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Human-like hip joint loading in *Australopithecus africanus* and *Paranthropus robustus*

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ABSTRACT

Adaptations indicative of habitual bipedalism are present in the earliest recognized hominins. However, debate persists about various aspects of bipedal locomotor behavior in fossil hominins, including the nature of gait kinematics, locomotor variability across different species, and the degree to which various australopith species engaged in arboreal behaviors. In this study, we analyze variation in trabecular bone structure of the femoral head using a sample of modern humans, extant non-human hominoids, baboons, and fossil hominins attributed to *Australopithecus africanus*, *Paranthropus robustus*, and the genus *Homo*. We use μ CT data to characterize the fabric anisotropy, material orientation, and bone volume fraction of trabecular bone to reconstruct hip joint loading conditions in these fossil hominins. Femoral head trabecular bone fabric structure in australopiths is more similar to that of modern humans and Pleistocene *Homo* than extant apes, indicating that these australopith individuals walked with human-like hip kinematics, including a more limited range of habitual hip joint postures (e.g., a more extended hip) during bipedalism. Our results also indicate that australopiths have robust femoral head trabecular bone, suggesting overall increased loading of the musculoskeletal system comparable to that imposed by extant apes. These results provide new evidence of human-like bipedal locomotion in Pliocene hominins, even while other aspects of their musculoskeletal systems retain ape-like characteristics.

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1. Introduction

Pliocene hominins display a variety of adaptations for habitual terrestrial bipedalism (Stern, 2000; Ward, 2013), but some aspects of their gait kinematics, locomotor variability, and the amount and nature of arboreality in their behavioral repertoires (i.e., its selective importance) remain unresolved (Ward, 2002; Lovejoy et al., 2009; Harcourt-Smith, 2016). Recent fossil evidence suggests that there may have been considerable locomotor variability among early hominins, and among australopiths in particular (Lovejoy

et al., 2009; Zipfel et al., 2011; Haile-Selassie et al., 2012; DeSilva et al., 2013; Harcourt-Smith, 2016). Reconstruction of australopith gait kinematics has typically relied on interpretations of a variety of morphological characteristics, biomechanical models, fossilized trackways, and experimental studies of locomotor energetics (Ruff, 1995, 2010; Stern, 2000; Wang et al., 2003, 2004; Lovejoy, 2005b, a, 2007; Nagano et al., 2005; Sellers et al., 2005; Sockol et al., 2007; Raichlen et al., 2008, 2010; Lovejoy and McCollum, 2010; Kibii et al., 2011; Ward et al., 2011; Barak et al., 2013; Hatala et al., 2016; Dowdeswell et al., 2017; Raichlen and Gordon, 2017). While many of these studies agree that australopiths likely walked with relatively extended lower limbs rather than with a bent-hip, bent-knee (BHBK) gait (e.g., similar to the bipedal kinematics of

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chimpanzees; Sockol et al., 2007; Crompton et al., 2008), debate continues as to whether other kinematic aspects of their gait may have differed from those of later hominins and modern humans (DeSilva et al., 2013; Harcourt-Smith, 2016; Hatala et al., 2016; Su and Carlson, 2017). Recent fossil discoveries and comparative analyses have also refocused attention on the degree to which australopiths engaged in selectively advantageous arboreal locomotor behaviors (DeSilva, 2009; Zipfel et al., 2011; Green and Alemseged, 2012; Haile-Selassie et al., 2012; Churchill et al., 2013; Kappelman et al., 2016; Ruff et al., 2016; Rein et al., 2017). Debate about locomotor kinematics and the degree of arboreality in australopiths and other early hominins often centers on interpretation of the functional significance of apparently primitive traits associated with arboreal locomotion in these fossil taxa (Ward, 2002). The retention of primitive features associated with arboreality in australopiths suggests either that these traits were not detrimental or that they may have provided some adaptive advantage (Ward, 2002), although differentiating between these scenarios is difficult (Lauder, 1996).

Biomechanically informative phenotypically plastic traits, or ecophenotypic traits, have the potential to provide significant insight into the mechanical environment and specific behaviors that an animal engaged in throughout its life (Ruff et al., 1999, 2016; Barak et al., 2013; Ward, 2013). Because of the mechanosensitivity of bone during development, structural variation in both cortical and trabecular bone provides insight into limb use and joint loading in extant and extinct organisms (Pearson and Lieberman, 2004; Ruff et al., 2006). Trabecular bone, in particular, not only has the potential to reveal important information about the magnitude and frequency of loading, but also can inform interpretations of the directionality of joint reaction forces and, by extension, provide insight into joint posture and loading. The distribution of trabecular bone material in three-dimensional space is highly correlated with its mechanical behavior (Mittra et al., 2005). In particular, the principal material direction of trabeculae corresponds closely to the principal elastic direction (Odgaard et al., 1997). Barak et al. (2017) recently demonstrated that the principal trabecular orientation represents a robust metric reflecting habitual joint loading differences between chimpanzees and humans in the third metacarpal. When considered together with the phenotypic plasticity of trabecular bone as a site-specific local response (Sugiyama et al., 2012) to locomotor loading (Pontzer et al., 2006; Barak et al., 2011; Wallace et al., 2013), this structure-function relationship provides a direct functional signal of loads incurred during habitual locomotor and postural behavior (Ryan and Ketcham, 2005; Kivell, 2016; Barak et al., 2017). Experimental and comparative work has demonstrated that the principal orientation of trabeculae in a joint reflects the orientation of peak compressive forces experienced during locomotion (Pontzer et al., 2006; Barak et al., 2011, 2013, 2017). Previous work within primates indicates that humans have highly oriented trabeculae (high structural anisotropy) in the femoral head (Ryan and Shaw, 2015), suggesting that trabecular bone organization reflects unique aspects of joint loading during bipedal locomotion (Ryan and Krovitz, 2006; Raichlen et al., 2015), and providing the opportunity to assess whether fossil hominins possess femoral head trabecular bone structure reflective of modern human-like hip joint loading.

The goal of this study is to use microcomputed tomography (μ CT) to characterize variation in trabecular bone anisotropy, material orientation, and bone volume fraction in the femoral head using a diverse extant primate sample that includes five modern groups of *Homo sapiens*, *Pan troglodytes*, *Gorilla* ssp., *Pongo* ssp., and *Papio* ssp. We also assess trabecular bone structure in six specimens of *Australopithecus africanus*, four of *Paranthropus robustus*, and four Pleistocene specimens of *Homo*, including two *Homo*

neanderthalensis, one Paleolithic *H. sapiens*, and the *Homo* sp. femur from Berg Aukas, Namibia. We hypothesize that primate groups that are primarily terrestrial, including quadrupedal baboons and bipedal humans, and therefore exhibit a relatively constrained range of motion at the hip joint, will display more anisotropic hip joint trabecular bone. Further, the primary trabecular bone material orientations in these terrestrial groups will reflect adaptation to repetitive, mostly unidirectional loading. The African apes are primarily terrestrial quadrupeds, but also engage in a variety of locomotor activities on arboreal substrates, including climbing, bridging, and below-branch suspension. As a result, this more diverse loading environment in chimpanzees and gorillas relative to modern humans should be reflected by a relatively more isotropic trabecular bone structure within the hip joint. Orangutans are the most arboreal of the great apes, and therefore should have relatively isotropic femoral head trabecular structure, reflecting their more diverse joint postures and hip joint loading directions. If the trabecular bone degree of anisotropy in the femoral head of australopiths resembles that of modern humans and extinct members of the genus *Homo*, it would indicate that australopiths have rather stereotypical hip joint loading, suggesting less variable hip postures and substrate types. By contrast, if australopith femoral head anisotropy is more like that of extant great apes, it would indicate that, while bipedal, australopiths exhibited much greater variability in hip joint loading conditions and, possibly, more varied substrate use. Bone volume fraction is expected to vary in relation to inferred activity pattern with non-human primates and fossil hominins having higher bone volume compared to Holocene modern humans (Chirchir et al., 2015).

2. Materials and methods

2.1. Sample

The sample of extant species consisted of adult individuals from five modern populations of *H. sapiens* ($n = 60$) and four non-human primate taxa (Table 1): *Pan troglodytes* ($n = 17$), *Gorilla* ssp. ($n = 8$; 4 *Gorilla gorilla*, 4 *Gorilla beringei*), *Pongo* ssp. ($n = 7$; 5 *Pongo pygmaeus*, 2 *Pongo abelii*), and *Papio* ssp. ($n = 11$; 4 *Papio hamadryas*, 3 *Papio cynocephalus*, 3 *Papio ursinus*, 1 *Papio anubis*). See Supplementary Online Material (SOM) Table S1 for details about extant and fossil specimens used in this study and their museum information. All individuals used in the study were adult based on epiphyseal fusion and free of pathology. Age-at-death estimates for the human samples were taken from museum collection records when available. Most humans in the sample were young adults between 20 and 35 years, although some individuals were as old as 45. The fossil sample included six femora from Sterkfontein assigned to *A. africanus* (StW 99, StW 311, StW 392, StW 403, StW 479, StW 501), four femora from Swartkrans attributed to *P. robustus* (SK 19, SK 82, SK 97, SK 3121), and four Pleistocene *Homo* individuals including the Berg Aukas femur (*Homo* sp.), La Ferrassie 1 and 2 (*H. neanderthalensis*), and Cro-Magnon 4321 (*H. sapiens*). We include the StW 311 proximal femur as *A. africanus*, but note that it comes from the younger Sterkfontein Member 5 (Kuman and Clarke, 2000) and therefore may not be attributable to *Australopithecus* (DeSilva, 2011).

2.2. Data collection

One proximal femur from each extant individual was scanned using μ CT, with voxel dimensions ranging from 0.020 to 0.069 mm. The range of voxel dimensions used from each taxon are listed in Table 1 and voxel sizes for each individual in the sample are listed in the SOM Table S1. Two femora of *Pa. hamadryas* were imaged with

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