Cross-Sectional Structural Variation Relative to Midshaft Among Hominine Diaphyses. II. The Hind Limb

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ABSTRACT Objectives: In comparative analyses of hominine hind limb diaphyseal structure, homologous cross sections are located according to half bone length (midshaft). Here, we address three questions. First, how accurately must midshaft be defined to yield comparable data? Second, does variation in midshaft location due to different ways of measuring length fall within error ranges such that data gathered using different metrics are comparable? Third, do error ranges and length metric ranges such that data gathered using different methods accurately must midshaft be defined to yield comparable data? Second, does variation in midshaft location due to different definitions of bone length fall within error ranges defined by any one metric?

Materials and Methods: Femora and tibiae of Homo, Pan, and Gorilla were CT-scanned longitudinally and error ranges for multiple structural parameters (CSA, J, I_max/I_min) were calculated around midshafts.

Results: Distances proximally and distally from midshaft where structural values differ significantly from midshaft values vary between bones, species, and structural traits. Femoral error ranges are typically larger than tibial ranges. In the femur, error ranges are generally largest for chimpanzees and smallest for gorillas. A similar taxonomic pattern is not evident in the tibia. No structural trait consistently displays larger or smaller error ranges across both elements and all species. Variation in midshaft locations stemming from different length definitions is small and falls within observed error ranges defined by any one metric.

Discussion: Incorporating fragmentary specimens (e.g., fossils) for which midshaft location is unknown in comparisons of diaphyseal structure necessitates evaluation on a case-by-case basis, with thought to element, taxon, and structural traits of interest. Midshaft data recorded from distinct length measurements are generally comparable. Am J Phys Anthropol 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

Cross-sectional geometric properties of limb bone diaphyses have been studied to address a variety of topics in primate and human skeletal biology, ranging from long-term evolutionary trends in mechanical design (e.g., Grine et al., 1995; Ruff, 2002, 2005, 2009; Holt, 2003; O’Neill and Dobson, 2008; Shaw and Ryan, 2012; Trinkaus and Ruff, 2012; Ruff et al., 2015a) to lifetime adaptations related to factors such as physical activity patterns and subsistence strategies (e.g., Ruff and Hayes, 1982, 1983; Ruff et al., 1984, 2015a; Ruff, 1987; Bridges, 1989; Trinkaus et al., 1998; Holt, 2003; Marchi et al., 2006; Stock, 2006; Carlson et al., 2007; Shackelford, 2007; Shaw and Stock, 2009; Lieverse et al., 2011; Carlson and Marchi, 2014; Macintosh et al., 2014; Wallace et al., 2014).

In such analyses, comparisons of shaft structural properties across different specimens typically employ equivalent (i.e., homologous) cross sections defined according to their position relative to bone length, with midshaft (i.e., half bone length) being the most frequently used. However, many important skeletal samples, particularly fossil collections, include fragmentary specimens for which exact bone length is unknown. For incomplete elements, locating the cross section of interest along the diaphysis requires estimation (e.g., Trinkaus and Ruff, 1989, 1999a, 1999b, 2012; Grine et al., 1995; Trinkaus et al., 1998; Ruff, 2009; Puymeraud et al., 2012; Ruff et al., 2015b), which raises uncertainty about the soundness of structural comparisons with other specimens (Sládek et al., 2010). Moreover, the fact that not all researchers employ the same set of landmarks to measure bone length may also preclude direct comparisons between midshaft structural data acquired by different workers.

In this study of the hind limb elements, as in a companion paper on the forelimb (Mongle et al., 2015), we consider three questions. First, how accurately must the level of midshaft be located to produce comparable diaphyseal structural data? Or, stated a different way, what is the distance proximally and distally away from midshaft at which structural values become significantly different from those at midshaft? Second, does variation in midshaft level due to different definitions of bone length fall within the proximal to distal error range such that...
structural data acquired using distinct length metrics can be reasonably compared? Third, do error ranges and the effects of differences in length definitions vary between skeletal elements or among taxa such that analyses of particular elements or species are more or less susceptible to issues of comparability? Only a single previous study has addressed any of these questions explicitly, and it focused exclusively on the hind limb of humans (Sládek et al., 2010). Comparative analyses would be greatly facilitated by establishing the degree of structural variation along limb bone diaphyseal lengths in a wider sample of primates.

To address these questions as they relate to elements of the hind limb, we here examine structural variation relative to midshaft along the diaphyses of the femur and tibia of three extant hominine species (Homo sapiens, Pan troglodytes, and Gorilla gorilla). These taxa were chosen for study because they are especially relevant for testing hypotheses about hominin evolution (e.g., Ruff, 2009). Three particular structural properties were studied: cross-sectional area (CSA), polar moment of area (J), and the shaft bending strength index (I\text{max}\!/I_{\text{min}}) (see Mongle et al., 2015, for explanation). To determine the accuracy with which midshaft must be located to yield comparable structural data, samples of femora and tibiae from each taxon were CT-scanned along and perpendicular to their long axes, and error ranges for the three structural traits were established around the midshaft of each element. Location of midshaft was determined using a standard definition of bone length; then, other commonly employed bone length measurements were used to locate alternative midshaft levels, and to determine if these other levels are encompassed by the observed error ranges surrounding the standard midshaft position. Data were then used to investigate whether error ranges and length metric effects differ between limb elements or among taxa.

**MATERIALS AND METHODS**

**Sample**

This study included femora and tibiae of adult Homo sapiens (males: n = 10, females: n = 10, sex unknown: n = 10), Pan troglodytes (males: n = 9, females: n = 10), and Gorilla gorilla (males: n = 8, females: n = 8). The human sample included archaeological specimens of prehistoric Inuit foragers (Wallace et al., 2014), as well as recent cadaveric specimens housed in the Department of Anatomical Sciences, Stony Brook University. Chimpanzee and gorilla samples were composed primarily of wild-shot animals housed at the American Museum of Natural History (New York City) and the Museum of Comparative Zoology (Harvard University). Individuals were judged to be adult on the basis of complete epiphyseal fusion. All specimens lacked obvious pathologies and healed fractures. Limb elements from the right side were analyzed when possible.

**Length metrics and midshaft locations**

In analyses of femoral diaphyseal structure, bone length (and thus the location of midshaft) has been defined in one of three ways (Fig. 1). One commonly employed definition, which has been designated “maximum” length (F1 of Martin and Saller, 1957), describes the distance between the proximal surface of the head and the most distal point of the medial condyle (e.g., Kimura and Takahashi, 1982; Stock and Shaw, 2007; Gosman et al., 2013; Davies and Stock, 2014; Pearson et al., 2014). This measurement is equivalent to Gieseler’s (1927) “Caput-Condylennlänge” and FeL of Pearson (1899). A second measurement of length that takes into account the valgus inclination of the shaft in relation to the bicondylar horizontal plane is commonly designated as “bicondylar,” “oblique,” or “physiological” length (e.g., Carlson et al., 2007; Wallace et al., 2014). It is defined as the distance between the proximal surface of the head and a line that passes tangent to the distal surfaces of the medial and lateral condyles (F2 in Martin and Saller, 1957) (Fig. 1). A third measure of femoral length that was popularized by Ruff and Hayes (1983), and frequently employed in studies of diaphyseal cross-sectional geometry (e.g., Ruff, 1984, 2002, 2003; Trinkaus and Ruff, 1999a; Carlson, 2002, 2005; Holt, 2003; Sládek et al., 2006, 2010; Shackelford, 2007; Ruff et al., 2013), is referred to as “mechanical” length. This measurement describes the distance from a line that passes tangent at the distal surfaces of the medial and lateral condyles to the intersection of the longitudinal axis of the shaft with the deepest (i.e., most distal) point on the superior surface of the femoral neck. As such, it takes into account the longitudinal axis of the shaft in physiological valgus but does not include the size of the femoral head or the length and angle of inclination of the neck to the shaft. Here, we designate this metric FML (Fig. 1).

In the present study, maximum femoral length (Fig. 1, F1) was used to establish the standard midshaft cross section around which error ranges for structural properties were calculated. Femoral bicondylar and mechanical lengths (Fig. 1, F2 and FML, respectively) were also measured in order to determine whether their associated midshaft locations fall within the observed error ranges determined by maximum femoral length. Midshaft as defined by bicondylar length will generally be more proximal than midshaft defined by maximum length, whereas mechanical length midshaft will always be more distal.

Studies of tibial diaphyseal structure typically employ one of two length metrics (Fig. 1). Some workers (e.g., Gosman et al., 2013; Davies and Stock, 2014) have utilized the metric designated “maximum” length (T1 of Martin and Saller, 1957) it describes the distance from a line that passes tangent at the proximal surface of the medial or lateral condylar plateau and the distal tip of the medial malleolus (Fig. 1). This measurement is equivalent to Gieseler’s (1927) “medial Condylenn-Malleolennlänge” and T1b in Bräuer (1988). Another often-used length metric (e.g., Carlson et al., 2006, 2010; Shackelford, 2007; Ruff et al., 2013) is referred to as “physiological” length (T2 of Martin and Saller, 1957). It spans the distance between the proximal surface of the medial condyle and the distal articular surface for the talus at the base of the medial malleolus. A slight variant of this metric employs the midpoint along a line tangent to the centers of the medial and lateral condylar plateaus as the proximal terminus (e.g., Kimura and Takahashi, 1982; Ruff and Hayes, 1983; Sládek et al., 2006, 2010; Ruff et al., 2013). This distinction, however, is trivial given the nearly horizontal alignment of these plateaus in normal anatomical position. For example, Hsu et al. (1990) report an average varus tilt in the angle between the medial and lateral tibial plateaus and the horizontal plane of only 0.4° ± 1.6° in a large human sample.

In this study, tibial physiological length (Fig. 1, T2) was used to establish the standard midshaft cross sections.
around which error ranges for structural properties were calculated. Tibial maximum length (Fig. 1, T1) was also measured in order to determine whether its associated midshaft locations are within the observed error ranges determined by physiological length. Midshaft defined by tibial physiological length will invariably be more proximal than as determined from maximum length.

**CT scanning and image processing**

Bones were CT-scanned longitudinally at full length using a LightSpeed VCT scanner (GE Healthcare, Waukesha, WI) located in the Department of Radiology, Stony Brook University. Following Ruff and Hayes (1983), bones were positioned in a standardized alignment. Use of a custom-built Styrofoam rack allowed us to position both elements from an individual together with their longitudinal axes aligned on the scanner gantry for a single pass. Specimens were scanned dry, and a slice thickness of 2.5 mm was used. A bone reconstruction algorithm was used, and final CT images had a pixel dimension of ~0.50 mm. Images were saved as DICOM files.

Diaphyseal structural properties (CSA, \( I \), and \( I_{\text{max}} / I_{\text{min}} \)) were measured from DICOM files with the BoneJ plugin (Doube et al., 2010) for ImageJ software (NIH, Bethesda, MD). Elements were cropped from DICOM stacks and segmented by the BoneJ automated thresholding function “Optimize Threshold” to extract the bone phase. Structural properties were measured at 5% intervals away from midshaft (defined by F1 or T2 length metrics) along the diaphysis using the BoneJ “Slice Geometry” function.

**Data analysis**

For each element the mean percentage difference between values of a structural parameter recorded at midshaft (i.e., 50% F1 and T2) and values recorded at specific cross sections located at 5% intervals of bone length away from midshaft was calculated using the following formula from Sladek et al. (2010):

\[
\frac{\sum_{i=1}^{n} (\text{SP}_i - \text{SP}_{\text{mid}})}{\text{SP}_{\text{mid}}} \times 100
\]

where \( \text{SP}_{\text{mid}} \) is the value of the structural parameter at midshaft in the \( i \)th specimen, \( \text{SP}_i \) is the value of the same parameter at a particular 5% interval, and \( n \) is the sample size. Mean percentage difference constitutes the directional bias between midshaft values and other cross-sectional locations along the diaphysis. Intervals away from midshaft ranged between 30% (proximal) and 70% (distal) of bone length. At levels outside this range,
TABLE 1. Percentage differences from midshaft structural values along the femoral diaphysis

<table>
<thead>
<tr>
<th>Level</th>
<th>Level 30</th>
<th>Level 35</th>
<th>Level 40</th>
<th>Level 45</th>
<th>Level 50</th>
<th>Level 55</th>
<th>Level 60</th>
<th>Level 65</th>
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<td></td>
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<td></td>
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<tr>
<td>Homo</td>
<td>Mean</td>
<td>7.17</td>
<td>6.26</td>
<td>5.05</td>
<td>2.81</td>
<td>−</td>
<td>−3.42</td>
<td>−6.13</td>
<td>−10.54</td>
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<tr>
<td>SD</td>
<td></td>
<td>5.87</td>
<td>6.90</td>
<td>4.58</td>
<td>2.59</td>
<td>−</td>
<td>2.16</td>
<td>4.01</td>
<td>5.42</td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
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</table>

| Pan   | Mean    | 3.11    | 4.06    | 3.40    | 1.84    | −       | −2.66   | −5.48   | −7.01   | −7.26   |
| SD    |         | 5.01    | 4.89    | 3.55    | 2.18    | −       | 1.34    | 2.55    | 4.14    | 6.50    |
| P     | <0.01   | 0.02    | 0.09    | 0.80    | 0.36    | <0.01   | <0.01   | <0.01   | <0.01   |

| Gorilla | Mean | 7.80 | 5.24 | 3.60 | 1.89 | − | −3.61 | −6.54 | −6.65 | −6.19 |
| SD | 5.07 | 3.56 | 3.02 | 2.86 | 4.19 | 5.17 | 6.16 |
| P | <0.01 | 0.02 | 0.03 | 0.95 | 0.23 | <0.01 | <0.01 | <0.01 |

| J     | Mean    | 14.65   | 8.59   | 3.11   | 1.02   | −       | −1.14   | 4.49    | 10.59   | 20.36   |
| SD    | 16.28   | 12.93   | 7.13   | 3.49   | 3.33    | 15.65   | 19.04   | 20.55   |
| P     | 0.12    | 0.94    | 1.00   | 1.00   | 0.83    | 0.22    | <0.01   |

| Pan   | Mean    | 1.22    | 3.10   | 1.78   | 0.23   | −       | −1.78   | −3.74   | −0.15   | 2.19    |
| SD    | 12.80   | 10.06   | 8.00   | 3.63   | 1.67    | 3.77    | 20.71   | 23.46   |
| P     | 1.00    | 0.99    | 1.00   | 1.00   | 0.98    | 1.00    | 1.00    |

| Gorilla | Mean | 10.36  | 3.07  | 3.98  | 2.09  | −       | −3.10   | −4.66   | −1.75   | 4.37    |
| SD | 9.86 | 5.75   | 5.48   | 2.16   | 2.16   | 3.81    | 5.63    | 7.17    |
| P | <0.01 | 0.69   | 0.77   | 0.99   | 0.86   | 0.34    | 0.94    | 0.93    |

| Lmax/Lmin | Mean | 16.77  | 7.76  | 2.66  | 0.54  | −       | −3.26   | −5.71   | −4.66   | −1.00   |
| SD | 27.80  | 20.43  | 10.66  | 5.60  | 3.26   | 13.16   | 20.82   | 21.67   |
| P | 0.25   | 0.98   | 1.00   | 1.00   | 0.98   | 0.68    | 0.60    | 0.90    |

| Pan   | Mean    | 11.21   | 6.44   | 3.28   | 2.05   | −       | −0.89   | 0.95    | 8.12    | 10.13   |
| SD    | 27.94   | 24.59   | 11.42  | 4.28   | 3.93   | 7.63    | 22.64   | 21.62   |
| P     | 0.63    | 0.99    | 1.00   | 1.00   | 1.00   | 0.76    | 0.51    |

| Gorilla | Mean | −15.78 | −18.10 | −16.04 | −10.55 | −9.51   | 16.04   | 18.80   | 21.74   |
| SD | 10.35  | 9.17   | 6.56   | 3.58   | 4.09   | 9.92    | 15.34   | 19.33   |
| P | <0.01  | <0.01  | <0.01  | <0.01  | <0.01  | <0.01   | <0.01   | <0.01   |

Significant differences from midshaft values are indicated in bold.

cross sections ordinarily passed through bone areas that were not part of the diaphysis (i.e., trabecular-rich metaphyses and epiphyses). To visualize variation in structural values along the diaphysis relative to midshaft values, data were fitted by locally weighted regression of absolute values of mean percentage differences (i.e., \(|\text{mean } \% \text{ difference}|\).

The null hypothesis of no directional bias between structural values at midshaft locations and at 5% length intervals away from midshaft was tested with repeated-measures ANOVA followed by Tukey’s HSD post hoc tests. The tests were two-tailed, and significance level was \(P \leq 0.05\). The results of these tests were used to establish error ranges around midshaft, defined as the proximo-distal distance (in % length intervals) away from midshaft at which structural values are not significantly different from midshaft values. Power analyses were conducted to calculate the sample sizes required to detect significant differences using repeated-measures ANOVA (Cohen, 1988). Assuming an effect size of 0.81 (the largest across all hind limb bones) and a significance level of \(P \leq 0.05\), it was determined that to yield statistical power of \(\geq 0.95\), a sample size of \(\geq 16\) individuals was required. Thus, our sample sizes were judged to be sufficiently large for the purposes of this study.

All analyses were performed in R software (v3.1.1; R Core Development Team, 2014).

**RESULTS**

Descriptive statistics for raw values of structural parameters for the femur and tibia of each taxon at midshaft and at 5% intervals along bone length (i.e., femoral maximum length and tibial physiological length) are provided in the Supporting Information (Tables S1 and S2).

**Femur**

Table 1 reports the mean percentage differences between structural trait values recorded at femoral midshaft (defined by F1 in Fig. 1) and values recorded at levels proximal and distal to midshaft between 30% and 70% of maximum femoral length. Error ranges around midshaft determined by Tukey’s HSD tests are also reported in Table 1. Data are presented visually in Figure 2 as the absolute value of mean percentage differences to facilitate comparison between proximal and distal variation.

Patterns of variation in cross-sectional area (CSA) along femoral diaphyses are generally similar across taxa, such that absolute percentage differences from midshaft CSA are greatest at levels distant from midshaft and least at levels nearest to midshaft. In the human femur, absolute percentage differences from midshaft CSA increase gradually proximally to a maximum of 7.2% at 30% length \((P < 0.01)\) and distally to a maximum of 14.2% at 70% length \((P < 0.01)\). Differences at proximal levels are significant starting at 40% length, where CSA is 5.1% greater than at midshaft \((P = 0.02)\). Differences at distal levels are significant by 60% length, where CSA is 6.1% less than at midshaft \((P < 0.01)\). In the chimpanzee femur, proximal to midshaft, percentage differences from midshaft CSA are generally smaller compared to humans, reaching a maximum of only 4.1% at 35% length \((P = 0.02)\). Differences at all other proximal levels are not statistically significant \((P \geq 0.09)\) for all levels). Distally, absolute percentage differences
from midshaft CSA is 7.8% at 30% length ($P < 0.01$), while distally it is 6.7% at 65% length ($P < 0.01$). Similar to the chimpanzee pattern, significant differences are detected away from midshaft starting proximally at 35% length and distally at 60% length, where CSA is 5.2% more ($P = 0.02$) and 6.5% less ($P < 0.01$) than at midshaft, respectively.

In all taxa, few significant differences were detected between femoral midshaft polar moment of area ($J$) and values at levels either proximal or distal to midshaft. In the human femur, absolute percentage differences from midshaft $J$ increase proximally to a maximum of 14.7% at 30% length ($P = 0.12$) and distally to a maximum of 20.4% at 70% length ($P < 0.01$); but at all levels except 70% length, differences from midshaft $J$ are not significant ($P > 0.1$ for all levels). In chimpanzees and gorillas, absolute percentage differences from midshaft $J$ are smaller than in humans, increasing at proximal levels to maxima of only 3.1% at 35% length ($P = 0.99$) in chimpanzees and 10.4% at 30% length ($P < 0.01$) in gorillas. At distal levels, absolute percentage differences reach maxima of only 3.7% ($P = 0.98$) and 4.7% ($P = 0.99$) at 60% length in chimpanzees and gorillas, respectively. Differences from midshaft $J$ are not significant at any level in the chimpanzee femur ($P > 0.9$ for all levels) and no level except 30% length in the gorilla femur ($P > 0.3$ for all other levels).

The profile of variation in the femoral bending strength index ($I_{\text{max}}/I_{\text{min}}$) differs among taxa, particularly between gorillas and the other two species. In humans and chimpanzees, proximally, absolute percentage differences from midshaft $I_{\text{max}}/I_{\text{min}}$ increase gradually to maxima of 16.8% ($P = 0.25$) and 11.2% ($P = 0.03$) at 30% length, respectively. Distally, absolute percentage differences in $I_{\text{max}}/I_{\text{min}}$ increase to maxima of 5.7% at 60% length ($P = 0.68$) in humans and 10.1% at 70% length ($P = 0.51$) in chimpanzees. In both groups, at no level is the difference from midshaft $I_{\text{max}}/I_{\text{min}}$ significant ($P > 0.2$ for all levels). By contrast, in gorillas, at all levels proximally and distally, differences from midshaft $I_{\text{max}}/I_{\text{min}}$ were found to be significant ($P < 0.01$). This includes 45% and 55% length levels closest to midshaft where $I_{\text{max}}/I_{\text{min}}$ is 10.6% lower ($P < 0.01$) and 9.5% greater ($P < 0.01$) than at midshaft, respectively. Proximal and distal maxima for absolute percentage differences from midshaft $I_{\text{max}}/I_{\text{min}}$ are 18.1% at 35% length ($P < 0.01$) and 21.7% at 70% length ($P < 0.01$) in the gorilla.

Therefore, based on statistical analyses, in humans, the error range around midshaft for CSA conservatively (i.e., based on 5% intervals) spans the distance between 45% and 55% of maximum femoral length, whereas in chimpanzees and gorillas, error ranges conservatively span the distance between 40% and 55% of maximum length. For chimpanzees, the $J$ error range extends along the entire diaphysis between 30% and 70% length. This is also true for $I_{\text{max}}/I_{\text{min}}$ in humans and chimpanzees. In humans and gorillas, $J$ error ranges are also large, spanning the distances between 30% and 65% length in humans and 35% and 70% length in gorillas. The error range around midshaft $I_{\text{max}}/I_{\text{min}}$ in gorillas is narrower than ±5% maximum femoral length and was thus undetectable in this study.

For all taxa, differences between midshaft locations defined by femoral maximum length (F1 in Fig. 1) and femoral bicondylar length (F2 in Fig. 1) are very small. The latter is located, on average (± standard deviation)
only 0.2% ± 0.4%, 0.4% ± 0.6%, and 0.2% ± 0.6% more proximal than F1 midshaft in humans, chimpanzees, and gorillas, respectively. Differences between midshaft locations defined by maximum length and femoral mechanical length (FML in Fig. 1) are only slightly greater. Midshaft sites defined by mechanical length are located 3.7% ± 1.0%, 3.8% ± 0.5%, and 4% ± 0.6% more distal relative to maximum length in humans, chimpanzees, and gorillas, respectively. Thus, for all taxa, midshaft locations defined by either bicondylar or mechanical length fall clearly within the observed error ranges for midshaft as determined by maximum length for CSA and J, as well as the I_max/I_min error ranges for humans and chimpanzees but not gorillas.

### Tibia

Table 2 presents the mean percentage differences between structural trait values recorded at tibial midshaft (defined by T2 in Fig. 1) and values recorded at levels proximal and distal to midshaft between 30% and 70% of tibial physiological length. Error ranges around midshaft based on statistical analyses are also reported in Table 2. Data are presented graphically in Figure 3 as the absolute value of mean percentage differences.

In general, variation in CSA along the diaphysis is low compared to that of the two other tibial structural properties, particularly among chimpanzees and gorillas. In humans, absolute percentage differences from midshaft CSA increase gradually proximally to a maximum of 5.1% at 40% length (P < 0.01) and much more steeply distally to a maximum of 20.8% at 70% length (P < 0.01). At levels distal to midshaft, differences are significant at 60% length, where CSA is 7.3% less than at midshaft (P < 0.01), and at all other more distal levels. For chimpanzee and gorilla tibiae, absolute percentage differences from midshaft CSA increase proximally to maxima of 5.7% (P < 0.01) and 8.4% (P < 0.01) at 50% length, respectively; distally, absolute percentage differences increase to maxima of 12% (P < 0.01) and 10.5% (P < 0.01) at 70% length, respectively. In chimpanzees and gorillas, differences from midshaft CSA at proximal levels are significant beginning at 35% length, where CSA is 3.6% (P = 0.05) and 4% (P = 0.04) greater than at midshaft, respectively. At distal levels, differences are significant by 55% length and 60% length, where CSA is 3.5% (P = 0.03) and 5.2% (P < 0.01) less than at midshaft, respectively.

In all three taxa, J displays the greatest degree of variation along the tibial diaphysis, which contrasts with the patterns observed in the femur. In humans, proximally, absolute percentage differences from midshaft J increase sharply to a maximum of 65.8% at 30% length (P < 0.01) and distally to a maximum of 30% at 70% length (P < 0.01). At all levels proximally and distally, differences from midshaft J are significant (P < 0.03), including at 45% and 55% length levels closest to midshaft where J is 10.7% greater (P = 0.01) and 9.6% lower (P = 0.03) than at midshaft, respectively. Similarly, in chimpanzees and gorillas, absolute percentage differences increase steeply proximally to maxima of 52.7% (P < 0.01) and 74.2% (P < 0.01) at 30% length and distally to maxima of 25% (P < 0.01) and 16.5% (P = 0.02)
from midshaft $J$ are significant starting at 60% length ($P < 0.01$), where $J$ is 16.4% less than midshaft $J$. In gorillas, differences from midshaft $J$ were found to be significant by 65% length ($P = 0.02$), where $J$ is 16.5% less than midshaft $J$.

Variation in $I_{\text{max}}/I_{\text{min}}$ along the tibial diaphysis is generally greater than that observed in the femur in all three taxa, but particularly among humans and chimpanzees. In humans, absolute percentage differences from midshaft $I_{\text{max}}/I_{\text{min}}$ increase gradually away from midshaft proximally to a maximum of 8.1% at 30% length ($P = 0.03$). Distally, they increase more steeply to a maximum of 24.6% at 70% length ($P < 0.01$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$). Differences at proximal levels are significant at only 30% length, and distally starting at 60% length ($P = 0.02$).

Thus, as indicated by statistical analyses, for humans, error ranges around midshaft for CSA and $I_{\text{max}}/I_{\text{min}}$ conservatively span the distances between 45% and 55%, and 35% and 55%, of tibial physiological length, respectively. The error range around midshaft $J$ in humans is narrower than ±5% physiological length and thus undetectable in this study. For chimpanzees, the CSA error range extends only proximally to 40% length, whereas the error ranges for $J$ and $I_{\text{max}}/I_{\text{min}}$ extend between 45% and 55% length. For gorillas, the CSA and $J$ error ranges span between 40% and 55% length, and 45% and 60% length, respectively. The $I_{\text{max}}/I_{\text{min}}$ error range for gorillas extends only distally to 55% length.

As in the femur, for all groups, differences between midshaft locations defined by tibial physiological length (T2 in Fig. 1) and tibial maximum length (T1 in Fig. 1) are generally rather small. In humans, chimpanzees, and gorillas, midshaft sites defined by maximum length are located, on average, at 1.7% ± 0.3%, 2.7% ± 0.4%, and 2.6% ± 0.3% more distal relative to physiological length, respectively. Therefore, midshaft locations defined by maximum length are within the observed error ranges determined by physiological length for CSA in humans and gorillas, $J$ in chimpanzees and gorillas, and $I_{\text{max}}/I_{\text{min}}$ in all taxa.

**DISCUSSION**

This study addressed three questions. First, how accurately does midshaft need to be defined to yield comparable hind limb diaphyseal structural data? Second, does variation in midshaft position caused by different definitions of bone length fall within error ranges such that...
data gathered using different length measurements are comparable? Third, do error ranges and effects of length metric variation differ between elements or species, such that analyses of certain bones or taxa are more prone to issues of comparability? To address these questions, femora and tibiae from *Homo*, *Pan*, and *Gorilla* were CT-scanned at full length and error ranges for three commonly examined structural parameters (CSA, *J*, and \( I_{\text{max}}/I_{\text{min}} \)) were calculated around the midshaft of each element.

The results show that the distances proximally and distally away from midshaft where structural values become significantly different from midshaft values vary between elements as well as among taxa and structural traits. Between elements, error ranges for the femur are generally larger than those for the tibia, especially among humans and chimpanzees. Among taxa, in the femur, error ranges for chimpanzees are generally the largest, and those for gorillas are generally the smallest; whereas no consistent taxonomic pattern is evident in the tibia. Among structural traits, error ranges depend on the bone for which such data exist such that no trait consistently displays larger or smaller error ranges across both bones or across all species. In humans, especially large error ranges (spanning >20% length around midshaft) exist for femoral *J* and \( I_{\text{max}}/I_{\text{min}} \), while a notably small error range (spanning <10% length around midshaft) exists for tibial *J*. In chimpanzees, particularly large error ranges also pertain to femoral *J* and \( I_{\text{max}}/I_{\text{min}} \), whereas a particularly small range exists for tibial CSA. In gorillas, a large error range is evident only for femoral *J*, while especially small error ranges are shown by femoral and tibial \( I_{\text{max}}/I_{\text{min}} \).

In general, variation in the location of midshaft that stems from different definitions of bone length is fairly small and, with only three exceptions, falls within error ranges defined by femoral maximum length or tibial physiological length. The three exceptions relate to *J* in the human tibia, CSA in the chimpanzee tibia, and \( I_{\text{max}}/I_{\text{min}} \) in the gorilla femur. Ultimately, these findings indicate that the soundness of incorporating fragmentary specimens for which exact midshaft location is unknown (e.g., many fossils) in comparative studies of hind limb structural traits of interest.

This study builds on a previous investigation by Sládek et al. (2010) of the effect of midshaft location on error ranges of femoral and tibial diaphyseal cross-sectional properties (CSA, *J*) in a sample of Eneolithic and Bronze Age humans. Our results are consistent in that both studies found that in the femur, the error range for CSA was smaller than that for *J*, while the opposite pattern was found in the tibia. Also, both studies found significant differences from midshaft CSA at levels <5% (mechanical) length away from midshaft, whereas in our human sample the femoral CSA error range was found to span at least 10% (maximum) length around midshaft. This discrepancy between our results and those of Sládek et al. (2010) is likely due to differences in the statistical methods employed to establish error ranges, or potentially our smaller sample sizes, rather than any biological difference between our samples. In both studies, absolute percentage differences between femoral midshaft CSA and values at levels 10% length around midshaft were all <5%, but while we employed Tukey’s HSD tests to detect significant differences, Sládek et al. (2010) used paired-samples *t*-tests. When paired-samples *t*-tests are applied to the present human data, differences between our results and those of Sládek et al. (2010) are no longer apparent (Supporting Information Tables S3 and S4). Therefore, the results of this study generally confirm those of Sládek et al. (2010), in addition to expanding the scope of inquiry by providing novel data from chimpanzees and gorillas.

For studies that focus on isolated and fragmentary specimens such as fossils, individual variation is an important consideration. Within taxa, individual differences in structural variation along bone shafts could arise from a variety of sources, including variation in genetics (Judex et al., 2004), age and sex (Ruff and Hayes, 1982; Gosman et al., 2013), and mechanical loading conditions (Hsieh et al., 2001). None of these were stringent criteria in our sample selection (e.g., sexes were pooled) because they are not always certain when reference to archaeological and paleontological samples. Thus, we predicted that individual variation in our samples would be relatively high and, likewise, our statistical analyses would be fairly conservative. The extent of individual variation among elements analyzed here can be assessed by inspecting standard deviations surrounding mean percentage differences in Tables 1 and 2. Based on these data, it is clear that individual variation differs greatly depending on element, taxon, and structural parameter, as well as on the location of the cross section along the length of the shaft.

Nevertheless, two general patterns are apparent. First, for all elements and taxa, *J* and \( I_{\text{max}}/I_{\text{min}} \) generally exhibit much larger degrees of individual variation than CSA. This is likely attributable, to some extent, to differences in the dimensionality of the parameters (Lande, 1977). Second, not surprisingly, when *J* and \( I_{\text{max}}/I_{\text{min}} \) are highly variable, the degree of individual variation is generally greatest at levels distant from midshaft and least at levels nearest to midshaft. These patterns suggest that prudence is required when *J* and \( I_{\text{max}}/I_{\text{min}} \) are assessed in isolated specimens for which midshaft location is unknown, but that individual variation in CSA is probably less of an issue. Ultimately, however, in any such analysis, researchers must bear in mind how individual variation may influence interpretations, according to specific element, taxon, and/or structural traits of interest.

Our results have relevance for a number of previous interpretations of the diaphyseal morphology of fragmentary hominine hind limb fossils. To illustrate this point, it is worth considering the example of Grine and coworkers’ (1995) analysis of the cross-sectional geometry of the mid-Pleistocene *Homo* proximal femur from Berg Aukas, Namibia. The fossil fragment is 244-mm long, and its original bicondylar length was estimated to be ~518 mm. Therefore, the distal break is roughly 15 mm proximal to the predicted midshaft location. Grine et al. (1995) found that CSA and *J* values recorded at its distal break exceed the average midshaft values (by multiple standard deviations) of several recent human samples (including hunter-gatherers),
highlighting the fossil's exceptional robusticity. Assuming that the authors were correct in that the distal break is located 2.9% of bicondylar length proximal to midshaft, their interpretations are generally supported by the results of our study, given that femoral CSA among humans exhibits an error range that spans between 45% and 55% maximum length, and J displays an error range spanning the entire diaphysis. Moreover, midshaft defined by bicondylar length is negligibly different from maximum length midshaft. Nevertheless, some caution is warranted when interpreting the CSA value of the Berg Aukas femur since individual differences in variation for this property are relatively high, even between 45% and 55% maximum length. Ultimately, this example underscores that the validity of interpretations of midshaft structure in fragmentary fossils must be considered separately for each specimen according to the traits of interest.

Finally, it should be emphasized that in this study we defined error ranges for structural traits in an entirely statistical sense as the interval from midshaft where structural values become significantly different (i.e., $P < 0.05$) from midshaft values to be suitably accurate (e.g., Trinkaus and Ruff, 1989; Slädek et al., 2010). Following this definition, error ranges for hominine hind limb elements generally become narrower than ranges based on statistical analyses. Yet, for many traits, error ranges remain fairly wide, spanning at least the region around midshaft between 45% and 55% bone length (i.e., F1 and T2 in Fig. 1). In the femur, this includes all structural traits of all taxa except femoral $I_{\text{max}}/I_{\text{min}}$ in gorillas. In the tibia, this includes CSA in all taxa and $I_{\text{max}}/I_{\text{min}}$ in humans. Nevertheless, regardless of the exact definition of error that is preferred, this study highlights the necessity for researchers to specify and justify the degree of error that is acceptable to them according to their study goals.

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LITERATURE CITED


