ABSTRACT

Trabecular fabric in the distal tibia has been shown to be sensitive to subtle variation in ankle sagittal plane kinematics during locomotor-related loading in both mammals (Barak *et al* 2011) and birds (Pontzer *et al* 2006). Differences or similarities within hominoid trabecular structure can be insightful for interpreting gait kinematic experimentation in the hominin lineage leading to the evolution of obligate bipedalism. This study assessed trabecular structure in the distal tibia of extant hominoids, and an outgroup of baboons, to infer locomotor kinematics of the ankle joint in fossil hominin species. Four hypotheses were tested through analyses of trabecular properties in the distal tibia:

Trabecular architecture deep to the tibial plafond of primates is effective at distinguishing species characterized by divergent locomotor behaviours.
Trabecular structure deep to the tibial plafond in primates mirrors known kinematics of extant species and will therefore reflect loading conditions imposed by posture and locomotion.
Trabecular structure in the distal tibiae of *Australopithecus africanus* specimens from Sterkfontein Member 4 is more human-like than ape-like in structure, reflective of bipedality.
Trabecular structure of the medial malleolus in the primate ankle contains a locomotor signal.

High resolution computed tomography (MicroCT) images (25µm -48µm voxels) were used to quantify trabecular bone structure deep to the tibial plafond and the medial malleolus in extant comparative species attributed to modern human hunter-gatherers (*Homo sapiens*), *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus* and *Papio hamadryas* as well as four fossil hominins from Sterkfontein Cave (Member 4), South Africa attributed to *A. africanus*. Nine trabecular subregions were isolated beneath the articular surface of the tibial plafond and two subregions were isolated beneath the articular surface of the medial malleolus. Subregions were segmented into spherical trabecular volumes for quantification of localized structure. Descriptive statistics were used to visualize variation among and within species, followed by an analysis of variance (ANOVA) of trabecular parameters between species to test for statistical significance of observed group differences ($p=0.05$). A further stepwise discriminant function analysis (DFA) was conducted to assess the capability of trabecular structure to discriminate between species with divergent locomotor behaviours based on trabecular structural properties.

The results of this study suggest that trabecular bone structure in the distal tibia of the primate species sampled is effective at distinguishing between species that are characterized by different locomotor behaviour repertoires. Differentiation in homologous regions is greater in presumed highly loaded regions (anterior) and less in regions of presumed low locomotor imposed loading. Trabecular structure in the distal tibia of extant comparative species sometimes matched predictions based on known kinematic data, indicating that these trabecular signals are functionally driven by posture and locomotion. Trabecular fabrics of the medial malleolus in extant non-human primates exhibited structural properties that reflected increased bone strength in their anterior region, suggesting a difference in loading exists across the anteroposterior axis of the medial malleolus (e.g., possibly differentiating relative amounts of climbing), although this difference could not be statistically tested due to small sample sizes.

Trabecular structure of *A. africanus* distal tibiae was highly variable, with some properties exhibiting greater variation than observed in any single extant species. The extent of this intraspecific variability in trabecular structure suggests the presence of two potentially different morphs in Sterkfontein Member 4. One morph resembled a baboon-like structure, composed of numerous thin trabecular struts that were highly oriented (i.e., anisotropically distributed), while the other morph resembled overlapping human-like and ape-like traits observed in previous studies of trabecular architecture in *A. africanus*. Based on the findings of this study, it can be concluded that trabecular structure in the distal tibia is effective at distinguishing species based on locomotor behaviour repertoires, provided that homologous regions are sampled, and that trabecular bone structure and organization mirrors kinematic indicators of ankle loading regimes. When these criteria are met, trabecular fabrics may be a useful tool for reconstructing behaviour in fossil hominin specimens in order to corroborate external morphological studies.

Keywords: Hominin, locomotion, bipedality, bone functional adaptation, evolution, ankle, tibia