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

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Abstract

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

Keywords: Metacarpal, Trabeculae, Hominid, Locomotion

Introduction

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

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

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

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

Hand use and locomotion

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

Pongo

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

The McP joints in *Pongo* possess a limited degree of possible hyper-extension at 19 degrees (Susman, 1979; Rose, 1988). Mc2-4 are also dorso-palmarly thicker at the diaphysis, and all the non-pollical metacarpal heads possess palmarly wide articular heads suggestive of habitual McP flexion (Susman, 1979). As the fourth proximal phalanx may often equal or exceed the length of the third phalanx in orangutans (40%; Susman, 1979), Rose (1988) has argued that the fourth ray is more in line with the second and third rays, which would be advantageous for both hook and double-locked grips in which rays 2-5 are typically all engaged. While body size in *Pongo* is sexually dimorphic (Rodman, 1984) and there is some evidence for differential locomotion between the sexes (Sugardjito and van Hooff, 1986), further work has found these differences to be relatively slight (Thorpe and Crompton, 2005). Therefore we do not expect habitual prehensile postures to differ between male and female *Pongo*.

Gorilla

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

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

Pan troglodytes

Generally *P. troglodytes* is thought to be more arboreal than *Gorilla* (Remis, 1995;Doran, 1996; Thorpe and Crompton, 2006) though this may be the result of comparisons to mountain gorillas that are better habituated to humans than their more arboreal lowland counterparts (Doran 1997; Hunt 2004, Neufuss et al., 2017). There is a large degree of variation in the chimpanzee locomotor repertoire depending on the local ecology (Doran and Hunt 1994; Carlson et al., 2006). *Pan troglodytes verus* engages in knuckle-walking, both arboreal and terrestrial, in ~85% of their locomotion and spend more time in the trees than *P. troglodytes schweinfurthii* (Doran and Hunt, 1994; Carlson et al., 2006). Compared with *Gorilla, P. troglodytes* uses more varied hand postures during knuckle-walking (Tuttle, 1969; Inouye, 1994; Matarazzo, 2013). Chimpanzees have been thought to primarily load digits 3 and 4 during knuckle walking (Tuttle, 1969; Tuttle and Basmajian, 1978). Inouye (1994) found that during captive terrestrial knuckle-walking, larger chimpanzees used their second digit significantly less often than gorillas of equivalent size and both chimpanzees and bonobos generally used their fifth digit significantly less often than gorillas. Pressure studies also found that the fifth digit of chimpanzees did not touch-down in 20% of knuckle-walking steps and that this digit experienced significantly less load than the other digits when it was used (Wunderlich and Jungers, 2009; Matarazzo, 2013). Further, *P. troglodytes* uses both 'palm-back' (~40%) and 'palm-in' (~60%) postures, compared with a more consistent use of mainly 'palm-back' (~86%) knuckle-walking postures in *Gorilla* (Wunderlich and Jungers, 2009; Matarazzo, 2013). During 'palm-in' knuckle-walking the intermediate phalanges roll radially in the direction of travel and the second or third digit usually experiences the highest pressures (Wunderlich and Jungers, 2009; Matarazzo, 2013). In 'palm-back' knuckle-walking the third digit is typically placed in front the others and usually is the last to touch off, which may be related to the fact that the third ray may be relatively longer in chimpanzees than in gorillas (Matarazzo, 2013; 2013b). Compared to *Gorilla*, the peak pressures experienced by digits 2-4 are more variable in chimpanzees (Wunderlich and Jungers, 2009; Matarazzo, 2013).

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

Pan paniscus

While bonobos have a relatively similar locomotor repertoire to chimpanzees, they are thought to be more arboreal (Alison and Badrian, 1977; Susman et al., 1980; Susman, 1984) and have been shown to use significantly more palmigrady in the trees (Doran, 1993; Doran and Hunt, 1994; Crompton et al., 2010). Though, the former claim may be an artefact of incomplete habituation of the individuals in these studies and more data is needed (Hunt, 2016), the relatively longer and heavier lower limbs of this species make for more generalised anatomy than that of chimpanzees (Zihlman, 1984; D'Août et al., 2004). During terrestrial knuckle-walking bonobos use the fifth digit even less than chimpanzees and Mc5 is shorter than the rest of the metacarpals in bonobos (Inouye, 1994). In a pressure study of arboreal locomotion, Samuel et al., (2018) found that captive bonobos used ‘palm-back’ (64%) or ‘palm-in’ (36%) knuckle-walking hand postures and that peak pressure was experienced by or around the third digit. However, unlike chimpanzees (Wunderlich and Jungers, 2009), they did not roll radially across their digits and the fifth digit always made contact with the substrate (Samuel et al., 2018). During vertical climbing and suspensory postures, bonobos used flexed-finger power grips similar to those described in other great apes and again peak pressure was experienced by or around the third digit (Samuel et al., 2018). In summary, the hand postures used during locomotion in *P. paniscus* can be characterised as similar to those of *P. troglodytes*, including a relatively low level of sexual dimorphism compared to other great apes (Doran, 1996), although more frequent palmigrady and arboreal grasping differentiate this species from *P. troglodytes*.

Predictions

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

Materials

Subchondral trabecular bone was analysed in the metacarpus of *Pan paniscus* (*n*=10), *Pan troglodytes verus* (*n*=12), *Gorilla gorilla gorilla* (*n*=12), *Pongo* sp. indet. (*n*=2), *Pongo pygmaeus* (*n*=7) and *Pongo abelii* (*n*=3). Metacarpi were sampled from the Royal Museum for Central Africa, Tervuren, the Max Planck Institute for Evolutionary Anthropology, Leipzig, the Powell-Cotton Museum, Birchington, Bavarian State Collection of Zoology, Munich, the Natural History Museum, Berlin, the Senckenberg Natural History Museum, Frankfurt and the Smithsonian National Museum of Natural History, Washington D.C. (Table1). All specimens were adult, wild shot and free from external signs of pathology. Within each taxon the samples were sex balanced with even numbers of right and left metacarpi, apart from *Gorilla* in which there were 7 left and 5 right metacarpi, as well as 5 females and 7 males. While great ape locomotion is sexually biased (Doran, 1996) and there has been some evidence for lateralized asymmetry in both the trabecular (Stephens et al., 2016) and cortical bone of hominid metacarpals (Sarringhaus et al., 2005) we argue that neither of these signals is greater than species locomotion differences under investigation here. Further, the use of evenly mixed samples should ameliorate these effects (see discussion).

Methods

MicroCT Scanning

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

Image processing

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

Geometric morphometric mapping

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

Anatomical Landmark definitions

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

Repeatability

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

Geometric morphometric procedure

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

Data mapping

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

Relative trabecular volume

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

Statistical analysis

We employ a 'mass-univariate' approach as advocated by Friston et al., (1995) similar to that used to statistically analyse cortical bone in ape metacarpals (Tsegai et al., 2017). Specifically, the trabecular values between species and rays at each landmark are independently analysed using univariate statistics. Inter-ray comparisons do not include comparisons between rays two and four or between rays three and five as they are not biologically contiguous and thus are less informative when prehensile hand postures are considered. However, comparisons of rays two and five are included to test for significant differences between the most ulnar and radial aspects of the metacarpus. Shapiro-Wilk tests found a non-normal distribution of data at one or more landmarks in one or both groups in every pair-wise, inter-ray and interspecific, comparison. To maintain consistent comparisons a non-parametric Kruskal-Wallis was applied at each landmark and a post-hoc test was used to test for pair-wise differences if the omnibus test was significant. Dunn's test was chosen as it uses the pooled variance of the Kruskal-Wallis tests and so is conservative. The level of significance was set at $p<0.05$ subsequent to a Bonferroni correction in each case. This univariate approach means that homologous landmark values are compared across groups rather than with spatially correlated neighbouring landmarks. *Z*-scores were used to determine the polarity, as well as the effect size, of significant differences between groups. These *Z*-scores were transformed into absolute, rather than signed, values and summarised for significant landmark differences, in both interspecific and inter-ray pairwise comparisons (Supp. Table 1 & 2). Resulting plots of significant univariate differences map regional differences between species and rays but were only considered meaningful if they were found at nine contiguous landmarks, as this represents just over 5% of the sub-articular surface, in order to further ameliorate any Type I error. Despite the fact this univariate method can identify where regions of significant difference lie it can be susceptible to Type I error and so to provide a multivariate corollary to this approach, a principle components analysis (PCA) of trabecular values, using landmarks as individual variables, was also run for all comparisons. Subsequent omnibus and pairwise one-way permutational MANOVAs were run with a Bonferroni correction, using the Vegan package (Oksanen et al., 2018) package in Rv3.3.0 (R Core Development team 2016), on the principal component scores of these PCAs to test for significant overall, rather than regional, differences in trabecular patterns.

Results

Univariate landmark comparisons

Pongo

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

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

Gorilla

The highest RBV/TV values in *Gorilla* were concentrated in the disto-dorsal portion of each metacarpal head extending dorsally on the medio-lateral edges of Mc3 and 4 but toward the mid-line of the hand in the Mc2 and Mc5 heads (Fig.3). This latter pattern was clear in the inter-ray comparison, with significantly greater RBV/TV found at the radial aspect of Mc5 relative to Mc2 and Mc4 as well as on the ulnar aspect of these rays relative to Mc5 (Fig. 5). Interspecifically, *Gorilla* was significantly higher in RBV/TV dorsally compared to *Pongo*, though the radio-palmar aspect of Mc5 was not significantly different between these groups. Compared with *Pan*, *Gorilla* generally had significantly higher RBV/TV dorsally but this was restricted to the medio-lateral edges of each metacarpal head in the regional comparison (Fig. 7). Specifically, *Gorilla* had significantly higher RBV/TV than *Pan* species on the radio-dorsal aspect of Mc5 and both medio-lateral edges of Mc4, as well as the ulno-dorsal aspect of Mc2, though this is extended across the dorsal aspect in the *P. troglodytes* comparison. The Mc3 of *Gorilla* was also had significantly higher RBV/TV than *P. paniscus* at landmarks on its dorso-ulnar aspect but was not significantly different from *P. troglodytes* in any region*. Gorilla* had less significant regional differences with *P. troglodytes* than with *P. paniscus* in RBV/TV.

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

Pan troglodytes

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

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

Pan paniscus

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

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

Multivariate whole-surface comparisons

Interspecific results

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

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

Inter-ray results

Figure 10 depicts the results of PCA of RBV/TV values, showing inter-ray differences within each species. Overall Mc head variation in RBV/TV across rays was different for each species but generally consistent with individual landmark comparisons described above. In *Pongo,* PC1 explained 33% of the variation and was driven by dorso-palmar landmark values, while PC2 explained 16% of the variation and reflected radio-ulnar landmark RBV/TV. The significant omnibus result was driven solely by a Mc2 configuration that had significantly higher disto-ulnar RBV/TV than Mc4 and Mc5.In *Gorilla,* PC1 reflected 27% of the variation as a result of radio-ulnar landmark values, while PC2 reflected 18% of the variation in RBV/TV due to distal and more dorso-palmarly located landmarks (Fig. 10). Permutational MANOVAs on PC1-3 demonstrated the *Gorilla* Mc5 had significantly higher RBV/TV disto-radially relative to all other rays. *Gorilla* Mc2 had significantly higher disto-ulnar RBV/TV than the other rays, whereas Mc3 and Mc4 had significantly higher RBVTV dorsally than Mc2 and Mc5 and were not significantly different from each other (Table 3). For *P. troglodytes* variation in overall RBV/TV was chiefly driven by dorso-palmar landmarks on PC1, which explained 31% of the variation, while PC2 explained 15% of the variation and reflected differences in the disto-ulnar landmarks. PC3 in *P. troglodytes* RBV/TV describes 12% of the variation and is driven by radio-ulnar landmarks (Fig. 10). *P. troglodytes* Mc2 had significantly higher RBTV/TV disto-palmarly on its ulnar aspect relative to all other rays whereas Mc5 had significantly higher RBV/TV disto-palmarly on its ulnar aspect compared to Mc2 and Mc3. While Mc3 and Mc4 were not significantly different from each other as both had higher dorsal RBV/TV, Mc4 was not significantly different from Mc5. In *Pan paniscus* PC1 explained 36% of the variance in RBV/TV and was driven by dorso-palmar landmarks while PC2 explained 25% of the variance and reflected distal and non-distal landmarks. However, no significant differences in RBV/TV were found between *P. paniscus* rays (Table3).

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

Discussion

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

Relative trabecular bone volume fraction

Pongo

We predicted the orangutans would show significantly higher RBV/TV in the disto-palmar region of the metacarpal heads compared to other hominids and that there would be no significant differences between rays, reflecting the flexed or neutral McP joint posture of all the fingers that characterises flexed-finger power, hook and double-locked grips typically used during arboreal locomotion (Rose, 1988; Sarmiento, 1988). We found general support for these predictions. Orangutans demonstrated significantly higher RBV/TV in the disto-palmar aspect of the subchondral trabeculae in all non-pollical metacarpal heads compared to that of all other taxa. We also found few inter-ray differences, with orangutans generally showing fewer significantly different landmarks in RBV/TV compared with gorillas and chimps (Fig. 5) and no significant difference in overall RBV/TV between adjacent rays (Table 3). The only exception to this was Mc2 of orangutans, which had significantly higher RBV/TV in the disto-dorsal region of its radial aspect, relative to the Mc4 and Mc5 (Figs. 5 and 10). Overall, our results are consistent with previous studies using differing methodologies that also found a higher BV/TV in the disto-palmar region of the orangutan Mc3 head (Zeininger et al., 2011; Tsegai et al., 2013; Skinner et al., 2015; Chirchir et al., 2017) and Mc5 head (Skinner et al. 2015).It should be noted, however, that present study sample includes five of the same Mc3 specimens and three of the Mc5 specimens used by Tsegai et al. (2013) and Skinner et al. (2015), respectively. The generally similar pattern of RBV/TV distribution across the Mc2-5 heads is consistent with using all of the fingers during power, hook and double-lock grips to grasp arboreal substrates (Rose, 1988). The diverging pattern found in the orangutan Mc2 could reflect the relatively more extended second digit posture during a diagonal double-locked grip of very thin substrates, as pictured by Napier (1960) in captivity (Supp. Fig.4). However, although challenging data to collect, more behavioural studies of types and frequency of hand grips used by orangutans during arboreal locomotion are needed to substantiate this.

Gorilla

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

Pan troglodytes

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

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

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

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

Pan paniscus

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

Trabecular anisotropy

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

High DA in orangutans did not support our predictions and appears contradictory to previous results showing significantly lower DA in orangutans and other suspensory taxa (Tsegai et al., 2013). However, Tsegai et al. (2013) quantified and averaged trabecular DA throughout the entire Mc3 head, as opposed to just the subchondral trabeculae, which can mask the signal of higher DA in particular regions of the head. In particular, subchondral trabeculae are responsible for the initial dissipation of load from the articular, compact cortical bone through to the more internal trabecular structure in long bones such as metacarpals (Currey, 2002). Thus it may be possible that trabeculae in this region are more constrained in their orientation, as they must link the cortical shell of the metacarpal head and the deeper trabecular structure, explaining the lack of variability in DA in our sample. If this is true, the variation in DA we did find, significantly higher DA in orangutans than in other species, might be due to a general lower number of trabeculae in orangutans. However, Chirchir et al. (2017) also found that DA was consistently, if not significantly, higher in orangutans compared with chimpanzees in all three of their VOIs which sampled most of the Mc3 head. Further higher DA has been found at superior-central region than in other regions of in the proximal *Pongo* humerus (Kivell et al. 2018).Therefore it is unlikely the significantly higher DA in orangutans is solely an artefact of sampling subchondral trabeculae.

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

Inferring bone functional adaptation

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

In the same vein, it could be argued that the lack of differences between chimpanzees and bonobos is due to their close phylogenetic distance rather than their similar locomotor regimes. Trabecular bone structure is controlled, at least to some extent, by genetic factors (Lovejoy et al., 2003, Havill et al., 2010, Judex et al., 2013, Almécija et al., 2015) and role of trabecular remodelling is not solely functional (Skinner et al., 2015, 2015b); for example, trabecular bone is also important for mineral homeostasis (Clarke, 2008). There were clear differences in absolute BV/TV, however, such that bonobos demonstrated much greater subchondral BV/TV in all elements of the hand studied compared to chimpanzees (Supp.Fig.7). This difference has been previously reported within the Mc3 of the same individuals in this study, for which the phylogenetic influence was assessed (Tsegai et al., 2013). The relative measure used here appears to have effectively controlled for this difference in subchondral metacarpal head BV/TV. This suggests that the absolute difference in BV/TV is not functional in origin, as it is unlikely bonobos practise a form of locomotion very similar to chimpanzees but with remarkably greater force. The only comparable kinematic data available demonstrates both captive chimpanzees and captive bonobos experience similar peak pressures on their fingers during arboreal knuckle walking (Wunderlich and Jungers, 2009; Samuel et al., 2018). If not functional in origin the absolute difference in BV/TV between chimpanzees and bonobos may be systemic. Though a study of metatarsal trabeculae failed to find this difference in absolute BV/TV between chimpanzees and bonobos (Griffin et al., 2010), Tsegai et al. (2018) have noted that systemic differences in BV/TV between species may be variably pronounced at different anatomical sites. While the reasons for systemic differences in trabeculae might be varied, including hormones, diet and disparate intestinal biomes (Tsegai et al., 2018), the difference is marked between these phylogenetically close species. As a corollary it would seem that there is little reason to suspect non-functional systematic forces are driving the similarities between RBV/TV in *Pan* species. Although the relative measure appears to have effectively controlled for possible systemic differences in subchondral trabeculae of the non-pollical metacarpal heads there are still small differences between the species which, by process of elimination, appear to be functional origin.

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

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

Conclusion

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

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Supplementary material

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

Supporting Information Figure 2. DA plots showing species differences within each metacarpal head. Each plot shows the first two principle components (PC) in each ray. 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.

Supporting Information Figure 3. DA PCA plots showing ray differences within each species. Each plot shows the first two principle components (PC) in each ray. For *Gorilla*, PC3 is depicted with PC1, inset, as PC2 and PC3 explain a similar amount of the variance (11% and 9% 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.

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

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

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

Supporting Information Figure 7. Species average absolute BV/TV, mapped to average models of each Mc head in **a)** distal, **b)** palmar and **c)** dorsal views. Note that absolute BV/TV interspecies or inter-ray comparisons are more likely to reveal overall differences in subchondral BV/TV than differences in the regional distribution of BV/TV, which are consistent with certain McP postures, as 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 - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - 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 - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - Ptv	Ggg - Pp	Ggg - Ppy	Ggg - Ptv	Pp - Ppy	Pp - Ptv	Ppy - 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.

	Gorilla gorilla				*Pan paniscus*				*Pongo spp.*				*Pan troglodytes*			
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

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

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

Pan paniscus	MRAC_15293	Female	Left	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_15294	Male	Left	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_20881	Male	Left	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_27696	Male	Right	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_27698	Female	Left	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_29042	Female	Right	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_29044	Male	Right	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_29045	Female	Left	Royal Museum for Central Africa, Tervuren
Pan paniscus	MRAC_29052	Male	Right	Royal Museum for Central Africa, Tervuren
Pan paniscus	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.

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