LJMU Research Online

Georgiou, L, Kivell, TL, Pahr, DH, Buck, LT and Skinner, MM

Trabecular architecture of the great ape and human femoral head

http://researchonline.ljmu.ac.uk/id/eprint/12621/

Article

For more information please contact researchonline@ljmu.ac.uk

Trabecular architecture of the great ape and human femoral head

Leoni Georgiou[1], Tracy L. Kivell[1,2], Dieter H. Pahr[3,4], Laura T. Buck[5], Matthew M. Skinner[1,2]

[1] Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom

[2] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[3] Institute for Lightweight Design and Structural Biomechanics, Vienna University of Technology, Vienna, Austria

[4] Department of Anatomy and Biomechanics, Karl Landsteiner Private University of Health Sciences, Krems an der Donau, Austria

[5] Department of Anthropology, University of California, Davis, California, United States of America

Corresponding Author:
Leoni Georgiou[1]
School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom
Email address: lg400@kent.ac.uk

Trabecular architecture of the great ape and human femoral head

Abstract

Studies of the femoral trabecular structure have shown that the orientation and volume of bone is associated with variation in loading and could be informative about individual joint positioning during locomotion. In this study we analyse for the first time trabecular bone patterns throughout the femoral head using a whole-epiphysis approach to investigate how potential trabecular variation in humans and great apes relates to differences in locomotor modes. Trabecular architecture was analysed using microCT scans of *Pan troglodytes* (n=20), *Gorilla gorilla* (n=14), *Pongo* sp. (n=5) and *Homo sapiens* (n=12) in medtool 4.1. Our results revealed differences in bone volume fraction (BV/TV) distribution patterns, as well as overall trabecular parameters of the femoral head between great apes and humans. *Pan* and *Gorilla* showed two regions of high BV/TV on the femoral head, consistent with hip posture and loading during two discrete locomotor modes; knuckle-walking and climbing. Most *Pongo* specimens also displayed two regions of high BV/TV, but these regions were less discrete and there was more variability across the sample. In contrast, *Homo* showed only one main region of high BV/TV on the femoral head and had the lowest BV/TV, as well as the most anisotropic trabeculae. The *Homo* trabecular structure is consistent with stereotypical loading with a more extended hip compared with great apes, which is characteristic of modern human bipedalism. Our results suggest that holistic evaluations of femoral head trabecular architecture can reveal previously undetected patterns linked to locomotor behaviour in extant apes and can provide further insight into hip joint loading in fossil hominins and other primates.

Key words: hominid, African apes, *Gorilla*, *Pan*, *Pongo*, cancellous bone, functional morphology.

Introduction

The morphology of the proximal femur has played a key role in the reconstruction of locomotion in extant and extinct primates (e.g. McHenry and Corruccini, 1978; Burr et al. 1982; Ruff et al. 1991; Ruff and Runestad, 1992; Ruff, 1995; Harmon, 2007; Harmon, 2009a; Ruff and Higgins, 2013) and particularly to understand the form of bipedalism used by australopiths (Stern and Susman, 1983; Susman et al. 1984; Crompton, et al. 1998; Carey and Crompton, 2005; Harmon, 2009b; Lovejoy and McCollum, 2010; Raichlen et al. 2010; DeSilva et al. 2013). External morphology provides ample evidence about functional links between morphology and locomotion. However, due to phylogenetic lag, inferences about behaviour based on external traits alone have been questioned (e.g. Ward, 2002). Variation in internal trabecular bone structure across different regions of the skeleton can provide additional evidence to help reconstruct joint postures and to infer potential differences in locomotor behaviour in extant and extinct primates (e.g. Thomason 1985a,b; Ryan and Ketcham, 2002; Volpato et al. 2008; Ryan and Shaw, 2012; Tsegai et al. 2013; Skinner et al. 2015; Stephens et al. 2016). Indeed, the ability of trabecular bone to reflect mechanical loading was first noted in the human proximal femur (Ward, 1838; Wolff 1870, 1892). It is not yet fully understood how mechanical or non-mechanical factors trigger and ultimately affect the organisation of trabeculae. For example, a range of activities, including high strain/low frequency loading or low strain/high frequency loading have been shown to elicit trabecular reorganisation (Rubin et al. 1990; Rubin et al. 2001; Judex et al. 2003; Wallace et

78 al. 2014). Furthermore, differences in body mass (Scherf, 2008; Cotter et al. 2009; Doube et
79 al. 2011; Fajardo et al. 2013; Ryan and Shaw, 2013), hormones (e.g. Gunness-Hey and Hock,
80 1984; Miyakoshi, 2004; Walsh, 2015), and genetic or systemic factors (Havill et al. 2010;
81 Tsegai et al. 2018) have been shown to influence aspects of trabecular structure as well.
82 However, computational (e.g. Huiskes et al. 2000; Keaveny et al. 2001) and experimental
83 studies have demonstrated that modelling of trabeculae is correlated with applied loads, and
84 trabecular strut reorganisation can be instigated by changes in the direction, magnitude and/or
85 frequency of load (Biewener et al. 1996; Mittra et al. 2005; Pontzer et al. 2006; Polk et al,
86 2008; Barak et al. 2011). Furthermore, trabecular bone volume fraction (BV/TV) and
87 trabecular strut alignment (degree of anisotropy, or DA) explain up to 98% of bone stiffness
88 (i.e. Young's modulus of elasticity) (Stauber et al. 2006; Maquer et al. 2015; Odgaard et al.
89 1997). Thus, variation in the distribution of BV/TV and DA can provide insight into joint
90 loading and, in turn, locomotor behaviours in primates.
91
92 Several studies have revealed that variation in the trabecular architecture of the primate hip
93 and proximal femur is associated with differences in locomotion (e.g. Rafferty and Ruff,
94 1994; MacLatchy and Muller, 2002; Volpato et al. 2008; Ryan and Shaw, 2012; Saers et al.
95 2016). For example, Volpato and colleagues (2008) demonstrated that the orientation of
96 trabecular struts in the ilium and femoral neck is associated with joint positioning in the hip
97 of bipedally-trained Japanese macaques and reflects alterations in the direction of load.
98 Comparable changes in trabecular structure that reflect differences in joint orientation were
99 found in the distal femora of guinea fowls (Pontzer et al. 2006) and distal tibiae of sheep
100 (Barak et al. 2011). Furthermore, Scherf (2008) found that trabecular structure within the
101 femoral head, neck and both trochanters of climbing primates (e.g. *Alouatta seniculus*) had
102 more isotropic architecture, while specialised primates (e.g. *Homo sapiens*) in which the
103 femur experienced more stereotypical loading had more anisotropic structure. Similar results
104 were found in leaping primates, which in comparison to non-leaping primate species, had
105 more anisotropic trabeculae in the inferior aspect of the femoral head (Ryan and Ketcham,
106 2002), and a different principal strut orientation (Ryan and Ketcham, 2005).
107
108 More recently, Ryan and Shaw (2012) investigated the trabecular patterns of the femoral head
109 of several anthropoid taxa and found that different suites of trabecular variables could
110 distinguish among taxa and locomotor groups. In particular, modern humans were distinct in
111 having relatively few, highly anisotropic trabeculae that are thin and plate-like, *Pan* had
112 relatively numerous, thick and isotropic trabeculae, while *Pongo* had relatively few and
113 isotropic. Additional studies investigating different human samples have also shown that
114 femoral head trabecular structure reflects variation in mobility levels, with more sedentary
115 agriculturalists having relatively low BV/TV compared with more active foragers (Ryan and
116 Shaw, 2015; Saers et al. 2016; Ryan et al. 2018). Interestingly, more active human foragers
117 have relatively high BV/TV that falls within the range of most extant hominoids apart from
118 *Pan* (Ryan et al. 2018). Despite this overlap in BV/TV between some human samples and
119 other hominoids, humans have consistently been shown to have the most anisotropic femoral
120 head structure compared to other great apes (Ryan and Shaw, 2015; Ryan et al. 2018).
121 Furthermore, the human trabecular pattern has been shown to develop during ontogeny when
122 independent bipedalism develops and the gait matures (Ryan and Krovitz, 2006; Reissis and
123 Abel, 2012; Milovanovic et al. 2017). Altogether, these studies suggest that the trabecular
124 studies suggest that the trabecular bone of the femoral head may hold a strong functional
125 signal of locomotor loading within primates.
126

127 Conversely, other studies have failed to detect a strong locomotor signal in the femoral head
128 (Ryan and Walker, 2010; Shaw and Ryan, 2012), femoral neck (Fajardo et al. 2007) and
129 distal femur (Carlson et al. 2008). Carlson and colleagues (2008) did not detect differences in
130 the DA of the distal femoral metaphysis between mice with turning locomotion and mice
131 with non-turning locomotion. Similarly, Ryan and Walker (2010) did not find any significant
132 differences in the DA and BV/TV patterns of the femoral head in a broad sample of
133 platyrrhines and catarrhines. Furthermore, Shaw and Ryan (2012), who examined the
134 subarticular trabecular and mid-diaphyseal cortical patterns in the femur and humerus of a
135 sample of primates, concluded that only the mid-diaphyseal cortical bone contains a clear
136 functional signal linked to the differential use of the two limbs between different locomotor
137 groups.
138
139 The discrepancy in the findings of previous studies may, in part, be an artefact of the volume-
140 of-interest (VOI) method that was used. A VOI quantifies only a subsample of trabecular
141 structure within a given region and results can vary depending on its size and position
142 (Fajardo and Müller, 2001; Kivell et al. 2011). Additionally, challenges arise when extracting
143 homologous VOIs in taxa that vary in external morphology. Prior research has demonstrated
144 that additional functional insight can be gained from investigating the trabecular architecture
145 within an epiphysis as a whole (Tsegai et al. 2013; Skinner et al. 2015; Stephens et al. 2016;
146 Sylvester and Terhune, 2017; Tsegai et al. 2018). Here we apply a whole-epiphysis approach
147 to study the trabecular structure throughout the femoral head of chimpanzees (*Pan
148 troglodytes*), lowland gorillas (*Gorilla gorilla*), orangutans (*Pongo* sp.) and humans (*Homo
149 sapiens*), which vary in locomotor behaviours and are relevant to the reconstruction of
150 locomotion in fossil hominins.
151
152 *Locomotion, hip morphology and predicted joint posture*
153
154 Habitual locomotor activities and the associated hip joint angles vary between great apes and
155 humans (Fig. 1). Chimpanzees are predominantly terrestrial/arboreal quadrupedal knuckle-
156 walkers, but also engage frequently in arboreal climbing and, less so, bipedalism (Hunt,
157 1991; Doran, 1992, 1993). In all these locomotor modes, the hindlimb plays key role in
158 propulsion and experiences higher vertical force than the forelimb (Demes et al. 1994;
159 Hannah et al. 2017). During terrestrial quadrupedalism in chimpanzees, the mean hip angle at
160 foot touchdown is 65° and at toe-off it is 98.2° (Finestone et al. 2018). Kinematics during
161 chimpanzee vertical climbing have, to our knowledge, only been studied in one individual
162 and show that the flexion-extension range at the hip increases substantially compared with
163 terrestrial quadrupedalism, with hip angles ranging from ~25° to ~105° (Nakano et al. 2006).
164 A more comprehensive study of bonobos (n=4 adults), which share similar hindlimb anatomy
165 to chimpanzees (e.g. Payne et al. 2006; Myatt et al. 2011), yielded hip angles ranging from
166 55° to 135° during vertical climbing (Isler, 2005).
167
168 Lowland gorillas are also predominantly quadrupedal knuckle-walkers (Remis, 1995;
169 Crompton et al. 2010). They often engage in arboreal climbing and bipedalism, but less
170 frequently than chimpanzees (Remis, 1995; Crompton et al. 2010). During terrestrial
171 quadrupedalism in gorillas, hip angles range from 77° at foot touchdown to 120.6° at toe-off
172 (Finestone et al. 2018). During vertical climbing, their hip angle range is similar to that of
173 bonobos, ranging from approximately 45° to 135° (Isler, 2005). *Gorilla* climbing frequency
174 and technique varies with sex and body size, with the range of hip flexion-extension being
175 reduced in larger males compared to smaller females (Remis, 1995; Remis, 1999; Isler,

4

176 2005). However, gorillas show less intraspecific variation in climbing techniques than
177 bonobos (Isler, 2005).
178
179 Orangutans employ a complex set of locomotor behaviours, which are mostly torso
180 orthograde, including vertical climbing, bridging, suspension from various limbs, and
181 terrestrial quadrupedalism (Cant, 1987; Isler and Thorpe, 2003; Thorpe and Crompton, 2006;
182 Thorpe et al. 2009). Their hips are more mobile than those of other apes, which allows them
183 to use their hindlimbs in more varied ways (Morbeck and Zihlman, 1988; Tuttle and
184 Cortright, 1988; Isler, 2005). During terrestrial locomotion, the orangutan hip angle is 68.3°
185 at touchdown and 107.3° at toe-off (Finestone et al. 2018). During vertical climbing,
186 orangutans are able to lift their feet further above their hips than African apes, such that their
187 flexion-extension angle ranges from around 30° to 135° (Isler, 2005).
188
189 Adult humans walk exclusively terrestrially on two legs, extending both their hips and knees
190 (Alexander, 1994). During the gait cycle, hip extension reaches 160° at touchdown and 175°
191 at toe-off (Abbass and Abdulrahman, 2014). Humans also engage in running, which alters the
192 joint angle of the hip and the resulting load on the femoral head (Ounpuu, 1990; Ounpuu,
193 1994; van den Bogert et al. 1999; Giarmatzis et al. 2015). Increase in speed is linked to more
194 flexed hip joints and a generally increased range of motion at the hip (Mann and Hagy, 1980;
195 Novacheck, 1998). At touchdown during running the hip is flexed at 30-40°, while also being
196 externally rotated, and at push off it is extended and internally rotated (Slocum and James,
197 1968). Furthermore, during running (3.5m/s), loads have been shown to increase to greater
198 than double that of walking (1.5 m/s) (van den Bogert et al.1999).
199
200   [Insert **Figure 1** about here]
201
202 Great apes and humans vary in the external morphology of the hip joint. Chimpanzees and
203 gorillas have a relatively small femoral head, a short femoral neck as well as a
204 superoinferiorly expanded greater trochanter compared to orangutans (McHenry and
205 Corruccini, 1978; Harmon, 2007). Chimpanzees have a "laterally facing acetabulum"
206 (Jenkins, 1972), however comparative quantitative data between apes do not exist
207 (Hogervorst et al. 2009 and references therein). Furthermore, in gorillas the acetabulum is
208 relatively deep, compared to other apes (Schultz, 1969), perhaps reducing capacity for
209 mobility at the hip. In orangutans the greater trochanter is less superoinferiorly expanded than
210 in the African apes and is positioned inferiorly to the femoral head, which may enhance
211 rotational capacity at the hip joint (Aiello and Dean, 2002; Harmon 2007). Orangutans also
212 have a relatively large head, long neck, and a greater trochanter that is less superoinferiorly
213 expanded than that of African apes and positioned inferiorly relative to the femoral head
214 (Aiello and Dean, 2002; Harmon, 2007). These features of the orangutan proximal femur,
215 plus the absence of a subchondral ligamentum teres insertion at the centre of the femoral head
216 (Crelin, 1988; Ward, 1991; Ruff, 2002; Harmon, 2007), enhance rotational capacity and
217 allow greater mobility at the hip joint compared to other hominoids.
218
219 Humans have a long femoral neck and valgus angle at the knee, which compensate for the
220 mechanical disadvantage of the increased bi-acetabular distance (Lovejoy, 1975; McHenry
221 and Corruccini, 1978; Rafferty, 1998; Lovejoy et al. 2002; Harmon, 2007) and result in
222 adduction of the hips during the stance phase (O'Neill et al. 2015). The greater trochanter is
223 less superoinferiorly expanded compared to other apes (Harmon, 2007). Furthermore, the
224 human acetabulum is relatively deep and the femoral head is relatively large (Schultz, 1969;
225 Jungers, 1988). This hip morphology is thought to help dissipate the increased load that

226 occurs when supporting body mass over two, rather than four, limbs. Biomechanical studies
227 have revealed that the peak contact force on the human hip during walking is directed
228 posteriorly, laterally and inferiorly (Pedersen et al. 1997), is located at the posterior aspect
229 (Paul, 1976; English and Kilvington, 1979), and pressure on the acetabulum is mainly located
230 posteriorly during different activities, such as standing up or sitting down (Yoshida et al.
231 2006). Lack of congruence between the femoral head and the acetabulum, combined with an
232 anterior-facing acetabulum result in the anterior region of the femoral head not being fully
233 covered by the acetabulum during bipedal locomotion (Hogervorst et al. 2009; Bonneau et al.
234 2014). Thus, the anterior region of the femoral head and acetabulum play a smaller role in
235 load transmission compared to other regions of the hip joint.

237 Examining the potential links between internal femoral bone structure and extant ape
238 locomotion will greatly facilitate attempts to reconstruct the locomotion of extinct hominins.
239 Here we provide this comparative context by analysing the trabecular architecture throughout
240 the entire femoral head in extant great apes and humans that vary in their locomotor
241 behaviours. We quantify BV/TV, DA, trabecular number (Tb.N), trabecular separation
242 (Tb.Sp) and trabecular thickness (Tb.Th) throughout the femoral head. Based on locomotor
243 and biomechanical studies reviewed above, we make the following predictions regarding
244 species variation in femoral head trabecular structure:

246 *1. BV/TV distribution in the femoral head*

248 The distribution of BV/TV throughout the femoral head will reflect joint positioning and
249 loading during habitual locomotion. In *Pan* we expect high BV/TV to extend from the
250 posterior and superior aspect of the femoral head to the anterior region, reflecting hip angles
251 and loading during knuckle-walking locomotion and vertical climbing (Finestone et al. 2018;
252 Isler 2005). We predict that *Gorilla* will show a similar pattern of BV/TV distribution,
253 although the region of high BV/TV is expected to extend over a smaller area of the femoral
254 head compared with that of *Pan*, reflecting a reduced range of motion (Hammond, 2014) and
255 different flexion/extension angles at the *Gorilla* hip during knuckle-walking and climbing
256 (Finestone et al. 2018; Isler 2005). We predict that *Pongo* will show the most variable
257 BV/TV distribution pattern, reflecting loading of the femoral head at different hip joint
258 angles, with high BV/TV spanning the whole of the superior area of the femoral head.
259 Finally, we expect a more restricted region of high BV/TV in *Homo* that will be concentrated
260 superiorly and posteriorly on the femoral head, reflecting the stereotypical loading pattern of
261 bipedal locomotion.

263 *2. Mean trabecular parameters in the femoral head*

265 Relative interspecific differences in mean BV/TV values will be consistent with those of
266 previous trabecular studies on the femur (e.g. Georgiou et al. 2018; Ryan et al. 2018; Tsegai
267 et al. 2018) and other postcranial elements (e.g. Maga et al. 2006; Cotter et al. 2009; Scherf et
268 al. 2013; Tsegai et al. 2013; Tsegai et al. 2017), such that *Pan* will have the highest BV/TV,
269 *Homo* will have the lowest, and *Gorilla* and *Pongo* will be intermediate between these two
270 taxa. Furthermore, mean DA of the entire femoral head will reflect the range of motion of the
271 hip joint during habitual locomotion. *Pan* and *Gorilla* will display intermediate DA values,
272 showing less anisotropic femoral heads than *Homo*, because they engage in both terrestrial
273 and arboreal behaviours that employ an increased range of motion at the hip. *Pongo* will be
274 the most isotropic, reflecting their highly mobile hip joint and diverse positioning of the
275 proximal femur during their varied quadrumanous locomotor behaviours. *Homo* will be the

276 most anisotropic, consistent with more stereotypical loading of the hip joint during bipedal
277 locomotion.
278
279 In addition to BV/TV and DA, we quantify mean Tb.N, Tb.Sp and Tb.Th within the femoral
280 head to better understand potential variation in the trabecular architecture across our sample
281 and for comparison with previous studies (e.g. Ryan and Shaw, 2012; Ryan and Shaw, 2015;
282 Ryan et al. 2018). In primates these parameters scale negatively allometrically to body size
283 (Barak et al. 2013; Ryan and Shaw, 2013) meaning results may be affected by body mass.
284 BV/TV and DA are expected to better reflect functional adaptations, as DA does not to scale
285 with body mass and BV/TV either shows no relationship (Doube et al. 2011; Barak et al.
286 2013) or a weak positively allometric relationship (Ryan and Shaw, 2013) with body mass.
287
288
289 **Methodology**
290
291 *Study sample*
292
293 Micro-computed tomographic scans were used to analyse trabecular morphology in the
294 femoral head of great apes and humans. Details of the study sample are provided in Table 1.
295 The *P. troglodytes* sample (n=20) is comprised of two subspecies; *Pan troglodytes verus*
296 (n=15) from the Taï Forest collection curated at the Max Planck Institute for Evolutionary
297 Anthropology in Leipzig, Germany, and *Pan troglodytes troglodytes* (n=5) curated at the
298 Smithsonian National Museum of Natural History in Washington, D.C., USA. The *Gorilla*
299 *gorilla gorilla* sample (n=14) is from the Powell-Cotton Museum, UK, of which 13
300 individuals are from Cameroon and one is from the Democratic Republic of the Congo. The
301 *Pongo* sample (n=5 and all female) is from the Zoologische Staatssammlung München,
302 Germany. Four of the individuals are *P. pygmaeus*, while one is *P. abelii*. The *H. sapiens*
303 sample (n=12) is curated at the Georg-August-Universität Göttingen, Germany. Ten of the
304 individuals come from a Catholic cemetery in Göttingen, which was used between 1851 and
305 1889, and two come from a cemetery in the village of Inden that was used between 1877 and
306 1924. All specimens were adult based on complete epiphyseal fusion throughout the skeleton
307 and none showed obvious signs of pathology.
308
309 The *Pan*, *Pongo* and *Homo* samples were scanned at the Department of Human Evolution in
310 the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany using a BIR
311 ACTIS 225/300 industrial microCT scanner. The *Gorilla* sample was scanned at the
312 Cambridge Biotomography Centre in the Department of Zoology at the University of
313 Cambridge, Cambridge, UK using a Nikon XT 225 ST microCT scanner. All specimens were
314 scanned at the highest possible resolution based on the size of the bone, ranging from 0.029-
315 0.082 mm, and were reconstructed into 16-bit TIFF stacks with isometric voxel sizes.
316 Reconstructed datasets were re-oriented to the same anatomical position and cropped in
317 AVIZO 6.3 ® (Visualization Sciences Group, SAS). All specimens, except six gorillas, were
318 re-sampled due to computational limitations of medtool 4.1 and resultant resolutions are
319 given in Table 1. Bone was segmented from air using the Ray Casting Algorithm (Scherf and
320 Tilgner, 2009).
321
322 *Trabecular architecture analysis*
323
324 Patterns of trabecular bone distribution throughout the whole femoral head were analysed in
325 medtool 4.1 (www.dr-pahr.at), following the protocol described by Gross and colleagues

(2014). A series of morphological filters were applied to identify and remove the cortical shell, thus isolating the trabecular structure. The resulting isolated trabecular structure was used to calculate trabecular thickness using the BoneJ plug-in (version 1.4.1, Doube et al. 2010) for ImageJ (Schneider et al. 2012) to validate the parameters used in the morphological filters for the separation of the cortical shell (see Gross et al. 2014). The original dataset and trabecular structure were used to create a trinary mask defining the outer air, inner air and trabecular bone. A 3D rectangular background grid with a size of 3.5mm was superimposed on the trabecular structure and a sphere with a diameter of 7.5mm was used to measure BV/TV at each node in medtool 4.1. BV/TV was calculated as the ratio of bone to total volume in the sampling spheres. The isolated trabecular structure and a mesh size of 0.6mm were used to create 3D tetrahedral meshes of all individuals, using CGAL 4.4 (CGAL, Computational Geometry, http://www.cgal.org) and BV/TV values were then interpolated on the tetrahedral elements of each mesh. Distribution maps of BV/TV were visualised using Paraview v4.0.1 (Ahrens et al. 2005). The femoral head for each specimen was manually isolated in AVIZO 6.3 ® by positioning the mediolateral axis facing superoinferiorly and cropping at the head-neck junction to ensure homology across specimens. Mean trabecular parameters (BV/TV, DA, Tb.N, Tb.Sp, Tb.Th) for the entire head were calculated using an in-house script. DA was calculated as DA= 1 – [smallest eigenvalue/largest eigenvalue], as they were calculated using the mean-intercept-length method (Whitehouse, 1974; Odgaard, 1997). Tb.Sp and Tb.Th were calculated based on the Hildebrand and Ruesegger (1997) method; Tb.N was then calculated as Tb.N=1/(Tb.Th+Tb.Sp). Mean BV/TV, DA, Tb.Sp and Tb.Th were calculated by averaging the values at each voxel of the trinary mask throughout the epiphysis. Mean Tb.N was calculated from the means of Tb.Sp and Tb.Th.

Statistical analysis

Statistical analysis was performed in R v3.4.1 (R Core Team, 2017). The Kruskal-Wallis test was used to evaluate interspecies differences in mean trabecular parameters (BV/TV, DA, Tb.N, Tb.Sp, Tb.Th) of the femoral head and a Wilcoxon rank sum test with Bonferroni correction was used for post-hoc pairwise comparisons.

Results

BV/TV distribution in the femoral head

In *Pan*, BV/TV distribution maps of the femoral head reveal concentrations of high BV/TV in the superior aspect of the femoral head (Fig. 2). In most *Pan* individuals (n=12) there are two distinct concentrations, one located more posteriorly and one located more anteriorly, whereas in some individuals one concentration spans across the whole of the superior region of the articulation. While the posterior concentration is always present in *Pan*, the location, extent and isolation of the anterior concentration varies between individuals.

[Insert **Figure 2** about here]

The pattern of BV/TV distribution in *Gorilla* is similar to that found in *Pan* (Fig. 3). Two concentrations of high BV/TV are seen in the superior aspect, one located anteriorly, and one located posteriorly. Unlike in *Pan* however, these concentrations are distinct from each other in all but three *Gorilla* individuals, in which a region of high BV/TV spans across the

375 superior region of the femoral head. There is no apparent difference in the size of the two
376 regions of high BV/TV.
377
378   [Insert **Figure 3** about here]
379
380 *Pongo* shows a slightly different BV/TV pattern compared to *Pan* and *Gorilla* (Fig. 4)*. The
381 P. pygmaeus* individuals show the two concentrations of high BV/TV, one in the anterior and
382 one in the posterior, similar to what is found in the African apes, however intermediate values
383 persist over the superior portion of the femoral head. The extent of this concentration differs
384 between *P. pygmaeus* individuals; in two individuals it is restricted more in the superior
385 aspect of the head, whereas in the other two it is enlarged and covers the majority of the
386 femoral head, from the anterior to the posterior. When the two concentrations are more well
387 defined, the posterior concentration is generally more mediolaterally expanded than the
388 anterior concentration. The *P. abelii* individual shows lower BV/TV than the other specimens
389 and does not show two distinct concentrations.
390
391   [Insert **Figure 4** about here]
392
393 *Homo* shows a different pattern to the great apes (Fig. 5). All individuals show one region of
394 high BV/TV located in the posterior and superior aspect of the femoral head. Intermediate
395 values of BV/TV expand across the whole of the superior aspect of the head of *Homo*, but
396 with no apparent second concentration of high BV/TV in the anterior region as found in great
397 apes. *Homo* individuals also display intermediate BV/TV on the inferior aspect of the head.
398 This expansion of intermediate BV/TV values along the inferior is not seen in the other apes.
399
400   [Insert **Figure 5** about here]
401
402
403 *Quantitative analysis of trabecular parameters in the femoral head*
404
405 Quantitative analysis of the mean trabecular parameters over the femoral head revealed
406 several differences across taxa. Results for each parameter in the different taxa are presented
407 in Table 2 and statistical results of species pairwise comparisons, after Bonferroni
408 corrections, are presented in Table 3. *Pan* shows significantly higher BV/TV in the femoral
409 head than *Pongo* ($p=0.05$) and *Homo* ($p<0.001$), and although its mean BV/TV value was
410 higher than that of *Gorilla*, this difference was not statistically significant (Tables 2 and 3).
411 *Homo* has the lowest mean BV/TV compared with all the great apes but is only significantly
412 different from *Pan*. *Homo* has significantly higher DA in the femoral head than all other apes
413 (*Pan* $p< 0.001$; *Gorilla* $p<0.05$; *Pongo* $p<0.01$), while *Pan, Pongo* and, less so, *Gorilla* are
414 more isotropic and not significantly different from each other. With regards to the
415 architectural parameters, *Pan* shows the most distinct trabecular structure with significantly
416 higher Tb.N than all other apes (*Gorilla* $p<0.001$; *Homo* $p<0.001$; *Pongo* $p<0.01$) and
417 significantly lower Tb.Sp (all $p<0.001$) and lower Tb.Th than *Gorilla* ($p<0.001$) and *Homo*
418 ($p<0.05$).
419
420 Differences in mean BV/TV and DA across taxa were further evaluated using a bivariate plot
421 (Fig.6) and a line histogram of the distribution of values in each taxon (Fig. 7). The data
422 depicted in these figures are mean values for each individual across the entire femoral head.
423 In the bivariate plot *Pan* shows a combination of high BV/TV and low DA, in contrast to
424 humans that show the opposite pattern. *Gorilla* overlaps with both of these taxa but shows

9

425 higher BV/TV than humans. *Pongo* individuals overlap with the African apes, with lower DA
426 values than humans, but with BV/TV values that overlap with all other taxa.
427
428 [Insert **Figure 6** about here]
429
430 This was also supported by the distribution of BV/TV and DA values in the taxa (Fig. 7). *Pan*
431 shows the highest mean BV/TV and high density close to the mean (0.39), whereas *Gorilla*
432 shows a lower mean value but high density between 0.3 and 0.4. *Pongo* shows a similar mean
433 to *Gorilla*, however the distribution of values more greatly resembles that of *Pan*. *Homo*
434 shows the lowest BV/TV values distributed over a wider area. The DA plot shows that *Pan,*
435 *Gorilla* and *Pongo* present similarly low mean DA values, but *Pongo* differs in distribution
436 with higher density around the mean. *Homo* shows a different distribution with the highest
437 mean DA but a wider distribution of values in the sample.
438
439 [Insert **Figure 7** about here]
440
441
442 **Discussion**
443
444 Our study investigated the variation in trabecular patterns of the femoral head in great apes
445 and humans. Qualitative and quantitative results supported our hypotheses that trabecular
446 bone would reflect differences in locomotor patterns, but not necessarily in the way we
447 predicted. *Pan* and *Gorilla* displayed a trabecular structure consistent with their terrestrial as
448 well as arboreal quadrupedal locomotion, while *Homo* showed a distinct trabecular pattern
449 indicative of stereotypical loading during bipedal locomotion. However, the African apes
450 showed a BV/TV distribution pattern that was different to what was expected, and their
451 trabecular structure did not differ significantly from *Pongo.*
452
453 *Distribution of BV/TV within the femoral head*
454
455 We predicted that African apes would display a region of high BV/TV extending from the
456 posteriosuperior to the anterior region of the femoral head, reflecting the flexed hip postures
457 and loading incurred during knuckle-walking and vertical climbing. However, instead of a
458 continuous ban of high BV/TV across the femoral head, *Pan* displayed two main regions of
459 high BV/TV, indicating two regions of high loading; one in the posterosuperior aspect of the
460 femoral head and one located more anteriorly. The majority of Taï chimpanzee (75% of the
461 *Pan* sample) locomotion is terrestrial quadrupedalism (Doran, 1993). Ground reaction forces
462 remain high throughout the stance phase during terrestrial knuckle-walking (Barak et al.
463 2013) and the hip remains flexed (Finestone et al. 2018), both of which are consistent with
464 high loading of the posterosuperior region of the femoral head and the high BV/TV
465 concentration that was found in this region. While Taï chimpanzees engage less frequently in
466 vertical climbing (Doran, 1993a), it is possible that this results in similarly high loading of
467 the femoral head, as it involves high propulsive forces from the hindlimbs (Hanna et al.
468 2017). During climbing, the hip can be flexed to a maximum of 25° to 55° (Isler, 2005;
469 Nakano et al. 2006), which would result in the anterior aspect of the head contacting the
470 lunate surface of the acetabulum. This is consistent with the second region of high BV/TV
471 found in the anterior portion of the femoral head in *Pan*. The anterior concentration was more
472 variable between individuals, but this could not be explained by subspecies differences within
473 the sample. Thus, the more variable anterior BV/TV pattern may reflect interindividual

10

474   variability in vertical climbing frequency (Doran, 1993b) or hip range of motion during
475   climbing (Isler, 2005; Nakano et al. 2006).
476
477   *Gorilla* displayed a similar pattern to *Pan*, with two regions of high BV/TV within the
478   femoral head. The two regions, one in the posterior and one in the anterior aspect of the head,
479   are, as in *Pan*, consistent with hip posture and loading during terrestrial quadrupedalism and
480   vertical climbing, as these modes of locomotion comprise the majority of *Gorilla* locomotion
481   (Doran, 1997; Crompton et al. 2010; Remis, 1995). However, unlike *Pan*, these regions were
482   better defined and more discrete in most *Gorilla* individuals (11 out of 14 individuals). This
483   more discrete pattern is perhaps due to their greater body mass. Greater mass is related to
484   restricted range of motion in joints (Hammond, 2014), which could result in less variability in
485   joint positioning during locomotion and may explain the more well-defined concentrations in
486   *Gorilla*. The two concentrations appeared closer to each other in *Gorilla* than in *Pan*, which
487   is also consistent with the reduced range of motion at the hip joint of *Gorilla* (Isler, 2005;
488   Hammond, 2014). Significant sex and body size related differences in joint mobility are
489   prominent in *Gorilla*, with females showing a larger range of motion than males and flexion-
490   extension ranges varying between the sexes by up to or even more than 30º (Isler, 2005;
491   Hammond, 2014). These differences were not detected in the BV/TV distribution maps and
492   *Gorilla* does not seem to be more variable than *Pan*. However, this could not be tested
493   statistically in the current study.
494
495   We predicted that the BV/TV distribution pattern of the *Pongo* femoral head would differ
496   from that of African apes and humans because of their more varied quadrumanous locomotor
497   behaviours (Thorpe and Crompton, 2005; Thorpe and Crompton, 2006), more mobile hip
498   joints (Crelin, 1988; Ward, 1991), and increased range of motion at the hip during vertical
499   climbing compared to African apes (Isler, 2005). Four of the five *Pongo* individuals in our
500   sample showed the same two regions of high BV/TV found in African apes, however these
501   were not as distinct and, instead, there was a continuous concentration of BV/TV spanning
502   across the superior aspect of the femoral head. This is perhaps unsurprising since *Pongo* use a
503   variety of hip postures while navigating their arboreal environment (Thorpe and Crompton,
504   2005; Thorpe and Crompton, 2006; Payne et al. 2006; Thorpe et al. 2009), which potentially
505   results in higher loading across the whole superior surface of the femoral head. *Pongo* also
506   vertically climbs less frequently than African apes (Thorpe and Crompton, 2006), which may
507   be reflected by the less defined anterior concentration of high BV/TV in *Pongo* compared
508   with *Pan* and, especially, *Gorilla*. Although our sample of *Pongo* is small (n=5) and all
509   individuals were female, there was greater variation in the BV/TV distributions along the
510   anterior and posterior aspects of the femoral head than was found in African apes. The one *P.*
511   *abelii* specimen in our sample differed from the *P. pygmaeus* individuals in having only one
512   superior concentration of high BV/TV. Although locomotor differences have been
513   documented between *P. pygmaeus* and *P. abelii* (Sugardjito and van Hooff, 1986; Cant,
514   1987), a larger sample of both species is needed to determine if this variation in the trabecular
515   pattern is characteristic of each species.
516
517   *Homo* showed a distinct trabecular pattern that is consistent with our predictions and similar
518   to previous results showing the density distribution of trabeculae adjacent to cortical bone
519   (Treece and Gee, 2014). All *Homo* individuals displayed one main region of high BV/TV,
520   located posteriorly and superiorly on the femoral head. This concentration was positioned
521   more medially than the posterior concentration seen in great apes and closer to the fovea
522   capitis, which is consistent with loading of the femur at a valgus angle. Intermediate BV/TV
523   values continued along the superior aspect of the femoral head in *Homo*. This is consistent

with loading that occurs throughout the gait cycle over the articulating surface but suggests that peak loading is occurring at the posterosuperior region, which is in contact with the acetabulum during walking (Bonneau et al. 2012; Bonneau et al. 2014). Of course, humans also engage in other activities that involve more flexed hip joint postures, such as running, jumping, or climbing stairs, all of which impose high loads on the lower limb (van den Bogert et al. 1999; Giarmatzis et al. 2015) and could result in some trabecular reorganisation, explaining the extended area of intermediate BV/TV values we found across the femoral head. Unfortunately, it is not yet known exactly how the peak load is distributed over the femoral head during these activities. However, all individuals lack the anterior concentration found in apes, further supporting the interpretation that high BV/TV in the anterior region could be linked to arboreal behaviours or more specifically vertical climbing.

Quantitative analysis of trabecular structure

Quantitative analysis of the femoral head trabecular structure only partially supported our hypotheses. As expected, *Homo* displayed the lowest mean BV/TV in our sample but was only significantly different from that of *Pan*. Our results confirm previous studies showing that modern humans, particularly those that are less active, have relatively lower BV/TV across the skeleton compared with highly mobile modern humans and other primates (Chirchir et al. 2015; Ryan and Shaw, 2015; Saers et al. 2016; Chirchir et al. 2017). Furthermore, *Homo* showed significantly higher DA than great apes, which is consistent with the more stereotypical loading of the hip joint during bipedal locomotion and in accordance with previous results from the proximal (Ryan and Shaw, 2015; Ryan et al. 2018) as well as the distal femur (Georgiou et al. 2018). *Homo* has narrower acetabulae than other great apes, with expanded cranial lunate surfaces, as well as shortened dorsal surfaces, which results in a distinctively-shaped dorso-cranially expanded lunate surface that may restrict movement in the parasagittal plane (San Millán et al. 2015). Furthermore, in *Homo* the iliofemoral ligament limits extension and external rotation (Myers et al. 2011), the ischiofemoral ligament limits internal rotation, while the pubofemoral ligament limits abduction (Wagner et al. 2012), all of which result in a more restrictive and stereotypical motion and loading of the femoral head that is reflected in the trabecular structure.

As predicted, mean BV/TV was highest in *Pan*, which is consistent with previous studies showing relatively high BV/TV in the African ape femur (Ryan and Shaw, 2015; Georgiou et al. 2018; Ryan et al. 2018; Tsegai et al. 2018) and other postcranial elements (e.g. Cotter et al. 2009; Scherf et al. 2013; Tsegai et al. 2017). BV/TV in *Pan* did not differ significantly from *Gorilla*, reflecting their generally similar locomotor repertoire. Overall, the quantitative analysis highlighted *Pan* as being distinct from the other taxa. *Pan* not only showed the highest BV/TV values, but also differed significantly to all taxa in Tb.N and Tb.Sp, showing consistently higher Tb.N and lower Tb.Sp, again resembling previous findings (Ryan and Shaw, 2015). Furthermore, *Pan* showed significantly lower Tb.Th than *Gorilla* and *Homo*. Additionally, mean DA was lowest in *Pan*, as well as *Pongo*, but only differed significantly from *Homo*. Less data is available about femoral ligaments of non-human apes however *Pan* and *Pongo* seem to have less restrictive ligaments than *Homo* (Sonntag, 1923; 1924).

The trabecular structure of *Gorilla* and *Pongo* was not as distinct. *Gorilla* mean BV/TV did not differ significantly from any other taxon, and they only differed significantly in Tb.N, Tb.Sp and Tb.Th from *Pan*, as well as in DA from *Homo*. *Gorilla* has less variable positioning of their lower limbs during locomotion, compared to other non-human apes, as was shown in vertical climbing (Isler, 2005), however this is not displayed as clearly in their

574   DA values as was initially predicted. The lack of significant differences in BV/TV and DA
575   with *Pan* can perhaps be explained by the similar shape of their hip joints (San Millán et al.
576   2015) and overall similarities in locomotion (Doran, 1997). None of great apes differed
577   significantly in DA, despite clear differences in locomotor behaviours and hip morphology.
578   *Pongo* has a cranio-ventrally expanded lunate surface and a smaller acetabular fossa than
579   other apes. They also show the largest articular surfaces and a relatively shallow acetabulum
580   (Schultz, 1969), which may be responsible for the increased mobility of the femoral head.
581   Furthermore, *Pongo* has a greater capacity for abduction and external rotation than non-
582   suspensory taxa (Hammond, 2014). Thus, *Pongo* was expected to display significantly lower
583   DA values than all other taxa, which was not the case, but this result may also reflect our
584   small sample size of this taxon.
585
586   Our result showed that *Pan* has relatively numerous, thinner and compactly organised
587   trabeculae, while *Gorilla* and *Homo* have relatively few, thicker and more separated
588   trabeculae. *Pongo* has relatively few, thinner and more separated trabeculae. These results are
589   largely in accordance with previous analyses of femoral head trabeculae (Ryan and Shaw,
590   2012; 2015) which showed that humans have relatively less numerous, thin and highly
591   anisotropic trabeculae compared to other anthropoids, *Pan* have relatively high numbers of
592   thick, isotropic trabeculae and *Pongo* have relatively few, isotropic trabeculae. *Gorilla*
593   showed the thickest trabeculae (Table 2), in support of previous studies suggesting that larger
594   taxa have absolutely thicker trabeculae (Barak et al. 2013; Ryan and Shaw, 2013; Tsegai et
595   al. 2013). However, the difference was not found to be significant, possibly due to the small
596   sample sizes in our study. Allometric relationships were not tested in our study because our
597   sample sizes were not large enough to test this intraspecifically, however previous research
598   has shown that these trabecular parameters can vary predictably with body size
599   interspecifically (Cotter et al. 2009; Doube et al. 2011; Barak et al. 2013; Ryan and Shaw,
600   2013). Across a large sample of mammals, Tb.Th and Tb.Sp were shown to increase with
601   size (Doube et al. 2011). In primates, Tb.N, Tb.Th and Tb.Sp present negatively allometric
602   relationships with body mass (Barak et al. 2013; Ryan and Shaw, 2013), resulting in more,
603   thinner and less separated trabeculae in larger taxa. These studies suggest that absolute
604   trabecular parameters, and specifically Tb.N, Tb.Sp and Tb.Th, do not necessarily directly
605   reflect locomotor modes as they could reflect body-size related or systemic differences
606   between taxa. Nevertheless, since our sample includes apes that are relatively similar in body
607   size compared to the more diverse samples of previous studies (Doube et al. 2011; Barak et
608   al. 2013; Ryan and Shaw, 2013), we would expect that allometry does not have a significant
609   effect on the variation observed here.
610
611   The absence of a clear functional signal in the mean trabecular parameters may be biased by
612   methodological limitations of the whole-epiphysis approach. The mean value of any given
613   trabecular parameter can obscure or homogenise any potential distinct variation in specific
614   regions of the femoral head, as demonstrated by the BV/TV distribution maps and previous
615   studies (Sylvester and Terhune, 2017). This is where the traditional VOI approach, in which
616   the trabecular architecture of specific regions of an epiphysis can be quantified and
617   compared, is potentially more functionally informative (e.g. Ryan and Shaw, 2012; 2015;
618   Ryan et al. 2018). Additionally, the lack of a strong functional signal in these parameters
619   could be due to non-mechanical factors affecting trabecular structure. Trabecular bone also
620   functions as a reserve of minerals and is important in maintaining homeostasis, hence its
621   structure will, to some extent, be affected by this (Rodan, 1998; Clarke, 2008). Genes control
622   for the rate of remodelling and bone mineral density, as well as the response to mechanical
623   strain in different skeletal sites (Smith et al. 1973; Dequeker et al. 1987; Kelly et al. 1991;

624 Garnero et al. 1996; Hauser et al. 1997; Judex et al. 2002; Judex et al. 2004). These along
625 with the fact that trabecular bone remodels in response to a range of magnitudes and
626 frequencies of load (Whalen et al. 1988; Rubin et al. 1990; Rubin et al. 2001; Judex et al.
627 2003; Scherf et al. 2013), complicate interpretations. Age, hormones, sex and other factors
628 (e.g. Simkin et al. 1987; Pearson and Lieberman, 2004; Suuriniemi et al. 2004; Kivell, 2016;
629 Wallace et al. 2017; Tsegai et al. 2018) influence trabecular bone modelling, thus these
630 factors should not be ignored.
631
632 **Conclusion**
633
634 This study showed that the trabecular architecture of the femoral head in great apes and
635 humans reflects habitual hip postures during locomotion. *Pan* and *Gorilla* showed similar
636 BV/TV distribution patterns, with generally two distinct high BV/TV regions that are
637 consistent with hip postures during knuckle-walking and vertical climbing. *Pongo* showed a
638 BV/TV distribution pattern that is characteristic of their highly mobile hips and complex
639 locomotion, however they do not differ as significantly as predicted from African apes.
640 Finally, *Homo* showed a distinct pattern of BV/TV distribution, with one posterosuperior
641 region of high BV/TV, the lowest overall BV/TV values and highest DA values, which is
642 consistent with stereotypical loading during locomotion. Despite mean trabecular parameters
643 not demonstrating locomotor differences as clearly as predicted, they largely match results
644 from previous VOI studies (Ryan and Shaw, 2015; Ryan et al. 2018). Our research reveals
645 that there are distinct patterns of BV/TV distribution that generally distinguish the locomotor
646 groups and provide a valuable comparative sample for future research on the evolution of gait
647 in hominins.
648
662
663
671
672
673 **References**

674

675 **Abbass SJ, Abdulrahman G** (2014) Kinematic Analysis of Human Gait Cycle. *Nahrain*
676 *University College of Engineering Journal (NUCEJ)* **16**, (2), 208-222.

677 **Ahrens J, Geveci B, Law C** (2005) ParaView: An end-user tool for large data visualization.
678 in Hansen CD, Johnson CR (eds). *Visualization handbook.* Butterworth- Heinemann,
679 Burlington. MA, 717-731.

680 **Aiello l, Dean C** (2002) *An Introduction to Human Eutionary Anatomy.* Academic Press, San
681 Diego.

682 **Alexander CJ** (1994) Utilisation of joint movement range in arboreal primates compared
683 with human subjects: an evolutionary frame for primary osteoarthritis. *Annals of the*
684 *Rheumatic Diseases* **53** (11), 720-725.

685 **Barak MM, Lieberman DE, Hublin J** (2011) A Wolff in sheep's clothing: Trabecular bone
686 adaptation in response to changes in joint loading orientation. *Bone* **49** (6), 1141-1151.

687 **Barak MM, Lieberman DE, Hublin J** (2013) Of mice rats and men: Trabecular bone
688 architecture in mammals scales to body mass with negative allometry. *Journal of Structural*
689 *Biology* **183** (2), 123-131

690 **Barak MM, Lieberman DE, Raichlen D, et al.** (2013) Trabecular Evidence for a Human-
691 Like Gait in Australopithecus africanus. *PLOS ONE* **8** (11), e77687

692 **Biewener AA, Fazzalari NL, Konieczynski DD, et al.** (1996) Adaptive changes in
693 trabecular architecture in relation to functional strain patterns and disuse. *Bone* **19**, 1-8.

694 **Bonneau N, Baylac M, Gagey O, et al.** (2014) Functional integrative analysis of the human
695 hip joint: The three-dimensional orientation of the acetabulum and its relation with the
696 orientation of the femoral neck. *The Journal of Human Evolution* **69**, 55-69.

697 **Bonneau N, Gagey O, Tardieu C** (2012) Biomechanics of the human hip joint. *Computer*
698 *Methods in Biomechanics and Biomedical Engineering*, **15**, 197-199.

699 **Burr DB, Piotrowski G, Martin RB, et al.** (1982) Femoral mechanics in the lesser
700 bushbaby (Galago senegalensis): Structural adaptations to leaping in primates. *Anatomical*
701 *Record* **202**, 419-429.

702 **Cant JG** (1987) Positional behavior of female bornean orangutans (Pongo pygmaeus).
703 *American Journal of Primatology* **12** (1), 71-90

704 **Carey TS, Crompton RH** (2005) The metabolic costs of 'bent-hip bent-knee' walking in
705 humans. *The Journal of Human Evolution* **48** (1), 25-44.

706 **Carlson KJ, Lublinsky S, Judex S** (2008) Do different locomotor modes during growth
707 modulate trabecular architecture in the murine hind limb? *Integrative and Comparative*
708 *Biology* **48** (3), 385–393.

709 **Chirchir H, Kivell TL, Ruff CB, et al.** (2015) Recent origin of low trabecular bone density
710 in modern humans. *Proceedings of the National Academy of Sciences* **112** (2), 366-371.

711 **Chirchir H, Ruff CB, Junno JA, et al.** (2017) Low trabecular bone density in recent
712 sedentary modern humans. *American Journal of Physical Anthropology* **162** (3), e23138.

713 **Clarke B** (2008) Normal Bone Anatomy and Physiology. *Clinical Journal of the American*
714 *Society of Nephrology* **3**, 131-139.

715 **Cotter MM, Simpson SW, Latimer BM, et al.** (2009) Trabecular Microarchitecture of
716 Hominoid Thoracic Vertebrae. *The Anatomical Record* **292** (8), 1098-1106.

717 **Crelin ES** (1988) Ligament of the head of the femur in the orangutan and Indian elephant.
718 *The Yale journal of biology and medicine* **61** (5), 383-388.

719 **Crompton RH, Sellers WI, Thorpe SKS** (2010) Arboreality terrestriality and bipedalism.
720 *Philosophical Transactions of the Royal Society B: Biological Sciences* **365** (1556), 3301-
721 3314.

722 **Crompton RH, Weijie LYW, Günther M, et al.** (1998) The mechanical effectiveness of
723 erect and) bent-hip bent-knee. bipedal walking in *Australopithecus afarensis*. *The Journal of*
724 *Human Evolution* **35** (1), 55-74.

725 **Demes B, Larson SG, Stern JT Jr, et al.** (1994). The kinetics of primate quadrupedalism:
726 "hindlimb drive" reconsidered. *Journal of human evolution* **26**, 353-374.

727 **Dequeker J, Nijs J, Verstraeten A, et al.** (1987) Genetic determinants of bone mineral
728 content at the spine and radius: A twin study. *Bone* **8** (4), 207-209.

729 **DeSilva JM, Holt KG, Churchill SE, et al.** (2013) The Lower Limb and Mechanics of
730 Walking in *Australopithecus sediba*. *Science* **340**, (6129).

731 **Doran DM** (1993a) Comparative locomotor behavior of chimpanzees and bonobos: The
732 influence of morphology on locomotion. *American Journal of Physical Anthropology* **91** (1),
733 83-98.

734 **Doran DM** (1993b) Sex differences in adult chimpanzee positional behavior: the influence of
735 body size on locomotion and posture. *American Journal of Physical Anthropology* **91**, 99-
736 115.

737 **Doran DM** (1997) Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal*
738 *of human evolution* **32** (4), 323-344.

739 **Doube M, Kłosowski MM, Wiktorowicz-Conroy A, et al.** (2011) Trabecular bone scales
740 allometrically in mammals and birds. *Proceedings of The Royal Society: Biological sciences*
741 **278** (1721), 3067-3073

742 **Doube M, Kłosowski MM, Arganda-Carreras I, et al.** (2010) BoneJ: Free and extensible
743 bone image analysis in ImageJ. *Bone* **47** (6), 1076-1079

744 **English TA, Kilvington M** (1979) In vivo records of hip loads using a femoral implant with
745 telemetric output (a prelimary report). *Journal of Biomedical Engineering* **1** (2), 111-115.

746 **Fajardo RJ, DeSilva JM, Manoharan RK, et al.** (2013) Lumbar vertebral body bone
747 microstructural scaling in small to medium-sized strepsirhines. *Anatomical Record* **296**, 210-
748 226.

749 **Fajardo RJ, Müller R** (2001) Three-dimensional analysis of nonhuman primate trabecular
750 architecture using micro-computed tomography *American Journal of Physical Anthropology*
751 **115**, 327-336.

752 **Fajardo RJ, Müller R, Ketcham RA, et al.** (2007) Nonhuman anthropoid primate femoral
753 neck trabecular architecture and its relationship to locomotor mode. *The Anatomical Record:*
754 *Advances in Integrative Anatomy and Evolutionary Biology* **290** (4), 422-436.

755 **Finestone EM, Brown MH, Ross SR, et al.** (2018) Great ape walking kinematics:
756 Implications for hominoid eution. *American Journal of Physical Anthropology* **166** (1), 43-
757 55.

758 **Garnero P, Arden NK, Griffiths G, et al.** (1996) Genetic influence on bone turnover in
759 postmenopausal twins. *The Journal of Clinical Endocrinology, Metabolism* **81** (1), 140-146

Giarmatzis G, Ilse J, Mariska W, et al. (2015) Loading of Hip Measured by Hip Contact Forces at Different Speeds of Walking and Running. *Journal of Bone and Mineral Research* **30** (8), 1431-1440.

Gross T, Kivell TL, Skinner MM (2014) A CT-image-based framework for the holistic analysis of cortical and trabecular bone morphology. *Palaeontologia Electronica* **17** (3), 1-13.

Gunness-Hey M, Hock JM (1984) Increased trabecular bone mass in rats treated with human synthetic parathyroid hormone. *Metabolic Bone Disease and Related Research* **5** (4), 177-181.

Hammond AS (2014) In vivo baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. *American Journal of Physical Anthropology* **153** (3), 417-434.

Hanna JB, Granatosky MC, Rana P, et al. (2017) The evolution of vertical climbing in primates: Evidence from reaction forces. *Journal of Experimental Biology* https://doiorg/101242/jeb157628.

Harmon EH (2007) The shape of the hominoid proximal femur: a geometric morphometric analysis. *Journal of anatomy* **210** (2), 170-185.

Harmon EH (2009a) The shape of the early hominin proximal femur. *American Journal of Physical Anthropology* **139** (2), 154-171.

Harmon EH (2009b) Size and shape variation in the proximal femur of Australopithecus africanus. *Journal of Human Evolution* **56** (6), 551-559.

Harris M, Nguyen TV, Howard GM, et al. (1998) Genetic and Environmental Correlations Between Bone Formation and Bone Mineral Density: A Twin Study. *Bone* **22** (2), 141-145.

Hauser DL, Fox JC, Sukin D, et al. (1997) Anatomic variation of structural properties of periacetabular bone as a function of age: A quantitative computed tomography study. *The Journal of arthroplasty* **12** (7), 804-811.

Havill LM, Allen MR, Bredbenner TL, et al. (2010) Heritability of lumbar trabecular bone mechanical properties in baboons. *Bone* **46**, 835-840.

Hildebrand T, Rüegsegger P (1997) A new method for the model-independent assessment of thickness in three-dimensional images. *Journal of microscopy* **185** (1), 67-75

Hogervorst T, Bouma HW, de Vos J (2009) Evolution of the hip and pelvis. *Acta Orthopaedica* **80**, 1-39.

Huiskes R, Ruimerman R, van Lenthe GH, et al. (2000) Effects of mechanical forces on maintenance and adaptation of form in trabecular bone. *Nature* **405**, 704-706.

Hunt KD (1991) Positional behavior in the Hominoidea. *International Journal of Primatology* **12**, 95-118.

Isler K, Thorpe SKS (2003) Gait parameters in vertical climbing of captive rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*). *Journal of Experimental Biology* **206** (22), 4081-4096.

Isler K (2005) 3D-kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology* **126** (1), 66-81.

Jenkins FA (1972) Chimpanzee Bipedalism: Cineradiographic Analysis and Implications for the Evolutionof Gait. *Science* **178** (4063), 877-879.

803 **Judex S, Boyd S, Qin Y, et al.** (2003) Adaptations of Trabecular Bone to Low Magnitude
804 Vibrations Result in More Uniform Stress and Strain Under Load. *Annals of Biomedical*
805 *Engineering* **31** (1), 12-20.

806 **Judex S, Donahue L, Rubin C** (2002) Genetic predisposition to low bone mass is paralleled
807 by an enhanced sensitivity to signals anabolic to the skeleton. *The FASEB Journal* **16** (10),
808 1280-1282.

809 **Judex S, Garman R, Squire M, et al.** (2004) Genetically Based Influences on the Site-
810 Specific Regulation of Trabecular and Cortical Bone Morphology. *Journal of Bone and*
811 *Mineral Research* **19** (4), 600-606.

812 **Jungers WL** (1988) Relative joint size and hominoid locomotor adaptations with
813 implications for the evolution of hominid bipedalism. *Journal of Human Evolution* **17** (1–2),
814 247-265.

815 **Keaveny TM, Morgan EF, Niebur GL, et al.** (2001) Biomechanics of trabecular bone.
816 *Annual Review of Biomedical Engineering* **3**, 307-333.

817 **Kelly PJ, Hopper JL, Macaskill GT, et al.** (1991) Genetic Factors in Bone Turnover. *The*
818 *Journal of Clinical Endocrinology and Metabolism* **72** (4), 803-813.

819 **Kivell TL** (2016) A review of trabecular bone functional adaptation: what have we learned
820 from trabecular analyses in extant hominoids and what can we apply to fossils? *Journal of*
821 *anatomy* **228** (4), 569-594.

822 **Kivell TL, Skinner MM, Richard L, et al.** (2011) Methodological considerations for
823 analyzing trabecular architecture: an example from the primate hand. *Journal of anatomy* **218**
824 (2), 209-225.

825 **Lovejoy CO, McCollum MA** (2010) Spinopelvic pathways to bipedality: why (hominids
826 ever relied on a bent-hip–bent-knee gait. *Philosophical Transactions of the Royal Society of*
827 *London B: Biological Sciences* **365** (1556), 3289-3299.

828 **Lovejoy CO** (1975) Biomechanical perspectives on the lower limb of early hominids. In
829 Tuttle RH (editor). *Primate Functional Morphology and Evolution.* Mouton, The Hague.
830 291–326.

831 **Lovejoy OC, Meindl RS, Ohman JC, et al.** (2002) The Maka femur and its bearing on the
832 antiquity of human walking: Applying contemporary concepts of morphogenesis to the
833 human fossil record. *American Journal of Physical Anthropology* **119** (2) 97-133.

834 **MacLatchy L, Müller R** (2002) A comparison of the femoral head and neck trabecular
835 architecture of Galago and Perodicticus using micro-computed tomography (µCT). *Journal of*
836 *Human Evolution* **43** (1), 89-105.

837 **Maga M, Kappelman J, Ryan TM, et al.** (2006) Preliminary observations on the calcaneal
838 trabecular microarchitecture of extant large-bodied hominoids. *American Journal of Physical*
839 *Anthropology* **129**, 410-417.

840 **Mann RA, Hagy J** (1980) Biomechanics of walking running and sprinting. *The American*
841 *Journal of Sports Medicine* **8** (5), 345-350.

842 **McHenry HM, Corruccini RS** (1978) The femur in early human evolution. *American*
843 *Journal of Physical Anthropology* **49** (4), 473-487.

844 **Milovanovic P, Danijela D, Michael H, et al.** (2017) Region-dependent patterns of
845 trabecular bone growth in the human proximal femur: A study of 3D bone microarchitecture
846 from early postnatal to late childhood period. *American Journal of Physical Anthropology*
847 **164** (2), 281-291.

848 **Mittra E, Rubin C, Qin Y** (2005) Interrelationship of trabecular mechanical and
849 microstructural properties in sheep trabecular bone. *Journal of Biomechanics* **38**, 1229-1237.

850 **Miyakoshi N** (2004) Effects of Parathyroid Hormone on Cancellous Bone Mass and
851 Structure in Osteoporosis. *Current Pharmaceutical Design* **10** (21), 2615-2627.

852 **Morbeck ME, Zihlman AL** (1988) Body composition and limb proportions. In: Schwartz
853 JH editor. *Orangutan biology*. Oxford: Oxford University Press. 285–297.

854 **Myatt JP, Crompton RH, Thorpe SKS** (2011) Hindlimb muscle architecture in non-human
855 great apes and a comparison of methods for analysing inter-species variation. *Journal of
856 Anatomy* **219** (2), 150-166.

857 **Myers CA, Register BC, Lertwanich P, et al.** (2011) Role of the Acetabular Labrum and
858 the Iliofemoral Ligament in Hip Stability: An in vitro Biplane Fluoroscopy Study. *The
859 American Journal of Sports Medicine* **39** (1), 85-91.

860 **Nakano Y, Hirasaki E, Kumakura H** (2006) Patterns of Vertical Climbing in Primates. In:
861 Ishida H Tuttle R Pickford M Ogihara N Nakatsukasa M (eds). *Human Origins and
862 Environmental Backgrounds Developments in Primatology: Progress and Prospects*.
863 Springer Boston, MA.

864 **Novacheck TF** (1998) The biomechanics of running. *Gait and Posture* **7**, 77-95.

865 **Odgaard A** (1997) Three-dimensional methods for quantification of cancellous bone
866 architecture. *Bone* **20** (4), 315-328.

867 **O'Neill MC, Lee L, Demes B, et al.** (2015) Three-dimensional kinematics of the pelvis and
868 hind limbs in chimpanzee (*Pan troglodytes*) and human bipedal walking. *Journal of Human
869 Evolution* **86**, 32-42.

870 **Ounpuu S** (1990) The biomechanics of running: a kinematic and kinetic analysis. *AAOS
871 Instructional Course Lectures* **39**, 305-318.

872 **Ounpuu S** (1994) The biomechanics of walking and running. *Clinics in Sports Medicine* **13**
873 (4), 843-863.

874 **Paul JP** (1976) Approaches to design- Force actions transmitted by joints in the human body.
875 *Proceedings of the Royal Society of London B* **192**, 163-172.

876 **Payne RC, Crompton RH, Isler K, et al.** (2006) Morphological analysis of the hindlimb in
877 apes and humans II Moment arms. *Journal of anatomy* **208** (6), 725-742.

878 **Pearson OM, Lieberman DE** (2004) The aging of Wolff's) law: Ontogeny and responses to
879 mechanical loading in cortical bone. *American Journal of Physical Anthropology* **125** (39),
880 63-99.

881 **Pedersen DR, Brand RA, Davy DT** (1997) Pelvic muscle and acetabular contact forces
882 during gait. *Journal of biomechanics* **30** (9), 959-965.

883 **Polk JD, Blumenfeld J, Ahlumwalia D** (2008) Knee posture predicted subchondral apparent
884 density in the distal femur: an experimental validation. *Anatomical Record* **291**, 293-302.

885 **Pontzer H, Lieberman DE, Momin E, et al.** (2006) Trabecular bone in the bird knee
886 responds with high sensitivity to changes in load orientation. *Journal of Experimental
887 Biology* **209** (1), 57-65.

888 **R Development Core Team** (2017) R: A language and environment for statistical
889 computing. Vienna, Austria: The R Foundation for Statistical Computing.

890 **Rafferty KL, Ruff CB** (1994) Articular structure and function in Hylobates Colobus and
891 Papio. *American Journal of Physical Anthropology* **94** (3), 395-408.

892 **Rafferty KL** (1998) Structural design of the femoral neck in primates. *Journal of Human*
893 *Evolution* **34** (4), 361-383.

894 **Raichlen DA, Gordon AD, Harcourt-Smith WEH, et al.** (2010*)* Laetoli Footprints
895 Preserve Earliest Direct Evidence of Human-Like Bipedal Biomechanics. *PLOS ONE* **5** (3),
896 e9769.

897 **Reissis D, Abel RL** (2012) Development of fetal trabecular micro-architecture in the
898 humerus and femur. *Journal of anatomy* **220** (5), 496-503.

899 **Remis MJ** (1995) Effects of body size and social context on the arboreal activities of
900 lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*
901 **97** (4), 413-433.

902 **Remis MJ** (1999) Tree structure and sex differences in arboreality among western lowland
903 gorillas (*Gorilla gorilla gorilla*) at Bai Hokou Central African Republic. *Primates* **40** (2),
904 383.

905 **Rodan GA** (1998) Bone homeostasis. *Proceedings of the National Academy of Sciences* **95**
906 (23), 13361-13362.

907 **Rubin CT, Turner AS, Bain S, et al.** (2001) Low mechanical signals strengthen long bones.
908 *Nature* **412**, 603.

909 **Rubin CT, McLeod KJ, Bain SD** (1990) Functional strains and cortical bone adaptation:
910 Epigenetic assurance of skeletal integrity. *Journal of Biomechanics* **23**, 43-49.

911 **Ruff CB, Scott WW, Liu AY-C** (1991) Articular and diaphyseal remodeling of the proximal
912 femur with changes in body mass in adults. *American Journal of Physical Anthropology* **86**,
913 397-413.

914 **Ruff CB, Higgins R** (2013) Femoral neck structure and function in early hominins.
915 *American Journal of Physical Anthropology* **150** (4) 512-525.

916 **Ruff CB, Runestad JA** (1992) Primate limb bone structural adaptations. *Annual Review of*
917 *Anthropology* **21**, 407–433.

918 **Ruff CB** (1995) Biomechanics of the hip and birth in early Homo. *American Journal of*
919 *Physical Anthropology* **98** (4), 527-574.

920 **Ruff CB** (2002) Long bone articular and diaphyseal structure in old world monkeys and apes
921 I: Locomotor effects. *American Journal of Physical Anthropology* **119** (4), 305-342.

922 **Ryan TM, Carlson KJ, Gordon AD, Jablonski N, Shaw CN, Stock JT** (2018) Hyman-like
923 hip joint loading in *Australopithecus africanus* and *Paranthropus robustus*. *Journal of*
924 *Human Evolution* **121**, 12-24.

925 **Ryan TM, Ketcham RA** (2002) The three-dimensional structure of trabecular bone in the
926 femoral head of strepsirrhine primates. *Journal of human evolution* **43** (1), 1-26.

927 **Ryan TM, Ketcham RA** (2005) Angular orientation of trabecular bone in the femoral head
928 and its relationship to hip joint loads in leaping primates. *Journal of Morphology* **265** (3),
929 249-263.

930 **Ryan TM, Krovitz GE** (2006) Trabecular bone ontogeny in the human proximal femur.
931 *Journal of Human Evolution* **51** (6), 591-602.

932 **Ryan TM, Shaw CN** (2012) Unique Suites of Trabecular Bone Features Characterize
933 Locomotor Behavior in Human and Non-Human Anthropoid Primates. *PLOS ONE* **7** (7),
934 e41037.

935 **Ryan TM, Shaw CN** (2013) Trabecular bone microstructure scales allometrically in the
936 primate humerus and femur. *Proceedings of the Royal Society B: Biological Sciences* **280**
937 (1758), 20130172.

938 **Ryan TM, Shaw CN** (2015) Gracility of the modern *Homo sapiens* skeleton is the result of
939 decreased biomechanical loading. *Proceedings of the National Academy of Sciences* **112** (2),
940 372-377

941 **Ryan TM, Walker A** (2010) Trabecular Bone Structure in the Humeral and Femoral Heads
942 of Anthropoid Primates. *The Anatomical Record: Advances in Integrative Anatomy and*
943 *Evolutionary Biology* **293** (4), 719-729.

944 **Saers JPP, Cazorla-Bak Y, Shaw CN, et al.** (2016) Trabecular bone structural variation
945 throughout the human lower limb. *Journal of Human Evolution* **97**, 97-108.

946 **San Millán M, Kaliontzopoulou A, Rissech C, et al.** (2015) A geometric morphometric
947 analysis of acetabular shape of the primate hip joint in relation to locomotor behaviour.
948 *Journal of Human Evolution* 83, 15-27.

949 **Scherf H, Tilgner R** (2009) A new high-resolution computed tomography (CT)
950 segmentation method for trabecular bone architectural analysis. *American Journal of*
951 *Physical Anthropology* **140** (1), 39-51.

952 **Scherf H** (2008) Locomotion-related Femoral Trabecular Architectures in Primates — High
953 Resolution Computed Tomographies and Their Implications for Estimations of Locomotor
954 Preferences of Fossil Primates. in Endo H, Frey R (eds). *Anatomical Imaging: Towards a*
955 *New Morphology.* Springer Japan, Tokyo. 39-59.

956 **Scherf H Harvati K, Hublin J-J** (2013) A comparison of proximal humeral cancellous bone
957 of great apes and humans *Journal of Human Evolution* **65** (1), 29-38.

958 **Schneider CA, Rasband WS, Eliceiri KW** (2012) NIH Image to ImageJ: 25 years of Image
959 Analysis. *Nature methods* **9** (7), 671-675.

960 **Schultz AH** (1969) Observations on the Acetabulum of Primates. *Folia Primatologica* **11**
961 (3), 181-199.

962 **Shaw CN, Ryan TM** (2012) Does skeletal anatomy reflect adaptation to locomotor patterns?
963 cortical and trabecular architecture in human and nonhuman anthropoids. *American Journal*
964 *of Physical Anthropology* **147** (2), 187-200.

965 **Simkin A, Ayalon J, Leichter I** (1987) Increased trabecular bone density due to bone-
966 loading exercises in postmenopausal osteoporotic women. *Calcified tissue international* **40**
967 (2), 59-63.

968 **Skinner MM, Stephens NB, Tsegai ZJ, et al.** (2015) Human-like hand use in
969 *Australopithecus africanus*. *Science* **347** (6220), 395-399.

970 **Slocum DB, James SL** (1968) Biomechanics of Running. *JAMA* **205** (11), 721-728.

971 **Smith DM, Nance WE, Kang KW, et al.** (1973) Genetic Factors in Determining Bone
972 Mass. *The Journal of clinical investigation* **52** (11), 2800-2808.

973 **Sonntag CF** (1923) On the Anatomy Physiology and Pathology of the Chimpanzee.
974 *Proceedings of the Zoological Society of London* **93** (2), 323-429.

975 **Sonntag CF** (1924) 17 On the Anatomy Physiology and Pathology of the Orang-Outan.
976 *Proceedings of the Zoological Society of London* **94** (2), 349-450.

Stephens NB, Kivell TL, Thomas G, et al. (2016) Trabecular architecture in the thumb of *Pan* and *Homo*: implications for investigating hand use loading and hand preference in the fossil record. *American Journal of Physical Anthropology* **161** (4), 603-619.

Stern Jr JT, Susman RL (1983) The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology* **60** (3), 279-317.

Sugardjito J, van Hooff JARAM (1986) Age-Sex Class Differences in the Positional Behaviour of the Sumatran Orang-Utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park Indonesia. *Folia Primatologica* **47** (1), 14-25.

Susman RL, Stern J JT, Jungers WL (1984) Arboreality and Bipedality in the Hadar Hominids *Folia Primatologica* 43 (2-3), 113-156.

Suuriniemi M, Anitta M, Vuokko K, et al. (2004) Association Between Exercise and Pubertal BMD Is Modulated by Estrogen Receptor α Genotype. *Journal of Bone and Mineral Research* **19** (11), 1758-1765.

Suwa G, Lovejoy CO, Asfaw B, et al. (2012) Proximal Femoral Musculoskeletal Morphology of Chimpanzees and its Evolutionary Significance: A Critique of Morimoto et al (2011). *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* **295** (12), 2039-2044

Sylvester AD, Terhune CE (2017) Trabecular mapping: Leveraging geometric morphometrics for analyses of trabecular structure. *American Journal of Physical Anthropology* **163** (3), 553-569.

Thomason JJ (1985a) Estimation of locomotory forces and stresses in the limb bones of Recent and extinct equids. *Paleobiology* **11** (2), 209-220.

Thomason JJ (1985b) The Relationship of Trabecular Architecture to Inferred Loading Patterns in the Third Metacarpals of the Extinct Equids Merychippus and Mesohippus. *Paleobiology* **11** (3), 323-335.

Thorpe SKS, Crompton RH (2005) Locomotor ecology of wild orangutans (Pongo pygmaeus abelii) in the Gunung Leuser Ecosystem Sumatra Indonesia: A multivariate analysis using log-linear modelling. *American Journal of Physical Anthropology* **127** (1), 58-78.

Thorpe SKS, Crompton RH (2006) Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *American Journal of Physical Anthropology* **131** (3), 384-401.

Thorpe SKS, Holder R, Crompton RH (2008) Orangutans employ unique strategies to control branch flexibility. *Proceedings of the National Academy of Sciences of the United States of America* **106** (31), 12646-12651.

Treece GM, Gee AH (2014) Independent measurement of femoral cortical thickness and cortical bone density using clinical CT. *Medical Image Analysis* **20** (1), 249-264.

Tsegai ZJ, Kivell TL, Gross T, et al. (2013) Trabecular Bone Structure Correlates with Hand Posture and Use in Hominoids. *PLOS ONE* **8** (11), e78781.

Tsegai ZJ, Skinner MM, Gee AH, et al. (2017) Trabecular and cortical bone structure of the talus and distal tibia in Pan and Homo. *American Journal of Physical Anthropology* **163**, 784-805.

Tsegai ZJ, Skinner MM, Pahr DH, et al. (2018) Systemic patterns of trabecular bone across the human and chimpanzee skeleton. *Journal of anatomy* **232** (4), 641-656.

1021 **Tuttle RH, Cortright W** (1988) Positional behavior adaptive complexes and evolution. In:
1022 Schwartz JH editor. *Orangutan biology*. Oxford: Oxford University Press. 311-330.

1023 **Van der Bogert AJ, Read L, Nigg BM** (1999) An analysis of hip joint loading during
1024 walking running and skiing. *Medicine, Science in Sports, Exercise* **31** (1), 131-142.

1025 **Volpato V, Viola TB, Nakatsukasa M, et al.** (2008) Textural characteristics of the iliac-
1026 femoral trabecular pattern in a bipedally trained Japanese macaque. *Primates* **49** (1), 16-25.

1027 **Wagner FV, Negrão JR, Campos J, et al.** (2012) Capsular Ligaments of the Hip: Anatomic
1028 Histologic and Positional Study in Cadaveric Specimens with MR Arthrography. *Radiology*
1029 **263** (1), 189-198.

1030 **Wallace IJ, Demes B, Judex S** (2017) Ontogenetic and Genetic Influences on Bone's
1031 Responsiveness to Mechanical Signals. In Percival CJ, Richtsmeier JT (eds). *Building Bones:*
1032 *Bone Formation and Development in Anthropology*. Cambridge University Press, Cambridge.
1033 233-253

1034 **Wallace IJ, Demes B, Mongle C, et al.** (2014) Exercise-Induced Bone Formation Is Poorly
1035 Linked to Local Strain Magnitude in the Sheep Tibia. *PLOS ONE* **9** (6), e99108.

1036 **Walsh JS** (2015) Normal bone physiology remodelling and its hormonal regulation. *Surgery*
1037 *(Oxford)* **33** (1), 1-6.

1038 **Ward CV** (1991) Functional anatomy of the lower back and pelvis of the Miocene hominoid
1039 *Proconsul nyanzae* from Mfanga Island Kenya. PhD Dissertation Johns Hopkins University.

1040 **Ward CV** (2002) Interpreting the posture and locomotion of *Australopithecus afarensis*:
1041 Where do we stand? *American Journal of Physical Anthropology* **119** (35), 185-215.

1042 **Ward FO** (1838) *Outlines of Human Osteology.* London: Henry Renshaw.

1043 **Whalen RT, Carter DR, Steele CR** (1988) Influence of physical activity on the regulation
1044 of bone density. *Journal of Biomechanics* **21** (10), 825-837.

1045 **Whitehouse WJ** (1974) The quantitative morphology of anisotropic trabecular bone. *Journal*
1046 *of microscopy* **101** (2), 153-168.

1047 **Wolff J** (1892) *Das Gesetz der Transformation der Knochen.* Berlin: A Hirchwild.

1048 **Wolff J** (1986) *The law of bone remodeling.* Berlin: Springer-Verlag.

1049 **Yoshida H, Faust A, Wilckens J, et al.** (2006) Three-dimensional dynamic hip contact area
1050 and pressure distribution during activities of daily living. *Journal of Biomechanics* **39** (11),
1051 1996-2004.

1052
1053
1054
1055
1056
1057
1058
1059
1060
1061
1062
1063
1064
1065
1066
1067
1068
1069
1070
1071
1072
1073
1074
1075
1076
1077
1078
1079
1080
1081
1082
1083
1084
1085
1086
1087
1088
1089
1090
1091
1092
1093
1094
1095
1096

1097
1098 **Tables**
1099

Table 1. Study sample taxonomic composition, re-sampled voxel size range, sex, and microCT scanning parameters. All specimens were re-sampled except six of the gorillas that were scanned at lower resolutions.

Taxon	Locomotor mode	N	Sex	Voxel size (mm)	Scanning
Pan troglodytes	Arboreal/ knuckle-walker	20	13 female, 6 male, 1 unknown	0.04-0.05	kV:120-130, μA: 80-100, 0.25 or 0.5mm brass
Gorilla gorilla gorilla	Terrestrial knuckle-walker	14	7 female, 7 male	0.05-0.08	kV:130-170, μA: 110-160, 0.1-0.5mm copper
Pongo sp.	Arboreal/ torso-orthograde suspension	5	5 female	0.04-0.045	kV:140, μA: 140, 0.5mm brass
Homo sapiens	Bipedal	12	3 female, 8 male, 1 unknown	0.06-0.07	kV:130-140, μA: 100-140, 0.5mm brass

Table 2. Trabecular architecture results. Mean, standard deviation (in parentheses) and coefficient of variation for five trabecular parameters quantified throughout the femoral head.

Taxon	*Pan*	CV	*Gorilla*	CV	*Pongo*	CV	*Homo*	CV
BV/TV	0.39 (0.03)	8.6	0.35 (0.05)	14.8	0.33 (0.04)	13.4	0.30 (0.05)	16.0
DA	0.15 (0.03)	21.6	0.18 (0.04)	21.8	0.15 (0.02)	14.7	0.23 (0.04)	17.9
Tb.N (1/mm)	1.19 (0.11)	9.4	0.83 (0.09)	10.7	0.92 (0.04)	4.4	0.87 (0.1)	11.4
Tb.Sp (mm)	0.56 (0.06)	10.0	0.81 (0.08)	9.8	0.78 (0.07)	8.4	0.84 (0.14)	16.6
Tb.Th (mm)	0.29 (0.03)	11.8	0.40 (0.08)	19.1	0.31 (0.03)	10.9	0.32 (0.03)	9.9

Table 3. Results of pairwise comparisons between taxa. Bonferroni-corrected p-values of each pairwise comparison for all trabecular parameters. Significant results are indicated by grey shading.

	Pan-Gorilla	*Pan - Pongo*	*Pan - Homo*	*Gorilla - Pongo*	*Gorilla - Homo*	*Pongo - Homo*
BV/TV	0.14	<0.05	<0.001	1	0.14	1
DA	0.24	1	<0.001	1	<0.05	<0.01
Tb.N	<0.001	<0.01	<0.001	0.33	1	1
Tb.Sp	<0.001	<0.001	<0.001	1	1	1
Tb.Th	<0.001	1	<0.05	0.09	0.05	1

Figure legends

Figure 1. Comparison of hip posture during different habitual locomotor activities in great apes (A-B) and humans (C-D). (A) Great ape hip posture in maximum hip flexion (~55-60 degrees) during climbing (Isler, 2005). (B) Great ape hip posture at toe-off (~110 degrees) during terrestrial knuckle-walking (Finestone et al. 2018). (C) Human hip posture at toe-off (~175 degrees). (D) Human hip posture at heel-strike (~160 degrees).

Figure 2. *Pan* BV/TV distribution in the femoral head. Five *Pan* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (F-female, M-male): MPITC 14996 (F), USNM 220063 (F), USNM 176228 (M), MPITC 11781 (M), MPITC 11786 (F).

Figure 3. *Gorilla* BV/TV distribution in the femoral head. Five *Gorilla* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (F-female, M-male): M96 (F), M264 (M), M372 (M), M856 (F), FC123 (M).

Figure 4. *Pongo* BVTV distribution in the femoral head. Five *Pongo* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (All female): ZSM 1909 0801, 1907 0660, 1973 0270, 1907 0483, 1907 0633b.

Figure 5. *Homo* BV/TV distribution in the femoral head. Five *Homo* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (F-female, M-male): CAMPUS 36 (F), CAMPUS 93 (M), CAMPUS 74 (F), CAMPUS 417 (sex unknown), CAMPUS 81 (M).

Figure 6. Bivariate plot of mean bone volume fraction (BV/TV) and mean degree of anisotropy (DA) for each individual and species in the sample.

Figure 7. A histogram of mean BV/TV and DA value distributions in the studied taxa.