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## Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins

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## ABSTRACT

Previous attempts to estimate body mass in pre-Holocene hominins have relied on prediction equations derived from relatively limited extant samples. Here we derive new equations to predict body mass from femoral head breadth and proximal tibial plateau breadth based on a large and diverse sample of modern humans (avoiding the problems associated with using diaphyseal dimensions and/or cadaveric reference samples). In addition, an adjustment for the relatively small femoral heads of non-*Homo* taxa is developed based on observed differences in hip to knee joint scaling. Body mass is then estimated for 214 terminal Miocene through Pleistocene hominin specimens. Mean body masses for non-*Homo* taxa range between 39 and 49 kg (39–45 kg if sex-specific means are averaged), with no consistent temporal trend (6–1.85 Ma). Mean body mass increases in early *Homo* (2.04–1.77 Ma) to 55–59 kg, and then again dramatically in *Homo erectus* and later archaic middle Pleistocene *Homo*, to about 70 kg. The same average body mass is maintained in late Pleistocene archaic *Homo* and early anatomically modern humans through the early/middle Upper Paleolithic (0.024 Ma), only declining in the late Upper Paleolithic, with regional variation. Sexual dimorphism in body mass is greatest in *Australopithecus afarensis* (log[male/female] = 1.54), declines in *Australopithecus africanus* and *Paranthropus robustus* (log ratio 1.36), and then again in early *Homo* and middle and late Pleistocene archaic *Homo* (log ratio 1.20–1.27), although it remains somewhat elevated above that of living and middle/late Pleistocene anatomically modern humans (log ratio about 1.15).

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### 1. Introduction

Because of the mechanical role of the lower limbs in supporting body weight, their bone breadths have frequently been used to estimate body mass in past hominins (McHenry, 1976, 1988, 1992; Rightmire, 1986; Jungers, 1988a; Grine et al., 1995; Ruff et al., 1997; Churchill et al., 2012; Grabowski et al., 2015; Will and Stock, 2015). Many questions remain regarding the best approach in such analyses, however, including the most appropriate modern reference groups and which specific skeletal dimensions to employ, as well as broader issues regarding possible variation in the scaling of dimensions to body mass in different hominin taxa. For example, it has been clear for more than half a century that compared to

modern humans, australopiths generally have small femoral heads relative to their proximal femoral shaft breadths (Napier, 1964; Wood, 1976; Ruff et al., 1999; Richmond and Jungers, 2008; Harmon, 2009); thus, when using equations based on modern humans, femoral head breadths produce smaller body mass estimates for australopiths than do shaft breadths (McHenry, 1992; also see below). Body mass estimation equations based on different modern human reference samples also produce variable results when applied to earlier hominins, with some possible size-related effects (Auerbach and Ruff, 2004; Kurki et al., 2010). Statistical methods for calculating prediction equations, particularly where target samples extend outside the size range of the reference sample, can also have an important effect on estimates (Sjøvold, 1990; Aiello, 1992; Konigsberg et al., 1998).

In this paper, we address some of these issues using large recent samples and develop new body mass estimation equations based on hip and knee joint size. These are then applied to a sample of 214

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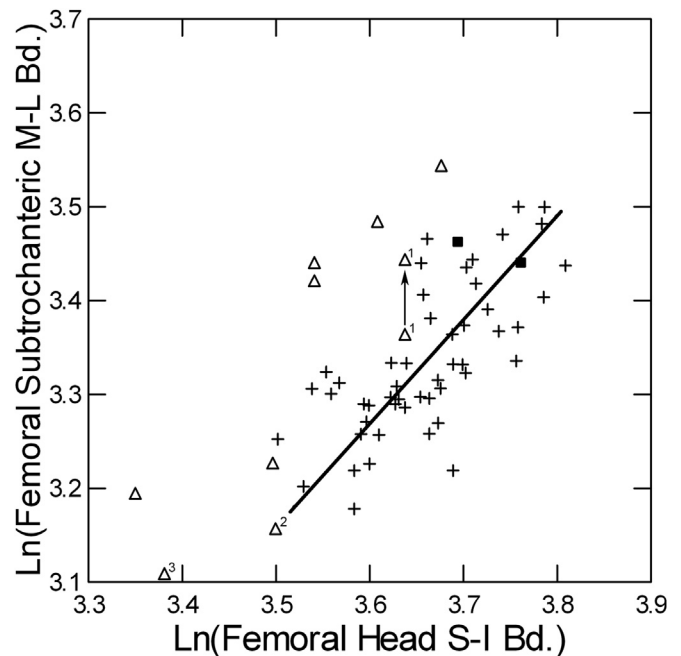
hominin specimens spanning from ~6 Ma to the end of the Pleistocene (0.012 Ma). Temporal trends and inter-taxon variation in average body mass and sexual dimorphism in body mass are examined, and compared with previous estimates. Differences relative to earlier estimates in some of the results obtained here are discussed with respect to both functional and statistical factors.

We note at the outset that we are considering only human-based body mass estimation equations in these analyses. Although there is evidence for arboreal behavior in some early hominin taxa (Stern and Susman, 1983; Ruff, 2009; Ruff et al., 2016a), early hominins show many adaptations for terrestrial bipedality (Ward, 2013); thus, equations based on a habitual biped should provide more accurate body mass reconstructions than ones based on hominoids more generally. This does not mean that such equations can be used uncritically—as discussed in the next two sections, some are likely to provide more accurate estimations than others, or to require adjustment before being applied. But beginning with a bipedal rather than quadrupedal (e.g., great ape or hominoid) model is most reasonable on morphological and functional grounds.

### 1.1. Use of articular versus diaphyseal breadths for body mass estimation

Both mechanical considerations and empirical observations support a strong association between body mass and articular and diaphyseal cross-sectional dimensions of weight-bearing long bones (Selker and Carter, 1989; Polk et al., 2000; Ruff, 2000b), although other considerations such as degree of joint excursion and locomotor mode may also affect these relationships (Godfrey et al., 1991; Ruff, 2002a). Diaphyseal breadths or the products of femoral shaft breadths have been used by a number of researchers to develop body mass estimation equations for early hominins (McHenry, 1976, 1988, 1992; Rightmire, 1986; Grabowski et al., 2015). It has been noted from early on, though, that these dimensions may produce different estimates than articular-based estimates in australopiths because of their different articular/shaft proportions compared to those of modern humans (McHenry, 1976, 1992). McHenry (1992) found that, among 10 non-*Homo* specimens, femoral shaft breadths produced estimates 1.34 times higher on average than lower limb articular breadths of the same specimens. Based on other considerations, he felt that the articular estimates were more reasonable than the shaft estimates, and subsequently used them exclusively in comparisons among both australopiths and *Homo* (McHenry, 1994; McHenry and Coffing, 2000).

The uniformity of this proportional difference between australopiths and modern humans was recently challenged by Grabowski et al. (2015), who pointed out that some specimens, notably A.L. 152-2, A.L. 827-1, and Sts 14, do not appear to have relatively small femoral heads. Figure 1 is a plot of subtrochanteric mediolateral (M-L) breadth of the femoral shaft against superoinferior (S-I) breadth of the femoral head in the 11 australopith and two early *Homo* specimens included in Grabowski et al.'s (2015) study, along with a sample of 50 Late Stone Age specimens (LSA; Will and Stock, 2015; Stock, pers. comm.), chosen for comparison because of their small body size, within or close to the range of the early hominins. The larger shaft dimensions relative to femoral head size for australopiths in general are clearly apparent. The three specimens highlighted by Grabowski et al. (2015) are indeed partial exceptions; however, in each case the femoral shaft dimension is open to question (see Supplementary Online Material [SOM] Text 1). As shown by Grabowski et al. (2015): their Fig. 4), australopiths have systematically much lower femoral head/shaft breadth proportions than modern humans, and if the three above



**Figure 1.** Femoral subtrochanteric mediolateral (M-L) breadth (Bd.) versus femoral head superoinferior (S-I) breadth in early hominins and a modern southern African Late Stone Age (LSA) sample. Ln = natural log, crosses = modern LSA, filled squares = early *Homo* (KNM-ER 1472 and 1481a), open triangles = australopiths (*Australopithecus afarensis*, *Australopithecus africanus*, *Paranthropus robustus*, *Paranthropus boisei*). Reduced major axis line plotted through modern data. The three specimens discussed in SOM Text 1 are indicated with numbers: 1 = A.L. 827-1, 2 = A.L. 152-1, 3 = Sts 14. Arrow indicates position of A.L. 827-1 using more traditional definition of subtrochanteric position (see SOM Text 1). Early hominin data from Grabowski et al. (2015); modern data from Stock (pers. comm.; also see Will and Stock [2015]).

specimens are not included there is minimal overlap in individual proportions with an extensive series of modern human samples. In contrast, early *Homo* femora have head/shaft proportions well within modern human ranges (Fig. 1 and Grabowski et al., 2015: their Fig. 3). (The one adult *Homo erectus* specimen, OH 28, included in Figure 3 of Grabowski et al. [2015] appears to have a low head/shaft breadth ratio, but this is in part due to an incorrect femoral head breadth estimate for this specimen—see SOM Text 2.)

Even within *Homo*, however, there is evidence for systematic taxonomic and temporal variation in lower limb bone cross-sectional diaphyseal size relative to body size and shape, pelvic shape, and lower/upper limb bone proportions (Ruff, 1995, 2009; Trinkaus and Ruff, 2012; Ward et al., 2015; Ruff et al., 2015a, b). Some of these differences are due to variation in overall body proportions and some to more specific mechanical/behavioral factors, but in either case, they argue for extreme caution in applying body mass equations based on living or very recent human shaft dimensions. The substantial variation in diaphyseal morphology among even closely related taxa/populations is likely in part attributable to the developmental plasticity of long bone diaphyses (Trinkaus et al., 1994; Ruff, 2003b; Ruff et al., 2006, 2013b; Warden et al., 2014; Sparacello et al., 2017). This raises issues regarding individual as well as broader group differences in morphology that are not directly related to differences in body size. In other words, lower limb bone diaphyseal breadths are likely to be influenced by a combination of body size and other mechanical influences, but in ways that are difficult to predict. This argues against their use in body mass prediction, unless the target sample is known to be very similar in other respects (e.g., body shape and locomotor behavior) to the reference sample (as might be the case, for example, in forensic applications—see Robbins et al., 2010; Ruff

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