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Georgiou, Leoni, Kivell, Tracy L., Pahr, Dieter H., Buck, Laura T. and Skinner, Matthew M. (2019) *Trabecular architecture of the great ape and human femoral head*. *Journal of Anatomy*, 234 (5). pp. 679-693. ISSN 0021-8782.

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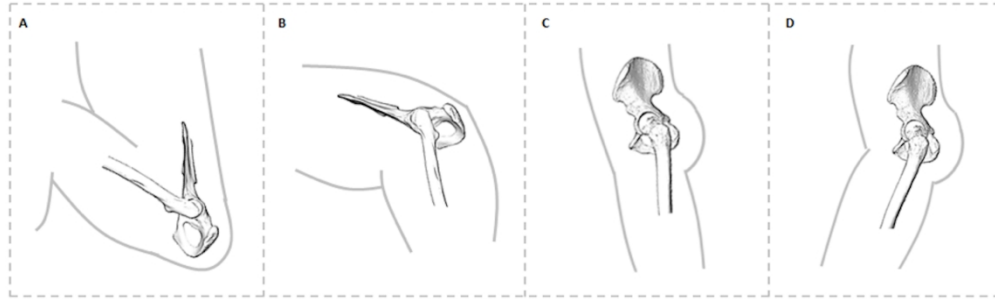


Figure 1. Comparison of hip posture during different habitual locomotor activities in great apes (A-B) and humans (C-D). (A) Great ape hip posture in maximum hip flexion ( $\sim 55$ - $60$  degrees) during climbing (Isler, 2005). (B) Great ape hip posture at toe-off ( $\sim 110$  degrees) during terrestrial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

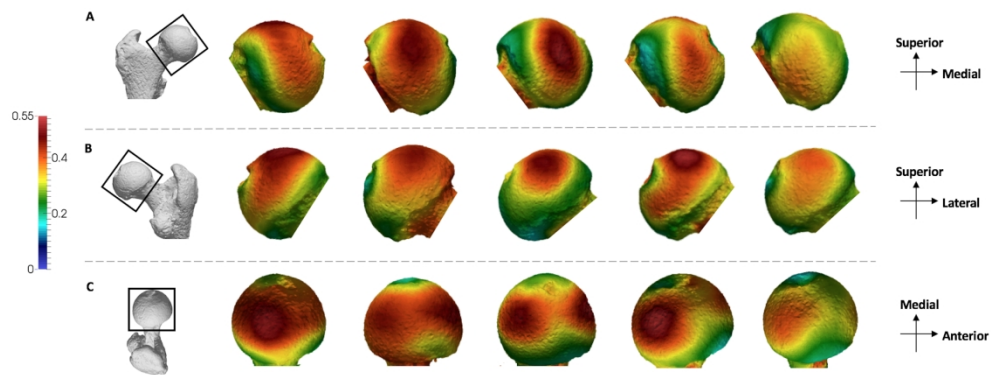


Figure 2. *Pan* BV/TV distribution in the femoral head. Five *Pan* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0–0.55. All specimens are from the right side. Specimens from left to right (F-female, M-male):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

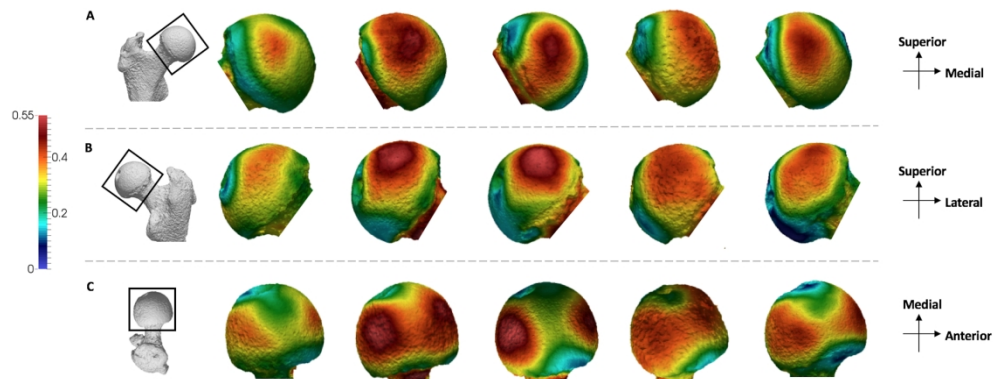


Figure 3. *Gorilla* BV/TV distribution in the femoral head. Five *Gorilla* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (F-female,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

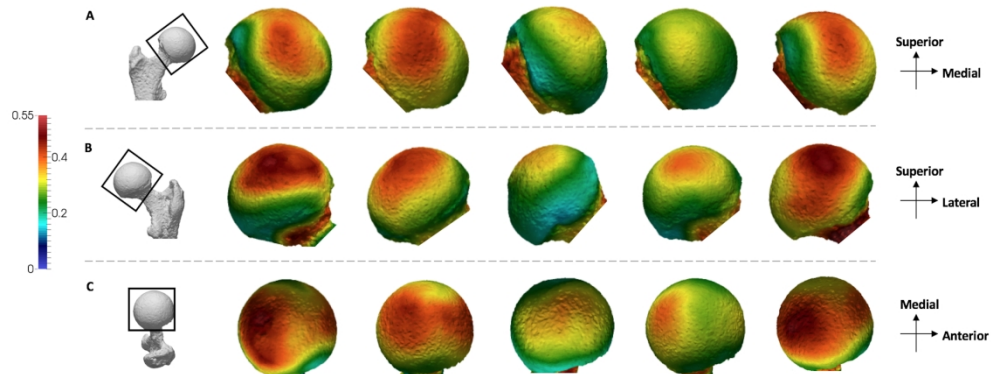


Figure 4. *Pongo* BVTV distribution in the femoral head. Five *Pongo* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (All female):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

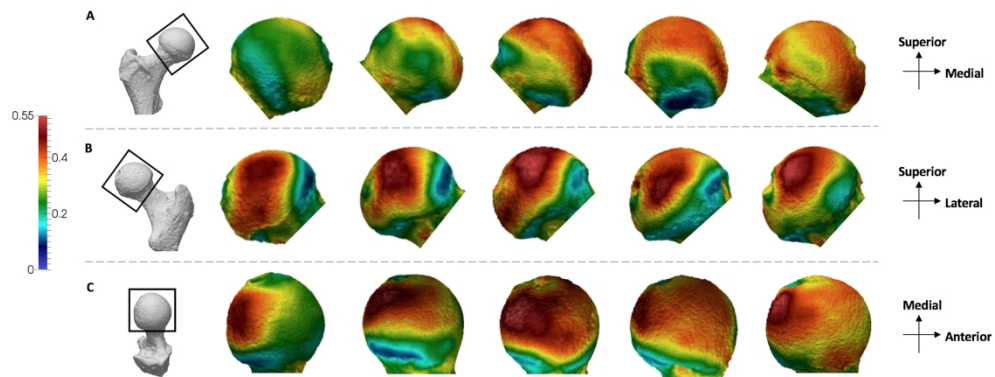


Figure 5. *Homo* BV/TV distribution in the femoral head. Five *Homo* specimens showing variation in the BV/TV distribution across the sample in (A) anterior, (B) posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from the right side. Specimens from left to right (F-female,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

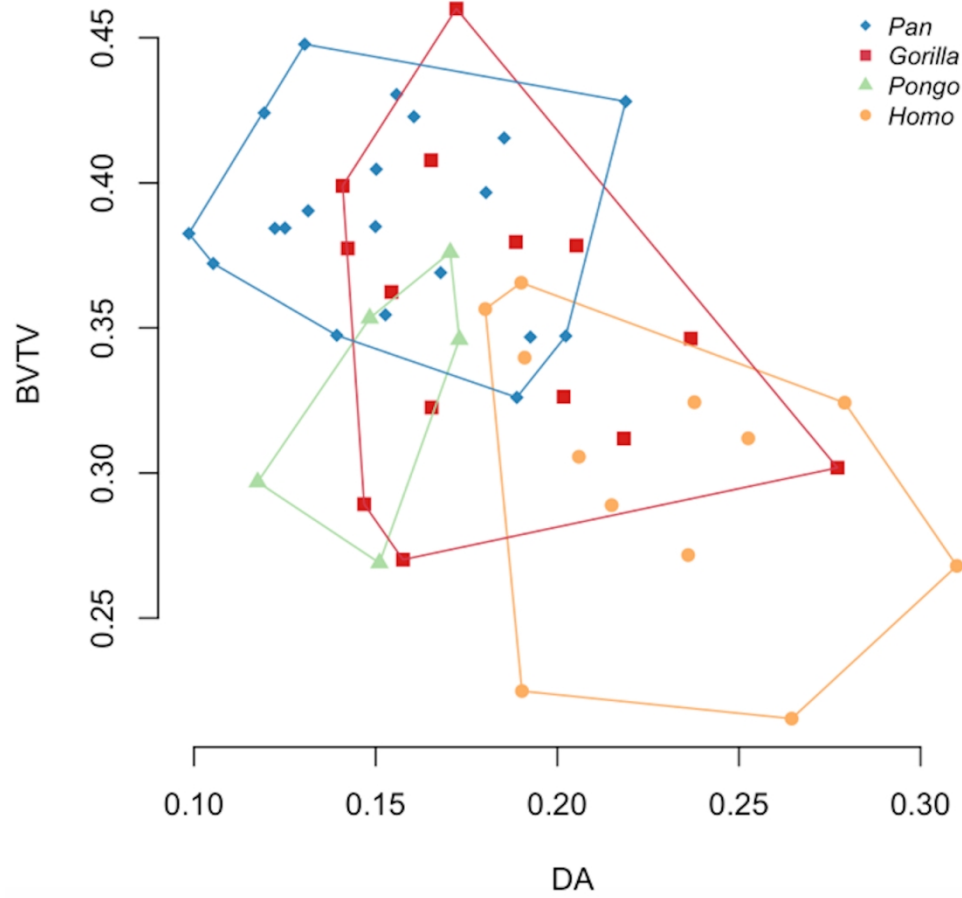


Figure 6. Bivariate plot of mean bone volume fraction (BV/TV) and mean degree of anisotropy (DA) for each individual and species in the sample.

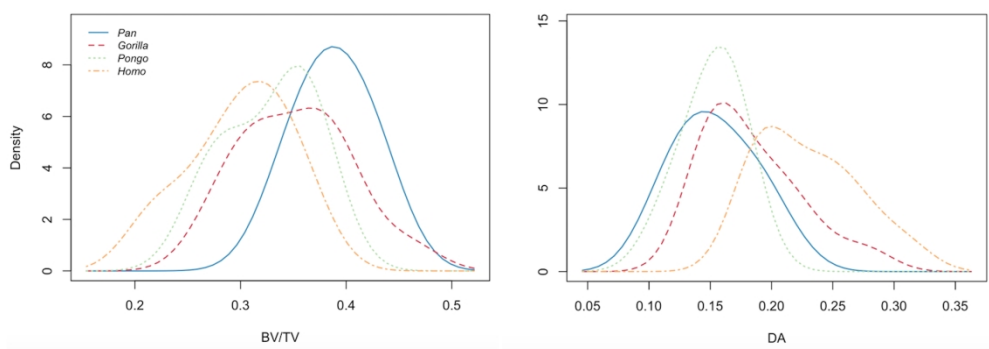


Figure 7. A histogram of mean BV/TV and DA value distributions in the studied taxa.



# 1 **Trabecular architecture of the great ape and human** 2 **femoral head**

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28

## 29 **Trabecular architecture of the great ape and human femoral head**

30

### 31 **Abstract**

32

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

54

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

57

58

### 59 **Introduction**

60

61 The morphology of the proximal femur has played a key role in the reconstruction of  
62 locomotion in extant and extinct primates (e.g. McHenry and Corruccini, 1978; Burr et al.  
63 1982; Ruff et al. 1991; Ruff and Runestad, 1992; Ruff, 1995; Harmon, 2007;  
64 Harmon, 2009a; Ruff and Higgins, 2013) and particularly **in understanding** the form  
65 of bipedalism used by australopiths (Stern and Susman, 1983; Susman et al. 1984;  
66 Crompton, et al. 1998; Carey and Crompton, 2005; Harmon, 2009b; Lovejoy and  
67 McCollum, 2010; Raichlen et al. 2010; DeSilva et al. 2013). External morphology  
68 provides **considerable** evidence of functional links between morphology and  
69 locomotion. However, due to **possible** phylogenetic lag, **which results in traits that**  
70 **are no longer functionally significant being present**, inferences about behaviour  
71 based on external traits alone have been questioned (e.g. Ward, 2002). Variation in

72 internal trabecular bone structure across different regions of the skeleton can  
73 provide additional evidence to help reconstruct joint postures and to infer potential  
74 differences in locomotor behaviour in extant and extinct primates (e.g. Thomason  
75 1985a,b; Ryan and Ketcham, 2002; Volpato et al. 2008; Ryan and Shaw, 2012; Tsegai  
76 et al. 2013; Skinner et al. 2015; Stephens et al. 2016). Indeed, **the ability of trabecular**  
77 **bone** to reflect mechanical loading was first **noted** in the human proximal femur  
78 (Ward, 1838; Wolff 1870, 1892). It is not yet fully understood how mechanical or non-  
79 mechanical factors trigger and ultimately affect the organisation of trabeculae. For  
80 example, a range of activities, including **high strain/low frequency loading and low**  
81 **strain/high frequency** loading have been shown to elicit trabecular reorganisation  
82 (Rubin et al. 1990; Rubin et al. 2001; Judex et al. 2003; Wallace et al. 2014).  
83 Furthermore, differences in body mass (Scherf, 2008; Cotter et al. 2009; Doube et al.  
84 2011; Fajardo et al. 2013; Ryan and Shaw, 2013), hormones (e.g. Gunness-Hey and  
85 Hock, 1984; Miyakoshi, 2004; Walsh, 2015), and genetic or systemic factors (Havill et  
86 al. 2010; Tsegai et al. 2018) have been shown to influence aspects of trabecular  
87 structure as well. However, computational (e.g. Huiskes et al. 2000; Keaveny et al.  
88 2001) and experimental studies have demonstrated that modelling of trabeculae is  
89 correlated with applied loads, and trabecular strut reorganisation can be instigated  
90 by changes in the direction, magnitude and/or frequency of load (Biewener et al.  
91 1996; Mittra et al. 2005; Pontzer et al. 2006; Polk et al, 2008; Barak et al. 2011).  
92 Furthermore, trabecular bone volume fraction (BV/TV) and trabecular strut alignment  
93 (degree of **anisotropy**, or DA) explain up to 98% of bone stiffness (i.e. Young's  
94 modulus of elasticity) (Stauber et al. 2006; Maquer et al. 2015; Odgaard et al. 1997).  
95 Thus, variation in the distribution of BV/TV and DA can provide insight into joint  
96 loading and, in turn, locomotor behaviours in primates.

97  
98 Several studies have revealed that variation in the trabecular architecture of the  
99 primate hip and proximal femur is associated with differences in locomotion (e.g.  
100 Rafferty and Ruff, 1994; MacLatchy and Muller, 2002; Volpato et al. 2008; Ryan and  
101 Shaw, 2012; Saers et al. 2016). For example, Volpato and colleagues (2008)  
102 demonstrated that the orientation of trabecular struts in the ilium and femoral neck  
103 is associated with joint positioning in the hip of bipedally-trained Japanese macaques  
104 and reflects alterations in the direction of load. **Comparable** changes in trabecular  
105 structure **that reflect** differences in joint orientation were **also** found in the distal  
106 femora of guinea fowls (Pontzer et al. 2006) and distal tibiae of sheep (Barak et al.  
107 2011). **Furthermore, Scherf (2008) found that trabecular structure within the femoral**  
108 **head, neck and both trochanters of climbing primates (e.g. *Alouatta seniculus*) had**  
109 **more isotropic architecture, while specialised primates (e.g. *Homo sapiens*) in which**  
110 **the femur experienced more stereotypical loading had more anisotropic structure.**  
111 **Similar results were found in leaping primates, which in comparison to non-leaping**  
112 **primate species, had more anisotropic trabeculae in the inferior aspect of the femoral**  
113 **head (Ryan and Ketcham, 2002), and a different principal strut orientation (Ryan and**  
114 **Ketcham, 2005).**

115  
116 More recently, Ryan and Shaw (2012) investigated the trabecular patterns of the  
117 femoral head in several anthropoid taxa and found that different suites of trabecular  
118 variables could distinguish among taxa and locomotor groups. In particular, modern  
119 humans were distinct in having relatively few, highly anisotropic trabeculae that are  
120 thin and plate-like, *Pan* had relatively numerous, thick and isotropic trabeculae, while  
121 *Pongo* had relatively few and isotropic trabeculae. Additional studies investigating  
122 different human samples have also shown that femoral head trabecular structure  
123 reflects variation in mobility levels, with more sedentary agriculturalists having  
124 relatively low BV/TV compared with more active foragers (Ryan and Shaw, 2015;  
125 Saers et al. 2016; Ryan et al. 2018). Interestingly, more active human foragers have  
126 relatively high BV/TV that falls within the range of most extant hominoids apart from  
127 *Pan* (Ryan et al. 2018). Despite this overlap in BV/TV between some human samples  
128 and other hominoids, humans have consistently been shown to have the most  
129 anisotropic femoral head structure compared to other great apes (Ryan and Shaw,  
130 2015; Ryan et al. 2018). Furthermore, the human trabecular pattern has been shown  
131 to develop during ontogeny when independent bipedalism develops and the gait  
132 matures (Ryan and Krovitz, 2006; Reissis and Abel, 2012; Milovanovic et al. 2017).  
133 Altogether, these studies suggest that the trabecular bone of the femoral head holds  
134 a strong functional signal of locomotor loading in primates.

135  
136 Conversely, other studies have failed to detect a strong locomotor signal in the  
137 femoral head (Ryan and Walker, 2010; Shaw and Ryan, 2012), femoral neck (Fajardo  
138 et al. 2007) and distal femur (Carlson et al. 2008). Carlson and colleagues (2008) did  
139 not detect differences in the DA of the distal femoral metaphysis between mice with  
140 turning locomotion and mice with non-turning locomotion. Similarly, Ryan and  
141 Walker (2010) did not find any significant differences in the DA and BV/TV patterns  
142 of the femoral head in a broad sample of platyrrhines and catarrhines. Furthermore,  
143 Shaw and Ryan (2012), who examined the subarticular trabecular and mid-diaphyseal  
144 cortical patterns in the femur and humerus of a sample of primates, concluded that  
145 only the mid-diaphyseal cortical bone contains a clear functional signal linked to the  
146 differential use of the two limbs between different locomotor groups.

147  
148 The discrepancy in the findings of previous studies may, in part, be an artefact of the  
149 volume-of-interest (VOI) method that was used. A VOI quantifies only a subsample of  
150 trabecular structure within a given region and results can vary depending on its size  
151 and position (Fajardo and Müller, 2001; Kivell et al. 2011). Additionally, challenges  
152 arise when extracting homologous VOIs in taxa that vary in external morphology.  
153 Prior research has demonstrated that additional functional insight can be gained  
154 from investigating the trabecular architecture within an epiphysis as a whole (Tsegai  
155 et al. 2013; Skinner et al. 2015; Stephens et al. 2016; Sylvester and Terhune, 2017;  
156 Tsegai et al. 2018). Here we apply a whole-epiphysis approach to study the trabecular  
157 structure throughout the femoral head of chimpanzees (*Pan troglodytes*), lowland

158 gorillas (*Gorilla gorilla*), orangutans (*Pongo* sp.) and humans (*Homo sapiens*), which  
159 vary in locomotor behaviours and are relevant to the reconstruction of locomotion in  
160 fossil hominins.

161

162 *Locomotion, hip morphology and predicted joint posture*

163

164 **Habitual locomotor activities and associated hip joint angles vary between great apes**  
165 **and humans (Fig. 1).** Chimpanzees are predominantly terrestrial/arboreal  
166 quadrupedal knuckle-walkers, but also engage frequently in arboreal climbing and,  
167 less so, bipedalism (Hunt, 1991; Doran, 1992, 1993). **In all these locomotor modes,**  
168 the hindlimb plays key role in propulsion and experiences higher vertical force than  
169 the forelimb (Demes et al. 1994; Hannah et al. 2017). During terrestrial  
170 quadrupedalism in chimpanzees, the mean hip angle at foot touchdown is 65° and at  
171 toe-off it is 98.2° (Finestone et al. 2018). **Kinematics during chimpanzee vertical**  
172 **climbing have, to our knowledge, only been studied in one individual and show that**  
173 **the flexion-extension range at the hip increases substantially compared with**  
174 **terrestrial quadrupedalism, with hip angles ranging from ~25° to ~105° (Nakano et**  
175 **al. 2006). A more comprehensive study of bonobos (n=4 adults), which share similar**  
176 **hindlimb anatomy with chimpanzees (e.g. Payne et al. 2006; Myatt et al. 2011),**  
177 **yielded hip angles ranging from 55° to 135° during vertical climbing (Isler, 2005).**

178

179 Lowland gorillas are also predominantly quadrupedal knuckle-walkers (Remis, 1995;  
180 Crompton et al. 2010). **They** often engage in arboreal climbing and bipedalism, **but**  
181 **less frequently than chimpanzees** (Remis, 1995; Crompton et al. 2010). During  
182 terrestrial quadrupedalism in gorillas, hip angles range from 77° at foot touchdown  
183 to 120.6° at toe-off (Finestone et al. 2018). During vertical climbing, **hip angle range**  
184 is similar to that of bonobos, ranging from approximately 45° to 135° (Isler, 2005).  
185 *Gorilla* climbing frequency and technique varies with sex and body size, with the  
186 range of hip flexion-extension being reduced in larger males compared to smaller  
187 females (Remis, 1995; Remis, 1999; Isler, 2005). However, gorillas show less  
188 intraspecific variation in climbing techniques than bonobos (Isler, 2005).

189

190 Orangutans employ a complex set of locomotor behaviours, which are mostly torso  
191 orthograde, including vertical climbing, bridging, suspension from various limbs, and  
192 terrestrial quadrupedalism (Cant, 1987; Isler and Thorpe, 2003; Thorpe and  
193 Crompton, 2006; Thorpe et al. 2009). **Their hips are more mobile than those of other**  
194 **apes**, which allows them to use their hindlimbs in more varied ways (Morbeck and  
195 Zihlman, 1988; Tuttle and Cortright, 1988; Isler, 2005). During terrestrial locomotion,  
196 the orangutan hip angle is 68.3° at touchdown and 107.3° at toe-off (Finestone et al.  
197 2018). During vertical climbing, orangutans are able to lift their feet **further above**  
198 **their hips than African apes**, such that their flexion-extension angle ranges from  
199 around 30° to 135° (Isler, 2005).

200

201 Adult humans walk exclusively terrestrially on two legs, extending both their hips and  
202 knees (Alexander, 1994). During the gait cycle, hip extension reaches 160° at  
203 touchdown and 175° at toe-off (Abbass and Abdulrahman, 2014). Humans also  
204 engage in running, which alters the joint angle of the hip and the resulting load on  
205 the femoral head (Ounpuu, 1990; Ounpuu, 1994; van den Bogert et al. 1999;  
206 Giarmatzis et al. 2015). Increase in speed is linked to more flexed hip joints and a  
207 generally increased range of motion at the hip (Mann and Hagy, 1980; Novacheck,  
208 1998). At touchdown during running the hip is flexed at 30-40°, while also being  
209 externally rotated, and at push off it is extended and internally rotated (Slocum and  
210 James, 1968). **Furthermore**, during running (3.5m/s), loads have been shown to  
211 increase to greater than double that of walking (1.5 m/s) (van den Bogert et al.1999).

212  
213 [Insert **Figure 1** about here]  
214

215 Great apes and humans vary in the external morphology of the hip joint.  
216 Chimpanzees and gorillas have a relatively small femoral head, a short femoral neck  
217 **as well as** a superoinferiorly expanded greater trochanter compared to orangutans  
218 (McHenry and Corruccini, 1978; Harmon, 2007). Chimpanzees have a “laterally facing  
219 acetabulum” (Jenkins, 1972), however comparative quantitative data **of acetabulum**  
220 **anteversion do not exist for apes and humans** (Hogervorst et al. 2009 and references  
221 therein). Furthermore, in gorillas the acetabulum is relatively deep, compared to  
222 other apes (Schultz, 1969), perhaps reducing capacity for mobility at the hip. In  
223 orangutans the greater trochanter is less superoinferiorly expanded than in the  
224 African apes and is positioned inferiorly to the femoral head, which may enhance  
225 rotational capacity at the hip joint (Aiello and Dean, 2002; Harmon 2007). Orangutans  
226 also **have** a relatively large head, long neck, and a greater trochanter that is less  
227 superoinferiorly expanded than that of African apes and which is **positioned** inferiorly  
228 relative to the femoral head (Aiello and Dean, 2002; Harmon, 2007). **These features of**  
229 **the orangutan proximal femur, plus the absence of a subchondral ligamentum teres**  
230 **insertion at the centre of the femoral head (Crelin, 1988; Ward, 1991; Ruff, 2002;**  
231 **Harmon, 2007), enhance rotational capacity and allow greater mobility at the hip**  
232 **joint compared to other hominoids.**

233  
234 Humans have a long femoral neck and a valgus angle at the knee, which compensate  
235 for the mechanical disadvantage of increased bi-acetabular distance (Lovejoy, 1975;  
236 McHenry and Corruccini, 1978; Rafferty, 1998; Lovejoy et al. 2002; Harmon, 2007) and  
237 result in adduction of the hips during the stance phase (O’Neill et al. 2015). The  
238 greater trochanter is less superoinferiorly expanded compared to other apes  
239 (Harmon, 2007). Furthermore, the human acetabulum is relatively deep and the  
240 femoral head is relatively large (Schultz, 1969; Jungers, 1988). This hip morphology is  
241 thought to help dissipate the increased load that occurs when supporting body mass  
242 over two, rather than four, limbs. Biomechanical studies have revealed **that** the peak  
243 contact force on the human hip during walking is directed posteriorly, laterally and

244 inferiorly (Pedersen et al. 1997) and is located at the posterior aspect (Paul, 1976;  
245 English and Kilvington, 1979). Furthermore, pressure on the acetabulum is mainly  
246 located posteriorly during different activities, such as standing up or sitting down  
247 (Yoshida et al. 2006). Lack of congruence between the femoral head and the  
248 acetabulum, combined with an anterior-facing acetabulum result in the anterior  
249 region of the femoral head not being fully covered by the acetabulum during bipedal  
250 locomotion (Hogervorst et al. 2009; Bonneau et al. 2014). Thus, the anterior region of  
251 the femoral head and acetabulum play a smaller role in load transmission compared  
252 to other regions of the hip joint.

253

254 Examining the potential links between internal femoral bone structure and extant ape  
255 locomotion will greatly facilitate attempts to reconstruct the locomotion of extinct  
256 hominins (e.g. Skinner et al. 2015). Here we provide this comparative context by  
257 analysing the trabecular architecture throughout the entire femoral head in extant  
258 great apes and humans that vary in their locomotor behaviours. We quantify BV/TV,  
259 DA, trabecular number (Tb.N), trabecular separation (Tb.Sp) and trabecular thickness  
260 (Tb.Th) throughout the femoral head. Based on the locomotor and biomechanical  
261 studies reviewed above, we make the following predictions regarding species  
262 variation in femoral head trabecular structure:

263

#### 264 *1. BV/TV distribution in the femoral head*

265

266 The distribution of BV/TV throughout the femoral head will reflect joint positioning  
267 and loading during habitual locomotion. In *Pan* we expect high BV/TV to extend  
268 from the posterior and superior aspect of the femoral head to the anterior region,  
269 reflecting hip angles and loading during knuckle-walking locomotion and vertical  
270 climbing (Finestone et al. 2018; Isler 2005). We predict that *Gorilla* will show a similar  
271 pattern of BV/TV distribution, although the region of high BV/TV is expected to  
272 extend over a smaller area of the femoral head compared with that of *Pan*, reflecting  
273 a reduced range of motion (Hammond, 2014) and different flexion/extension angles  
274 at the *Gorilla* hip during knuckle-walking and climbing (Finestone et al. 2018; Isler  
275 2005). We predict that *Pongo* will show the most variable BV/TV distribution pattern,  
276 reflecting loading of the femoral head at different hip joint angles, with high BV/TV  
277 spanning the whole of the superior area of the femoral head. Finally, we expect a  
278 more restricted region of high BV/TV in *Homo* that will be concentrated superiorly  
279 and posteriorly on the femoral head, reflecting the stereotypical loading pattern of  
280 bipedal locomotion.

281

#### 282 *2. Mean trabecular parameters in the femoral head*

283

284 We hypothesise that relative interspecific differences in mean BV/TV values will be  
285 consistent with those of previous trabecular studies on the femur (e.g. Georgiou et al.  
286 2018; Ryan et al. 2018; Tsegai et al. 2018) and other postcranial elements (e.g. Maga

287 et al. 2006; Cotter et al. 2009; Scherf et al. 2013; Tsegai et al. 2013; Tsegai et al. 2017),  
288 such that *Pan* will have the highest BV/TV, *Homo* will have the lowest, and *Gorilla* and  
289 *Pongo* will be intermediate between these two taxa. Furthermore, mean DA of the  
290 entire femoral head will reflect the range of motion of the hip joint during habitual  
291 locomotion. *Pan* and *Gorilla* will display intermediate DA values, showing less  
292 anisotropic femoral heads than *Homo*, because they engage in both terrestrial and  
293 arboreal behaviours that employ an increased range of motion at the hip. *Pongo* will  
294 be the most isotropic, reflecting their highly mobile hip joint and diverse positioning  
295 of the proximal femur during their varied quadrumanous locomotor behaviours.  
296 *Homo* will be the most anisotropic, consistent with more stereotypical loading of the  
297 hip joint during bipedal locomotion.

298  
299 In addition to BV/TV and DA, we quantify mean Tb.N, Tb.Sp and Tb.Th within the  
300 femoral head to better understand potential variation in the trabecular architecture  
301 across our sample and for comparison with previous studies (e.g. Ryan and Shaw,  
302 2012; Ryan and Shaw, 2015; Ryan et al. 2018). In primates these parameters scale  
303 negatively allometrically with body size (Barak et al. 2013; Ryan and Shaw, 2013)  
304 meaning results may be affected by body mass. BV/TV and DA are expected to better  
305 reflect functional adaptations, as DA does not to scale with body mass and BV/TV  
306 either shows no relationship (Doube et al. 2011; Barak et al. 2013) or a weak  
307 positively allometric relationship (Ryan and Shaw, 2013) with body mass.

308

309

## 310 **Methodology**

311

### 312 *Study sample*

313

314 Microcomputed tomographic scans were used to analyse trabecular morphology in  
315 the femoral head of great apes and humans. Details of the study sample are  
316 provided in Table 1. The *P. troglodytes* sample (n=20) is comprised of two subspecies;  
317 *Pan troglodytes verus* (n=15) from the Tai Forest collection curated at the Max Planck  
318 Institute for Evolutionary Anthropology in Leipzig, Germany, and *Pan troglodytes*  
319 *troglodytes* (n=5) curated at the Smithsonian National Museum of Natural History in  
320 Washington, D.C., USA. The *Gorilla gorilla gorilla* sample (n=14) is from the Powell-  
321 Cotton Museum, UK, of which 13 individuals are from Cameroon and one is from the  
322 Democratic Republic of the Congo. The *Pongo* sample (n=5 and all female) is from  
323 the Zoologische Staatssammlung München, Germany. Four of the individuals are *P.*  
324 *pygmaeus*, while one is *P. abelii*. The *H. sapiens* sample (n=12) is curated at the  
325 Georg-August-Universität Göttingen, Germany. Ten of the individuals come from a  
326 Catholic cemetery in Göttingen, which was used between 1851 and 1889, and two  
327 come from a cemetery in the village of Inden that was used between 1877 and 1924.  
328 All specimens were adult based on complete epiphyseal fusion throughout the  
329 skeleton and none showed obvious signs of pathology.



330

331 The *Pan*, *Pongo* and *Homo* samples were scanned at the Department of Human  
332 Evolution in the Max Planck Institute for Evolutionary Anthropology, Leipzig,  
333 Germany using a BIR ACTIS 225/300 industrial microCT scanner. The *Gorilla* sample  
334 was scanned at the Cambridge Biotomography Centre in the Department of Zoology  
335 at the University of Cambridge, Cambridge, UK using a Nikon XT 225 ST microCT  
336 scanner. All specimens were scanned at the highest possible resolution based on the  
337 size of the bone, ranging from 0.029-0.082 mm, and were reconstructed into 16-bit  
338 TIFF stacks with isometric voxel sizes. Reconstructed datasets were re-oriented to the  
339 same anatomical position and cropped in AVIZO 6.3 ® (Visualization Sciences Group,  
340 SAS). All specimens, except six gorillas, were re-sampled due to computational  
341 limitations of medtool 4.1 ([www.dr-pahr.at](http://www.dr-pahr.at)) and resultant resolutions are given in  
342 Table 1. Bone was segmented from air using the Ray Casting Algorithm (Scherf and  
343 Tilgner, 2009).

344

#### 345 *Trabecular architecture analysis*

346

347 Patterns of trabecular bone distribution throughout the whole femoral head were  
348 analysed in medtool 4.1 ([www.dr-pahr.at](http://www.dr-pahr.at)), following the protocol described by Gross  
349 and colleagues (2014). A series of morphological filters were applied to identify and  
350 remove the cortical shell, thus isolating the trabecular structure. The resulting  
351 isolated trabecular structure was used to calculate trabecular thickness using the  
352 BoneJ plug-in (version 1.4.1, Doube et al. 2010) for ImageJ (Schneider et al. 2012) to  
353 validate the parameters used in the morphological filters for the separation of the  
354 cortical shell (see Gross et al. 2014). The original dataset and trabecular structure  
355 were used to create a trinary mask defining the outer air, inner air and trabecular  
356 bone. A 3D rectangular background grid with a size of 3.5mm was superimposed on  
357 the trabecular structure and a sphere with a diameter of 7.5mm was used to measure  
358 BV/TV at each node in medtool 4.1. BV/TV was calculated as the ratio of bone to  
359 total volume in the sampling spheres. The isolated trabecular structure and a mesh  
360 size of 0.6mm were used to create 3D tetrahedral meshes of all individuals, using  
361 CGAL 4.4 (CGAL, Computational Geometry, <http://www.cgal.org>) and BV/TV values  
362 were then interpolated on the tetrahedral elements of each mesh. Distribution maps  
363 of BV/TV were visualised using Paraview v4.0.1 (Ahrens et al. 2005). The femoral head  
364 for each specimen was manually isolated in AVIZO 6.3 ® by positioning the  
365 mediolateral axis facing superoinferiorly and cropping at the head-neck junction to  
366 ensure homology across specimens. Trabecular parameters (BV/TV, DA, Tb.N, Tb.Sp,  
367 Tb.Th) for the femoral head were calculated using an in-house script in medtool 4.1.  
368 Mean BV/TV, DA, Tb.Sp and Tb.Th were quantified within the entire epiphysis and  
369 Tb.N was calculated from the means of Tb.Sp and Tb.Th. DA was calculated as  $DA = 1$   
370  $- [\text{smallest eigenvalue}/\text{largest eigenvalue}]$ , as they were calculated using the mean-  
371 intercept-length method (Whitehouse, 1974; Odgaard, 1997). Tb.Sp and Tb.Th were

372 calculated based on the Hildebrand and Ruesegger (1997) method; Tb.N was then  
373 calculated as  $Tb.N = 1 / (Tb.Th + Tb.Sp)$ .

374

### 375 *Statistical analysis*

376

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

381

382

## 383 **Results**

384

### 385 *BV/TV distribution in the femoral head*

386

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

394

395 [Insert **Figure 2** about here]

396

397 The pattern of BV/TV distribution in *Gorilla* is similar to that found in *Pan* (Fig. 3).  
398 Two concentrations of high BV/TV are seen in the superior aspect, one located  
399 anteriorly, and one located posteriorly. Unlike in *Pan* however, these concentrations  
400 are distinct from each other in all but three *Gorilla* individuals, in which a region of  
401 high BV/TV spans across the superior region of the femoral head. There is no  
402 apparent difference in the size of the two regions of high BV/TV.

403

404 [Insert **Figure 3** about here]

405

406 *Pongo* shows a slightly different BV/TV pattern compared to *Pan* and *Gorilla* (Fig. 4).  
407 The *P. pygmaeus* individuals show the two concentrations of high BV/TV, one in the  
408 anterior and one in the posterior, similar to what is found in the African apes,  
409 however intermediate values persist over the superior portion of the femoral head.  
410 The extent of this concentration differs between *P. pygmaeus* individuals: in two  
411 individuals it is restricted more in the superior aspect of the head, whereas in the  
412 other two it is enlarged and covers the majority of the femoral head, from the  
413 anterior to the posterior. When the two concentrations are more well-defined, the  
414 posterior concentration is generally more mediolaterally expanded than the anterior

415 concentration. The *P. abelii* individual shows lower BV/TV than the other specimens  
416 and does not show two distinct concentrations.

417

418 [Insert **Figure 4** about here]

419

420 *Homo* shows a different pattern to the great apes (Fig. 5). All individuals show one  
421 region of high BV/TV located in the posterior and superior aspect of the femoral  
422 head. Intermediate values of BV/TV expand across the whole of the superior aspect  
423 of the head of *Homo*, but with no apparent second concentration of high BV/TV in  
424 the anterior region as found in great apes. *Homo* individuals also display  
425 intermediate BV/TV on the inferior aspect of the head. This expansion of  
426 intermediate BV/TV values along the inferior is not seen in the other apes.

427

428 [Insert **Figure 5** about here]

429

430

431 *Quantitative analysis of trabecular parameters in the femoral head*

432

433 Quantitative analysis of the mean trabecular parameters over the femoral head  
434 revealed several differences across taxa. Results for each parameter in the different  
435 taxa are presented in Table 2 and statistical results of species pairwise comparisons,  
436 after Bonferroni corrections, are presented in Table 3. *Pan* shows significantly higher  
437 BV/TV in the femoral head than *Pongo* ( $p=0.05$ ) and *Homo* ( $p<0.001$ ), and although  
438 its mean BV/TV value was higher than that of *Gorilla*, this difference was not  
439 statistically significant (Tables 2 and 3). *Homo* has the lowest mean BV/TV compared  
440 with all the great apes but is only significantly different from *Pan*. *Homo* has  
441 significantly higher DA in the femoral head than all other apes (*Pan*  $p<0.001$ ; *Gorilla*  
442  $p<0.05$ ; *Pongo*  $p<0.01$ ), while *Pan*, *Pongo* and, less so, *Gorilla* are more isotropic and  
443 not significantly different from each other. With regards to the architectural  
444 parameters, *Pan* shows the most distinct trabecular structure with significantly higher  
445 Tb.N than all other apes (*Gorilla*  $p<0.001$ ; *Homo*  $p<0.001$ ; *Pongo*  $p<0.01$ ) and  
446 significantly lower Tb.Sp (all  $p<0.001$ ) and lower Tb.Th than *Gorilla* ( $p<0.001$ ) and  
447 *Homo* ( $p<0.05$ ).

448

449 Differences in mean BV/TV and DA across taxa were further evaluated using a  
450 bivariate plot (Fig.6) and a line histogram of the distribution of values in each taxon  
451 (Fig. 7). The data depicted in these figures are mean values for each individual across  
452 the entire femoral head. In the bivariate plot *Pan* shows a combination of high BV/TV  
453 and low DA, in contrast to humans that show the opposite pattern. *Gorilla* overlaps  
454 with both of these taxa but shows higher BV/TV than humans. *Pongo* individuals  
455 overlap with the African apes, with lower DA values than humans, but with BV/TV  
456 values that overlap with all other taxa.

457

458 [Insert **Figure 6** about here]

459

460 These differences are reflected in the distribution of BV/TV and DA values in the taxa  
461 (Fig. 7). *Pan* shows the highest mean BV/TV and **most individuals** close to the mean  
462 (0.39), whereas *Gorilla* shows a lower mean value but **most individuals** between 0.3  
463 and 0.4. *Pongo* shows a similar mean to *Gorilla*, however the distribution of values  
464 **more greatly resembles** that of *Pan*. *Homo* shows the lowest BV/TV values distributed  
465 over a wider area. The DA plot shows that *Pan*, *Gorilla* and *Pongo* present similarly  
466 low mean DA values, but *Pongo* differs in distribution with **more individuals** around  
467 the mean. *Homo* shows a different distribution with the highest mean DA but a wider  
468 distribution of values in the sample.

469

470 [Insert **Figure 7** about here]

471

472

## 473 **Discussion**

474

475 Our study investigated the variation in trabecular patterns of the femoral head in  
476 great apes and humans. Qualitative and quantitative results supported our  
477 hypotheses that trabecular bone would reflect differences in locomotor patterns, but  
478 not necessarily in the way we predicted. *Pan* and *Gorilla* displayed trabecular  
479 structures consistent with their terrestrial as well as arboreal quadrupedal  
480 locomotion, while *Homo* showed a distinct trabecular pattern indicative of  
481 stereotypical loading during bipedal locomotion. However, the African apes showed  
482 a BV/TV distribution pattern that was **different to what was expected**, and their  
483 trabecular structure did not differ significantly from *Pongo*.

484

### 485 *Distribution of BV/TV within the femoral head*

486

487 We predicted that African apes would display a region of high BV/TV extending from  
488 the posterosuperior to the anterior region of the femoral head, reflecting the flexed  
489 hip postures and loading incurred during knuckle-walking and vertical climbing.  
490 However, instead of a continuous band of high BV/TV across the femoral head, *Pan*  
491 displayed two main regions of high BV/TV, indicating two regions of high loading;  
492 one in the **posterosuperior** aspect of the femoral head and one located more  
493 anteriorly. The majority of Tai chimpanzee (75% of the *Pan* sample) locomotion is  
494 terrestrial quadrupedalism (Doran, 1993). Ground reaction forces remain high  
495 throughout the stance phase during terrestrial knuckle-walking (Barak et al. 2013)  
496 and the hip remains flexed (Finestone et al. 2018), both of which are consistent with  
497 high loading of the posterosuperior region of the femoral head and the high BV/TV  
498 concentration that was found in this region. While Tai chimpanzees engage less  
499 frequently in vertical climbing (Doran, 1993a), it is possible that this results in  
500 similarly high loading of the femoral head, **as it involves high propulsive forces from**

501 **the hindlimbs** (Hanna et al. 2017). During climbing, the hip can be flexed to a  
502 maximum of 25° to 55° (Isler, 2005; Nakano et al. 2006), which would result in the  
503 anterior aspect of the head contacting the lunate surface of the acetabulum. This is  
504 consistent with the second region of high BV/TV found in the anterior portion of the  
505 femoral head **in Pan**. The anterior concentration was more variable between  
506 individuals, but **this** could not be explained by subspecies differences within the  
507 sample. Thus, the more variable anterior BV/TV pattern may reflect interindividual  
508 variability in vertical climbing frequency (Doran, 1993b) or hip range of motion  
509 during climbing (Isler, 2005; Nakano et al. 2006).

510

511 *Gorilla* displayed a similar pattern to *Pan*, with two regions of high BV/TV within the  
512 femoral head. The two regions, one in the posterior and one in the anterior aspect of  
513 the head, are, as in *Pan*, consistent with hip posture and loading during terrestrial  
514 quadrupedalism and vertical climbing, as these modes of locomotion comprise the  
515 majority of *Gorilla* locomotion (Doran, 1997; Crompton et al. 2010; Remis, 1995).  
516 However, unlike *Pan*, these regions were better defined and more discrete in most  
517 *Gorilla* individuals (**11 out of 14 individuals**). This more discrete pattern is perhaps  
518 due to their greater body mass. Greater mass is related to restricted range of motion  
519 in joints (Hammond, 2014), which could result in less variability in joint positioning  
520 during locomotion and may explain the more **well-defined** concentrations in *Gorilla*.  
521 The two concentrations appeared closer to each other in *Gorilla* than in *Pan*, which is  
522 also consistent with the reduced range of motion at the hip joint of *Gorilla* (Isler,  
523 2005; Hammond, 2014). Significant sex and body size related differences in joint  
524 mobility are prominent in *Gorilla*, with females showing a larger range **of motion**  
525 **than** males and flexion-extension ranges varying between the sexes by up to or even  
526 more than 30° (Isler, 2005; Hammond, 2014). These differences were not detected in  
527 the BV/TV distribution maps and *Gorilla* does not seem to be more variable than  
528 *Pan*. However, this could not be tested statistically in the current study.

529

530 We predicted that the BV/TV distribution pattern of the *Pongo* femoral head would  
531 differ from that of African apes and humans because of their more varied  
532 quadrumanous locomotor behaviours (Thorpe and Crompton, 2005; Thorpe and  
533 Crompton, 2006), more mobile hip joints (Crelin, 1988; Ward, 1991), and increased  
534 range of motion at the hip during vertical climbing compared to African apes (Isler,  
535 2005). Four of the five *Pongo* individuals in our sample showed the same two regions  
536 of high BV/TV found in African apes, however these were not as distinct and, instead,  
537 there was a continuous concentration of BV/TV spanning the superior aspect of the  
538 femoral head. This is perhaps unsurprising since *Pongo* uses a variety of hip postures  
539 while navigating their arboreal environment (Thorpe and Crompton, 2005; Thorpe  
540 and Crompton, 2006; Payne et al. 2006; Thorpe et al. 2009), which potentially results  
541 in higher loading across the whole superior surface of the femoral head. *Pongo* also  
542 vertically climbs less frequently than African apes (Thorpe and Crompton, 2006),  
543 which may be **reflected by** the less defined anterior concentration of high BV/TV in

544 *Pongo* compared with *Pan* and, especially, with *Gorilla*. Although our sample of  
545 *Pongo* is small (n=5) and all individuals were female, there was greater variation in  
546 the BV/TV distributions along the anterior and posterior aspects of the femoral head  
547 than was found in African apes. The one *P. abelii* specimen in our sample differed  
548 from the *P. pygmaeus* individuals in having only one superior concentration of high  
549 BV/TV. Although locomotor differences have been documented between *P.*  
550 *pygmaeus* and *P. abelii* (Sugardjito and van Hooff, 1986; Cant, 1987), a larger sample  
551 of both species is needed to determine if this variation in the trabecular pattern is  
552 characteristic of each species.

553

554 *Homo* showed a distinct trabecular pattern that is consistent with our predictions and  
555 similar to previous results showing the density distribution of trabeculae adjacent to  
556 cortical bone (Treece and Gee, 2014). All *Homo* individuals displayed one main region  
557 of high BV/TV, located posteriorly and superiorly on the femoral head. This  
558 concentration was positioned more medially than the posterior concentration seen in  
559 great apes and closer to the fovea capitis, which is consistent with loading of the  
560 femur at a valgus angle. Intermediate BV/TV values continued along the superior  
561 aspect of the femoral head in *Homo*. This is consistent with loading that occurs  
562 throughout the gait cycle over the articulating surface but suggests that peak  
563 loading is occurring at the posterosuperior region, which is in contact with the  
564 acetabulum during walking (Bonneau et al. 2012; Bonneau et al. 2014). Of course,  
565 humans also engage in other activities that involve more flexed hip joint postures,  
566 such as running, jumping, or climbing stairs, all of which impose high loads on the  
567 lower limb (van den Bogert et al. 1999; Giarmatzis et al. 2015) and could result in  
568 some trabecular reorganisation, explaining the extended area of intermediate BV/TV  
569 values we found across the femoral head. Unfortunately, it is not yet known exactly  
570 how the peak load is distributed over the femoral head during these activities.  
571 However, all individuals lack the anterior concentration found in apes, further  
572 supporting the interpretation that high BV/TV in the anterior region could be linked  
573 to arboreal behaviours or more specifically vertical climbing.

574

#### 575 *Quantitative analysis of trabecular structure*

576

577 Quantitative analysis of the femoral head trabecular structure only partially  
578 supported our hypotheses. As expected, *Homo* displayed the lowest mean BV/TV in  
579 our sample but was only significantly different from that of *Pan*. Our results confirm  
580 previous studies showing that modern humans, particularly those that are less active,  
581 have relatively lower BV/TV across the skeleton compared with highly mobile modern  
582 humans and other primates (Chirchir et al. 2015; Ryan and Shaw, 2015; Saers et al.  
583 2016; Chirchir et al. 2017). Furthermore, *Homo* showed significantly higher DA than  
584 great apes, which is consistent with the more stereotypical loading of the hip joint  
585 during bipedal locomotion and in accordance with previous results from the proximal  
586 (Ryan and Shaw, 2015; Ryan et al. 2018) as well as the distal femur (Georgiou et al.

587 2018). *Homo* has narrower acetabulae than other great apes, with expanded cranial  
588 lunate surfaces, as well as shortened dorsal surfaces, which result in a distinctively-  
589 shaped dorso-cranially expanded lunate surface that may restrict movement in the  
590 parasagittal plane (San Millán et al. 2015). Furthermore, in *Homo* the iliofemoral  
591 ligament limits extension and external rotation (Myers et al. 2011), the ischiofemoral  
592 ligament limits internal rotation and the pubofemoral ligament limits abduction  
593 (Wagner et al. 2012), all of which result in a more restrictive and stereotypical motion  
594 and loading of the femoral head that is reflected in the trabecular structure.

595

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

609

610 The trabecular structure of *Gorilla* and *Pongo* was not as distinct. *Gorilla* mean BV/TV  
611 did not differ significantly from any other taxon, and they only differed significantly  
612 in Tb.N, Tb.Sp and Tb.Th from *Pan*, as well as in DA from *Homo*. *Gorilla* has less  
613 variable positioning of their lower limbs during locomotion, compared to other non-  
614 human apes, as was shown in vertical climbing (Isler, 2005), however this is not  
615 displayed as clearly in their DA values as was initially predicted. The lack of significant  
616 differences in BV/TV and DA with *Pan* can perhaps be explained by the similar shape  
617 of their hip joints (San Millán et al. 2015) and overall similarities in locomotion  
618 (Doran, 1997). None of great apes differed significantly in DA, despite clear  
619 differences in locomotor behaviours and hip morphology. *Pongo* has a cranio-  
620 ventrally expanded lunate surface and a smaller acetabular fossa than other apes.  
621 They also show the largest articular surfaces and relatively shallow acetabulae  
622 (Schultz, 1969), which may be responsible for the increased mobility of the femoral  
623 head. Furthermore, *Pongo* has a greater capacity for abduction and external rotation  
624 than non-suspensory taxa (Hammond, 2014). Thus, *Pongo* was expected to display  
625 significantly lower DA values than all other taxa, which was not the case, but this  
626 result may also reflect our small sample size for this taxon.

627

628 Our results showed that *Pan* has relatively numerous, thinner and compactly  
629 organised trabeculae, while *Gorilla* and *Homo* have relatively few, thicker and more

630 separated trabeculae. *Pongo* has relatively few, thinner and more separated  
631 trabeculae. These results are largely in accordance with previous analyses of femoral  
632 head trabeculae (Ryan and Shaw, 2012; 2015) which showed that humans have  
633 relatively less numerous, thin and highly anisotropic trabeculae compared to other  
634 anthropoids, *Pan* have relatively high numbers of thick, isotropic trabeculae and  
635 *Pongo* have relatively few, isotropic trabeculae. *Gorilla* showed the thickest  
636 trabeculae (Table 2), in support of previous studies suggesting that larger taxa have  
637 absolutely thicker trabeculae (Barak et al. 2013; Ryan and Shaw, 2013; Tsegai et al.  
638 2013). However, the difference was not found to be significant, possibly due to the  
639 small sample sizes in our study. Allometric relationships were not tested in our study  
640 because our sample sizes were not large enough to test this intraspecifically,  
641 however previous research has shown that these trabecular parameters can vary  
642 predictably with body size interspecifically (Cotter et al. 2009; Doube et al. 2011;  
643 Barak et al. 2013; Ryan and Shaw, 2013). Across a large sample of mammals, Tb.Th  
644 and Tb.Sp were shown to increase with size (Doube et al. 2011). In primates, Tb.N,  
645 Tb.Th and Tb.Sp present negatively allometric relationships with body mass (Barak et  
646 al. 2013; Ryan and Shaw, 2013), resulting in more, thinner and less separated  
647 trabeculae in larger taxa. These studies suggest that absolute trabecular parameters,  
648 and specifically Tb.N, Tb.Sp and Tb.Th, do not necessarily directly reflect locomotor  
649 modes as they could reflect body-size related or systemic differences between taxa.  
650 Nevertheless, since our sample includes apes that are relatively similar in body size  
651 compared to the more diverse samples of previous studies (Doube et al. 2011; Barak  
652 et al. 2013; Ryan and Shaw, 2013), we would expect that allometry does not have a  
653 significant effect on the variation observed here.

654  
655 The absence of a clear functional signal in the mean trabecular parameters may be  
656 due to methodological limitations of the whole-epiphysis approach. The mean value  
657 of any given trabecular parameter can obscure or homogenise any potential distinct  
658 variation in specific regions of the femoral head, as demonstrated by the BV/TV  
659 distribution maps and previous studies (Sylvester and Terhune, 2017). This is where  
660 the traditional VOI approach, in which the trabecular architecture of specific regions  
661 of an epiphysis can be quantified and compared, is potentially more functionally  
662 informative (e.g. Ryan and Shaw, 2012; 2015; Ryan et al. 2018). Additionally, the lack  
663 of a strong functional signal in these parameters could be due to non-mechanical  
664 factors affecting trabecular structure. Trabecular bone also functions as a reserve of  
665 minerals and is important in maintaining homeostasis, hence its structure will, to  
666 some extent, be affected by this (Rodan, 1998; Clarke, 2008). Genes control for the  
667 rate of remodelling and bone mineral density, as well as the response to mechanical  
668 strain in different skeletal sites (Smith et al. 1973; Dequeker et al. 1987; Kelly et al.  
669 1991; Garnerio et al. 1996; Hauser et al. 1997; Judex et al. 2002; Judex et al. 2004).  
670 These factors, along with the fact that trabecular bone remodels in response to a  
671 range of magnitudes and frequencies of load (Whalen et al. 1988; Rubin et al. 1990;  
672 Rubin et al. 2001; Judex et al. 2003; Scherf et al. 2013), complicate interpretations.



673 Age, hormones, sex and other factors (e.g. Simkin et al. 1987; Pearson and  
674 Lieberman, 2004; Suuriniemi et al. 2004; Kivell, 2016; Wallace et al. 2017; Tsegai et al.  
675 2018) influence trabecular bone modelling, thus these factors should not be ignored.  
676 **Nonetheless, future research will aim to use techniques that will allow statistical**  
677 **comparisons of the trabecular distribution patterns in the femoral head of apes,**  
678 **rather than mean parameters, for more accurate interpretation of locomotor patterns**  
679 **in extinct hominins.**

680

## 681 **Conclusion**

682

683 **This study showed that** the trabecular architecture of the femoral head in **great apes**  
684 **and humans** reflects habitual **hip** postures during locomotion. *Pan* and *Gorilla*  
685 **showed** similar BV/TV distribution patterns, **with generally two distinct high BV/TV**  
686 **regions that are consistent with hip postures during knuckle-walking and vertical**  
687 **climbing.** *Pongo* **showed a BV/TV distribution pattern that is characteristic of their**  
688 highly mobile hips and complex locomotion, however **they** do not differ as  
689 significantly as predicted **from** African apes. Finally, *Homo* **showed** a distinct pattern  
690 of BV/TV distribution, **with one posterosuperior region of high BV/TV,** the lowest  
691 overall BV/TV values and highest DA values, **which is** consistent with stereotypical  
692 loading during locomotion. **Despite mean trabecular parameters not demonstrating**  
693 **locomotor differences as clearly as predicted, they largely match results from**  
694 **previous VOI studies (Ryan and Shaw, 2015; Ryan et al. 2018). Our research reveals**  
695 **that there are distinct patterns of BV/TV distribution that generally distinguish the**  
696 **locomotor groups and provide a** valuable comparative sample for future research on  
697 the evolution of gait in hominins.

698

## 699 **Acknowledgements**

700

701 We thank the following researchers for access to specimens: Anneke Van Heteren  
702 (Zoologische Staatssammlung München), Inbal Livne (Powell-Cotton Museum),  
703 Christophe Boesch and Jean-Jacques Hublin (Max Planck Institute for Evolutionary  
704 Anthropology), and Brigit Grosskopf (Georg-August University of Goettingen). We  
705 also thank David Plotzki (Max Planck Institute for Evolutionary Anthropology) and  
706 Keturah Smithson (University of Cambridge) for the CT scanning of specimens. We  
707 thank Zewdi Tsegai for facilitating access to CT data and Kim Deckers for discussions  
708 that improved this manuscript. **We are grateful to two anonymous reviewers for their**  
709 **valuable feedback that improved this manuscript.** This research is supported by a  
710 50th Anniversary Research Scholarship, University of Kent (LG), European Research  
711 Council Starting Grant 336301 (MMS, TLK), and the Max Planck Society (MMS, TLK).

712

713

## 714 **Author contributions**

715

716 L. Georgiou, T.L. Kivell and M.M. Skinner contributed to the design of the study and  
717 acquisition of data, **L. T. Buck facilitated and collected data**, D.H Pahr contributed to  
718 the analysis tools, L. Georgiou processed, analysed and interpreted the data, L.  
719 Georgiou drafted the manuscript, L. Georgiou, T.L. Kivell, D.H. Pahr, **L.T. Buck** and  
720 M.M. Skinner revised and approved the final manuscript submitted for review.  
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1169 **Tables**

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1171 **Table 1. Study sample taxonomic composition, re-sampled voxel size range,**  
 1172 **sex, and microCT scanning parameters. All specimens were re-sampled except six**  
 1173 **of the gorillas that were scanned at lower resolutions.**

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

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1198 **Table 2. Trabecular architecture results.** Mean, standard deviation (in parentheses)  
1199 and coefficient of variation for five trabecular parameters quantified throughout the  
1200 femoral head.

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

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1231 **Table 3. Results of pairwise comparisons between taxa.** Bonferroni-corrected p-  
1232 values of each pairwise comparison for all trabecular parameters. Significant results  
1233 are indicated by grey shading.

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

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### 1270 **Figure legends**

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**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).

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**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).

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**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).

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**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

1294 the right side. Specimens from left to right (All female): ZSM 1909 0801, 1907 0660,  
1295 1973 0270, 1907 0483, 1907 0633b.

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1297 **Figure 5. *Homo* BV/TV distribution in the femoral head.** Five *Homo* specimens  
1298 showing variation in the BV/TV distribution across the sample in (A) anterior, (B)  
1299 posterior and (C) superior views. BV/TV is scaled to 0-0.55. All specimens are from  
1300 the right side. Specimens from left to right (F-female, M-male): CAMPUS 36 (F),  
1301 CAMPUS 93 (M), CAMPUS 74 (F), CAMPUS 417 (sex unknown), CAMPUS 81 (M).

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1303 **Figure 6. Bivariate plot of mean bone volume fraction (BV/TV) and mean**  
1304 **degree of anisotropy (DA) for each individual and species in the sample.**

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1306 **Figure 7. A histogram of mean BV/TV and DA value distributions in the studied**  
1307 **taxa.**