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Title: Ape femoral-humeral rigidities and arboreal locomotion

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Objectives:
This study investigates patterns of bone functional adaptations in extant apes through comparing hindlimb to forelimb bone rigidity ratios in groups with varying levels of arboreality.

Materials and Methods:
Using CT scans, bone rigidity (J) was calculated at three regions of interest (ROI) along femoral and humeral diaphyses in *Homo, Pongo, Pan,* and *Gorilla* with further comparisons made between species and subspecies divisions within *Pan* and *Gorilla.*

Results:
Consistent with previous work on extant hominoids, species exhibited differences in midshaft F/H rigidity ratios. Results of the present study confirm that these midshaft differences extend to 35% and 65% diaphyseal ROIs. Modern humans, exhibiting larger ratios, and orangutans, exhibiting smaller ratios, bracketed the intermediate African apes in comparisons. Within some African apes, limb rigidity ratios varied significantly between taxonomic groups. Eastern gorillas exhibited the highest mean ratios and chimpanzees the lowest at all three ROIs. In posthoc comparisons, chimpanzees and bonobos did not differ in relative limb rigidity ratios at any of the three ROIs. However, western gorillas were more similar to bonobos than eastern gorillas at 50% and 35% ROIs, but not at the 65% ROI.

Conclusion:
Species, and to a lesser extent subspecies, can be distinguished by F/H (femoral to humeral) limb rigidity ratios according to broad positional behavior patterns at multiple regions of interest along the diaphyses. Similarity of bonobos and western gorillas is in line with behavioral data of bonobos being the most terrestrial of *Pan* species and western gorillas the most arboreal of the *Gorilla* groups.

1. Introduction

Long bone diaphyseal strength and robusticity proportions are useful indicators of relative limb involvement and loading during the locomotor repertoires of primates (Burr, Ruff, & Johnson, 1989; Demes & Jungers, 1993; Kimura, 2002; Ruff, Harper, Goldstein, Daegling, & McGaw, 2019; Schaffler, Burr, Jungers, & Ruff, 1985; Ruff, 2002; Carlson, 2005; Shaw and Ryan, 2012). This form-function relationship has been formalized as bone functional adaptation (Ruff et al., 2006). According to the mechanostat proposed by Frost (1973, 1987, 1996, 2003), cortical bone modeling is responsible for the formation and redistribution of bone mass in a long bone diaphysis when mechanical usage exceeds a minimum loading threshold but falls below an upper threshold corresponding to overloading situations (Martin, Burr, Sharkey, & Fyhrie, 2015; Barak, 2020). Other factors besides mechanical usage, however, also clearly affect the modeling process (i.e., these factors can operate to adjust mechanostat thresholds), often complicating a straightforward interpretation of bone functional adaptations (Martin, Burr, Sharkey, & Fyhrie, 2015; Frost, 2003; Wergedal et al., 2005; Devlin et al., 2010; Devlin, 2011; Wallace et al., 2010, 2012).

Investigating patterns in the expression of bone functional adaptations in humeral and femoral diaphyses, especially in comparisons of great apes, has proven to be informative in differentiating their relative frequencies of arboreal versus terrestrial locomotor behavior. *Pongo* exhibits more arboreal locomotion than other great apes (Thorpe & Crompton, 2006). Arboreal *Pongo* also exhibits greater forelimb to hindlimb strength ratios compared to relatively more terrestrial African apes (Ruff, 2002; Shaw & Ryan, 2012; see Table 1) and even more so when compared to terrestrial *Homo* (Shaw & Ryan, 2012). Within African apes, *Pan* exhibits higher humeral to femoral ratios compared to those of *Gorilla* (Ruff, 2002). The vast majority of these efforts have focused on humeral and femoral evaluations in higher taxonomic levels of extant apes (e.g., interspecific comparisons), while finer scaled investigations (e.g., intraspecific comparisons) have been less numerous (Carlson, 2005; Carlson et al., 2006, 2011; Ruff et al. 2018). Additionally, attempts to coordinate structural patterns in bone functional adaptations with frequencies of specific positional modes, irrespective of substrate considerations, have been less successful at establishing clear behavior-specific relationships (Runestad, 1997; Carlson, 2005; Carlson et al., 2011; Ruff et al., 2018; but see Runestad, Connour, Glander, & Vincent, 2000 and Demes, Jungers, & Selpien, 1991).

Limited upper limb involvement in locomotor behavior distinguishes modern humans from other extant hominoids, and has long been recognized as a feature that evolutionarily distinguishes the human lineage (Huxley, 1863; Darwin, 1871). While it is a widely held view that *Homo erectus* was an obligate biped by 1.5-1.7 mya (Ruff, 2007; Pontzer, 2012; Hatala et al., 2016), exactly when the shift in the human lineage from facultative to obligate bipedality occurred--along with the concomitant de-emphasis of the upper limb in weight-bearing locomotor activities--remains vigorously debated (Stern & Susman, 1983; Ward, 2002; Lovejoy, Suwa, Spurlock, Asfaw, & White, 2009; White et al., 2009; Churchill et al., 2013; Ruff, Burgess, Ketcham, & Kappelman, 2016; Kozma et al., 2018; Macchiarelli et al., 2020; Carlson et al., 2021). While extant great apes are the most informative modern analogs for framing utilization of the upper limbs in positional repertoires of hominins, it is increasingly clear that no living ape provides an exact replica of a hominin positional repertoire (see Almécija et al., 2021). Nonetheless, with the upper limb serving in some capacity as a weight-bearing instrument during locomotor behavior over the evolutionary history of early hominins, as opposed to an absence of this capacity as in modern humans,

relative humeral and femoral diaphyseal rigidities should differ from those of modern humans and approach those of other extant great apes to varying degrees. The aim of the present study is to quantify femoral-humeral limb rigidities, along multiple diaphyseal locations, across a diverse sample of extant great apes to provide an interpretive framework for early hominin relative limb rigidities that may facilitate recognition of subtle pattern shifts in limb use. Specifically, we evaluate taxonomic and ecomorphological diversity within this framework by quantifying femoral-humeral rigidity ratios in all commonly recognized African ape species and subspecies.

1.1. African ape taxonomy

Genetically derived phylogenetic relationships among the great apes are generally agreed upon with competing alternatives emphasizing differences in divergence times rather than differences in branching patterns. The family Hominidae consists of two subfamilies, Ponginae and Homininae[1], that diverged more than 15 mya (Locke et al., 2011, Prado-Martinez et al., 2013, Moorjani, Amorim, Arndt, & Przeworski, 2016, Almécija et al., 2021). *Pongo* is the only extant genus encompassed within Ponginae, and comprises two species, *Pongo pygmaeus* and *Pongo abelii* (Groves, 2001). The Homininae, on the other hand, include three extant genera: *Gorilla, Pan*, and *Homo* with *Gorilla* the first to diverge from stem hominines, and separate *Homo* and *Pan* lineages subsequently arising 6.5-9.3 mya (Moorjani, Amorim, Arndt, & Przeworski, 2016; Almécija et al., 2021). *Gorilla* consists of two species, *G. beringei* and *G. gorilla* (Groves, 2018; Xue et al., 2015), with both species further consisting of two subspecies (summarized in Groves, 2018). *Gorilla beringei* consists of *G.b. graueri* and *G.b. beringei*, while *Gorilla gorilla* includes the subspecies *G.g. gorilla* and *G.g. diehli*. The genus *Pan* also is split into two species, *P. paniscus* and *P. troglodytes* (Groves, 2018). While no subspecies have been designated within *P. paniscus*, we adhere to the consensus view that *Pan troglodytes* comprises four subspecies; *P.t. verus, P.t. ellioti, P.t. troglodytes, P.t. schweinfurthii* [Das, 2014, although see Groves (2018) for a fifth subspecies].

Among free-ranging great apes, admixture has been documented between geographically adjacent taxa such as *P.t. troglodytes* and *P.t. schweinfurthii* (Hvilsom et al., 2013). Even modern ranges being geographically separated by 1000 km or more (e.g., those of *Gorilla* species) has not prevented small amounts of hypothesized admixture within the last 100,000 years (Scally et al., 2012; de Manuel et al., 2016). By comparison, hybridization within *Pan* or *Gorilla* species during captivity, such as in zoos, occurs to a substantially greater extent than has been documented in free-ranging populations in natural habitats (Hvilsom et al., 2013). Admixture has practical implications in morphological studies such as the present one, for example, when trying to isolate unique features of specific taxa (e.g., cross-sectional geometric properties of diaphyses) that may be under varying degrees of genetic control. While bone functional adaptations in limb diaphyses are genetically constrained to some extent, and likely are influenced by multiple other non-behavioral factors such as diet, temperature, and hormonal fluctuations, there is a strong case to be made for activity patterns over the lifetime as being their primary determinant (Pearson and Lieberman, 2004; Ruff, Holt, Trinkaus, 2006; Shaw & Stock, 2009; Carlson & Marchi, 2014; Saers et al. 2021). Thus, by prioritizing skeletal material from wild-caught individuals in comparisons of diaphyseal structure, the potential signal in form-function relationships will be less obscured by the possibility of taxonomic uncertainty due to admixture.

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[1] In this study, we adopt the use of crown/stem terminology introduced by Ax (1985) and motivated by others (e.g., Strait, 2013). Here, the human clade (Hominina) and the chimpanzee clade (Panina) represent subtribes within the tribe Hominini.

1.2. African ape form-function diversity

Behavioral observation studies of African apes have documented variability in positional behavior attributable to subspecies or population (Table 1; Hunt, 1992; Doran and Hunt, 1994; Doran, 1996), age (Doran, 1997; Sarringhaus et al., 2014), sex (Doran, 1993b; White et al., 2020), and body size (Hunt, 1994). Some have broadly characterized chimpanzees as more arboreal (climbing) than gorillas in comparative investigations of hominoid long bone diaphyseal structure (Ruff, 2002; Marchi, 2005, 2007, 2015a), as well as when inferring form-function relationships in homininan long bones (Marchi, 2015b; Marchi et al., 2019). While there are no behavioral observation data on percentage of time spent arboreal vs. terrestrial for western gorillas, they are thought to be more arboreal than the better studied eastern gorillas (especially mountain gorillas), based off of seasonal arboreal feeding and nesting behavior (Brugiere & Sakom, 2006, Doran, 1997, Masi, 2004; Masi, Cipolletta & Robbins, 2009, Mehlman & Doran, 2002; Ostrofsky & Robbins, 2020; Remis, 1999, Tutin, Parnell, White & Fernandez, 1995). Additionally, lower elevation eastern gorilla groups have been recently shown to utilize arboreal behaviors more than previously thought (Neufuss et al., 2017, 2018). Bonobos were long thought to be more arboreal than chimpanzees (Susman, 1985, Doran, 1993, Crompton et al., 2010), however, lack of full habituation made accurate estimates of rates of overall levels of both arboreality and arboreal locomotion impossible (Doran, 1993). More recent positional behavior work from a habituated community, Lui Katole, suggests that bonobos are not more arboreal than chimpanzees, calling into question this long-held belief (Lomako: Doran, 1989, 1993a; Lui Kotale: Ramos, 2014; Table 1). Re-evaluation of relative rigidities in African ape humeri and femora would be timely in light of these behavioral studies. Ultimately, we encourage caution when broadly characterizing behavioral repertoires across great ape genera to avoid obscuring potentially informative form-function links in their postcranial skeleton, especially in features that are demonstrably plastic (e.g., long bone diaphyseal cross-sectional geometric properties).

Within extant ape species, limited subspecific comparisons of (and between) forelimb and hindlimb strengths have mirrored relative differences observed in apparent limb involvement in positional repertoires. More arboreal western gorillas (*Gorilla gorilla*) exhibited greater forelimb to hindlimb strength proportions compared to more terrestrial eastern gorillas (*Gorilla beringei;* Ruff, 2002; Ruff, Burgess, Bromage, Mudakikwa, & McFarlin, 2013; Ruff et al. 2018). In an examination of ratios of cross-sectional diaphyseal properties of gorilla species and subspecies, Ruff and colleagues (2018) observed an altitudinal trend among groups whereby high elevation *G.b. graueri* were more similar to *G.b. beringei* than *G.g. gorilla* in both cross-sectional geometric properties and the likely degree of arboreality, while low elevation *G.b. graueri* were more similar to *G.g. gorilla* in these respects.

Investigating free-ranging populations in archetypal habitats where locomotor patterns have been documented at the individual level through observation studies could maximize the likelihood of uncovering form-function signals associated with representative positional behavior patterns. Carlson and colleagues (2008, 2011) documented humeral diaphyseal differences in shape ratios (I_{max}/I_{min}) in more arboreal Taï chimpanzees (*P.t. verus*) compared to several habituated chimpanzee populations (*P.t. schweinfurthii*) occupying more open habitats with more variable vertical relief in the terrain. This previous work attributed the unique aspects of the Taï chimpanzee humeri to potentially more multidirectional loading of their upper limb during more frequent arboreal behavior (Carlson et al., 2008, 2011). Unfortunately, Carlson and colleagues (2008, 2011) did not conduct comparisons between upper versus lower limb diaphyses in these groups.

1.3. Study objectives

In this study, we aim to compare a large and geographically diverse extant ape sample at generic and species levels using free-ranging individuals. We also aim to assess subspecies level patterns within both *Pan* and *Gorilla.* We test two hypotheses using a series of predictions. First, we investigate whether extant great ape species exhibit similar rigidity ratios in their femoral and humeral diaphyses (Hypothesis 1). We predict that orangutans and humans will bracket African apes, whereby orangutans will exhibit the lowest femoral-humeral ratios given their propensity for greater frequencies of forelimb-dominated arboreal and suspensory positional behaviors and modern humans will exhibit the highest femoral-humeral ratios given their obligate bipedalism. Additionally, we predict that *Pan* and *Gorilla* species will be intermediate given greater overlap in their limb use during documented positional repertoires. Amongst the African apes, we further predict that the relationship between limb ratios will inversely rank according to degree of arboreality and arboreal locomotion recorded in behavioral observation studies (i.e., the highest femoral-humeral ratios are expected in eastern gorillas followed by western gorillas, bonobos, and then the lowest femoral-humeral ratios are expected in chimpanzees).

Secondly, we investigate whether African ape species and subspecies within *Pan* and *Gorilla* exhibit similar rigidity ratios of femoral and humeral diaphyses (Hypothesis 2). We predict that *P. t. verus* will exhibit the lowest limb ratios of any chimpanzee subspecies because of a greater arboreal component in its positional repertoire (i.e., greater forelimb involvement in arboreal weight-bearing activities, Table 1). We also predict that bonobos will exhibit a similar ratio to chimpanzee subspecies because of the recent behavioral evidence suggesting less emphasis in their positional behavior on arboreal locomotion than long thought (Table 1). Finally, we evaluate the prediction that *G. b. graueri* will exhibit intermediate limb ratios to those of *G.g. gorilla* and *G. b. beringei*, similar to what has been previously reported by Ruff et al. (2018) because of the presumed intermediate (in frequency) arboreal component in the overall positional repertoire of this group.

2. Materials and Methods
2.1 Samples

Humeri and femora from 254 free-ranging, adult great apes were investigated (Table 2). Cumulatively, these samples incorporate a majority of the currently recognized taxonomic diversity in *Pan* and *Gorilla* (Table 2). We excluded *P. t. ellioti* and *G. g. diehli* as discrete groups in this study, however, due to unavailable or small samples of specimens from both taxa. Data from non-human African apes in this sample have been published previously (Sumner, Morbeck, & Lobick, 1989; Carlson, 2005; Carlson et al., 2006; Carlson et al., 2008; Carlson et al., 2011, Sarringhaus et al., 2016). The chimpanzee sample also includes known individuals from free-ranging habituated groups (Carlson et al., 2006; Carlson et al., 2011). The orangutan sample consists of six adult *Pongo abelii* individuals from the collection of the National Museum of Natural History (NMNH), Washington DC, USA. The modern human sample consists of adult *Homo sapiens* individuals from the Raymond A. Dart Collection of Modern Human Skeletons in the School of Anatomical Sciences of the University of the Witwatersrand, Johannesburg, South Africa (Dayal et al., 2009). Adult status of each individual was assessed according to epiphyseal fusion and, where possible, eruption of third molars. Sex determination was based on information obtained from collection records. When sex information was not recorded, individuals were designated as 'unknown' sex. Only humeri and femora of individuals with no apparent trauma or movement-altering pathologies were used in this study. In addition to the targeted humeri and femora, we inspected other bones in each skeleton for trauma or pathology. Minor evidence of a degenerative joint condition was not considered an exclusionary criterion for the purposes of this study.

Preference was given to using the ipsilateral humerus and femur, but in a minority of cases it was necessary to mix sides within an individual.

2.2 Data acquisition

Single slice computed tomography (CT) images were collected from three specific regions of interest (ROI) along diaphyses corresponding to 35%, 50% and 65% femoral mechanical length and humeral maximum length (Figure 1), where the distal ends of femora and humeri represent 0% length (see Carlson, 2005 for additional protocol details on specimen positioning and leveling). For the majority of African apes, this resulted in three CT slices being obtained from each diaphysis. While there is some indication that adjacent diaphyseal regions may show broad similarities with these targeted ROIs (Davies and Stock, 2014; Mongle et al. 2015a, b), we chose these three specific locations to create representative comparisons with published data and also incomplete bones, such as fossils, that may not preserve entire diaphyses.

Other samples were represented by serial image data sets of entire bones. Orangutan cross-sectional data were collected following the same protocol as African apes, but with modifications made for digitally positioning and extracting cross sections of interest from three-dimensional image data sets of whole bones rather than physically positioning bones on a scanner bed prior to the image acquisitions and collecting single slice CT scans of leveled bones (see Carlson et al., 2008 for protocol details). Modern human data were also collected from serial image acquisitions of entire bones. The human image data were processed according to a published protocol for conducting structural analyses of hominoid metatarsals (Jashashvili et al. 2015; Dowdeswell et al., 2017) that was adapted for use with humeri and femora in the present study.

Scan parameters for use with medical CT scanners [e.g., a range of pixel dimensions (0.352 - 0.500 mm) and slice thicknesses (1.0 - 2.0 mm)] and high resolution CT scanners (e.g., voxel dimensions of 45 um or 93 um) during the acquisition of non-human African ape data have been reported elsewhere (i.e., medical CT scanners: Sumner, Morbeck, & Lobick, 1989; Carlson 2002; Carlson, 2005; Yamanaka, Gunji, & Ishida, 2005; Carlson, Doran-Sheehy, Hunt, Nishida, Yamanaka, & Boesch, 2006; Carlson, Sumner, Morbeck, Nishida, Yamanka, & Boesch, 2008; Carlson, Wrangham, Muller, Sumner, Morbeck, Nishida, Yamanaka, & Boesch 2011; high resolution CT scanners: Sarringhaus, MacLatchy, & Mitani, 2016). Orangutan femora and humeri were scanned using a Siemens Emotion 6 medical CT scanner in the Department of Anthropology at the National Museum of Natural History, Washington D.C. (Smithsonian). Scan parameters included: tube voltage = 130 kVp, tube current = 98 mA, exposure time = 600 ms, slice thickness = 0.63 mm, pixel resolutions between 0.199 - 0.371 mm, a 512x512 matrix, and an inner ear 'bone' reconstruction kernel (H90s). From scan data, we generated 16-bit DICOM images. Modern human femora and humeri were scanned using the Nikon Metrology XTH 225/320 LC dual source high resolution CT scanner in the Evolutionary Studies Institute of the University of the Witwatersrand (see https://wits.ac.za/microct). Scan parameters included tube voltage = 55 - 85 kV, tube current = 180 - 500 uA, isotropic voxel dimensions (0.100 - 0.129 mm), 360 projections, 3 frame averaging, and 1.8 mm or 3.6 mm of aluminum pre-filtration of x-rays. Cross-sectional data sets generated from CT-derived image data using single slice images or from virtual sectioning of volumes have been shown to generate mean cross-sectional shapes (i.e., I_{max}/I_{min} values) and also mean cortical areas (CA) within one standard deviation of one another (Carlson et al., 2008).

2.3 Measurements

Once slices corresponding to 35%, 50%, and 65% ROIs were identified in non-human ape diaphyses, they were processed in the freeware program, Scion Image (release Beta 4.0.2; see Carlson, 2005 for additional details), with a customized macro modeled after the SLICE program (Nagurka and Hayes, 1980; see Carlson,

2005 for additional details). Modern human cross sections were analyzed in BoneJ (Doube et al., 2010) using the Slice Geometry macro. We use the polar moment of area, J (mm^4), to assess (twice average) bending rigidities, or torsional rigidity. It is equivalent to the sum of any two perpendicular second moments of area in a cross section (e.g., $I_{max} + I_{min}$ or $I_x + I_y$). The polar moment of area has been argued to be the single best estimator of bone loading, better than any second moment of area, when direct diaphyseal loading data are unavailable (Lieberman, Polk, & Demes, 2004). Since relative limb rigidity measures are of primary interest, we do not standardize bone-specific structural properties (i.e., J) by bone length nor by the product of bone length and body mass since these would be scalar values in ratios calculated from the same individuals. The range of reported body sizes for great ape taxa in our study is within an order of magnitude (Smith & Jungers, 1997), thus log-transforming structural properties was deemed unnecessary for the purposes of this investigation.

2.4 Analyses

In order to conduct group comparisons at species and subspecies levels with subsample sizes that permitted statistical rigor, we followed others who pooled males and females (Shaw & Ryan, 2012; Patel, Ruff, Simons, & Organ, 2013; Ruff et al., 2018). Prior to performing statistical testing, we explored variables of interest using several approaches. We assessed normality of distributions using Kolmogorov-Smirnov (K-S) tests. In practically all cases, data distributions did not depart significantly from normal distributions (*Gorilla gorilla* K-S test, $p = 0.05$; all other group K-S tests, $p > 0.05$). Thus, transforming data (e.g., log-transformation) was deemed unnecessary. Following these assessment methods, we used a one-way ANOVA to evaluate statistical differences in femoral-humeral J ratios between groups of species or subspecies (i.e., to test Hypotheses 1 & 2, respectively; Sokal & Rohlf, 1995). All pairwise comparisons evaluating explicit predictions were assessed using the Tamhane post hoc test due to unequal variances at species (i.e., 35% ROI: Levene Statistic = 23.124, df = 5, $p < 0.001$; 50% ROI: Levene Statistic = 25.663, df = 5, $p < 0.001$; 65% ROI: Levene Statistic = 20.944, df = 5, $p < 0.001$) and subspecies levels (i.e., 35% ROI: Levene Statistic = 4.112, df = 6, $p = 0.001$; 50% ROI: Levene Statistic = 3.101, df = 6, $p = 0.006$; 65% ROI: Levene Statistic = 3.902, df = 6, $p = 0.001$).

3. Results
3.1 Hominoid interspecific differences (Hypothesis 1)

Hominoid species exhibit significant differences in femoral-humeral (F/H) J ratios at all three ROIs (35%: ANOVA F =105.800, df = 5, $p < 0.001$; 50%: ANOVA F = 128.766, df = 5, $p < 0.001$; 65%: ANOVA F = 97.937, df = 5, $p < 0.001$; Tables 3 & 4, Figure 2). Tamhane post hoc analyses consistently reveal that *P. abelii* exhibits significantly lower F/H J ratios than those of all other great ape species at each of the three ROIs (i.e., for all 15 pairwise comparisons, $p \leq 0.005$; Table 4, Figure 2). Humans, on the other hand, consistently exhibit significantly larger F/H J ratios compared to those of all other great ape species at each of the three ROIs (i.e., for all 15 pairwise comparisons, $p \leq 0.011$; Tables 3 & 4, Figure 2). Among the other African ape species, *P. troglodytes* exhibits significantly lower F/H J ratios compared to those of both *Gorilla* species: *G. gorilla* and *G. beringei* (Tables 3 & 4, Figure 2). Interestingly, *P. paniscus* exhibits F/H J ratios that are intermediate between those of *P. troglodytes* and *Gorilla* species (Figure 2), although only the differences from *Gorilla* species are statistically significant (Table 4). Specifically, *P. paniscus* exhibits F/H J ratios that are lower than those of both *Gorilla* species at the 65% ROI, but only lower than *G. beringei* at 35% and 50% ROIs (Table 4).

3.2 Hominoid intraspecific differences (Hypothesis 2)

Intraspecific comparisons within *Pan* and *Gorilla* also reveal significant differences in F/H J ratios at all three ROIs (35%: ANOVA F = 40.119, df = 6, p < 0.001; 50%: ANOVA F = 17.997, df = 6, p <0.001; 65%: ANOVA F = 34.730, df = 6, p < 0.001; Table 5, Figure 3). Subspecies of *Pan troglodytes* do not differ significantly from one another at any of the three ROIs (i.e., for all 6 pairwise comparisons, p > 0.735; Table 5, Figure 3). Notably, only *P. t. verus* among the chimpanzee subspecies exhibits a significantly lower F/H J ratio than that of *P. paniscus*, and only at the 35% ROI (p = 0.016; Table 5, Figure 3). All F/H J ratios of *G. b. graueri* do not differ significantly from the lower ratios of *G. g. gorilla*, while all F/H J ratios of *G. b. beringei* are significantly greater than those of *G. g. gorilla* (Table 5, Figure 3). The F/H J ratios of *G. b. beringei* also consistently exceed those of *G. b. graueri*, although this difference is significant only at the 65% ROI (Table 5; Figure 3).

4. Discussion
4.1 Species level diversity in interlimb rigidity ratios

Femoral-humeral J ratios varied significantly between great ape species with post hoc tests confirming that *Pongo* and *Homo* bracket the African apes, with arboreal *Pongo* exhibiting lower F/H J ratios and terrestrial bipedal *Homo* exhibiting higher F/H J ratios compared to all other groups in the study (Table 4). These results were consistent across the three ROIs and support broad comparability of our results with those from previous investigations of diaphyseal rigidity at hominoid femoral and humeral midshafts (Ruff, 2002; Shaw & Ryan, 2012). Among great apes, the relative ranking of mean F/H J ratios was as predicted, with chimpanzees < bonobos < western gorillas < eastern gorillas for all ROIs (Table 3). Diaphyseal rigidity ratios of chimpanzees and bonobos differed significantly from western gorillas, including at some non-midshaft ROIs. Specifically, chimpanzees exhibited significantly lower F/H J ratios than western gorillas at all three ROIs, while bonobos exhibited significantly lower F/H J ratios than western gorillas only at the 65% ROI, which is the only ROI where the two gorilla species did not differ significantly (Figure 2). In the present study, non-midshaft ROIs ultimately expanded the diaphyseal signal that differentiates groups.

While mean F/H J ratios were indeed higher in bonobos than chimpanzees (Table 3), as predicted based on the behavioral data from Lui Kotale (Ramos, 2014), it must be noted that post hoc tests did not support this prediction with statistical significance (Table 4). Compared to chimpanzees, bonobos from Lui Kotale spend less overall time arboreally and less locomotor time arboreally, (Table 1). Morphological results of the present study appear to confirm what the behavioral data from Lui Kotale may lead one to infer (Ramos, 2014), the absence of significant differences in F/H J ratios of bonobos and chimpanzees suggests that long-held beliefs about arborealism in bonobos must be revised (Susman, 1985, Doran, 1993, Crompton et al., 2010). The general behavioral similarity between bonobos and western gorillas may partially explain why F/H J ratios did not differ significantly at either the 35% or 50% ROIs between these two groups, even though chimpanzees did exhibit lower F/H J ratios than western gorillas (Table 4). Further behavioral observation studies of ape taxa (e.g., bonobos and western gorillas) would be helpful in corroborating these results, as may targeted comparisons between bonobos and groups of chimpanzees with known contextual information on habitat and behavioral repertoires.

To the extent that F/H J ratios may reflect ape body plans, the bonobo results offer additional insights. Bonobos have been previously suggested to represent the subadult form of chimpanzees in both morphology and behavior (i.e. paedomorphism and greater arboreality, Doran, 1992). Results of the

present study, however, do not support this idea since bonobo F/H J ratios were not indicative of a significantly more arboreal body plan in the former compared to chimpanzees. Bonobos have also been argued to exhibit a more basal body plan with regards to the human-chimpanzee last common ancestor (HCLCA: Diogo, Molnar, and Wood, 2017; Hunt, 2020). Their apparent intermediate degree of arboreality between that of chimpanzees and gorillas, supported by their somewhat intermediate F/H J ratios in this study, are consistent with the notion that arboreal locomotor behavior in the HCLCA may have been more bonobo-like than chimpanzee-like in frequency. Additional behavioral observation studies of bonobos would offer opportunities to more robustly contextualize the Lui Kotale results.

Intrageneric differences between gorilla species were observed at the midshaft ROI in the present study, which is consistent with the overall pattern reported in studies by Ruff et al. (2013, 2018). These authors observed that western gorillas exhibited lower femoral/humeral Z_p ratios compared to eastern gorillas in comparisons of 50% femur Z_p to 40% humerus. In the present study, we have extended the range of significant differences between gorilla species to include non-midshaft ROIs. Femoral-humeral J ratios differed between gorilla species at both 35% and 50% ROIs, but no significant differences were observed at the 65% ROI (Table 4). This suggests that interlimb structural differences between gorilla groups are highest in the midshaft or mid-distal diaphysis compared to more proximal diaphyseal locations (we address variation later in the discussion).

In addition to calling for more observational studies of habituated apes, as in any interspecific analysis, we point to the possibility that phylogeny influences patterns of F/H J ratios. One way to incorporate phylogeny into these analyses would be to conduct a phylogenetic ANOVA on F-H J ratios and the degree of arboreality. The small sample size (e.g., n = 6 species) and an incomplete behavioral record for degree of arboreality in all our subgroups (e.g., *P. t. troglodytes*), however, limits the utility of this approach in the current study. Specifically, estimates of phylogenetic signal are unreliable when phylogenies include fewer than 20 taxa (Freckleton et al., 2002; Münkemüller et al., 2012), often resulting in large confidence intervals on phylogenetic signal estimates such as Pagel's lambda.

4.2 Intraspecific diversity in interlimb rigidity ratios

Counter to our predictions of intraspecific differences (Hypothesis 2), *P. t. verus* did not exhibit lower F/H J ratios compared to the two other *P. troglodytes* subspecies investigated in the present study. Notably, *P. t. verus* did exhibit a significantly lower F/H J ratio at the 35% ROI compared to *P. paniscus*, but analogous F/H J ratios of *P. t. schweinfurthii* and *P. t. troglodytes* were not significantly lower than that of *P. paniscus*. Since the *P. t. verus* sample largely consisted of individuals from the Taï Forest population (Carlson et al., 2006, 2008), which has a relatively high component of closed forest in their home range, a more substantial difference in F/H J ratios was expected due to their higher levels or arboreality. It may be the case that comparisons undertaken at a subspecies level, such as in the present study, inadvertently conflate localized differences in habitat conditions. For example, we would predict that chimpanzees from the opposite end of the habitat spectrum to the Taï Forest population (e.g., groups occupying dry, open habitats, such as those at Fongoli, Mt. Assirik, or Semliki) may show a more dramatic difference in F/H J ratios. Such a comparison would more effectively dichotomize documented variation in chimpanzee habitat conditions and probably behavioral repertoires too. The existence of a potentially distinct signal in F/H J ratios of dry habitat chimpanzees is especially intriguing given recent reporting of other ecomorphological skeletal features in such groups, e.g., more human-like bicondylar angles characterize femora of Semliki chimpanzees compared to femora from forest-dwelling chimpanzees (Hunt, Dunevant, Yohler, & Carlson, 2021).

Our prediction that *G. b. graueri* would exhibit intermediate F/H J ratios to those of *G. g. gorilla* and *G. b. beringei* was partially supported in all three ROIs. *G. g. gorilla* exhibited significantly lower F/H J ratios than did *G. b. beringei*, but the former did not differ significantly from *G. b. graueri* at any of the three diaphyseal locations (Table 5). Moreover, *G. b. graueri* exhibited lower F/H J ratios at the 65% ROI, but not at the 35% and 50% ROIs compared to *G. b. beringei*. These results are consistent with the findings of Ruff et al. (2018) who compared 50% femur Z_p to 40% humerus, observing that *G.b. graueri* was intermediate between *G.b. beringei* and *G.g. graueri.* Ruff et al. (2018) further divided *G.b. graueri* into lowland and highland groups, noting that lowland *G.b. graueri* was more similar to *G.g. gorilla* than *G.b. beringei*, with highland individuals being intermediate between the groups. Our results extend this intermediate designation of *G.b.graueri* between *G. g. gorilla* and *G.b.beringei* to additional areas of the diaphysis beyond the midshaft.

Across species groups, the F/H J ratios at 35% ROIs were consistently higher compared to those at 50% and 65% ROIs (Figures 2 and 3). Changes in ratios along the shaft may be a reflection of an increase in humeral values more than a decrease in femoral values between the 35% ROI on the one hand and the 50% and 65% ROIs on the other hand (e.g., see trends in supplemental scatterplot Figures). One potential explanation for the observed pattern along diaphyses may be the presence of the deltoid insertion, which spans parts of the proximal and lateral surface of the great ape humerus (see Gómez et al. 2020). The most prominent area of the diaphyseal attachment site is typically the most distal portion of the attachment, which often coincides with the midshaft region in great ape humeri (Swindler and Wood, 1973). For example, Larson (1998) reported that the distal extent of the deltoid insertion in great apes (*Pongo* 52%, *Pan* 45%, *Gorilla* 46%) narrowly varied in its distance from the distal end of the humerus. There is precedence in the literature for avoiding the deltoid tuberosity when measuring humeral cross-sectional properties (e.g., see Marchi, Ruff, Capobianco, Rafferty, Habib, Patel, 2016; Patel, Ruff, Simons, & Organ, 2013), as it has been suggested to unduly complicate diaphyseal loading of the shaft as estimated by cross-sectional properties (Ruff, 2002). Here, we deliberately chose to sample the midshaft to intentionally incorporate this complexity, as other ROIs of the diaphysis also do not exclude consideration of local muscle attachments.

Based on comparisons of cross-sectional geometric properties from the three ROIs in the present study, the 35% ROIs appear to be more successful in differentiating groups than midshafts or 65% ROIs. This again underscores the value of diaphyseal ROIs in addition to midshaft when differentiating internal structure in hominoid femoral and humeral diaphyses. Interestingly, Mongle, Wallace, & Grine (2015) observed that *Pan* exhibited a change in J values along the humeral shaft when comparing other ROIs to midshaft while *Gorilla* did not display the same trend. In the present study, this difference between the African ape genera was supported by F/H J ratios in *Pan* being smaller at 65% ROIs and greater at 35% ROIs when comparing them to midshaft F/H J ratios, while *Gorilla* did not exhibit the same trends across the three ROIs (i.e., midshaft ROIs tended to exhibit the lowest F/H J ratios in gorillas rather than intermediate ratios).

More fully documenting variability in F/H J ratios within African apes, including extending investigations to non-midshaft locations, offers a more rigorous framework for evaluating F/H J ratios in stem homininans. In the present study, African ape subspecies displayed a range of F/H J ratios where *P. t. verus* generally exhibited the lowest ratios (e.g., mean F/H J ratios in ROIs ranging between 1.30 - 1.38), while *G. b. beringei* generally exhibited the highest ratios (e.g., mean F/H J ratios of ROIs between 1.74 - 2.15). Obtaining finer resolution within these ranges may be possible by grouping individuals according to habitat conditions rather than taxonomic status. In particular, adding F/H J ratios from a sample of dry habitat chimpanzees could be especially illuminating for developing insights into relative limb use by stem homininans. Ruff (2008) reported F/H J ratios in two *H. erectus* partial skeletons as 3.04 (KNM-WT 15000) and 5.31 (KNM-ER 1808). Values for both of these partial skeletons fall comfortably within the range of values obtained from the small

representative sample of *H. sapiens* in the present study, and well above ranges of values observed in any other ape group. Midshaft F/H J ratios from early stem homininans, such as *Homo habilis* at 1.70 (OH 62: Ruff, 2009) and *Australopithecus afarensis* at 2.16 (A.L. 288-1: Ruff et al., 2016), on the other hand, are more like those of the extant African ape groups in the present study, even overlapping with the ranges of some of these taxa. Discoveries of additional partial skeletons (e.g., Berger et al., 2010; Clarke, 2019; Heaton et al., 2019) offer critical and exciting opportunities to more fully explore variation in relative limb use among early stem homininans.

As noted earlier, small sample sizes acted as a limitation in this study, including during the analysis of intraspecific variation. In some cases, this is unavoidable given the rarity of postcranial material of wild-caught, adult bonobos and orangutans curated in museum collections. The substantial variation in F/H J ratios observed in our small modern human sample (i.e., 10 right humeri, 2 left humeri) may be partly attributable to humeral bilateral asymmetry. Humeral bilateral asymmetry is typically attributed to handedness in studies of human upper limb activity (Sparacello et al., 2017; Wei et al., 2020), but it is not similarly expressed at the population level in other apes (Marchant & McGrew, 2013). Exploring sources of variation in the modern human sample, such as handedness, however, is beyond the scope of the present study. Finally, while it is commonly believed that western gorillas are more arboreal than eastern gorillas (Doran, 1997; Remis, 94 & 94 & 98; Ruff et al. 2018), another limitation in this study is the lack of available positional behavior data on fully habituated western gorilla individuals. Future observational studies providing more positional behavioral data on habituated *G.g. gorilla*, *G.b. graueri,* and *P.t. troglodytes* individuals would be helpful in this regard.

5. Conclusions

Differences in F/H J ratios according to positional behavior patterns were easily discernible between ape groups at the species level, strengthening the call to use these ratios for interpreting the limb use and behavior of fossil specimens where femoral and humeral remains are present. This study expands on midshaft usage to demonstrate that both 35% and 65% length from the distal ends of diaphyses can be informative areas for exploring species differences in relative limb rigidity (J) ratios.

Behavioral data suggest that bonobos may be intermediate in degree of arboreality between chimpanzees and western gorillas. Diaphyseal femoral to humeral J ratios documented in the present study, in part, corroborate this aspect of their reassessed behavioral repertoire since they are also somewhat intermediate between chimpanzees and western gorillas, further indicating that diaphyseal J ratios can be useful for interpreting relative limb involvement in broad behavioral repertoires of fossil taxa. Comparisons of chimpanzee subspecies J ratios were less informative for insights into behavioral differences, likely due to the smaller shifts in behavioral repertoires that occur at this level. Evaluating chimpanzees according to habitat differences, however, may provide additional, new information. Subspecies differences in relative J ratios at one ROI (65%) were observed in eastern gorillas (*Gorilla beringei)*, possibly due to the behavioral differences between these subspecies being more drastic.

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7. References

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8. Figure legends

Figure 1. Locations of femoral (left) and humeral (right) diaphyseal regions of interest (35%, 50%, and 65% length) analyzed in the present study.

Figure 2. Species Boxplot of Femoral J to Humeral J Ratios for Each Region of Interest. Reference line = 1.0 in which the femur and humerus are equivalent in value. Two human outliers were removed for easier visualization of data but the original figure has been included in supplementary figures for the sake of transparency.

Figure 3. Subspecies Boxplot of Femoral J to Humeral J Ratios for Each Region of Interest.

Supplementary Figure Legends

Supplementary Figure 1. Scatterplot of Femoral and Humeral J Values for Each Species at 35% Region of Interest.

Supplementary Figure 2. Scatterplot of Femoral and Humeral J Values for Each Species at 50% Region of Interest.

Supplementary Figure 3. Scatterplot of Femoral and Humeral J Values for Each Species at 65% Region of Interest.

Supplementary Figure 4. Original Species Boxplot of Femoral J to Humeral J Ratios for Each Region of Interest. The two human outliers excluded in Figure 2 are present.

Appendix. Excel data set. The Mahale, Gombe, and Kibale chimpanzees have been excluded from this file.
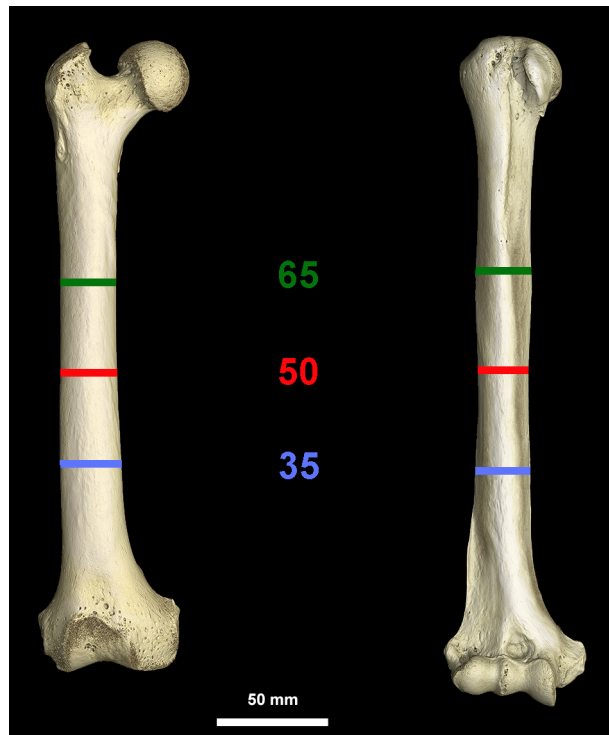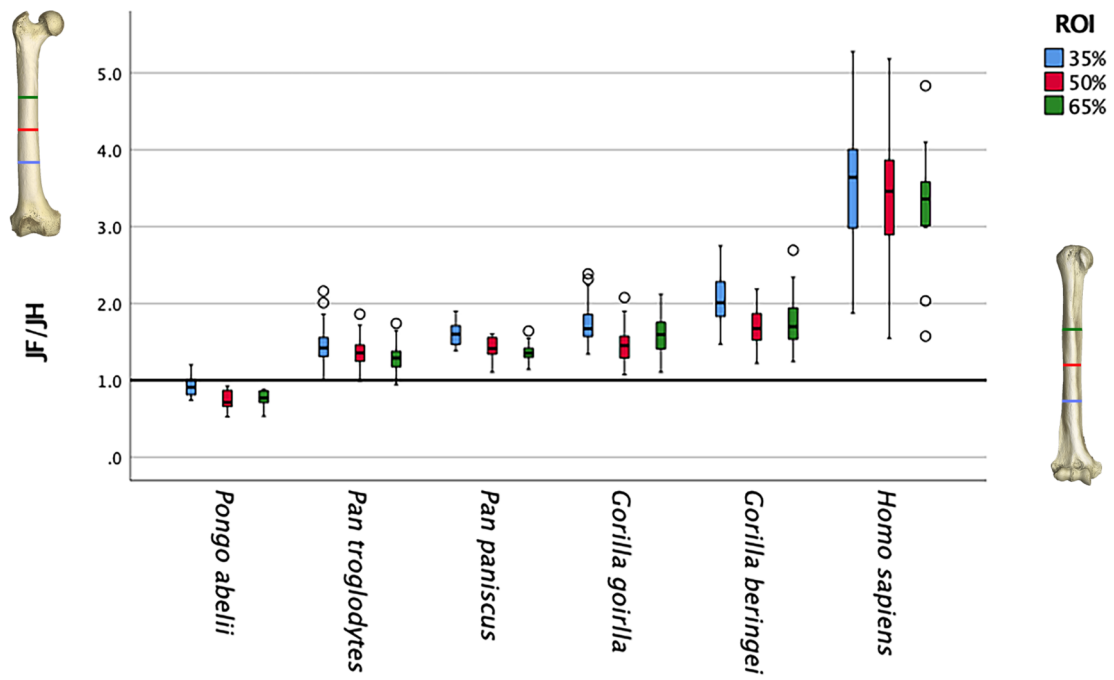
Figure 1. ROIs copy.tif

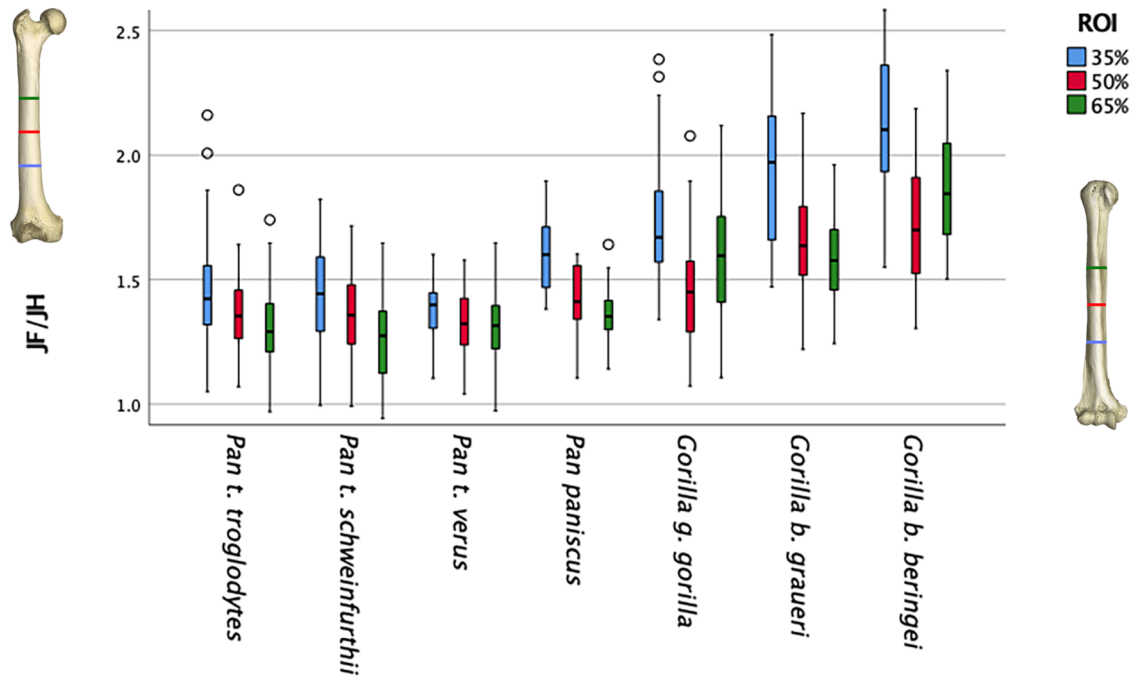Figure 2. Species F H ratio boxplot with bones copy.tif

Figure 3. Subspecies F H ratios boxplot with bones copy.tif

Table 1. Arboreal behavior percentages for different hominin species and subspecies.

Species Subspecies	%Time Arb F/M	% Loc Arb F/M	Arboreal Locomotion		
			%susp F/M	%climb F/M	%scramble F/M
Pongo abelii	~100[a]	100	17-18	20-25	31-44[b]
Pan troglodytes					
P.t.troglodytes					
P.t. schweinfurthii	52/34[c]	12/8[d]	8/7	49/52	10/3
P.t verus	65/49[c]	18/15[d]	7/6	51/59	8/8
Pan paniscus	47/41[e]	9[f]	2	40	33
Gorilla gorilla					
G. g. gorilla		9/2[d]	11/4	39/48	31/25
Gorilla beringei					
G. b. beringei	7/2[g]	8/2[d]	3/0	33/27	3/9
G. b graueri					

*F = female, M = male; if only one number provided it is for sexes combined

a = Suaq Balimbing flanged males spend <0.25% of their time terrestrial and habituated females spend <0.05% terrestrial (personal communication with C. Schuppli referenced in Ashbury et al., 2015) and approximately 0% terrestrial for Sumatran orangutans from personal communication with S.K.S. Thorpe.

b = Pongo data from Manduell et al. 2012, Data 1-min instantaneous focal sampling. Ranges are from two study sites, Ketambe and Suaq Balimbing, Sumatra. Orangutans are highly arboreal but the breakdown of their arboreal behavior depends on habitat structure to a high degree (Manduell et al., 2012; Manduell, 2013). Suspend (includes brachiation and forelimb swing; torso pronograde suspensory behavior) Quadrupedal scrambling (includes orthograde clamber and transfer, drop and leap, sway, ride, and bridge); Quadrupedal climb (includes vertical climb and descent);

c = from Doran & Hunt, 1994 Table 4, Mahale and Gombe combined for P.t.s,

d = Data from *Pan* troglodytes and *Gorilla* from Carlson, 2005 Suspend (includes brachiate, arm swing, and drop), Quadrupedal scrambling (includes scramble, bridge, fireslide, tree sway, ride, and leap), and Quadrupedal climbing (on vertical or inclined substrates) within arboreal locomotor behaviors only (Carlson used original data from D. Doran and K. Hunt as well as data from Doran, 1989; Doran & Hunt, 1994; Hunt, 1989, 1992; Remis, 1994, 1995, 1998)

e = % time arboreal and arboreal locomotion for bonbons from Lui Kotale taken from Ramos, 2014 Table 4.13 and 4.23. Doran 1993 reported that Lomako bonobos engaged in 19% suspensory, 28% climb, 2% scramble for arboreal locomotion.

f = Percentage of arboreal locomotion data for *Pan paniscus* reflect 69 arboreal locomotor bouts out of 789 total locomotor bouts. (Ramos, personal communication)

g = Doran, 1997

Table 2. Taxonomic distribution of samples (N = 254).

Species Subspecies	Sex				Museum or location
	F	M	U	T	
Pongo abelii	1	5	0	6	NMNH
Pan troglodytes	50	43	37	130	AIMUZ, AMNH, BMNH, CMNH, LHU, MNHU, NMNH, PCM, RMCA
P.t. troglodytes[a]	22	16	18	56	Gombe, Kibale
P.t. schweinfurthii	15	22	17	54	
P.t verus	13	5	2	20	
Pan paniscus	8	4	0	12	RMCA
Gorilla gorilla[b]	19	27	7	53	AIMUZ, AMNH, BMNH, MNHU, NMNH, PCM, RMCA,
Gorilla beringei[c]	18	19	4	41	AIMUZ, AMNH, BMNH, MNHU, NMNH, RMCA
G. b. beringei	11	11	0	22	
G. b graueri	7	8	4	19	
H. sapiens	5	7	0	12	RADUW

*M = male, F = female, U = undetermined, T = total number

Museum Abbreviations: AIMUZ = Anthropolisches Institut und Museum der Universität Zürich-Irchel, Zürich, Switzerland; AMNH = American Museum of Natural History, New York, NY; BMNH = British Museum of Natural History, London; CMNH = Cleveland Museum of Natural History, Cleveland, USA; LHU = Laboratory of Human Evolution, Kyoto University, Japan; MNHU = Museum für Naturkunde der Humboldt Universität, Berlin, Germany; NMNH National Museum of Natural History, Washington, DC, USA; PCM = Powell-Cotton Museum, Birchington, Kent, UK; RADUW = Raymond A. Dart Collection University of the Witwatersrand, Johannesburg, SA; RMCA = Musée Royal de l' Afrique Centrale, Tervuren, Belgium

a= Including two individuals (50% ROI only) who may be *P.t. ellioti* based on their port of origin provided collection records. These two individuals were included in the *P.t.t* group as results did not differ with the inclusion or exclusion of the specimens.

b= *Gorilla gorilla* is comprised of 52 *G.g. gorilla* specimens and one *G.g.diehli* specimen which was included as results did not vary with the inclusion or exclusion of this specimen.

c= Subspecies divided by geographic information in accordance with range data provided by Plumptre *et al.* 2016, Tocheri *et al*. 2016, and van der Valk *et. al.* 2018.

Table 3. Species mean RAW J_F/J_H.

	35%	50%	65%
Pongo abelii	**0.930**	**0.733**	**0.755**
	(0.162)	**(0.145)**	**(0.129)**
	0.740-1.202	**0.524-0.924**	**0.532-0.883**
Pan troglodytes[a]	**1.441**	**1.351[b]**	**1.289**
	(0.196)	**(0.160)**	**(0.172)**
	0.995-2.161	**0.991-1.861**	**0.944-1.740**
P. t. troglodytes	1.460	1.356	1.316
	(0.212)	(0.153)	(0.172)
	1.050-2.161	1.069-1.861	0.969-1.740
P. t. schweinfurthii	1.445	1.354	1.261
	(0.202)	(0.173)	(0.172)
	0.995-1.822	0.991-1.716	0.944-1.646
P. t. verus	1.382	1.328	1.303
	(0.118)	(0.148)	(0.167)
	1.104-1.601	1.041-1.578	0.973-1.647
Pan paniscus	**1.611**	**1.429**	**1.370**
	(0.171)	**(0.148)**	**(0.129)**
	1.382-1.896	**1.105-1.603**	**1.141-1.641**
Gorilla gorilla	**1.734**	**1.455**	**1.597**
	(0.242)	**(0.224)**	**(0.251)**
	1.340-2.385	**1.073-2.077**	**1.105-2.119**
Gorilla beringei	**2.044**	**1.705**	**1.748**
	(0.321)	**(0.244)**	**(0.293)**
	1.471-2.750	**1.220-2.187**	**1.243-2.692**
G. b. graueri	1.917	1.658	1.589
	(0.298)	(0.237)	(0.204)
	1.471-2.485	1.220-2.168	1.243-1.961
G. b. beringei	2.153	1.744	1.886
	(0.305)	(0.247)	(0.291)
	1.550-2.750.	1.304-2.187	1.503-2.692
Homo sapiens[a]	**3.767**	**3.400[b]**	**3.537**
	(1.291)	**(1.005)**	**(1.327)**
	1.871-6.565	**1.546-5.181**	**1.574-6.781**

Mean values (standard deviation) and then minimum and maximum ranges given for each region of interest.

a. The human ratios have a large range which may be due in part to the sample being comprised of individuals from different ages (20-90 years) and ethnic groups. The mean for the 50% is similar to published values (Shaw and Ryan, 2012).

Table 4. Species ANOVA post hoc results for RAW J_F/J_H at each ROI.

J 35%

	P. abelii	P. troglodytes	P. paniscus	G. gorilla	G. beringei	H. sapiens[a]
P. abelii	X	**0.005***	**<0.001***	**<0.001***	**<0.001***	**<0.001***
P. troglodytes		X	*0.086*	**<0.001***	**<0.001***	**0.001***
P. paniscus			X	0.537	**<0.001***	**0.002***
G. gorilla				X	**<0.001***	**0.003***
G. beringei					X	**0.011***

J 50%

	P. abelii	P. troglodytes	P. paniscus	G. gorilla	G. beringei	H. sapiens
P. abelii	X	**0.001***	**<0.001***	**<0.001***	**<0.001***	**<0.001***
P. troglodytes		X	0.811	**0.042***	**<0.001***	**<0.001***
P. paniscus			X	1.000	**0.001***	**<0.001***
G. gorilla				X	**<0.001***	**<0.001***
G. beringei					*X*	**0.002***

J 65%

	P. abelii	P. troglodytes	P. paniscus	G. gorilla	G.. beringei	H. sapiens[a]
P. abelii	X	**0.001***	**<0.001***	**<0.001***	**<0.001***	**<0.001***
P. troglodytes		X	0.631	**<0.001***	**<0.001***	**0.002***
P. paniscus			X	**0.001***	**<0.001***	**0.002***
G. gorilla				X	0.136	**0.005***
G. beringei					X	**0.010***

* & **Bold** Denotes a significant result. *Italicized* Denotes borderline non-significant result (0.05-0.099). Regular font denotes nonsignificant results.

Species ANOVA results RAW data. Tamhane used for post hoc analysis as Levene's test significant.

35% ANOVA F =105.800, df = 5, p < 0.001

50% ANOVA F = 128.766, df = 5, p <0.001

65% ANOVA F = 97.937, df = 5, p < 0.001

[a] Results between the other species remained the same when humans were removed at all ROI. i.e. the same post hoc comparisons were sig/nonsig.

Table 5. Subspecies ANOVA post hoc results for RAW J_F/J_H at each ROI.

Table 5. Subspecies ANOVA post hoc results for RAW J_F/J_H at each ROI.

J35%	P .t. s.	P. t. v.	P. p.	G. g. g.	G.b.g.	G. b. b.
P.t.t.	1.000	0.735	0.311	**<0.001***	**<0.001***	**<0.001***
P.t.s.	X	0.909	0.168	**<0.001***	**<0.001***	**<0.001***
P.t.v.		X	**0.016***	**<0.001***	**<0.001***	**<0.001***
P. p.			X	0.659	**0.022***	**<0.001***
G.g.g.				X	0.388	**<0.001***
G.b.g.					X	0.305

J50%	P. t. s.	P. t. v.	P. p.	G. g. g.	G. b. g.	G. b. b.
P.t.t.	1.000	1.000	0.959	0.161	**0.001***	**<0.001***
P.t.s.	X	1.000	0.957	0.191	**0.001***	**<0.001***
P.t.v.		X	0.821	0.169	**<0.001***	**<0.001***
P. p.			X	1.000	*0.051*	**0.001***
G.g.g.				X	*0.059*	**0.001***
G.b.g.					X	0.998

J65%	P. t. s.	P. t. v.	P. p.	G. g. g.	G. b. g.	G. b. b.
P.t.t.	0.993	1.000	0.997	**<0.001***	**<0.001***	**<0.001***
P.t.s.	X	1.000	0.385	**<0.001***	**<0.001***	**<0.001***
P.t.v.		X	0.994	**<0.001***	**0.001***	**<0.001***
P. p.			X	**0.002***	**0.022***	**<0.001***
G.g.g.				X	1.000	**0.005***
G.b.g.					X	**0.010***

* & **Bold** Denotes a significant result. *Italicized* Denotes borderline non-significant result (0.05-0.099). Regular font denotes nonsignificant results. Species ANOVA results RAW data. Tamhane used for post hoc analysis as Levene's test significant. 35% ANOVA F = 40.119, df = 6, p < 0.001; 50% ANOVA F = 17.997, df = 6, p <0.001; 65% ANOVA F = 34.730, df = 6, p < 0.001