)	-	278			250		Lovejoy et al. (2009)
A.L. 288-1 (*Au. afarensis*)	-	236.8	26.8	30.1	174-215	15	Richmond et al. (2002); Asfaw et al. (1999); Johanson et al. (1982); see text
KNM-WT 15000 (*H. erectus*)	130.5 (r) 130.4 (l)	319	-	40.8	255	-	Ruff and Walker (1993); see text
Dmanisi 4507/4161/4162 (*H. erectus*)	135.6 (r) 137.3 (l)	295	-		-	-	Lordkipanidze et al. (2007)
Liang Bua 1 (*H. floresiensis*)	91 (r)	243	-		190	-	Brown et al. (2004); Larson et al. (2009)

TABLE 3. SUMMARY STATISTICS FOR THE CRURAL INDEX (100*tibia maximum length/femur bicondylar length) FOR THE AFRICAN HOMINID (*sensu lato*) SAMPLE.

Taxon	*Homo sapiens*	*Pan troglodytes*	*Gorilla* spp.
Mean	83.6	83.9	80.3
SD	2.7	3.2	3.5
n	1156	62	54
Range	74.9–91.6	75.5–91.1	72.8–88.2

long bone lengths from radiographs of subadult individuals from the Denver growth study. Ruff (2007) provides predictive ratios between diaphyseal length and the combined epiphyseal-diaphyseal long bone length in anatomical position for the 13–17 year age group. For the femur, the recommended ratio is 1.097 (Ruff 2007). When maximum length of the MH1 left femoral diaphysis (262mm) without its epiphyses is multiplied by this ratio, the result (287.4mm) is an estimate nearly identical (a difference of ca. 0.1%) to that derived via the methodology used here.

Finally, the MH1 right proximal femur lacks its epiphysis, and the metaphyseal plate has suffered some taphonomic damage (and presents as two conjoined fragments). Uncertainty exists as to whether the two portions conjoin cleanly or if the specimen has suffered some loss of bone in the area of the break. Berger at al. (2010) operated on the assumption that the pieces refit cleanly, and from the size of the metaphyseal plate they estimated a femoral head anteroposterior diameter of 29.8mm. However, if indeed some bone loss has occurred, a larger estimate (on the order of 33mm as reported in [DeSilva et al. 2013]) would be appropriate. Recent efforts (conducted by Ashley Hammond) to fit a sphere to the preserved portion of the metaphyseal plate support the use of a larger estimate, and suggest an anteroposterior diameter of 32.5mm, which is the estimate used here.

Comparative data for *H. sapiens*, *P. troglodytes* and *Gorilla* spp. were measured by TWH, with some additional *Pan* and *Gorilla* data provided courtesy of Campbell Rolian. Descriptions of these data sets are found elsewhere (Garvin et al., 2017; Holliday 1995; Holliday and Friedl 2013; Holliday and Hilton 2010). Comparative fossil data were either measured by the authors or their colleagues, or are taken from the literature (see Tables 1 and 2; Table 5).

METHODS

BODY MASS ESTIMATION

With the exception of the ARA-VP-6/500 *Ardipithecus ramidus* individual, for which body mass estimates are taken from Lovejoy et al. (2009), body mass (Y) was estimated from femoral head anteroposterior diameter (*X*) for the extant African hominid (*sensu lato*) samples as well as for fossil hominins, using regression analyses. Estimated body mass (EBM) data for *Pan* and *Gorilla* were derived from anteroposterior femoral head diameter. For these taxa, EBM is calculated from the generic formulae (*Pan* and *Gorilla*) reported in Almécija et al. (2015).

Humans support a higher percentage of their body weight on their hindlimbs than do the apes, and therefore,

TABLE 4. ORDINARY LEAST-SQUARES REGRESSIONS OF FEMORAL BICONDYLAR LENGTH (FL) ON TIBIAL MAXIMUM LENGTH (TL), *HOMO SAPIENS* AND *PAN TROGLODYTES*, AND THE PREDICTED FEMORAL LENGTH OF MH4 (with standard error of the prediction and its 95% confidence limits).*

***H. sapiens* OLS regression of FL on TL: Y=1.002*X*+70.669; r=0.93, n=1156**

Tibial Length	Pred. Femur L.	S.E.	95% LL	95% UL
267	338.13	12.66	313.31	362.94
275.5	346.6	12.65	321.85	371.44

***P. troglodytes* OLS regression of FL on TL: Y=0.807*X*+95.562; r=0.81, n=62**

Tibial Length	Pred. Femur L.	S.E.	95% LL	95% UL
267	310.96	9.57	291.82	330.11
275.5	317.82	9.68	298.45	337.19

*Both the MH4 and the A.L. 288-1 tibiae have a range of estimated maximum lengths, here represented by a maximum and a minimum.

TABLE 5. COMPARATIVE SAMPLES FOR REGRESSION ANALYSES–MAXIMUM SAMPLE SIZES.

Taxon	Male	Female	Sex Unknown
Homo sapiens	551	397	25
Pan troglodytes	45	69	5
Gorilla spp.	40	39	0

for any given body mass, have larger femoral head diameters. For this reason, body mass for fossil hominins is likely better estimated from human than nonhuman hominoid formulae (McHenry 1992), since unlike the quadrupedal extant African apes, *Australopithecus* and early *Homo* were obligate bipeds. Thus, for these analyses, fossil and recent hominin body mass was estimated from anteroposterior femoral head diameter (Table 6) following formulae from Ruff et al. (1997) and Grine et al. (1995). Specifically, the result of the combined-sex OLS formulae in Ruff et al. (1991) was averaged with the result of the OLS combined-sex formula from Grine et al. (1995). Auerbach and Ruff (2004) note that the Grine et al. (1995) equation tends to overestimate body mass, while the Ruff et al. (1997) formula tends to underestimate body mass; they therefore recommend using an average of the two methods to reduce directional bias. Note, however, that while the Grine et al. (1995) formula does tend to yield higher body mass estimates, it is nonetheless useful to use in light of the fact that for any given body mass, an australopith will most likely have a smaller femoral head than a modern human.

Note, too, that when *Australopithecus* body mass data are estimated using the *Pan*-specific formula (see Table 6), the "human" and "nonhuman hominoid" estimates differ little for smaller body-sized hominins, but there is a greater disparity for the larger hominins. For example, the average difference between the *Pan* vs. hominin body mass estimate for the smallest five fossil hominins in Table 6 is 7.3%, ranging from 3.2% to 9.6%. By way of contrast, for the largest six hominins, the average difference between the two estimates is 14.9% (the hominin regression always yields the heavier of the two estimates), with a range of 13.4% to 17.4%.

Based on the remains of three individuals, body size of *Au. sediba* appears to be uniformly small. As revealed in Table 6, estimated body mass (from femoral head size) of the juvenile MH1 is ca. 35kg, while that of the adult MH2 is ca. 35.5kg. It also appears that the presumed adult MH4 (thus far represented solely by a partial tibia) was characterized by a similarly small body size. Specifically, using the tibial distal articular (talar) surface area to estimate the size of the femoral head yields an estimated anteroposterior femoral head diameter of ca. 30.7mm, with a standard

TABLE 6. BODY MASS ESTIMATES FOR FOSSIL HOMININS BASED ON HUMAN AND NONHUMAN HOMINOID REGRESSION ANALYSES OF FEMORAL ANTEROPOSTERIOR DIAMETER ON BODY MASS.

Specimen	**Grabowski et al. (2015) estimate[1] (kg)**	**Grine (1995) formula estimate (kg)**	**Ruff et al. (1997) formula estimate (kg)**	**Ruff et al. (2012) formulae estimate[2] (kg)**	**Almécija et al. (2015) *Pan* formula estimate (kg)**	**Current study estimate[3] (kg)**
MH1	29.7	37.2	32.9	29.7	32.2	**35**
MH2	29.1	37.7	33.3	30.2	32.5	**35.5**
A.L. 152-2	28.6	38.6	34.2	31.2	33.2	**36.4**
A.L. 288-1	26	27.7	23.5	19.2	24.8	**25.6**
A.L. 827-1	38.2	50.1	45.6	43.9	42.1	**47.9**
KSD-VP-1/1	40.9*	49.7	45.2	43.4	41.8	**47.4**
KNM-ER 1472	45.4	51	46.5	44.9	42.8	**48.8**
KNM-ER 1481	40.9	59	54.4	53.6	48.9	**56.7**
KNM-WT 15000	53.3	67.8	63.1	63.3	55.8	**65.5**
Dmanisi 4507	40.7	54.2	49.7	48.3	45.3	**51.9**
LB1	27.5	33.8	29.5	25.9	29.6	**31.7**

[1] The multivariate estimate unless indicated by an asterisk, in which case it is the univariate estimate.

[2] The arithmetic average of the male- and female-specific formula results.

[3] The arithmetic average of the Ruff et al. (1997) estimates with the Grine et al. (1995) estimates.

error of the estimate of 2.36mm (based on a human OLS regression), which is ca. 5.5% smaller than the anteroposterior femoral head diameter of either MH1 (32.5mm, itself estimated from the metaphyseal surface; see above) or MH2 (32.7mm). With a (likely) smaller femoral head than either MH1 or MH2, then, MH4 was almost certainly smaller in body mass. As the three Malapa individuals share similarly small size, the MH4 tibial length (267mm and 275.5mm), and femoral lengths estimated from it (319.4mm and 329.5mm), are combined with the upper limb skeleton of MH2 to form a "composite individual" for the evaluation of interlimb proportions (i.e., intermembral and humerofemoral proportions). Note that if MH2, which has a complete humerus, were in fact characterized by a humerofemoral index identical to that of A.L. 288-1, the MH2 femur would be 318mm in length, nearly identical to the lower of the two estimates given above. Also, as MH4 appears to have been slightly smaller than MH2 based on the distal tibia comparison, the lower limb length estimates used here should be viewed as conservative; the actual MH2 lower limb segment lengths (which may be recovered in the future) could have been longer.

REGRESSION ANALYSES

Bivariate scatterplots were generated to investigate body proportions using data available for *Au. sediba*; specifically, the position in bivariate space of the *Au. sediba* specimens were compared to samples of *H. sapiens*, *P. troglodytes*, and *Gorilla* spp. using two approaches. First, 95% confidence ellipses were calculated for the extant samples and positions of the *Au. sediba* specimens and other fossil hominins were evaluated relative to them, and, second, Smith's (1980) d_{yx} "prediction errors" metric was used. This method quantifies the percentage deviation of an individual from expectation (i.e., from the X-axis position along the OLS line of the sample in question), and is calculated as (observed value–predicted value)/predicted value*100.

The radius of A.L. 288-1 is incomplete, and therefore for the investigation of intermembral proportions its length had to be estimated from the left ulna. The problem is that this latter bone is broken into two pieces joined only by an ambiguous contact with one another. Häusler (2001) argues that there is bony contact between these two pieces, and that when joined, the ulna measures 191mm in length, which he suggests gives a radius ca. 181mm in length. However, Richmond et al. (2002) generated a shorter, more "human-like" radius of 174mm in length for the specimen using the Schmid (1983) A.L. 288-1 reconstruction. Longer radius lengths were estimated by Kimbel et al. (1994) at 206mm, and Asfaw et al. (1999) at 215mm. We therefore generated two A.L. 288-1 individuals, one with a radius 174mm long, and a second with a radius length of 215mm in order to bracket the range of estimates that have been produced.

RESULTS

Forelimbs of African apes bear a sizable portion of their body weight during terrestrial locomotion, up to 100% of their weight during suspensory behavior (Demes et al. 1994), and are characterized by humeral heads that are larger than their femoral heads. In contrast, the femoral head is larger than the humeral head in *H. sapiens*, for which the upper limb is featured in manipulatory activities rather than locomotor activities. These differences are elucidated in Figure 1, a scatterplot of humeral head diameter regressed on femoral head diameter. MH2 follows the human trend, lying almost directly on the *H. sapiens* ordinary least-squares (OLS) regression line for the humeral head diameter to femoral head diameter relationship, and falling just on the lower margin of the 95% confidence ellipse about the *H. sapiens* sample (see Figure 1). Its percentage deviation (or d_{yx}) from the human OLS regression line is +3.9%, approximating the mean absolute d_{yx} value of *H. sapiens* individuals used to generate the OLS line (3.6%). In contrast, its d_{yx} from the *P. troglodytes* line is a more marked –19.1%, which according to its Z-score of –6.84, is significantly different (at $p<0.01$) from the mean absolute d_{yx} value of the chimpanzees used to generate the *Pan* OLS regression (2.8%). The 3.18 Ma A.L. 288-1 (*Au. afarensis*) specimen has a much smaller humeral and femoral head than any of the human individuals in the sample (which includes small-bodied "Pygmies," San, and Andaman Islanders), and for this reason the specimen lies far outside the human 95% confidence ellipse. However, A.L. 288-1's d_{yx} from the human line is –1.9% which is not significantly different from the *H. sapiens* individuals used to calculate the regression. By way of contrast, its (negative) d_{yx} from the *Pan* line (–24.1%) is significantly different from the chimpanzee sample (Z-score=–8.9; $p<0.01$).

Another consequence of weight-bearing in the African ape forelimb (either in below-branch activity or in knuckle-walking) is that chimpanzees and gorillas tend to have larger elbow articular dimensions than do comparably-sized humans. This trend is evident when humeral distal articular breadth (i.e., combined ML breadth of the trochlea and capitulum) is regressed on humeral length (Figure 2), although there is considerable overlap between the *P. troglodytes* and *H. sapiens* 95% confidence ellipses. For this relationship, MH1 falls outside of both the *P. troglodytes* and *H. sapiens* 95% confidence ellipse, primarily due to its overall small size. It does fall close to the *H. sapiens* OLS line, with a d_{yx} of +9%, the Z-score of which (0.94) is not significantly different from the absolute mean d_{yx} value of the *H. sapiens* individuals. However, its d_{yx} from the *Pan* OLS line is only slightly more marked at –10.5%; its Z-score of –1.76 indicates it is not significantly different (at $p<0.05$) than the absolute mean d_{yx} value of the *P. troglodytes* individuals used to calculate the *Pan* regression. The presumed female MH2 has a smaller distal articular breadth than the adolescent male MH1, but also falls just beyond the margins of the human 95% confidence ellipse, and well outside the *P. troglodytes* 95% confidence ellipse. The MH2 percentage deviation (d_{yx}) from the human OLS line is –12.5%, the Z-score of which (–1.82 is not significant a $p<0.05$), while its deviation from the *Pan* OLS line is over twice as great at –25.6% (and with a Z-score of –6.52 that is significantly

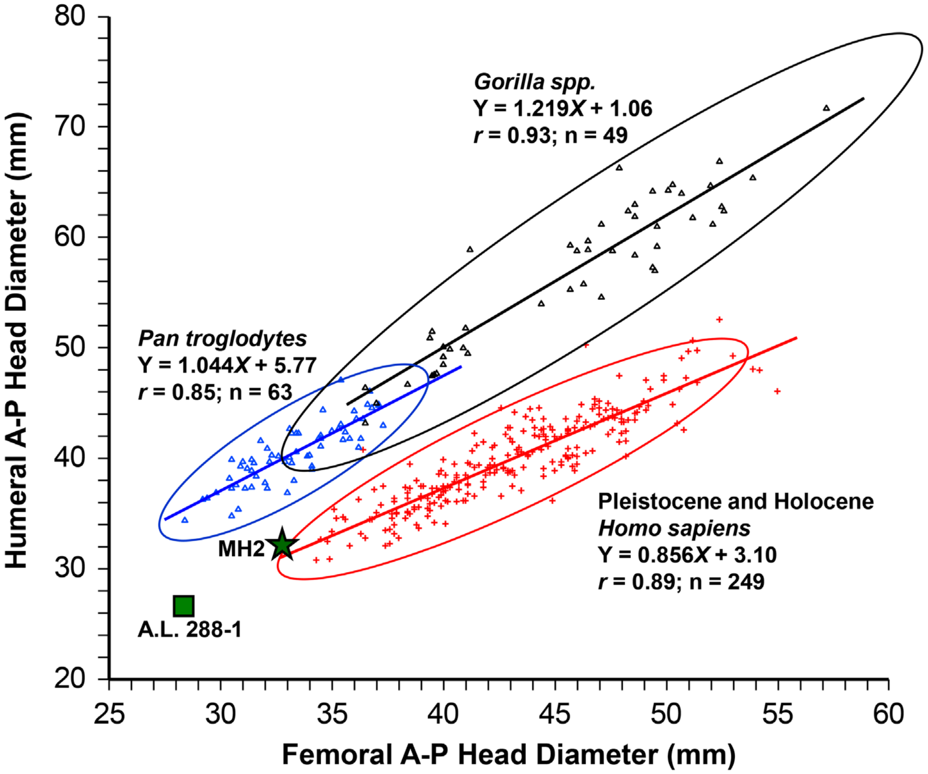

Figure 1. Anteroposterior head diameter of the humerus regressed on that of the femur for Pleistocene/Holocene H. sapiens, Pan, Gorilla, *MH2 (*Au. sediba*) and A.L. 288-1 (*Au. afarensis*).* H. sapiens *is indicated by red crosses,* Pan *by blue triangles,* Gorilla *by black triangles.* Australopithecus *is indicated in green, with Malapa represented by a star. The OLS regression lines for the comparative samples are represented by solid lines. Ninety-five percent confidence ellipses about each extant sample are also indicated.*

different at p<0.01). As in the previous analysis, A.L. 288-1 falls below the *H. sapiens* size range, but like the other fossil hominins examined here, does not fall far from the human regression; its deviation (d_{yx}) from the human OLS line is –9.5%, with a Z-score of 1.82, is not significantly different (at p<0.05) from the absolute mean d_{yx} value of the *H. sapiens* individuals used in the OLS regression. A.L. 288-1's deviation from the *Pan* line is much more marked at –27.2%, with a Z-score of –7.0 that is significantly different from the absolute mean d_{yx} value of the *P. troglodytes* individuals at p<0.01. By way of contrast, KNM-WT 15000 falls well within the *H. sapiens* 95% confidence ellipse, just below the *H. sapiens* OLS regression line, with a d_{yx} from the human OLS line of –4.9% (not significantly different from the *H. sapiens* individuals), and a much more marked –13.2% deviation from the *Pan* OLS line that, with a Z-score of –2.6, is significantly different from the *P. troglodytes* individuals used to generate the *Pan* OLS line.

Interlimb length proportions have long been known to distinguish hominins from the African apes (Drapeau and Ward 2007; Jungers 1982; Schultz 1937), and in this light, the interlimb proportions of *Au. sediba* can be assessed via analysis of upper limb long bone lengths relative to preserved and/or estimated lower limb bone lengths. Figure 3 is a scatterplot of upper limb (humerus + radius) length regressed on lower limb (femur + tibia) length for *H. sapiens*, *P. troglodytes*, *Gorilla*, and those fossil hominins for which these measurements are preserved and/or can be reliably estimated. As evident in the plot, *H. sapiens* is characterized by what are on average the longest lower limbs and the shortest upper limbs, while *Pan* and *Gorilla* have longer upper limbs than lower limbs—a long-recognized pattern.

What is important to note is that of the fossil hominins preserving sufficient upper and lower limb bone lengths for this analysis, only KNM-WT 15000, the 1.49 Ma *H. erectus* skeleton, falls within the *H. sapiens* 95% confidence ellipse, with a modest d_{yx} from the human OLS line of +3.3%; its Z-score of 0.61 indicates its d_{yx} is not significantly different from that of the *H. sapiens* individuals, but its d_{yx} of –31.2% has a Z-score of –14.6, significantly different from the *Pan* individuals' mean absolute value d_{yx} at p<0.01. All of the other fossil hominins fall well outside of the 95% confidence ellipses of all the extant hominids (*sensu lato*). *Australopithecus sediba*, represented by the composite MH2 / MH 4 individual, and given a range of potential lower limb lengths, lies far from the hominin scatter; its d_{yx} from their relationship ranges from +18% to +21.6% (its respective Z-scores of 8.9 and 11 are significantly different from *H. sapiens*' mean absolute d_{yx} at p<0.01). However, the specimen is just as markedly different from *P. troglodytes*, albeit in the opposite direction, with d_{yx} values of –20.3% to – 22.5%, respectively. The Z-scores for these d_{yx} values are –9.1 and

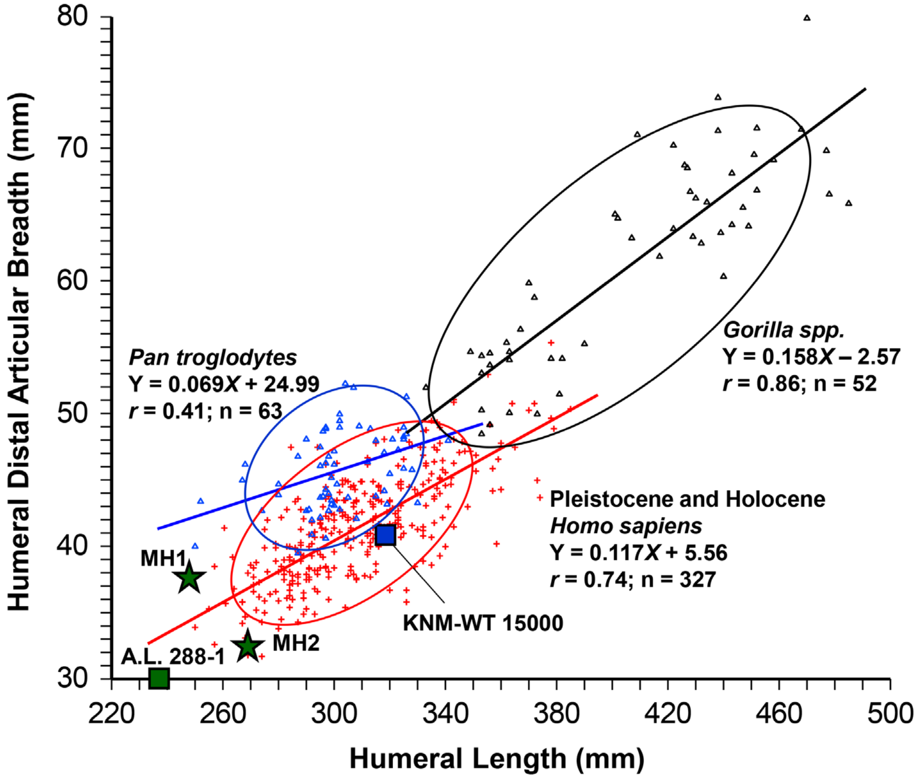

Figure 2. Humeral distal articular breadth on humeral maximum length. Symbols, ellipses, and regression lines as in Figure 1. KNM-WT 15000 is represented by a dark blue square.

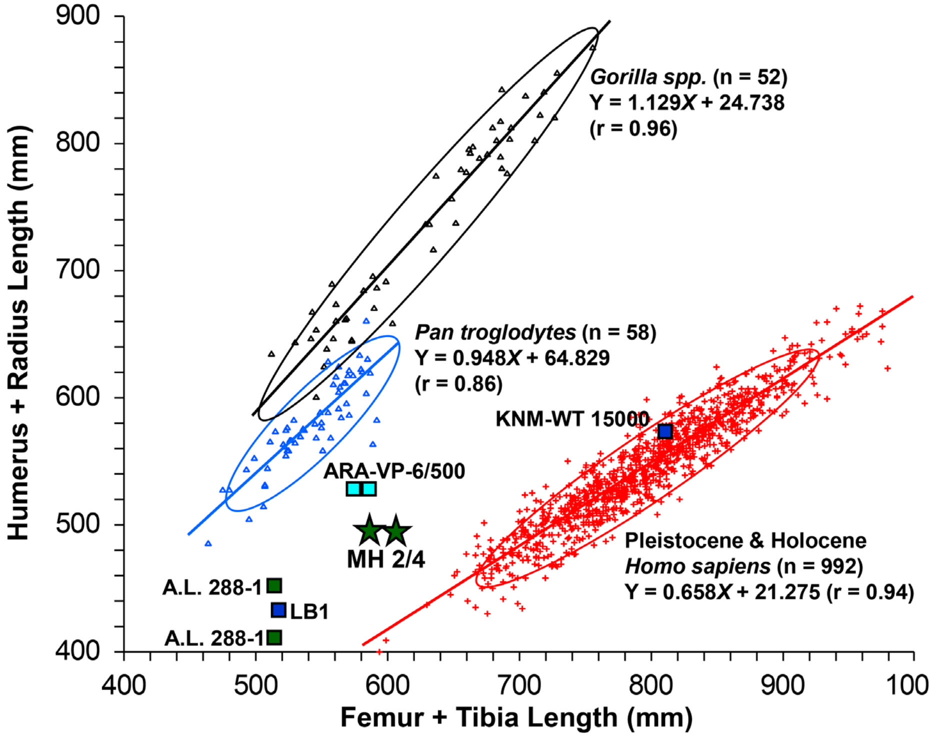

Figure 3. Upper limb (humerus + radius) skeletal length regressed on lower limb (femur + tibia) skeletal length for H. sapiens, P. troglodytes, Gorilla, *and those fossil hominins for which these measurements are preserved and/or can be reliably estimated. Symbols, ellipses, and regression lines as in Figure 1. Fossil* Homo *is represented by dark blue squares;* Ardipithecus ramidus *is represented by light blue squares. A.L. 288-1 is represented by two radius length estimates.*

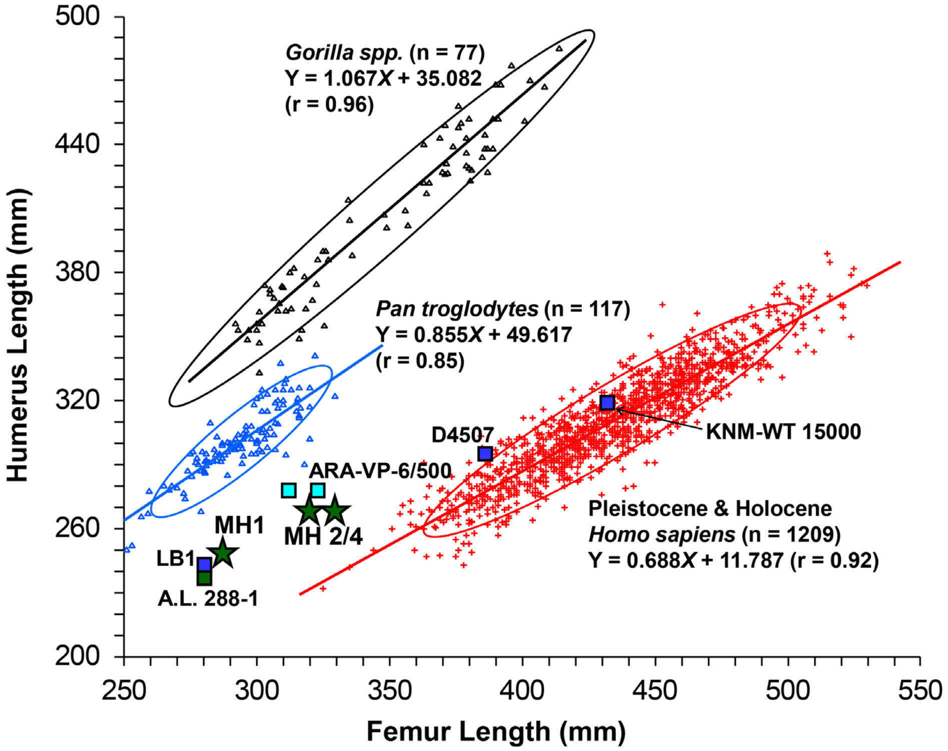

Figure 4. Humerus maximum length regressed on femoral bicondylar length for H. sapiens, P. troglodytes, Gorilla, *and those fossil hominins for which these measurements are preserved and/or can be reliably estimated. Note the high degree of overlap in pairwise comparisons of groups along the y-axis (humeral length), except for* Pan *versus* Gorilla. *Symbols, ellipses, and regression lines as in previous figures.*

–11.5, respectively, which are significantly different from *Pan* at p<0.01. The *Au. afarensis* specimen A.L. 288-1, represented by two different radius lengths, shows a similar pattern; its d_{yx} from the human line is +14.2% to +25.7% (respective Z-scores of 6.8 and 13.3 indicate these d_{yx} values are significantly different from the *H. sapiens* individuals at p<0.01). Its d_{yx} from the *P. troglodytes* regression ranges from –18.2% to –25.8%, respectively; Z-scores of –8 and –11.9, respectively, also indicate that A.L. 288-1's d_{yx} is significantly different from those of the *P. troglodytes* individuals used to calculate the *Pan* OLS line at p<0.01. The *H. floresiensis* holotype (Liang Bua 1) occupies nearly the same morphospace as A.L. 288-1, and its d_{yx} from the human line is +19.7%, while its d_{yx} from the *Pan* line is –22%; Z-scores relative to each taxon are +/–9.9, both of which are significantly different from their respective extant taxon at p<0.01. Finally, the ARA-VP-6/500 *Ar. ramidus* specimen, represented by two femoral length estimates, has d_{yx} values from the human line ranging from +30% to +32.3%, respectively, and d_{yx} values from the *Pan* line of – 13.3% to –14.8%, respectively, making it the most apelike hominin in terms of its intermembral proportions, as has been previously noted (White et al. 2015). However, Z-scores indicate that *Ar. ramidus* is significantly different from both *Pan* and *Homo* at p<0.01.

Humerofemoral proportions are highly correlated with intermembral proportions (Jungers, 2009), and are therefore expected to show similar patterning. Differences in humerofemoral proportions between the extant apes and hominins will not be as marked, however, as those of their intermembral proportions, since the former do not include the antebrachium. However, the pattern revealed is much the same as in the prior analysis, with the added benefit of the inclusion of more fossil hominins. Figure 4 is a scatterplot of humeral length regressed on femoral length. Note that (with the exception of *Pan* vs. *Gorilla*) there is a high degree of overlap in humeral length among the extant hominids (*sensu lato*); the proportional differences that are manifest between these extant taxa are primarily due to differences in femoral length. With regard to fossil hominins, only the two *H. erectus* (*sensu lato*) specimens fall among the *H. sapiens* scatter. Of these two specimens, KNM-WT 15000 falls nearer the middle of the *H. sapiens* scatter close to the human OLS line; the specimen's d_{yx} from the OLS line is +3.2%, close to the mean absolute value d_{yx} (2.5%) for the *H. sapiens* sample (Z-score of 0.3 is not significantly different at p<0.05). By way of contrast, the Dmanisi 4507/4167 *H. erectus* specimen lies just outside the *H. sapiens* 95% confidence ellipse; its d_{yx} is more marked at +6.4%, with a Z-score of 1.95 that is borderline non-significant at the $p < 0.05$ level. However, both these *H. erectus* specimens lie much farther away from the *P. troglodytes* OLS line, with d_{yx} values of –23.9% and –22.3%, respectively. Their respective Z-scores of –10.7 and –11.6 are significantly different from *P. troglodytes* at p<0.01.

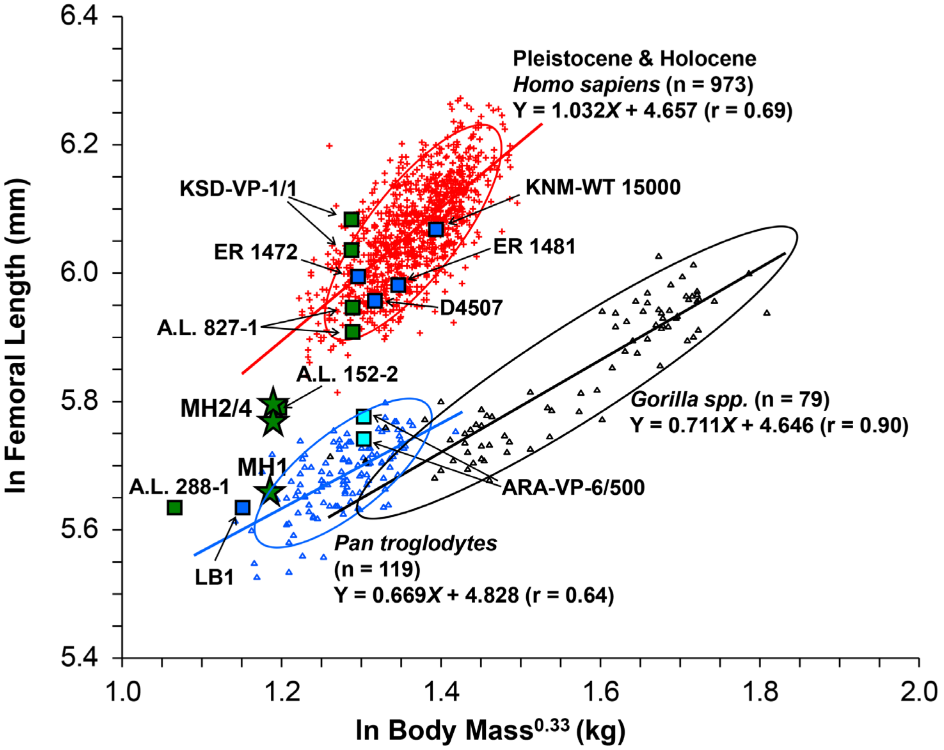

Figure 5. Log femur bicondylar length regressed on the cube root of estimated body mass for Pleistocene/Holocene H. sapiens, Pan, Gorilla, *and fossil hominins. Symbols, ellipses, and regression lines as in previous figures.*

The *Au. afarensis* specimen A.L. 288-1 and the *H. floresiensis* holotype LB1 show nearly identical placement for this relationship, lying well outside the 95% confidence ellipses for both *H. sapiens* and *P. troglodytes*, and falling in the morphological space between these two extant taxa. This is also reflected in their d_{yx} values; A.L. 288-1 and LB1 deviate +15.8% and +18.9% from the *H. sapiens* OLS line and –18.1% and –15.9% from the *P. troglodytes* line, respectively. For both of these cases, Z-scores indicate these specimens are significantly different from both *Pan* and *Homo* at $p<0.01$. As was the case with the combined proximal and distal limb segments, the *Ar. ramidus* ARA-VP-6/5 00 specimen, represented here by two potential femoral lengths, is again the most apelike of the fossil hominins in its limb proportions, although it, too, falls well outside the 95% confidence ellipses of both the extant chimpanzees and humans. Its d_{yx} values from the *H. sapiens* line are +18.8% and +22.8%, while its d_{yx} values from the *P. troglodytes* line are somewhat smaller at –12.1% to –14.7%; Z-scores indicate ARA-VP-6/500 is significantly different from both extant taxa at $p<0.01$.

With regard to *Au. sediba*, both MH1 and MH2/4 fall well outside the 95% confidence ellipses of both the extant chimpanzees and humans. This is reflected in their d_{yx} values, as MH1 shows a deviation of +18.5% from the human OLS line and a deviation of –15.9% from the chimpanzee OLS line, both of which are significantly different from the extant taxa in question at $p<0.01$. Similarly, the MH2/MH4 composite individual, represented by two potential femoral lengths, shows deviations (d_{yx}) of +12.8% to +16.2% from the human OLS regression line and d_{yx} values of –18.8% to –23.1% from the chimpanzee OLS regression, respectively; all of these d_{yx} values are significantly different from *P. troglodytes* or *H. sapiens* at $p<0.01$.

The relationship of femur length relative to estimated body mass is a utile means by which to elucidate differences between *H. sapiens* and the African apes in proportional lower limb length. A scatterplot of this relationship is found in Figure 5; due to the large number of fossil hominins included in this analysis, d_{yx} data and their associated Z-scores are presented in Table 7. Note that in Figure 5 the human (isometric) and African ape (negatively allometric) lines start to converge in the smaller body size range, as has been previously documented (Holliday 2012; Holliday and Franciscus 2009; Pontzer 2012). This means that small-bodied hominins (even those assigned to *Homo*) are also more likely to fall among African apes for the lower-limb to body size relationship than are larger hominins. However, with regard to *Au. sediba*, the pattern is a bit more complex. Specifically, when MH1 femur length is plotted against the estimated body mass for this individual, the relatively small-bodied MH1 juvenile falls just within the chimpanzee 95% confidence ellipse close to the *Pan* OLS line. In this, the Z-score of the specimen's d_{yx} from the *Pan* OLS line indicates that MH1's deviation from that line is not significantly different from those of the chimpanzees used to calculate it (see Table 7). By way of contrast, MH1 falls well outside of the 95% confidence ellipse about the *H. sapiens*

TABLE 7. PERCENTAGE DEVIATIONS (d_{yx}; [observed value–predicted value]/predicted value*100) FROM *H. SAPIENS*, *P. TROGLODYTES*, and *GORILLA* spp. OLS REGRESSION LINES (ln femoral length regressed on ln body mass$^{0.33}$; Z-scores calculated using absolute values of d_{yx} within each taxon).

Specimen	d_{yx} from *H. sapiens* regression	d_{yx} from *P. troglodytes* regression	d_{yx} from *G.* spp. regression	Z-score (*H. sapiens* distribution)	Z-score (*Pan* distribution)	Z-score (*Gorilla* distribution)
MH1	-3.74	+0.67	+1.62	**-5.27****	0.21 n.s.[1]	**+2.17***
MH2 (2 FL)	-1.47	+3.08	+4.04	-1.28 n.s.	**+5.61****	**+7.43****
	-2.00	+2.52	+3.48	**2.21***	**+4.36****	**+6.22****
ARA-VP-6/500 (2 FL)	-3.73	+0.73	+1.58	**-5.25****	+0.34 n.s.	**+2.09***
	-4.31	+1.35	+2.19	**-6.27****	+1.73 n.s.	**+3.42****
A.L. 152-2	-1.74	+2.84	+3.79	-1.75 n.s.	**+5.07****	**+6.89****
A.L. 288-1	-2.36	+1.5	+2.55	**-2.84****	**+2.07***	**+4.20****
A.L. 827-1 (2 FL)	-1.32	+3.81	+4.69	-1.01 n.s.	**+7.25****	**+8.84****
	-0.69	+4.64	+5.35	-0.1 n.s.	**+9.11****	**+10.27****
KSD-VP-1/1 (2 FL)	+0.87	+6.09	+6.99	0.21 n.s.	**+12.37****	**+13.83****
	+1.65	+6.91	+7.82	1.59 n.s.	**+14.21****	**+15.63****
KNM-ER 1472	+0.01	+5.24	+6.13	1.29 n.s.	**+10.46****	**+11.97****
KNM-ER 1481	-1.05	+4.41	+5.25	-0.54 n.s.	**+8.6****	**+10.06****
KNM-WT 15000	-0.43	+5.33	+6.14	-0.55 n.s.	**+10.66****	**+11.99****
Dmanisi 4507	-0.98	+4.32	+5.18	-0.41 n.s.	**+8.04****	**+9.9****
LB1	-3.59	+0.64	+1.61	**-5****	+0.14 n.s.	**+2.16***

[1] n.s.=not significantly different at $p<0.05$.

*=significantly different at $p<0.05$.

**=significantly different at $p<0.01$.

individuals, and the MH1 Z-score indicates a significantly larger (negative) deviation (at $p<0.01$) from the human OLS line than do the humans used in its calculation. At the same time, MH1 also falls near LB1 (*H. floresiensis*) and A.L. 288-1 (*Au. afarensis*), both of which remain outside the *Pan* 95% confidence ellipse. Z-scores indicate that A.L. 288-1 shows a significant positive deviation from *Pan*, while the likely heavier LB1 specimen does not show a significant deviation (see Table 7).

Unlike MH1, the MH2/MH4 composite skeleton (while approximately the same body size as MH1), has a longer reconstructed femur length, and as a result falls farther from the African ape scatter (its d_{yx} Z-score of from *Pan* shows a significantly more pronounced deviation (at $p<0.01$) than those of the individual chimpanzees [see Table 7]). Also in contrast to MH1, MH2 is less divergent from *Homo sapiens* (although it falls well outside of the human 95% confidence ellipse). In fact, the d_{yx} Z-score of the longer of the two femoral length estimates is not significantly different from those of the humans, but the shorter femur length estimate's d_{yx} Z-score is significantly different from those of the humans at $p<0.05$ (see Table 7). MH2/4 also closely approximates the position of the A.L. 152-2 *Au. afarensis* specimen in bivariate space; its d_{yx} Z-scores show it is not significantly different from humans, but is significantly different (at $p<0.01$) from chimpanzees (see Table 7). By way of comparison, larger-bodied early *Homo* specimens (KNM-ER 1472; KNM-ER 1481; KNM-WT 15000; Dmanisi 4507) and larger members of the paleospecies *Au. afarensis* (KSD-VP-1/1; A.L. 827-1) fall among recent humans, lying within (or in the case of KSD-VP-1/1, perhaps just beyond) the *H. sapiens* 95% confidence ellipse, and away from the African apes. Z-scores of d_{yx} indicate that none of these specimens is significantly different from the humans, while all are significantly different (at $p<0.01$) from *Pan* (see Table 7). Finally, based on the Lovejoy et al. (2009) body mass estimate, *Ar. ramidus* (ARA-VP-6/500) is characterized by ape-like lower limb length proportions, again highlighting the fact that this hominin was not an obligate biped. Z-scores of its d_{yx} values indicate it is significantly different from *H. sapiens* at $p<0.01$. In contrast, the shorter femur length estimate (which falls well within the *Pan* 95% confidence ellipse) is not significantly different from *P. troglodytes*, whereas the longer femur length estimate (which falls at the margins of the *Pan* 95% confidence ellipse) just achieves significance at $p<0.05$.

Tibial length can also serve as a useful proxy of lower limb length among hominins (Haile-Selassie et al. 2010; Lovejoy et al. 2016). Tibial length regressed on the square root of tibial distal articular area (a reflection of body mass) tends to separate *H. sapiens*, who have long tibiae, from *Pan* and *Gorilla*, who do not, albeit with some overlap between these groups (Figure 6). MH4, represented by two estimated tibial lengths, falls outside of the *H. sapiens* 95% confi-

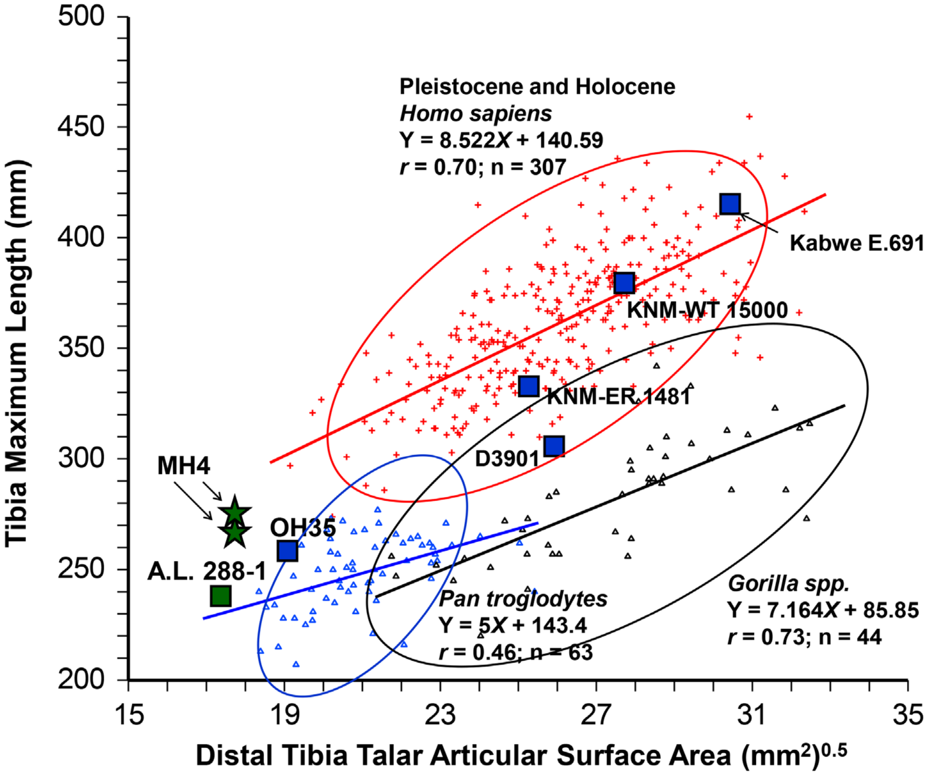

Figure 6. Tibia maximum length regressed on the square root of tibial talar distal articular facet area for Pleistocene/Holocene H. sapiens, Pan, Gorilla, *and fossil hominins. Symbols, ellipses, and regression lines as in previous figures, with two tibial length estimates shown for MH4.*

dence ellipse, but not far below the human OLS line. In fact, the specimen's d_{yx} from the human OLS line ranges from –5.4% to –8.3%, with respective Z-scores (–0.15 and –0.95) showing they are not significantly different from *H. sapiens* at $p<0.05$. In contrast, its deviation from the *Pan* OLS line is more marked at +15.2% to +18.9%; the respective Z-scores (2.86 and 3.85) are significantly different from *P. troglodytes* at $p<0.01$. Two other fossil hominins, both of which are small in body size, also fall outside the human 95% confidence ellipse—A.L. 288-1 (*Au. afarensis*) and OH 35 (*H. habilis*?). OH 35 lies at the margin of the *P. troglodytes* 95% confidence ellipse, showing a d_{yx} from the *Pan* line of +8.6% (not significantly different from *Pan*), and a d_{yx} from the human line of –14.4% (Z-score of –2.63 is significantly different from *H. sapiens* at $p<0.01$). While smaller than any of the chimpanzees, A.L. 288-1 lies almost directly on an extension of the *Pan* OLS line, showing a d_{yx} from the line of only +1.8% (not significantly different from *Pan*). In contrast, the specimen shows a much larger d_{yx} from the human OLS line of –18.8% (Z-score of –3.86 is significantly different at $p<0.01$). The remaining fossil hominins, which are larger in body size: KNM-ER 1481 (*H. sp.*), KNM-WT 15000 and Dmanisi 3901 (*H. erectus*), and Kabwe E.691 (*H. rhodesiensis / heidelbergensis*), all lie within the *H. sapiens* 95% confidence ellipse (although Dmanisi 3901 also lies within the *Gorilla* 95% ellipse; and the Z-score [1.83] of its d_{yx} [+12.85] is not significantly different from the *Gorilla* sample). Their d_{yx} values from the human line range from –15.2% (Dmanisi, the Z-score of which [–2.86] is significantly different from *H. sapiens* at $p<0.01$) to +4.1% (Kabwe). With the exception of the Dmanisi tibia, none of the d_{yx} values of these other tibiae is significantly different from the *H. sapiens* sample, and all are significantly different (at $p<0.01$) from the African apes.

DISCUSSION AND CONCLUSIONS

Australopithecus sediba shows body size and proportions long considered characteristic of the genus *Australopithecus*. Data thus far available for this taxon do not suggest that *Au. sediba* was characterized by the increased body size that has been documented for (at least some) early members of the genus *Homo*, but rather was smaller, with an estimated body mass of ca. 30–36 kg. In terms of its upper- to lower-limb articular proportions, *Au. sediba*, like *H. sapiens* and *Au. afarensis*, and unlike extant nonhuman apes, is characterized by smaller upper limb articular dimensions and larger lower limb articular dimensions. This indicates (unsurprisingly) that, despite adaptations for arboreal locomotor behaviors evident in the shoulder, arm, and hand (Churchill et al. 2013; Kivell et al. 2011), the upper limb is not used in locomotion in the same manner of that of the extant African apes, since unlike these extant knuckle-walkers, *Au. sediba* was terrestrially bipedal. Like other member species of its genus, *Au. sediba* also exhibits significantly longer lower limbs relative to its upper limbs, and somewhat longer femora relative to its humeri than the African apes. However, at the same time it does not fall among *Homo sapiens* for this relationship; rather, when it comes to limb and body proportions, *Au. sediba* (and apparently all other species of *Australopithecus*) appears to occupy morphological space intermediate between *H. sapiens* and the extant African apes, and different from both.

Note that while the length of the MH1 femur relative to its estimated body mass falls among the *P. troglodytes* individuals, and significantly (at p<0.05) below the *H. sapiens* sample, it is uncertain whether the femur of this juvenile would have shown significant growth had he survived to adulthood. In contrast, the (presumed adult) MH4 tibia (and by extension, its estimated femur, had it been preserved), shows some degree of lower limb elongation, lying close to the *H. sapiens* scatter, and outside the *P. troglodytes* scatter, for this relationship. However, the lower of the two estimated MH4 femoral lengths falls significantly (at p<0.05) below the human sample relative to its estimated body mass, so as was the case with MH1, lower limb elongation does not appear to have reached the extent it has reached in *H. sapiens* (or in *H. erectus*).

In terms of interlimb proportions, *Au. sediba* resembles other australopiths and *H. floresiensis* (which despite its late date [ca. 100–60 ka] appears to have diverged early from another species of *Homo*, as it retains many *Australopithecus*-like features; Morwood and Jungers 2009), in that it occupies morphological space between extant chimpanzees and *H. sapiens*; i.e., the upper limb bones of *Au. sediba* are slightly elongated relative to those of extant humans, but shorter than those of chimpanzees, while their lower limbs show the converse pattern; i.e., they are elongated relative to extant chimpanzees while at the same time somewhat shorter on average than those of *H. sapiens* (and *H. erectus*).

Taken as a whole, then, body size and proportions of *Au. sediba* are similar to *Au. afarensis* and *H. floresiensis*. Given the relatively recent date of *Au. sediba* at ca. 1.98 Ma, it seems possible that many of its more australopith-like proportional features are not merely selectively neutral plesiomorphic characters, but may in fact reflect retention of some degree of arboreal competency, as has been suggested by earlier studies of the upper limb and foot (Churchill et al. 2013; DeSilva et al. 2013; Rein et al. 2017). Nonetheless, as was the case for the pelvis (Kibii et al. 2011), elongation of the lower limb is also consistent with some degree of selection for efficient terrestrial bipedality, albeit perhaps not to the degree one observes in later *Homo*, reflecting once again the morphologically mosaic nature of this taxon.

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