



Using principal trabecular orientation to differentiate joint loading orientation in the 3rd metacarpal heads of humans and chimpanzees



Meir M. Barak ^{a, b, *}, Emma Sherratt ^c, Daniel E. Lieberman ^b

^a Department of Biology, Winthrop University, Rock Hill, SC 29730, USA

^b Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

^c Department of Genetics and Evolution, School of Biological Sciences, The University of Adelaide, Adelaide, South Australia 5005, Australia

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ABSTRACT

If Wolff's law is valid, then quantifying the three-dimensional architecture of trabecular bone, specifically 3D principal trabecular orientation (3D-PTO), can reveal joint loading direction among different taxa. This study measured the architecture of trabecular bone in the 3rd metacarpal head of humans and chimpanzees, and then tested their association with expected joint loading direction. We postulate that since chimpanzees, unlike humans, directly load their metacarpal bones during knuckle-walking, trabecular structure in the dorsal aspect of the 3rd metacarpal head will be significantly more organized and robust in chimpanzees. To test this hypothesis, we micro-CT scanned the 3rd metacarpal from 11 chimpanzees and 12 humans. Three 6 mm volumes of interest (VOI; palmar, center and dorsal) were selected and trabecular bone properties and 3D-PTO were measured. The results revealed many similarities between humans and chimpanzees: in both taxa the dorsal VOI demonstrated the lowest bone volume fraction (BV/TV), the most rod-like trabecular structure, the fewest and thinnest trabeculae, and low organization of the trabecular architecture (degree of anisotropy). Nevertheless, 3D-PTO in the dorsal VOI differed significantly between humans and chimpanzees. While 3D-PTO in humans was clustered together and aligned nearly along the bone long axis, in chimpanzees 3D-PTO was divided into two distinct groups and aligned with an angle toward either the medial or lateral orientations. Our results suggest that loading effects on trabecular bone properties such as BV/TV might be partially constrained by genetic factors. On the other hand, 3D-PTO is continually affected by active loading (i.e., modeling) and thus may serve as a useful tool to infer differences in joint loading directions.

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1. Introduction

One key area of research in human evolution is the question of when hominins became bipeds and what was the locomotor repertoire of the last common ancestor of chimpanzees and humans (Stern and Susman, 1983; Lovejoy, 1988; Latimer and Lovejoy, 1989; Stern, 2000; Richmond et al., 2001; Ward, 2002; Richmond and Jungers, 2008; DeSilva, 2009; Lovejoy et al., 2009; Ward et al., 2011). Although the external morphology of bones, including fossils, is an important source of information on function, it is highly influenced by many genetic and non-genetic stimuli and thus often difficult to interpret (Wolff, 1892; Murray and Huxley,

1925; Niven, 1933; Lieberman, 1997; Hsieh and Turner, 2001; Mariani and Martin, 2003; Wallace et al., 2013). In contrast, internal trabecular bone has a clear advantage for making inferences about how bones were loaded as numerous comparative and experimental studies have demonstrated a relationship between the architecture of trabecular bone and applied loads (MacLachy and Müller, 2002; Ryan and Rietbergen, 2005; Pontzer et al., 2006; Barak et al., 2011; Christen et al., 2012; Tsegai et al., 2013; Skinner et al., 2015; Scherf et al., 2016). Comparisons of trabecular bone structural properties such as trabecular bone volume fraction (BV/TV), trabecular thickness, number and separation (Tb.Th, Tb.N and Tb.Sp, respectively), connectivity density (ConnD) and degree of anisotropy (DA) are thus important sources of evidence for inferring and testing differences in loading regimes. Nonetheless, previous studies have yielded conflicting results demonstrating that these trabecular bone parameters sometimes reflect differences in joint loading directions (MacLachy and

* Corresponding author.

E-mail addresses: barakm@winthrop.edu (M.M. Barak), emma.sherratt@gmail.com (E. Sherratt), danlieb@fas.harvard.edu (D.E. Lieberman).

Müller, 2002; Ryan and Krovitz, 2006; Volpato et al., 2008; Fajardo et al., 2013; Su et al., 2013; Tsegai et al., 2013; Skinner et al., 2015) but do not always (Ryan and Rietbergen, 2005; Fajardo et al., 2007; Carlson et al., 2008; Ryan et al., 2010; Ryan and Walker, 2010; Shaw and Ryan, 2012; Wallace et al., 2012, 2013). This variation implies that the relation between predicted joint loading direction and the morphology of trabecular bone is complex and cannot be always depicted by measuring several individual trabecular bone properties (Zeininger et al., 2011; Tsegai et al., 2013; Alméjija et al., 2015; Chirchir et al., 2017).

More consistent results were achieved when studies used a suite of trabecular bone properties to infer differences in locomotion behavior and joint loading direction (Shaw and Ryan, 2012; Scherf et al., 2013, 2016; Matarazzo, 2015). A study by Matarazzo (2015) demonstrated that measuring a suite of trabecular bone properties (BV/TV, DA and elongation index) in the metacarpal head, and proximal and middle phalanges of the third ray was able to differentiate between knuckle-walking, quadrupedal, and suspensory primates. Similarly, Ryan and Shaw (2012) showed that a suite of trabecular bone properties (Tb.N, ConnD, DA and the relative proportion of trabecular rods and plates) in the femoral head was able to differentiate accurately between different locomotor groups among eight anthropoid primate genera. However, the same suite of trabecular bone properties in the humeral head revealed a much weaker relationship with the same locomotor groups. In contrast, Scherf et al. (2013) did find that a suite of trabecular bone properties (BV/TV, relative proportion of trabecular rods and plates, and Tb.N, Tb.Th and Tb.Sp) in the humeral head was able to clearly differentiate between knuckle-walker (chimpanzees), arboreal (orangutans) and bipedal (human) primates. Thus, it seems that even the use of a suite of trabecular bone properties may yield inconsistent results.

Recent studies have introduced another method, “principal trabecular orientation” (PTO), to assess joint loading direction from trabecular bone tissue structure (Pontzer et al., 2006; Barak et al., 2011, 2013b). PTO is based on Wolff’s law of trabecular transformation, first proposed as a strict mathematical law in 1892 (Wolff, 1892), and now accepted as a more general concept of bone functional adaptation, that links mechanical loading to bone structure (Ruff et al., 2006). In particular, PTO predicts that trabecular struts just below the cortex of the joint surface respond to external loads by preferentially aligning their long axes along the trajectories of peak principal stresses. Several recent studies have provided experimental and observational support for this approach. Pontzer et al. (2006) found a 13.6° difference in the distal femur sagittal plane 2D-PTO between two groups of guinea fowl running on flat vs. inclined treadmills. This 13.6° difference corresponded closely to a 13.7° difference in knee angle joint between these two groups. In another study, Barak et al. (2011) compared 2D-PTO in the distal tibia and 3D-PTO in the distal radius of sheep running on flat versus inclined treadmills. They found a difference of 2.7–4.3° and no difference (0°) in distal tibia and distal radius sagittal plane 2D-PTO, respectively, between the groups. Again, these values corresponded closely to a 3–4.5° and 0° differences in tarsal and carpal joints angle, respectively, between the flat and inclined sheep groups. Finally, Barak et al. (2013b) demonstrated a highly predictive relationship between ankle joint orientation of chimpanzees and humans during loading, and their distal tibia sagittal plane 2D- and 3D-PTO. Moreover, these results showed that the sagittal plane 2D-PTO of two fossil distal tibiae assigned to *Australopithecus africanus* was comparable to humans but not to chimpanzees, indicating that *A. africanus* loaded their ankles in a relatively extended posture like modern humans and unlike chimpanzees.

This study uses 3D-PTO to examine if there is a significant difference in trabecular bone structure in the 3rd metacarpal (MC)

head between humans and chimpanzees, suggesting a signal of joint loading direction in the bone structure. We focused on trabecular properties of the 3rd MC because there is substantial evidence that the third ray experiences the highest loads while human fingers are in flexed or natural posture, during striking, grasping and the swing and strike phases of tool production (Marzke and Marzke, 1987; Tamai et al., 1988; Rolian et al., 2011; Williams et al., 2012; Horns et al., 2015), and during chimpanzee knuckle-walking (Matarazzo, 2008, 2009; Wunderlich and Jungers, 2009). As a result of these peak stresses, the 3rd MC of humans and chimpanzees was shown to have distinct subchondral mineralization density patterns (Zeininger et al., 2011), significant differences in BV/TV distribution and DA (Tsegai et al., 2013), and diverse concentration of BV/TV (Skinner et al., 2015).

Chimpanzees use quadrupedal knuckle-walking as their principal mode of terrestrial locomotion (Hunt, 1992). In this form of locomotion, fingers are flexed and body-weight is supported by the dorsal surface of middle phalanges 2, 3, 4 and, to lesser extent, 5. From there, load is transmitted via the proximal phalanges and the dorsal aspect of the distal MC bones (metacarpophalangeal joint) to the more proximal elements of the upper extremities (Wunderlich and Jungers, 2009). Chimpanzees, however, knuckle-walk only about 2–3 km a day (Pontzer and Wrangham, 2004). In addition to knuckle-walking, chimpanzees engage to a lesser extent in arboreal suspension (often using transverse and diagonal hook grip) and climbing (often using power grip), where the metacarpophalangeal joints are flexed to a variable degree and the palmar and palmar-distal surfaces of the metacarpal heads likely experience the greatest joint loads (Marzke and Wullstein, 1996). In contrast, bipedal humans rarely load their hands during locomotion. Most stresses applied to the human MC bones are generated during manual manipulation while the fingers are flexed (e.g., grasping, squeezing, carrying and punching), although infrequently these stresses may involve extended metacarpophalangeal joint postures (e.g., pushing an object or to open a door). Thus, loading via the metacarpophalangeal joint is transmitted mainly through the palmar and palmar-distal aspects of the MC head (Marzke and Marzke, 1987; Jones and Lederman, 2006).

Several other studies have used different methods to investigate the correlation between joint loading direction and trabecular bone architecture in the 3rd MC head of humans and chimpanzees. Zeininger et al. (2011) employed backscattered electron microscopy analysis to measure subchondral and trabecular bone mineral density in sagittal sections of chimpanzee, orangutan and human 3rd MC heads. Their results revealed significantly lower bone mineralization (indicative of bone modeling) in the dorsal and palmar regions of chimpanzees, and the distal region of orangutans. These diverse mineralization patterns correlate to chimpanzee knuckle-walking and climbing, and orangutan suspensory and climbing locomotion behavior. In contrast, humans demonstrated a much more uniform distribution of mineralization throughout the metacarpal head, corresponding to the lower stresses and their more homogenous use of the hand during manual manipulation. Rather than looking at a specific volume of interest (VOI), Tsegai et al. (2013) applied a whole-epiphyseal analysis to test whether trabecular bone architecture in the 3rd MC head demonstrates differences in relation to hand posture and joint loading in knuckle-walking, suspension and manipulation across several primate taxa. Their results demonstrate that BV/TV distribution and regions of greatest bone stiffness generally corresponded well with expected joint loading direction in each locomotor category. The authors concluded that their results support a relationship between locomotion behavior and trabecular architecture in extant primates and that this relation can assist in inferring locomotor behavior in extinct primates. Skinner et al. (2015) also used the technique

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