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1 **Metacarpal trabecular bone varies with distinct hand-positions used in**  
2 **hominid locomotion.**

3 Christopher J. Dunmore<sup>1\*</sup>, Tracy L. Kivell<sup>1,2</sup>, Ameline Bardo<sup>1</sup>, Matthew M. Skinner<sup>1,2</sup>

4  
5 1 - Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, UK

6 2 - Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

7 \* Corresponding author  
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30 **Abstract**

31 Trabecular bone remodels during life in response to loading and thus should, at least in part, reflect  
32 potential variation in the magnitude, frequency and direction of joint loading across different  
33 hominid species. Here we analyse the trabecular structure across all non-pollical metacarpal distal  
34 heads (Mc2-5) in extant great apes, expanding on previous volume of interest and whole-epiphysis  
35 analyses that have largely focussed on only the first or third metacarpal. Specifically, we employ  
36 both a univariate statistical mapping and a multivariate approach to test for both inter-ray and  
37 interspecific differences in relative trabecular bone volume fraction (RBV/TV) and degree of  
38 anisotropy (DA) in Mc2-5 subchondral trabecular bone. Results demonstrate that while DA values  
39 only separate *Pongo* from African apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*), RBV/TV  
40 distribution varies with the predicted loading of the metacarpophalangeal (McP) joints during  
41 locomotor behaviours in each species. *Gorilla* exhibits a relatively dorsal distribution of RBV/TV  
42 consistent with habitual hyper-extension of the MCP joints during knuckle-walking, whereas *Pongo*  
43 has a palmar distribution consistent with flexed MCP joints used to grasp arboreal substrates. Both  
44 *Pan* species possess a disto-dorsal distribution of RBV/TV, compatible with multiple hand postures  
45 associated with a more varied locomotor regime. Further inter-ray comparisons reveal RBV/TV  
46 patterns consistent with varied knuckle-walking postures in *Pan* species in contrast to higher RBV/TV  
47 values toward the midline of the hand in Mc2 and Mc5 of *Gorilla*, consistent with habitual palm-back  
48 knuckle-walking. These patterns of trabecular bone distribution and structure reflect different  
49 behavioural signals that could be useful for determining the behaviours of fossil hominins.

50 Keywords: Metacarpal, Trabeculae, Hominid, Locomotion

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64 **Introduction**

65 Trabecular, or cancellous, bone has been experimentally shown to remodel (Cowin, 1986; Frost,  
66 1987) in response to loading across a range of phylogenetically disparate taxa (Biewener et al., 1996;  
67 Pontzer et al., 2006; Barak et al., 2011). Therefore trabecular architecture can provide additional  
68 information about how a bone was loaded during life, compared to external morphology alone (Ruff  
69 and Runestad, 1992; Tsegai et al., 2013). The term ‘remodeling’ is used here, rather than ‘modeling’,  
70 as it occurs throughout life and is therefore key to a bone’s “ability to function in a changing  
71 mechanical environment” (Martin et al., 1998 pp. 96; see Allen and Burr, 2014). When trabeculae  
72 are preserved in fossil hominins they have been used to infer habitual loading and reconstruct both  
73 locomotor (DeSilva and Devlin, 2012; Barak et al. 2013; Su et al., 2013; Zeininger et al., 2016; Ryan et  
74 al., 2018) and manipulative (Skinner et al., 2015, Stephens et al., 2018) behaviours during human  
75 evolution. These functional inferences rely on comparative analyses that associate known  
76 behaviours of extant primates with variation in trabecular architecture at particular joints (Orr,  
77 2016).

78 The hand makes direct contact with the substrate during non-human primate locomotion and  
79 therefore its trabecular structure may provide a clearer functional signal than skeletal elements that  
80 are further removed from substrate reaction forces, such as the humerus (Ryan and Walker 2010;  
81 Scherf et al., 2016). Indeed, previous studies of the internal bone structure of hand bones have  
82 found substantial differences between primate species with distinct habitual locomotor modes  
83 (Zeininger et al., 2011; Lazenby et al., 2011; Tsegai et al., 2013; Skinner et al., 2015; Matarazzo, 2015;  
84 Stephens et al., 2016; Chirchir et al., 2017; Barak et al., 2017). The majority of these studies have  
85 investigated trabecular bone structure in the third metacarpal (Mc3) head because the central ray is  
86 buffered from mediolateral forces, is consistently involved in weight bearing during locomotion, and  
87 often experiences peak reaction forces in ape locomotion (Zeininger et al., 2011; Tsegai et al., 2013;  
88 Matarazzo, 2015; Chirchir et al., 2017; Barak et al., 2017).

89 Different methodological approaches to the analysis of trabecular structure in the primate Mc3 head  
90 have yielded varied results. Tsegai et al., (2013) applied a whole-epiphysis approach and found that  
91 African apes had higher trabecular bone volume fraction (BV/TV) and degree of anisotropy (DA) than  
92 suspensory hominoids, especially in the dorsal region of the Mc3 head, consistent with an extended  
93 metacarpophalangeal (McP) joint during knuckle-walking. Suspensory orangutans and hylobatids  
94 were found to have more isotropic trabeculae and lower overall BV/TV that was highest in the  
95 palmar aspect of the Mc3, consistent with flexed-finger arboreal grips. Using fewer volumes of  
96 interest (VOI) Chirchir et al., (2017) found that there were no significant differences in DA across a  
97 sample of chimpanzees, orangutans, baboons and humans, but that BV/TV was significantly higher in  
98 distal and palmar portions of the Mc3 head in orangutans and, to a lesser extent in humans,  
99 consistent with flexed-finger grips used during arboreal locomotion and manipulation, respectively.  
100 In contrast, Barak et al., (2017), using a similar method, found the dorsal VOI in both chimpanzees  
101 and humans had significantly lower BV/TV and DA than the distal or palmar VOIs. Despite these  
102 conflicting results, these studies uniformly found that humans possessed significantly less BV/TV  
103 throughout the Mc3 head relative to other primate species (Tsegai et al., 2013; Barak et al., 2017,  
104 Chirchir et al., 2017). This finding is consistent with other skeletal elements (Chirchir et al., 2015;  
105 Ryan and Shaw, 2015) and may reflect, at least in part, lower loading of the hand during  
106 manipulation compared with that of locomotion (Tsegai et al., 2013), or sedentism in recent human  
107 populations, or both (Ryan and Shaw, 2015).

108 Although the whole-epiphysis approach has found a relationship between variation in metacarpal  
109 trabecular structure and hand use (Tsegai et al., 2013), this approach has been limited to  
110 comparisons of average trabecular parameters (Tsegai et al., 2013; Skinner et al., 2015; Stephens et  
111 al., 2016) or sections thereof (Georgiou et al., 2018). Recently some researchers have called for  
112 (Chirchir et al., 2017), or developed (Sylvester and Terhune, 2017), new methods that can better  
113 quantify and statistically compare trabecular structure across different individuals and species. Here,  
114 we build on this previous work by analysing trabecular structure across all of the non-pollical  
115 metacarpal heads (Mc2-Mc5) and applying a geometric morphometric, statistical mapping method  
116 to trabecular bone data produced by the whole-epiphysis approach. We compare relative trabecular  
117 bone volume fraction (RBV/TV) and degree of anisotropy (DA) between Mc2-5 both within and  
118 across the following species: bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes verus*), gorillas  
119 (*Gorilla gorilla gorilla*) and orangutans (*Pongo abelii* and *Pongo pygmaeus*). RBV/TV values are BV/TV  
120 values divided by the average BV/TV of each metacarpal head (see methods). This approach allows  
121 for the quantification of trabecular architecture in a heuristic sample, less affected by issues of sub-  
122 sampling of a continuous structure, to infer differences in habitual hand loading and posture  
123 associated with hominid locomotor modes.

#### 124 ***Hand use and locomotion***

125 Hand postures vary greatly during different types of arboreal and terrestrial locomotion in apes  
126 (Hunt et al., 1996; Schmitt et al., 2016). However, detailed studies of hominid hand postures in the  
127 wild (Hunt, 1991; Neufuss et al., 2017; Thompson et al., 2018) and captive settings (Wunderlich and  
128 Jungers 2009; Matarazzo, 2013; Samuel et al., 2018) can inform predictions of frequent McP joint  
129 positions and loading across the hand in different species. While frequent McP joint postures may  
130 only reflect part of a large and varied locomotor repertoire, previous research suggests (Tsegai et al.,  
131 2013; Chirchir et al., 2017; Barak et al., 2017) that subchondral trabecular patterns of the metacarpal  
132 head can be statistically discerned among species with different locomotor modes.

#### 133 *Pongo*

134 *P. pygmaeus* and *P. abelii* are primarily arboreal, engaging in suspensory locomotion to move  
135 through the canopy via tree branches and lianas (Cant 1987; Sugardjito and Cant, 1994; Thorpe and  
136 Crompton 2005). Specifically, researchers have emphasized the use of multiple supports and  
137 quadrumanous orthograde locomotion in *Pongo* (Thorpe and Crompton, 2006; Manduell et al.,  
138 2011), though specific hand grips have not been reported in detail (Thorpe and Crompton 2005).  
139 However, during suspension orangutans are thought to employ a hook-grip, in which the proximal  
140 phalanges align with the proximo-distal axis of the metacarpal, such that the distal McP joint is  
141 thought to be loaded in tension (Sarmiento, 1988; Rose, 1988; Schmitt et al., 2016; Fig 1a.). Similarly  
142 a double-locked grip, in which all joints of the ray, including the McP, are greatly flexed around a  
143 small substrate, is also adopted in orangutan locomotion (Napier, 1960; Rose, 1988; Fig 1b.).

144 The McP joints in *Pongo* possess a limited degree of possible hyper-extension at 19 degrees  
145 (Susman, 1979; Rose, 1988). Mc2-4 are also dorso-palmarly thicker at the diaphysis, and all the non-  
146 pollical metacarpal heads possess palmarly wide articular heads suggestive of habitual McP flexion  
147 (Susman, 1979). As the fourth proximal phalanx may often equal or exceed the length of the third  
148 phalanx in orangutans (40%; Susman, 1979), Rose (1988) has argued that the fourth ray is more in  
149 line with the second and third rays, which would be advantageous for both hook and double-locked

150 grips in which rays 2-5 are typically all engaged. While body size in *Pongo* is sexually dimorphic  
151 (Rodman, 1984) and there is some evidence for differential locomotion between the sexes  
152 (Sugardjito and van Hooff, 1986), further work has found these differences to be relatively slight  
153 (Thorpe and Crompton, 2005). Therefore we do not expect habitual prehensile postures to differ  
154 between male and female *Pongo*.

#### 155 *Gorilla*

156 The most frequent locomotor mode of *Gorilla* is terrestrial knuckle-walking (Inouye, 1994; Doran,  
157 1996; Remis, 1998), however they can vary substantially in their degree of arboreality based on the  
158 species, sex and local ecology (Doran, 1996; Remis, 1998; Neufuss et al., 2017). The western lowland  
159 gorilla (*Gorilla gorilla gorilla*) is reported to probably spend at least 20% of its time in trees (Tuttle  
160 and Watts, 1985; Remis, 1998). During knuckle-walking, the McP joint is hyper-extended to place the  
161 arm above the weight-bearing intermediate phalanges (Tuttle, 1969; Matarazzo 2013; Fig. 1c).  
162 *Gorilla* usually uses a 'palm-back' hand posture during knuckle-walking, which places the McP  
163 orthogonal to the direction of travel while consistently loading rays 2-5, that differs from the more  
164 variable hand postures, as well as digit loading, found in *Pan* and probably reflects the relatively  
165 longer fifth digit of *Gorilla* (Tuttle, 1969; Susman, 1979; Inouye, 1992; 1994; Wunderlich and Jungers,  
166 2009; Matarazzo, 2013; but see Thompson et al., 2018). In a study of digit pressures during knuckle-  
167 walking in captive gorilla, Matarazzo (2013) found that the fifth digit always touches down first with  
168 weight moving radially until the second (61%) or third (39%) digit lifts off. Peak pressures were  
169 significantly lower on the fifth digit and highest on the third, but overall gorilla maintained a more  
170 even distribution of pressure across rays 2-5 than that of captive chimpanzees.

171 Compared to terrestrial knuckle-walking, far less is known about hand postures used by gorillas  
172 during arboreal locomotion. In captivity, *Gorilla* is described as using a power grip with little McP  
173 flexion when vertically climbing large-diameter substrates (Sarmiento, 1994). Neufuss et al., (2017)  
174 also described a similar type of power grip using all five digits and the palm in wild mountain gorillas  
175 (*Gorilla beringei*) when climbing larger substrates. However, when climbing medium-sized substrates  
176 (6-10 cm diameter), mountain gorillas used a diagonal power grip, in which the substrate lies  
177 diagonally across the fingers and palm, with an extremely ulnarly-deviated wrist posture (Neufuss et  
178 al., 2017; Fig. 1d). In this diagonal power grip, weight appeared to be frequently borne by digits 2-4  
179 while the fifth McP joint was unable to flex to the same extent due to the irregular shape of some  
180 substrates. Although similar data on arboreal hand postures is not available for *G. gorilla*, we assume  
181 that during arboreal locomotion, the *G. gorilla* McP joints are moderately flexed, and that this  
182 flexion increases as the substrate diameter decreases, with potentially less flexion at the fifth McP  
183 joint. However, this arboreal McP posture is likely less frequent than that associated with knuckle-  
184 walking in *Gorilla*. Indeed, while female individuals are more arboreal than larger males in *Gorilla*  
185 (Remis, 1995), the primary locomotor mode for both sexes is knuckle-walking (Tuttle and Watts,  
186 1985; Remis, 1995; Crompton et al., 2010).

#### 187 *Pan troglodytes*

188 Generally *P. troglodytes* is thought to be more arboreal than *Gorilla* (Remis, 1995; Doran, 1996;  
189 Thorpe and Crompton, 2006) though this may be the result of comparisons to mountain gorillas that  
190 are better habituated to humans than their more arboreal lowland counterparts (Doran 1997; Hunt  
191 2004, Neufuss et al., 2017). There is a large degree of variation in the chimpanzee locomotor

192 repertoire depending on the local ecology (Doran and Hunt 1994; Carlson et al., 2006). *Pan*  
193 *troglydytes verus* engages in knuckle-walking, both arboreal and terrestrial, in ~85% of their  
194 locomotion and spend more time in the trees than *P. troglodytes schweinfurthii* (Doran and Hunt,  
195 1994; Carlson et al., 2006). Compared with *Gorilla*, *P. troglodytes* uses more varied hand postures  
196 during knuckle-walking (Tuttle, 1969; Inouye, 1994; Matarazzo, 2013). Chimpanzees have been  
197 thought to primarily load digits 3 and 4 during knuckle walking (Tuttle, 1969; Tuttle and Basmajian,  
198 1978). Inouye (1994) found that during captive terrestrial knuckle-walking, larger chimpanzees used  
199 their second digit significantly less often than gorillas of equivalent size and both chimpanzees and  
200 bonobos generally used their fifth digit significantly less often than gorillas. Pressure studies also  
201 found that the fifth digit of chimpanzees did not touch-down in 20% of knuckle-walking steps and  
202 that this digit experienced significantly less load than the other digits when it was used (Wunderlich  
203 and Jungers, 2009; Matarazzo, 2013). Further, *P. troglodytes* uses both 'palm-back' (~40%) and  
204 'palm-in' (~60%) postures, compared with a more consistent use of mainly 'palm-back' (~86%)  
205 knuckle-walking postures in *Gorilla* (Wunderlich and Jungers, 2009; Matarazzo, 2013). During 'palm-  
206 in' knuckle-walking the intermediate phalanges roll radially in the direction of travel and the second  
207 or third digit usually experiences the highest pressures (Wunderlich and Jungers, 2009; Matarazzo,  
208 2013). In 'palm-back' knuckle-walking the third digit is typically placed in front the others and usually  
209 is the last to touch off, which may be related to the fact that the third ray may be relatively longer in  
210 chimpanzees than in gorillas (Matarazzo, 2013; 2013b). Compared to *Gorilla*, the peak pressures  
211 experienced by digits 2-4 are more variable in chimpanzees (Wunderlich and Jungers, 2009;  
212 Matarazzo, 2013).

213 *P. troglodytes verus* most often uses climbing and scrambling locomotion in trees (60-77%, Doran,  
214 1992; 1993). Chimpanzees are described as using power grips, diagonal power grips and hook grips  
215 during arboreal locomotion, all of which typically involve some degree of flexion at the MCP joint  
216 (Alexander, 1994; Hunt, 1991; Marzke et al., 1992; Marzke and Wullstein, 1996; Napier, 1960).  
217 Climbing often encompasses vertical climbing and clambering in naturalistic studies. Hunt (1991) has  
218 emphasized the role of vertical climbing in wild *P. troglodytes* and while the grips employed tend to  
219 be ulnarly deviated at the wrist, they are dependent on substrate diameter. Neufuss et al., (2017)  
220 also found that chimpanzees used both power grips and diagonal power grips, but with a less ulnarly  
221 deviated wrist than in *Gorilla*. A diagonal power grip involves greater flexion of the more ulnar rays  
222 and in some cases flexion at the fifth carpometacarpal joint, which may likely be associated with  
223 wrist adduction (Marzke and Wullstein, 1996; Fig. 1d). Therefore the locomotor hand postures of *P.*  
224 *troglydytes verus* may be characterised as primarily those of knuckle-walking but with a more  
225 frequent arboreal grasping component than in *Gorilla*. Given the lower sexual dimorphism relative to  
226 *Gorilla* and *Pongo* (Doran, 1996), there may be less variation in grasping postures in this species.

#### 227 *Pan paniscus*

228 While bonobos have a relatively similar locomotor repertoire to chimpanzees, they are thought to  
229 be more arboreal (Alison and Badrian, 1977; Susman et al., 1980; Susman, 1984) and have been  
230 shown to use significantly more palmigrady in the trees (Doran, 1993; Doran and Hunt, 1994;  
231 Crompton et al., 2010). Though, the former claim may be an artefact of incomplete habituation of  
232 the individuals in these studies and more data is needed (Hunt, 2016), the relatively longer and  
233 heavier lower limbs of this species make for more generalised anatomy than that of chimpanzees  
234 (Zihlman, 1984; D'Août et al., 2004). During terrestrial knuckle-walking bonobos use the fifth digit

235 even less than chimpanzees and Mc5 is shorter than the rest of the metacarpals in bonobos (Inouye,  
236 1994). In a pressure study of arboreal locomotion, Samuel et al., (2018) found that captive bonobos  
237 used 'palm-back' (64%) or 'palm-in' (36%) knuckle-walking hand postures and that peak pressure  
238 was experienced by or around the third digit. However, unlike chimpanzees (Wunderlich and  
239 Jungers, 2009), they did not roll radially across their digits and the fifth digit always made contact  
240 with the substrate (Samuel et al., 2018). During vertical climbing and suspensory postures, bonobos  
241 used flexed-finger power grips similar to those described in other great apes and again peak  
242 pressure was experienced by or around the third digit (Samuel et al., 2018). In summary, the hand  
243 postures used during locomotion in *P. paniscus* can be characterised as similar to those of *P.*  
244 *troglydytes*, including a relatively low level of sexual dimorphism compared to other great apes  
245 (Doran, 1996), although more frequent palmigrady and arboreal grasping differentiate this species  
246 from *P. troglodytes*.

### 247 **Predictions**

248 Based on the summary above, we predict RBV/TV and DA in *Pongo* will be significantly higher in the  
249 disto-palmar region of the metacarpal heads compared to other hominids and no significant inter-  
250 ray differences in both measures due to the more consistent recruitment of rays 2-5 during hook  
251 and double-locked grasping. In *Gorilla* we predict a significantly higher dorsal distribution of RBV/TV  
252 and DA in each metacarpal head compared with all other hominids, reflecting McP joints frequently  
253 loaded in a hyper-extended posture during knuckle-walking. As *P. troglodytes* may be more arboreal  
254 and uses more variable knuckle-walking postures, we predict this species will have significantly  
255 lower dorsal RBV/TV and DA, with more significant differences across rays, than that of *Gorilla*. We  
256 also predict this mixture of arboreality and terrestriality in *P. troglodytes* will elicit higher dorsal  
257 RBV/TV and DA than *Pongo* but with a more homogeneous distribution within each metacarpal  
258 head. We predict *P. paniscus* trabecular patterning will be similar to that of *P. troglodytes*, and thus  
259 possess significantly higher palmar distribution of RBV/TV and DA compared to *Gorilla* and a more  
260 dorsal distribution of these measures than in *Pongo*. However, we also expect *P. paniscus* to have  
261 lower DA and further homogenised distribution of RBV/TV than *P. troglodytes* due to more frequent  
262 use of palmigrady and arboreal grips.

### 263 **Materials**

264 Subchondral trabecular bone was analysed in the metacarpus of *Pan paniscus* ( $n=10$ ), *Pan*  
265 *troglydytes verus* ( $n=12$ ), *Gorilla gorilla gorilla* ( $n=12$ ), *Pongo* sp. indet. ( $n=2$ ), *Pongo pygmaeus* ( $n=7$ )  
266 and *Pongo abelii* ( $n=3$ ). Metacarpi were sampled from the Royal Museum for Central Africa,  
267 Tervuren, the Max Planck Institute for Evolutionary Anthropology, Leipzig, the Powell-Cotton  
268 Museum, Birchington, Bavarian State Collection of Zoology, Munich, the Natural History Museum,  
269 Berlin, the Senckenberg Natural History Museum, Frankfurt and the Smithsonian National Museum  
270 of Natural History, Washington D.C. (Table1). All specimens were adult, wild shot and free from  
271 external signs of pathology. Within each taxon the samples were sex balanced with even numbers of  
272 right and left metacarpi, apart from *Gorilla* in which there were 7 left and 5 right metacarpi, as well  
273 as 5 females and 7 males. While great ape locomotion is sexually biased (Doran, 1996) and there has  
274 been some evidence for lateralized asymmetry in both the trabecular (Stephens et al., 2016) and  
275 cortical bone of hominid metacarpals (Sarringhaus et al., 2005) we argue that neither of these



276 signals is greater than species locomotion differences under investigation here. Further, the use of  
277 evenly mixed samples should ameliorate these effects (see discussion).

## 278 **Methods**

### 279 *MicroCT Scanning*

280 Specimens were scanned with BIR ACTIS 225/300 and Diondo D3 high resolution microCT scanners  
281 at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology,  
282 Germany, as well as with the Nikon 225/XTH scanner at the Cambridge Biotomography Centre,  
283 University of Cambridge, UK. Scan parameters were 100-160kV and 100-140 $\mu$ A, using a brass or  
284 copper filter of 0.25-0.5mm, resulting in reconstructed images with an isometric voxel size of 24-  
285 45 $\mu$ m.

### 286 *Image processing*

287 Micro-CT scans of each metacarpal were isolated in Avizo 6.3 (Visualization Sciences Group; Fig. 2a)  
288 and segmented using the Ray Casting Algorithm (Scherf and Tilgner, 2009). The segmented volume  
289 images were then processed as per the whole-epiphysis method, outlined in Gross et al., (2014).  
290 Briefly, a series of filters run in medtool 4.2 (Dr. Pahr Ingenieure e.U.) isolated the inner trabecular  
291 structure (Fig. 2b) by casting rays at different angles from the outer cortical shell and terminating  
292 them on contact with background, non-bone, voxels. A spherical kernel, with a diameter equal to the  
293 measured average trabecular thickness in that bone, was then used to close this inner structure  
294 (Pahr & Zysset, 2009). The 3D edge of this solid inner structure defined the boundary between  
295 subchondral trabecular and cortical bone. Subsequently, a regular 3D background grid, spaced at  
296 2.5mm intervals, was overlaid and a spherical VOI 5 mm in diameter was centred at each vertex of  
297 the grid in which BV/TV and DA was measured (Fig. 2c). Previous studies have shown that these two  
298 variables are correlated with the mechanical properties of trabecular bone, reflect bone functional  
299 adaptation (Odgaard et al., 1997; Uchiyama et al., 1999; Pontzer et al., 2006; Barak et al., 2011;  
300 Lambers et al., 2013; 2013b) and that they are not strongly allometric (Doube et al., 2011; Barak et  
301 al., 2013b; Ryan and Shaw, 2013). DA was measured via the mean intercept length (MIL) method and  
302 was bounded between 0, total isotropy, and 1, total anisotropy, using the calculation:  $1 - (\text{lowest}$   
303  $\text{eigenvalue of the fabric tensor} / \text{greatest eigenvalue fabric tensor})$ . Both trabecular values were then  
304 separately interpolated on a regular 3D tetrahedral mesh of the trabecular model (Fig. 2d), created  
305 using CGAL ([www.cgal.org](http://www.cgal.org)). The surface of the trabecular mesh was extracted using Paraview  
306 ([www.paraview.org](http://www.paraview.org)) and it was smoothed, to permit landmark sliding (see below), in Meshlab  
307 (Cignoni et al., 2008) via a screened Poisson surface reconstruction filter (Kazhdan and Hoppe, 2013;  
308 Fig. 2e). For left hand bones this surface mesh was mirrored in Meshlab so that it was oriented in the  
309 same manner as those from right hands to permit homologous functional comparisons.

### 310 *Geometric morphometric mapping*

311 While the whole-epiphysis method maps the entire volumetric trabecular model, we focus our  
312 analysis on the trabecular bone beneath the articular surface of the metacarpal heads because  
313 external loads necessarily pass through these subchondral trabeculae before they can be  
314 transmitted to any other part of the trabecular structure (Zhou et al., 2014, Sylvester and Terhune,  
315 2017). We employ a 3D geometric morphometric (GM) approach (Gunz and Mitteroecker, 2013) to

316 trabecular analysis similar to that of Sylvester and Terhune (2017) and test for significant differences  
317 between groups using homologous landmarks on the subchondral trabecular surface.

#### 318 *Anatomical Landmark definitions*

319 Many landmarks have been identified on the non-pollical metacarpals for morphometric studies  
320 (Susman, 1979; Inouye, 1992; Drapeau, 2015) but there have been relatively few studies that have  
321 applied GM methods to the primate metacarpus and these have focussed on the Mc1 base  
322 (Niewoehner, 2005; Marchi et al., 2017). Metatarsals are developmental serial homologues of  
323 metacarpals (Rolian et al., 2010) and a relatively recent study captured their shape variation using a  
324 patch of 3D landmarks (Fernández et al., 2015). A recent study of Mc3 head shape used most of the  
325 same landmarks that bordered this metatarsal patch, at the homologous metacarpal locations (Rein,  
326 2018). Based on these studies, the location and type (Bookstein, 1991) of anatomical landmarks used  
327 here are given in Table 2. Although the internal trabecular subchondral surface is landmarked,  
328 cortical bone is very thin at the metacarpal head in hominids (Tsegai et al., 2017) and so the  
329 correspondence between these surfaces is generally high. Though the articular surface may not  
330 reach the same extent in all species studied, the same landmarks are used for comparison as they  
331 are present on all metacarpal heads studied.

#### 332 *Repeatability*

333 Landmarks were manually placed in Checkpoint (Stratovan Corporation, Davis, CA) and repeated ten  
334 times on three randomly selected specimens from each species over several days. A different ray  
335 was used from each species to ensure landmarks were repeatable across elements following  
336 Fernández et al., (2015). The landmarks were then aligned using Procrustes superimposition in the  
337 Morpho package in Rv3.3.0 (Schlager, 2017; R Development Core team, 2016). Landmark  
338 configurations were then plotted in the first two principal components (PC) of shape space.  
339 Landmarks were considered stable if repeated measures were more clustered than those of  
340 different individuals. Significant pair-wise permutational MANOVAs conducted on PC1 and PC2  
341 scores demonstrated that group means, the three individuals and their repeats, are significantly  
342 different in each case and that variance in landmark placement is significantly less than that  
343 between specimens (Supp. Fig.1).

#### 344 *Geometric morphometric procedure*

345 To create the landmark template a random specimen was selected and eight curves were defined at  
346 the margins of the sub-articular surface, in Checkpoint (Stratovan Corporation, Davis, CA ), each  
347 bordered by anatomical landmarks as recommended by Gunz et al. (2005). Three sliding semi-  
348 landmarks were placed on each of these curves and an additional 140 were equally distributed over  
349 the sub-articular surface in Avizo 6.3 (Visualization Sciences Group, Germany) to create a 173  
350 landmark template. The anatomical landmarks were subsequently placed on every specimen and  
351 then the landmark template (Fig. 2f) was projected onto each of the 183 other metacarpal heads  
352 and relaxed onto the surface of each metacarpal using the Morpho package in R (Schlager, 2017) by  
353 minimising bending energy. This package was then used to slide the semi-landmarks along their  
354 respective curves and over the surface by minimising Procrustes distances. This slid template is  
355 plotted on an individual Mc3 from each species to provide a sense of the shape variation present  
356 (Supp. Fig.6.).

357 *Data mapping*

358 Using a custom Python script plugin for Paraview ([www.paraview.org](http://www.paraview.org)) the non-smoothed surface  
359 mesh triangles inherited trabecular values from their originating tetrahedra. The Python module  
360 SciPy (Jones et al., 2001) was then used in medtool 4.2 (Dr. Pahr Ingenieure e.U.) to interpolate the  
361 trabecular values to the nearest landmark; this was done separately for BV/TV and DA. Interpolating  
362 these trabecular values from the outer tetrahedra of the trabecular model is analogous to using  
363 spherical VOIs, 1 mm in diameter, centred 0.5 mm beneath an inner trabecular surface landmark.  
364 Finally the geomorph package (Adams et al., 2017) in R was used to perform a generalised  
365 Procrustes procedure, resulting in 184 sets of 173 homologous landmarks each with two associated  
366 trabecular values (Fig. 2g).

367 *Relative trabecular volume*

368 We employ a relative measure of bone volume fraction (RBV/TV), in which the raw BV/TV value of  
369 each landmark is divided by the mean of all landmark BV/TV values on that metacarpal head. Thus  
370 RBV/TV values  $\sim 1$  indicate landmarks close to the average BV/TV of that Mc head, while values  
371 above or below 1 indicate a deviation from this average at these landmarks. This relative measure  
372 was preferred because, while BV/TV can vary systemically across extant hominid species (Tsegai et  
373 al., 2018) and may show considerable intraspecific variation, the relative patterns of trabecular  
374 architecture appear to preserve a functional signal superimposed on this variation (Saers et al.,  
375 2016). RBV/TV measures the position of the greatest subchondral trabecular bone of a given Mc  
376 head rather the absolute volume of bone and therefore is argued to reflect the habitually loaded  
377 joint positions of extant hominids while controlling, at least in part, for intra-species and systemic  
378 inter-species differences. Species average absolute BV/TV landmark values are depicted for  
379 comparison with RBV/TV values in Figure 3 (see supporting information).

380

381 *Statistical analysis*

382 We employ a 'mass-univariate' approach as advocated by Friston et al., (1995) similar to that used to  
383 statistically analyse cortical bone in ape metacarpals (Tsegai et al., 2017). Specifically, the trabecular  
384 values between species and rays at each landmark are independently analysed using univariate  
385 statistics. Inter-ray comparisons do not include comparisons between rays two and four or between  
386 rays three and five as they are not biologically contiguous and thus are less informative when  
387 prehensile hand postures are considered. However, comparisons of rays two and five are included to  
388 test for significant differences between the most ulnar and radial aspects of the metacarpus.  
389 Shapiro-Wilk tests found a non-normal distribution of data at one or more landmarks in one or both  
390 groups in every pair-wise, inter-ray and interspecific, comparison. To maintain consistent  
391 comparisons a non-parametric Kruskal-Wallis was applied at each landmark and a post-hoc test was  
392 used to test for pair-wise differences if the omnibus test was significant. Dunn's test was chosen as it  
393 uses the pooled variance of the Kruskal-Wallis tests and so is conservative. The level of significance  
394 was set at  $p < 0.05$  subsequent to a Bonferroni correction in each case. This univariate approach  
395 means that homologous landmark values are compared across groups rather than with spatially  
396 correlated neighbouring landmarks. Z-scores were used to determine the polarity, as well as the  
397 effect size, of significant differences between groups. These Z-scores were transformed into  
398 absolute, rather than signed, values and summarised for significant landmark differences, in both

399 interspecific and inter-ray pairwise comparisons (Supp. Table 1 & 2). Resulting plots of significant  
400 univariate differences map regional differences between species and rays but were only considered  
401 meaningful if they were found at nine contiguous landmarks, as this represents just over 5% of the  
402 sub-articular surface, in order to further ameliorate any Type I error. Despite the fact this univariate  
403 method can identify where regions of significant difference lie it can be susceptible to Type I error  
404 and so to provide a multivariate corollary to this approach, a principle components analysis (PCA) of  
405 trabecular values, using landmarks as individual variables, was also run for all comparisons.  
406 Subsequent omnibus and pairwise one-way permutational MANOVAs were run with a Bonferroni  
407 correction, using the Vegan package (Oksanen et al., 2018) package in Rv3.3.0 (R Core Development  
408 team 2016), on the principal component scores of these PCAs to test for significant overall, rather  
409 than regional, differences in trabecular patterns.

## 410 **Results**

411

### 412 *Univariate landmark comparisons*

#### 413 *Pongo*

414 RBV/TV was highest in the palmar aspect of all metacarpal heads in *Pongo* (Fig. 3). The only  
415 significant differences among the rays were between Mc2 and Mc5, in which each had a small patch  
416 of significantly higher RBV/TV at the ulnar and radial aspects of the metacarpal head, respectively  
417 (Fig. 5). Interspecifically, *Pongo* RBV/TV was significantly higher at landmarks in the palmar region of  
418 the metacarpal heads than in *P. troglodytes* and especially *Gorilla* (Fig. 7). Compared with *P.*  
419 *paniscus*, *Pongo* was again significantly higher at more palmar landmarks in Mc4 and Mc5 but there  
420 were fewer significantly higher landmarks in Mc3 and almost none in the Mc2 comparison.

421 *Pongo* had high DA values throughout the sub-articular metacarpal heads with few significant  
422 differences between rays (Figs. 4, 6, Supp. Fig. 3). Interspecifically, *Pongo* DA was significantly  
423 greater than that of *Gorilla* in all metacarpal heads except for the central disto-palmar aspects of  
424 Mc3-4 and radio-palmar aspects of Mc5. *Pongo* had significantly higher DA on the disto-dorsal  
425 aspects of Mc2 and Mc5 as well the disto-radial aspect of Mc4 relative to both *P. troglodytes* and *P.*  
426 *paniscus*. *Pongo* also had higher DA at landmarks situated on the dorsal aspects of Mc 3 and 4  
427 relative to *P. paniscus* (Fig. 8).

#### 428 *Gorilla*

429 The highest RBV/TV values in *Gorilla* were concentrated in the disto-dorsal portion of each  
430 metacarpal head extending dorsally on the medio-lateral edges of Mc3 and 4 but toward the mid-  
431 line of the hand in the Mc2 and Mc5 heads (Fig.3). This latter pattern was clear in the inter-ray  
432 comparison, with significantly greater RBV/TV found at the radial aspect of Mc5 relative to Mc2 and  
433 Mc4 as well as on the ulnar aspect of these rays relative to Mc5 (Fig. 5). Interspecifically, *Gorilla* was  
434 significantly higher in RBV/TV dorsally compared to *Pongo*, though the radio-palmar aspect of Mc5  
435 was not significantly different between these groups. Compared with *Pan*, *Gorilla* generally had  
436 significantly higher RBV/TV dorsally but this was restricted to the medio-lateral edges of each  
437 metacarpal head in the regional comparison (Fig. 7). Specifically, *Gorilla* had significantly higher  
438 RBV/TV than *Pan* species on the radio-dorsal aspect of Mc5 and both medio-lateral edges of Mc4, as

439 well as the ulno-dorsal aspect of Mc2, though this is extended across the dorsal aspect in the *P.*  
440 *trogloodytes* comparison. The Mc3 of *Gorilla* was also had significantly higher RBV/TV than *P. paniscus*  
441 at landmarks on its dorso-ulnar aspect but was not significantly different from *P. troglodytes* in any  
442 region. *Gorilla* had less significant regional differences with *P. troglodytes* than with *P. paniscus* in  
443 RBV/TV.

444 *Gorilla* had low DA throughout the subchondral metacarpal head trabeculae with slightly higher  
445 values distally on Mc3 and Mc4, though only the ulnar-distal aspect of Mc3 had values that were  
446 significantly larger than Mc2 (Figs. 4 and 6). Mc5 had significantly higher DA on its radial side relative  
447 to Mc2 (Fig. 6). *Gorilla* was not significantly higher in DA than other taxa, apart from the radial  
448 border of the distal Mc5 head compared with *Pan* (Fig. 8).

#### 449 *Pan troglodytes*

450 *P. troglodytes* had disto-dorsally higher RBV/TV values in the subchondral trabeculae of all the  
451 metacarpal heads, though this pattern was more dorsally-positioned in Mc3 and Mc4 (Fig. 3). Mc2  
452 and Mc5 showed significantly higher RBV/TV at their most palmar extent relative to Mc3 and Mc4,  
453 respectively (Fig. 5). Interspecifically, *P. troglodytes* showed almost no significant differentiation  
454 from *P. paniscus* in RBV/TV in any ray, though landmarks on the disto-ulnar aspect of Mc3 were  
455 significantly higher (Fig. 7). *P. troglodytes* had significantly higher RBV/TV across the palmar extent of  
456 Mc2, and disto-palmarly on the ulnar aspect of Mc5 compared to that of *Gorilla*, and significantly  
457 higher RBV/TV dorsally than *Pongo* in each ray.

458 *P. troglodytes* generally had low DA through all of the metacarpal heads, although DA values were  
459 slighter higher in the palmar regions of Mc3 and Mc4 (Fig. 4). DA values were significantly higher in  
460 Mc4 relative to Mc5 and higher in Mc3 relative to Mc2 (Fig. 6). *P. troglodytes* showed the fewest  
461 significant differences in DA with *P. paniscus*, higher DA in the palmar aspects of Mc2 and Mc3  
462 compared with *Gorilla*, and significantly lower DA than *Pongo* throughout all the rays, except Mc3  
463 (Fig. 8).

#### 464 *Pan paniscus*

465 Like *P. troglodytes*, *P. paniscus* had the highest RBV/TV values at the disto-dorsal aspect of  
466 metacarpal heads but subchondral trabeculae structure was more homogenous within and between  
467 the rays (Figs. 3 and 5). Interspecifically, *P. paniscus* showed the fewest significant differences with  
468 *P. troglodytes* apart from a small concentration of higher RBV/TV landmarks in the most palmar  
469 extent of Mc3 (Fig. 7). *P. paniscus* possessed significantly higher RBV/TV dorsally than *Pongo* across  
470 the rays and significantly higher palmar RBV/TV in all of the rays than *Gorilla* and this pattern  
471 extended distally on Mc2 and Mc5 (Figs 3 and 7).

472 *P. paniscus* had a similar DA pattern to *P. troglodytes*, with similar inter-ray significant differences  
473 and almost no significant differences between these species (Figs. 4, 6 and 8). *P. paniscus* showed  
474 significantly higher DA than *Gorilla* in landmarks across the Mc2 and Mc3 heads, in the palmar  
475 regions (Fig. 8). As with all other African apes, *P. paniscus* had significantly lower DA than *Pongo*  
476 across the metacarpal heads, particularly in the dorsal regions.

477

#### 478 *Multivariate whole-surface comparisons*

479 *Interspecific results*

480 Figure 9 depicts the results of the PCA on RBV/TV values, showing species differences within each  
481 metacarpal head. Within the Mc2-5 of all the taxa, the first principal component (PC1) explains 38-  
482 46% variation in RBV/TV and was driven by dorsal and palmar landmarks. PC2 in Mc2-Mc5 described  
483 13-17% of the variation and reflected variation of values in landmarks that were distally and non-  
484 distally situated, respectively. In Mc5, PC3 described 14% of RBV/TV variation in values at radio-ulnar  
485 landmarks. Permutational MANOVA omnibus tests were run using PC1-3 in each case, as for some  
486 comparisons the PC2 and PC3 explained a similar amount of variance whereas further PCs each  
487 explained less than 10% of the variance. These omnibus tests were significant in every ray. As with  
488 the individual landmark comparisons described above, *Pongo* had significantly higher palmar RBV/TV  
489 compared to all other species, especially *Gorilla*. The overall configuration of *Gorilla* RBV/TV was  
490 significantly higher dorsally compared to all other species in Mc2-4 and radio-dorsally in Mc5 (Fig. 9,  
491 Table 3). *P. troglodytes* and *P. paniscus* were not significantly different from each other in any of the  
492 species comparisons (Table 3).

493 Following the limited interspecific differences in DA described above, a PCA of DA values yielded  
494 poor separation among the sampled taxa. As such, the results are depicted in the Supporting  
495 Information. PC1 in DA for each ray, across species, described 34-36% of the variation and was  
496 driven by higher values at most landmarks. PC2 described 10-14% of the variation and was driven by  
497 landmarks situated dorsally and disto-palmarly, respectively (Supp. Fig. 2). While *Pongo* tended to  
498 occupy the positive end of PC1, reflecting higher DA, permutational MANOVAs on PC1-3 revealed,  
499 they were only significantly different in every ray from *Gorilla*. This result may be partially driven by  
500 the larger intra-species variation in *Pongo* DA relative to other species studied (Supp. Fig. 2, see  
501 discussion). *Pongo* was significantly different from *P. paniscus* in Mc2, Mc4 and Mc5 as well as from  
502 *P. troglodytes* in Mc2 and Mc5 by having generally higher DA (Table 3). Again, *P. paniscus* and *P.*  
503 *troglodytes* were not significantly different from each other at any ray, though both species were  
504 slightly, but significantly, higher in DA than *Gorilla* in Mc2-4 and lower than *Gorilla* in the radio-distal  
505 aspect of Mc5.

506 *Inter-ray results*

507 Figure 10 depicts the results of PCA of RBV/TV values, showing inter-ray differences within each  
508 species. Overall Mc head variation in RBV/TV across rays was different for each species but generally  
509 consistent with individual landmark comparisons described above. In *Pongo*, PC1 explained 33% of  
510 the variation and was driven by dorso-palmar landmark values, while PC2 explained 16% of the  
511 variation and reflected radio-ulnar landmark RBV/TV. The significant omnibus result was driven  
512 solely by a Mc2 configuration that had significantly higher disto-ulnar RBV/TV than Mc4 and Mc5. In  
513 *Gorilla*, PC1 reflected 27% of the variation as a result of radio-ulnar landmark values, while PC2  
514 reflected 18% of the variation in RBV/TV due to distal and more dorso-palmarly located landmarks  
515 (Fig. 10). Permutational MANOVAs on PC1-3 demonstrated the *Gorilla* Mc5 had significantly higher  
516 RBV/TV disto-radially relative to all other rays. *Gorilla* Mc2 had significantly higher disto-ulnar  
517 RBV/TV than the other rays, whereas Mc3 and Mc4 had significantly higher RBV/TV dorsally than Mc2  
518 and Mc5 and were not significantly different from each other (Table 3). For *P. troglodytes* variation  
519 in overall RBV/TV was chiefly driven by dorso-palmar landmarks on PC1, which explained 31% of the  
520 variation, while PC2 explained 15% of the variation and reflected differences in the disto-ulnar  
521 landmarks. PC3 in *P. troglodytes* RBV/TV describes 12% of the variation and is driven by radio-ulnar

522 landmarks (Fig. 10). *P. troglodytes* Mc2 had significantly higher RBT/TV disto-palmarly on its ulnar  
523 aspect relative to all other rays whereas Mc5 had significantly higher RBV/TV disto-palmarly on its  
524 ulnar aspect compared to Mc2 and Mc3. While Mc3 and Mc4 were not significantly different from  
525 each other as both had higher dorsal RBV/TV, Mc4 was not significantly different from Mc5. In *Pan*  
526 *paniscus* PC1 explained 36% of the variance in RBV/TV and was driven by dorso-palmar landmarks  
527 while PC2 explained 25% of the variance and reflected distal and non-distal landmarks. However, no  
528 significant differences in RBV/TV were found between *P. paniscus* rays (Table3).

529 Variation in DA values did not show many significant differences across the Mc heads but was  
530 broadly consistent with the individual landmark comparisons. For all species sampled, PC1 was  
531 driven by higher values at most landmarks in PC1 and explained 19-41% of the variation. PC2  
532 described 10-14% of the variation in DA and reflected distal as opposed to non-distal landmarks in all  
533 species (Supp. Fig. 3). In *Pongo* no ray was significantly different from any other in overall  
534 configuration of DA values (Table3). In *Gorilla* PC3 explained 9% of the variance and was driven by  
535 radio-ulnar landmarks. Mc5 in *Gorilla* had significantly higher DA at radial landmarks than Mc2 and  
536 Mc3. The *Gorilla* Mc4 had slightly, but significantly, higher DA over most landmarks relative to Mc2.  
537 Both *P. troglodytes* and *P. paniscus* had significantly lower DA at landmarks on the distal aspect of  
538 Mc5 compared to Mc3 and Mc4. *P. paniscus* alone, also had significantly lower DA over most  
539 landmarks on Mc2 compared to Mc3.

## 540 **Discussion**

541

542 The aim of this study was to associate inferred loading during particular hand postures in great apes  
543 during locomotion with subchondral trabecular architecture across the non-pollical metacarpal  
544 heads. The results confirm and build upon previous studies of trabecular bone, most often focussed  
545 on only the Mc3 head (Tsegai et al., 2013; Barak et al., 2017; Chichir et al., 2017), demonstrating that  
546 not only is this association possible but that regional trabecular patterns within metacarpal heads,  
547 both within and across species, can be statistically discerned. Further, locomotor signals within  
548 trabecular structure are not limited to the Mc3 and analysis of all non-pollical metacarpals can  
549 provide greater insight into inter-ray and interspecific differences in digit loading.

### 550 *Relative trabecular bone volume fraction*

#### 551 *Pongo*

552 We predicted the orangutans would show significantly higher RBV/TV in the disto-palmar region of  
553 the metacarpal heads compared to other hominids and that there would be no significant  
554 differences between rays, reflecting the flexed or neutral McP joint posture of all the fingers that  
555 characterises flexed-finger power, hook and double-locked grips typically used during arboreal  
556 locomotion (Rose, 1988; Sarmiento, 1988). We found general support for these predictions.  
557 Orangutans demonstrated significantly higher RBV/TV in the disto-palmar aspect of the subchondral  
558 trabeculae in all non-pollical metacarpal heads compared to that of all other taxa. We also found few  
559 inter-ray differences, with orangutans generally showing fewer significantly different landmarks in  
560 RBV/TV compared with gorillas and chimps (Fig. 5) and no significant difference in overall RBV/TV  
561 between adjacent rays (Table 3). The only exception to this was Mc2 of orangutans, which had

562 significantly higher RBV/TV in the disto-dorsal region of its radial aspect, relative to the Mc4 and  
563 Mc5 (Figs. 5 and 10). Overall, our results are consistent with previous studies using differing  
564 methodologies that also found a higher BV/TV in the disto-palmar region of the orangutan Mc3 head  
565 (Zeininger et al., 2011; Tsegai et al., 2013; Skinner et al., 2015; Chirchir et al., 2017) and Mc5 head  
566 (Skinner et al. 2015). It should be noted, however, that present study sample includes five of the  
567 same Mc3 specimens and three of the Mc5 specimens used by Tsegai et al. (2013) and Skinner et al.  
568 (2015), respectively. The generally similar pattern of RBV/TV distribution across the Mc2-5 heads is  
569 consistent with using all of the fingers during power, hook and double-lock grips to grasp arboreal  
570 substrates (Rose, 1988). The diverging pattern found in the orangutan Mc2 could reflect the  
571 relatively more extended second digit posture during a diagonal double-locked grip of very thin  
572 substrates, as pictured by Napier (1960) in captivity (Supp. Fig.4). However, although challenging  
573 data to collect, more behavioural studies of types and frequency of hand grips used by orangutans  
574 during arboreal locomotion are needed to substantiate this.

#### 575 *Gorilla*

576 We predicted gorillas would show a significantly higher dorsal distribution of RBV/TV in each  
577 metacarpal head compared with all other hominids, reflecting McP joints loaded in a hyper-  
578 extended posture during frequent knuckle-walking and this prediction was supported. RBV/TV in the  
579 gorilla subchondral trabeculae was significantly higher dorsally than in all other species (Figs. 7 and  
580 9). This RBV/TV pattern was also found previous studies of the Mc3 in gorillas (Tsegai et al., 2013;  
581 Skinner et al., 2015). The present results, however, also revealed high RBV/TV along the disto-ulnar  
582 region of the Mc2 head and disto-radial region of the Mc5 head, which was not predicted, although  
583 a similar pattern was also found in the Mc5 by Skinner et al. (2015). This pattern is present in both  
584 the average male and female RBV/TV distribution (Supp. Fig. 5). The gorilla fifth digit is more  
585 frequently used in knuckle-walking (Inouye, 1994) and is more similar in length to the other rays  
586 than that of chimpanzees (Susman, 1979; Inouye, 1992), which may explain the more even  
587 distribution of knuckle-walking pressure across the digits in captive gorillas (Matarazzo, 2013). As the  
588 fifth digit is often not involved in grips of thinner arboreal substrates (Neufuss et al., 2017) and this  
589 RBV/TV pattern is mirrored in the Mc2, it seems parsimonious to argue it reflects more frequent and  
590 less variable knuckle-walking hand postures in gorillas relative to chimpanzees and bonobos (Tuttle  
591 and Basmajian, 1978; Matarazzo, 2013; Thompson et al., 2018). The Mc3 and Mc4 of gorillas also  
592 showed high RBV/TV dorsally, especially at the radio-ulnar margins (Figs. 3 and 5), which is  
593 consistent with the idea that the fingers work in concert to buffer medio-lateral forces during  
594 locomotion (Chirchir et al., 2017). The medio-lateral forces generated during 'palm-back' knuckle-  
595 walking, which places the McP joints orthogonal to the direction of travel, may be considerable.

#### 596 *Pan troglodytes*

597 We predicted that chimpanzees would have significantly higher dorsal RBV/TV than orangutans but  
598 lower than in gorillas, with a more homogeneous distribution of RBV/TV within each metacarpal  
599 head and more inter-ray differences, reflecting their more varied locomotor regime. These  
600 predictions were generally supported. The disto-dorsal pattern of higher RBV/TV across the  
601 subchondral metacarpus of chimpanzees (Fig. 3) was more dorsally concentrated than that of  
602 orangutans and more distally-extended than in gorillas (Figs. 7 and 9). This RBV/TV pattern is  
603 consistent with previous studies of chimpanzee subchondral trabecular bone (Zeininger et al., 2011)  
604 and whole-epiphyseal analyses that found a similar signal in the subchondral trabeculae of Mc3 and



605 Mc5 (Tsegai et al., 2013; Skinner et al., 2015). It should be noted, however, that present study  
606 sample includes five of the same Mc3 specimens and four of the Mc5 specimens used by Tsegai et al.  
607 (2013) and Skinner et al. (2015), respectively. In contrast to these analyses, studies using larger  
608 volume of interest (VOI) methods have found higher BV/TV in centrally-placed VOIs relative to  
609 palmar or dorsally placed VOI's in the chimpanzee Mc3 head (Barak et al., 2017; Chirchir et al.,  
610 2017). However the use of fewer large VOIs in these studies, as opposed to the many smaller VOIs  
611 produced by the whole-epiphysis approach employed here, may exacerbate issues of VOI placement  
612 and size that have been shown to dramatically effect trabecular measures in the primate Mc3 (Kivell  
613 et al., 2011).

614 In partial support of our prediction, we found that chimpanzees showed several significant  
615 differences in RBV/TV between the Mc heads, although there were not more differences than those  
616 found in gorillas. Specifically, RBV/TV was significantly higher palmarly in Mc2 and Mc5 but higher  
617 distally in Mc3 and Mc4 in chimpanzees (Figs.5 and 10). This pattern may reflect relatively more  
618 weight bearing by digits 3 and 4 during knuckle-walking than in the second or fifth digit (Tuttle and  
619 Basmajian, 1978). Some captive chimpanzees with injuries to digits 2 and 5 appeared to be  
620 unimpaired when knuckle-walking and some healthy individuals were observed flexing these digits  
621 so that they did not bear weight during this mode of locomotion (Tuttle, 1967). Larger captive  
622 chimpanzees have been observed using their second digit significantly less often than gorillas of  
623 equivalent size during knuckle-walking and chimpanzees of all sizes used their fifth digit significantly  
624 less often and loaded it less than gorillas did (Inouye, 1994, Wunderlich and Jungers, 2009;  
625 Matarazzo, 2013). Matarazzo (2013) found the third digit regularly lifted-off last during 'palm-back'  
626 knuckle-walking in captive chimpanzees and that peak pressure was often experienced by the third  
627 digit. Wunderlich and Jungers (2009) also found that peak pressures were higher on digits 3 and 4  
628 than on digits 2 and 5 when young chimpanzees practised arboreal knuckle-walking and when they  
629 used a 'palm-back' posture during terrestrial knuckle-walking. Therefore it could be argued that the  
630 more palmar RBV/TV distribution in Mc2 and Mc5, relative to Mc3 and Mc4, might reflect less  
631 loading in McP hyper-extension during knuckle-walking and a need to flex digits 2 and 5 during  
632 arboreal grasping. Marzke and Wullstein (1996) have argued that the fifth digit should be the most  
633 flexed in diagonal power grips, known to be used by wild chimpanzees while vertically climbing  
634 (Hunt, 1991; Neufuss et al., 2017).

635 That being said, in previous hand pressure studies, all mature chimpanzees experienced peak  
636 pressures on digits 2-4 when terrestrially knuckle-walking and the second digit usually lifts-off during  
637 'palm-in' knuckle-walking (Wunderlich and Jungers,2009; Matarazzo, 2013). Further, the second  
638 digit should be the most extended during diagonal power grips (Marzke and Wullstein, 1996) which  
639 opposes the relative flexion thought to be indicated here by the relatively palmar RBV/TV pattern  
640 found in the chimpanzee Mc2 head. Therefore, in the absence of kinematic and kinetic studies of  
641 locomotor hand postures in wild chimpanzees, we suggest that this pattern may reflect a more  
642 varied hand postures and distribution of pressure across the digits during knuckle-walking  
643 (Wunderlich and Jungers, 2009; Matarazzo, 2013) or more frequent arboreal grasping compared  
644 with gorillas, or a combination of both (Remis, 1995; Doran, 1996; Thorpe and Crompton, 2006).

#### 645 *Pan paniscus*

646 Given the general similarities in locomotion and hand use between chimpanzees and bonobos, we  
647 predicted that bonobos would have a RBV/TV pattern that was very similar to that of chimpanzees,

648 but with a more homogenised distribution of RBV/TV within each metacarpal head. Our results  
649 supported these predictions; bonobos showed disto-dorsally higher RBV/TV was more distally-  
650 extended than in gorillas and more dorsally concentrated than that of orangutans (Figs. 3, 7 and 9).  
651 Bonobos differed from chimpanzees in that they possessed almost no significant inter-ray  
652 differences and they showed the most landmarks closest to the mean of BV/TV throughout each  
653 head's trabecular surface (i.e., RBV/TV being  $\sim 1$ ; Figs. 3, 5 and 10). This RBV/TV distribution is  
654 consistent with the expectation raised by Tsegai et al. (2013), that bonobos would have an  
655 intermediate Mc3 trabecular structure between that of African apes and Asian apes (Fig.9) and the  
656 intermediate thickness of Mc3 cortical bone in this species (Susman, 1979). If the relatively higher  
657 dorsal RBV/TV in chimpanzee Mc3 and Mc4 is a knuckle-walking signal then the lack of it in bonobos,  
658 as well as the significantly higher palmar RBV/TV of Mc3, may either reflect more loading of a flexed  
659 McP joint consistent with the presumed greater arboreality in this species (Alison and Badrian, 1977;  
660 Susman et al., 1980; Susman 1984; Crompton et al., 2010) or direct palmar loading of the metacarpal  
661 head as a result of a significant amount of arboreal palmigrady (Doran, 1993, Doran and Hunt, 1994).

#### 662 *Trabecular anisotropy*

663 In contrast to the RBV/TV results, the degree of anisotropy (DA) in the subchondral trabecular bone  
664 was less variable, both in inter-species and inter-ray comparisons. Interestingly, every species  
665 studied possesses higher average DA values across the most dorsal aspect of each metacarpal  
666 (Fig.4). As this pattern also appears in orangutans, it is likely not reflective of hyper-extension of the  
667 McP during knuckle-walking but may instead reflect fewer trabeculae at the limit of the sub-articular  
668 surface. Fewer subchondral trabecular struts would reduce the variability of alignment and thus  
669 increase DA. The main significant differences in DA were found in orangutans, which were generally  
670 more anisotropic than any other taxon, especially gorillas (Figs. 4 and 6, Supp. Figs 2, 3 and Table 3).  
671 This did not support our prediction that orangutan DA would be significantly higher in the disto-  
672 palmar region, nor that gorilla DA would be significantly higher in the dorsal region of the  
673 metacarpal heads compared to other hominids. Given this lack of specific regional differences it is  
674 difficult to attribute the general lack of inter-ray differences in orangutans and gorillas to functional  
675 grips as per our predictions (Fig.6; Supp.Fig.3). Conversely, chimpanzees and bonobos did partially  
676 support our predictions as they showed the least significantly different landmarks in DA, between  
677 them (Fig.8) and the most inter-ray differences within each species (Fig.6), though again it is difficult  
678 to link this to specific hand postures.

679 High DA in orangutans did not support our predictions and appears contradictory to previous results  
680 showing significantly lower DA in orangutans and other suspensory taxa (Tsegai et al., 2013).

681 However, Tsegai et al. (2013) quantified and averaged trabecular DA throughout the entire Mc3  
682 head, as opposed to just the subchondral trabeculae, which can mask the signal of higher DA in  
683 particular regions of the head. In particular, subchondral trabeculae are responsible for the initial  
684 dissipation of load from the articular, compact cortical bone through to the more internal trabecular  
685 structure in long bones such as metacarpals (Currey, 2002). Thus it may be possible that trabeculae  
686 in this region are more constrained in their orientation, as they must link the cortical shell of the  
687 metacarpal head and the deeper trabecular structure, explaining the lack of variability in DA in our  
688 sample. If this is true, the variation in DA we did find, significantly higher DA in orangutans than in  
689 other species, might be due to a general lower number of trabeculae in orangutans. However,  
690 Chirchir et al. (2017) also found that DA was consistently, if not significantly, higher in orangutans

691 compared with chimpanzees in all three of their VOIs which sampled most of the Mc3 head. Further  
692 higher DA has been found at superior-central region than in other regions of in the proximal *Pongo*  
693 humerus (Kivell et al. 2018). Therefore it is unlikely the significantly higher DA in orangutans is solely  
694 an artefact of sampling subchondral trabeculae.

695 High subchondral DA in orangutans may reflect a lower extension range of motion (19°) compared to  
696 that of African apes (50°) (Napier, 1960; Rose, 1988). Although orangutans have been assumed to  
697 load their hands in a greater range of postures to accommodate their diverse arboreal locomotor  
698 repertoire relative to the frequent and consistent knuckle-walking postures of African apes (Tsegai et  
699 al., 2013), the orangutan McP joint will, presumably, always been in a neutral-to-flexed posture  
700 when grasping arboreal substrates. Indeed, while variability in DA values for orangutans appears to  
701 be higher than in other taxa studied, higher average DA values are not solely driven by outlying  
702 individuals (Fig. 8) nor, on further interrogation, those of a particular species or sex. An analysis of  
703 trabeculae in the whole Mc3 head has reported similar intra-species variability in orangutans (Tsegai  
704 et al., 2013). Yet one constant across orangutan species and sexes is their high frequency of arboreal  
705 locomotion requiring flexed McP grasping and perhaps a more stereotypically-aligned trabecular  
706 structure, reflected in the high average DA found here. In contrast, African apes load their McP joints  
707 in both hyper-extension during knuckle-walking and a range of neutral-to-flexed postures during  
708 arboreal locomotion. The greater isotropy found within African apes subchondral trabeculae may  
709 reflect loading of the McP joint from multiple directions during arboreal, as well as terrestrial,  
710 behaviours.

#### 711 *Inferring bone functional adaptation*

712 Many explorative comparative anatomy analyses, including the present study, can be thought of as  
713 adaptationist (Gould and Lewontin, 1979), presenting functionally adaptive explanations for the  
714 observed data that are not easily falsified (Smith, 2016). Here, however, we submit that as the  
715 clearest differences in subchondral RBV/TV and DA patterns in the metacarpal heads are between  
716 the two species with the most disparate locomotor modes (orangutans and gorillas) and the least  
717 differences are between the two species with the most similar locomotor modes (chimpanzees and  
718 bonobos), this offers a kind of informal falsification. If the chimpanzees and bonobos were the most  
719 disparate in trabecular pattern this would effectively falsify the broad underlying logic of our  
720 predictions. Conversely, with respect to our more specific predictions that were not met, for  
721 example those regarding regional DA in *Pongo* and *Gorilla*, alternative data must be sought to  
722 explain these results (as detailed above). For example, future work that scales DA by trabecular  
723 number, analyses of the differences between subchondral and deeper trabecular structure, or  
724 detailed studies of locomotor hand postures in wild *Pongo*, could all potentially falsify some of these  
725 explanations. Nevertheless, it must be noted that the broader logic underlying more predictions  
726 holds for DA, as chimpanzees and bonobos did not display the most significant differences.

727 In the same vein, it could be argued that the lack of differences between chimpanzees and bonobos  
728 is due to their close phylogenetic distance rather than their similar locomotor regimes. Trabecular  
729 bone structure is controlled, at least to some extent, by genetic factors (Lovejoy et al., 2003, Havill et  
730 al., 2010, Judex et al., 2013, Almécija et al., 2015) and role of trabecular remodelling is not solely  
731 functional (Skinner et al., 2015, 2015b); for example, trabecular bone is also important for mineral  
732 homeostasis (Clarke, 2008). There were clear differences in absolute BV/TV, however, such that  
733 bonobos demonstrated much greater subchondral BV/TV in all elements of the hand studied

734 compared to chimpanzees (Supp.Fig.7). This difference has been previously reported within the Mc3  
735 of the same individuals in this study, for which the phylogenetic influence was assessed (Tsegai et  
736 al., 2013). The relative measure used here appears to have effectively controlled for this difference  
737 in subchondral metacarpal head BV/TV. This suggests that the absolute difference in BV/TV is not  
738 functional in origin, as it is unlikely bonobos practise a form of locomotion very similar to  
739 chimpanzees but with remarkably greater force. The only comparable kinematic data available  
740 demonstrates both captive chimpanzees and captive bonobos experience similar peak pressures on  
741 their fingers during arboreal knuckle walking (Wunderlich and Jungers, 2009; Samuel et al., 2018). If  
742 not functional in origin the absolute difference in BV/TV between chimpanzees and bonobos may be  
743 systemic. Though a study of metatarsal trabeculae failed to find this difference in absolute BV/TV  
744 between chimpanzees and bonobos (Griffin et al., 2010), Tsegai et al. (2018) have noted that  
745 systemic differences in BV/TV between species may be variably pronounced at different anatomical  
746 sites. While the reasons for systemic differences in trabeculae might be varied, including hormones,  
747 diet and disparate intestinal biomes (Tsegai et al., 2018), the difference is marked between these  
748 phylogenetically close species. As a corollary it would seem that there is little reason to suspect non-  
749 functional systematic forces are driving the similarities between RBV/TV in *Pan* species. Although the  
750 relative measure appears to have effectively controlled for possible systemic differences in  
751 subchondral trabeculae of the non-pollical metacarpal heads there are still small differences  
752 between the species which, by process of elimination, appear to be functional origin.

753 Work on intra-species variation in a large sample of a single species also supports this idea of both a  
754 systemic and functional signal in trabecular architecture. While current studies have focused on  
755 humans, likely due to the availability of specimens, data from several anatomical sites has  
756 demonstrated lower BV/TV in sedentary humans relative to mobile forager populations primarily  
757 due to lower mechanical loading (Chirchir et al., 2015; Ryan and Shaw, 2015). Within the lower limb,  
758 this trabecular difference appears to be superimposed on a pattern of increasing trabecular gracility  
759 with increasingly distal elements of the limb (Saers et al., 2016). The transition to sedentism in  
760 human populations provides a natural experiment that allows the identification of a trabecular  
761 functional signal superimposed onto a structural limb tapering signal, which is also found in cortical  
762 bone (Saers et al., 2016). We argue that the phylogenetic proximity and similar locomotion of *Pan*  
763 also provides a natural experiment that begins to separate functional and systemic differences  
764 between these species, as seen in the present RBV/TV results. Future work should consider the  
765 possibility of clarifying functional and systemic signals in trabecular bone.

766 It would be interesting to apply these methods to the pollical metacarpal of hominids, and perhaps  
767 a larger sample of primates, in order to test for manipulative behaviour signals that may lie in the  
768 subchondral trabecular bone. Even this relatively small comparative sample may be used to  
769 contextualise fossil hominin trabeculae to shed light on their habitually loaded hand postures.  
770 Though relatively complete fossil hominin hands are rare in the archaeological record, this  
771 comparative sample demonstrates that isolated Mc2 or Mc5 elements are more important than  
772 previously thought for identifying habitual hand use in our ancestors.

### 773 **Conclusion**

774 Using a geometric morphometric approach, we demonstrated significant differences in the  
775 distribution of subchondral trabecular RBV/TV across great apes that were consistent with our

776 predicted differences in McP joint loading during locomotion. Results of this study generally confirm  
777 previous analyses of metacarpal head trabecular structure that have largely focused only on the  
778 Mc3, but provide for the first time statistically robust comparison using the whole-epiphysis  
779 approach. By building upon previous work to look at trabecular structure across all of the non-  
780 pollical metacarpals, we revealed novel RBV/TV patterns in the inter-ray comparisons within *Gorilla*  
781 and *Pan* that are consistent with differences in hand posture during knuckle-walking and the  
782 frequency of arboreal locomotion. However, these inferences require testing with more detailed  
783 kinematic and kinetic analyses of the hand, ideally in wild African apes. Contrary to our predictions,  
784 we found few significant differences in DA across taxa, with *Pongo* demonstrating significantly  
785 higher DA than African ape taxa. We conclude that the interspecific variation in subchondral  
786 trabecular RBV/TV revealed here is consistent with what is currently known about great ape hand  
787 use and McP joint loading and, as such, provides a valuable comparative context in which to  
788 interpret the trabecular structure of fossil hominoid or hominin metacarpal heads.

789

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1094 **Supplementary material**

1095

1096 **Supporting Information Figure 1. Repeatability tests of landmarks.** Each individual metacarpal was  
1097 landmarked 10 times on different days. The same rays from three individuals of the same species  
1098 were then subjected to Procrustes transformation in each case. Subsequent permutational omnibus  
1099 and pairwise MANOVA's were run on the PC1 and PC2 scores, as these cumulatively explained >80%  
1100 of the variation: **a) Gorilla** Mc2's (Culm. Var. 83%); **b) Pongo** Mc3's (Culm. Var. 80%); **c) Pan paniscus**  
1101 Mc4's (Culm. Var. 85%); **d) Pan troglodytes** Mc5's (Culm. Var. 87%). All individual specimen repeats  
1102 were significantly different from each other subsequent to a Bonferroni correction ( $p \leq 0.0006$ ).

1103

1104 **Supporting Information Figure 2. DA plots showing species differences within each metacarpal**  
1105 **head.** Each plot shows the first two principle components (PC) in each ray. Landmarks at each  
1106 extreme of a PC are coloured in grayscale, according to their signed contribution to that PC and  
1107 plotted on a Mc3 in distal view. White landmarks indicate the highest signed contribution to the PC  
1108 and black the least.

1109

1110 **Supporting Information Figure 3. DA PCA plots showing ray differences within each species.** Each  
1111 plot shows the first two principle components (PC) in each ray. For *Gorilla*, PC3 is depicted with PC1,  
1112 inset, as PC2 and PC3 explain a similar amount of the variance (11% and 9% respectively) in this case.  
1113 Landmarks at each extreme of a PC are coloured in grayscale, according to their signed contribution  
1114 to that PC and plotted on a Mc3 in distal view. White landmarks indicate the highest signed  
1115 contribution to the PC and black the least.

1116

1117 **Supporting Information Figure 4. A captive orangutan engaged in a diagonal 'double-locked' grip**  
1118 **around a piece of string.** Note the extension of the second metacarpophalangeal joint. Image  
1119 adapted from Napier (1960).

1120

1121 **Supporting Information Figure 5. Gorilla average RBV/TV by sex,** mapped to average models of  
1122 right Mc heads in distal view for **a) Male** Mc5, **b) Male** Mc2, **c) Female** Mc5 and **d) Female** Mc2,  
1123 specimens. Note that the radio-ulnar bias is present in both sexes (see main text for details).

1124

1125 **Supporting Information Figure 6.** Landmark template projected onto Mc3s of individual **a) Gorilla**  
1126 **gorilla,** **b) Pan troglodytes,** **c) Pan paniscus** and **d) Pongo pygmaeus** specimens. Note the homology  
1127 of these landmarks across shape variation in species.

1128

1129 **Supporting Information Figure 7. Species average absolute BV/TV**, mapped to average models of  
1130 each Mc head in **a)** distal, **b)** palmar and **c)** dorsal views. Note that absolute BV/TV interspecies or  
1131 inter-ray comparisons are more likely to reveal overall differences in subchondral BV/TV than  
1132 differences in the regional distribution of BV/TV, which are consistent with certain McP postures, as  
1133 is the case for the scaled RBV/TV (See text for further information).

**Supporting Information Table 1. Descriptive statistics** of absolute Z-scores from significant pairwise inter-species landmark comparisons. Species abbreviations are: Ggg = *Gorilla*, Ptv = *Pan troglodytes*, Pp = *Pan paniscus*, Ppy = *Pongo* spp. . The minimum differences between species at a given landmark are over 2.4 normalized standard deviations from each other.

	Mc2						Mc3						Mc4						Mc5					
RBV/TV	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv
Min	2.43	2.40	2.40	2.40	2.40	2.40	2.40	2.45	2.45	2.40	2.42	2.48	2.40	2.40	2.43	2.40	2.48	2.46	2.47	2.40	2.40	2.41	n/s	2.42
Max	4.28	5.38	4.68	3.56	3.60	3.51	4.13	5.40	3.00	4.15	3.25	4.78	3.82	5.92	3.50	5.07	3.16	4.88	4.55	5.38	4.35	3.67	n/s	4.91
SD	0.47	0.77	0.66	0.30	0.50	0.36	0.46	0.69	0.18	0.40	0.21	0.55	0.33	0.75	0.30	0.67	0.23	0.60	0.46	0.80	0.46	0.36	n/s	0.69
Mean	3.10	3.66	3.25	2.84	2.93	2.87	3.06	3.89	2.58	2.91	2.65	3.28	2.93	3.93	2.87	3.34	2.66	3.32	3.22	3.84	3.18	2.92	n/s	3.23
DA	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy	Ggg	Ggg	Ggg	Pp	Pp	Ppy
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv	Pp	Ppy	Ptv	Ppy	Ptv	Ptv
Min	2.40	2.43	2.40	2.44	2.42	2.40	2.41	2.43	2.40	2.46	2.46	2.40	2.40	2.40	2.49	2.40	2.55	2.43	2.42	2.40	2.40	2.40	2.40	2.42
Max	3.28	4.76	3.88	4.56	3.21	3.77	3.57	4.59	3.63	4.06	3.34	2.86	3.39	4.12	3.85	3.44	3.16	3.82	3.78	4.68	3.70	4.62	2.67	4.85
SD	0.26	0.59	0.35	0.50	0.27	0.41	0.27	0.47	0.32	0.42	0.27	0.16	0.30	0.46	0.38	0.32	0.24	0.35	0.41	0.44	0.34	0.59	0.13	0.68
Mean	2.72	3.49	2.80	3.14	2.65	2.89	2.86	3.20	2.93	3.08	2.78	2.56	2.76	3.10	2.99	2.84	2.84	2.80	3.02	3.04	2.86	3.08	2.49	3.33



**Supporting Information Table 2. Descriptive statistics** of absolute Z-scores from significant pairwise inter-ray landmark comparisons. The minimum differences between rays at a given landmark are over 2.4 normalized standard deviations from each other.

	<i>Gorilla gorilla</i>				<i>Pan paniscus</i>				<i>Pongo spp.</i>				<i>Pan troglodytes</i>			
RBV/TV	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5
Min	2.41	n/s	2.42	2.49	2.51	2.60	2.41	2.43	2.46	2.55	2.42	2.42	2.41	2.43	2.41	2.43
Max	3.59	n/s	4.51	5.39	3.02	2.60	3.60	3.52	2.76	2.89	3.08	4.58	4.01	2.60	3.88	4.37
SD	0.40	n/s	0.45	0.71	0.26	0.00	0.37	0.38	0.11	0.12	0.23	0.52	0.48	0.08	0.40	0.48
Mean	2.95	n/s	3.19	3.69	2.76	2.60	2.75	2.85	2.58	2.75	2.61	3.25	3.11	2.52	2.95	2.96
DA	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5	2 - 3	3 - 4	4 - 5	2 - 5
Min	2.42	2.48	2.45	2.42	2.41	2.47	2.41	2.43	2.46	n/s	2.54	2.42	2.42	n/s	2.41	2.42
Max	3.97	3.02	3.65	4.33	3.71	3.44	3.42	3.35	3.24	n/s	3.28	3.19	3.25	n/s	3.86	3.95
SD	0.50	0.22	0.35	0.59	0.37	0.41	0.30	0.28	0.39	n/s	0.26	0.28	0.28	n/s	0.33	0.43
Mean	2.86	2.63	2.79	3.11	2.86	2.96	2.85	2.69	2.85	n/s	2.95	2.74	2.80	n/s	2.82	2.85

**Tables**

**Table 1. Study sample**

<b>Taxonomy</b>	<b>Accession ID</b>	<b>Sex</b>	<b>Side</b>	<b>Institution</b>
<i>Gorilla gorilla gorilla</i>	PC_MER_300	Female	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_264	Male	Right	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_372	Male	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_95	Female	Right	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_962	Male	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_CAMI_230	Male	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_138	Female	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_174	Male	Right	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_696	Female	Right	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_856	Female	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_MER_879	Male	Left	Powell-Cotton Museum
<i>Gorilla gorilla gorilla</i>	PC_ZVI_32	Male	Right	Powell-Cotton Museum
<i>Pan troglodytes verus</i>	MPITC_11789	Male	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_11778	Female	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_13439	Female	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_15002	Female	Left	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_11800	Female	Right	Max Planck Institute for Evolutionary Anthropology

<i>Pan troglodytes verus</i>	MPITC_11903	Male	Left	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_11781	Male	Left	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_14996	Female	Left	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_15012	Male	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_15013	Female	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_15014	Male	Right	Max Planck Institute for Evolutionary Anthropology
<i>Pan troglodytes verus</i>	MPITC_15032	Male	Left	Max Planck Institute for Evolutionary Anthropology
<i>Pongo abelii</i>	SMF_6785	Male	Right	Senckenberg Natural History Museum, Frankfurt
<i>Pongo abelii</i>	SMF_6779	Female	Left	Senckenberg Natural History Museum, Frankfurt
<i>Pongo pygmaeus</i>	ZSM_1907_0633b	Female	Right	Bavarian State Collection of Zoology
<i>Pongo sp.</i>	ZSM_AP_122	Male	Right	Bavarian State Collection of Zoology
<i>Pongo pygmaeus pygmaeus</i>	ZSM_1907_0660	Female	Right	Bavarian State Collection of Zoology
<i>Pongo sp.</i>	ZSM_AP-120	Male	Left	Bavarian State Collection of Zoology
<i>Pongo pygmaeus pygmaeus</i>	ZSM_1907_0483	Female	Right	Bavarian State Collection of Zoology
<i>Pongo pygmaeus pygmaeus</i>	ZSM_1909_0801	Male	Right	Bavarian State Collection of Zoology
<i>Pongo abelii</i>	NMNH_267325	Male	Left	Smithsonian Institution National Museum of Natural History
<i>Pongo pygmaeus</i>	ZMB_6948	Female	Left	Natural History Museum, Berlin
<i>Pongo pygmaeus</i>	ZMB_6947	Male	Left	Natural History Museum, Berlin
<i>Pongo pygmaeus</i>	ZMB_87092	Female	Right	Natural History Museum, Berlin

<i>Pan paniscus</i>	MRAC_15293	Female	Left	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_15294	Male	Left	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_20881	Male	Left	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_27696	Male	Right	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_27698	Female	Left	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_29042	Female	Right	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_29044	Male	Right	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_29045	Female	Left	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_29052	Male	Right	Royal Museum for Central Africa, Tervuren
<i>Pan paniscus</i>	MRAC_29060	Female	Right	Royal Museum for Central Africa, Tervuren

**Table 2. Anatomical landmark definitions**, types (Bookstein, 1991) and their provenance. Each article describes the landmark, uses it as the terminus of a linear measure or directly uses it for GM analysis.

Number	Type	Description	Provenance
1	Type II	Most proximal point under the ulnar palmar epicondyle (anterior eminence)	(Yeh and Wolf, 1977, Fernández, 2015, Rein, 2018)
2	Type III	The point of maximum curvature on the inter-epicondylar ridge between points 1 and 3	(Drapeau, 2015, Fernández, 2015, Rein, 2018)
3	Type II	Most proximal point under the radial palmar epicondyle (anterior eminence)	(Yeh and Wolf, 1977, Fernández, 2015, Rein, 2018)
4	Type III	Point of maximum curvature on the radial ridge separating the articular surface from the radial lateral sulcus	(Yeh and Wolf, 1977, Fernández, 2015, Rein, 2018)
5	Type II	Most radially projecting point under the ulnar dorsal tubercle	(Yeh and Wolf, 1977, Susman, 1979, Inouye, 1992, Fernández, 2015, Rein, 2018)
6	Type III	Mid-point between the posterior tubercles on the intertubercular ridge, underlying the dorsal ridge if present.	(Yeh and Wolf, 1977, Fernández, 2015)
7	Type II	Most ulnarly projecting point under the ulnar posterior tubercle	(Yeh and Wolf, 1977, Susman, 1979, Inouye, 1992, Fernández, 2015, Rein, 2018)
8	Type III	Point of maximum curvature on the ulnar ridge separating the articular surface from the radial lateral sulcus	(Yeh and Wolf, 1977, Fernández, 2015, Rein, 2018)
9	Type II	Most distally projecting point on the subchondral surface	(Fernández, 2015; Susman, 1979; Inouye, 1992, Rein, 2018)

**Table 3. Permutational MANOVAs** on the first three principle components between all groups. Species abbreviations are: Ggg = *Gorilla*, Ptv = *Pan troglodytes*, Pp = *Pan paniscus*, Ppy = *Pongo* spp. . Subsequent pair-wise tests were carried out if the omnibus test was significant; otherwise pair-wise tests are marked as non-significant (N/S). All *p*-values reported are subsequent to a Bonferroni correction and are marked in bold where significant.

	<i>RBV/TV MC2</i>	<i>RBV/TV MC3</i>	<i>RBV/TV MC4</i>	<i>RBV/TV MC5</i>		<i>RBV/TV Ggg</i>	<i>RBV/TV Pp</i>	<i>RBV/TV Ppy</i>	<i>RBV/TV Ptv</i>
<i>All</i>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<i>All</i>	<b>0.0001</b>	0.1209	<b>0.0006</b>	<b>0.0001</b>
<i>Ppy-Pp</i>	<b>0.0312</b>	<b>0.0024</b>	<b>0.0006</b>	<b>0.0200</b>	2-3	<b>0.0258</b>	n/s	<b>0.1374</b>	<b>0.0006</b>
<i>Ptv-Pp</i>	1.0000	0.5196	1.0000	1.0000	3-4	1.0000	n/s	1.0000	1.0000
<i>Pp-Ggg</i>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0006</b>	4-5	<b>0.0006</b>	n/s	1.0000	0.1044
<i>Ptv-Ggg</i>	<b>0.0006</b>	<b>0.0168</b>	<b>0.0006</b>	<b>0.0006</b>	2-5	<b>0.0006</b>	n/s	<b>0.0018</b>	<b>0.0456</b>
<i>Ptv-Ppy</i>	<b>0.0402</b>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0006</b>	3-5	<b>0.0006</b>	n/s	0.7434	<b>0.0030</b>
<i>Ppy-Ggg</i>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0006</b>	2-4	<b>0.0012</b>	n/s	<b>0.0036</b>	<b>0.0090</b>
	<i>DA MC2</i>	<i>DA MC3</i>	<i>DA MC4</i>	<i>DA MC5</i>		<i>DA Ggg</i>	<i>DA Pp</i>	<i>DA Ppy</i>	<i>DA Ptv</i>
<i>All</i>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<i>All</i>	<b>0.0003</b>	<b>0.0001</b>	0.5848	<b>0.0018</b>
<i>Ppy-Pp</i>	<b>0.0018</b>	0.0582	<b>0.0450</b>	<b>0.0018</b>	2-3	0.4032	<b>0.0264</b>	n/s	0.3690
<i>Ptv-Pp</i>	0.4872	1.0000	0.8700	1.0000	3-4	1.0000	0.4302	n/s	1.0000
<i>Pp-Ggg</i>	<b>0.0402</b>	<b>0.0102</b>	<b>0.0378</b>	<b>0.0006</b>	4-5	0.0900	<b>0.0012</b>	n/s	<b>0.0348</b>
<i>Ptv-Ggg</i>	<b>0.0426</b>	<b>0.0342</b>	<b>0.0486</b>	<b>0.0132</b>	2-5	<b>0.0096</b>	0.3318	n/s	0.2832
<i>Ptv-Ppy</i>	<b>0.0054</b>	0.3018	0.0870	<b>0.0018</b>	3-5	<b>0.0108</b>	<b>0.0012</b>	n/s	<b>0.0012</b>
<i>Ppy-Ggg</i>	<b>0.0006</b>	<b>0.0006</b>	<b>0.0042</b>	<b>0.0030</b>	2-4	<b>0.0114</b>	0.0930	n/s	1.0000

### **Figure captions**

**Figure 1.** Diagrammatic representations of the metacarpophalangeal postures during **a)** a hook grip, **b)** a 'double-locked' grip and **c)** knuckle-walking and **d)** a diagonal power-grip. Images are adapted from Lewis (1977), Rose (1988), and Tsegai et al. (2013).

**Figure 2.** Methodological stages of metacarpal trabecular analysis, shown in a third metacarpal as an example: **a)** isosurface model; **b)** segmented trabecular structure inside cortical shell; **c)** diagram of the background grid and one of the VOI's at a vertex (purple); **d)** volume mesh coloured by BV/TV (0-45%); **e)** smoothed trabecular surface mesh; **f)** surface landmarks (anatomical = red, semi-sliding landmarks on curves = blue and on surfaces = green); **g)** RBV/TV interpolated to each surface landmark.

**Figure 3. Species average RBV/TV,** mapped to average models of each Mc head in **a)** distal, **b)** palmar and **c)** dorsal views. RBV/TV values around one (white) indicate landmarks close to the average BV/TV of that Mc head, while values above (red) or below one (blue) indicate a deviation from this average at these landmarks.

**Figure 4. Species average DA** mapped to average models of each Mc head in **a)** distal, **b)** palmar and **c)** dorsal views.

**Figure 5. Inter-ray significant differences in RBV/TV,** mapped to an average right Mc3 head in each case in dorsal (top), distal (middle) and palmar (bottom) views. Where RBV/TV values at landmarks are significantly higher in one ray than the other, they are coloured as per the ray numbers in each comparison.

**Figure 6. Inter-ray significant differences in DA,** mapped to an average right Mc3 head in each case in dorsal (top), distal (middle) and palmar (bottom) views. Where DA values at landmarks are significantly higher in one ray than the other, they are coloured as per the ray numbers in each comparison.

**Figure 7. Significant differences in RBV/TV between species,** mapped to average models of each Mc head in **a)** distal **b)** palmar and **c)** dorsal views. Where RBV/TV values at landmarks are significantly higher in one species than the other, they are coloured as per the species in each comparison.

**Figure 8. Significant differences in DA between species,** mapped to average models of each Mc head in **a)** distal **b)** palmar and **c)** dorsal views. Where DA values at landmarks are significantly higher in one species than the other, they are coloured as per the species in each comparison.

**Figure 9. RBV/TV PCA plots showing species differences within each metacarpal head.** Each plot shows the first two principle components (PC) in each ray. For Mc5, PC3 is depicted with PC1, inset, as PC2 and PC3 explain a similar amount of the variance (16% and 14% respectively) in this case. Landmarks at

each extreme of a PC are coloured in grayscale, according to their signed contribution to that PC and plotted on a Mc3 in distal view. White landmarks indicate the highest signed contribution to the PC and black the least.

**Figure 10. RBV/TV PCA plots showing ray differences within each species.** Each plot shows the first two principle components (PC) in each ray, except for *Pan troglodytes* where PC3 is depicted with PC1, inset, as PC2 and PC3 explain a similar amount of the variance (15% and 12% respectively) in this case. Landmarks at each extreme of a PC are coloured in grayscale, according to their signed contribution to that PC and plotted on a Mc3 in distal view. White landmarks indicate the highest signed contribution to the PC and black the least.