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The ontogeny of bipedalism: insights from trabecular changes during growth

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Many primates are capable of facultative upright locomotion for short periods of time, but this differs from the committed terrestrial bipedalism that is a hallmark of our species. For this reason the evolutionary acquisition of bipedal locomotion, and its relationship to our own transition from a crawling infant to striding bipedalism (5-7 years), have been topics of great interest within paleoanthropology. Research into this transition have highlighted cultural influences that change the timing of milestones (e.g., crawling and unaided walking), and others factors that affect the development of locomotion (e.g. stance, step length, and pace) [1]. In regard to ontogenetic changes in bone morphology, there are many questions about the interplay between genetic canalization and the bones biomechanical response to loading. While there is evidence for a bone functional adaption response to gait maturation, in the form of trabecular architectural (re)modelling of the femur [2], very little is known about trabecular architectural changes in the human foot during the transition from crawling to walking. In humans the morphology of the talus provides a wide range of movements during locomotion while efficiently dividing weight between its anterior and posterior parts. Being that locomotor variation arises during development [1], it is important to understand the morphological differences that coincide. To better understand the internal differences during these periods we quantified the trabecular architecture in an ontogenetic sample of 28 human tali (8 weeks – 13 years) from the known age/sex/death collection in Bologna, Italy (n = 18), and an archaeological collection from Norris Farms #36, Illinois, USA (n = 10). Tali representing five age classes (8 weeks-1 year, n = 5; 1.1-3 years, n = 9; 3.1-6 years, n = 8; 6.1-10 years, n = 3; 10.1-15 years, n = 3) were microCT scanned (20-40 µm voxel resolution) and reconstructed as 16bit tif stacks. Segmentation of the images into bone and non-bone voxels was performed using the MIA-clustering algorithm [3] with trabecular bone isolation and quantification (bone volume fraction [BV/TV], degree of anisotropy [DA], elastic modulus in gigapascals [E], thickness [TbTh], spacing [TbSp], number [TbN], total surface [TS], and total volume [TV]) performed in Medtool 4.2 (Dr. Pahr Ingenieurs.e.U. [4]). Logistic regression was run in R 3.5.3 (The R Foundation for Statistical Computing, 2019) with trabecular variables as responses, and age class along with population as predictors. Significant results ($p<0.05$) between age class were found for E (8wk-1 and 1.1-3 years), and TS (3.1-6, 6-10, and 10.1-15 years). Among the age classes TbTh, TbSp, TS, and TV steadily increase with age. BV/TV and E are lowest for individuals in the second oldest class (14%, 6.7), and highest in the oldest class (17.9%, 10.8). For DA, the youngest class is relatively isotropic (.16), which increases towards more anisotropic trabeculae and plateaus in the older classes (.22-.23). The increase in architectural variables (TbTh, TbSp, TS, and TV), relative to age, is expected. The variables associated with fracture resistance (BV/TV and E) are at their lowest in the age class (1.1-3 years), which coincides with the developmental period when modern children begin walking unassisted. Interestingly, these preliminary results agree with a similar study on the radius [5], which suggests the ontogenetic trajectory may be similar between skeletal elements during the transition from crawling to walking. Future analyses will consider also the external morphology and cortical bone thickness, which will provide a more complete picture of these differences. These results could then be used to compare the external and internal morphologies of non-human primates and fossil taxa, which would be useful in identifying developmental milestones related to the evolutionary history of committed terrestrial bipedalism.

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