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## Body mass estimates of hominin fossils and the evolution of human body size

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### ABSTRACT

Body size directly influences an animal's place in the natural world, including its energy requirements, home range size, relative brain size, locomotion, diet, life history, and behavior. Thus, an understanding of the biology of extinct organisms, including species in our own lineage, requires accurate estimates of body size. Since the last major review of hominin body size based on postcranial morphology over 20 years ago, new fossils have been discovered, species attributions have been clarified, and methods improved.

Here, we present the most comprehensive and thoroughly vetted set of individual fossil hominin body mass predictions to date, and estimation equations based on a large ( $n = 220$ ) sample of modern humans of known body masses. We also present species averages based exclusively on fossils with reliable taxonomic attributions, estimates of species averages by sex, and a metric for levels of sexual dimorphism. Finally, we identify individual traits that appear to be the most reliable for mass estimation for each fossil species, for use when only one measurement is available for a fossil.

Our results show that many early hominins were generally smaller-bodied than previously thought, an outcome likely due to larger estimates in previous studies resulting from the use of large-bodied modern human reference samples. Current evidence indicates that modern human-like large size first appeared by at least 3–3.5 Ma in some *Australopithecus afarensis* individuals. Our results challenge an evolutionary model arguing that body size increased from *Australopithecus* to early *Homo*. Instead, we show that there is no reliable evidence that the body size of non-*erectus* early *Homo* differed from that of australopithecids, and confirm that *Homo erectus* evolved larger average body size than earlier hominins.

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### 1. Introduction

An animal's overall body size is directly related to how it interacts with the natural world. Factors such as energy requirements, home-range size, social organization, relative brain size, locomotion, and numerous other morphological, ecological, and life history characteristics are all tied in some way to body size. Thus, interpreting the evolution of any of these factors demands accurate estimates of body size in extinct species. This is true for our own lineage, where almost all of the hows and whys of human

evolution are directly tied to estimates of body size at particular points in time. (Note that we define body size as body mass.)

The last major review of hominin body size based on postcranial traits was more than 20 years ago – the classic contribution of McHenry (1992), who presented size predictions for individual fossils, species averages, species averages by sex, and a comprehensive set of regression equations that have been used extensively to estimate body size in newly described fossil hominins since its publication. McHenry (1992: 412) presented his results as an “important first step toward establishing the average body size and range of variation of early hominid species” (referring to hominins). It was considered to be a first step because the size estimates required a number of unavoidable assumptions, and the species body mass averages were in many cases based on tentative species

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attributions that may or may not be valid today. McHenry's (1992) analysis has proven to be a very important step in understanding the evolution of human body size. However, despite McHenry's (1992) caveats about uncertainty regarding some of the estimates, the results of this study have often been used with more confidence than might be warranted in the development of prominent models and hypotheses regarding human evolutionary history.

Since then, very few studies have attempted a large review of hominin body size estimation. Ruff et al. (1997) presented a large number of individual fossil body size estimates in their supplementary information, though these estimates were not the focus of this analysis (see also Trinkaus and Ruff, 2012). Hartwig-Scherer (1993) used a slightly different approach than McHenry (1992), though Hartwig-Scherer (1993) provided estimates of a smaller number of individuals. Manger et al. (2012) presented a large number of body size estimates for individual fossils but these were taken from various sources and the focus of that review was on relative brain size. A number of recent articles on the origin of our genus (Antón, 2012; Antón and Snodgrass, 2012; Plavcan, 2012; Antón et al., 2014) used a combination of published and new individual estimates of body mass compiled by Pontzer (2012) that were then used to calculate species means (Antón, 2012). But most of the early hominin body mass estimates from this compilation (Pontzer, 2012) were taken directly from McHenry (1992), and the majority of the rest were based on regression equations taken from the same source. Therefore, while these represent updated estimates of hominin body size, they rely heavily on McHenry's (1992) analyses. There have also been a number of attempts to estimate fossil hominin body mass based on cranial traits, for example using the regression of orbit size and body mass in modern humans or other primates (Aiello and Wood, 1994; Kappelman, 1996), although Elliott et al. (2014) suggest caution due to the large amount of error present around these estimates, at least within taxa.

We argue that, for a number of reasons, it is time for an analysis to build on and update McHenry's (1992: 412) "important first step." First, many hominin fossils have been discovered since 1992. Second, more taxa have been discovered since that time and, for many species, the taxonomic attributions of postcranial fossils are better understood. Third, more comprehensive comparative samples of known mass, especially smaller-bodied humans, are available to improve estimates of body mass from skeletal remains similar in size to those of early hominins. Finally, methodological advances (e.g.; Brown, 1982; Brown and Sundberg, 1987; Brown, 1993; Konigsberg et al., 1998; Hens et al., 2000; Uhl et al., 2013), including the ability to test for differences in scaling between fossil traits and modern humans (see below), can provide more reliable estimates including prediction and confidence intervals.

The objectives of this study are to:

- 1) Provide body mass predictions, with confidence intervals, for the largest possible current sample of early hominin lower postcranial elements using a combination of multivariate and univariate approaches. For our multivariate estimates, we first determine which traits within a particular fossil shared the same scaling relationship among each other as in modern humans, and only those traits with similar relationships were used in our final body mass estimates. We also include body mass predictions using the same methods for a worldwide sample of smaller-bodied modern human populations and include these in the [Supplementary Online Material \[SOM\]](#).
- 2) Present a series of equations for estimating body mass from univariate postcranial trait measurements based on a large sample ( $n = 220$ ) of modern human skeletons with known body mass.

- 3) Determine individual traits for each hominin species that produce univariate body mass estimates equivalent to those calculated using our multiple regression approach.
- 4) Provide body mass species means, species means by sex (both with confidence intervals), and a metric of sexual dimorphism for fossil hominin species. Importantly, these are restricted to fossils with relatively reliable species attributions.
- 5) Provide all fossil postcranial measurements used in this analysis to aid future researchers.

## 2. Materials and methods

### 2.1. Overview of our approach

This study follows previous analyses (Brown, 1982; Brown and Sundberg, 1987; Brown, 1993; Konigsberg et al., 1998; Uhl et al., 2013) that use a calibration approach. In the simplest terms, a calibration approach involves using a large training sample (i.e., the sample used to build, or train, the model) with known body mass and multiple trait measurements per individual to construct regression equations that are then used to predict body mass in a sample with an unknown body mass. But this is where the simplicity ends. The questions of what training sample is most appropriate, which traits to use in the analysis, and the particulars of the statistical model employed are all paramount. These are discussed in detail below. In brief, we use a training sample of generally smaller-bodied modern humans of known body mass because modern humans provide the best available model (i.e. better than an all-hominoid sample) for predicting body mass from lower limb size in hominins that are committed bipeds (i.e. those that only travel bipedally on the ground). Traits are limited to dimensions of the lower limb skeleton because of its direct functional role in supporting body mass. We use the "inverse calibration" approach, which has been exclusively used to estimate hominin body mass in most (e.g. McHenry, 1992) but not all (e.g. Nakatsukasa et al., 2007) previous works. We select the inverse calibration approach for theoretical reasons (see below) and because the alternative "classic calibration" approach can produce mass estimates that deviate substantially away from the true mass of the individual (see below).

### 2.2. Training sample

Estimating hominin body mass requires that the training samples comprise individuals from closely related species of known body mass and available skeletal elements. Two possibilities are the living species most closely related to early hominins, modern humans and chimpanzees. Modern humans are the obvious choice here, as there are a number of large collections of individuals with known body mass and matched skeletal elements. Modern human regressions based on lower limb elements are likely to be the most appropriate for early hominins because it appears that some form of bipedal locomotion evolved early in our lineage (Pickford et al., 2002; Richmond and Jungers, 2008; Kimbel and Delezene, 2009; Lovejoy et al., 2009b; Almécija et al., 2013), though they may be less appropriate for fossils argued to be the earliest members of our clade (White et al., 1994; Senut et al., 2001; Brunet et al., 2002). Functional similarity could argue against using a chimpanzee training sample even for early hominins that may have been only facultative bipeds because their lower limbs, while still different from those of humans, appear to possess certain adaptations to some form of bipedal locomotion that are absent in chimpanzees (e.g. Ruff, 1988; Jungers, 1988a). In addition, though skeletal material from chimpanzees is readily available, matched body masses for individuals are extremely

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