Trabecular structure of the elbow reveals divergence in knuckle-walking biomechanical strategies of African apes

Julia Arias-Martorell[1,2]*, Angel Zeininger[3], Tracy L. Kivell[2,4]

1. Institut Català de Paleontologia Miquel Crusafont, Edifici ICTA-ICP, Carrer Columnes s/n, Campus de la UAB, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain.

2. Animal Postcranial Evolution (APE) Lab, School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury, CT2 7NR, UK

3. Department of Evolutionary Anthropology, Duke University, Durham, North Carolina, 27708, USA.

4. Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, Germany 01403, Germany

*Corresponding author: Dr Julia Arias-Martorell

Correspondence to: julia.arias@icp.cat

Running Head: Trabecular structure of the African ape elbow

Abstract

African apes engage in a distinct form of locomotion called knuckle-walking, but there is much ambiguity as to when and how this locomotor behaviour evolved. This study aims to elucidate potential differences in knuckle-walking elbow posture and loading in African apes through the study of trabecular bone. Using a whole-epiphysis approach, we quantified variation in trabecular structure of the distal humerus of chimpanzees, western lowland gorillas, and mountain gorillas in comparison to orang-utans, siamangs and a sample

of Old and New World monkeys. Results demonstrate differences in the distribution of trabecular bone within the distal humerus that are consistent across taxa that habitually use a flexed-elbow posture in comparison to those that use an extended-elbow during locomotion. Western lowland gorillas show an extended-elbow pattern consistent with the straight forelimb position during knuckle-walking, whereas chimpanzees show a flexed-elbow pattern. Unexpectedly, mountain gorillas show an intermediate pattern between their western counterparts and chimpanzees. The differences found in elbow joint posture between chimpanzees and gorillas, and between gorilla species, point to diversification in the knuckle-walking biomechanical strategies among African apes, which has implications in the debate regarding the locomotor behaviour from which human bipedalism arose.

Keywords: bone functional adaptation; joint posture; hominoid; locomotion; chimpanzee; gorilla

Introduction

Knuckle-walking is the most frequent form of locomotion used by African apes (Hunt, 1991; Doran, 1996; Doran, 1997; Remis, 1995). In this quadrupedal locomotion, the hand is in a vertical posture with the digits flexed such that weight is born on the dorsal side of the intermediate phalanges of the second to fifth rays. Although there is variation across genera and species in how often knuckle-walking is used, all African apes knuckle-walk both on the ground and in trees at least 85% of their locomotor time (Hunt, 1991; Doran, 1997; Crompton et al., 2010). As such, there has been much discussion about the potential adaptive and evolutionary significance associated with this distinct form of locomotion (reviewed in Richmond et al., 2001). The presence or absence of potential knuckle-walking adaptations, particularly of the wrist and hand, is a dominant feature in debates about the locomotor behaviour of the last common ancestor of *Pan* (i.e., chimpanzees and bonobos) and hominins and whether knuckle-walking might have independently evolved in gorillas and chimpanzees (Begun, 1992; Richmond and Strait, 2002; Dainton and Macho, 1999; Kivell and Schmitt, 2009; Lovejoy, 2009; Williams, 2010). As an alternative to external features associated with the hand and wrist, this study aims to identify variation in the internal anatomy (trabecular structure) at the elbow (distal humerus) in extant African apes to investigate the presence of a knuckle-walking signal.

The external elbow morphology of primates provides stability in a wide range of pronation-supination and flexion-extension movements (Rose, 1988; Drapeau, 2008). Of particular importance is the distal humerus, which articulates with both forearm bones and for which extant apes, including humans, share a derived morphology with a spool-shaped trochlea (which articulates with the ulna) and a globular capitulum (which articulates with the radius) (Supporting Information [SI] Fig. S1). Morphological variation of the distal humerus across apes is traditionally thought to reflect their locomotor differences (Rose, 1988;

65 Drapeau, 2008). Relative to more suspensory Asian apes (Schmitt, 1994; Zihlman et al.,
66 2011), African apes have more distally expanded and flatter joints to sustain loading of the
67 forelimb during terrestrial locomotion with an extended forearm (Drapeau, 2008). Powerful
68 forearm flexor and extensor muscles, which are essential during below-branch locomotor
69 behaviours and which generate transverse forces that are resisted by the spool-shaped
70 trochlear morphology, insert on the medial and lateral epicondyles of the distal humerus.
71 External bone morphology, and particularly joint morphology, is potentially more
72 genetically constrained compared with internal bone architecture (Rafferty and Ruff, 1994;
73 Lieberman et al., 2001). Experimental evidence demonstrates that trabecular bone in
74 particular can respond to the magnitude, frequency and direction of mechanical load during
75 life (Biewener et al., 1996; Pontzer et al., 2006; Barak et al., 2011; reviewed in Kivell, 2016).
76 Although other non-functional factors can influence trabecular structure, such as genetics
77 (Ryan et al., 2017), age (Macho et al., 2005), hormones (Khosla et al., 2006) or systemic
78 differences (Tsegai et al., 2018), numerous comparative studies have demonstrated strong
79 correlations between variation in trabecular structure and differences in behaviour among
80 primates in many bones/joints of the postcranial skeleton (e.g., Ryan and Shaw, 2012; Tsegai
81 et al., 2013; Saers et al., 2019). The proximal humerus has been the anatomical focus of many
82 of these studies, with some showing clear functional signals within the trabecular structure
83 across primates (Rafferty and Ruff, 1994; Scherf et al., 2013; Kivell et al., 2018), while
84 others are more ambiguous (Ryan and Walker, 2010; Ryan and Shaw, 2012). Other studies
85 focused on the capitate and third metacarpal of African apes concluded that changes in
86 trabecular structure reflected changes in locomotor frequencies throughout ontogeny (Ragni,
87 2020), while additional studies of the capitate x found that capitate trabecular patterns in
88 African apes differed from the Asian apes in relation to their particular locomotor behaviour
89 (i.e., knuckle-walking; Bird et al., 2021); however, to date, no study has focused on the distal

humerus in spite of its significance (and of the elbow in general) to forelimb posture and loading during locomotion.

The locomotor and postural repertoire of the African apes has been extensively studied (e.g., Inouye, 1994; Inouye, 1992; Doran, 1997; Isler, 2005; Neufuss et al., 2017; Finestone et al., 2018; Thompson et al., 2020). African apes are the most terrestrial of the non-human apes, with gorillas being more terrestrial than chimpanzees in adulthood (Hunt, 1991; Doran, 1993; Doran, 1996; Crompton et al., 2010). Additional variation in terrestriality exists within species of chimpanzees and gorilla (e.g., mountain gorillas are more terrestrial than western lowland gorillas; Doran, 1993; Inouye, 1993; Remis, 1994). There are also postural differences in African ape knuckle-walking such that gorillas typically use a pronated hand posture (palm facing backwards), while chimpanzees are more variable but most often use a palm-in posture (Tuttle, 1969; Wunderlich and Jungers, 2009; Matarazzo, 2013; but see Thompson et al., 2020). In addition to knuckle-walking, African apes also use a large diversity of other locomotor behaviours, including vertical climbing, clambering, and suspension (Hunt, 1991; Doran, 1993; Remis, 1994; Crompton et al., 2010). These arboreal behaviours are more frequent during early ontogeny (i.e., <5 years of age) in both chimpanzees and gorillas (Doran, 1997).

To investigate the potential knuckle-walking signals in humeral trabecular bone, we compare African apes to the more suspensory Asian apes (orang-utans and hylobatids), semi-suspensory spider monkeys, and both arboreal and terrestrial quadrupedal monkeys (howler monkeys and long-tailed macaques, and Hamadryas baboons, respectively) that vary in both their locomotor behaviours and habitual elbow postures (see below).

Elbow joint loading predictions

The main movement of the primate elbow is flexion-extension, the range of which is mostly determined by the shape of the olecranon process of the ulna (Harrison, 1982). Apes

have a short olecranon processes that allows full (and even hyper-) extension of the elbow, whereas monkeys have a long olecranon process that impedes full extension at the elbow when it articulates with the olecranon fossa of the humerus. Stabilisation of the ape elbow is achieved in part by a keeled humeroulnar joint. In apes, the humeral trochlea has a medial and lateral keel (creating the spool-shape), in which the medial keel, particularly in monkeys, helps to resist mediolateral forces generated by the elbow and digit extensors that threaten to rotate and displace the ulna medially (Preuschoft, 1973; Schmitt, 2003; Hunt, 2016). The median keel in the trochlear notch of the ulna further enhances mediolateral stabilization. Apes have a round radial head that articulates with a globular capitulum and deep zona conoidea (an indentation between the lateral keel and the capitulum) of the distal humerus, which provides greater stabilization of the radiohumeral joint in all positions of pronosupination (although pronosupination itself occurs at proximal and distal radioulnar joints) and stabilizes the radial head during the movement. Habitual elbow postures during locomotion can include full (or hyper-) extension, full flexion, or a variety of postures involving semi-flexion of the elbow (Rose, 1988). While elbow joint angle can be measured directly, it is not possible to directly quantify joint reaction forces (loading). However, relative loading conditions (e.g., higher loads on one region of the joint) can be reasonably predicted given variation in anatomy and joint posture.

Therefore, we predict that an elbow habitually loaded in (1) **extension** (~180º) will result in a distal humerus showing a relatively high density of trabeculae (bone volume fraction, bone volume/total volume [BV/TV]) concentrated in the distal and/or posterior aspects of the trochlea and the distal capitulum, while **hyperextension** (>180º) might be reflected in higher BV/TV in the posterior aspect of the trochlea as the olecranon impinges into the humerus' fossa; (2) **semi-flexion** (>90º and <180º) will result in a distal humerus showing high BV/TV concentrated more anterodistally in the capitulum and trochlea, and

potentially the medial keel of the trochlea, which resists the medial forces of the muscles acting at the elbow; (3) **flexion** (≤90º) will result in a distal humerus showing high BV/TV concentrated only in the anterior regions of the capitulum and trochlea.

Based on the model above, we make the following predictions for habitual loading of the elbow of African apes, Asian apes and non-hominoid taxa studied:

Gorillas and chimpanzees The elbow is generally held in an extended posture during knuckle-walking in all African apes during stance phase (Zylstra, 1999; Hunt, 1996). The mean elbow joint angle of gorillas (*Gorilla*) is closer to 180 degrees (i.e., fully extended) at midstance than chimpanzees (*Pan*), which display more variability (Isler, 2005; Finestone et al., 2018; Thompson et al., 2020); however, both taxa occasionally use hyperextended elbow postures (Inouye, 1994; Zylstra, 1999; Finestone et al., 2018). As such, we predict that African apes will show a trabecular pattern consistent with habitual loading of a relatively extended elbow during knuckle-walking.

Siamangs and orang-utans Orang-utans (*Pongo*) engage most frequently in torso-orthograde suspension, such that the torso is vertically oriented with the hands and feet bearing weight typically in tension with the elbow extended, while during vertical climbing/descent, the elbow is most often flexed (Thorpe and Crompton, 2005; Thorpe and Crompton, 2006; Thorpe et al., 2009). Hylobatids prefer to move through the canopy using brachiation, including ricochetal brachiation, as the primary form of locomotion (Hunt, 1991) in which the elbow of the support limb is extended (Swartz, 1989; Swartz et al., 1989). We include siamangs (*Symphalangus*) in our sample whose positional behaviour is more similar to that of orangutans than other hylobatids, likely due to their larger body size (Hunt, 2016). Thus, the expected pattern for the more suspensory Asian apes is habitual loading of an extended elbow. However, if found, we expect potential variation in BV/TV values between the African versus Asian ape extended-elbow trabecular pattern given that African apes more

165 frequently load their forelimb in compression (higher BV/TV) and the Asian apes in tension
166 (lower BV/TV) (Swartz et al., 1989). Additionally, due to their more varied locomotor
167 regimes, orang-utans may alternatively show a more diffuse or unspecific trabecular pattern
168 consistent with an elbow loaded in a variety of different postures.

169 Pronograde monkeys Howler monkeys (*Alouatta* sp.), macaques (*Macaca*
170 *fascicularis*), and baboons (*Papio hamadryas*), most often engage in pronograde
171 quadrupedalism either in the trees (*Alouatta* sp., *M. fascicularis*) or almost exclusively on the
172 ground (*P. hamadryas*) (Cant, 1986; Cant, 1988; Schmidt, 2011). During quadrupedal
173 walking and running the elbow is most often semi-flexed during stance phase (Larney and
174 Larson 2004; Youlatos, 2008) and we predict that quadrupedal monkeys will show a
175 trabecular pattern consistent with a habitually semi-flexed or flexed elbow that primarily
176 incurs load in the parasagittal plane. Spider monkeys most frequently engage in arboreal
177 quadrupedalism but also use semi-brachiation with the aid of a prehensile tail and the elbow
178 is used in extended and semi-flexed postures (Schmitt et al., 2005; Youlatos, 2008). Thus, it
179 is reasonable to predict that spider monkeys may converge with orang-utans in showing a
180 trabecular pattern consistent with an elbow loaded in a variety of different postures due to
181 their more varied locomotor regime.
182
183 **Materials and Methods**

184 The sample used in this study (see Table 1 for details) includes (1) apes: chimpanzees,
185 Virunga mountain gorillas, western lowland gorillas, orang-utans, and siamangs; (2) Old
186 World monkeys: long-tailed macaques and hamadryas baboons; and (3) New World
187 monkeys: howler monkeys and spider monkeys. All individuals were wild-shot adults and
188 showed no obvious signs of pathology.

189 Specimens were scanned using a BIR ACTIS 225/300 industrial microCT scanner
190 (Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology,
191 Germany) and two Nikon XT H 225 ST microCT scanner (Cambridge Biotomography
192 Centre, Department of Zoology, University of Cambridge, UK and Shared Materials
193 Instrumentation Facility, Duke University, USA). The isotropic voxel size range for the
194 sample is 21.9–99.9 µm (Table 1). Scan parameters were 100–160 kV and 100–140 µA,
195 using a brass or copper filter of 0.2–0.5 mm. All scans were reconstructed as 16-bit TIFF
196 image stacks.
197 All scans were oriented to a homologous position in AVIZO 6.3® (Visualization
198 Sciences Group, SAS) and cropped at the end of the medial and lateral ridges, which marks
199 the start of the humeral shaft and the most proximal extent of trabecular bone (SI Fig. S1,
200 S2). All data were segmented using the Ray Casting Algorithm (Scherf and Tilgner, 2009).
201 Medtool 4.2 (www.dr-pahr.at) was used to quantify trabecular bone throughout the
202 distal epiphysis of the humerus using a Holistic Morphometric Analysis (HMA) following
203 the methods described in Gross et al. (2014) and Tsegai et al. (2013). Briefly, cortical bone is
204 separated from the trabeculae (SI Fig. S2) by casting rays at different angles from the outer
205 cortical shell and terminating them on contact with background voxels. The inner structure is
206 then closed with a spherical kernel the size of the average trabecular thickness in that bone
207 (Pahr and Zysset, 2009), and the 3D edge of this inner structure defines the boundary
208 between subchondral trabecular and cortical bone (Gross et al., 2014).
209 Bone volume fraction (BV/TV), quantified as a ratio of bone volume to total volume,
210 and degree of anisotropy (DA), quantified following the mean intercept length (MIL) method
211 and bounded between 0 (isotropy) and 1 (anisotropy), were measured throughout the distal
212 epiphysis using a sampling sphere with a 5-mm diameter on a 2.5- mm background grid.
213 Regions with marked concavities, such as the olecranon fossa, were defined with a bounding

box and a correction filter was applied, following Georgiou et al. (2018). An additional protocol was followed to quantify the BV/TV and DA values in the trochlea and capitulum separately, given the complexity of the distal humeral morphology (see SI Fig. S1 for details).

Statistical analyses

Descriptive statistics were conducted for BV/TV and DA values for the whole epiphysis, capitulum and trochlea for each genus (SI Table S1; BV/TV and DA individual values can be found in SI Data S1). We tested differences between gorillas and chimpanzees with Mann-Whitney U-tests given their larger sample sizes (n=7) (see also SI Appendix S1). However, sample sizes for the comparative taxa were too small (ranging n=2–4) to apply probability-based statistical tests (but see SI Appendix S1). Box-and-whisker plots for BV/TV and DA values for the whole epiphysis (Fig. 2), capitulum and trochlea (SI Fig S3) were used instead to evaluate and compare trabecular parameters across taxa. All statistical tests were done in R v.3.6.1 (R Core Team) using the 'dyplr' package (Wickham et al., 2018). A bivariate plot of mean DA and BV/TV for all specimens in the sample was generated in R to explore the relationship between BV/TV, DA and the distribution of groups in relation to these two parameters (Fig. 3).

Finally, allometry was investigated by means of linear regression of log transformed variables following Jungers (1991). We obtained the average humeral head diameter (linear dimension 2: mean of two chords perpendicular to greater and lesser tubercles; Jungers, 1991: 392) and log-transformed them with natural logarithms (ln). The result was used as an independent variable of body size (SI Dataset S1). We also applied natural logarithms to the BV/TV and DA values of each individual for the whole epiphysis, and obtained the linear regression models between these dependent variables and body size (SI Table S2).

239

240 *Qualitative analyses*

241 Three-dimensional tetrahedral meshes with a 1-mm mesh size were created using
242 CGAL 4.4 (CGAL, Computational Geometry; http://www.cgal.org) and BV/TV values were
243 interpolated from the background grid onto the elements creating BV/TV distribution colour
244 maps. Internal BV/TV distribution was visualised in Paraview (Ahrens et al., 2005).

245

246 **Results**

247 Colour maps of BV/TV for all individuals in all taxonomic groups in the sample are
248 presented in the SI Fig. S3, with one representative specimen in Fig. 1. Variation in the
249 distribution of trabeculae in the distal humerus is described below in detail.

250 Chimpanzees (*P. t. verus*) All chimpanzees display a very similar pattern in BV/TV
251 distribution (SI Fig. S3). High BV/TV values are concentrated anteriorly on the capitulum
252 and anteriorly, distally and posteriorly on the trochlea, with the highest values typically
253 located on the medial keel of the trochlea. All individuals have relatively high BV/TV
254 distribution throughout the articular surfaces of the distal humerus compared with other taxa.
255 Both epicondyles show high BV/TV with the medial epicondyle generally exhibiting
256 markedly higher BV/TV than that of the lateral epicondyle.

257 Western lowland gorillas (*G. g. gorilla*) For the western lowland gorillas, three out of
258 four individuals display high BV/TV on the disto-posterior trochlea and slightly less on the
259 capitulum (SI Fig. S3). There are small areas of high BV/TV in the medial epicondyle,
260 situated distally to the medial ridge, but notably low BV/TV in the lateral epicondyle. The
261 fourth individual (PC M29) displays exceptionally high BV/TV throughout the distal
262 humerus, and particularly at both the distal trochlea and the anterior capitulum.

Mountain gorillas (*G. b. beringei*) All mountain gorillas present a pattern that is distinct from that of lowland gorillas. There is high BV/TV on the antero-distal capitulum as well as the anterior portion of both the medial and lateral trochlear keels that extend distally and posteriorly with minimal connection. Mountain gorillas show high BV/TV at both epicondyles, with higher concentrations in the medial epicondyle and in the posterior aspect of the lateral epicondyle, expanding into the lateral crest, with the exception of one individual (GP 78; SI Fig. S3).

Asian apes In both suspensory orang-utans (*P. pygmaeus*) and siamangs (*S. syndactylus*), high BV/TV is mainly concentrated on the distal and posterior trochlea. There are two exceptions to this pattern: one orang-utan (ZMS 1982-0092), which shows high BV/TV throughout the epiphysis, and particularly at the epicondyles and the medial trochlear keel, and one siamang (ZMB 38573), which shows high BV/TV at the anterior capitulum, the distal and posterior trochlea, and the medial epicondyle (SI Fig. S3). Overall, both taxa show low or very low BV/TV in the medial and lateral epicondyles.

Monkeys Pronograde quadrupedal monkeys (macaques, baboons, howler monkeys) as well as spider monkeys with a more varied locomotor repertoire, all display a common pattern of high BV/TV throughout the epiphysis. On the trochlea, BV/TV is concentrated anteriorly as well as distally, while it is distally and anteriorly concentrated on the capitulum. Howler monkeys display higher BV/TV in the capitulum than spider monkeys, while baboons and macaques display higher BV/TV throughout the distal humerus relative to all the other taxa in our sample (SI Fig. S3). Monkeys generally have relatively lower BV/TV in the epicondyles compared with apes, however, some individuals (ZMB 44814, ZMB 35764, ZMB 48496) show slightly higher BV/TV values in the medial epicondyle.

Despite these qualitative differences in BV/TV distribution, two-tailed Mann-Whitney *U*-tests reveal no significant differences between chimpanzees and gorillas in BV/TV (p =

288 0.165), or separately for the capitulum ($p = 0.710$) and trochlea ($p = 0.535$). Although small
289 sample sizes prohibited statistical testing among the rest of the sample, box-and-whisker plots
290 reveal that baboons consistently showed the highest BV/TV for the whole epiphysis,
291 capitulum and trochlea, followed closely by gorillas and then chimpanzees. In contrast,
292 atelines (howler and spider monkeys) and macaques consistently showed the lowest BV/TV
293 for each region (Fig. 2; SI Fig. S3).
294 Degree of anisotropy (DA) colour maps (Fig. 1) do not reveal clear regional
295 interspecific differences that can be readily associated to locomotor behaviour. However, the
296 Mann-Whitney *U*-tests found significant differences in DA between African apes, with
297 chimpanzees showing higher DA values than gorillas for the whole epiphysis ($p = 0.002$),
298 capitulum ($p = 0.038$) and trochlea ($p = 0.038$). Box-and-whisker plots reveal that
299 chimpanzees and baboons display the highest DA for each region, whereas gorillas show
300 relatively low DA (albeit, with a wide range of variation), similar to those of siamangs,
301 atelines and macaques. Orang-utans display the greatest variation in DA values for each
302 region.
303 A bivariate plot of BV/TV and DA (Fig. 3) distinguishes siamangs, atelines and
304 macaques from the remainder of the sample with relatively low BV/TV and DA. Great apes
305 and baboons generally have higher BV/TV values, but as a group are more variable in their
306 DA values.
307 The linear regressions between our proxy for body size and BV/TV is significant ($p =$
308 <0.000) but the R^2 and adjusted R^2 values are not very high ($R^2 = 0.61$, $_{Adj}R^2 = 0.60$) (SI
309 Table S2). The linear regression between body size and DA is not significant ($p = 0.058$, $R^2 =$
310 0.11, $_{Adj}R^2 = 0.08$).
311
312 **Discussion**

313 This study found that trabecular bone holds functional signals of variation in elbow
314 joint loading that are consistent with differences between taxa that more often use a semi-
315 flexed elbow posture during locomotion compared with those that use an extended elbow
316 posture. Importantly, most individuals across our entire sample showed relatively high
317 BV/TV at the medial epicondyle, which likely reflects the high loading incurred by
318 antebrachial flexor muscles, highlighting the importance of internal muscle forces on bone
319 modelling (which can be up to seven times higher than external reaction forces; e.g.,
320 Preuschoft, 1973). We found a significant but weak allometric relationship between body size
321 and BV/TV in our sample; the low R^2 and $_{Adj}R^2$ indicate that other factors explain the BV/TV
322 patterns found here beside body size (Bird et al., 2021) BV/TV (together with DA, which
323 was not significantly associated with body size in our sample) determines most of the
324 mechanical stiffness of trabecular bone (Maquer et al., 2015), with the underlying assumption
325 that higher BV/TV reflects higher habitual mechanical loading. Based on previous studies
326 (e.g. Doube et al., 2011; Barak et al., 2013) and given that BV/TV values inherently account
327 for variation in size (i.e. as a ratio), our finding that BV/TV is at least partially influenced by
328 body size was unexpected. However, given our sample sizes are relatively small (more so for
329 the comparative sample than for *Pan* and *Gorilla*), further studies are needed to explore the
330 allometric influence on BV/TV in the distal humerus within species and how this might differ
331 from other skeletal regions. Finally, some specimens display sections of compact cortical
332 bone (e.g., in specimen ZMB 44079 (*Ateles*), the crest arising from the medial epicondyle)
333 which may be replacing trabecular bone; the biomechanical information and potential bias
334 this might introduce should be further explored in relation to trabecular bone patterns and
335 locomotor behaviours in the distal humerus in the future.
336 Old and New World monkeys, chimpanzees, and, slightly less evidently, mountain
337 gorillas showed a semi-flexed elbow pattern. The BV/TV distribution pattern on the articular

surfaces of the trochlea and capitulum they exhibited included high BV/TV anteriorly in the capitulum that merged with regions of high BV/TV on the trochlea, which expanded anteriorly, distally and posteriorly. The highest BV/TV concentration for the semi-flexed elbow pattern was found in the medial keel of the trochlea. Thus, the BV/TV pattern found for the pronograde quadrupeds (macaques, baboons and howler monkeys) was consistent with our predictions. In the semi-flexed elbow joint posture during stance phase of quadrupedal gait, there is increased contact at the humeroradial joint (Rose, 1988). This is consistent with the anterodistally high BV/TV values in the capitulum in these taxa. High BV/TV across the trochlea in general, with particularly high BV/TV at the medial keel, is consistent with the medially-directed, compressive forces exerted by the forearm flexor muscles (Preuschoft, 1973; Hunt, 2016) and the subsequent mediolateral substrate reaction forces (which are greater during terrestrial locomotion than on arboreal substrates) trying to displace the ulna medially (Schmitt, 2003).

Spider monkeys are substantially less quadrupedal than the other monkeys in our sample, but contrary to our predictions, they aligned with the semi-flexed elbow trabecular pattern. Nevertheless, this is consistent with their most frequent locomotor behaviour, quadrupedal walking and running, which they may engage in over 50% of their locomotor time, depending on the species (Youlatos, 2008). Spider monkeys only engage in suspensory behaviours ~25% of time (Cant, 1986) and use their prehensile tails (and occasionally their feet) for support. As such, their forelimbs do not always support full body weight during suspension as in hylobatids and orang-utans (Swartz et al., 1989; Youlatos, 2008). Moreover, during tail-assisted suspension, the trailing limb elbow is oftentimes held in a semi-flexed position at the beginning of a swing (Youlatos, 2008), which is consistent with the trabecular pattern observed.

Baboons are the most terrestrial taxon among our sample (Schmidt, 2011) and their high DA values are consistent with a joint loaded in a highly stereotypical manner (Tsegai et al., 2013), facilitated by a limb joint morphology advantageous for movement in the parasagittal plane (Rose, 1988). The comparatively lower DA values in macaques and atelines, in contrast, may reflect a greater range of movement needed to navigate an arboreal environment.

Orang-utans, siamangs and western lowland gorillas each showed an extended-elbow pattern, consisting of low BV/TV in the capitulum coupled with high BV/TV in the trochlea, where it was mostly restricted to its distal and posterior aspects. The shared pattern of siamangs and orang-utans (African apes will be discussed separately below) is consistent with an extended-elbow position during brachiation and torso-orthograde suspension, and also consistent with our predictions. The forelimb of brachiating gibbons and, presumably, siamangs experiences maximum strain at the extended-elbow midsupport phase of the swing, as the animal reaches the bottom of the brachiating arc, with the humerus experiencing tensile loading (Swartz, 1989; Swartz et al., 1989). The slightly lower BV/TV values in Asian apes relative to gorillas may reflect this tensile loading compared to compressive loading of an extended elbow in gorillas (see below). The relatively low DA values of siamangs are also consistent with highly mobile joints. In contrast, orang-utans displayed extremely variable (including the lowest and highest in the sample) DA values. High intraspecific variability in orang-utan trabecular structure, including DA, has also been found in the distal femur (Georgiou et al., 2018) and capitate (Bird et al., 2020).

We predicted that African great apes would share the same extended (or near-extended)-elbow pattern that is typically described for knuckle-walking (Tuttle, 1969; Inouye, 1993; Zylstra, 1999; Finestone et al., 2018). Our results did not fully support this prediction. Instead, chimpanzees (and to a lesser extent, mountain gorillas, discussed

separately below) presented a flexed-elbow BV/TV pattern similar to the monkeys. Recent studies (Finestone et al., 2018; Thompson et al., 2020) have demonstrated that there is more variability in chimpanzee elbow joint kinematics during knuckle-walking than previously understood, which could explain the flexed-elbow pattern of chimpanzees found in our study. Our results suggest that chimpanzees load their elbow differently from that of gorillas, with a more flexed posture (Inouye, 1993; Zylstra, 1999; Finestone et al., 2018), which has been observed in captive chimpanzees (A.Z. unpublished research). It should be noted that our sample consists of Taï chimpanzees, one the most arboreal and acrobatic chimpanzee groups (Doran, 1994), and the flexed-elbow trabecular pattern may alternatively reflect a bony response to the stresses of arboreal behaviours, such as vertical climbing or clambering (Doran, 1996). Although we have found clear patterns of flexed vs. extended elbow postures in relation to habitual behaviour in the other taxa studied, other species and subspecies of chimpanzee such as bonobos or East African chimpanzees (*P. paniscus* and *P. troglodytes schweinfurthii*, respectively, which, unfortunately, were not available for this study) with different ecolocomotor characteristics should be studied to see if they also demonstrate a flexed-elbow trabecular pattern.

In comparison to chimpanzees, western lowland gorillas generally exhibited a BV/TV distribution pattern similar to that of suspensory Asian apes, and consistent with habitual loading in an extended-elbow joint posture (albeit, with the stated difference in loading regimes, i.e., compression vs. tension respectively; Swartz et al., 1989). Our African ape sample is skewed towards females, which display different frequencies of locomotor behaviours with respect to their males counterparts (Inouye, 1994; Doran, 1996; Doran, 1997). Owing to their dense-canopy environment, all western lowland gorillas, including large males, spend up to a 35% of their time in trees, even in adulthood (Ruff et al., 2018 and references therein), but the likelihood of the extended-elbow pattern being related to a more

412 suspensory behaviour is low, since lowland gorillas and chimpanzees engage in roughly the
413 same, almost negligible amount of suspensory locomotion, ranging from less than 1% to
414 3.6% of their locomotor time (Crompton et al., 2010). If western lowland gorillas follow a
415 similar pattern to mountain gorillas, then they most often vertically climb with an extended
416 elbow only on large or extra-large diameter substrates (Neufuss et al., 2017). In addition,
417 gorillas display an elbow morphology (i.e., generally flatter joints; Rose, 1993) that are
418 advantageous for coping with loads incurred during terrestrial locomotion with an extended
419 forearm. Finestone et al. (2018) showed that, although there is general similarity in knuckle-
420 walking kinematic pattern in both captive chimpanzees and lowland gorillas, gorillas used a
421 slightly more (but not significantly so) extended elbow posture at midstance. Although it is
422 uncertain how less frequent, but potentially higher loading, behaviours may drive modelling
423 of the trabeculae (e.g., Umemura, 2002), the trabecular pattern in lowland gorillas (as well as
424 in chimpanzees) most likely reflects posture and load during knuckle-walking over any other
425 behaviour, as previously found for other forelimb structures, e.g., capitate and third
426 metacarpal (Ragni, 2020) and the capitate (Bird et al., 2021).

427 Surprisingly, mountain gorillas displayed a BV/TV distribution pattern that was
428 intermediate between the extended-elbow posture of western lowland gorillas and the flexed-
429 elbow posture of chimpanzees. Mountain gorillas had high BV/TV at the anterior capitulum
430 and at both trochlear keels, but without the high BV/TV throughout the distal humerus found
431 in chimpanzees and monkeys. Mountain gorillas are the most terrestrial of all *Gorilla* species
432 (and apes, in general) due to their montane forest habitat (Tocheri et al., 2011; Jabbour and
433 Pearman, 2016; Ruff et al., 2018). Analyses of forelimb diaphyseal strength proportions show
434 mountain gorillas have stronger ulnae with respect to radii (Ruff et al., 2018), possibly due
435 their high humeral torsion (greater than in any other ape; Inouye, 1993) and a more pronated
436 hand during knuckle-walking, which leads to more load being transferred through the ulna.

Mountain gorillas have shorter fingers than their western counterparts, and, while knuckle-walking kinematics of mountain gorillas have not yet been studied, Thompson et al. (2020) documented a surprising amount of variability in the hand postures used during terrestrial locomotion, in which 40% of the hand postures included fist-walking, loading of the dorsal metacarpus or modified palmigrady. More data on elbow joint kinematics in African apes is needed to fully ascertain whether mountain gorillas use and load their forelimb differently from that of western lowland gorillas during knuckle-walking and in a way that is more similar biomechanically at the elbow to that of chimpanzees. Furthermore, the mountain gorillas in our sample displayed high variability in both BV/TV values and distribution, and thus future studies incorporating larger samples in comparison to other apes would be able to reveal the potential functional significance of this intraspecific variability.

Further trabecular differences between gorillas (including mountain gorillas) and chimpanzees were found in DA values. Chimpanzees exhibited significantly higher DA than gorillas, which was not expected given the generally higher amount of arboreal locomotion and, presumably, more varied joint loading at the elbow in chimpanzees. Although the variability in mountain gorilla hand postures noted above (Thompson et al., 2020) may partly explain lower DA in this taxon, we suggest that generally low DA in gorillas might also reflect a different bone functional adaptation response within the trabecular structure. Gorillas might offset the need of highly aligned trabeculae (i.e., high DA) to diffuse the incurred stress acting on the distal humerus by possessing thicker trabecular struts, as is suggested might be the case in their distal femur (Georgiou et al., 2018). Future investigation of additional trabecular parameters, including trabecular thickness and separation, are needed to test this hypothesis.

The resolution of the functional signal in the distal humerus did not differentiate each locomotor behaviour but did provide a clear distinction between a flexed-elbow *versus* an

extended-elbow posture that is generally consistent with the most frequent locomotor behaviours. Moreover, inferred joint posture and loading differences found between chimpanzees and gorillas, and between gorilla species, pinpoint possible divergent biomechanical strategies adopted by African apes during knuckle-walking (Kivell and Smith, 2009; Ragni, 2020). More studies are needed to better understand potential variation in knuckle-walking and its evolution; however, differences revealed by trabecular structure within African apes add further evidence to the hypothesis that knuckle-walking is not a unified biomechanical phenomenon (Dainton and Macho, 1999; Kivell and Schmitt, 2009; Hunt, 2016) with potential bearing on the role knuckle-walking played, if any, in the origin(s) of hominin bipedalism.

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Ethics statement

All methods were carried out in accordance with the University of Kent ethical guidelines and were approved by both the University of Kent and the Institut Català de Paleontologia Ethics Committee.

Author contributions

JAM and TLK designed the research, JAM and AZ acquired the data, JAM performed the analyses, and JAM, TLK and AZ interpreted the data, JAM wrote the manuscript. All authors reviewed the manuscript.

Competing interests

The author(s) declare no competing interests.

Data availability

All data analysed can be found as a csv dataset in Dryad:

https://doi.org/10.5061/dryad.9ghx3ffhz

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Figure legends

Figure 1. Colour map of differences between taxa in bone volume fraction (BV/TV) and degree of anisotropy (DA) patterns for a representative individual. The original trabecular structure (i.e., a slice from the CT scanned bone) is also presented (Trabeculae).

Figure 2. Box-and-whisker plots of bone volume fraction (BV/TV) and degree of anisotropy (DA), grouped by genus.

Figure 3. Bivariate plot of mean values per specimen (at species level) of bone volume fraction (BV/TV) and degree of anisotropy (DA). Convex hulls denote species distribution limits except for those species for which only two specimens are available.

Table 1. Details of the sample of the study.

Taxon	Common name	N	Side R/L	Sex M/F/Un	Preferred Locomotor Behaviour	Collections/Project and Housing Institution	CT Resolution range in µm
Gorilla gorilla gorilla	Western lowland gorilla	4	2/2	1/3/0	Knuckle-walking	Powell-Cotton Museum (Birchington, UK)	40.7-57.9
Gorilla beringei beringei	Mountain gorilla (Virungas)	3	0/3	1/2/0	Knuckle-walking	Mountain Gorilla Skeletal Project, Dian Fossey Gorilla Fund International's Karisoke Research Centre (Rwanda)	89.8-99.9
Pan troglodytes verus	Common chimpanzee	7	1/6	1/6/0	Knuckle-walking	Taï Forest Collection, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany)	23.7-30.1
Pongo pygmaeus	Orang-utan	5	2/3	2/3/0	Quadrumanous climbing/clambering	ZMB[1], ZMS[2]	26.6-28.3
Symphalangus syndactylus	Siamang	3	2/1	0/2/1	Brachiation	ZMB	25.6-27.5
Macaca fascicularis	Long-tailed macaque	3	0/3	0/0/3	Arboreal quadrupedalism	ZMB	23.8-30
Papio hamadryas	Hamadryas baboon	2	1/1	2/0/0	Terrestrial quadrupedalism	ZMB	27.5 (single scan)
Ateles sp.	Spider monkey	4	2/2	1/1/2	Arboreal quadrupedalism	ZMB	24.7-26.5
Alouatta sp.	Howler monkey	2	1/1	1/0/1	Arboreal quadrupedalism	ZMB, ZMS	21.9, 26.5

[1] Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science (Berlin, Germany).
[2] Zoologische Staatssammlung Munchen (Munich, Germany).

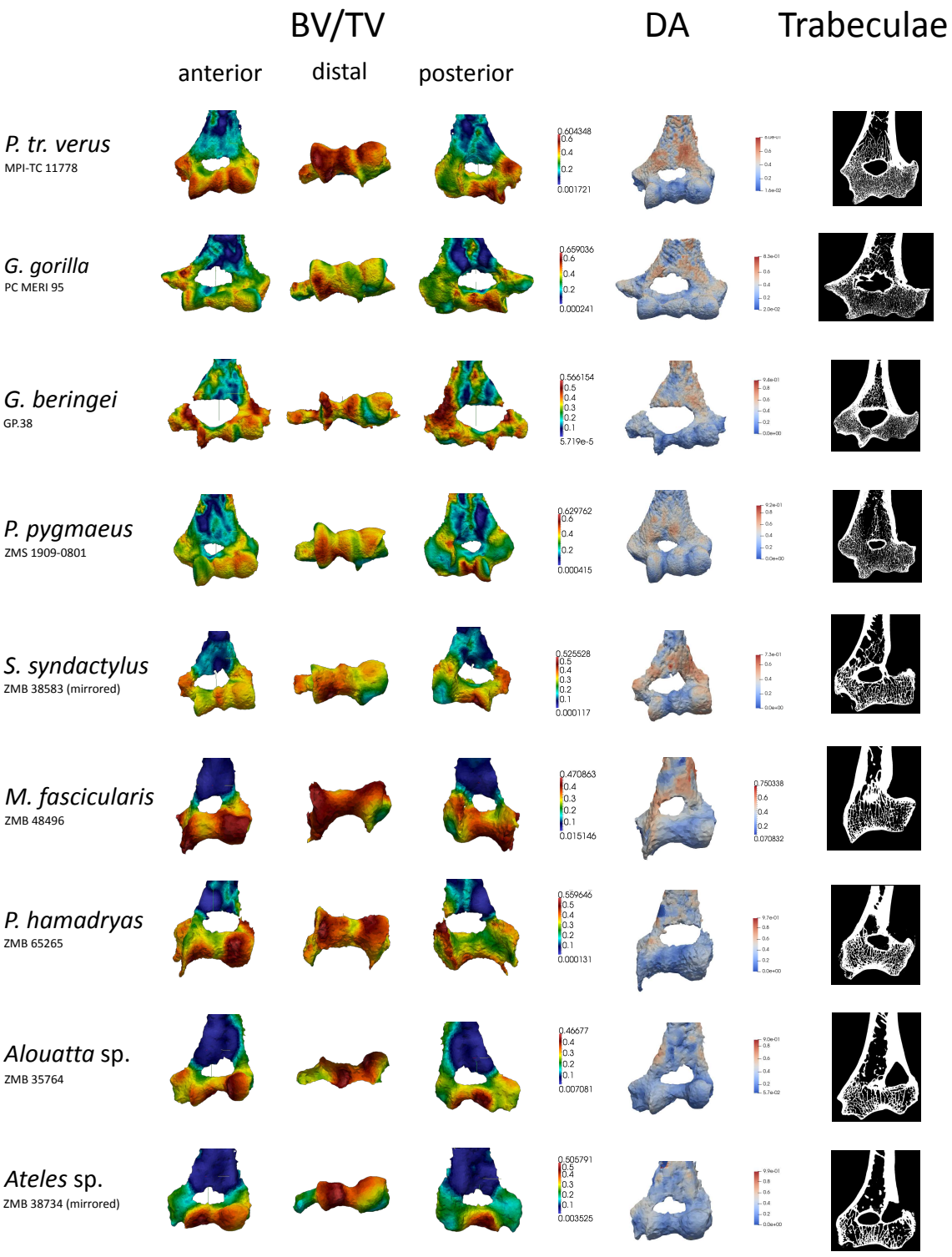
BV/TV
DA
Trabeculae
anterior
distal
posterior
P. tr. verus
MPI-TC 11778
G. gorilla
PC MERI 95
G. beringei
GP.38
P. pygmaeus
ZMS 1909-0801
S. syndactylus
ZMB 38583 (mirrored)
M. fascicularis
ZMB 48496
P. hamadryas
ZMB 65265
Alouatta sp.
ZMB 35764
Ateles sp.
ZMB 38734 (mirrored)

Figure 1.

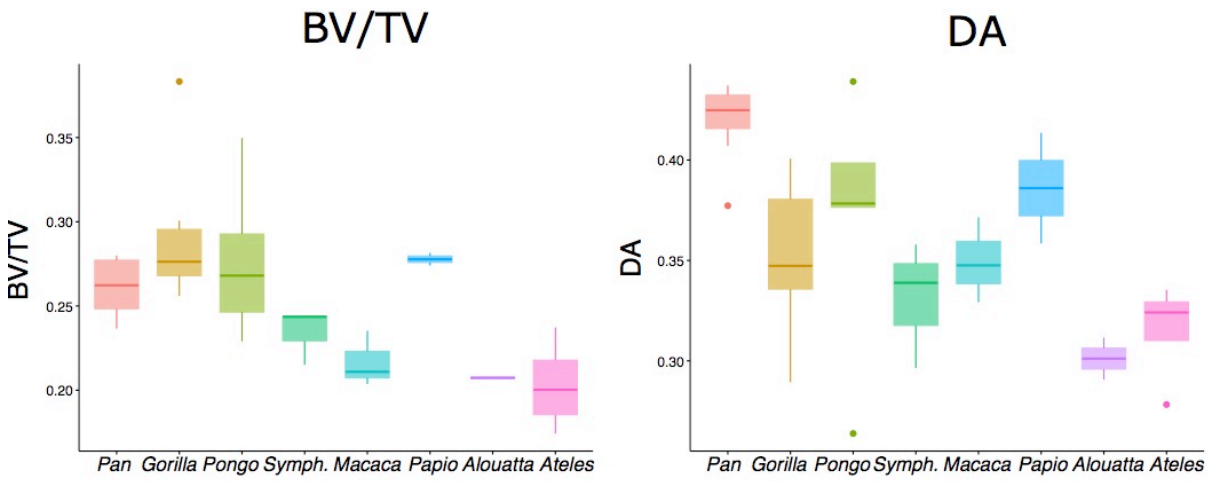
BV/TV
BV/TV
0.35
0.30
0.25
0.20
Pan
Gorilla
Pongo
Symph.
Macaca
Papio
Alouatta
Ateles
DA
DA
0.40
0.35
0.30
Pan
Gorilla
Pongo
Symph.
Macaca
Papio
Alouatta
Ateles

Figure 2.

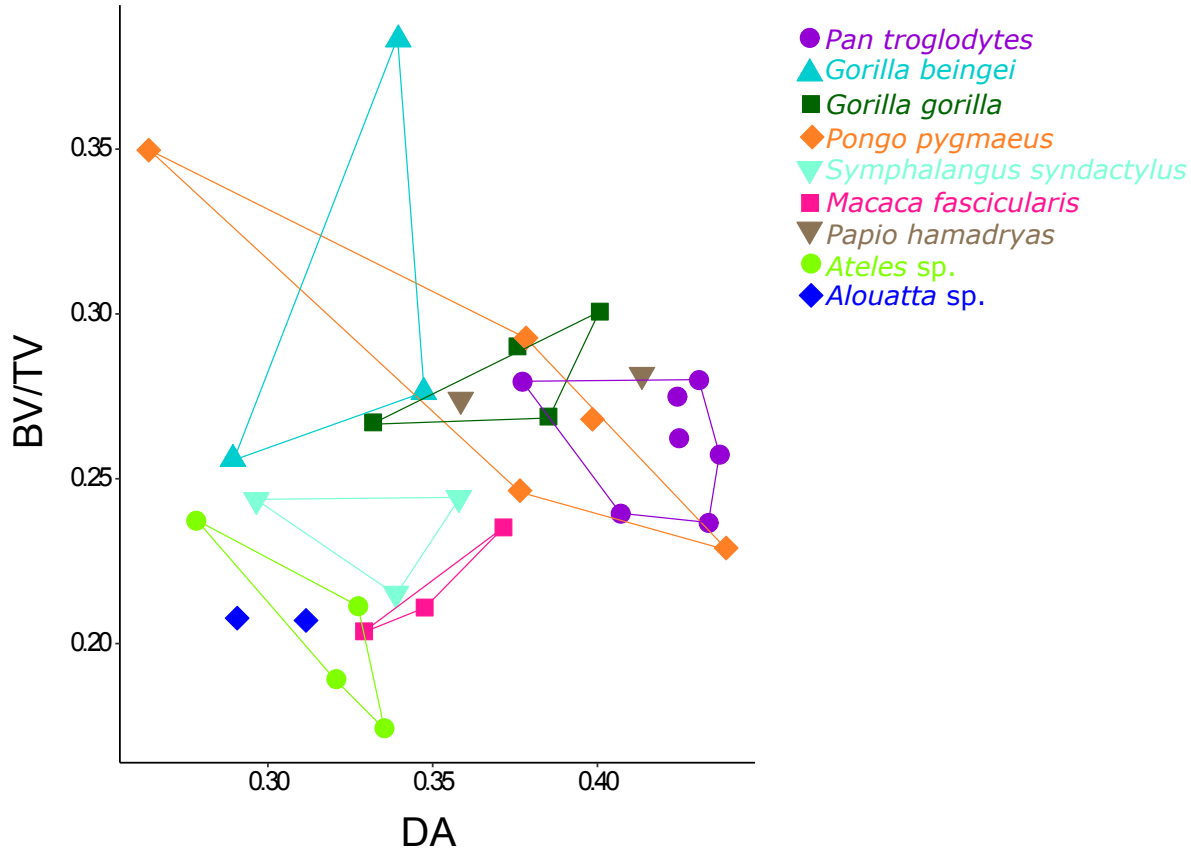
Pan troglodytes
Gorilla beingei
Gorilla gorilla
Pongo pygmaeus
Symphalangus syndactylus
Macaca fascicularis
Papio hamadryas
Ateles sp.
Alouatta sp.
BV/TV
0.35
0.30
0.25
0.20
0.30
0.35
0.40
DA

Figure 3.