Title: Ontogenetic and morphological variation in primate long bones reflect signals of size and behavior

Short title: Ontogeny and morphology of primate long bones

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Abstract:

Objectives

Many primates change their locomotor behavior as they mature from infancy to adulthood. Here we investigate how long bone cross-sectional geometry in *Pan*, *Gorilla*, *Pongo*, Hylobatidae and *Macaca* varies in shape and form over ontogeny, including whether specific diaphyseal cross sections exhibit signals of periosteal adaptation or canalization.

Materials and Methods

Diaphyseal cross sections were analyzed in an ontogenetic series across infant, juvenile and adult subgroups. Three-dimensional laser-scanned long bone models were sectioned at midshaft (50% of biomechanical length) and distally (20%) along the humerus and femur. Traditional axis ratios acted as indices of cross-sectional circularity, while geometric morphometric techniques were used to study cross-sectional allometry and ontogenetic trajectory.

Results

The humeral midshaft is a strong indicator of posture and locomotor profile in the sample across development, while the mid-femur appears more reflective of shifts in size. By comparison, the distal diaphyses of both limb elements are more ontogenetically constrained, where periosteal shape is largely static across development relative to size, irrespective of a given taxon's behavior or ecology.

Discussion

Primate limb shape is not only highly variable between taxa over development, but at discrete humeral and femoral diaphyseal locations. Overall, periosteal shape of the humeral and femoral midshaft cross sections closely reflects ontogenetic transitions in behavior and size, respectively, while distal shape in both bones appears more genetically constrained across intraspecific development, regardless of posture or size. These findings support prior research on tradeoffs between function and safety along the limbs.

Key words: development; primate; locomotion; morphometrics; long bone

1. Introduction

Many primates change their locomotor behavior and posture as they mature (Doran, 1997; Dunbar and Badam, 1998). Unlike precocial mammals, some species take months or years to reach locomotor independence (Young and Shapiro, 2018). The mechanical loads placed on infant long bones thus differ from those experienced by adults (Sarringhaus et al., 2014; Morimoto et al., 2018). There is a close relationship between size and posture between and within species: as young primates become more independent, their smaller body masses allow them to exploit environments inaccessible to larger-bodied adults, influencing locomotor activity (Doran et al., 1997; Young et al., 2010). As a primate matures, its body shape, including long bone dimensions, changes as its size increases, carrying biomechanical implications (Ruff et al., 2018). Although most of the literature on primate movement and posture focuses on adults, ontogenetic research is gaining momentum, with considerable work focused on quadrupedalism and relatively little examining other forms of locomotion, like brachiation (see review in Young and Shapiro, 2018). Though all share an orthograde body plan, the apes are divergent in locomotion, ecology, size, and maturation pattern, all of which have direct implications to functional morphology over development (Rose, 1983; Jungers and Susman, 1984; Leigh, 1993).

The Asian apes are more committed to arboreal locomotion and use forelimb suspensory behaviors more frequently than the African apes (Hunt, 2016). When moving, small apes employ brachiation much of the time (with estimates varying from ~60% to ~80% of locomotor time; Fleagle, 1974, 1980; Hunt, 2004; Michilsens et al., 2009) and have musculoskeletal adaptations to facilitate specialized locomotion (Swartz et al., 1989; Michilsens et al., 2009). Both hylobatids and orangutans exhibit a relatively elongated and circular humeral diaphysis in response to the increased torsion and reduced bending and compressive loads experienced during suspensory locomotion (Swartz et al., 1989; Ki-Kydd and Piper, 2004; Patel et al., 2013). Compared to the hylobatids, orangutan locomotor and positional behaviors are less easily characterized, incorporating suspensory activity, quadrupedal and bipedal walking in trees, and climbing (Thorpe and Crompton, 2006). They reach locomotor independence by at least six years and as early as three (van Adrichem et al., 2006), and exhibit limited positional and locomotor differences across age-sex categories (Thorpe and Crompton, 2005, 2006; but see Sugardjito and van Hooff, 1986;

Cant, 1987). Rather, gap-crossing maneuvers are adopted early in life and are performed at different frequencies over development (Chappell et al., 2015).

Gorillas and chimpanzees employ knuckle-walking, which likely evolved in parallel in the two genera (Dainton and Macho, 1999; Kivell and Schmitt, 2009). The extent to which gorillas and chimpanzees exploit terrestrial versus arboreal substrates varies by taxon, sex and developmental stage. Mountain gorillas are competent quadrupeds (knuckle-walking and palmigrade locomotion) by 6–23 months, becoming increasingly more terrestrial by juvenility into adulthood, when up to 86% of total locomotor time is terrestrial (Doran, 1997). Across the genus, females tend to be more arboreal than their larger male counterparts, while western lowland gorillas exhibit arboreal behavior more frequently than other species (Remis, 1999; Masi, 2004; Doran-Sheehy et al., 2009). In contrast to gorillas, which adopt quadrupedalism early in life, the chimpanzee locomotor profile continues to be characterized by climbing and suspension into juvenility (Doran, 1997; Sarringhaus et al., 2014), although the extent to which common chimpanzees use arboreal substrates also varies with habitat (Doran, 1992a,b; Doran and Hunt, 1994).

Unsurprisingly, differences in adult mass across primates result in variation of maturation patterns among taxa and between sexes. Gorillas grow faster than chimpanzees and bonobos, but relative to *Pan*, growth terminates earlier in female gorillas than in males (Leigh, 1992; Leigh and Shea, 1996). Consequently, gorillas arrive at the same developmental junctures at larger sizes than chimpanzees or bonobos (Shea, 1985). A longer growth period in male gorillas compared to females contributes to sexual size dimorphism, which is also true in bonobos but not in chimpanzees, where faster male growth accounts for adult differences with females (Leigh and Shea, 1996). Albeit based only on the cranium, dimorphism is present from infancy in orangutans, with males being larger than females at all age stages, and a growth spurt occurring in males at adolescence (Hens, 2005).

There are also ontogenetic differences in body proportions between ape taxa. Femoral diaphyseal shape seems to develop differently in chimpanzees and gorillas, which is not explained by size variation (Morimoto et al., 2018). Support for this concept comes from observations that interlimb diaphyseal strength proportions in gorillas correlate closely with transitions in locomotor behavior over development, rather than scaling isometrically, suggesting that increases in bone strength relative to length are not soley products of normal growth, but adaptive responses to behavioral change (Ruff et al., 2013, 2018). The effects of locomotor behavior over gorilla development also impact diaphyseal shape (Canington et al., 2018). Similar research on chimpanzee limb strength proportions determined that femoral strength becomes relatively greater than humeral strength over development as a means of supporting a transition to hindlimb locomotor dominance (Sarringhaus et al., 2016).

Macaques have served as insightful functional and phylogenetic points of comparison to apes (Ruff, 1988; Ruff et al., 2002), as they employ a diversity of locomotor modes, including quadrupedal walking, running, galloping, leaping and clambering (Cant, 1988; Demes et al., 2001; Patel, 2009). Accordingly, macaque locomotor adaptations can inform about the mechanical pressures placed on their postcranial skeletons in both terrestrial and arboreal contexts. The locomotor behavior and skeletal morphology of rhesus macaques are tightly linked as they develop, where caudal to cranial shifts in mass are tied to postural and positional changes in growing infants (Wells and Turnquist, 2001). In the limbs, an increase in mass is shifted to the hindlimb compared to the forelimb early in infancy (about 4–6 months) (Turnquist and Kessler, 1989; Schneider and Zernicke, 1992), driving the transition to hindlimb propulsion and locomotor independence (Wells and Turnquist, 2001), like that observed in the hominids (Kimura, 1979, 1992; Demes et al., 1994). A comparative study of human and baboon limb ontogeny also demonstrated how behavioral changes over development are associated with species-specific femoral-to-humeral strength and length proportions (Ruff, 2003).

1.1 Postcranial development and adaptation

Notwithstanding underlying genetic components (Lovejoy et al., 2003; Wallace et al., 2010; Morimoto et al., 2018), the limb diaphyses have the capacity to morphologically adapt in response to environmental forces (Robling et al., 2006). Modeling limbs after engineering beams to study their cross-sectional geometry (Huiskes, 1982, Biewener, 1982; Lanyon, 1987) can grant insight into diaphyseal form-function relationships at important ontogenetic stages (Burgess et al., 2016; Ruff et al., 2018). Prior studies on human and nonhuman long bone form and function have demonstrated that there is a close correspondence between cross-sectional geometry and loading regime (Ruff, 2002; Shaw and Ryan, 2012; Marchi, 2015; Macintosh and Stock, 2019; Ruff et al., 2019). For example, loading patterns restricted to movement in the saggital plane (i.e., unidirectional or uniform loading) correspond to a more elliptical cross-sectional shape in African apes, while multidirectional or other variable loading patterns are more closely tied to a circular shape (Carlson, 2002, 2005). Locomotor patterns associated with multidirectional loading and turning apear to result in bone deposition in the mediolateral (ML) axis compared to the anteroposterior (AP) axis along femoral diaphyses as well, as demonstrated among modern humans (Shaw and Stock, 2009) and in murine models (Carlson and Judex, 2007). Primate limb morphology is also highly dependent on the variable forces encountered during locomoton in arboreal compared to terrestrial contexts (e.g., substrate reaction forces) (Schmitt, 2003). With respect to the analysis of cross-sectional shape, some previous studies have focused primarily on deviations from circularity in either the principal plane or the anatomical plane alone. However, the two indices can describe the distribution of bone about a cross section more effectively when used together, as maximum and minimum second moments of area are often independent of those about the ML and AP axes (Ohman, 1993; Carlson, 2005).

Metaphyses and epiphyses transfer mechanical loads across elements via trabeculae, instead of solely relying on the cortex for energy absorption (Currey, 2002; Kivell, 2016). Accordingly, bone regions adjacent to joints should not adapt their cortical structure to the same extent as midshafts, as major modifications in joint morphology could influence safety or function negatively (Currey, 2002; Skedros et al., 2003; Lazenby et al., 2008). Indeed, rigidity and cortical area were virtually indistinguishable between locomotor-variable groups of modern humans at their metaphyses, but significantly different at midshaft (Nadell and Shaw, 2016). A morphometric study of skeletal variation across 11 catarrhine genera, including the extant hominoids, also identified significantly less epiphyseal compared to diaphyseal long bone variation, likely due to greater adaptive constraints in the joints (Buck et al., 2010). Just as marked morphological differences between the epiphyses and diaphyses grant insight into their respective adaptive capacities, it is also possible that differences in development between midshaft and more peripheral diaphyseal sections may serve as effective behavioral signals.

The application of geometric morphometrics (GM) in morphological research has informed relationships between the behavioral ecology and skeletal morphology of primate taxa, including in apes (Lockwood et al., 2002; Smith et al., 2015) and monkeys (Cardini and Elton, 2008a,b; Ito et al., 2014). Geometric morphometrics can define skeletal variation within (Baab and McNulty, 2009; Lordkipanidze et al., 2013), and between populations and species (Almécija et al., 2013; Lordkipanidze et al., 2013; Tallman et al., 2013; Püschel and Sellers, 2016). A GM approach to the study of cross-sectional shape was utilized by Wilson and Humphrey (2015), where bilateral asymmetry of the humerus was compared among a modern human population. The authors determined that a GM approach to shape analysis can offer more accurate information than second moment of area ratios alone (Wilson and Humphrey, 2015). To study the way adult morphological characters arise from infancy, ontogenetic craniofacial trajectories of extant hominids have been compared by regressing cranial shape with size (Mitteroecker et al., 2004). Similar studies investigated the sexual dimorphism of apes over development, by measuring the angles formed between shape vectors (Cobb and O'Higgins, 2004, 2007; Klingenberg and Marugán-Lobón, 2013). The size of a vector angle formed between two taxa can determine how much their developmental trajectories diverge. A greater representation of cranial over postcranial data in GM growth trajectory studies may be related to the stronger phylogenetic compared to functional signals incorporated in the skull (Lieberman, 1996). Even so, comparing ontogenetic trajectories through a functional adaptive lens can be an intuitive way to study postcranial shape, especially when infant populations exhibit greater morphological similarity to each other than their adult counterparts (Schultz, 1924; Canington et al., 2018).

To attain a better understanding of hominoid ontogeny and form-function relationships, this study compares the development and functional morphology of humeral and femoral cross sections from *Pan*, *Gorilla*, *Pongo*, and Hylobatidae, using *Macaca* as a functional and phylogenetic outgroup (Wells and Turnquist, 2001; Patel, 2005; Patel et al., 2013). We use ratios of second moments of area (bending rigidities) about the principal and anatomical axes to measure cross-sectional circularity (Ohman, 1993), while geometric morphometric analyses are used to study variation in cross-sectional shape and form (Klingenberg et al., 2002; Slice, 2007; Zelditch et al., 2012). A GM approach also accounts for size differences in relation to shape, as analyses can be used to scale an object’s dimensions by its centroid in order to consider all aspects of its shape together (Zelditch et al., 2012). An ontogenetic series is included to determine whether important developmental events, like locomotor transitions or increases in body size, can be measured as physical signals along each skeletal element. To study how different aspects of the diaphyses develop, cross-sectional geometry is measured at the distal diaphysis and at midshaft. Accounting for variation at two discrete sections along each element will elucidate how humeral and femoral diaphyses develop.

We address the following questions:

1) For both intra- and interspecific analyses, how do shape patterns differ at discrete cross sections of the humerus and femur?

2) How does diaphyseal form change ontogenetically in each taxon, and does that map onto locomotor/postural changes?

3) For each developmental stage, how does shape vary between taxa?

Specific to these questions, we predict that distal diaphyses will maintain their shape to a greater degree than midshafts over development, irrespective of a taxon's locomotor profile, due to the different strains they experience and their relative proximity to joints compared to midshafts. By comparison, midshafts are expected to adapt their periosteal shape in response to the peak strains they experience during loading and as they grow. Bone deposition patterns at midshaft should reflect the locomotor profile of a given taxon (e.g., terrestrial vs. arboreal), with consideration of the transitions they undertake (if any) as they grow. Supporting Information Tables 1–5 outline the predictions and observations for each taxon and skeletal element.

2. Material and Methods

2.1 Sample

Information on the sample, comprising infant, juvenile and adult long bones of *Pan* (*n*=54), *Gorilla* (*n*=52), *Pongo* (*n*=54), Hylobatidae (*n*=55) and *Macaca* (*n*=56), is detailed in Supporting Information Tables 6 and 7. Most of the sample (94%) was wild-caught, although a total of 21 macaques across all developmental stages were captive. Though studies have found significant differences in cross-sectional geometric properties between captive and wild apes (Venkataraman et al., 2013; Canington et al., 2018), others have found few or none in lemurs (Demes and Jungers, 1993), macaques (Burr et al., 1989) and apes (Marchi, 2007; Morimoto et al., 2011; Marchi et al., 2019). To decide whether the captive macaques should be included for analysis, the dispersion of wild and captive macaque circularity ($I_{\max}/I_{\min}$) was compared at the humeral and femoral midshafts, due to their locomotor adaptive capacities. Circularity was deemed not significantly different between captive and wild macaques in the femur and humerus following a Kolmogorov–Smirnov (KS) independent samples test (mid-femoral P=0.425; mid-humeral P=0.061). Due to the greater overall shape variation in the humerus, a Mann–Whitney U (MW) test and a second KS test were conducted on the captive and wild adult sample, because adult midshafts were expected to exhibit the most adaptive variation. The captive and wild adult humeri did not vary significantly in either comparison (KS: P=0.356; MW: P=0.409), so the captive macaques were included in the general sample.

Developmental stage was scored dentally for each individual using taxon-specific crown eruption benchmarks of deciduous and permanent dentition (Wintheiser et al., 1977; Smith et al., 1994; Dirks and Bowman, 2007; Breuer et al., 2009; Smith and Boesch, 2011; Smith et al., 2013) as detailed in Supporting Information Table 8. The eruption benchmarks were compared against general age-class categories for each taxon to determine whether an individual should be classified as an infant, juvenile or adult. Though some primates experience a brief adolescent stage after juvenility (Sarringhaus et al., 2014), adolescent and subadult individuals were pooled with adults in this study, as rates of load-induced periosteal modeling decline following juvenility (Bertram and Swartz, 1991; Lieberman et al., 2003; Pearson and Lieberman, 2004), in favor of an increased endosteal response in adolescence (Ruff et al., 1994; Kontulainen et al., 2003). Sexes were pooled for infants and juveniles in intra- and interspecific analyses. Male and female adults were only pooled in interspecific comparisons, as the primary interest of those analyses was to identify broader locomotor differences between taxonomic groups (Patel et al., 2013). Male and female adults were analyzed separately in intraspecific analyses except for hylobatids, for which no significant sex-shape differences were identified. For examination of broad form-function relationships among multiple taxonomic groups, such pooling is justifiable based on the relative homogeneity of the family (Bartlett, 2007; Buck et al., 2010), as the hylobatids share similar ecologies (Palombit, 1994; Asensio et al., 2017), musculoskeletal anatomy (Vereecke and Channon, 2013) and locomotor repertoires (Fleagle, 1974; Michilsens et al., 2009).

2.2. Cross section generation and analysis

Fore- and hindlimb data were collected from the same side in each individual (i.e., left humerus; left femur) (Carlson, 2005). All elements were scanned and fused using a NextEngine laser scanner and ScanStudio HD software (NextEngine Inc.). A single scan family consisting of 12 scan divisions was recorded at the highest possible definition (360K points per inch^2) for each bone (Davies et al., 2012; Davies, personal communication). The articular surfaces of each bone were digitally fused to their diaphyses to calculate biomechanical length, as defined by Ruff (2002), and to identify the midshaft and distal locations for sequencing. All digital models were aligned in three dimensions (X, Y, and Z axes), facing posteriorly, following Ruff (2002; Appendix B), to ensure that orientation was consistent between each bone (Davies et al., 2012). Each digital model was exported to the freeware program, AsciiSection (Davies et al. 2012) and segmented into cross sections at midshaft (50% of biomechanical length) and distally (20%). The humeral and femoral cross section locations were selected based on acceptable error ranges for solid-sectional compared to "true" (endosteal and periosteal) cross-sectional shape ($I_{\max}/I_{\min}$) of human humeral and femoral diaphyses, presented in a human archaeological sample ($N = 20$) (Macintosh et al., 2013).

Previous studies interested in cross-sectional strength and rigidity have controlled for muscle attachment sites like the deltoid tuberosity; typically by evaluating cross sections distal to the humeral-midshaft (Ruff, 2002; Alba et al., 2011; Marchi et al., 2016). Analyses of mid-humeral cross-sectional shape ratios in a sample of humans, chimpanzees, and gorillas identified significant differences between the 50% and 40% locations among humans, but not among chimpanzees or gorillas (Mongle et al., 2015). Similarly, an ontogenetic study of chimpanzees found no relationship between shape and age between the 50% and 40% humeral diaphyseal locations (Sarringhaus et al., 2016). Because the current study was specifically interested in cross-sectional shape and form rather than measures of strength and rigidity, true midshaft (50% of length) was analyzed.. A graphing program called gnuplot illustrated 2D solid section images based on the coordinate data extracted by AsciiSection. After each model was sectioned, four second moments of area were calculated in AsciiSection: maximum bending rigidity ($I_{\max}$), minimum bending rigidity ($I_{\min}$), bending rigidity about the AP axis (I_x) and bending rigidity about the ML axis (I_y). After values for I were established, ratios were calculated for the principal and anatomical axes and expressed as I_{max}/I_{min} and I_x/I_y, respectively. A Shapiro-Wilk test was conducted to determine whether the circularity data were normally distributed (Shapiro and Wilk, 1965). Equality of variance in each of the developmental subgroups was evaluated using Levene's test. Univariate analysis of variance (ANOVA) and, where appropriate, corrections from the Tukey HSD or Games-Howell post hoc tests were used to interpret circularity at 50% and 20% length for each taxon and age-class. In one instance (infant distal humerus), the data were deemed not normally distributed following a Brown-Forsythe test and a Welch test. To control for variance in group size in this instance, shape comparisons were assessed with a Kruskal-Wallis H test. Coefficients of variation (CV%) were calculated to highlight intragroup shape variation.

2.3. Geometric morphometric analysis

To quantify periosteal contour form, 21 semilandmarks were placed equidistantly around the circumference of each 2D cross-sectional image, beginning at the anterior-most portion of the section, using tpsDig (Rohlf, 2015). To preserve lateral symmetry across the sample, images of all left elements were mirrored to reflect the right side prior to landmarking. The semilandmarks were slid along each digitized curve using tpsUtil (Rohlf, 2015), to minimize shape differences and spacing (Gunz and Mitteroecker, 2013). Models from each age class were checked for outliers by evaluating the theoretical and observed landmark distribution through comparisons of squared Mahalanobis distance—indicative of dissimilarity between individuals relative to the group (Klingenberg and Monteiro, 2005)−in MorphoJ (Klingenberg, 2011). Generalized Procrustes Analysis (GPA), a method used to superimpose objects upon each other to compare their shapes (Gower, 1975; Rohlf, 2015), was also performed using MorphoJ (Klingenberg,

2011) prior to further analysis (Figure 1). Multivariate regressions of Procrustes distance and the natural logarithm of centroid size (log CS) were used to define how much shape variation was attributed to size at each developmental stage. Specifically, allometry was presented as a percentage in each model by calculating the predicted sum of squares as a proportion of the total sum of squares (Klingenberg, 2016).

For the GM data, covariance matrices of the aligned Procrustes coordinates were created (Klingenberg and Spencer, 1993). Principal component analysis (PCA) was conducted for each taxon and element to compare shape variation at midshaft across each developmental stage, and between sexes among adults. Eigenvalues were <1.0 in each PCA, so Cattell's scree test informed which principal components (PCs) were most meaningful (Jackson, 1993). The first several PCs describe the majority of total variance (Jackson, 1993), while the first PC typically serves as the allometric shape component in single-species ontogenetic samples (Cobb and O'Higgins, 2004; Mitteroecker et al., 2004). Therefore, interspecific PC1 vectors were compared for a more comprehensive view of ontogenetic change than can be found comparing discrete age classes alone. Interspecific pairwise comparisons of vector angles ranging between 0° and 90° were conducted using MorphoJ (Klingenberg, 2011), where larger angles corresponded to greater ontogenetic divergence between taxa and smaller angles corresponded to a similar ontogenetic trajectory (Cobb and O'Higgins, 2004, 2007; Klingenberg and Marugán-Lobón, 2013). Canonical variate analyses (CVA) were also used to compare midshaft shape between taxa at each developmental stage, where permutation tests of 10,000 iterations determined significant differences of Procrustes distances between taxonomic groups.

3. Results

3.1. Intraspecific ontogeny of the humerus

Descriptive statistics of distal and mid-humeral circularity across development are given in Table 1. Coefficients of variation generally revealed a greater degree of shape variation at the distal diaphysis compared to midshaft. No intraspecific differences in shape (neither I_{max}/I_{min} or I_x/I_y) were identified among the hominids or macaques at the distal humerus across any developmental stage (Table 2). Only hylobatids exhibited distal humeral shape variation (I_x/I_y), with adults distributing significantly more bone mediolaterally compared to infants or juveniles (Table 2).

Unlike the distal humerus, varying degrees of developmental shape variation were identified at the humeral midshafts of gorillas, hylobatids and macaques (Table 3). Principal component analyses (Table 4; Figures 2 – 4) demonstrated that gorilla midshafts are more circular in infancy, becoming more ML-elliptical over development. Shape differences were also identified between sexes at the adult gorilla mid-humerus. Multivariate allometric regressions further established that size accounted for a significant degree of humeral midshaft shape variation in each taxon, although orangutans and gorillas showed a somewhat weaker allometric relationship than the other taxa (Table 5). A similar pattern was identified among chimpanzees following PCA, where a circular configuration in infancy gave way to a more ML-oriented midshaft in adulthood. The orangutan sample displayed the greatest developmental overlap in shape, where infant, juvenile and adult scatters were distributed relatively evenly across the first two PCs, indicative of a circular cross section spanning development. Compared to the hominids, infant hylobatids and macaques were both aligned on the high end of PC1, presenting more elliptical mid-humeri than their juvenile or adult counterparts.

3.2. Interspecific ontogeny of the humerus

No significant differences in distal humeral circularity were observed between the infant hominid subgroups or juvenile hominid subgroups in either the principal or anatomical planes (Table 6). Among adult hominids, the African apes each exhibited a similar shape configuration characterized by significantly more ML-oriented distal humeri compared to orangutans. No differences were observed between the three adult hominid taxa about the principal axes, however. Shape ratios further demonstrated that hylobatids possess significantly more circular distal humeri compared to any of the great apes, as well as macaques at any stage of their development. Mid-humeral shape about the principal axes did not differ between the five infant taxa (Table 6), though distribution about the anatomical axes revealed that infants were associated with either an approximately circular (gorillas and macaques) or AP-oriented (chimpanzees, orangutans and hylobatids) periosteal shape. Interspecific differences in shape were more pronounced in juveniles and adults.

Permutation tests of Procrustes distance are given in Table 7. Among the infant age classes, chimpanzee, orangutan and hylobatid mid-humeral shape did not significantly differ from one another but each differed from both gorillas and macaques. In alignment with the multiple comparison tests about the anatomical axes, GM analyses identified that hylobatids were distinguishable from the other taxa following infancy. Mid-humeral shape variation was greatest between adult subgroups, where the cross-sectional shape of each taxon differed significantly from each other apart from orangutans and chimpanzees, which overlapped at each developmental stage. Ontogenetic PC1 vector angles of the humeral midshaft are presented in Table 8. The size-range of the angles indicated that humeral midshaft shape change is highly variable over development. The smallest angle was formed between chimpanzees and orangutans, which exhibited a similar AP-oriented mid-humeral shape across all stages of development. The largest angle was formed between the hylobatids and macaques, which developed a relatively circular compared to ML-oriented mid-humerus, respectively. Shape trajectories between the hominids were smaller, ranging between 20.8° and 50.6°.

3.3. Intraspecific ontogeny of the femur

Descriptive statistics of distal and midshaft femoral circularity across development are given in Table 9. Like the humerus, intraspecific CV% at the distal diaphyses were generally greater than at midshaft within each taxon. The three hominid taxa exhibited ML-oriented distal femora that did not significantly deviate in shape about either the principal or anatomical axes at any developmental stage (Table 10). The distal femora of the hylobatid and macaque samples were also predominantly ML-oriented over their respective ontogenies, but shape varied between development stages. For instance, the hylobatid distal femur was significantly more circular among adults than infants while juvenile macaques exhibited a significantly more circular distal femur than infants (Table 10).

Shape variation was generally more pronounced at the femoral midshaft compared to the distal femur (Table 11). Across the sample, only adult gorillas revealed a sexually dimorphic shape signal, where males were associated with a significantly more ML-oriented mid-femur compared to females. Multivariate regressions of mid-femoral form underscored a positive allometric effect among the hominids, with size accounting for 17.2%–21.7% of midshaft shape variation (Table 5), greater than that in the humeral midshaft. Size had a smaller effect on shape among the hylobatids and macaques but allometry was also a statistically significant factor in the model for both taxa. Principal component analyses were aligned to the results derived from shape ratio analyses, demonstrating that all three hominid taxa transition from a relatively circular to ML-elliptical midshaft as they develop (Table 4; Figures 5–7). Comparatively, adult hylobatids and macaques possessed circular midshafts relative to infants. Among the gorillas and orangutans, sexual dimorphism was distinguishable along PC1 relative to the adult chimpanzee, hylobatid and macaque samples.

3.4. Interspecific ontogeny of the femur

Distal femoral circularity ratios were more effective at distinguishing taxa than mid-femoral ratios across development (Table 12). Among adult subgroups, the hominids each exhibited significantly more elliptical, ML-oriented distal femora compared to hylobatids or macaques. Moreover, distal femoral shape distinguished all three hominids at each stage of their development, in contrast to comparisons at the distal humerus. At the femoral midshaft, gorillas displayed significantly more ML-oriented cross sections than all other taxa over development (Table 12). Following Procrustes distance analysis at midshaft, mid-femoral shape was also found to vary significantly between all taxa at all developmental stages apart from the infant chimpanzee and orangutan subgroups, which exhibited comparatively circular midshafts (Table 7). While midshaft shape did not differ between infant chimpanzees and orangutans, juvenile and adult orangutan mid-femora were characterized by significantly more ML-oriented elliptical cross sections compared to chimpanzees.

Mid-femoral vector angles of PC1 ranged between 23.2° and 57.4° across the total ontogenetic sample (Table 8). Femoral trajectories did not resemble the angles formed in the humerus, in that they were generally smaller in range and size. Relatively small angles were formed between the sampled hominids. The chimpanzee-gorilla femoral angle was the smallest in the analysis, contrasting with the relatively large angles formed between both taxa at the mid-humerus.

4. Discussion

We investigated the ontogeny of hominoid and macaque limb cross-sectional shape and form both within and between taxa, as well as between limb elements. The results highlighted several distinct developmental strategies employed by the sampled taxa, contextualizing the relationship between long bone morphology and its association with locomotor ecology and body size. In alignment with our predictions, distal diaphyseal shape in both the humerus and femur exhibited relatively little change over development, regardless of phylogeny or locomotor behavior. An ontogenetically static distal cortex is likely a beneficial adaptation for transferring loads between limb elements in a manner similar to the function of articular surfaces and their adjacent epiphyses (Ruff and Runestad, 1992; Currey, 1984, 2002; Lazenby et al., 2008; Kivell, 2016), regardless of developmental stage. By comparison, regions exposed to greater bending loads, such as midshafts, more clearly reflect signals of posture or size in a given taxon, dependent on the element. While mid-humeral shape appears to be linked to locomotor transitions, the relationship between shape and behavior over development was not as apparent at the mid-femur, contra to our prediction. Instead, changes in femoral shape may more accurately reflect shifts in body mass over development. Similar to hominid craniofacial development (Cobb and O'Higgins, 2004), the sampled primates do not appear to share common limb ontogenies, or a common point of periosteal shape divergence for either bone. Rather, it appears that most interspecific limb morphological variation is established early in life and develops through adaptive and genetic pathways thereafter (Canington et al., 2018).

To the authors' knowledge, this is the first investigation of nonhuman primate diaphyseal shape and form using laser scanner-derived periosteal data. The laser scanning method used here is equally applicable to human and nonhuman primate postcrania, contingent on the capability of the scanner to accurately reproduce digital models of the periosteal contour (Davies et al., 2012). That said, a limiting factor of the method is the degree to which the variation of percent cortical area (%CA) may impact the predictive accuracy of second moment of area values, as the errors between solid- and true cross-sectional properties are a function of $\%CA^2$ (Sparacello and Pearson, 2010). It follows that the predictive accuracy of bone regions where cortical area is relatively small, such as at the distal femur, are most susceptible to error (Macintosh et al., 2013). While human humeral and femoral solid section values for shape (I_{max}/I_{min}) were supported by computed tomography (CT) comparisons at the same midshaft and distal locations studied here (Macintosh et al., 2013), the current study compared shape across an interspecific and ontogenetic sample of nonhuman primates, the %CA of which could vary considerably compared to a single homogeneous human population (Ruff et al., 1994; Shaw and Ryan, 2012). While the second moment of area shape analyses and GM analyses each evaluated periosteal solid section data, the findings of both approaches largely supported each other. The GM method was also able to reveal subtle shape patterns that went undetected by circularity ratios alone.

4.1. Intraspecific patterns of variation

Our results demonstrate that allometry is a critical component to the development of primate limb form, and that its effects are element-dependent. The relatively low shape variation (CV%) identified at both the mid-humerus and -femur compared to their respective distal cross sections may reflect the midshaft's adaptive capacity, irrespective of taxonomy or developmental stage. Indeed, prior research on diaphyseal strength and rigidity in modern human athletes identified less intragroup variation at long bone midshafts relative to epiphyses, suggesting that individuals who assume comparable locomotor profiles also exhibit a convergence around similar midshaft morphological characteristics (Nadell and Shaw, 2016). By comparison, the greater intraspecific distal shape CV% may better reflect body size variation or phenotypic factors not as closely related to load-induced bone modeling, as distal diaphyses are exposed to different forces than those at midshaft (Biewener and Taylor, 1986). While the present study did not compare midshaft and epiphyseal or metaphyseal shape, it is apparent that a similar pattern of convergence exists at midshaft relative to the distal diaphysis (20% length).

The more elliptical mid-humeri observed in juvenile and adult male gorillas maps onto increased terrestriality after infancy (Doran, 1997; Ruff et al., 2018. The sexual shape variation at the adult gorilla humeral midshaft may be accounted for by male-female locomotor differences as well. Both adult female mountain gorillas and western lowland gorillas spend more time in arboreal contexts than adult males (Kuroda, 1992; Remis, 1995, 1999; Doran, 1997); the relatively variable loading pattern of which may reinforce midshafts in multiple dimensions, supporting fairly unidirectional loading patterns like knuckle-walking, while also reinforcing the planes of bending brought on by multi-directional suspensory loads (but see Ruff et al., 2018 for an analysis of interlimb strength proportions in male and female gorillas). The influence of the deltoid tuberosity on shape at the gorilla midshaft may also impact dimorphic variation within the sample. By comparison, the transition from forelimb- to hindlimb-dominant locomotion between infant and adult chimpanzees (Doran, 1992a) was not exhibited by humeral shape, in agreement with previous findings demonstrating that chimpanzee mid-humeral shape is relatively static over development (Sarringhaus et al., 2016). Instead, a clearer chimpanzee ontogenetic signal may be reflected by femoral periosteal shape.

While allometry explained a statistically significant proportion of mid-humeral periosteal form among all of the sampled hominids, its effects were disproportionately greater at the mid-femur. Whether the allometric disparity between the humerus and femur is more a product of locomotor function or a body size effect can be addressed in light of each taxon's ecology. Among the hominids, the most pronounced developmental change in both humeral and femoral midshaft form was identified in chimpanzees. Chimpanzees are also characterized by a well-defined locomotor transition, from an arboreal, forelimb-driven posture, to a semi-arboreal and terrestrial, hindlimb-driven posture, in late infancy (Doran, 1997). The infant mid-humeral configuration exhibited some shape overlap with, but was easily distinguishable from both juvenile and adult patterns, implying a correspondence between locomotor pattern and midshaft morphology. If femoral morphology was impacted by locomotor behavior to the same extent, a similar adaptive pattern between infancy and juvenility would likely be discernible. Rather than mirroring the locomotor signals of the humerus, the timing of femoral midshaft shape change more closely corresponds to body size increases exclusive to *P. troglodytes* (Leigh and Shea, 1996). Male and female chimpanzees follow a highly similar growth trajectory until about eight years of age, when female growth velocity peaks (approximately 4kg per year), and males experience a growth spurt (approximately 8kg per year) (Leigh and Shea, 1996). Adopting an ML-oriented mid-femur late in juvenility may therefore provide an important means of body mass support to accommodate growth and postural change. Compared to chimpanzees, quadrupedalism already accounts for 56% of gorilla locomotor activity between 6–23 months of age while orangutans are capable of arboreal gap crossing maneuvers by the time they are one (albeit less frequently than juveniles and adults) (Doran, 1997; Chappell et al., 2015). The early adoption of these enduring positional behaviors in both taxa is reflected by the least mid-humeral size variance across the sample (8.1% in gorillas and 6.7% in orangutans; Table 5). Like chimpanzees though, gorillas and orangutans exhibit a pronounced allometric effect at the femoral midshaft, suggesting that increases in size rather than changes in posture may account for a high degree of variability in adult mid-femoral form. While the present study pooled infant gorillas (0 – 4 years) into a single group, the transition from more frequent suspensory to quadrupedal locomotion over development has been captured through limb strength comparisons of younger (0 – 2 years) and older (2 – 7 years) gorilla age groups (Ruff et al., 2018). An ontogenetic analysis of midshaft section moduli, second moments of area and cortical area across the sample could further explicate how diaphyses grow and adapt with respect to unique locomotor profiles (Ruff et al., 2013, 2018; Sarringhaus et al., 2016).

Gorillas and orangutans experience growth spurts earlier than chimpanzees while expressing greater dimorphic variability in growth duration and rate (Shea, 1983; Leigh, 1993; Leigh and Shea, 1995). Although their growth rates differ, both gorilla and orangutan males initiate a growth spurt around five years of age, while females of both taxa begin earlier (~4.5 years in gorillas; ~3.5 years in orangutans) (Leigh and Shea, 1995). These differences were reflected in analyses of femoral shape, where gorillas and orangutans exhibited a sexual dimorphic signal that chimpanzees did not. The early adoption of quadrupedal and suspensory behaviors in gorillas and orangutans, respectively, indicates that mid-femoral shape variation after infancy is unlikely an adaptation to a changing locomotor repertoire. The relationship between body size and femoral form can be expanded to the smaller-bodied hylobatids and macaques as well, which displayed the smallest allometric effect (5% and 7%, respectively). This observation is unsurprising among the hylobatids, which employ forelimb-driven brachiation above other forms of travel (50%–80% of locomotor time) (Fleagle, 1974; Michilsens et al., 2009), relying on the hindlimb to support their mass to a lesser extent than any hominid taxon. Though research on hylobatid locomotor ontogeny is limited, it has been established that locomotor independence is not achieved by infants until around two years of age in siamangs and gibbons (Harvey and Clutton-Brock, 1985; Lappan, 2009; Morino and Borries, 2016). While there is considerable overlap in humeral shape across hylobatid developmental stages, differences are still discernible between infants and the other developmental subgroups, suggesting that the acquisition of new locomotor techniques, or their increased intensity and frequency, may be expressed as physical signals in the humerus following infancy. Additional experimental and wild focal studies can confirm whether these observations are products of developmental locomotor adaptations. The small influence of size on shape in the hylobatid femur on the other hand, is more likely a product of the forelimb's greater weight-bearing role during brachiation and suspension (Fleagle and Lieberman, 2015).

Because terrestrial knuckle-walking places higher peak vertical forces on the hindlimb than the forelimb (Demes et al., 1994), it seems likely that hindlimb-driven primates such as adult African apes would adapt their femora to mitigate substrate reaction forces produced during terrestrial locomotion. However, it is evident that habitual quadrupeds such as macaques, which are also hindlimb-dominant locomotors (Wells and Turnquist, 2001), distribute cortical bone virtually equally between the AP and ML axes, producing a circular mid-femur in adulthood. Thus, mid-femoral ML-distribution may not be a broad adaptive solution to uniform quadrupedal loading. Compared to midshafts, distal diaphyses experience less bending during locomotion (Biewener and Taylor, 1986), and thus, were predicted to maintain rather than adapt their shape to support adjacent synovial joints (Currey, 1984; Ruff and Runestad, 1992). Accordingly, results from periosteally-derived data demonstrate that distal diaphyseal sections do not adapt their cortical shape to the same extent as midshaft sections, likely due to constraints on their periosteal morphology associated with their relative proximity to articular surfaces. Instead, changes in size rather than shape appear to be more adaptive to changing mechanical loads in these areas.

4.2. Interspecific patterns of variation

Analysis of adult orangutan and gorilla mid-humeral circularity (I_{max}/I_{min}) initially determined that despite their distinctly different locomotor profiles and ecologies, the two genera overlapped in shape, in agreement with previous findings (Carlson, 2005; Patel et al., 2013). However, the inclusion of I_x/I_y ratios revealed that orangutans distribute significantly more bone in the AP plane, compared to the ML distribution found in gorillas, distinguishing the genera by mid-humeral shape. This finding further demonstrates that cross-sectional circularity is an effective indicator of behavior when paired with information on bone distribution in both the principal and anatomical planes. As such, using both ratios together can delineate fine differences in bone distribution, rather than relying on a single ratio as a general index of circularity.

While mid-humeral morphology across infant taxa is more comparable than in adulthood, the variation that is present appears to reflect more of a locomotor than phylogenetic signal, in support of previous findings in human and nonhuman primates (Stock, 2006; Buck et al., 2010). From infancy, both chimpanzees and orangutans feature relatively circular mid-humeri which may facilitate an arboreal lifestyle. Chimpanzees are not completely adapted to either arboreal or terrestrial locomotion (Rose, 1991), though both are important components of their daily active periods (Hunt, 1991, 1992; Fleagle, 1999), especially among infants (Doran, 1997). Even after chimpanzees transition to a more terrestrial lifestyle following infancy (Doran, 1997), vertical climbing remains a more energy efficient form of locomotion than terrestrial travel (Pontzer and Wrangham, 2004), emphasizing the importance of arboreality to their positional repertoire. The dynamic loads associated with suspension and climbing appear to govern chimpanzee and orangutan cross-sectional humeral morphology into adulthood, even after chimpanzees adopt a more terrestrial lifestyle. If humeral cross-sectional shape were more a product of phylogeny, the gorilla condition would be expected to bear some resemblance to chimpanzees, at least in infancy.

While evaluating whether these morphological differences are a genetic or epigenetic phenomenon is beyond the scope of this study, trajectory analyses of hominoid postcranial shape suggests that behavioral and developmental plasticity each play important roles in ontogeny (Turley et al., 2018).

To determine if a similar shared suspensory signal existed in the femur as it did in the humerus, the adult chimpanzee sample was compared to the adult orangutans. Unlike the close shape overlap found at their humeral midshafts across development, femoral midshaft shape differed significantly between the taxa, highlighting that the two long bones do not reflect the same adaptive signals. Furthermore, hylobatid and macaque mid-femoral shape did not vary between samples at any stage, despite the distinctly different locomotor strategies they evolved (Fleagle, 1976; Cant, 1988). Thus, mid-femoral morphology may be a stronger indicator of intraspecific locomotion, as demonstrated between human populations (Larsen, 2002; Stock and Pfeiffer, 2001, 2004) and primate subspecies (Carlson, 2002, 2005; Ruff et al., 2013), and a better indicator of size in broad generic comparisons. Subsequent studies of interlimb strength proportions could further clarify the functional roles of the humerus and femur among the ontogenetic series.

Femoral ontogenetic trajectories also formed relatively small vector angles compared to the humerus and did not delineate any clear interspecific locomotor signals. While chimpanzees and gorillas generated a smaller angle at the mid-femur than at the mid-humerus, their trajectory was still significantly different, consistent with the foundation of their independent evolutionary histories and locomotor adaptations (Kivell and Schmitt, 2009; Morimoto et al., 2018). From an ontogenetic standpoint, primate skeletons are mosaics, with each limb element indicating different adaptive signals at different developmental stages. For instance, humeral and femoral form follow a relatively similar ontogenetic trajectory among chimpanzees and orangutans (humerus = 20.8°;

femur = 28.1°), whereas the same comparison between chimpanzees and gorillas (humerus = 50.6°; femur = 23.2°) demonstrates that the fore- and hindlimbs develop in distinctly different ways. To place this disparity in perspective, the craniofacial development of close relatives like chimpanzees and bonobos yield an angle of approximately 22° (Cobb and O'Higgins, 2004), suggesting that even highly genetically canalized structures of like-species develop and adapt along unique trajectories.

5. Conclusions

This research further contextualizes the relationship between diaphyseal morphology and its association with locomotor ecology and body size, through intra- and interspecific comparisons. It is apparent that limb development is not only highly variable between taxa over ontogeny but at discrete locations of skeletal elements. Overall, distal cross sections of the humeral and femoral periosteal contour appear more adaptively constrained across ontogenetic stages, irrespective of posture or size. Adapting size rather than shape over development enables distal diaphyseal cortices to support congruent joint surfaces, while transferring loads between them (Ruff and Runestad, 1992), all without undergoing the structural changes that regions prone to bending otherwise might. By comparison, adaptive signals varied widely between humeral and femoral midshafts. Specifically, locomotor signals more closely corresponded to mid-humeral morphology, while signals of pubertal shifts in body mass better explained mid-femoral morphology, especially among hominids. Applying GM methods to midshaft cross sections successfully distinguished shape between age-classes and taxa, building upon prior research (Wilson and Humphrey, 2015; Morimoto et al., 2018) and complementing traditional beam modeling methods.

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Conflict of Interest Statement

The authors of this research article have no conflict of interest to declare.

References

Alba DM, Moyà-Solà S, Almécija S. 2011. A partial hominoid humerus from the middle miocene of Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). Am J Phys Anthropol 144:365–381.

Almécija S, Tallman M, Alba DM, et al. 2013. The femur of Orrorin tugenensis exhibits morphometric affinities with both Miocene apes and later hominins. Nat Commun. 4:2888.

Asensio N, José-Domínguez JM, Kongrit C, Brockelman WY. 2017. The ecology of white-handed and pileated gibbons in a zone of overlap and hybridization in Thailand. Am J Phys Anthropol:716–728.

Baab KL, McNulty KP. Size, shape, and asymmetry in fossil hominins: the status of the LB1 cranium based on 3D morphometric analyses. 2009. J Hum Evol. 57(5):608-622.

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

Bartlett TQ. 2007. The Hylobatidae: small apes of Asia. In CJ Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder (eds.) Primates in perspective, pp. 274–289. Oxford: Oxford University Press.

Bertram JE, Swartz SM. 1991. The 'law of bone transformation': a case of crying Wolff? Biol. Rev. 66(3):245-73.

Biewener AA. 1982. Bone Strength In Small Mammals And Bipedal Birds: Do Safety Factors Change With Body Size? J Exp Biol 98:289–301.

Biewener AA, Taylor CR. 1986. Bone strain: a determinant of gait and speed? J Exp Biol 123:383–400.

Breuer T, Breuer-Ndoundou Hockemba M, Olejniczak C, Parnell RJ, Stokes EJ. 2009. Physical maturation, life-history classes and age estimates of free-ranging western gorillas — insights from Mbeli Bai, Republic of Congo. Am J Primatol 71:106–119.

Buck LT, Stock JT, Foley RA. 2010. Levels of Intraspecific Variation Within the Catarrhine Skeleton. Int J Primatol 31:779–795.

Burgess ML, Schmitt D, Zeininger A, McFarlin SC, Zihlman AL, Polk JD, Ruff CB. 2016. Ontogenetic scaling of fore limb and hind limb joint posture and limb bone cross-sectional geometry in vervets and baboons. Am J Phys Anthropol. 161(1):72-83.

Burns BL, Judge DS. 2016. The varied path to adulthood: Plasticity in developmental timing in hylobatids. Am J Primatol. 78(6):610-625.

Burr DB, Ruff CB, Johnson C. Structural adaptations of the femur and humerus to arboreal and terrestrial environments in three species of macaque. 1989. Am J Phys Anthropol. 79(3):357-367.

Canington SL, Sylvester AD, Burgess ML, Junno JA, Ruff CB. 2018. Long bone diaphyseal shape follows different ontogenetic trajectories in captive and wild gorillas. Am J Phys Anthropol. 167(2):366–376.

Cant JGH. 1987. Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (Pongo pygmaeus). Am J Phys Anthropol 74:143–148.

Cant JG. 1988. Positional behavior of long-tailed macaques (Macaca fascicularis) in northern Sumatra. Am J Phys Anthropol 76:29–37.

Cardini A, Elton S. 2008a. Variation in guenon skulls (I): species divergence, ecological and genetic differences. J Hum Evol. 54(5):615-637.

Cardini, A. and Elton, S., 2008b. Variation in guenon skulls (II): sexual dimorphism. J Hum Evol. 54(5):638-647.

Carlson KJ. 2002. Shape and material properties of African pongid femora and humeri: their relationship to observed positional behaviors. Ph.D. dissertation, Indiana University, Bloomington.

Carlson KJ. 2005. Investigating the form-function interface in African apes: Relationships between principal moments of area and positional behaviors in femoral and humeral diaphyses. Am J Phys Anthropol 127:312–34.

Carlson KJ, Judex S. 2007. Increased non-linear locomotion alters diaphyseal bone shape. J Exp Biol 210:3117–3125.

Channon AJ, Crompton RH, Günther MM, D'Août K, Vereecke EE. 2010. The biomechanics of leaping in gibbons. Am J Phys Anthropol 143:403–416.

Chappell J, Phillips AC, Van Noordwijk MA, Setia TM, Thorpe SKS. 2015. The ontogeny of gap crossing behaviour in bornean orangutans (*Pongo pygmaeus wurmbii*). PLoS One 10:1–15.

Cheverud JM. 1981. Epiphyseal union and dental eruption in *Macaca mulatta*. Am J Phys Anthropol. 56(2):157-167.

Cobb SN, O'Higgins P. 2004. Hominins do not share a common postnatal facial ontogenetic shape trajectory. J Exp Zool Part B, Mol Dev Evol 302:302–321.

Cobb SN, O'Higgins P. The ontogeny of sexual dimorphism in the facial skeleton of the African apes. J Hum Evol. 2007. 53(2):176-190.

Currey J. 1984. The Mechanical Adaptations of Bones. Princeton: Princeton University Press.

Currey JD. 2002. Bones: Structure and Mechanics. Princeton Univ Press, Princeton. pp. 28-79.

Dainton M, Macho GA. 1999. Did knuckle walking evolve twice? J Hum Evol. 36(2):171-194.

Davies TG, Shaw CN, Stock JT. 2012. A test of a new method and software for the rapid estimation of cross-sectional geometric properties of long bone diaphyses from 3D laser surface scans. Archaeol Anthropol Sci 4:277–290.

Demes B, Jungers WL. Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. 1993. J Hum Evol 25(1):57-74.

Demes B, Larson SG, Stern JT, Jungers WL, Biknevicius AR, Schmitt D. 1994. The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. J Hum Evol 26:353–374.

Demes B, Qin YX, Stern Jr JT, et al. 2001. Patterns of strain in the macaque tibia during functional activity. Am J Phys Anthropol. 116(4):257-265.

Dirks W, Bowman JE. 2007. Life history theory and dental development in four species of catarrhine primates. J Hum Evol 53:309–20.

Doran DM. 1992a. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. Journal of Human Evolution 23:139–157.

Doran DM. 1992b. Comparison of instantaneous and locomotor bout sampling methods: a case study of adult male chimpanzee locomotor behavior and substrate use. American Journal of Physical Anthropology 89:85–99.

Doran DM. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. J Hum Evol 32:323–344.

Doran DM, Hunt KD. 1994. Comparative locomotor behavior of chimpanzees and bonobos: Species and habitat differences. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds.), Chimpanzee cultures pp. 93–106. Cambridge, MA: Harvard University Press.

Doran-Sheehy D, Andrianady M, Lodwick J. 2009. Sex differences in western gorilla arboreality. Am. J. Phys. Anthropol. Vol 48 S, 120.

Dunbar DC, Badam GL. 1998. Development of posture and locomotion in free-ranging primates. Neurosci Biobehav Rev. 22(4):541-546.

Fleagle JG. 1974. Dynamics of a brachiating siamang [Hylobates (*Symphalangus*) syndactylus]. Nature 248:259–260.

Fleagle JG. 1976. Locomotion and Posture of the Malayan Siamang and Implications for Hominoid Evolution. Folia Primatol 26:245–269.

Fleagle JG. 1980. Locomotion and posture. In: Chivers, DJ (ed.) Malayan Forest Primates: Ten Years' Study in Tropical Rain Forests. Plenum Press, New York, pp. 191-209.

Fleagle JG. 1999. Primate Adaptation and Evolution (Academic Press, New York). 15.

Fleagle JG, Lieberman DE. 2015. Major Transformations in the Evolution of Primate Locomotion. In: Great Transformations in Vertebrate Evolution. 1st ed. London: University of Chicago Press. p 257–282.

Gower JC. 1975. Generalised Procrustes analysis. Psychmetrika 40:33–50.

Gunz P, Mitteroecker P. 2013. Semilandmarks: A method for quantifying curves and surfaces. Hystrix 24:103–109.

Harvey PH, Clutton-Brock TH. 1985. Life History Variation in Primates. Soc Study Evol 39:559–581.

Hens SM. 2005. Ontogeny of craniofacial sexual dimorphism in the orangutan (Pongo pygmaeus). I: face and palate. Am J Primatol 65(2):149-166.Hsieh Y, Robling AG, Ambrosius WT, Burr DB, Turner CH. 2001. Mechanical Loading of Diaphyseal Bone In Vivo : The Strain Threshold for an Osteogenic Response Varies with Location. J Bone Miner Res 16:2291–2297.

Huiskes R. 1982. On the modeling of long bones in structural analyses. J Biomech 15:65–69.

Hunt KD. 1991. Positional behavior in the Hominoidea. Int J Primatol 12, 95–118.

Hunt KD. 1992. Positional Behavior of Pan Troglodytes in the Mahale Mountains and Gombe

Stream National Parks, Tanzania. Am J Phys Anthropol 87:83–105.

Hunt KD. 2004. The special demands of great ape locomotion and posture. In: Russon AE, Begun DR, editors. The evolution of thought: evolutionary origins of great ape intelligence. Cambridge: Cambridge University Press. p 172–189.

Hunt KD. 2016. Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. J Anat 228:630–685.

Ito T, Nishimura TD, Hamada Y, et al. 2015. Contribution of the maxillary sinus to the modularity and variability of nasal cavity shape in Japanese macaques. Primates. 56(1):11-9.

Jackson DA. 1993. Stopping Rules in Principal Components Analysis : A Comparison of Heuristical and Statistical Approaches Stable. Stat Approaches 74:2204–2214.

Jungers WL, Susman RL. 1984. Body size and skeletal anatomy in the African apes. In: RL Susman (ed.) The Pygmy Chimpanzee: Evolutionary Biology and Behavior. New York: Plenum Press.

Jungers WL, Hartmann SE. 1988. Relative growth of the locomotor skeleton in orang-utans and other large-bodied hominoids. In: Schwartz JH (ed.) Orang-utan Biology, pp. 347–359.

Jungers WL, Godfrey LR, Simons EL, et al. 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP (eds.) Reconstructing Behavior in the Primate Fossil Record. Kluwer Academic/Plenum Publishers, New York, pp. 371-411.

Ki-Kydd K, Piper PJ. 2004. Identification of morphological variation in the humeri of Bornean primates and its application to zooarchaeology. Archaeofauna. 13(85):e95.

Kimura T. 1992. Hindlimb dominance during primate high-speed locomotion. Primates 33: 465–476.

Kimura T. Kinesiological characteristics of primate walking. Environment, behavior, and morphology: Dynamic interactions in primates. 1979:297-311.

Kivell TL, Schmitt D. 2009. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. Proc Natl Acad Sci USA 106(34):14241-14246.

Kivell TL 2016. A review of trabecular bone functional adaptation: what have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? J Anat. 228, 569-594.

Klingenberg CP. 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol. Ecol. Resour. 11, 353–357.

Klingenberg CP. 2016. Size, shape, and form: concepts of allometry in geometric morphometrics. Dev Genes Evol. 226(3):113-137.

Klingenberg CP, Spence JR. 1993. Heterochrony and allometry: lessons from the water strider genus *Limnoporus*. Evolution (NY) 47:1834–1853.

Klingenberg CP, Monteiro LR. 2005. Distances and directions in multidimensional shape spaces: implications for morphometric applications. Syst Biol 54:678–688.

Klingenberg CP, Marugán-Lobón J. 2013. Evolutionary covariation in geometric morphometric data: analyzing integration, modularity, and allometry in a phylogenetic context. Syst Biol. 62(4):591-610.

Kontulainen S, Sievänen H, Kannus P, Pasanen M, Vuori I. 2003. Effect of long-term impact-loading on mass, size, and estimated strength of humerus and radius of female racquet-sports players: a peripheral quantitative computed tomography study between young and old starters and controls. J Bone Miner Res. 18(2):352-359.

Kuroda S. 1992. Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabale Reserve, Northern Congo. In Itoigawa N, Sugiyama Y, Sackett G, Thompson RKR (eds.), Topics in Primatology. vol. 2: Behavior, Ecology and Conservation, pp 385–394. Tokyo: University of Tokyo Press.

Lanyon L. 1987. Functional Strain In Bone Tissue As An Objective And Controlling Stimulus For Adaptive Bone Remodelling. J Biomech 20:1083–1093.

Lappan S. 2009. The effects of lactation and infant care on adult energy budgets in wild siamangs (*Symphalangus syndactylus*). Am J Phys Anthropol, 140, 290–301.

Lazenby RA, Cooper DM, Angus S, et al. 2008. Articular constraint, handedness, and directional asymmetry in the human second metacarpal. J Hum Evol. 54(6):875-885.

Lordkipanidze D, de León MS, Margvelashvili A, et al. 2013. A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. Science. 342(6156):326-31.

Leigh SR. 1992. Patterns of variation in the ontogeny of primate body size dimorphism. J Hum Evol 23:27–50.

Leigh SR. 1993. Ontogeny and body size dimorphism in extant hominoid primates. Am J Phys Anthropol Suppl. 16:133.

Leigh SR, Shea BT. 1995. Ontogeny and the evolution of adult body size dimorphism in apes. Am J Primatol 36:37–60.

Leigh SR, Shea BT. 1996. Ontogeny of body size variation in African apes. Am J Phys Anthropol 99:43–65.

Leigh SR, Blomquist GE. 2011. Life history. In Campbell CJ. Primates in perspective, pp. 418-428, New York: Oxford University Press.

Lieberman DE. How and why humans grow thin skulls: experimental evidence for systemic cortical robusticity. 1996. Am J Phys Anthropol. 101(2):217-36.

Lieberman DE, Pearson OM, Polk JD, Demes B, Crompton AW. 2003. Optimization of bone growth and remodeling in response to loading in tapered mammalian limbs. J Exp Biol

206:3125–3138.

Lockwood CA, Lynch JM, Kimbel WH. 2002. Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. J Anat. 201(6):447-464.

Lovejoy CO, McCollum MA, Reno PL, Rosenman BA. 2003. Developmental Biology and Human Evolution. Annu Rev Anthropol 32:85–109.

Macintosh AA, Davies TG, Ryan TM, Shaw CN, Stock JT. 2013. Periosteal versus true cross-sectional geometry: a comparison along humeral, femoral, and tibial diaphyses. Am J Phys Anthropol 150:442–452.

Macintosh AA, Stock JT. 2019. Intensive terrestrial or marine locomotor strategies are associated with inter- and intra-limb bone functional adaptation in living female athletes. Am J Phys Anthropol. 168:566-581.

Marchi D. 2007. Relative strength of the tibia and fibula and locomotor behavior in hominoids. J Hum Evol. 53(6):647-655.

Marchi D. 2015. Variation in tibia and fibula diaphyseal strength and its relationship with arboreal and terrestrial locomotion: extending the investigation to non-hominoid primates. J Anthropol Sci. 20;93:1-4.

Marchi D, Ruff CB, Capobianco A, et al. 2016. The locomotion of Babakotia radofilai inferred from epiphyseal and diaphyseal morphology of the humerus and femur. J Morphol. 277(9):1199-1218.

Marchi D, Harper CM, Chirchir H, et al. 2019. Relative fibular strength and locomotor behavior in KNM-WT 15000 and OH 35. 2019. J Hum Evol 131:48-60.

Masi S. 2004. Tree use by a western gorilla group (*Gorilla gorilla gorilla*) in the Dzanga-Ndoki National Park, Central African Republic. Folia Primatol. 75, 385–414.

Michilsens F, Vereecke EE, D'Août K, Aerts P. 2009. Functional anatomy of the gibbon forelimb: Adaptations to a brachiating lifestyle. J Anat 215:335–354.

Mitteroecker P, Gunz P. 2009. Advances in Geometric morphometrics. Evol Biol 36:235–247.

Mitteroecker P, Gunz P, Bernhard M, et al. 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. J Hum Evol 46:679–698.

Mongle CS, Wallace IJ, Grine FE. 2015. Cross-sectional structural variation relative to midshaft along hominine diaphyses. I. The forelimb. Am J Phys Anthropol. 158:386-397.

Morimoto N, De León MSP, Zollikofer CPE. 2011. Exploring Femoral Diaphyseal Shape Variation in Wild and Captive Chimpanzees by Means of Morphometric Mapping: A Test of Wolff's Law. Anat Rec 294:589–609.

Morimoto N, Nakatsukasa M, de León MS, Zollikofer CP. Femoral ontogeny in humans and great apes and its implications for their last common ancestor. 2018. Sci Rep. 8:1930.

Morino L, Borries C. 2016. Offspring loss after male change in wild siamangs: The importance of abrupt weaning and male care. Am J Phys Anthropol:180–185.

Nadell JA, Shaw CN. 2016. Phenotypic plasticity and constraint along the upper and lower limb diaphyses of Homo sapiens. Am J Phys Anthropol 422:410–422.

Nicholson CL, Firth EC. 2010. Assessment of bone response to conditioning exercise in the radius and tibia of young thoroughbred horses using pQCT. J Musculoskelet Neuronal Interact 10:199–206.

Ohman JC. 1993. Computer software for estimating cross-sectional geometric properties of long bones with concentric and eccentric elliptical models. J Hum Evol 25:217–227.

Palombit RA. 1994. Dynamic pair bonds in hylobatids: Implications regarding monogamous social systems. Behaviour 128:65–101.

Patel BA. 2005. The hominoid proximal radius: re-interpreting locomotor behaviors in early hominins. J Hum Evol. 48(4):415-432.

Patel BA. 2009. Not so fast: speed effects on forelimb kinematics in cercopithecine monkeys and implications for digitigrade postures in primates. Am J Phys Anthropol. 140(1):92-112.

Patel BA, Ruff CB, Simons ELR, Organ JM. 2013. Humeral cross-sectional shape in suspensory primates and sloths. Anat Rec 296:545–56.

Pearson OM, Lieberman DE. 2004. The aging of Wolff's "law": ontogeny and responses to mechanical loading in cortical bone. Am J Phys Anthropol. 125(S39):63-99.

Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. J Hum Evol 46(3):315-333.

Püschel TA, Sellers WI. 2016. Standing on the shoulders of apes: analyzing the form and function of the hominoid scapula using geometric morphometrics and finite element analysis. Am J Phys Anthropol. 159(2):325-41.

Püschel TA, Marcé-Nogué J, Gladman JT, et al. 2018. Inferring locomotor behaviours in Miocene New World monkeys using finite element analysis, geometric morphometrics and machine-learning classification techniques applied to talar morphology. J R Soc Interface. 15:20180520.

Rawlinson SC, Mosley JR, Suswillo RF, et al. 1995. Calvarial and limb bone cells in organ and monolayer culture do not show the same early responses to dynamic mechanical strain. J Bone Miner Res. 10(8):1225-32.

Remis MJ. 1995. The effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. Amer. J. Phys. Anthropol., 97: 413-433.

Remis M. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. Primates 40:383–396.

Robling AG, Castillo AB, Turner CH. 2006. Biomechanical and Molecular Regulation of Bone

Remodeling. Annu Rev Biomed Eng 8:455–498.

Rohlf FJ. 2015. The tps series of software. Hystrix, Ital J Mammal 26:9–12.

Rose MD. 1983. Miocene Hominoid Postcranial Morphology; Monkey-like, Ape-like, Neither, or Both? In: Ciochon, RL, Corruccini RS (ed.). New Interpretations of Ape and Human Ancestry. 1st Edition, pp. 405–413. New York: Springer.

Rose MD. 1991. The process of bipedalization in hominids. In: Senut B, Coppens Y (eds.) Origines de la bipedie chez les Hominides. pp. 37–48. Paris: CNRS.

Ruff C. 1988. Hindlimb articular surface allometry in Hominoidea and Macaca, with comparisons to diaphyseal scaling. J Hum Evol. 17(7):687-714.

Ruff CB. 2002. Long bone articular and diaphyseal structure in old world monkeys and apes. I: locomotor effects. Am J Phys Anthropol 119:305–42.

Ruff C. 2003. Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. J Hum Evol. 45(4):317-349.Ruff CB, Runestad JA. 1992. Primate Limb Bone Structural Adaptations. Annu Rev Anthropol 21:407–433.

Ruff CB, Walker A, Trinkaus E. 1994. Postcranial robusticity in Homo. III: ontogeny. Am J Phys Anthropol. 93(1):35-54.

Ruff CB, Burgess ML, Bromage TG, Mudakikwa A, McFarlin SC. 2013. Ontogenetic changes in limb bone structural proportions in mountain gorillas (*Gorilla beringei beringei*). J Hum Evol 65:693–703.

Ruff CB, Burgess ML, Junno JA, Mudakikwa A, Zollikofer CP, Ponce de León MS, McFarlin SC. 2018. Phylogenetic and environmental effects on limb bone structure in gorillas. Am J Phys Anthropol. 166:353-372.

Ruff CB, Harper CM, Goldstein DM, Daegling DJ, McGraw WS. 2019. Long bone structural proportions and locomotor behavior in Cercopithecidae. J Hum. 132:47-60.

Sarringhaus LA, Maclatchy LM, Mitani JC. 2014. Locomotor and postural development of wild chimpanzees. J Hum Evol. 66:29–38.

Sarringhaus LA, MacLatchy LM, Mitani JC. 2016. Long bone cross-sectional properties reflect changes in locomotor behavior in developing chimpanzees. Am J Phys Anthropol 60:16-29.

Schaffler MB, Burr DB, Jungers WL, Ruff CB. 1985. Structural and mechanical indicators of limb specialization in primates. Folia Primatol (Basel) 45:61–75.

Schmitt D. 2003. Mediolateral reaction forces and forelimb anatomy in quadrupedal primates: Implications for interpreting locomotor behavior in fossil primates. J Hum Evol 44:47–58.

Schneider K, Zernicke RF. 1992. Mass, center of mass, and moment of inertia estimates for infant limb segments. J Biomech. 25(2):145-148.

Schultz AH. 1924. Growth studies on primates bearing upon man's evolution. Am J Phys Anthropol. 7(2):149-64.

Shaw CN, Ryan TM. 2012. Does skeletal anatomy reflect adaptation to locomotor patterns? Cortical and trabecular architecture in human and nonhuman anthropoids. Am J Phys Anthropol 147(2), 187-200.

Shaw CN, Stock JT. 2009. Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. Am J Phys Anthropol 140:149–59.

Shea BT. 1983. Allometry and heterochrony in the African apes. Am J Phys Anthropol 62:275–89.

Shea BT. 1985. The ontogeny of sexual dimorphism in the African Apes. Am J Primatol 8:183–188.

Siegal ML, Bergman A. 2002. Waddington's canalization revisited: developmental stability and evolution. Proc Natl Acad Sci USA 99:10528–10532.

Simmen B, Darlu P, Hladik CM, Pasquet P. 2015. Scaling of free-ranging primate energetics with body mass predicts low energy expenditure in humans. Physiol. Behav. 138:193–99.

Skedros JG, Sybrowsky CL, Parry TR, Bloebaum RD. 2003. Regional differences in cortical bone organization and microdamage prevalence in Rocky Mountain mule deer. Anat Rec A Discov Mol Cell Evol Biol 274:837–50.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–59.

Smith BH, Crummett TL, Brandt KL. 1994. Ages of Eruption of Primate Teeth: A Compendium for Aging Individuals and Comparing Life Histories. Yearb Phys Anthropol 37:177–231.

Smith BH, Boesch C. 2011. Mortality and the magnitude of the "wild effect" in chimpanzee tooth emergence. J Hum Evol 60:34–46.

Smith TM, Machanda Z, Bernard AB, Donovan RM, Papakyrikos AM, Muller MN, Wrangham R. First molar eruption, weaning, and life history in living wild chimpanzees. 2013. PNAS. 19:2787-2791.

Smith AL, Benazzi S, Ledogar JA, et al. 2015. Biomechanical implications of intraspecific shape variation in chimpanzee crania: moving toward an integration of geometric morphometrics and finite element analysis. Anat Rec. 298(1):122-144.

Sparacello VS, Pearson OM. 2010. The importance of accounting for the area of the medullary cavity in cross-sectional geometry: a test based on the femoral midshaft. Am J Phys Anthropol. 143(4):612-624.

Stock J, Pfeiffer S. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. Am J Phys Anthropol 115:337–48.

Stock JT, Pfeiffer SK. 2004. Long bone robusticity and subsistence behaviour among Later StoneAge foragersofthe forest andfynbosbiomes of South Africa. JArch Sci 31(7):999–1013.

Sugardjito J, van Hooff J. 1986. Sex–age class differences in positional behavior of Sumatran orangutan (*Pongo pygmaeus abelii*) in Gunung Leuser National Park, Indonesia. Folia Primatol 47, 14–25.

Swartz SM, Bertram JE, Biewener AA. 1989. Telemetered in vivo strain analysis of locomotor mechanics of brachiating gibbons. Nature. 342(6247):270.

Tallman M, Almécija S, Reber SL, et al. 2013. The distal tibia of *Hispanopithecus laietanus*: more evidence for mosaic evolution in Miocene apes. J Hum Evol. 64(5):319-327.

Terhune CE, Robinson CA, Ritzman TB. 2014. Ontogenetic variation in the mandibular ramus of great apes and humans. Journal of morphology. 275(6):661-677.

Thorpe SK, Crompton RH, Günther MM, Ker RF, McNeill Alexander R. 1999. Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (*Pan troglodytes*). Am J Phys Anthropol. 110:179–99.

Thorpe SK, Crompton RH. 2005. Locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modelling. Am J Phys Anthropol. 127(1):58-78.

Thorpe SKS, Crompton RH. 2006. Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea. Am J Phys Anthropol. 131(3):384-401.

Turley K, Simons EA, Frost SR. Trajectory analysis among African hominoids can provide insights into genetic and epigenetic influences during ontogeny. 2018. Am J Phys Anthropol. 167:173-177.

Turnquist JE, Kessler MJ. 1989. Free-ranging Cayo Santiago rhesus monkeys (*Macaca mulatta*): I. Body size, proportion, and allometry. Am J Primatol. 19(1):1-3.

Turnquist JE, Wells JP. 1994. Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. J Hum Evol. 26(5-6):487-499.

van Adrichem GG, Utami SS, Wich SA, van Hooff JA, Sterck EH. 2006. The development of wild immature Sumatran orangutans (Pongo abelii) at Ketambe. Primates. 47(4):300-9.

Venkataraman VV, Kraft TS, Dominy NJ. Tree climbing and human evolution. 2013. PNAS. 110(4):1237-1242.

Vereecke EE, Channon AJ. 2013. The role of hind limb tendons in gibbon locomotion: springs or strings? J Exp Biol 216:3971–3980.

Wallace IJ, Middleton KM, Lublinsky S, Kelly SA, Judex S, Garland Jr T, Demes B. 2010. Functional significance of genetic variation underlying limb bone diaphyseal structure. Am J Phys Anthropol. 143(1):21-30.

Watts DP. 1991. Mountain gorilla reproduction and sexual behavior. Am J Primatol. 24(3-4):211-

225.

Wells JP, Turnquist JE. 2001. Ontogeny of locomotion in rhesus macaques (Macaca mulatta): II. Postural and locomotor behavior and habitat use in a free-ranging colony. Am J Phys Anthropol. 115(1):80-94.

Wilson LAB, Humphrey LT. 2015. A Virtual geometric morphometric approach to the quantification of long bone bilateral asymmetry and cross-sectional shape. Am J Phys Anthropol 158(4), 541-556.

Wintheiser J, Clauser D, Tappen N. 1977. Sequence of eruption of permanent teeth and epiphyseal union in three species of African monkeys. Folia Primatol 27:178–197.

Young JW, Shapiro LJ. Developments in development: What have we learned from primate locomotor ontogeny? 2018. Am J Phys Anthropol. 165:37-71.

Young JW, Ferna D, Fleagle JG. 2010. Ontogeny of long bone geometry in capuchin monkeys (*Cebus albifrons* and *Cebus apella*): implications for locomotor development and life history. Biol Lett 6:197–200.

Zelditch ML, Swiderski DL, Sheets H.D. 2012. Geometric Morphometrics for Biologists: a primer (Second Edition). Academic Press.

Figure Captions:

Figure 1. The 21 semilandmarks of the adult (aggregate) mid-femur following Procrustes superimposition and sliding. The large blue dots and their corresponding red numbers depict the semilandmark position of the cumulative reference configuration, the small grey dots surrounding them depict the semilandmark positions of each specimen in the sample.

Figure 2. Scatter plot of chimpanzee (top) and gorilla (bottom) humeral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.

Figure 3. Scatter plot of orangutan (top) and hylobatid (bottom) humeral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.

Figure 4. Scatter plot of macaque humeral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.

Figure 5. Scatter plot of chimpanzee (top) and gorilla (bottom) femoral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.

Figure 6. Scatter plot of orangutan (top) and gorilla (bottom) femoral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.

Figure 7. Scatter plot of macaque femoral periosteal midshaft developmental variation projected onto PC1 and PC2 in shape space. Wireframes along the axes represent shape variation; the light blue outlines depict shape at the low ends of their respective axes and the dark blue outlines depict the high ends.