Skeletal dimorphism of *Australopithecus afarensis* and its significance for behavioral reconstructions in early hominids

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Diet and locomotor behavior can, to a certain extent, be reliably determined from the dentition and postcranial skeleton. In each case, inferences can be made reasonably from a single well-preserved specimen. An analysis of secondary sexual characteristics that permits the reconstruction of reproductive behavior, however, requires a substantial sample of individuals with which to accurately estimate variation across a population or species. The most commonly cited estimate of body mass dimorphism suggested a level intermediate between moderately dimorphic humans and chimpanzees and extreme dimorphism of gorillas and orangutans (McHenry 1991). However, estimating mass from isolated skeletal specimens necessarily introduces error that when accounted for precludes eliminating any particular primate degree of dimorphism (McHenry 1994). As the relationship between body mass and skeletal size cannot be known for extinct species, recent analyses have focused on measuring *skeletal* variation in *Australopithecus afarensis* and comparing it to similar quantities in extant ape species. Still, different researchers have come to remarkably different conclusions ranging from moderate levels of dimorphism similar to humans (Reno et al. 2010; Reno et al. 2003) to extremely high levels similar to gorillas (Gordon et al. 2008).

Our measure of *Au. afarensis* dimorphism was attained using the template method, which takes advantage of the largely complete Lucy skeleton (A.L. 288-1) to estimate size ratios for many Afar specimens (Reno et al. 2010; Reno et al. 2003). This method permits an inclusion of large samples to accurately infer skeletal size variation. Briefly, the template method is calculated as follows: Using the Lucy skeleton we first make a series of simple ratios between a skeletal dimension of an individual fossil (i.e., the A.L. 333-7 distal tibia) and the equivalent dimension on Lucy. Multiplying these ratios by Lucy's femoral head size derives a sample of estimated femoral heads for the fossils. This procedure expands the available sample size to 26 from the single site A.L. 333 and to 41 incorporating fossils from across the Afar region (Combined Afar). To provide a measure of dimorphism we calculated the coefficient of variation of the computed ratios. Each ratio is simply computed between two similar metrics—therefore no assumptions are required concerning the scaling relationships between different skeletal sites.

To compare the degree of variation in *A. afarensis* to those of extant species we performed random simulations using modern humans, chimpanzees, and gorillas. In each case an individual was randomly chosen to serve as the template specimen (i.e., stand in for Lucy) to calculate species-specific size ratios. Then a sample was randomly selected to match the anatomical composition of the *Au. afarensis* assemblage. Size

variation was then measured using the template specimen, and the process was repeated 1000 times to provide a distribution of dimorphism estimates for each species.

An additional strength of the template method is the ability to modify the extant species simulations to model specific taphonomic properties (formative and sampling characteristics) of the fossil assemblage. As A.L. 333 is a single locality, it is possible that a number of the separate fossils represent the same *afarensis* individuals. Given the dental remains, it is known that at least 9 individuals were recovered from A.L. 333 (White and Johanson 1989). Therefore, we modified our simulations to randomly sample the 26 anatomical measurements representing the A.L. 333 fossils from a subsample of 9 randomly selected individuals, guaranteeing the multiple representation of single individuals in the sample.

Our results show that the A.L. 333, non-A.L.333 and Combined Afar assemblages all have a low probability of being sampled from a low dimorphic chimpanzee-like or high dimorphic gorilla-like population. The template method also has advantages over other methods that estimated higher degrees of dimorphism in that it maximizes sample size while not requiring an *a priori* assumption of sex for specific fossils (McHenry 1991) nor overemphasizing the influence of more complete but extreme sized individuals (Gordon et al. 2008). Such a degree of dimorphism accords well with estimates of other early hominid species such as *Ardipithecus ramidus* (White et al. 2009), *Au. africanus* (Harmon 2009), and recent *Homo,* which displayed low to moderate degrees of skeletal dimorphism.

Estimating skeletal dimorphism is of course not an end unto itself. More important are the behavioral inferences available from such patterns of dimorphism, which can then be used to reconstruct early hominid diet, locomotion, and reproductive strategy. An intermediate level of dimorphism suggests a wholly different form of reproductive behavior from other hominoids and indicates that no extant ape can serve as an appropriate model for reconstructing early hominid behavior. More compelling, however, is the reduced, 'feminized' male canine found in all hominid species (Kimbel and Delezene 2009). Such reduction is now known to have occurred prior to systematic tool usage and major dietary shifts seen in australopithecines (Suwa et al. 2009). Large canines are highly associated with strong intrasexual competition. Such reduction as seen in hominids suggests a reduction in male agonistic behavior is a key behavior of the hominid lineage.

It is unsurprising that the unique combination of reduced canines and moderate body size dimorphism in *Au. afarensis* has garnered significant attention and interest. However, it should also be unsurprising that this early hominid species would display a

unique pattern of dimorphism compared to its primate relatives, thus confounding simple behavioral analogies to extant apes. Recent discoveries from *Ardipithecus ramidus* demonstrate that the African apes represent highly derived relic species with respect to our last common ancestor (White et al. 2009). In contrast to the arboreal, knuckle/fist-walking, fruit/foliage specialized great apes, australopithecines were bipedal terrestrial omnivores with remarkable demographic success compared to any other Pliocene hominoid except for subsequent species of *Homo*. Modern humans also exhibit a unique suite of socially-related anatomical and physiological characters, such as concealed ovulation and poor sperm competition capability (Dixson 1998). It is therefore entirely possible that much of the derived physiology and anatomy of Pleistocene humans had also evolved by the early Pliocene. One behavioral reconstruction that accords well with these characteristics of *Au. afarensis* is a pair-bonded social reproductive strategy that includes male provisioning behavior of his mate and offspring (Lovejoy 1981; Lovejoy 2009). This would account for the canine reduction, indicating low intermale agonism and moderate body size dimorphism associated with distinct male and female foraging behaviors. Most importantly, such a strategy would account for the increased reproductive rate with simultaneous increase in the juvenile dependency period necessary for permitting the dramatic demographic success of early hominids and subsequent brain expansion observed in the Pleistocene.

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