

Gracility of the modern *Homo sapiens* skeleton is the result of decreased biomechanical loading

Timothy M. Ryan^{a,b,1} and Colin N. Shaw^{c,d,e}

^aDepartment of Anthropology, ^bCenter for Quantitative Imaging, EMS Energy Institute, The Pennsylvania State University, University Park, PA 16802; and ^cPhenotypic Adaptability, Variation and Evolution Research Group, ^dMcDonald Institute for Archaeological Research, Department of Archaeology and Anthropology, and ^eCambridge BioTomography Centre, Department of Zoology, University of Cambridge, Cambridge CB2 3QG, United Kingdom

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The postcranial skeleton of modern *Homo sapiens* is relatively gracile compared with other hominoids and earlier hominins. This gracility predisposes contemporary humans to osteoporosis and increased fracture risk. Explanations for this gracility include reduced levels of physical activity, the dissipation of load through enlarged joint surfaces, and selection for systemic physiological characteristics that differentiate modern humans from other primates. This study considered the skeletal remains of four behaviorally diverse recent human populations and a large sample of extant primates to assess variation in trabecular bone structure in the human hip joint. Proximal femur trabecular bone structure was quantified from microCT data for 229 individuals from 31 extant primate taxa and 59 individuals from four distinct archaeological human populations representing sedentary agriculturalists and mobile foragers. Analyses of mass-corrected trabecular bone variables reveal that the forager populations had significantly higher bone volume fraction, thicker trabeculae, and consequently lower relative bone surface area compared with the two agriculturalist groups. There were no significant differences between the agriculturalist and forager populations for trabecular spacing, number, or degree of anisotropy. These results reveal a correspondence between human behavior and bone structure in the proximal femur, indicating that more highly mobile human populations have trabecular bone structure similar to what would be expected for wild nonhuman primates of the same body mass. These results strongly emphasize the importance of physical activity and exercise for bone health and the attenuation of age-related bone loss.

trabecular bone | gracilization | human evolution | biomechanics | mobility

Compared with other hominoids and extinct hominin species, more recent humans possess relatively gracile postcranial skeletons (1–9). One of the consequences of this gracility in contemporary humans is an increased fracture risk associated with age-related bone loss and osteoporosis [hip fractures alone are projected to reach 6.26 million per year globally by 2050 (10)] (11–15). The etiology of this relative gracility remains uncertain, and this uncertainty hinders the development of strategies for mitigating fracture risk and morbidity. The progressive gracilization of the *Homo* postcranial skeleton was originally detected in cortical bone structure (1, 2), but has now been demonstrated in the trabecular bone microstructure of joints (12, 14, 16–19), where osteoporotic fracture risk is highest (20). Most notably, in an analysis of thoracic vertebral bodies, Cotter et al. (12) found that young adult humans have significantly lower trabecular bone volume fraction (BV/TV) and thinner vertebral shells than similarly sized apes. Griffin et al. (16) also found significantly lower BV/TV in the human first and second metatarsal heads compared with hominoid primates. The results of these studies are corroborated by work on the hominoid calcaneus (17), the anthropoid proximal femur (18), and several other clinical studies of femoral head trabecular bone architecture in contemporary adult humans (21–24). The results of these studies

suggest that relative trabecular bone volume in the axial skeleton and lower limbs is significantly lower in modern humans compared with quadrupeds, despite the legs and vertebral column bearing a higher proportion of body mass and peak substrate reaction forces during bipedal locomotion (25–27). The high positive correlation between BV/TV and bone material properties (28–32) suggests that trabecular bone in the human lower limb and vertebral column is less stiff than in other primates. Ongoing debates aimed at enhancing our understanding of bone adaptation, skeletal health, and the prevention and treatment of osteoporosis would be greatly enhanced by the determination of the primary factors underlying the relatively gracile skeleton of living humans.

Several explanations for the skeletal gracility of recent modern humans have been offered. The most common explanation is that living populations are simply less physically active compared with extinct hominins or closely related contemporary wild apes (1–6). This hypothesis suggests that a shift in subsistence patterns away from hunting and gathering, combined with an increased reliance on technology, led to reductions in overall physical activity levels and mobility in more recent hominins (cf. 2). In contrast, some (12, 13) attribute lower trabecular bone volume in humans to the mechanical consequences of the larger vertebral cross-sectional areas and larger joint surface areas required of an obligate biped. The crux of this argument is that larger joint surfaces distribute loads across a greater area, thereby reducing strain in the underlying trabecular tissue and leading to lower bone volume. Cotter et al. (12) have suggested that even if

Significance

Compared with other primates and earlier human species, contemporary humans possess relatively lightly built skeletons. Previous studies suggest that skeletal gracility results from a lack of physical activity because of increased reliance on culture, is a biomechanical consequence of bipedal locomotion, or reflects systemic physiological differences between modern humans and other primates. We found that bone strength in the hip joint of human foragers is comparable to similarly sized nonhuman primates, and is significantly more robust than sedentary agriculturalists. These results conclusively demonstrate the utility of trabecular bone structure for differentiating activity and mobility patterns among prehistoric hominins and reveal that low levels of physical activity contribute to reduced bone strength, and consequently increased fracture risk, in contemporary human populations.

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¹To whom correspondence should be addressed. Email: tmr21@psu.edu.

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human activity levels were equal to those of wild apes, this loading would still be insufficient to illicit comparable trabecular bone growth. Alternatively, it has been suggested that the low bone-volume fraction observed in human thoracic vertebrae and the first and second metatarsals are the result of systemic physiological differences between humans and apes (14, 16). These studies do not suggest the mechanism or the function of this systemic gracility, but one potential explanation may be selection for increased tissue economy in hominins (5, 33–35).

The aim of this study is to assess explanations for the trabecular bone gracility found in contemporary populations by evaluating the skeletal structure of human groups with divergent behavioral patterns within the broader context of primate biology. The impact of this research is twofold: (i) the samples and methods (imaging of trabecular bone microstructure using microCT) allow us to address questions inaccessible to research focused on living participants, yet inform on prevention and treatment in the 21st century; and (ii) these novel analyses allow us to evaluate the efficacy of quantifying trabecular bone structure for the purpose of differentiating activity and mobility patterns among prehistoric hominins. For this assessment, trabecular bone architecture of the proximal femur is compared among human foragers, village agriculturalists, and a large sample of extant primates. One of three outcomes is possible: (i) trabecular bone architecture does not separate *Homo sapiens* from the general nonhuman primate pattern, indicating a high level of canalization in primates for specific trabecular architectural features; (ii) trabecular bone architecture separates all *H. sapiens* from the nonhuman primate allometric pattern, indicating that trabecular bone structure in humans is largely driven by postcranial joint size or a genetic predisposition to maintaining a relatively gracile skeleton; or (iii) trabecular bone architecture separates agriculturalists and foragers, indicating structural differences among the groups, highlighting the influence of biomechanical loading or other osteogenic factors on trabecular bone composition.

Results

Species mean and SD values for each measured trabecular bone variable are listed in Table S1 and definitions for each trabecular bone variable are provided in Table S2. There are no significant differences between the human populations for femoral head superoinferior height or estimated body mass (Table S3). Despite having similar body sizes, visual inspection of the reconstructed volumes of interest (VOI) and 2D cross-sections suggest structural variation in femoral head trabecular bone between these agriculturalist (Norris Farms, Dickson Mounds) and forager (Black Earth, Modoc Rock Shelter) populations from eastern North America (Illinois) (Fig. 1). Scatter plots of individual trabecular bone variables vs. estimated body mass reveal that the foragers and agriculturalists separate from each other in three important structural features: bone volume fraction (BV/TV), trabecular thickness (Tb.Th), and bone surface area relative to bone volume (BS/BV) (Fig. 2). The mean BV/TV for the agriculturalist groups both plot below the lower-bound 95% confidence interval for the nonhuman primate regression line, revealing that these groups have the lowest BV/TV relative to body mass of all primates, aside from *Tarsius*. In contrast, BV/TV of the forager sample falls within the 95% confidence interval for the nonhuman primates, plotting on top of *Pongo*. Tb.Th values for the agricultural sample lie well below the nonhuman primate regression line and outside of the 95% confidence interval, indicating that the trabeculae of agriculturalists are relatively thin compared with a primate of similar body mass. In contrast, the Tb.Th of the forager sample falls within the nonhuman primate 95% confidence interval. As a consequence of their lower BV/TV and thick trabeculae, the agriculturalists have relatively high BS/BV. Trabecular separation (Tb.Sp) for all

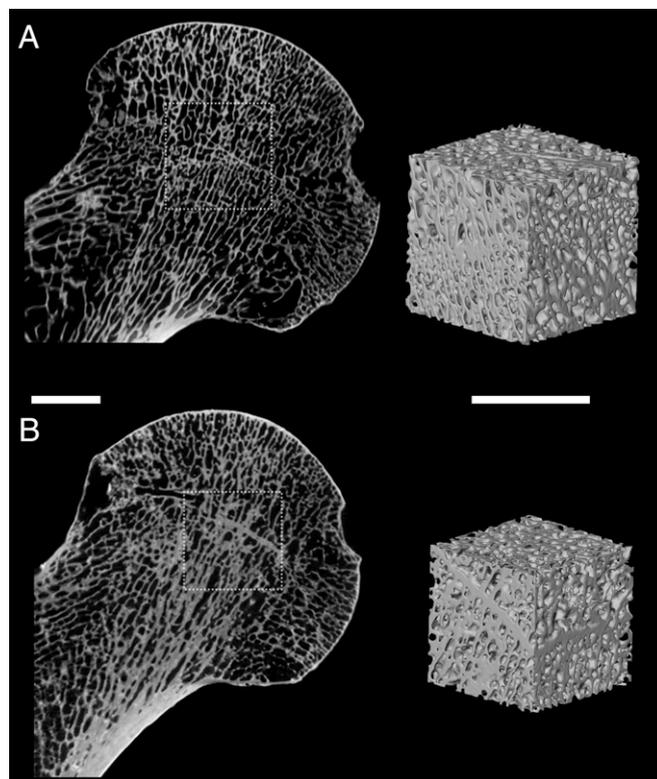


Fig. 1. Trabecular bone architecture in the proximal femur of human agriculturalists (A) and foragers (B). Shown are coronal microCT slices through the femoral head together with a 3D surface reconstruction of the cubic volume of interest extracted from the femoral head (denoted by the dotted line box in each femoral head). Note that both specimens are presented at the same scale, highlighting the significantly more robust trabecular bone in the forager (B). (Scale bars, 10 mm.)

human groups falls just above and outside of the nonhuman primate 95% confidence interval. Both foragers and agriculturalists also have lower trabecular number (Tb.N) relative to body mass compared with other hominoids, plotting just outside of the nonhuman primate 95% confidence interval. All human groups have relatively anisotropic trabecular bone structure.

The ANOVA comparisons for unstandardized residuals substantiate the scatter plot results, revealing significant structural differences between the foragers and agriculturalists, and also among the agricultural populations and most other hominoids (Table 1). No significant differences were found between the Norris Farms agriculturalists and Dickson Mounds agriculturalists for any variable, and are henceforth collectively referred to as “agriculturalists,” unless otherwise specified. Compared with the foragers, agriculturalists display significantly lower mass-corrected BV/TV and Tb.Th, and significantly higher BS/BV. There are no significant differences between the agriculturalist and forager populations for Tb.Sp, Tb.N, or degree of anisotropy (DA). The agriculturalists have significantly lower BV/TV than all other extant hominoids, except *Gorilla*. In contrast, BV/TV of the forager *H. sapiens* is comparable to all hominoid groups, other than *Pan*, a taxon with particularly high femoral BV/TV (see, for example, ref. 18). The Tb.Th values in the forager and agriculturalist humans do not differ from any of the extant hominoids. Both agriculturalists and foragers have significantly higher Tb.Sp and lower Tb.N than *Pan*. The foragers and Dickson Mounds agriculturalists also have significantly fewer trabeculae relative to their body mass compared with *Gorilla* (Norris Farms agriculturalists approach significance: $P = 0.056$). The Norris Farms agriculturalists also have significantly higher

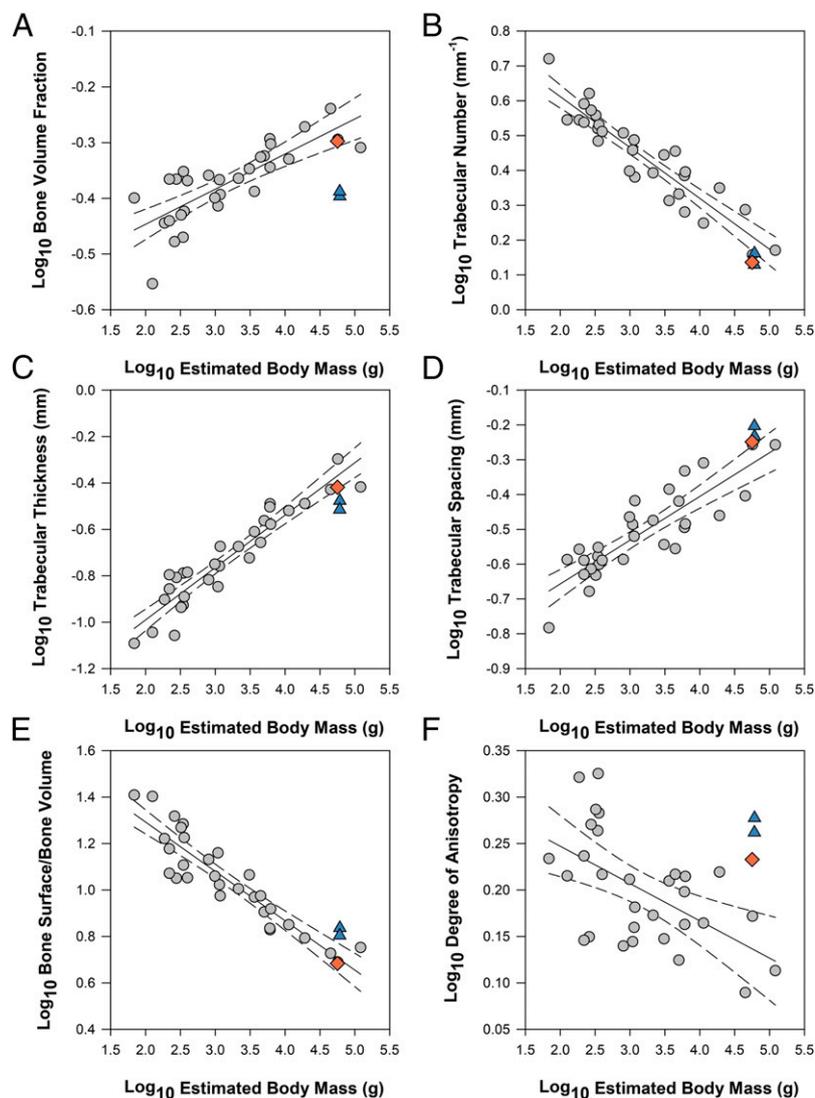


Fig. 2. Log-log plots of species mean femoral head trabecular bone variables vs. estimated body mass for all nonhuman primates (gray circles) in the sample. The two human agriculturalist samples (blue triangles) and the combined forager sample (orange diamond) are plotted onto each graph for comparison with the nonhuman primate sample. Solid and dashed lines represent the best-fit OLS regression line and 95% confidence intervals, respectively, for the nonhuman primate species, not including the three human samples. (A) BV/TV, (B) Tb.N, (C) Tb.Th, (D) Tb.Sp, (E) BS/BV, (F) DA.

BS/BV compared with *Pan*. Comparisons of DA in humans and other hominoids indicate that both agriculturalists and foragers have significantly more anisotropic trabeculae than all other hominoids; the one exception is a lack of difference between foragers and *Pongo* ($P = 0.069$).

Discussion

The findings of the present study have significant implications for understanding human skeletal form and its relationship to age-related bone loss in contemporary human populations. Osteoporosis is a systemic bone disease with significant global health impacts that is characterized by low bone mass and microarchitectural deterioration, leading to increased bone fragility and fracture risk (36). Although both cortical and trabecular bone, together, determine bone strength, trabecular architecture is particularly susceptible to age-related loss because of the extensive exposure of its metabolically active surfaces and the relatively thin plates and struts (37–40). Because of the documented gracilization of the human skeleton (2) and the diversity of subsistence strategies performed in the past, the

hominin fossil and skeletal record is ideal for addressing questions aimed at understanding contemporary human bone biology and health.

The results of the present study indicate that human populations with divergent activity patterns display significantly different trabecular bone structural characteristics in the proximal femur. Mobile foragers possess significantly higher BV/TV and significantly thicker trabeculae compared with more sedentary agriculturalists. The trabecular BV/TV, and consequently the relative stiffness, of the forager femoral head are comparable to most other hominoids. These results, therefore, reveal that more highly mobile human populations have trabecular bone structure in the femoral head that is similar to what would be expected for a nonhuman primate of the same body size. The comparatively gracile trabecular bone of the more sedentary village agriculturalists is composed of significantly thinner trabeculae, resulting in a much higher BS/BV ratio compared with the foragers. These results strongly suggest that BV/TV, Tb.Th, and consequently, BS/BV ratio in the human femoral head are inherently plastic traits influenced by the loading environment. In contrast, the finding of similar trabecular

Table 1. Results of post hoc (ANOVA) comparisons of body mass-corrected trabecular bone variables

| Bone variable | Foragers | Agr. (NF) | Agr. (DM) | Pan | Gorilla | Pongo | Symphalangus |
|------------------------------------|----------|-----------|-----------|--------|---------|-------|--------------|
| Bone volume fraction | | | | | | | |
| Agr. (NF) | <0.001 | | | | | | |
| Agr. (DM) | <0.001 | NS | | | | | |
| Pan | <0.01 | <0.001 | <0.001 | | | | |
| Gorilla | NS | NS | NS | <0.05 | | | |
| Pongo | NS | <0.01 | <0.01 | NS | NS | | |
| Symphalangus | NS | <0.05 | <0.05 | NS | NS | NS | |
| Trabecular thickness | | | | | | | |
| Agr. (NF) | <0.001 | | | | | | |
| Agr. (DM) | <0.001 | NS | | | | | |
| Pan | NS | NS | NS | | | | |
| Gorilla | NS | NS | NS | NS | | | |
| Pongo | NS | NS | NS | NS | NS | | |
| Symphalangus | NS | NS | NS | NS | NS | NS | |
| Trabecular spacing | | | | | | | |
| Agr. (NF) | NS | | | | | | |
| Agr. (DM) | NS | NS | | | | | |
| Pan | <0.001 | <0.001 | <0.001 | | | | |
| Gorilla | NS | NS | <0.01 | NS | | | |
| Pongo | NS | NS | NS | <0.001 | NS | | |
| Symphalangus | NS | NS | NS | <0.001 | NS | NS | |
| Trabecular number | | | | | | | |
| Agr. (NF) | NS | | | | | | |
| Agr. (DM) | NS | NS | | | | | |
| Pan | <0.001 | <0.001 | <0.001 | | | | |
| Gorilla | <0.001 | NS | <0.001 | NS | | | |
| Pongo | NS | NS | NS | <0.001 | NS | | |
| Symphalangus | NS | NS | NS | <0.001 | <0.01 | NS | |
| Bone surface to bone volume | | | | | | | |
| Agr. (NF) | <0.001 | | | | | | |
| Agr. (DM) | <0.001 | NS | | | | | |
| Pan | NS | <0.05 | NS | | | | |
| Gorilla | NS | NS | NS | NS | | | |
| Pongo | NS | NS | NS | NS | NS | | |
| Symphalangus | NS | NS | NS | NS | NS | NS | |
| Degree of anisotropy | | | | | | | |
| Agr. (NF) | NS | | | | | | |
| Agr. (DM) | NS | NS | | | | | |
| Pan | <0.001 | <0.001 | <0.001 | | | | |
| Gorilla | <0.001 | <0.001 | <0.001 | NS | | | |
| Pongo | NS | <0.01 | <0.05 | NS | NS | | |
| Symphalangus | <0.001 | <0.001 | <0.001 | <0.01 | NS | NS | |

Abbreviations for human agriculturalists (Agr): DM, Dickson Mounds; NF, Norris Farms #36; NS, not significant.

number and spacing in the femoral head of both agriculturalists and foragers, despite divergent loading patterns, suggests a higher level of canalization for these traits.

The three main hypotheses proposed to explain the relatively gracile skeleton of contemporary humans include: (i) a reduction in physical activity because of increased sedentism and reliance on culture (1–6, 41), (ii) selection for systemic reduction of bone mass in modern humans (14, 16), and (iii) attenuation of strain imposed upon trabecular bone because of larger joint surface areas (12, 13). The morphological differences between the highly mobile foragers and relatively sedentary village agriculturalists clearly point to physical activity as a major determinant of bone mass in the hip joint. The nonhuman primate-like BV/TV in the highly mobile foragers strongly suggests that modern humans are neither systemically gracile nor morphologically constrained by their bipedal anatomy.

Although ancestry and sex are osteoporotic risk factors (42), the influence of these variables have been considered; similar numbers of male and female humans are included in this study, and all individuals derive from geographically proximate archaeological sites in eastern North America (*Materials and Methods*). It is also possible that diet plays a role in the observed differences between these populations. The dietary shift toward cultivated grains is associated with reduced calcium intake and net calcium deficiencies in some populations reliant on agriculture (cf. 43, 44). The archaeological record provides insight into possible dietary differences between the forager and agriculturalist groups included in this study. The Dickson Mounds and Norris Farms populations appear to have engaged in a mixed-subsistence strategy that included hunting, fishing, and gathering of wild-plant resources in addition to the active cultivation of maize and other plants (45). Isotopic data, however, suggest that the Norris Farms site may have relied less on maize than did Dickson Mounds (45). Analyses of the forager's subsistence strategies suggest a similarly diverse diet that included fauna, such as large and small mammals, birds, and fish, as well as a diversity of seasonally available plant resources (46, 47). Floral and faunal remains from the Black Earth site indicate a highly mobile population with a large and diverse home-range, used for both seasonal and year-round foraging activities (46). Although dietary differences can contribute to a reduction in skeletal mass among agriculturalists relative to foragers, evidence from other localities (48, 49) strongly implicates activity, rather than diet, as the most important factor influencing skeletal strength and robusticity (the strength or mass of a bone in relation to body size) (41). The results, therefore, further corroborate the suggestion that exercise, perhaps most importantly activity performed during the adolescent growth period (50), is likely to be the best approach for the prevention of bone fragility and heightened fracture risk.

The results of the present study also provide insight into locomotor loading at the hip joint of hominoids. In contrast to the nonhuman apes, all four human populations display a highly anisotropic trabecular structure in the proximal femur. It seems likely that this human-specific trabecular construction relates to the stereotypical loading at the hip joint imposed during bipedal locomotion. In contrast, the proximal femur of quadrupedal and climbing apes is likely to experience more diverse postural and locomotor loads (51). This morphological consistency in humans may provide a tool for reconstructing locomotor behavior in the hominin fossil record.

The findings of the present study are relevant to various fields and inform debates involving the evolution of the human skeleton, bone adaptation, the reconstruction of past activity patterns, and the importance of skeletal loading and exercise for bone health in contemporary human populations. To our knowledge, this study provides the first clear evidence for a strong relationship between patterns of terrestrial mobility and trabecular bone architecture in the hip joint of modern humans. Increased loading magnitude and frequency in mobile human foragers led to relatively robust trabecular bone structure comparable to that seen in other primate species (52). With the emergence of *Homo erectus* ~1.8 million y ago, paleontological and archaeological evidence indicate a major shift in hominin evolution characterized by increases in brain and body size (53), improved locomotor efficiency (54), larger home ranges, and increased mobility (55). This long evolutionary history of high levels of terrestrial mobility in the genus *Homo*, together with the evidence of selection for endurance running (56, 57), strongly suggests that the human locomotor skeleton evolved in a mechanical and physiological context that involved persistent and frequent loading throughout life. This study provides support for the assertion that contemporary humans live in a cultural and technological milieu incompatible with our evolutionary adaptations (58), and highlights the importance of physical activity and exercise for bone health

and the attenuation of age-related bone loss, osteoporosis, and fracture risk.

Materials and Methods

Sample. The skeletal sample used in this study consisted of a total of 288 adult individuals from 32 primate species (Table S1). All nonhuman primate specimens derive from museum skeletal collections (52) and were wildshot adults except *Tarsius syrichta* and *Cheirogaleus medius*, which were captive adult skeletal specimens from the Duke University Lemur Center. Four archaeological human samples from Illinois were used. The Norris Farms #36 (~700 y B.P.) and Dickson Mounds (~700–860 y B.P.) samples both represent sedentary agriculturalists of the Oneota and Mississippian traditions, respectively (45). The Black Earth (~5,000 y B.P.) and Modoc Rock Shelter (~5,000–7,000 y B.P.) sites have been interpreted as multiseason forager base camps (46, 59–61). The Modoc individuals ($n = 3$) were combined with the Black Earth sample to create a combined forager sample, which was used for all analyses. Before this step, it was confirmed that for each Modoc individual all trabecular bone variables fell within one SD of the Black Earth mean. Only adult individuals were included in this study. Age-at-death estimates for the human samples were taken from existing museum collection records using standard aging methods (62, 63). Mean age for the combined forager group was 32.7 y (SD, 7.34). The median age for the Norris Farms agriculturalists, which were not normally distributed, was 32.5 y (interquartile range, 9.75). The Dickson Mounds skeletons were all classified as young adults between the ages of 20 and 35 y.

Data Collection. Human proximal femora were scanned on the OMNI-X HD600 microcomputed tomography scanner (Varian Medical Systems) at the Center for Quantitative Imaging, Pennsylvania State University. All nonhuman primates included in the study were scanned at the Center for Quantitative Imaging or at the University of Texas at Austin's High-Resolution X-Ray Computed Tomography Facility (18, 52, 64–66). Voxel dimensions ranged from 0.0068 and 0.0687 mm, depending on size of the specimen. A cubic VOI was defined within each femoral head using Avizo software (FEI Visualization Sciences Group), following previously described methods (18, 52, 66, 67). The center of each VOI was positioned at the center of the femoral head articular surface bounding box, defined as the center of the femoral head in this study. The size of each VOI was equal to one-sixth of the superoinferior height of the articular surface. The trabecular bone in each VOI was segmented using an iterative algorithm (68, 69) and the 3D trabecular bone structure was quantified using the Scanco image processing language (Scanco Medical) (18, 52, 66). Six morphometric variables were quantified using standard techniques (18, 22, 70): BV/TV, Tb.Th, Tb.Sp, Tb.N, DA, and BS/BV. The Tb.Th values were corrected for resolution dependency using a method outlined previously (18).

Statistical Analyses. Previous work has demonstrated the relationship between body mass and femoral head trabecular bone structure in primates

(52). Nonhuman primate species means for each trabecular bone variable (\log_{10}) were plotted against species mean body mass (\log_{10}) and a line of best fit was calculated. Log-transformed body mass and trabecular bone data for the human foragers and agriculturalists were then plotted overtop to visualize human variation in the context of nonhuman primate diversity. Ordinary least-squares (OLS) regression analyses were performed for each \log_{10} -transformed trabecular bone variable versus the \log_{10} -transformed body mass estimate for each individual in the sample, including humans. Body masses were estimated for each individual based on femoral head dimensions using equations taken from the literature and derived from analyses of the most appropriate taxonomic group (71–73). Although using body mass estimates based on regression equations may introduce error, the nonisometric scaling of femoral head size with body size in humans (74, 75), as well as variation in the relationship between femoral head size and body mass in primates because of differences in joint excursion (76), complicate the use of femoral head breadth as a proxy for body mass. Femoral head superoinferior height (FHSI) was measured to the nearest hundredth of a millimeter using digital calipers. The unstandardized residuals from each OLS regression analysis for trabecular bone properties vs. body mass were calculated for the human populations and the four other hominoid taxa in the sample. These residuals represent body mass-corrected trabecular bone structural variables.

Univariate ANOVA was used to identify significant differences among the hominoid taxa (human populations and the four ape species) for the unstandardized residuals of each trabecular bone variable. Differences in these properties were subsequently contrasted using either Hochberg's GT2 or Games Howell post hoc test, based on the results of Levene's Test for equality of variance. ANOVA and post hoc tests were conducted only for those variables where a significant relationship with body mass was found using OLS regression (Table S4). Finally, differences in body size among the three human groups were evaluated using ANOVA to compare FHSI and estimated body mass. All statistical analyses were performed in SPSS v19. Because the primary goal of the present analysis was to investigate structural differences between the human foragers and agriculturalist groups, and only secondarily to analyze interspecific differences in trabecular bone microstructure, phylogenetic correction was not performed. Recent work has found minimal phylogenetic effects on bone microstructure (66, 77).

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