Metacarpal head biomechanics: A comparative backscattered electron image analysis of trabecular bone mineral density in *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens*

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Abstract

Great apes and humans use their hands in fundamentally different ways, but little is known about joint biomechanics and internal bone variation. This study examines the distribution of mineral density in the third metacarpal heads in three hominoid species that differ in their habitual joint postures and loading histories. We test the hypothesis that micro-architectural properties relating to bone mineral density reflect habitual joint use. The third metacarpal heads of *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens* were sectioned in a sagittal plane and imaged using backscattered electron microscopy (BSE-SEM). For each individual, 72 areas of subarticular cortical (subchondral) and trabecular bone were sampled from within 12 consecutive regions of the BSE-SEM images. In each area, gray levels (representing relative mineralization density) were quantified.

Results show that chimpanzee, orangutan, and human metacarpal III heads have different gray level distributions. Weighted mean gray levels (WMGLs) in the chimpanzee showed a distinct pattern in which the ‘knuckle-walking’ regions (dorsal) and ‘climbing’ regions (palmar) are less mineralized, interpreted to reflect elevated remodeling rates, than the distal regions. *Pongo pygmaeus* exhibited the lowest WMGLs in the distal region, suggesting elevated remodeling rates in this region, which is loaded during hook grip hand postures associated with suspension and climbing. Differences among regions within metacarpal heads of the chimpanzee and orangutan specimens are significant (Kruskal–Wallis, p < 0.001). In humans, whose hands are used for manipulation as opposed to locomotion, mineralization density is much more uniform throughout the metacarpal head. WMGLs were significantly (p < 0.05) lower in subchondral compared to trabecular regions in all samples except humans. This micro-architectural approach offers a means of investigating joint loading patterns in primates and shows significant differences in metacarpal joint biomechanics among great apes and humans.

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Introduction

Joint loading is critical to our understanding of functional adaptations. Studies of trabecular bone structure (e.g., Fajardo and Müller, 2001; Ryan and Ketcham, 2002, 2005; Maclatchy and Müller, 2002; Ketcham and Ryan, 2004; Richmond et al., 2004; Maga et al., 2006; Griffin et al., 2010; Lazenby et al., 2011) are improving our understanding of joint biomechanics in primates, especially in light of experimental evidence that trabecular density, degree of mineralization, and direction change via remodeling in response to changes in load (e.g., Goldstein et al., 1991; Hou et al., 1994; Kambayashi et al., 1995; Sakata et al., 1999; Boyde, 2003; Pontzer et al., 2006). Joint loading in primates differs according to hand postures and form of locomotion. By better defining trabecular bone patterns associated with habitual arboreal and terrestrial locomotion in extant primate species, such as knuckle-walking and climbing, there is a potential for the analysis of these features in fossil hominins. Identifying bone morphology that is epigenetically sensitive to joint use could provide compelling evidence of the functional significance of primitive morphology in early hominins.
This study tests a micro-architectural approach as a means of better understanding how functional use affects subchondral and trabecular bone mineralization within metacarpal heads of *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens*. Previous studies have shown that gray levels in backscattered electron microscopy (BSE-SEM) images are directly correlated to the relative mineralization density, with more heavily mineralized bone being more reflective and appearing proportionately lighter in BSE-SEM images (e.g., Skedros et al., 1993a,b; Roschger et al., 1998). Relative mineralization density, in turn, is related to the rate of remodeling (e.g., Skedros et al., 1993a,b; Roschger et al., 1998; Kierdorf et al., 2000; Goldman et al., 2005; Fig. 1).

Remodeling occurs when primary osteons are replaced by secondary osteons (Haversian systems), and it is measured by quantifying variables that are directly representative of remodeling rates or the amount of remodeled bone (e.g., population densities of secondary osteons and/or semi-osteons, the fractional area of secondary osteonal bone, population densities of newly forming secondary osteons and resorption spaces, or the size of individual secondary osteons). Bone remodeling occurs in response to elevated or repetitive strain during normal functional loading (Rubin and Lanyon, 1984; Currey, 2002; Robling et al., 2006). Other factors may lead to bone remodeling (Young et al., 1983, 1986; Frost, 1990; Skedros et al., 2001), but the primary factor leading to substantial remodeling is repetitive or elevated strain (e.g., Rubin and Lanyon, 1984; Robling et al., 2006). New bone formed by remodeling is less mineralized than pre-existing bone in the area because mineral accumulates for six or more months in the new tissue, and the mineralization process may persist for as much as two decades (Martin et al., 1998; Akkus et al., 2003). By comparing gray levels in BSE-SEM images, and hence level of mineralization, it is possible to estimate the degree of remodeling which has taken place.

We hypothesize that the relative mineralization density of bone varies in a manner consistent with the ways that chimpanzee, orangutan, and human metacarpophalangeal (MP) joints are loaded. Joint postures during knuckle-walking (extended) and climbing (neutral or flexed) indicate that joint reaction forces occur at the dorsally expanded and distal-palmar aspects, respectively, of the third metacarpal head (Fig. 2; Tuttle, 1967; Inouye, 1994; Richmond et al., 2001). In contrast, orangutans are almost exclusively arboreal and use suspensory ‘hook grip’ and orthograde climbing postures and locomotion (Cant, 1985). These activities involve neutral (distal joint reaction force) and flexed (palmar joint reaction force) MP joint postures during grasping (Fig. 2). Human hand postures involved in carrying and manual manipulation (e.g., power and precision grips) also typically involve neutral and flexed joint postures, and rarely involve extended MP joint postures (Goldfarb and Dovan, 2006). However, human hands are undoubtedly subjected to lower forces on a daily basis, as they are not normally used for locomotion and body weight support.

The goal of this study is to examine the distribution of mineral density in the metacarpal III heads in three species that differ fundamentally in their habitual joint postures and loading histories. We test four hypotheses. We predict that ‘knuckle-walking’ regions (dorsal) and ‘climbing’ regions (palmar to distal) of the chimpanzee metacarpal heads will have significantly lower BSE-SEM gray levels and therefore be less mineralized than the distal, less stereotypically loaded regions. We hypothesize that the dorsal regions of the chimpanzee metacarpal will be less mineralized than the palmar regions of the chimpanzee metacarpal because it is suspected that peak loads are more common on the dorsal region during knuckle-walking compared to the varying degrees of flexion used during climbing (e.g., neutral MP joint during hook grips, more flexed MP joints when grasping small supports). We predict that in the metacarpal III heads of orangutans, the ‘climbing’ (palmar) and ‘hook grip’ (distal) regions will be less mineralized than the dorsal regions because of peak loads incurred during habitual climbing and suspending. If there is a difference in mineralization within the human metacarpal, a lower mineralization density is predicted in the distal-to-palmar regions compared to dorsal regions because those regions are loaded during power and precision grips. Finally, we predict that bone tissue at the articular surface (subchondral bone) will be less mineralized than trabeculae because of the proximity of the articular surface bone to the joint reaction force. Bone tissue farther from the surface experiences the collective forces transmitted and dissipated through trabecular connections, so it is expected to be less affected by local joint stresses (Currey, 2002).

**Materials and methods**

**Specimens**

Subchondral and trabecular bone within metacarpal heads of eight *Homo sapiens*, two *Pan troglodytes* and one *Pongo pygmaeus* were examined in this study. Table 1 shows the age, sex, hand side, and source for each of our 11 specimens. The sample sizes were limited by the availability of metacarpals for sectioning and the availability of the scanning electron microscope. Both chimpanzees are from the Yerkes Regional Primate Research Center in Atlanta, GA. The male chimpanzee was healthy until an attack by other chimpanzees led to his death at the age of 18 years, 10.5 months. The female chimpanzee was one of the oldest known captive chimpanzees on record and died at the age of 57 years, 11.5 months. Due to arthritis in her third metacarpal, the second metacarpal was chosen for analysis. The orangutan came from a cadaver at Arizona State University, originally from the Phoenix Zoo. Although he died of coccidioidomycosis (a fungal infection) at the age of 38 years, 6 months, the hand was not affected. Human third metacarpals from

![Backscattered electron microscopy (BSE-SEM) image from the dorsal aspect of a chimpanzee MC III head. Dorsal subchondral bone is visible on the left while trabecular bone appears on the right. Gray levels 0–255 are represented, where black equals gray level 0 and white equals gray level 255. Gray levels have been shown to be correlated with mineralization density and degree of remodeling (recently remodeled bone is less mineralized and yields lower gray levels). Darker gray levels indicate less mineralized, newly deposited bone. Lighter gray levels indicate highly mineralized, less recently deposited bone.](image-url)
Fig. 2. The black arrow illustrates the joint reaction force (JRF) acting on the metacarpal head. The JRF acts on the dorsal region of the metacarpal head in the hyperextended metacarpophalangeal (MP) joint posture during knuckle-walking in chimpanzees (left, adapted from Richmond and Strait, 2000). During the hook grip, often used by orangutans, the MP joint is in a neutral position and the JRF acts on the distal region of the metacarpal head (center, adapted from Sarmiento, 1988). A flexed MP joint posture during the power grip, used by chimpanzees and orangutans during climbing and humans during carrying and manual manipulation, results in a palmar JRF (right, modified from Legget and Meko, 2006).

5 males and 3 females were collected from recently embalmed cadavers at The George Washington University Medical School.

Specimen preparation

To remove excess soft tissue the metacarpals were gently simmered for 30 min in a washing soda solution and then rinsed under running tap water for 10 min following the hot water maceration protocol of the Caribbean Primate Research Center Museum. The distal heads were then removed from the shafts using a diamond saw, and the heads were cut in the mid–sagittal plane. These cross sections were embedded in a mixture of Epotek 301 A and B, 4:1 resin:hardener by weight, and placed under a vacuum hood to remove air bubbles. Finally, all specimens were serially ground on a lapidary wheel and polished using a 0.01 μm alumina suspension (Buehler Ltd). Although ultramilling is the preferred method for mineralization analysis via BSE-SEM imaging (Vajda et al., 1999), this method was unavailable to the authors. We consider our method sufficient given that variability induced from polishing does not affect results of relative gray level histograms (Skedros et al., 1993b). All specimens were vacuum pumped overnight to prepare for scanning.

BSE-SEM imaging

BSE-SEM scans were collected for each of the sagittally-sectioned metacarpal heads using a Philips XL-30 environmental scanning electron microscope (ESEM) at the National Museum of Natural History, Smithsonian Institution in Washington, DC. To ensure stable conditions, a new tungsten filament was installed at the beginning of the project. Scans were taken during six separate sessions over the course of two and a half weeks. Beam current delivered to the sample was held stable and measured by a Faraday cup. Images were captured at 100× magnification, 20 kV accelerating voltage, 0.65 nA beam current, at a working distance of 10.0 mm.

Histograms of aluminum (Al) and carbon (C) standards were used to calibrate gray levels during image capture (Roschger et al., 1998). An aluminum and a carbon wire were embedded in the specimen holder. A master image of the standards was captured at the beginning of the first session, from which a master standards histogram was made. After every 10 scans we returned to the standards. Brightness and contrast were adjusted when necessary in order to recreate the master standards histogram. Prior to image analysis, these standards were also used to standardize gray levels in bone images. In Scion Image (http://www.scioncorp.com), a calibration standard was set so that the mean value of the carbon standard was set equal to zero while the mean value of the aluminum standard was set equal to 255. Subsequent bone images retained this calibration system.

Individual BSE-SEM images were stitched together using Photoshop 7.0 in order to form a composite for each specimen. Each composite was then divided into 12 equally-spaced regions: 4 dorsal (D1–D4), 4 distal (Di5–Di8), and 4 palmar (P9–P12; Fig. 3). Three subchondral and three trabecular areas (typically

Table 1

Specimens used in this study.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Species</th>
<th>Side</th>
<th>Bone</th>
<th>Sex</th>
<th>Age (Years)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Pan troglodytes</em></td>
<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>18 years, 10.5 months</td>
<td>Yerkes Regional Primate Research Center</td>
</tr>
<tr>
<td>2</td>
<td><em>Pan troglodytes</em></td>
<td>Left</td>
<td>MC II</td>
<td>Female</td>
<td>57 years, 11.5 months</td>
<td>Yerkes Regional Primate Research Center</td>
</tr>
<tr>
<td>3</td>
<td><em>Pongo pygmaeus</em></td>
<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>38 years, 6 months</td>
<td>Arizona State University</td>
</tr>
<tr>
<td>4</td>
<td><em>Homo sapiens</em></td>
<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>81</td>
<td>George Washington University Medical School</td>
</tr>
<tr>
<td>5</td>
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<td>Right</td>
<td>MC III</td>
<td>Female</td>
<td>71</td>
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</tr>
<tr>
<td>6</td>
<td><em>Homo sapiens</em></td>
<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>92</td>
<td>George Washington University Medical School</td>
</tr>
<tr>
<td>7</td>
<td><em>Homo sapiens</em></td>
<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>92</td>
<td>George Washington University Medical School</td>
</tr>
<tr>
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<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>84</td>
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</tr>
<tr>
<td>9</td>
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<td>Right</td>
<td>MC III</td>
<td>Female</td>
<td>Unknown</td>
<td>George Washington University Medical School</td>
</tr>
<tr>
<td>10</td>
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<td>Right</td>
<td>MC III</td>
<td>Male</td>
<td>Unknown</td>
<td>George Washington University Medical School</td>
</tr>
<tr>
<td>11</td>
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<td>Right</td>
<td>MC III</td>
<td>Female</td>
<td>Unknown</td>
<td>George Washington University Medical School</td>
</tr>
</tbody>
</table>
Fig. 3. Composite of 31 individual BSE-SEM images along the articular surface of a sagittal cross section of the male chimpanzee third metacarpal head. First, a line was drawn to separate the head from the diaphysis. Next, the head was divided into 12 equal regions labeled from dorsal to palmar. Regions D1–D4 are dorsal regions, D5–D8 are distal regions, and P9–P12 are the palmar regions. Within each region, samples were chosen from subchondral and trabecular bone. In this study, subchondral bone was defined as the outermost rim of bone (within 400 μm of the joint surface) while trabecular refer to longer struts deep to the subchondral bone (between 400 and 1200 μm from the joint surface).

150 × 150 μm) of bone were sampled from within the 12 consecutive regions, resulting in a total of 72 areas for each individual. Subchondral bone is defined here as bone tissue within the contiguous bone within 400 μm of the bone perimeter, whereas trabecular are defined as trabecular bone struts within a band between 400 μm and 1200 μm deep to the joint surface. In each area, gray levels (representing degree of mineralization) were quantified using Scion Image.

Gray level histogram values were exported into Excel spreadsheets where they were converted to weighed mean gray levels (WMGLs) by multiplying each histogram value by the number of observations with that grayscale value, then calculating the average gray level across the total number of observations (Bloebaum et al., 1997). Black background values (gray levels 0–8), representing space (i.e., canaliculi and Haversian canals, not mineralized bone tissue), were deleted before calculating the WMGLs. WMGLs for each of the 72 samples for each specimen were imported into Statistica (Statsoft, Inc) to make boxplots and perform nonparametric Kruskal–Wallis tests.

Results

Results show that the pattern of bone mineral density, as reflected by grayscale values, differs between species in predictable ways. The two chimpanzee metacarpal heads show a distinct pattern in which WMGLs (combined subchondral and trabecular samples) are lowest in dorsal and palmar regions, and highest in the distal region (Fig. 4). From the low WMGLs in the dorsal-most regions, values increase to a peak in the distal regions, and subsequently decrease in the palmar region (Fig. 4). The difference among regions is statistically highly significant (female chimpanzee \( H = 39.79, p < 0.001 \); male chimpanzee \( H = 43.97, p < 0.001 \)).

In the orangutan metacarpal, the lowest WMGLs occur in the distal and slightly palmar regions (Fig. 4). The dorsal regions have the highest WMGLs, followed by decreasing values in the distal region then slightly increasing values in the palmar regions. Differences in WMGLs among regions (combined subchondral and trabecular) are significant \( (H = 24.11, p < 0.05) \). WMGLs in the human metacarpals are much more uniform across the sagittal section regions. Although values appear slightly lower in the dorsal regions of the human metacarpals, the variation in WMGLs among regions is not significant \( (H = 10.35, p > 0.05) \).

In all specimens, when subchondral and trabecular samples are distinguished from one another (Fig. 5), each maintains the specific trend of lowest and highest WMGL across regions. For example, in the male chimpanzee, subchondral WMGLs are lowest in the dorsal regions and highest in the distal regions. The same is true for trabecular WMGLs in the same specimen. However, articular surface gray levels have statistically significantly lower gray levels compared with gray levels in the deeper trabecular bone in both chimpanzees as well as the orangutan (female chimpanzee \( H = 5.54, p < 0.05 \); male chimpanzee \( H = 10.74, p < 0.01 \); orangutan \( H = 9.42, p < 0.05 \); Fig. 5).

Although results are not significant \( (H = 1.46, p > 0.05) \), the human samples show a similar pattern, with a typically lower mean WMGL in subchondral samples. These results support the hypothesis that bone nearer to the joint reaction force maintains lower gray levels and is therefore less mineralized than deeper trabecular struts. Alternatively, lower mineralization density in subchondral bone may be the result of early (not visible on external anatomy) osteoarthritis, especially in the older female chimpanzee, orangutan, and humans. Low mineralization density in association with early osteoarthritis has been reported in both weight-bearing and non-weight-bearing femoral head subchondral bone (Grynpas et al., 1991).

Absolute WMGLs

Differences in gray level ranges between specimens may reflect absolute differences in degree of mineralization associated with age (Bailey et al., 1999; Akkus et al., 2003) and species (Rowland...
et al., 1959). Results show absolutely low WMGLs in the young male chimpanzee (WMGL range = 100–160), and absolutely higher WMGLs in the older female chimpanzee and human sample (WMGL range = 150–185). The pattern in the two chimpanzees is consistent with the age-related increase in mineralization of bone tissue in humans, especially at advanced ages (Bailey et al., 1999; Akkus et al., 2003). The WMGL range (115–155) of the relatively old (38.5 years) orangutan is more similar to that of the young male chimpanzee than it is to the older chimpanzee and human sample, and may be due to early osteoarthritis (Grynpas et al., 1991).

However, little is known about inter-specific variation in bone mineralization and intraspecific variation within primate species. While data by Rowland et al. (1959) compare humans to other mammals, no such comparative data within a sample of primates exists. Therefore, further study will be required to examine inter-specific differences in bone mineralization and whether age-related changes (e.g., the onset of osteoarthritis) match the pattern observed in humans.

**Discussion**

The distributions of bone tissue gray levels in chimpanzee, orangutan, and modern human metacarpal heads differ from one another and broadly match biomechanical expectations.

Species variance: dorsal to palmar pattern

As hypothesized, the three species show different patterns. In both chimpanzee specimens, results provide strong support for the first hypothesis that relatively low WMGLs occur in the dorsal (‘knuckle-walking’) and palmar (‘climbing’) regions. Thus, it appears that the joint loads associated with knuckle-walking result in relatively low bone mineralization density, most likely due to elevated remodeling rates because this would reduce mean tissue age. It is much less likely that these variations are attributable to subtle histological, compositional, and/or crystallinity changes that could not be detected using the methods employed in this study.

The hypothesis that in chimpanzees the dorsal region would have lower WMGLs than the palmar region can be neither fully supported nor rejected. The prediction is upheld in the young male specimen but not the elderly female specimen. Various degrees of MP flexion are used by chimpanzees during climbing and suspension depending on body posture and support size and inclination; however, insufficient data are available to evaluate which hand postures are most common or involve the highest joint loads. The observation of significantly low WMGLs in the palmar metacarpal head regions of both chimpanzees is consistent with high loads in flexed MP joint postures associated with...
climbing and/or suspensory activities, and point to elevated remodeling rates in these regions. There may be variation among the metacarpals due to functional variation within the hand. For example, 7 year old chimpanzees experience higher pressures on digits 2 and 3 when knuckle-walking on the ground compared to knuckle-walking on a large branch (Wunderlich and Jungers, 2008). At present, little is known about primate hand postures and pressures during locomotion, how anatomical elements within the hand function during gait, as well as variation in internal skeletal structure.

The relatively low WMGLs in the distal and slightly palmar regions of the orangutan metacarpal head support the third hypothesis (tentatively, because only one specimen was available for sectioning). These regions of the metacarpal head are loaded during hook grip and power grip postures used in suspension and climbing, and the results suggest that these regions are less highly mineralized and likely more recently remodeled than the dorsal regions in Pongo. Orangutans do not knuckle-walk and rarely use extended MP joints during locomotion and therefore do not typically experience high strains in the dorsal regions of their metacarpal heads. Thus, these results help support the hypothesis that the lower mineralization density in the dorsal regions seen in the chimpanzee, and lacking in the orangutan, result from specific locomotor strains. Future work will be needed to confirm the results found here in the small samples available for the great apes.

The lack of significant regional WMGL variation in the human metacarpal heads contradicts expectations that distal-palmar regions involved in power and precision grips would show decreased gray values. However, the human metacarpal is not used in locomotor functions and therefore it is not surprising to see that no single region is statistically more or less mineralized than any other region, as reflected in gray levels. The human sample is comprised of elderly individuals that may, on average, have used their hands in less biomechanically-challenging ways than a sample of younger adults. However, several of the individuals sampled were robust, well-muscled individuals, suggesting that inactivity is unlikely to explain the gray level distribution pattern in the human metacarpal heads. Rather, the more likely explanation is that the non-locomotor MP joint loads within the modern human hand do not result in the regional patterning of remodeling and mineral turnover suggested by the mineral density variation within the ape hands.

Comparisons of grayscale values show that subchondral bone is slightly but significantly less highly mineralized, and likely underwent more recent remodeling, compared to the trabecular regions. This is true for both chimpanzees as well as the orangutan.
Although the pattern in the human sample is consistent with our hypothesis, results are not significant. These results support the hypothesis that bone nearer to the joint reaction force maintains lower gray levels and is therefore less mineralized than deeper trabecular struts. This suggests that subchondral bone tissue may be more sensitive to variation in joint loading than bone tissue deeper within the joint, and that bone tissue closer to the joint surface will provide more information about joint loading (in non-ostearthritic metacarpal heads), an association that has been confirmed with experimental (Polk et al., 2008) and comparative (Carlson and Patel, 2006; Patel and Carlson, 2007; Nowak et al., 2010) research.

This study offers a micro-architectural approach for studying trabecular bone mineralization in human and nonhuman primates, and points to a broad range of research questions that deserve further attention, from experimental studies of the relationship between joint loading and bone remodeling including variation in bone remodeling response within a joint and throughout ontogeny, to basic research on hand posture and pressure in primates.

Conclusions

Our preliminary data suggest that there is a strong correlation between bone tissue mineralization and functional loading history. Variation in the relative mineralization density of trabecular and subchondral bone may therefore preserve information about stress due to loading. Bone mineralization density variation is detectable through gray level analysis of BSE-SEM images.

The chimpanzee metacarpal has lower mineral density, and likely experienced more recent remodeling, in the palmar and especially dorsal regions of the joint subjected to joint reaction forces during climbing and knuckle-walking, respectively. In contrast, the orangutan metacarpal has lower mineral density, and likely experienced more recent remodeling, in the distal-to-palmar regions as opposed to the dorsal regions. This is consistent with loads that would occur with neutral and slightly flexed MP joint postures (e.g., hook grip) during habitual climbing and suspension. The human metacarpal has slightly lower mineralization in the dorsal-most regions, but the variation among regions is not significant, indicating that mineral density and potentially remodeling rates are broadly similar throughout the human metacarpal heads. The relatively homogeneous distribution of mineral density is consistent with the decreased remodeling rates that occur at advanced ages in humans and with the possibility of relatively low (non-locomotor) mechanical loads in this population.

Remodeling processes provide information about habitual biomechanical function in bones and offer a new avenue for investigating musculoskeletal biomechanics. By better defining joint loading patterns involved in various locomotor and potentially manual manipulation activities, we may reach a better understanding of the relationship between joint loading history and trabecular bone structure. This, in turn, might allow us to make more detailed inferences about joint function and functional adaptations in fossils.

Acknowledgements

We thank Scott Whitaker, Amelia Logan, and Ed Vicenzi for assistance in SEM data collection and permission to use the SEM facilities at the Smithsonian Institution’s National Museum of Natural History. We are grateful to Tim Gooding of the NMNH’s Mineral Sciences Department for aiding in sample preparation. We thank Mary Marzke and Caley Orr of Arizona State University for donating the Pongo specimen. Thanks also to Nicole Griffin and Matt Skinner for helpful discussions and assistance, and to Tim Bromage, the anonymous reviewers, the Associate Editor, Susan Antón, Liza Shapiro, and Shannon McFarlin for constructive comments and suggestions on an earlier version of this manuscript. This research was supported in part by an Undergraduate Research Internship to AZ funded by NSF–IGERT grant DGE-9587590, and NSF BCS-0521835 to BR.

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