Body mass estimates of the earliest possible hominins and implications for the last common ancestor

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A B S T R A C T

Many hypotheses regarding the paleobiology of the earliest possible hominins, *Orrorin tugenensis* and *Ardipithecus ramidus*, are dependent upon accurate body mass estimates for these taxa. While we have previously published body mass predictions for *Orrorin* and *Ardipithecus*, the accuracies of those estimates depend on the assumption that the postcranial skeletal dimensions and body masses of these taxa followed scaling patterns that were similar to those observed in modern humans. This assumption may not be correct because certain aspects of postcranial morphology in *Orrorin* and *Ardipithecus* differ from modern humans, and suggest that their overall body plans might be unique but more similar to modern non-human great apes than to modern humans. Here we present individual body mass predictions for *O. tugenensis* and *Ar. ramidus* assuming that they followed postcranial scaling patterns similar to those of chimpanzees. All estimates include individual prediction intervals as measures of uncertainty. In addition, we provide equations for predicting body mass from univariate postcranial measurements based on the largest sample ($n = 25$) yet compiled of common chimpanzee skeletons with known body masses, which is vital for calculating prediction intervals for individual fossils. Our results show that estimated body masses in *Orrorin* and *Ardipithecus* are generally larger when derived from a chimpanzee-like scaling pattern compared to estimates that assume a human-like pattern, though the prediction intervals of the two sets of estimates overlap. In addition, the more complete of the two known *Orrorin* femora has an overall scaling pattern that is more similar to common chimpanzees than to modern humans, supporting the application of a non-human great ape comparative model. Our new estimates fall near the male (*Ardipithecus*) average and in between the male and female averages (*Orrorin*) for wild-caught common chimpanzees. If a chimpanzee-like pattern of scaling between postcranial dimensions and body mass did exist in these earliest hominins, our results suggest the large body masses found in some early australopiths were already present in taxa near the origins of our lineage, and perhaps also in the *Pan-Homo* last common ancestor.

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1. Introduction

Current views on the earliest period of human evolution are based on fragmentary fossils from just a few individuals (e.g., White et al., 1994; Senut et al., 2001; Brunet et al., 2002) including one partial skeleton (White et al., 2009). Though their phylogenetic position is a matter of debate (e.g., Strait and Grine, 2004; Harrison, 2010; Kimbel et al., 2014), these fossils give us important information on a period of human evolution that is otherwise unknown. As body mass is related to both ecological and life-history characteristics, understanding its evolution in early hominins is a prerequisite for untangling the intricate web of ecological and life-

history traits that characterized the earliest members of the hominin clade.

While we previously used a series of methodological advances to estimate body mass for individual hominin fossils and to calculate species averages (Grabowski et al., 2015), our conclusions in that paper regarding some of the earliest possible hominins — Orrorin and Ardipithecus — made the assumption that postcranial traits and body mass in these fossil taxa followed scaling patterns similar to those seen in modern humans. It has been reported elsewhere (Ruff, 1988; Jungers, 1990; Hartwig-Scherer, 1993) that non-human great apes share a similar pattern of scaling between postcranial traits and body mass, while modern humans, and likely some earlier hominins, possess an apparently derived pattern. Modern humans possess large hindlimb joints for their mass due to our habitual bipedal mode of locomotion (Jungers, 1988a). Because of these divergences in scaling patterns, previous research suggested that substantial differences in predicted body mass can occur when estimating mass from relatively large skeletal traits using a modern human regression rather than a non-human great ape regression (Jungers, 1988b; McHenry, 1992). Many of our published body mass estimates for early hominins (e.g., most individuals of Australopithecus) fall within the lower part or just below the range of masses observed in modern humans, which led us to suggest (Grabowski et al., 2015) that using a modern human or non-human great ape regression might not have a substantial effect on these predicted body masses. However, prior estimates of body mass for Orrorin and Ardipithecus are larger than ours (e.g., Nakatsukasa et al., 2007; White et al., 2009), and it is possible that a non-human great ape-like scaling pattern could lead to greater body mass estimates for those taxa (see also Almécija et al., 2015). In addition, the locomotor repertoires of these earliest hominins likely differed from those of modern humans and later fossil hominins (e.g., Lovejoy et al., 2009b; Kuperavage et al., 2010; Almécija et al., 2013), which casts further doubt on the appropriateness of assuming a modern human pattern of scaling.

Given the alternative assumption that they followed a pattern of scaling similar to other extant great apes, rather than to modern humans, here we present individual body mass predictions for the earliest recognized hominins — individuals assigned to the taxa Orrorin tugenensis and Ardipithecus ramidus — based on metrics of their postcranial fossils. These individual estimates include 95% prediction intervals (PIs) to provide measures of uncertainty. In addition, we provide a new species "average" for Orrorin, based on the two individuals that are currently described, with a confidence interval. Here average is in quotes based on the fact that there are currently only two individuals from which complementary measurements can be obtained. We also present a series of equations for estimating body mass from univariate postcranial trait measurements based on the largest sample ($n = 25$) compiled to date of common chimpanzee skeletons with known body masses. Importantly, body masses, trait measurements, and complete information on these individuals (location, ID number, sex, etc.) are provided to aid future researchers.

2. Materials and methods

As in our previous work (Grabowski et al., 2015), this study follows analyses that use a calibration approach (Brown, 1982, 1993; Brown and Sundberg, 1987; Konigsberg et al., 1998; Uhl et al., 2013). A calibration approach involves using a training sample (i.e., the sample used to build, or train, the model) with known body mass and trait measurements for each individual to construct regression equations that are then used to predict body mass in a sample with an unknown body mass. While we previously used a training sample of generally smaller-bodied modern humans of

known body mass (Grabowski et al., 2015), here we use a training sample of common chimpanzees with known body masses and associated postcranial measurements.

2.1. Individuals vs. means

The primary difference between this study and most others that have predicted body mass for early hominins (e.g., McHenry, 1992; Nakatsukasa et al., 2007) or Miocene apes (e.g., Ruff et al., 1989) is that our comparative sample is composed of individuals with known body masses and skeletal elements rather than population or species/sex means (see also Grabowski et al., 2015). This distinction is important because a regression equation derived from species/sex means relates to a different biological question than a regression based on individuals. With a regression using data from individuals, the question being asked is: what is the predicted body mass for one individual, with a prediction interval around that estimate, given individual fossil measurements? With a regression using data from means, the question becomes: what is the predicted average value that a population or species would have had, with a prediction interval around that mean estimate, given an average value of a trait or traits? When using measurements from an individual fossil and a regression based on data from population or species means, the type of data being entered as the independent variable and the data that went into creating the regression are not on the same scale, which can lead to problems in the interpretation of the results. In this scenario, a prediction generated for an individual fossil does not represent the predicted mass of that individual. Instead, the prediction represents the average body mass of a population or species assuming that the averages of a particular set of measurements across that population or species are identical to the measurements of the individual fossil (e.g., Ruff et al., 2018). A large amount of error in estimation is inappropriately removed because species means do not take into account individual variation. This most often results in a reduced prediction interval (though it is actually a confidence interval around an mean estimated from a sample size of one) and gives the false impression that the resulting "mean" prediction is estimated much more accurately than it is in reality. A recent study (Lacoste Jeanson et al., 2017) focused on predicting body mass for individuals using equations based on species and population means, testing the ability of 11 different commonly used body mass estimation equations (Ruff, 1991; McHenry, 1992; Elliott et al., 2016) in predicting body masses in a modern human reference set of individuals with known masses. The researchers found that none of the equations was able to predict known body mass within 10% in more than half of the reference sample, and suggested that while the equations are generally reliable and accurate for calculating averages, none is suitable for calculating individual body masses. Thus, average fossil body masses and individual fossil body mass predictions should be calculated using separate reference data sets (among vs. within-species) depending on the question being asked.

2.2. Training sample

Estimating body mass with prediction intervals for individual hominin fossils requires that the training samples be comprised of individuals from closely related species, of known body mass, and with available skeletal elements that can be measured. Our training sample is comprised of skeletal material from common chimpanzees (Pan troglodytes) with known body masses. Though this sample is small ($n = 25$; 11 males, 14 females), it is the largest ever compiled for this species. It is comprised of both wild-collected and captive individuals (17 wild-collected, 8 captive). Including captive individuals can be problematic in terms of captivity's effect on body

mass (e.g., Isler et al., 2008). While no significant difference in body mass was found between these two subsamples when sex was taken into account (*p*-value: 0.187), we also tested if captivity affects how individual traits scale with body mass. To test for the effect of captivity on our sample, we performed a series of ANCOVAs with body mass as the dependent variable and each trait as the independent variable, with wild/captive as the covariate. Our results (Supplementary Online Material [SOM] Table S1; SOM Figs. S1—S12) show that captivity has no effect on the slope of relationship for any of the 12 traits, but has a significant effect on the intercept of body mass regressed on two traits — anteroposterior diameter of the femoral midshaft (Subtrochanteric ML) and mediolateral width at the femoral epicondyles (Femoral Bicondylar). We chose to leave these two traits out of our analysis but include the regression equation results here as they may be of use to other researchers. Based on these findings, measurements from both captive and wild animals were used in our subsequent analyses (see Tables 1 and 2 and SOM Table S2 for complete details on this data set).

2.3. Trait selection

Here we focus on traits from the lower limb skeleton, and use these to predict body mass in fossil hominins. Traits are limited to dimensions of the lower limb skeleton because of its direct functional role in supporting body mass, but we acknowledge that this issue may be more complex in the earliest hominins if they had diverse locomotor repertoires (e.g., Jungers, 1988a) (see SOM Table S2 for complete chimpanzee measurements).

The earliest fossil hominins may not share the same scaling relationship between body mass and our traits of interest as found in our training sample. We previously used the methods of Brown and colleagues (Brown and Sundberg, 1987; Brown, 1993) to determine first which postcranial traits in the fossil sample follow the same scaling relationship among each other as observed in our training sample, and then calculated our final multivariate estimate of body mass using these traits (Grabowski et al., 2015). We note

that here, as in our previous work, this approach tests which traits scale similarly with each other in the same manner as in the training sample, but also assumes that the final set of traits scales with body mass in a similar fashion as the training sample. Of course, it is possible that these traits might actually scale differently with body mass in the training and fossil samples, but this assumption is unavoidable in any study that seeks to estimate body mass in fossil species where the true masses cannot be known. Here we repeat this procedure with the caveat that because of the relatively small sample size ($n = 25$) of the chimpanzee training sample, the power to determine if fossil traits significantly differed in scaling from our training sample may be reduced. We believe the benefit of presenting multivariate estimates of body mass for the earliest hominins outweighs the potential costs of error in our results. See Grabowski et al. (2015) for additional details of this method.

2.4. Measurements

Metric traits from individuals in our training sample were collected using digital calipers by WLJ and MG. The traits in this study were chosen based on their significant relationship with body mass in the calibration sample used here, their relative abundance in the hominin fossil record, and their usage in previous hominin body mass analyses. As opposed to some previous studies (e.g., McHenry, 1992), here we focused on individual measurements, not areas produced by the product of two measurements, as this allows for a greater number of fossil individuals to be included and more easily shows the relationships between individual traits and body mass. The measurements taken for this analysis are presented in Table 3.

2.5. Fossil data

Measurements of *O. tugenensis* and *Ar. ramidus* postcranial fossils matching those of the training sample were taken from the literature and supplemented by measurements of the original

Table 1
Adult common chimpanzee individuals with known body masses.

Species	Collection No.	Subspecies	Locality	Sex	Wild\Captive	Mass (kg)
Pan troglodytes	AS-1763	*verus*	Liberia	F	captive	28.6
Pan troglodytes	AS-1784	unknown (Schultz)	NA	F	captive	33.0
Pan troglodytes	P.A.L. 217	unknown (Schultz)	NA	F	captive	44.4
Pan troglodytes	P.A.L. 219	unknown (Schultz)	NA	F	captive	33.8
Pan troglodytes	P.A.L. 96	unknown (Schultz)	NA	F	captive	36.7
Pan troglodytes	NMNH-236971	*schweinfurthii*	Uganda	F	wild	31.0
Pan troglodytes	NMNH-477333	*verus*	Cote d'Ivoire	F	wild	36.3
Pan troglodytes	NMNH-481803	*verus*	Liberia	F	wild	49.9
Pan troglodytes	RMCA-29073	*schweinfurthii*	R.D. Congo	F	wild	45.0
Pan troglodytes	RMCA-29074	*schweinfurthii*	R.D. Congo	F	wild	31.5
Pan troglodytes	Susman-SBU 94-4	*verus*	Liberia	F	wild	38.5
Pan troglodytes	AMNH-174860	*troglodytes*	Equatorial Guinea	F	wild	41.0
Pan troglodytes	PCM VII-23	*troglodytes*	Cameroon	F	wild	50.0
Pan troglodytes	PCM CAM-147	*troglodytes*	Cameroon	F	wild	42.3
Pan troglodytes	AS-1695	unknown (Schultz)	NA	M	captive	31.8
Pan troglodytes	AS-1810	unknown (Schultz)	NA	M	captive	48.5
Pan troglodytes	P.A.L. 220	unknown (Schultz)	NA	M	captive	54.0
Pan troglodytes	MCZ-19187	*troglodytes*	Cameroon	M	wild	46.0
Pan troglodytes	MCZ-48686	*troglodytes*	Equatorial Guinea	M	wild	62.0
Pan troglodytes	NMNH-481804	*verus*	Liberia	M	wild	46.0
Pan troglodytes	AMNH-174861	*troglodytes*	Equatorial Guinea	M	wild	55.0
Pan troglodytes	NMNH-220327	*troglodytes*	Gabon	M	wild	63.6
Pan troglodytes	PCM Z VII-25	*troglodytes*	Cameroon	M	wild	70.0
Pan troglodytes	PCM CAM-13	*troglodytes*	Cameroon	M	wild	50.0
Pan troglodytes	PCM Z VII-24	*troglodytes*	Cameroon	M	wild	60.0

Institution key: A. H. Schultz Collection and the collection of the Anthropological Institute & Museum, University of Zurich (AS, P.A.L.); National Museum of Natural History (NMNH); Royal Museum of Central Africa (RMCA); Department of Anatomical Sciences, RL Susman collection, Stony Brook University (Susman-SBU); American Museum of Natural History (AMNH); Powell-Cotton Museum (PC); Harvard Museum of Comparative Zoology (MCZ).

Table 2
Average body mass and sample size for chimpanzee sample used in this study compared to other samples and samples of modern humans used in previous analyses.

Known Body Mass	n=	Average Mass	Males n=	Male Average	Females n=	Female Average
P. troglodytes (this study)	25	46.0	11	53.4	14	38.7
Wild *P. troglodytes*[a]	60	45.0	27	49.6	33	40.4
Wild *P. troglodytes*[b]	60	41.0	27	46.0	33	35.9
P. troglodytes schweinfurthii[c]	47	38.2	21	42.7	26	33.7
P. troglodytes troglodytes[c]	9	52.8	5	59.7	4	45.8
P. troglodytes verus[c]	4	44.0	1	46.3	3	41.6
Worldwide *H. sapiens*[d]	51	58.2	28	61.0	23	54.7
Small bodied *H. sapiens*[e]	220	49.2	116	51.8	104	46.2

[a] From Smith and Jungers (1997) − mean of between sex − means for all *Pan troglodytes* subspecies.
[b] From Smith and Jungers (1997) − mean of between sex − means weighted by sample size for all *Pan troglodytes* subspecies.
[c] From Smith and Jungers (1997).
[d] From Ruff et al. (1997) based on 51 population means.
[e] From Grabowski et al. (2015).

Table 3
Postcranial measurements taken for this analysis.

Measurement	Description	Source
Femoral Head SI	Superoinferior diameter of the head	McHenry and Corruccini (1978)
Femoral Neck SI	Superoinferior height of the neck	McHenry and Corruccini (1978)
Femoral Head AP	Anteroposterior diameter of the head	−
Femoral Neck AP	Anteroposterior height of the neck	−
Subtrochanteric AP	Anteroposterior diameter of the shaft just below the lesser trochanter	McHenry and Corruccini (1978)
Subtrochanteric ML	Mediolateral diameter of the shaft just below the lesser trochanter	McHenry and Corruccini (1978)
Femoral Midshaft AP	Anteroposterior diameter of the shaft midway along its length	McHenry and Corruccini (1978)
Femoral Midshaft ML	Mediolateral diameter of the shaft midway along its length	McHenry and Corruccini (1978)
Femoral Bicondylar	Maximum mediolateral width of the distal end taken perpendicular to the shaft axis	McHenry and Corruccini (1978)
Tibial Plateau AP	Maximum anteroposterior width of proximal tibia taken perpendicular to the shaft axis	McHenry (1992)
Tibial Plateau ML	Maximum mediolateral width of proximal tibia taken perpendicular to the shaft axis	McHenry (1992)
Tibial Distal End ML	Maximum mediolateral width of distal end taken perpendicular to shaft	Langley et al. (2016)
Tibial Distal Articular Surface AP	Maximum anteroposterior width of articular surface of distal tibia	McHenry (1992)
Tibial Plafond	Maximum mediolateral width of articular surface of distal tibia	McHenry (1992)

Orrorin fossils (courtesy of Brian Richmond). For ARA-VP-6/500, Lovejoy et al. (2009c) estimated a range of values for the acetabular diameter between 36 and 42 mm, with a midpoint of 39. We used this range of values (midpoint, low end, high end) to estimate a range of femoral head diameters following Plavcan et al. (2014), using their regression for *P. troglodytes*. Because of the high correlation between femoral head diameter and acetabulum diameter ($r = 0.937$; Plavcan et al., 2014), these estimates should have relatively small error (see SOM Tables S3 and S4 for measurements and references).

2.6. Statistical model

We use the 'inverse calibration' approach, which was used to estimate hominin body mass in most (e.g., McHenry, 1992; Nakatsukasa et al., 2007) previous works. Inverse calibration is the regression of body mass on a single skeletal measurement in the univariate case and the multiple regression of body mass on skeletal measurements in the multivariate case. We use inverse calibration because the alternative 'classic calibration' approach, and the multivariate extension "profile likelihood," can produce mass estimates that deviate substantially away from the true mass of the individual when the unknown mass is far from the mass of the training sample (Grabowski et al., 2015). Note that the inverse calibration approach produces body mass predictions that are biased toward the mean of the training sample (in this case, the mean chimpanzee body mass; Table 2), as the final body mass prediction is based on the combination of the likelihood estimator and the informative prior − the distribution of known body masses from the training sample. We also calculate a multivariate "species mean" for *Orrorin* based on the two preserved individuals according to the procedure outlined in Grabowski et al. (2015). This

includes a 95% confidence interval. This method follows Borenstein et al. (2010) using an approach originally intended to be used with meta-analyses. It allows for determination of the species mean and the pooled confidence interval around this mean, taking into account the uncertainty of individual fossil predictions.

3. Analysis

3.1. Univariate regression equations

All analyses were performed using natural log-transformed data to improve model fit (Jungers, 1988b) and to correct for any heteroscedasticity in the residuals that may exist. Using natural log-transformed data also makes univariate coefficients roughly interpretable as proportional differences. For example, a coefficient of 1.57 from a regression of log body mass on log femoral head diameter can be interpreted as meaning that a 1% increase in femoral head diameter corresponds to a 1.57% increase in body mass. The final 10 traits used for this analysis were chosen first based on their use in previous analyses to estimate body mass (see references in Table 3) and their generally significant relationships with body mass (i.e., significant slopes), which are also reflected in their relatively high correlations with body mass.

The 10 traits included in this analysis had correlations with body mass ranging from 0.41 to 0.78 within our chimpanzee training sample. Though these correlations are lower than those of McHenry (1992), the results of that analysis were based on body mass regressions using sex-specific hominoid species means ($n = 16$) or partially sex-specific population means ($n = 4$) for intra-*Homo* regressions. Besides the extra error that is propagated from estimating means and then using these mean estimates to estimate hominin body mass (Smith et al., 1996), using means removes much

of the variation in body masses that is inherent to populations and needs to be included to produce robust prediction intervals for individual fossil body mass estimates.

All regression equations, standard errors for the parameter estimates, *p*-values for the intercept and slope, r^2, correlation (r), mean squared error (MSE), root mean square error (RMSE), as well as %SEE following Smith (1984) are shown in Table 4. For comparison, Table 5 (see also SOM Table S5) shows the same regression results but is taken from Grabowski et al. (2015) and is based on a small-bodied modern human sample of 220 individuals. Also note that both sets of equations include the mean of the measured trait and its variance, allowing future researchers to estimate prediction intervals for individual fossils using these results, and the quasi-maximum likelihood estimator (QMLE) to correct for de-transforming bias in body mass predictions (Smith, 1993).

3.2. Fossil body mass prediction

Using multivariate trait data from the relatively more complete fossil individuals (see Table 6), we tested which fossil traits followed the same scaling relationship among each other as in the training sample following Brown (1993) (see also Konigsberg et al., 1998; Uhl et al., 2013). If individual fossil traits were found to differ from this relationship, we used an iterative procedure described in Uhl et al. (2013; see also Brown and Sundberg, 1987) to drop them from the model, refit the model using the remaining traits, and repeat this procedure until the traits that remained were found to no longer be significantly different in terms of scaling from the training sample. The final multivariate estimate of a fossil's body mass was calculated based on the traits that had the same scaling relationship among each other as in the training sample. Table 6 presents the multivariate (where applicable) and univariate individual body mass predictions for *Orrorin* and *Ardipithecus* including 95% prediction intervals (see also SOM Table S6) using the common chimpanzee training sample. Also shown is a new multivariate species "average" for *O. tugenensis* with its CI (see also SOM Table S7). For comparative purposes, results using the modern human training sample from Grabowski et al. (2015) are included. We also included measurements and similarly calculated body mass predictions for A.L. 288-1 assigned to the species *Australopithecus afarensis* for comparison of the effects of using a different training sample on body mass predictions (Table 6 and SOM Table S6). Finally, Table 6 presents previously published body mass estimates based on the same metric traits as well as estimates from other sources.

We have corrected for bias that could result from back-transforming our predictions from log space into standard linear space (Smith, 1993) by multiplying our final untransformed body mass predictions by the QMLE for each multivariate and univariate equation discussed above. We have also done this for the results included here using the modern human training sample, resulting in small average increase (2.7%; range: 1.9–3.2%) in multivariate mass for BAR 1002′00, 1003′00, and A.L. 288-1 when compared to previous results (Grabowski et al., 2015).

4. Results

Table 4 presents the univariate regression equations to be used for predicting body mass from fossil traits based on a common chimpanzee training sample. Comparing these results with those using a modern human training sample (Table 5), one should note the substantially higher correlations between body mass and the individual traits in our chimpanzee sample when compared to the larger modern human sample from Grabowski et al. (2015). While this could be a statistical artifact due to sampling, it is more likely due to greater variation in the relationship between body mass and skeletal size in modern humans when compared to chimpanzees.

Based on the midpoint of the range of possible acetabular diameter dimensions (39 mm), Grabowski et al. (2015) estimated a body mass of 32.1 kg (PI: 19.4–53.3 kg) for ARA-VP-6/500, assigned to *Ar. ramidus* (Table 6). Our estimate shown here, 33.1 (PI: 20.0–55.0), is slightly higher than our previous estimate using the same modern human training sample as we apply the QMLE correction. Here, our point estimates for the body mass of ARA-VP-6/500 (50.2 kg; PI: 37.5–70.5 kg) are up to 20 kg larger than previously suggested when using a chimpanzee rather than a modern human pattern of scaling (Table 6; Grabowski et al., 2015). Similarly, while we (Grabowski et al., 2015) predicted body masses of 30.0 and 42.5 kg, respectively (PI: 17.0–50.2 and 25.5–70.9) for BAR 1002′00 and 1003′00, here we predict body masses of 30.9 (PI: 18.5–51.8) and 43.9 (26.4–73.2; Table 6) using the same modern human training sample and the QMLE correction. These estimates were based on 2–4 traits that were found to follow the same scaling relationship among each other as in modern humans, but equivalent results were found using only the superoinferior (SI) diameter of the femoral head for 1002′00. Here, we predicted body masses of 44.7 and 47.3 kg, respectively (PI: 31.3–63.8 and 30.2–74.1) for BAR 1002′00 and 1003′00, a large increase in body mass for BAR 1002′00 when compared to our previous estimate, though only a slight increase for BAR 1003′00. We note that here all but one of the traits in BAR 1002′00, mediolateral (ML) diameter of the subtrochanteric femur, were found to share a similar pattern of scaling as in the chimpanzee sample. We (Grabowski et al., 2015; SOM Table S6) previously found that two traits in both fossils did

Table 4
Regression parameter estimates using the chimpanzee training sample. Traits in bold were used in this study.

Traits	Intercept	SE	*p*-value	Slope	SE	*p*-value	r^2	r	MSE	RMSE	%SEE	Mean(X)	Var(X)	QLME
Femoral Head SI	−4.69	1.43	<0.01	2.44	0.41	<0.01	0.60	0.78	0.03	0.16	17.34	3.47	0.006	1.01
Femoral Neck SI	−0.69	1.37	0.62	1.45	0.44	<0.01	0.32	0.56	0.04	0.21	23.36	3.08	0.009	1.02
Femoral Head AP	−5.03	1.44	<0.01	2.53	0.41	<0.01	0.62	0.79	0.02	0.16	16.95	3.48	0.006	1.01
Femoral Neck AP	0.80	1.09	0.47	1.02	0.37	0.01	0.25	0.50	0.05	0.22	24.72	2.92	0.015	1.02
Subtrochanteric AP	−0.34	1.12	0.77	1.33	0.36	<0.01	0.37	0.61	0.04	0.20	22.39	3.11	0.013	1.02
Subtrochanteric ML	−2.05	1.42	0.16	1.80	0.44	<0.01	0.42	0.65	0.04	0.19	21.31	3.24	0.008	1.02
Femoral Midshaft AP[a]	−0.43	1.34	0.75	1.36	0.43	<0.01	0.30	0.55	0.05	0.21	23.66	3.09	0.010	1.02
Femoral Midshaft ML	−0.32	1.23	0.80	1.28	0.38	<0.01	0.32	0.57	0.04	0.21	23.25	3.21	0.012	1.02
Femoral Bicondylar[a]	−2.11	2.76	0.45	1.45	0.68	0.04	0.17	0.41	0.05	0.23	26.16	4.07	0.005	1.03
Tibial Plateau AP	−1.60	2.74	0.57	1.47	0.76	0.07	0.17	0.42	0.05	0.22	24.99	3.62	0.005	1.03
Tibial Plateau ML	−5.66	2.32	0.02	2.34	0.57	0.00	0.42	0.65	0.04	0.19	21.40	4.04	0.005	1.02
Tibial Distal End ML	−3.09	3.11	0.33	1.89	0.86	0.04	0.23	0.48	0.05	0.22	24.57	3.60	0.004	1.02
Tibial Distal Articular Surface	0.83	1.50	0.59	0.93	0.48	0.06	0.15	0.39	0.05	0.23	26.36	3.16	0.011	1.03
Tibial Plafond	0.18	1.81	0.92	1.20	0.61	0.07	0.20	0.44	0.05	0.22	25.23	2.95	0.008	1.03

[a] Traits that have a significant captivity effect.

Table 5
Regression parameter estimates using the MHS training sample. Traits in bold were used in this study.

Traits	Intercept	SE	p-value	Slope	SE	p-value	r^2	r	MSE	RMSE	%SEE	Mean(X)	Var(X)	QLME
Femoral Head SI	−2.10	0.85	0.01	1.57	0.22	<0.01	0.19	0.44	0.06	0.25	28.39	3.79	0.006	1.03
Femoral Neck SI	0.87	0.62	0.16	0.87	0.18	<0.01	0.10	0.32	0.07	0.26	30.13	3.43	0.010	1.04
Femoral Head AP	−1.92	0.86	0.03	1.53	0.23	<0.01	0.18	0.42	0.06	0.25	28.60	3.78	0.006	1.03
Femoral Neck AP	1.68	0.53	<0.01	0.66	0.16	<0.01	0.08	0.28	0.07	0.27	30.59	3.32	0.014	1.04
Subtrochanteric AP	1.30	0.72	0.07	0.78	0.22	<0.01	0.06	0.24	0.07	0.27	30.96	3.29	0.007	1.04
Subtrochanteric ML	−0.57	0.75	0.45	1.29	0.22	<0.01	0.15	0.38	0.07	0.26	29.30	3.44	0.007	1.03
Femoral Midshaft AP	1.76	0.71	0.01	0.64	0.22	<0.01	0.04	0.20	0.07	0.27	31.14	3.31	0.008	1.04
Femoral Midshaft ML	0.25	0.66	0.71	1.10	0.20	<0.01	0.13	0.36	0.07	0.26	29.57	3.29	0.008	1.03
Femoral Bicondylar	−3.35	1.15	<0.01	1.66	0.26	<0.01	0.16	0.40	0.06	0.25	28.85	4.35	0.004	1.03
Tibial Plateau AP	−1.04	1.05	0.33	1.25	0.27	<0.01	0.11	0.33	0.07	0.26	29.12	3.93	0.005	1.03
Tibial Plateau ML	−0.19	1.35	0.89	0.95	0.31	<0.01	0.06	0.25	0.07	0.26	29.10	4.29	0.005	1.04
Tibial Distal End ML	−2.81	0.50	<0.01	1.75	0.13	<0.01	0.47	0.69	0.04	0.20	22.13	3.82	0.012	1.02
Tibial Distal Articular Surface	0.41	0.70	0.56	1.00	0.20	<0.01	0.11	0.33	0.07	0.26	30.04	3.45	0.008	1.04
Tibial Plafond	1.02	0.73	0.16	0.86	0.22	<0.01	0.07	0.27	0.07	0.26	30.12	3.32	0.007	1.04

not scale in the same way as modern humans (leaving four and two traits, respectively, on which body mass was predicted).

The new species average for *Orrorin* of 45.7 kg (CI: 35.1–59.4 kg) is ~10 kg larger than we found previously (35.8 kg - CI: 25.0–51.3 kg; Grabowski et al., 2015; and 37.0 kg − CI 25.8–53.0 with the QMLE correction; Table 6) though we note that in both cases the species 'average' is unlikely to be an accurate measure of the true species mean due to the small number of individuals (two) that make up this estimate. The results of this analysis highlight how scaling differences among species can lead to large differences in predicted body masses.

5. Discussion

Overall, the differences between our previous results and those presented here are consistent with prior applications of regression equations based on modern human and non-human great ape data to predict body mass (Jungers, 1988b; Nakatsukasa et al., 2007), where the former generally predict smaller body masses than the latter (see also Almécija et al., 2015). It is important to note that though our point estimates of body mass are higher using the chimpanzee sample than the modern human sample, the new estimates fall within the prediction intervals of the former. Here we focused on intraspecific scaling (static allometry) rather than scaling between population averages (McHenry, 1992) or species means (Jungers, 1988b), levels of scaling that may or may not be consistent (Grabowski et al., 2015). We argue here and previously that regression equations based on individual data are most appropriate for the prediction of individual fossil body masses because they allow the construction of prediction intervals around individual estimates, rather than producing population or species mean estimates. These are necessarily more "messy" than predictions using means, but this is the result of them more accurately reflecting biological reality.

Though the body mass prediction of 1002′00 is 30.9 kg given the modern human pattern of scaling (Table 6), this result appears to be most consistent with the univariate results produced using only SI diameter of the femoral head and the modern human comparative data set (31.2 kg). Other traits predict larger body masses (ranging from 38.6 to 45.8 kg). This result is likely due to a combination of factors. Most importantly, *Orrorin* was identified as having a relatively small femoral head when compared to modern humans (relative to the overall size of the proximal femur), but slightly larger than some australopiths and African apes such as *Pan* (Richmond and Jungers, 2008; but see; Almécija et al., 2013) (see Fig. 1). A relatively small head when compared to modern humans could lead to smaller body mass predictions given a regression equation composed of individuals of that species.

Though these results could be used to argue that femoral head diameter is not an appropriate trait to use to predict body mass for early hominins when using a modern human training sample, as previously discussed (Grabowski et al., 2015), the picture of relative femoral head size in fossil hominins appears to be complex. Some australopith femoral heads are within the range of sizes observed in modern human populations, and some are below this range. With a large enough training sample and a relatively more complete hominin fossil, it appears possible to determine whether a particular femoral head is relatively small compared to modern humans, and base the final body mass estimates on traits that do not diverge from this pattern of scaling (e.g., A.L. 288-1; Grabowski et al., 2015). The finding here that most traits of BAR 1002′00, including the SI diameter of the femoral head, give roughly consistent results using the chimpanzee scaling model could suggest that generally the *Orrorin* femur scales more like those of chimpanzees than those of modern humans. With regard to *Ardipithecus*, the lack of any other relevant trait besides our estimate of SI diameter of the femoral head leaves this an open question.

We also note that there are some differences between our multivariate body mass estimates using the chimpanzee training sample for BAR 1002′00 and the body mass predicted by univariate traits - primarily those derived from ML diameter of the subtrochanteric femur. Correspondingly, this is the one trait that was dropped from our multivariate model using either training sample as it appeared to be significantly different in scaling than all other measured traits (Table 6). This result is encouraging in that it suggests that the ability of these methods to detect individual fossil traits that scale in a significantly different way than others is not substantially impacted by the small training sample size. This finding may be the result of an increase in power due to substantially higher correlations between body mass and most postcranial traits in chimpanzees when compared to modern humans, even when sample sizes are taken into account (Table 4 vs. Table 5), but we also note that the original presentation of this approach used example data sets that were smaller than our current sample size (Brown, 1982; Brown and Sundberg, 1987).

For A.L. 288-1, our results suggest that eight of nine traits in this fossil follow a similar pattern of scaling among each other as in chimpanzees. This result is quite distinct from that using a modern human comparative sample, where only two traits (ML diameter of the subtrochanteric femur and ML width at the femoral epicondyles) followed a similar pattern of scaling as traits in the comparative sample. Thus, issues with power may be problematic when testing which fossil traits followed the same scaling relationship among each other as in the chimpanzee training sample. On the other hand, the consistent univariate estimates for *Orrorin*

Table 6
Fossil individuals with measurements, body mass predictions with 95% PI using the chimpanzee and modern human training samples, and other published predictions. All measurements in kilograms (kg).

Species	Measurement (mm)	Body mass: Chimpanzee model - This study	Body mass: MHS model – From Grabowski et al. (2015)	Other Published Predictions
Orrorin tugenensis				
BAR 1002′00				
Multivariate Estimate	–	44.7 (31.3–63.8)	30.9 (18.5–51.8)	
Femoral Head SI	33.2	47.7 (34.0–66.9)	31.2 (18.7–51.9)	41.2[a]/31.5[b]
Femoral Neck SI	23.4	49.9 (31.9–78.1)	38.6 (22.7–65.6)	
Subtrochanteric AP	21.9	43.5 (28.5–66.7)	42.0 (24.5–72.1)	
Subtrochanteric ML	29.2	**56.4 (36.9–86.1)**	**45.4 (27.3–75.4)**	
Femoral Midshaft AP	21	–	41.8 (24.2–72.2)	50.1[c]
Femoral Midshaft ML	25	45.4 (29.2–70.5)	45.8 (27.4–76.5)	
Range	–	43.5–56.4	31.2–45.8	35–50[d]
BAR 1003′00				
Multivariate Estimate	–	47.3 (30.2–74.1)	43.9 (26.4–73.2)	
Subtrochanteric AP	21.1	41.4 (27.0–51.0)	40.8 (23.7–70.83)	
Subtrochanteric ML	27.6	51.0 (33.7–77.0)	**42.2 (25.3–70.3)**	
Femoral Midshaft AP	20.8	–	41.5 (24.0–71.8)	
Femoral Midshaft ML	26.4	48.7 (31.2–75.8)	48.6 (29.1–81.2)	55.1[d]
Range	–	41.4–51.0	40.8–48.6	
Multivariate species "average"		45.7 (35.1–59.4)	37.0 (25.8–53.0)	
Ardipithecus ramidus				
ARA-VP-6/500				51[e]
Femoral Head SI – Midpoint[f]	33.9/34.5	50.2 (35.7–70.5)	33.1 (20.0–55.0)	35.7/50.8[g]
Femoral Head SI - Lower limit[f]	31.5/31.9	41.9 (29.9–58.8)	29.3 (17.5–49.0)	
Femoral Head SI - Upper limit[f]	36.3/37.1	59.3 (41.7–84.3)	37.1 (22.5–61.2)	
Acetabular Diameter SI	Midpoint 39 (range: 36–42)			
Range		41.9–59.3	29.3–37.1	
Australopithecus afarensis				
AL 288-1				
Multivariate Estimate	–	27.4 (13.1–57.3)	26.5 (17.6–40.0)	
Femoral Head SI	28.5	32.9 (23.1–46.8)	**24.5 (14.4–41.47)**	
Femoral Neck SI	21.4	43.8 (28.1–68.2)	**35.7 (20.9–61.1)**	
Subtrochanteric AP	17.7	32.8 (20.7–52.0)	**35.6 (20.3–62.5)**	
Subtrochanteric ML	24.4	40.8 (27.1–61.5)	36.0 (21.4–60.4)	
Femoral Bicondylar	56.7	–	**29.3 (17.3–49.6)**	
Tibial Plateau AP	32.8	35.4 (21.0–59.6)	**28.9 (16.6–50.5)**	
Tibial Plateau ML	50.2	33.6 (21.8–51.8)	**35.8 (20.5–62.5)**	
Tibial Distal End ML	32.7	34.3 (20.3–57.9)	27.2 (18.1–40.07)	
Tibial Distal Articular Surface AP	14.9	**28.8 (14.7–56.26)**	**23.3 (12.8–42.4)**	
Tibial Plafond	17.2	37.7 (22.7–62.7)	**33.0 (18.8–57.7)**	
Range		32.8–49.8	23.3–35.8	

Multivariate estimates based on traits that follow the same scaling relationship as in each model species.
Results in bold refer to traits that differ from the scaling relationship of the model species.
Ranges show ranges of body mass point estimates for univariate traits that do not differ from the scaling relationship of the model species.
[a] Based on a non-human ape training sample from McHenry (1992).
[b] Based on a modern human training sample from McHenry (1992).
[c] Based on an ape training sample from Ruff (2003).
[d] From Nakatsukasa et al. (2007).
[e] Based on regression of body mass on geometric means of talus and capitate measurements using an anthropoid training sample.
[f] Range of estimates predicted for Femoral Head SI using acetabular diameter range and prediction equations of Plavcan et al. (2014).
[g] Values from Almécija et al. (2015) based on chimpanzee sample of known body mass and population means for small-bodied modern humans.

body mass argue that this issue is likely to have less effect on the multivariate estimates for this taxon. We also note that the final difference in body mass estimates for A.L. 288-1 using either training sample is less than a kilogram and, as previously noted (Jungers et al., 2016), this fossil may be unusual in size and shape when compared to many other hominins.

5.1. Comparisons with other studies

Nakatsukasa et al. (2007) estimated the body mass and stature of *O. tugenensis* using published univariate anthropoid, great ape, and modern human regressions that were based on available population and/or species means to predict the body mass of 1002′00 and 1003′00. Predicted body masses for both individuals combined were found to be somewhere between 35 and 50 kg using their range of regressions. Here, given a chimpanzee-like pattern of scaling, our

predictions for both fossils are in the middle of their range of estimates and support their conclusions. As discussed by the authors, "care should be taken because these estimates are accompanied by a wide CI" (Nakatsukasa et al., 2007, p. 177). These wide CIs are even wider when predicting the individual body mass of the fossil using regressions based on individuals rather than means, as we do in this study. As discussed above, these wider CIs more accurately reflect uncertainty in predictions for fossil individuals.

With regards to ARA-VP-6/500, it is notable that the numerous published papers discussing the evolutionary implications of *Ar. ramidus* (e.g., White et al., 2009; Lovejoy et al., 2009a, 2009b) relied upon one uncommon approach to estimate body mass. The researchers who calculated this estimate regressed the mean log of the cube root of body mass on the log of the geometric mean of measurements from the talus and capitate from a large number of anthropoids (Lovejoy et al., 2009b). This approach produced an

Figure 1. Proximal femur of BAR 1002′00 (*Orrorin tugenensis*, top center) compared to other early hominins including fossils attributed to *Paranthropus robustus* (SK 82, top left; SK 97, middle left), *P. boisei* (KNM-ER 1503, bottom left), *Au. afarensis* (cast of A.L. 288-1, bottom center), and early *Homo* (KNM-ER 1481, right). Photograph courtesy of Brian Richmond. For reference, femoral head diameter of BAR 1002′00 is 33.2 mm.

estimate of ~51 kg depending on the species composition. This is notable because an estimate of acetabular diameter, a trait that is commonly used in body mass estimation based on abundant research demonstrating its relationship with mass, was also available though they gave a range of estimates for this dimension. Here, taking the midpoint of this range and the low and high ends, our results are similar to those of Lovejoy et al. (2009b) given a chimpanzee-like pattern of scaling with body mass (50.2 kg; PI: 35.7—70.5 kg using the midpoint of acetabular diameter estimates), though they stand in sharp contrast with the results given a modern human pattern (33.1 kg; PI: 20.0—55.0 kg using the same midpoint). Similar results were found in Almécija et al. (2015), regressing estimated femoral head diameter against a mixed common chimpanzee and bonobo sample (*P. troglodytes* and *Pan paniscus*) with known body masses and a sample of sex-specific population means for small-bodied modern humans (Table 6), though our results include the prediction interval for our estimate and were based on a single chimpanzee species. The chimpanzee-sized body mass estimate is consistent with the observation that the sizes of many ARA-VP-6/500 skeletal elements are comparable to those of chimpanzees (e.g., Lovejoy et al., 2009c). How our results here and in our previous analysis complement or contrast that of Lovejoy et al. (2009c) depends on which, if any, comparative model is more appropriate for *Ardipithecus*.

6. Conclusion

The body mass predictions for *Orrorin* and *Ardipithecus* presented here, as well as all fossil body mass predictions, depend on the assumption that the pattern of scaling between skeletal traits and body mass in the fossil was similar to that of an extant model. Previously we used modern humans as this model, based on the assumption that because early hominins appear to share our mode of locomotion (Richmond and Jungers, 2008; Kimbel and Delezene, 2009; Lovejoy et al., 2009c; Almécija et al., 2013), postcranial dimensions may scale with body mass in a similar fashion. As we noted (Grabowski et al., 2015), evidence that *Orrorin* (Pickford et al., 2002; Richmond and Jungers, 2008) and *Ardipithecus* (Haile-Selassie, 2001; Lovejoy et al., 2009c; Russo and Kirk, 2013) had some adaptations for bipedalism could be used to argue that modern humans are the most appropriate extant great ape model for these species. On the other hand, it does not appear that either taxon had a complete suite of postcranial traits that mirrored the biomechanical complexes observed in australopiths or later hominins (Lovejoy et al., 2009c; Kuperavage et al., 2010). In addition, here we found the more complete 1002′00 scales overall in a way that is more similar to common chimpanzees than modern humans.

Our new estimates fall near the male (*Ardipithecus*) average and in between the male and female averages (*Orrorin*) for wild-caught common chimpanzees (49.6 for males, 40.4 for females, Table 2) (Smith and Jungers, 1997). If chimpanzee-like patterns of scaling existed in these earliest possible hominins, these results could mean that the larger body sizes found in some early australopiths (Pontzer, 2012; Grabowski et al., 2015; see also; Jungers et al., 2016; Masao et al., 2016) were already present in earlier taxa near the origins of our lineage. These results also point to a fairly large body mass for the last common ancestor of humans and chimpanzees, a conclusion that is consistent with the sizes of individual skeletal elements of late Miocene fragmentary fossils attributed to *Sahelanthropus* and earlier members of *Ardipithecus* (Haile-Selassie, 2001; Brunet et al., 2002) and a recent study using a different approach (Grabowski and Jungers, 2017). A common chimpanzee-like size has significant implications for the locomotor modes of the *Pan-Homo* last common ancestor, strongly arguing against small-bodied models (e.g., the hylobatidian model; Keith, 1923; Tuttle, 1981) and providing less support for an above-branch arboreal quadruped (Straus, 1949; Lovejoy, 2009).

Supplementary Online Material

Supplementary online material related to this article can be found at https://doi.org/10.1016/j.jhevol.2018.05.001.

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