Trabecular bone patterning across the human hand

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ABSTRACT

Hand bone morphology is regularly used to link particular hominin species with behaviors relevant to cognitive/technological progress. Debates about the functional significance of differing hominin hand bone morphologies tend to rely on establishing phylogenetic relationships and/or inferring behavior from epigenetic variation arising from mechanical loading and adaptive bone modeling. Most research focuses on variation in cortical bone structure, but additional information about hand function may be provided through the analysis of internal trabecular structure. While primate hand bone trabecular structure is known to vary in ways that are consistent with expected joint loading differences during manipulation and locomotion, no study exists that has documented this variation across the numerous bones of the hand. We quantify the trabecular structure in 22 bones of the human hand (early/extant modern *Homo sapiens*) and compare structural variation between two groups associated with post-agricultural/industrial (post-Neolithic) and foraging/hunter-gatherer (forager) subsistence strategies. We (1) establish trabecular bone volume fraction (BV/TV), modulus (E), degree of anisotropy (DA), mean trabecular thickness (Tb.Th) and spacing (Tb.Sp); (2) visualize the average distribution of site-specific BV/TV for each bone; and (3) examine if the variation in trabecular structure is consistent with expected joint loading differences among the regions of the hand and between the groups. Results indicate similar distributions of trabecular bone in both groups, with those of the forager sample presenting higher BV/TV, E, and lower DA, suggesting greater and more variable loading during manipulation. We find indications of higher loading along the ulnar side of the forager sample hand, with high site-specific BV/TV distributions among the carpals that are suggestive of high loading while the wrist moves through the 'dart-thrower's' motion. These results support the use of trabecular structure to infer behavior and have direct implications for refining our understanding of human hand evolution and fossil hominin hand use.

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1. Introduction

Interest in primate hand morphology and function is long-standing (e.g., Jones, 1916; Ashley-Montagu, 1931; Napier, 1960; Lewis, 1969; Susman, 1979; Diogo et al., 2012; Boyer et al., 2013), as the hand interacts with substrates during locomotion (e.g., Doran, 1993; Daver et al., 2012; Congdon and Ravosa, 2016) while also facilitating dexterous manipulation during social grooming (Whiten et al., 1999; Brand et al., 2017), food acquisition (Hunt, 1991; Boesch and Boesch, 1993; Visalberghi et al., 2009), communication (Hopkins et al., 2005; Zlatev, 2008), and complex object manipulations (Marzke and Wullstein, 1996; Viaro et al., 2017).

Among primates, humans are often cited as the most dexterous (Napier, 1960; Vereecke and Wunderlich, 2016), possessing a suite of morphological features that allow for a wide range of wrist movements, power 'squeeze' grips (Marzke et al., 1992), and the formation of stable precision grips via the forceful opposition of the thumb and finger-pads (Napier, 1956; Marzke, 1997; Susman, 1998). Early interpretations favored a view that human dexterity was derived, with researchers drawing strong causal links with hominin bipedal locomotion, the emergence of stone tool use, and/or increased carnivory (Young, 2003; Wood, 2014; Lemelin and Schmitt, 2016). Although most researchers still agree that the distinct aspects of human hand morphology are related to the selective pressures of at least three million years of tool-related behaviors (e.g., Napier, 1956; Washburn, 1960; Marzke, 1997; Harmand et al., 2015), there is less certainty about which features

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reflect a conserved ancestral state and which are derived (Tocheri et al., 2008; Rolian et al., 2010). This shift in our evolutionary understanding is the direct result of improved comparative techniques (Boyer et al., 2013, 2015; Almécija et al., 2015a), new fossil discoveries (Lorenzo et al., 1999, 2015; Kivell et al., 2011a, 2015; Almécija et al., 2012) and more comprehensive observational studies of non-human primate hand use (Hopkins et al., 2011; Marzke et al., 2015; Proffitt et al., 2016; Neufuss et al., 2017), which suggest that human-like hand morphology and use is more generalized and deep-rooted than previously appreciated (Alba et al., 2003; Almécija et al., 2010; Almécija and Alba, 2014; Rolian, 2016).

Thus, a greater understanding of how hand function may be reflected in hand morphology is needed. Variation in hand morphology has been key to informing hypotheses about not only manipulative behaviors and technological abilities in the human past (Leakey et al., 1964; Musgrave, 1971; Vlček, 1975; Susman, 1991, 1994; Niewoehner et al., 2003; Eren and Lycett, 2012; Wood, 2014), but also locomotor habits (Ricklan, 1987; Alba et al., 2003; Shrewsbury et al., 2003; Green and Gordon, 2008; Kivell et al., 2015), and—more indirectly—human neurological evolution and language acquisition (e.g., Falk, 1980; Hopkins, 2013; Putt et al., 2017). Interpreting hand function in the past is further complicated by the tendency for hominin fossil hand remains to be recovered in isolation or as unassociated collections (Bush et al., 1982; Schmid and Berger, 1997; Venkataraman et al., 2013; Ward et al., 2014; Domínguez-Rodrigo et al., 2015; Lorenzo et al., 2015; Stratford et al., 2016; Daver et al., in press). As such, it is useful to explore methods with the potential to provide additional functional information about how manual behavior may have varied in the past that can also be applied to isolated hand bone elements.

1.1. Bone functional adaptation

Traditionally, researchers have compared the external shape of fossil hominin hand bones to generate hypotheses about hand function and grip capacity. For example, the potential for forming the precision and power grips observed during tool manufacture/use tend to be inferred from the hand proportions (i.e., thumb length relative to finger length) and shape of the trapezium-first metacarpal joint (e.g., Napier, 1962; Trinkaus, 1989; Godinot and Beard, 1991; Susman, 1994; Alba et al., 2003; Tocheri et al., 2003; Marzke et al., 2010). These morphological associations are established through observational studies focusing on wild and captive primate manipulative habits (e.g., Pouydebat et al., 2009, 2011, 2014; Bardo et al., 2015, 2016; Marzke et al., 2015; Orr, 2017), which provide the basis for understanding if extinct taxa with similar morphologies had similar manipulative capacities (e.g., Almécija et al., 2010; Almécija and Alba, 2014; Kivell et al., 2015; Orr, 2018). However, as external morphology only allows inferences about manipulative capacity, and not necessarily actual behavior, many researchers have begun to quantify epigenetic changes to bone that result from repetitive loading (e.g., compression, tension, and shear; Frost, 1987).

This phenomenon, commonly referred to as bone functional adaptation, has been experimentally observed to alter the structure in ways that improve the mechanical competence of repeatedly-loaded bone (Lanyon and Rubin, 1985; Pontzer et al., 2006; Ruff et al., 2006; Barak et al., 2011; Schulte et al., 2013; Christen et al., 2014; Cresswell et al., 2016; Christen and Muller, 2017; Ritter et al., 2017). For instance, cortical bone adjusts in thickness for improved resistance to bending forces, while trabecular bone alters the thickness, spacing, and orientation of struts adjacent to loaded regions in a way that enhances the transfer of kinetic energy away from joint surfaces (Cowin et al., 1985; Keaveny et al., 2001;

Sugiyama et al., 2010; Currey, 2011; Barak et al., 2013; Reznikov et al., 2015; but see Demes et al., 1998; Ozcivici and Judex, 2014; Wallace et al., 2015a,b; Fairfield et al., 2017). In general, many regions of the primate skeleton exhibit evidence of adaptive modeling, with structural variation aligning with hypothesized loading differences (e.g., Rafferty and Ruff, 1994; Ryan and Ketcham, 2002; Stock, 2006; Marchi and Shaw, 2011; Ryan and Shaw, 2012; Su et al., 2013; Chirchir, 2015; Fabre et al., 2017; Reznikov et al., 2017; Stieglitz et al., 2017), and hand bone variation reflecting known locomotor, postural, and manipulatory habits (e.g., Marchi, 2005; Patel and Carlson, 2007; Lazenby et al., 2008a,b, 2011a; Zeininger et al., 2011; Tsegai et al., 2013; Barak et al., 2017; Chirchir et al., 2017b).

For hand trabecular bone, there are some studies that have reported ambiguous results between inferred loading and structure (e.g., Lazenby et al., 2011a; Schilling et al., 2014; Stephens et al., 2016a; Reina et al., 2017), with overlapping or unanticipated levels of bone volume fraction (BV/TV) and trabecular strut alignment (degree of anisotropy; DA). Explanations for such inconsistencies are found in well-controlled experiments, which utilize animal models to highlight how bone modeling may be influenced by genetic, systemic, or hormonal variation (e.g., Wallace et al., 2010, 2015a; Schlecht et al., 2014; Smith et al., 2014; Fairfield et al., 2017; see Wallace et al., 2017b for a recent review). Among humans, these factors are best understood as they relate to bone's role in maintaining homeostasis, with differences in bone structure arising from nutritional stress (e.g., anemia, pregnancy) or advanced age (e.g., menopause, osteoporosis; Agarwal, 2016). For trabecular bone these changes are documented in modern and archaeological contexts, with shifts from high BV/TV and low DA (more isotropic) to relatively low BV/TV and high DA (more anisotropic), which prioritizes resistance to load along a singular axis (Singh et al., 1970; Agarwal et al., 2004; Christen et al., 2014; Beauchesne and Agarwal, 2017). Much of this understanding has come from the ability to perform more comprehensive quantitative analyses, which better characterize local microstructural changes in bone (Poole et al., 2012; Gee and Treece, 2014; Gross et al., 2014; Hermann and Klein, 2015; Phillips et al., 2015). This is especially evident in trabecular studies, which have moved from single volume of interest (VOI) analyses to the simultaneous analyses of multiple VOIs (Su and Carlson, 2017; Sylvester and Terhune, 2017) or the whole-bone/epiphysis (Gross et al., 2014; Taghizadeh et al., 2017).

For hand bones, such methods have documented differences in the distribution of trabeculae in the primate third metacarpal (Mc3) that align with predicted joint loading during locomotion and manipulation (Tsegai et al., 2013; Barak et al., 2017; Chirchir et al., 2017b). Other studies have identified similar distributions of BV/TV in human and fossil hominin metacarpals, which suggests a shared pattern of joint loading that may be related to opposition on the thumb during the use of precision grips (Skinner et al., 2015a,b; Stephens et al., 2016a; but see Almécija et al., 2015b). Such results establish the value of trabecular bone analysis to examine aspects of extant and fossil primate manual behavior, which we explore here through the quantification of trabeculae from the articulated elements of the wrist, metacarpus, and phalanges of human (Homo sapiens) hands (excluding the pisiform and distal phalanges).

To assess if trabecular architecture of the hand is related to differences in manipulatory loading, we follow previous analyses of other skeletal regions (e.g., Ryan and Shaw, 2015; Scherf et al., 2016; Stieglitz et al., 2017), and compare two groups of humans broadly defined by subsistence strategy and assumed behavior (i.e., community dwelling post-Neolithic agriculturalists/industrialists and mixed foraging/hunter-gatherers; hereafter 'post-Neolithic' and