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An ontogenetic framework linking locomotion and trabecular bone architecture with applications for reconstructing hominin life history

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ABSTRACT

The ontogeny of bipedal walking is considered uniquely challenging, due in part to the balance requirements of single limb support. Thus, locomotor development in humans and our bipedal ancestors may track developmental milestones including the maturation of the neuromuscular control system. Here, we examined the ontogeny of locomotor mechanics in children aged 1–8, and bone growth and development in an age-matched skeletal sample to identify bony markers of locomotor development. We show that step-to-step variation in mediolateral tibia angle relative to the vertical decreases with age, an indication that older children increase stability. Analyses of trabecular bone architecture in the distal tibia of an age-matched skeletal sample (the Norris Farms #36 archaeological skeletal collection) show a bony signal of this shift in locomotor stability. Using a grid of eleven cubic volumes of interest (VOI) in the distal metaphysis of each tibia, we show that the degree of anisotropy (DA) of trabecular struts changes with age. Intra-individual variation in DA across these VOIs is generally high at young ages, likely reflecting variation in loading due to kinematic instability. With increasing age, mean DA converges on higher values and becomes less variable across the distal tibia. We believe the ontogeny of distal tibia trabecular architecture reflects the development of locomotor stability in bipeds. We suggest this novel bony marker of development may be used to assess the relationship between locomotor development and other life history milestones in fossil hominins.

Introduction

Bipedalism is a hallmark trait for the human lineage and its evolution generated changes in the hominin skeleton from the skull to the feet (Robinson, 1972; Stern and Susman, 1983). While studies of comparative biomechanics and functional anatomy have yielded key insights into how and why bipedalism may have evolved (Stern and Susman, 1983; Wheeler, 1984, 1991; Chaplin et al., 1994; Hunt, 1994; Sockol et al., 2007; Thorpe et al., 2007), most work has focused exclusively on adult subjects and fossil specimens. However, the study of locomotor development can provide a unique window into the evolution of morphology and behavior across species that is obscured when considering the adult phenotype alone (Inouye, 1994; Raichlen, 2005a, 2005b, 2006; Shapiro and Raichlen, 2005; Ryan and Krovitz, 2006; Shapiro and Raichlen, 2006; Gosman and Ketcham, 2009; Zollikofer and Ponce de León, 2010; Gosman et al., 2013; Harmon, 2013; Shapiro et al., 2014).

For example, previous studies used evidence of load-induced ontogenetic changes in bone morphology from living taxa to confirm the presence of locomotor behaviors such as climbing or terrestrial bipedalism in the fossil record (e.g., phalangeal curvature and bicondylar angle; Duncan et al., 1994; Tardieu and Trinkaus, 1994; Tardieu and Damsin, 1997; Tardieu, 1999, 2010; Shefelbine et al., 2002; Richmond, 2007). Due to the rising number of fossil elements attributed to juvenile hominins (e.g., Duarte et al., 1999; Alemseged et al., 2006; Cowgill et al., 2007), researchers may

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now have the unique ability to explore the *pattern* of locomotor development in early hominins, providing a novel perspective on the evolution of bipedal walking and hominin life history patterns. This concept of exploring locomotion itself as a life history characteristic was first introduced by Zihlman (1992), and we suggest this intriguing idea can be expanded by carefully examining bony development in the fossil record. To compare patterns of development across taxa, however, we must first determine how skeletal material reflects the ontogeny of human bipedalism. The goal of this study is to find skeletal markers of bipedal locomotor development that we can apply to fossil hominins in future studies.

One salient aspect of locomotion in bipeds that may have a major impact on the characteristics of skeletal loading during development (e.g., the magnitude and orientation of ground reaction forces), and consequently on bone growth, is the inherent instability of walking on two limbs (Sutherland et al., 1980; Beck et al., 1981; Bril and Brenière, 1992; Adolph, 2003; Adolph et al., 2003; Khammari and Poyil, 2013). Early in locomotor development, when this instability is most pronounced, walking is irregular with each step differing from the last as individuals work to maintain balance with an immature muscular control system (Sutherland et al., 1980; Adolph, 2003; Khammari and Poyil, 2013). As neuromuscular control improves, variation from step to step is reduced, and, therefore, forces become more predictable (Sutherland et al., 1980; Forssberg, 1985; White et al., 1999; Adolph et al., 2003). Since both cortical bone and trabecular bone respond to changes in loading patterns through remodeling processes (Wolff, 1892; Ruff and Hayes, 1982; Pontzer et al., 2006; Ruff et al., 2006; Carlson and Judex, 2007; Barak et al., 2011), the response of bone to irregular loading patterns early on, and more predictable loading patterns during late childhood, may provide a unique morphological indicator of the development of mature and stable gaits.

Here we examine trabecular bone in the distal tibia as a potential marker of bipedal maturation in humans. Trabecular bone architecture is highly responsive to changes in loading orientations (Ryan and Ketcham, 2002b, 2005; Pontzer et al., 2006; Barak et al., 2011; Wallace et al., 2013) and the distal tibia represents the fulcrum for the body over the fixed foot during single limb support. Additionally, recent work shows that trabecular architecture in the tibia differentiates loading patterns in bipedalism and quadrupedalism (humans vs. chimpanzees), and these gait-related differences are detectable in the hominin fossil record (Barak et al., 2013). Thus, we predict changes in stability and balance during human growth are reflected in distal tibia trabecular bone architecture. If supported, then researchers would have a powerful method to capture patterns of locomotor development and maturation using fossil tibiae in hominin taxa.

Linking locomotor and morphological maturation

As described earlier, bone growth may capture the shift from unstable to stable locomotion, driven by a combination of neuromuscular maturation and changes in muscle strength (McGraw, 1935, 1943; Thelen, 1984; Breniere and Bril, 1987; Assaiante et al., 1993). In order to predict how bone will respond to locomotor changes, however, we must first define the features of gait in new walkers that reflect instability and immaturity. One key marker of instability is step-to-step variation in locomotor parameters. For example, intra-individual coefficients of variation (CV) for spatio-temporal parameters (calculated over multiple steps within an individual) are generally higher in younger compared to older walkers (Lasko-McCarthey et al., 1990). Standard deviations (SD) of joint flexion/extension angles (hip, knee, and ankle) also decrease from new walkers to older children (Lasko-McCarthey et al., 1990). Mediolateral trunk oscillations are significantly higher in new walkers as well, reflecting variation in joint angles from the ankle through the pelvis (Bril and Brenière, 1992; Assaiante et al., 1993; Yaguramaki and Kimura, 2002; Ivanenko et al., 2005). Supporting new walkers (holding their hands or otherwise providing postural support) reduces CVs for spatio-temporal parameters and SDs of joint angles, suggesting step-to-step variation in these parameters is due to insufficient balance control (Lasko-McCarthey et al., 1990; Ivanenko et al., 2005). In addition to variation during a single set of walking trials, measurements of joint angles and spatio-temporal variables show lower day-to-day repeatability in younger children compared to older children (Gorton et al., 1997; Looper et al., 2006). Although more challenging to collect, ground reaction force (GRF) data from children also show greater variation than adults (Cowgill et al., 2010). Cowgill et al. (2010) show that GRFs in all three directions (vertical, fore-aft, mediolateral) are more variable at young ages and that peak magnitudes of mediolateral forces are highest at the youngest ages, possibly reflecting mediolateral instability in early walkers.

Shifts from unstable to stable locomotion (i.e., variable to less variable segment angles) may leave markers on bone during growth and development. For example, epiphyseal morphology, cortical bone morphology, and bone strength are all influenced by ontogenetic changes in loading patterns (Carter, 1987; Carter et al., 1989; Shefelbine et al., 2002; Ruff, 2003a, 2003b), and the shift from highly variable to highly predictable joint angles should lead to a significant change in load orientations throughout growth and development. While the response of cortical bone to loads during growth is well documented, less is known about ontogenetic changes in trabecular bone morphology in the hindlimb of growing humans (see Ryan and Krovitz, 2006; Gosman and Ketcham, 2009). We suggest that trabecular morphology may provide a sensitive marker of changes in locomotor stability, since the architecture of trabecular struts may hold more detailed information regarding both the magnitude and orientation of loading patterns during development (Pontzer et al., 2006; Barak et al., 2011).

One of the primary functions of trabecular bone is to transmit loads generated during activity through struts oriented to best resist these loads. Researchers have suggested a relationship between limb usage, inferred loading patterns (orientations), and trabecular architecture in extant adult primates (Ward and Sussman, 1979; Pauwels et al., 1980; Oxnard and Yang, 1981; Oxnard, 1993; Rafferty and Ruff, 1994; Oxnard, 1997; Rafferty, 1998; Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham, 2002b, 2005; Richmond et al., 2004; Fajardo et al., 2007), fossil primates (Galichon and Thackeray, 1997; Macchiarelli et al., 1999; Rook et al., 1999; Ryan and Ketcham, 2002a; Scherf et al., 2013; Su et al., 2013), archaeological populations (Mielke et al., 1972; Vogel et al., 1990; Brickley and Howell, 1999; Agarwal et al., 2004), a diversity of extant mammal species (Kummer, 1959), extant and extinct equids (Thomason, 1985a, 1985b), and experimentally in guinea fowl (Pontzer et al., 2006), mice (Wallace et al., 2013), and sheep (Barak et al., 2011).

We also note that there is some evidence that loading patterns are not always reflected in trabecular architecture (e.g., Carlson et al., 2008; Scherf, 2008; Ryan and Walker, 2010; DeSilva and Devlin, 2012). Some of these researchers suggest that the trabecular response to loading patterns depends on the bone (i.e., location in the body). For example, Carlson et al. (2008) suggested joints that are more constrained in their range of motion may show a lower trabecular response in DA to loading patterns than joints that have higher degrees of freedom (see also Wallace et al., 2013). The lack of consensus among studies suggests we must use caution when interpreting trabecular bone, but also argues for more direct studies linking locomotor mechanics and bony architecture. Thus, despite