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Trabecular architecture of the great ape and human femoral head

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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

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

The discrepancy in the findings of previous studies may, in part, be an artefact of the volume-of-interest (VOI) method that was used. A VOI quantifies only a subsample of trabecular structure within a given region and results can vary depending on its size and position (Fajardo and Müller, 2001; Kivell et al. 2011). Additionally, challenges arise when extracting homologous VOIs in taxa that vary in external morphology. Prior research has demonstrated that additional functional insight can be gained from investigating the trabecular architecture within an epiphysis as a whole (Tsegai et al. 2013; Skinner et al. 2015; Stephens et al. 2016; Sylvester and Terhune, 2017; Tsegai et al. 2018). Here we apply a whole-epiphysis approach to study the trabecular structure throughout the femoral head of chimpanzees (*Pan troglodytes*), lowland gorillas (*Gorilla gorilla*), orangutans (*Pongo* sp.) and humans (*Homo sapiens*), which vary in locomotor behaviours and are relevant to the reconstruction of locomotion in fossil hominins.

Locomotion, hip morphology and predicted joint posture

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

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

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 68.3º
185 at touchdown and 107.3º 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 30º to 135º (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 160º at touchdown and 175º
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 30-40º, 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

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

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

1. BV/TV distribution in the femoral head

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

2. Mean trabecular parameters in the femoral head

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

superior region of the femoral head. There is no apparent difference in the size of the two
regions of high BV/TV.

[Insert **Figure 3** about here]

Pongo shows a slightly different BV/TV pattern compared to *Pan* and *Gorilla* (Fig. 4). The
P. pygmaeus individuals show the two concentrations of high BV/TV, one in the anterior and
one in the posterior, similar to what is found in the African apes, however intermediate values
persist over the superior portion of the femoral head. The extent of this concentration differs
between *P. pygmaeus* individuals; in two individuals it is restricted more in the superior
aspect of the head, whereas in the other two it is enlarged and covers the majority of the
femoral head, from the anterior to the posterior. When the two concentrations are more well
defined, the posterior concentration is generally more mediolaterally expanded than the
anterior concentration. The *P. abelii* individual shows lower BV/TV than the other specimens
and does not show two distinct concentrations.

[Insert **Figure 4** about here]

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

[Insert **Figure 5** about here]

Quantitative analysis of trabecular parameters in the femoral head

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

Differences in mean BV/TV and DA across taxa were further evaluated using a bivariate plot
(Fig.6) and a line histogram of the distribution of values in each taxon (Fig. 7). The data
depicted in these figures are mean values for each individual across the entire femoral head.
In the bivariate plot *Pan* shows a combination of high BV/TV and low DA, in contrast to
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.

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.

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
664 **Author contributions**
665
666 L. Georgiou, T.L. Kivell and M.M. Skinner contributed to the design of the study and
667 acquisition of data, L. T. Buck facilitated and collected data, D.H Pahr contributed to the
668 analysis tools, L. Georgiou processed, analysed and interpreted the data, L. Georgiou drafted
669 the manuscript, L. Georgiou, T.L. Kivell, D.H. Pahr, L.T. Buck and M.M. Skinner revised
670 and approved the final manuscript submitted for review.
671
672
673 **References**

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1098 **Tables**
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1100 **Table 1. Study sample taxonomic composition, re-sampled voxel size range, sex, and**
1101 **microCT scanning parameters.** All specimens were re-sampled except six of the gorillas
1102 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

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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

1159 **Table 3. Results of pairwise comparisons between taxa.** Bonferroni-corrected p-values of
1160 each pairwise comparison for all trabecular parameters. Significant results are indicated by
1161 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

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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.