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Cross-sectional Morphology and Mechanical Loading in Plio-Pleistocene Hominins: Implications for Locomotion and Taxonomy

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CROSS-SECTIONAL MORPHOLOGY AND MECHANICAL LOADING IN PLIO-PLEISTOCENE HOMININS: IMPLICATIONS FOR LOCOMOTION AND TAXONOMY

(Spine title: Cross-sectional Morphology and Mechanical Loading in Fossil Hominins)

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by

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ABSTRACT

This study explores locomotion and locomotor variability in Plio-Pleistocene hominins by examining cross-sectional properties and mechanical loading patterns in the proximal and midshaft femur of *Paranthropus*, fossil *Homo* sp. and *H. erectus*. Modern human and *Pan* models are used for comparative purposes. Given the wide degree of locomotor variability in *Pan*, the first part of this study explores ranges of variation in forelimb and hindlimb cross-sectional properties and mechanical loading patterns among taxa of *Pan* to determine if groups can be combined in further analysis. Results suggest that combining the groups should not introduce significant noise into the *Pan* model.

Cross-sectional properties in the proximal and midshaft femur of fossil hominins are examined to test the hypothesis that members of the same genus should exhibit similar locomotor behavior. In the proximal femur, fossil *Homo* sp. cluster with modern humans (*Homo sapiens*) to the exclusion of *Paranthropus*, and East and South African *Paranthropus* cluster together. Group differences are primarily due to differences in average bending and torsional strength. KNM-ER 738, which has been allocated to both *Paranthropus* and *Homo*, is more similar to paranthropine samples than to modern and fossil *Homo*. In the midshaft femur, fossil *Homo* sp. and *H. erectus* cluster with modern humans. OH 62 (*H. habilis*), however, forms a cluster by itself. It is unclear if this indicates a non-*Homo* status or if locomotor behavior was highly variable in early *Homo*. KNM-ER 1592, which is generally attributed to *Paranthropus*, clusters with modern and fossil *Homo*. This either suggests that mechanical loading is comparable between *Paranthropus* and *Homo* or that KNM-ER 1592 is misclassified as *Paranthropus*. KNM-ER 736 and KNM-ER 1807, which have been allocated to both *Paranthropus* and *Homo*, cluster with modern and fossil *Homo*, and therefore cannot be excluded from this genus. Group differences in the midshaft femur are largely due to differences in average bending and torsional strength.

Relationships between cross-sectional properties in the proximal and midshaft femur are examined to investigate if mechanical loading patterns in fossil hominin femora suggest human-like locomotion, *Pan*-like locomotion or intermediate locomotor behavior. The relative amount of cortical bone is elevated in modern humans compared to *Pan*, and in fossil hominins compared to modern humans. Axial strength is greater relative to average bending and torsional strength in modern humans compared to *Pan*. Fossil *Homo* sp. and *H. erectus* are most similar to modern humans in this regard. OH 62, however, displays the *Pan*-like pattern. Mechanical loading patterns in *Paranthropus* are more similar to patterns in modern humans than to patterns in *Pan.* The relationship between bending strength in the medio-lateral plane relative to bending strength in the antero-posterior plane of the proximal and midshaft femur is not significantly different between modern humans and *Pan*. Thus, different mechanical demands could potentially yield similarities in diaphyseal shape.

Key Words:

cross-sectional morphology, biomechanics, femur, locomotion, *Paranthropus*, fossil *Homo* sp., *Homo erectus*, modern humans, *Pan*, taxonomy

DEDICATION

Nothing has such power to broaden the mind as the ability to investigate systematically and truly all that comes under thy observation in life.

—Marcus Aurelius Antoninus, *Meditations*

If everyone is thinking alike, then somebody isn't thinking.

—George S. Patton

To my family and Jeff, with love.

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CHAPTER I

INTRODUCTION

RESEARCH OBJECTIVES

Locomotion is the foundation from which models regarding early hominin[1] food procurement strategies, physical and physiological adaptations and interspecific relationships within an ecological community can be reconstructed. Interpreting locomotor behavior among fossil hominins has been difficult given the amalgamation of ancestral and derived traits, and the mosaic nature of human evolution. A biomechanical approach may help clarify questions regarding the locomotor behavior of various fossil hominin groups. The major goal of this dissertation is to investigate locomotion and locomotor variability among Plio-Pleistocene hominins by examining proximal and midshaft femoral cross-sectional morphology and mechanical loading patterns. The following research questions will be addressed: (1) how well do cross-sectional properties, which give an indication of mechanical loading and locomotion, reflect current taxonomic assignments of fossil samples; (2) what do proximal and midshaft cross-sectional morphologies in paranthropine femora suggest about locomotor behavior in *Paranthropus*[2]; and (3) what do proximal and midshaft cross-sectional morphologies in fossil *Homo* femora suggest about locomotor behavior in early *Homo*, *Homo* sp. and *H. erectus*. Before these questions can be addressed, it is necessary to examine ranges of variation in proximal and midshaft femoral cross-sectional properties and mechanical loading patterns in modern humans and *Pan*—the two logical reference groups for which to compare fossil hominins.

The significance of this dissertation is threefold. First, if a genus should consist of species that occupy the same or similar adaptive zone (Mayr, 1950; Cela-Conde and

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[1] Hominin is defined as species that postdate the separation of African apes and the lineage that led to modern humans (Delson, 1981).

[2] The genus name *Paranthropus* is used throughout this dissertation in support for the hypothesis that the “megadont” taxa from East and South Africa form a monophyletic group that is adaptively distinct from *Australopithecus* following Robinson (1972), Wood and Constantino (2007) and Wood and Lonergan (2008).

Ayala, 2003; Wood and Lonergan, 2008), then locomotor behavior should be comparable among species within a genus, and distinct from species of another genus. Cross-sectional morphology is used for the first time to examine if current taxonomic assignments of many isolated fossil femora are in agreement with generally accepted locomotor characterizations of genera within the hominin lineage. By including a behavioral aspect to classification, this approach may be valuable for helping to recognize the generic status of isolated femora in the human fossil record. Second, this dissertation indirectly tests if reconstructions of cross-sectional morphology and mechanical loading patterns based on direct measurements of cortical thicknesses at natural breaks in fossil femora are compatible with reconstructions based on advanced technology (e.g. x-ray, computed tomography). Third, original data from fossil hominin femora, the modern human sample and a subset of the *Pan* sample that have not previously been examined from a biomechanical approach are included in this study. This information will add to the growing database documenting femoral cross-sectional morphological variability in Plio-Pleistocene hominins, modern humans and *Pan*.

BIOMECHANICS

Mechanical loading stimulates bone modeling and remodeling (Frost, 1964, 1988; Huiskes, 1982; Lanyon, 1987; Martin and Burr, 1989; Rubin et al., 1990; Frost et al., 1998). As a result, the cross-sectional properties of a long bone at a given section describe structural modifications that reflect a lifetime of mechanical loading history (Enlow, 1963; Frost, 1964; Martin and Burr, 1989; Rubin et al., 1990; Ruff et al., 2006). Cross-sectional morphology can be used to provide clues into the habitual functional usage of skeletal elements. The significance of a biomechanical approach to skeletal morphology is that it indirectly enables us to reconstruct possible behavioral repertoires based on mechanical loading histories, and thus gives a better indication of function from form.

The primary roles of the skeletal system are to provide mechanical support for the body, to protect soft-tissued organs and to store minerals. Although the bauplan of the skeleton is genetically canalized, a certain degree of morphological plasticity exists that continues to guide skeletal form throughout life (Martin and Burr, 1989; Cubo and Casinos, 1998; Ruff, 2000; Cullinane and Einhorn, 2002; Ruff et al., 2006). This adaptability of bone is largely influenced by mechanical loading, although non-mechanical factors such as age, sex, disease and diet also influence skeletal variability (Rubin et al, 1990; Burr and Martin, 1992; Lanyon, 1996; Frost, 1998, 1999; Ruff, 2000, 2005; Cullinane and Einhorn, 2002; Tanck et al., 2006).

Effects of loading on bone

Bone is a dynamic, elastic tissue that is not as rigid as it appears. Its physical strength is determined by its material properties, mass and architecture, and its biological strength is determined by genetically programmed baseline conditions and tissue-level modifications, which are driven by the basic multicellular unit (BMU) (Martin and Burr, 1989; Keller et al., 1990; Frassica et al., 1997; Frost, 1999; Currey, 2003; Pearson and Lieberman, 2004). The BMU includes the biological mechanisms responsible for cortical and trabecular bone remodeling (i.e. the turn over of bone) throughout life (Martin and Burr, 1989; Frost, 1999).

Bone bends, stretches, shortens and/or twists when a load is applied to it (Rubin et al., 1990; Turner, 1998; Carter and Beaupré, 2001; Currey, 2002; Winwood et al., 2006). A load results from a force, or moment, that is exerted on the bone either internally (e.g. by muscles) or externally (e.g. by gravity) (Martin and Burr, 1989; Duda et al., 1997; Frost et al., 1998; Turner, 1998; Pearson and Lieberman, 2004). Over time, bone accommodates to such loads in an effort to maintain its supportive role for the body. Loading, then, is “a potent means of stimulating bone formation,” (Skerry, 2000:31). Indeed, the functional adaptations of bone due to loading are a compromise because the skeleton has to maintain many functions that are not necessarily related to its role as a support system for the body, and it has to maintain such functions in an energetically efficient manner (e.g. attain peak bone strength with as little material as possible) (Frost, 1988; Rubin et al., 1990; Schoenau et al., 2001).

During loading, a force simultaneously produces a stress, which then produces a strain (Martin and Burr, 1989; Rubin et al., 1990; Turner, 1998). Dynamic strains are the basic stimulus guiding adaptive responses of bone (Frost, 1988; Rubin et al., 1990; Lanyon, 1996; Turner, 1998; Ruff et al., 2006). The duration of the strain does not have to be long in order to elicit a bony response (Rubin and Lanyon, 1985; Turner, 1998). In fact, there is a diminishing effect on bone adaptation since bone cells can accommodate to strains (Rubin and Lanyon, 1984). A strain can be tensile, compressive or shear (Cullinane and Einhorn, 2002; Pearson and Lieberman, 2004). Tension occurs when two opposing forces are applied along the same line, compression results when two forces are applied towards each other along the same line and shearing occurs when two parallel forces act in opposite directions and produce rotation (Cullinane and Einhorn, 2002). Torsion, or twisting, occurs when shear strains are produced along the entire longitudinal length of a structure (Frassica et al., 1997; Frost, 1998; Cullinane and Einhorn, 2002). Tension and compression result from axial loads, which are placed longitudinally along the length of a structure and whose applied force passes through the center of area of the section (Ruff and Hayes, 1983). Most loading patterns involve a combination of strain types (Ruff and Hayes, 1983; Frost, 1988; Burr et al., 1989; Skerry, 2000; Lieberman et al., 2004). Bending results when a force (i.e. a bending moment) simultaneously produces tension and compression on opposite surfaces of the bone (Rubin et al., 1990; Frost et al., 1998; Turner, 1998). Tension occurs along the convex surface, and compression occurs along the concave surface (Cullinane and Einhorn, 2002). Bending is the primary loading regime on long bones during terrestrial locomotion, although axial loads (torsion and compression) are experienced on a much smaller scale (Biewener, 1982; Bertram and Biewener, 1988; Lanyon, 1996; Ruff, 2000; Demes, 2007).

Bone will continue to deform to accommodate strains so that it becomes reinforced in the plane(s) of loading. However, if loads (and strains) are reduced, bone is lost (resorption), it becomes weaker and it reverts to its initial ‘optimal strain’ state

(Rubin et al., 1990; Skerry, 2000). The effects of strains on bone, however, appear to be site-, age- and sex-specific (Skedros et al., 1994; Lieberman, 1996; Skerry, 2000; Currey, 2003; Pearson and Lieberman, 2004; Ruff et al., 2006). For example, bone modeling and remodeling primarily occur in the periosteum (i.e. the outer surface of the bone) during skeletal growth and development, but then shift to the endosteum (i.e. the inner surface of the bone) in adulthood (Goodship et al., 1979; Lanyon, 1982; Rubin and Lanyon, 1984; van der Meulen et al., 1996). Moreover, during puberty human males add bone primarily on the periosteal surface, whereas females add bone in the endocortical region of the endosteum (Schoenau et al., 2001).

Once a strain is produced, bone cells react in one of four ways. First, there may be no cellular response if the strain magnitude is not large enough to elicit a bony reaction (i.e. the BMU is not activated) or if there are physiological disruptions (e.g. inhibition of parathyroid hormone, growth hormone, insulin-like growth factors-I and II) (Frost, 1987, 1988; Turner, 1998; Bikle et al., 1995; Skerry, 2000; Schoenau, 2005). Second, bone forming cells (osteoblasts) may produce more bone tissue (i.e. modeling) in response to the strain (Rubin et al., 1990; Turner and Pavalko, 1998; Currey, 2003). Third, bone absorbing cells (osteoclasts) may resorb bone tissue if it recognizes disuse or unloading beyond a certain threshold (Turner and Pavalko, 1998; Bikle and Halloran, 1999; Frost, 1999). Finally, bone tissue may be remodeled via the BMU (Martin and Burr, 1989; Rubin et al., 1990; Frost, 1999; Currey, 2002, 2003).

The exact mechanisms guiding the responses of bone cells to loading (i.e. mechanotransduction) are unclear, although many studies have shown that osteocyte-osteoblast communication is key (Rubin et al., 1990; Cowin et al., 1991; Marotti et al., 1992; Mikuni-Takagaki, 1999; Cullinane and Einhorn, 2002). The multistep process of mechanotransduction involves: (1) mechanocoupling, the conversion of mechanical forces into local mechanical signals that initiate a response from bone cells; (2) biochemical coupling, the transduction of a mechanical signal to a biochemical response; (3) cell-to-cell signaling, which involves communication from sensor cells (e.g. probably osteocytes) to effector cells (osteoblasts or osteoclasts); and finally (4) effector response, which is the formation or resorption of bone depending on the mechanical signal (Turner and Pavalko, 1998). This communication likely acts within a larger complex system called the “mechanostat”, a term coined by Frost which describes the mechanisms that coordinate cellular responses to mechanical loading in osseous tissue (Frost, 1987, 1998, 2003; Turner, 1998; Schoenau, 2005).

Beam Theory

A long bone can be modeled as a beam "and standard beam theory [can be] used to predict stress, strength and rigidity under particular types of loading," (Ruff and Hayes, 1983:359). Beam theory applied to bone adaptation is rooted in a functional paradigm where long bone diaphyses are modeled as hollow tubes (beams), “optimized through the process of functional adaptation to offer a maximum of mechanical resistance with a minimum of bone substance,” (Demes, 2007:717).

Beam theory predicts that the stiffness (rigidity) and strength (torsional resistance) of a beam (bone) is optimized when the polar second moment of area or polar section modulus, a measure of average bending and torsional rigidity and strength, respectively, is maximized (Huiskes, 1982; Levenston et al., 1998; de Margerie et al., 2005). Conversely, when resistance is favored along a particular plane of bending (e.g. sagittal or transverse), the second moment of area or section modulus along that plane increases (de Margerie et al., 2005). The cortical area of a section is a measure of axial strength (i.e. resistance to tensile and compressive loadings) (Ruff, 2000). It has been shown that axial loading influences the size of the cross-section, but not the overall cross-sectional geometry (Levenston et al., 1998). Although, bones predominately subjected to axial loading will bend (buckle) about its weakest axis (i.e. the minimum second moment of area), this is highly unlikely in most long bones since they are not slender enough and/or because axial loading is an insignificant part of the typical loading regime (Demes, 2007). When pure axial loading on the lower limbs does occur, it is almost exclusively compressional (Ruff and Hayes, 1983).

The stiffness and strength of a beam (bone) is also determined from wall (cortical bone) thickness. Beam theory predicts that torsional resistance is favored in long bones with thin walls and a large diameter (i.e. more hollow) rather than in long bones with thick walls and a small diameter, because material is placed farther from the neutral axis[3], often assumed to run through the center of the section, which increases the polar second moment of area and polar section modulus (Alexander, 1968; Huiskes, 1982; Frassica et al., 1997). The magnitude of a force increases from the center of the bone (i.e. from the neutral axis) to the outer diameter, and resistance to bending increases as osseous material is placed away from the neutral axis (Ruff and Hayes, 1983; Bertram and Swartz, 1991; Frassica et al., 1997; Frost, 1998; Levenston et al., 1998; Martin et al., 1998; O'Neill and Ruff, 2004). Resistance to pure axial loading is not influenced by wall thickness (de Margerie et al., 2005). Thus, "when compared to bones habitually subjected to mixed bending/axial loading, torsion-resisting bones should theoretically have relatively thinner walls," (de Margerie et al., 2005:51).

Since the relationships among behavior, loading and resultant cross-sectional geometries are not completely understood, many have argued that functional interpretations, particularly when deducing activity patterns, should be approached with caution (Bertram and Swartz, 1991; Lieberman, 1997; Polk et al., 2000; Lovejoy et al., 2003; Lieberman et al., 2004; Pearson and Lieberman, 2004; Demes, 2007). For instance, Lieberman et al. (2004) found that sheep tibiae are not structurally reinforced in the direction of peak bending strains, and suggested that variations in bone design, speed and gait likely complicate efforts to interpret the relationship between the direction of peak bending and diaphyseal cross-sectional geometry. Moreover, absolute values of cross-

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[3] In straight, symmetrical beams under uniform bending, the neutral axis passes through the geometric centroid of the section and is therefore also known as the centroidal axis (Lieberman et al., 2004). However, since long bones are subjected to a combination of bending and axial loads, and since long bones are neither entirely straight nor symmetrical, the neutral axis may not always pass through the centroid of the section (Lieberman et al., 2004). Experimental studies have confirmed that under varied loading regimes, the neutral axis shifts away from the centroid and towards the cortex under tension (Carter et al., 1981; Demes et al., 1998; Lieberman et al., 2004). Lieberman et al. (2004) showed that patterns in cross-sectional properties are not affected when assumed centroidal axes are chosen over experimentally derived ones, although absolute values of cross-sectional properties differed depending on whether they were calculated about the centroidal axis or an experimentally derived neutral axis. In this dissertation, cross-sectional properties are calculated with reference to a neutral axis assumed to run through the cross-sectional area centroid.

sectional properties differed depending on whether they were calculated about the centroidal axis or an experimentally derived neutral axis (Lieberman et al., 2004). Despite our incomplete knowledge of cortical bone modeling/remodeling and the complexities associated with it, experimental research continues to reinforce the existence of a relationship between cortical bone functional adaptation and mechanical loading (Jones et al., 1977; Woo et al., 1981; van der Meulen et al., 1995; Levenston et al., 1998; Haapasalo et al., 2000; Robling et al., 2000; Lieberman et al., 2004; de Margerie et al., 2005; Modlesky et al., 2008). At the very least, patterns in cross-sectional geometries are a useful means of inferring bone adaptations to habitual mechanical loads.

LOCOMOTION AND TAXONOMY

As will become evident in the following discussion and throughout this dissertation, taxonomic uncertainty has hampered analyses of locomotion among early hominins because it is unclear if reconstructed locomotor behaviors, which are primarily based on isolated postcranial remains, are valid for species largely diagnosed craniodentally (e.g. Leakey, 1959; Wood, 1993; Rightmire, 1993, 1998; Grine et al., 1996; Wood and Lonergan, 2008). Since ranges of variation in postcranial morphology within several early hominin groups are unknown and/or poorly understood, it is difficult to allocate isolated postcranial specimens to a specific taxon. This is particularly the case where more than one species is presumably present based on craniodental evidence (e.g. Olduvai Gorge Bed II, Koobi Fora, Swartkrans) (Leakey et al., 1964; Leakey, 1972, 1973a, b; 1976, 1979; Grine, 1989). As succinctly stated by Constantino and Wood (2007:51), “the problem researchers have faced at Olduvai Gorge, Koobi Fora, and elsewhere is how to tell which of the unassociated hominin postcranial fossils should be assigned to *P. boisei* and which should be assigned to the contemporaneous species *Homo habilis*.”

Another difficulty is when the postcranial morphologies of presumably different species are similar (Day, 1976a, b; Leakey and Walker, 1976; Susman, 1993). For instance, OH 8 and OH 35, both isolated postcranial elements attributed to *H. habilis*, have been argued to share morphological resemblances to corresponding elements in KNM-ER 1500, an associated skeleton assigned to *Paranthropus* (Grausz et al., 1988). Morphological resemblance has been used to argue that the Olduvai samples should be attributed to *P. boisei*, or another non-*Homo* genus, rather than *H. habilis* (Day, 1976a; Grausz et al., 1988; Wood, 2000). Assuming that morphology follows function, morphological similarity *may* reflect functional similarity in the two genera, but it is also quite possible that similar morphology does not reflect similar function. Thus, it is unclear if OH 8, OH 35 and KNM-ER 1500 represent the same species misclassified as two different species or if certain aspects in the postcranial skeleton of *Paranthropus* and *H. habilis* are indeed similar.

OH 36, a partial ulna recovered from upper Bed II at Olduvai Gorge, was initially attributed to *H. erectus* based on its overall morphology and its stratigraphic location (Leakey, 1978; Day, 1986). However, functional morphological comparisons with ulnae recovered after the discovery of OH 36 suggest that it is likely a representative of *P.* cf. *boisei* rather than *H. erectus* (Walker and Leakey, 1993; Aiello et al., 1999; McHenry et al., 2007; Drapeau, 2008). According to McHenry et al. (2007:217), "since its [OH 36] morphology is entirely unlike other known member of early *Homo* (e.g. KNM-WT 15000), it is *reasonable* to assign it to *P. boisei*," [emphasis added]. L40-19, an ulna from Member E of the Shungura Formation in Ethiopia, was initially attributed to *Paranthropus* sp. (Howell and Wood, 1974), but according to Drapeau (2008), its morphology and functional anatomy align it with *Homo* (but see Feldesman, 1979; McHenry et al., 2007). The morphological distinctions and inferred functional differences between OH 36 and L40-19 strongly suggest separate taxonomic assignments where the more ancestral condition is retained in *Paranthropus* (e.g. OH 36) while the lack of arboreal adaptations likely signifies an allocation to the genus *Homo* (e.g. L40-19) (Drapeau, 2008) or Hominini gen. et sp. indet. (Aiello et al., 1999). However, since postcranial morphology does not appear to follow a linear trend toward hominization, postcranial elements with more primitive traits may not necessarily represent a more ancestral hominin (Richmond et al. 2002; Green et al., 2007; Lordkipanidze et al., 2007; McHenry and Brown, 2008).

Morphological and behavioral delineations among species and the characteristics a species must posses to be included in a genus are poorly defined in paleoanthropology. Moreover, the degree of differences between and among groups may depend on which traits (ancestral or human-like) are emphasized. Thus, a certain amount of subjectivity is inherent in any classification scheme. Examining locomotor behavior and locomotor variability from a biomechanical perspective is a means of functionally categorizing hominin groups, which may help define a species' adaptive zone, which should be "consistent and coherent across the species taxa in the putative genus," (Wood and Lonergan, 2008:374). Thus, all members of the same genus are expected to engage in similar locomotor behavior, which should be distinct, to some degree, from members of another genus.

Many of the Plio-Pleistocene samples examined in this study are allocated to more than one genus (e.g. KNM-ER 738), or their inclusion in a specific genus is dubious (e.g. OH 62). Given the taxonomic uncertainties of many isolated fossil hominin femora, the first goal of this dissertation is to ascertain if cross-sectional morphology, which can be cautiously used to reconstruct locomotor behavior, is consistent with generally recognized taxonomic identities of isolated fossil hominin femora. That is, all femora attributed to *Paranthropus* are expected to show similar mechanical loading patterns among each other, which should be distinct from patterns in femora attributed to *Homo*, and vice versa. It is of utmost importance to stress that while cross-sectional morphology *per se* is not suitable for taxonomic identifications, given its plasticity, the mechanical information that can be gleaned from long bone cross-sectional analyses, specifically with regard to locomotion, can be useful for taxonomic inferences, at least to the genus level, with the understanding that members of a genus occupy the same, or very similar, adaptive zone (Mayr, 1950).

PLIO-PLEISTOCENE LOCOMOTION

The first hominin to display anatomical traits fully consistent with the modern human form of obligate terrestrial bipedalism was *H. erectus* nearly 1.8 mya (Walker and Leakey, 1993; McHenry and Coffing, 2000; Antón, 2003; Bramble and Lieberman, 2004; Polk, 2004; Lordkipanidze et al., 2007; Ruff, 2008), and most certainly by ~1.5 mya (Bennett et al., 2009). Pre-*H. erectus* hominins (e.g. *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus* sp., *Australopithecus* sp., *Paranthropus* sp., early *Homo*) retain some anatomical evidence of ancestral adaptations to arborealism with apparently increasing adaptations to terrestrial bipedalism over time (Robinson, 1972; Susman and Creel, 1979; Susman and Stern, 1982; Stern and Susman, 1983; Susman et al., 1984; Susman and Brain, 1988; Clarke and Tobias, 1995; Leakey et al., 1995; Berger and Tobias, 1996; Duncan et al., 1997; Asfaw et al. 1999; Aiello and Andrews, 2000; Senut et al., 2001; Brunet et al., 2002; Harcourt-Smith, 2007; Green et al., 2007; Richmond and Jungers, 2008; Lovejoy et al., 2009).

Locomotion and locomotor variability among Plio-Pleistocene hominins are difficult to reconstruct given the fragmentary nature of the hominin fossil record and the mosaic nature of evolution. It has been argued that postcranial morphological differences between *Paranthropus* and early *Homo*[4] suggest that at least two patterns of locomotion, which were evolving in parallel, were in existence around the same time, and that such divergent locomotor behaviors likely helped to promote niche differentiation between coexisting paranthropine and early *Homo* groups (Davis, 1964; Leakey, 1973a; Day, 1976a, b; McHenry and Corruccini, 1978). Recent evidence and reevaluation of previous data, however, indicate that locomotor behavior in early *Homo*, specifically *H. habilis*, likely included an arboreal component, and in this way they were more similar to *Paranthropus* than to later *Homo* (Oxnard and Lisowski, 1980; Richmond et al., 2002; Gebo and Schwartz, 2006; Haeusler and McHenry, 2007; Ruff, 2009). Since the fossil

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[4] In this study, early *Homo* refers to members of the genus *Homo* that predate *H. erectus*, but whose species identification is uncertain or unknown (e.g. KNM-ER 1472), and *H. habilis* (i.e. OH 62). Although it has been suggested that the allocation of OH 62 to the genus *Homo* may not be valid (e.g. Wood, 1992; Wood and Collard, 1999a, b), it is included in the early *Homo* group since it is generally referred to as *H. habilis* in the literature.

evidence suggests that *Paranthropus* and early *Homo* likely co-existed in many parts of East and South Africa (Tobias, 1965; Leakey, 1972, 1973a, b; Grine et al., 1996; Susman et al., 2001; Wood and Constantino, 2007), similar locomotor behavior may have led to an increase in competition between the two genera (Wood and Strait, 2004).

***Paranthropus* locomotion**

Although far from conclusive, several lines of evidence suggest that the locomotor behavior in *Paranthropus* included both a rudimentary form of terrestrial bipedalism as well as a strong arboreal component (Day, 1969; Jolly, 1970; Leakey, 1971, 1972; Robinson, 1972; Grine, 1988; Susman and Brain, 1988; Susman, 1989; Harcourt-Smith and Aiello, 2004; Susman and deRuiter 2004; Gebo and Schwartz, 2006).

Indications of arborealism in *Paranthropus* derive from analyses of limb proportions (McHenry, 1978), semi-circular canal morphology (Spoor et al., 1994) and functional morphology of various postcranial elements (Lague and Jungers, 1996; Aiello et al., 1999; Patel, 2005; Gebo and Schwartz, 2006; McHenry et al., 2007). For instance, Grine and Susman (1991) found that proximal and distal radial morphology in *Paranthropus* was similar to that in *A. africanus* and *A. afarensis*, and that the radial morphologies in both australopithecines and paranthropines were distinct from *Homo*. The overall morphology of the *Paranthropus* radius indicated enhanced stability for the elbow joint, enhanced forearm flexion and wrist extension capabilities, which suggest that *Paranthropus* was an adept climber (Grine and Susman, 1991). Patel (2005) found that the proximal radius in *Paranthropus* was morphologically most similar to extant hylobatids (e.g. gibbons and siamangs), where the elbow joint is adapted for both stability and suspensory behaviors. Although *Paranthropus* was likely not participating in richochetal brachiation, the mode of locomotion specific to hylobatids, the morphology of the paranthropine proximal radius alludes to an arboreal function (Patel, 2005).

Evidence that *Paranthropus* was likely capable of a rudimentary form of terrestrial bipedalism, which was different from that in later *Homo,* stems from functional morphological analyses of manual and pedal remains (Susman, 1988, 1989; Susman and

Brain, 1988; Gebo, 1992)[5], limb proportions (McHenry, 1978; Grausz et al., 1988) and morphological analyses of various postcranial elements (e.g. Day, 1969; McHenry, 1975a, b, c, 1976). For instance, Lovejoy et al. (1973:78) argued that paranthropine (and australopithecine) pelves and proximal femora conformed to morphological and biomechanical patterns "fully commensurate with erect striding as is that of modern man." More recently, DeSilva (2009:6570) found that KNM-ER 1500, a possible associated skeleton of *P. boisei*[6], possessed the decidedly human-like trait of a "perpendicularly oriented ankle joint relative to the long axis of the tibia." In addition, the angle between the plane of the ankle joint and the long axis of the tibia in KNM-ER 1500 is within the modern human range of variation (DeSilva, 2009). The functional morphology of the ankle joint complex suggests that KNM-ER 1500 did not have an inverted ankle nor an ankle joint capable of extreme dorsiflexion, which would have compromised its ability to traverse arboreal substrates and climb in an ape-like manner (DeSilva, 2009).

Previous studies have addressed the issue of locomotor behavior in *Paranthropus* from a biomechanical perspective (e.g. Ruff et al., 1993; Ruff et al., 1999). Macchiarelli et al. (1999) examined the architecture of cancellous bone in the ilia of South African gracile and robust australopithecines, and found that the structure of the trabecular network indicated a loading regime commensurate with a bipedal gait somewhat different from that in modern humans. Ruff et al. (1999) found that femoral cross-sectional geometries in *P. robustus* were comparable to their robust East African counterparts (i.e. *P. boisei*), and both groups, as well as early *Homo*, were markedly different from *H. erectus* and modern humans. The distinction in cross-sectional geometries between the pre-*H. erectus* group and the *H. erectus* and modern human group indicated an "increased

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[5] Since there are no hand and foot bones that can be assigned with confidence to *P. boisei* (Wood and Constantino, 2007), interpretations of locomotion from manual and pedal morphologies are based on South African *Paranthropus* specimens (i.e. *P. robustus*). If hypotheses regarding *Paranthropus* monophyly are not rejected, then it is reasonable to assume that species within the same genus will generally have similar locomotor adaptations (Strait et al., 1997; Strait and Grine, 2004; Wood and Constantino, 2007). However, there may be some variability in locomotor behavior associated with the environment (Harmon, 2009).

[6] The taxonomic allocation of KNM-ER 1500 to *P. boisei* is not unanimously accepted (e.g. Constantino and Wood, 2007).

level of mechanical loading of the skeleton in non-*H. erectus*, [which] is consistent with a slightly altered pattern of bipedal gait relative to that of modern humans and *H. erectus*," (Ruff et al., 1999:519).

Multiple lines of evidence have not yielded consistent interpretations of the locomotor behavior in *Paranthropus*. Thus, for the time being, it is assumed that *Paranthropus* was capable of both arborealism and terrestrial bipedal locomotion, albeit the latter was different from that in later *Homo*. The second goal of this dissertation is to help shed light on paranthropine locomotion by examining cross-sectional diaphyseal geometric variation in femora attributed to *Paranthropus*.

Early *Homo* locomotion

Leakey et al. (1964) revised the definition of the genus *Homo* after recovering specimens at Olduvai Gorge from Bed I and the lower part of Bed II at the FLK NN I site. The new species, *Homo habilis* Leakey et al. (1964), was found in strata earlier than, contemporary with and later than specimens attributed to the robust australopithecines (or paranthropines) (Leakey et al., 1964). Concerning locomotion, Leakey and colleagues (1964:7-8) stated:

> …the structure of the pelvic girdle and of the hind-limb skeleton is adapted to habitual erect posture and bipedal gait; the fore-limb is shorter than the hind-limb; the pollex is well developed and fully opposable and the hand is capable not only of a power grip but of, at the least, a simple and usually well-developed precision grip;…the hallux is stout, adducted and plantigrade; there are well-marked longitudinal and transverse arches.

Since then, locomotor behavior in early *Homo* has been a controversial subject (Day and Wood, 1968; Day, 1976a; Oxnard and Lisowski, 1980; Clark and Tobias, 1995; Kidd et al.*,* 1996; Ruff, 2009). While most researchers agree that early *Homo* was a biped, differences of opinion center on the degree of bipedalism (i.e. facultative or obligate), gait kinematics and whether traits indicative of arborealism are primitive, nonfunctional retentions or functionally significant (Davis, 1964; Day and Napier, 1964; Lewis, 1972; Susman and Stern, 1979; McHenry and Berger, 1998; Haeusler and McHenry, 2004; Gebo and Schwartz, 2006).

One of the key anatomical traits necessary for human-like terrestrial bipedalism is an adducted hallux, which has a propulsive function and a supportive role for the medial and anterior foot during bipedal locomotion (Weidenreich, 1923). According to Leakey et al. (1964) and Day and Napier (1964), the OH 8 foot, which is generally attributed to *H. habilis*, had a stout, adducted hallux. More recently, McHenry and Jones (2006) found that the morphology of the articular areas between the first metatarsal and the medial cuneiform indicated complete hallucial convergence in OH 8. Others have argued, however, that the hallux of OH 8 is primitive, which indicates that the species represented by the foot was not a fully, committed terrestrial biped, but rather was adapted for both arborealism and terrestrial bipedalism (Lewis, 1972; Oxnard and Lisowski, 1980; Kidd et al., 1996). Gebo and Schwartz (2006:510) argued that the well-curved medial trochlear rims of OH 8 indicated an adaptation to “movements or postures, such as those used during arboreal activities,” and further suggested that its closest functional morphological affinities were with tali attributed to *Paranthropus*. The total morphological pattern of the foot suggests that early *Homo* was not a committed biped (Gebo and Schwartz, 2006).

The functional capabilities of the OH 7 hand, attributed by Leakey et al. (1964) to the *H. habilis* hypodigm, have also confounded reconstructions of early *Homo* locomotor behavior. Napier (1962) described the ancestral and human-like characteristics of the hand, and suggested that the presence of a fully opposable thumb and broad terminal phalanges indicated that OH 7 was likely capable of a precision grip, although not as effective as in modern humans. Susman and Stern (1979) also observed derived *Homo* characteristics in the pollex and distal phalanges of OH 7. At the same time, however, the prominent muscle markings for *flexor digitorum profundus* and *flexor digitorum superficialis* suggested that OH 7 was capable of suspensory climbing behaviors (Susman and Stern, 1979).

The OH 35 tibia and fibula, discovered in Bed I at Olduvai Gorge where the type specimen of *P. boisei* was recovered, have also weighed heavily on reconstructions of early *Homo* locomotion. According to Davis (1964), the forward tilt of the talar surface on the tibia allowed dorsiflexion of the ankle joint, which is necessary for bipedal plantigrade locomotion. Some aspects of the musculature in OH 35 are more similar to modern humans than to great apes, while other aspects, such as the extent of *soleus*, is intermediate between the human and great ape conditions (Davis, 1964). Davis (1964:968) suggested that the total morphological pattern of OH 35 indicates that "at the time of *Zinjanthropus* [*Paranthropus*] *boisei*, there lived a hominid in whom bony adaptation to bipedalism was well advanced at the ankle...while the fossil form was clearly a habitually bipedal plantigrade primate, its gait may well have differed considerably from that of modern man." Susman and Stern (1982) argued that the joint surfaces in OH 35 indicated a human-like form of bipedalism, and the suite of morphological traits in OH 7, OH 8 and OH 35, which may represent a single individual, indicated that *H. habilis* possessed a derived bipedal morphology while maintaining arboreal capabilities.

Limb proportions in *H. habilis* indicate adaptations to both arborealism and terrestrial bipedalism (McHenry and Berger, 1998; Richmond et al., 2002). Haeusler and McHenry (2004:460) suggested "the earliest species of the genus *Homo* [OH 62 and KNM-ER 3735] possessed an elongated hindlimb relative to that of *Australopithecus africanus* and *A. afarensis*, whereas the forelimb probably retained brachial proportions with long forearms." Relatively long hindlimbs may have been an adaptation to more energy efficient long distance terrestrial travel, whereas long forelimb proportions and the shoulder joint morphology, particularly in KNM-ER 3735, may indicate adaptations to arborealism (Haeusler and McHenry, 2004, 2007).

Biomechanical analyses of upper and lower limb loading in early *Homo* suggest different behavioral patterns compared to later *Homo*. Ruff (2009) found that femoral-to-humeral strength proportions in OH 62 were more similar to patterns observed among chimpanzees than to patterns noted in *H. erectus* and modern humans. Patterns in upper-to-lower limb strength were "consistent with locomotor differentiation between the two early *Homo* lineages, with *H. habilis* more reliant on arboreal climbing while *H. erectus* was a fully committed terrestrial biped," (Ruff, 2009:98).

The evidence to date suggest that locomotor behavior in early *Homo* may have been different from that in later *Homo* and more akin to that in pre-*H. erectus* hominins, particularly *Australopithecus* and *Paranthropus*. This possibility has several ramifications. First, it would indicate that all members of the genus *Homo* are not committed bipeds, which conflicts with one of the defining characteristics of *Homo* per Leakey et al. (1964). Second, if locomotor behavior was not distinct between *Paranthropus* and early *Homo*, which were speculated to be contemporaneous at many sites throughout East and South Africa, then competition between the two lineages may have been elevated and niche separation, to minimize competition, would have had to occur via other means (e.g. diet and culture) (Wood and Strait, 2004). Third, if the earliest members of the genus *Homo* were not committed to obligate bipedalism, then the locomotor precursor to human-like bipedalism must have been a successful strategy. Moreover, the commitment to obligate terrestrial bipedalism may have been adapted very late in human evolution with the advent of *H. erectus* nearly ~1.8 mya. Finally, if all members of the genus *Homo* were not obligate bipeds, then locomotor variability in the lineage may have been more pronounced than is generally recognized.

This study directly addresses the issue of locomotion and locomotor variability in the hominin fossil record by investigating femoral cross-sectional morphological and mechanical loading patterns. The final goal of this dissertation is to help elucidate locomotor behavior and locomotor behavioral variability in fossil *Homo* from a biomechanical perspective, which may help clarify interpretations of locomotion based on preserved morphology.

STRUCTURE OF DISSERTATION

This dissertation includes a collection of papers that examines locomotion and locomotor variability in Plio-Pleistocene hominins from a biomechanical perspective. Each chapter focuses on a specific problem related to the main goal of this work. The chapters provide a logical progression of interrelated topics that together culminate in an integrated final body of work.

Pan referential models are often used to infer locomotor behavior in fossil hominins since there is a close phylogenetic relationship between *Pan* and the lineage that led to modern humans (Rogers, 1993; D'Août et al., 2004; Sockol et al., 2007; Crompton et al., 2008; Tocheri et al., 2008; Pontzer et al., 2009). Although the primary mode of locomotion in *Pan* is defined as quadrupedal knuckle-walking, field observations have shown that qualitative and quantitative differences in particular locomotor behaviors do exist among different chimpanzee (*P. troglodytes* ssp.) and bonobo (*P. paniscus*) communities (e.g. Kortlandt, 1962; Van Lawick-Goodall, 1968; Susman et al., 1980; Hunt, 1989, 1992; Kano, 1992; White, 1992; Doran and Hunt, 1994; Boesch et al., 2002). Locomotor variation observed in *Pan* may reflect subtle differences in habitat, morphology, the composition of the groups under investigation (e.g. age and sex) and/or field methods (e.g. provisioning versus non-provisioning, the level of habituation). While links between cross-sectional geometric patterns and broad locomotor categories among non-human primates have been established, the relationship between cross-sectional geometries and specific locomotor behaviors have not been determined (e.g. Burr et al., 1989; Ruff, 1989; Ruff and Runestad, 1992; Polk et al., 2000; Carlson, 2002, 2005). Given field observations of locomotor variability among *Pan* communities, it cannot be assumed that all members of *Pan* will present with similar cross-sectional morphology, and the combining of *Pan* samples *a priori* may artificially inflate variation in the *Pan* model. Chapter II examines ranges of variation in femoral and humeral cross-sectional properties in chimpanzee subspecies and bonobos to determine baseline loading conditions in quadrupeds and to determine if cross-sectional properties are similar among *Pan* taxa so that the samples can be combined in further analyses. This analysis will also give insight into cross-sectional variability among different species within a genus, which will aid in determining if cross-sectional variation in species of *Paranthropus* and *Homo* are consistent with expected variability within genera.

Taxonomic uncertainty, propelled by the lack of associated skeletons and the fragmentary nature of many postcranial elements, has hampered inferences of locomotion among early hominins because it is unclear if reconstructed locomotor behaviors, which are primarily based on isolated postcranial remains, are actually valid for a species largely identified craniodentally. Although this problem is universally acknowledged among researchers, especially those working with postcranial material (e.g. Leakey, 1972, 1973a, b; Day, 1976a, b, 1978; Wood, 1978; Leakey and Walker, 1985; McHenry, 1991, 1992; Jungers, 1988; Ruff et al., 1999; Ruff, 1995; Harcourt-Smith, 2007; Harmon, 2009), an explicit examination of the relationship between inferred locomotor behavior, deduced from cross-sectional morphology and mechanical loading patterns, and presumed taxonomy has not been conducted. Since members of the same genus are expected to share a similar adaptive zone, there should be commonality in locomotor behavior among species within a genus (Mayr, 1950; Cela-Conde and Ayala, 2003; Wood and Lonergan, 2008). The goal of Chapter III is to investigate if members of the same genus are broadly homogeneous in their locomotor repertoires based on femoral cross-sectional properties and mechanical loading patterns.

The goal of Chapter IV is to examine cross-sectional morphology in femora attributed to *Paranthropus*, early *Homo* and *H. erectus*, within the working taxonomic hypotheses from Chapter III, to investigate locomotion and locomotor variability among Plio-Pleistocene hominins. Cortical area is plotted against total area to examine the relative amount of cortical bone in the cross-section, cortical area is plotted against the polar section modulus to examine if bones are preferentially adapted for axial strength or bending and torsional strength, and the polar section modulus about the medio-lateral plane is plotted against the polar section modulus about the antero-posterior plane to examine bending preferences in the anatomical axes, which give an overall indication of diaphyseal shape. Modern human and *Pan* comparative samples are used to examine if cross-sectional morphology in *Paranthropus*, early *Homo, Homo* sp. and *H. erectus* femora suggest mechanical loading patterns more akin to modern human locomotion, *Pan* locomotion or intermediate locomotor behavior.

Finally, Chapter V includes a summary of the research objectives and results, a discussion of the significance of this study to paleoanthropology and brief thoughts about future research directions. Supporting information is provided in the Appendices.

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CHAPTER II

VARIATION IN HUMERAL AND FEMORAL CROSS-SECTIONAL PROPERTIES IN MEMBERS OF THE GENUS *PAN*

Pan referential models are often used to infer locomotor behavior in fossil hominins since there is a close phylogenetic relationship between *Pan* and the lineage that led to modern humans (Corruccini and McHenry, 1979; Rogers, 1993; D’Août et al., 2004; Crompton et al., 2008; Tocheri et al., 2008; Pontzer et al., 2009). In addition, experimental research has shown that the mechanics of arboreal climbing and bipedalism are very similar to each other, which likely suggests that hindlimb morphology in vertical climbers may have been pre-adaptations to human bipedalism (Fleagle et al., 1981; Stern and Susman, 1981; Hirasaki et al., 2000). Indeed, pre-*Homo* hominins display many morphological traits consistent with locomotor adaptations to arborealism likely retained from the *Pan*/hominin last common ancestor (Robinson, 1972; Susman and Creel, 1979; Oxnard and Lisowski, 1980; Susman and Stern, 1982; Stern and Susman, 1983; Susman et al., 1984; Susman and Brain, 1988; Grine and Susman, 1991; Asfaw et al., 1999).

The primary mode of locomotion in *Pan* is defined as quadrupedal knuckle-walking, but field observations have shown that qualitative and quantitative differences in particular locomotor behaviors do exist among different chimpanzee (*P. troglodytes* ssp.) and bonobo (*P. paniscus*) communities (Kortlandt, 1962; Van Lawick-Goodall, 1968; Albrecht and Dunnett, 1971; Susman et al., 1980; Hunt, 1989, 1992; Kano, 1992; White, 1992; Doran, 1993a; Doran and Hunt, 1994; Boesch et al., 2002; Stanford, 2002, 2006; Carlson et al., 2008). Locomotor variation in *Pan* may reflect subtle differences in habitat, morphology, the composition of the groups under investigation (e.g. age and sex) and/or field methods (e.g. provisioning vs. non-provisioning, the level of habituation). For instance, Doran (1993a) argued that the hand and wrist anatomy of bonobos is adapted to palmigrady while that of chimpanzees is adapted to knuckle-walking. These morphological distinctions may explain, in part, “the overall reduced usage of arboreal quadrupedalism by chimpanzees since knuckle-walking would, on average, require a larger substrate than palmigrade quadrupedalism," (Doran, 1993a:69). McHenry and Corruccini (1981), however, found that when size differences were removed, chimpanzees and bonobos exhibit essentially identical wrist, elbow, hip and knee joint morphologies.

Given the locomotor behavioral variability observed among chimpanzees and bonobos in the wild, the range of variation in locomotor behavior and its effect on the skeleton should be established within a *Pan* model before that model is used to deduce locomotor behavior in the hominin fossil record. The purpose of the present study is to determine if species and/or subspecies locomotor differences in *Pan* are mechanically discernible by examining ranges of variation in the biomechanical properties of the primary load bearing bones of the fore- and hindlimbs (i.e. the humerus and femur, respectively). Within the broad observational understanding of locomotor behavioral flexibility in *Pan*, the following research questions will be addressed: (1) are femoral cross-sectional geometries distinct in *Pan* at the subspecies-level, species-level or both? And, (2) are humeral cross-sectional geometries distinct in *Pan* at the subspecies-level, species-level or both? If forelimb and hindlimb cross-sectional properties are similar among this specific sample of *Pan*, then taxa can be combined in further analysis. However, if there are significant differences among taxa, then combining taxa is unwarranted since it will introduce noise into the *Pan* model, which may render the model overly robust and less useful for comparative purposes.

Since osseous tissue responds to habitual, mechanical loading throughout life, structural modifications of a long bone at a given section can be examined to reconstruct mechanical loading history (Enlow, 1963; Frost, 1964; Martin and Burr, 1989; Rubin et al., 1990; Ruff et al., 2006). Several studies have applied a biomechanical approach to investigate functional differences in forelimb and hindlimb use within and among many non-human primate taxa (e.g. Schaffler et al., 1985; Burr et al., 1989; Ruff, 1989; Demes et al., 1991; Ruff and Runestad, 1992; Demes and Jungers, 1993; Polk et al., 2000; Demes et al., 2001; Carlson, 2002, 2005; Kimura, 2003; Marchi and Borgognini-Tarli, 2004; Yamanaka et al., 2005; Carlson et al., 2006; Matsumura et al., 2010). Although links between cross-sectional geometric patterns and broad locomotor categories have been established, the relationship between cross-sectional geometries and specific locomotor behaviors has not been determined. One of the reasons for this is the disconnect between field-based and laboratory-based research since behavioral information gathered from individuals observed in the field are generally not the same individuals analyzed in the laboratory. In addition, the relationship between cross-sectional geometry and loading is not completely understood, nor is it straightforward since non-mechanical factors (e.g. genetics, age-related changes, hormonal effects and pathology) can also influence skeletal morphology (Slemenda et al., 1996; Demes et al., 2001; Lovejoy et al., 2003; Volkman et al., 2003, 2004; Lieberman et al., 2004; Pearson and Lieberman, 2004; Demes, 2007). Given these limitations, reconstructing locomotor behavior from a biomechanical perspective should be approached with caution.

There are several mechanical similarities between chimpanzee and bonobo locomotion that have been elucidated from laboratory studies. *P. troglodytes* ssp. and *P. paniscus* display a “bent-hip, bent-knee” posture when walking bipedally and during quadrupedal locomotion (Berge, 1994; Li et al., 1996; Crompton et al., 1998; Schmitt, 2003). Although the “bent-hip, bent-knee” posture is largely a consequence of morphology (Crompton et al., 1998; Preuschoft, 2004), it has also been hypothesized that this posture acts to reduce overall vertical peak forces in the fore- and hindlimbs because weight is shifted posteriorly through the retracted hindlimbs (Taylor, 1985; Alexander, 1992; Schmitt, 1999). Quadrupedal walking in *Pan* involves a diagonal footfall sequence-diagonal couplets gait where a forelimb footfall follows the contralateral hindlimb footfall such that contralateral forelimb-hindlimb pairs are related in time (D’Août et al., 2004; Raichlen et al., 2008). Chimpanzees and bonobos tend to gallop at high velocities rather than trot (Schmitt, 1999; D’Août et al., 2004; Preuschoft 2004; Hanna et al., 2006). Trotting may be an energetically inefficient gait since it leads to high peak stresses on the limbs and high moments of inertia about the hip (D’Août et al., 2004). Vertical peak substrate reaction forces are generally higher in the hindlimbs than in the forelimbs (Preuschoft, 2004; Hanna et al., 2006). Moreover, since the hindlimbs carry and accelerate the body, they are more structurally reinforced relative to the forelimbs, which mainly act to balance and steer the body when quadrupedally moving on the ground (Demes et al., 1994; Kimura, 1995; Preuschoft, 2004).

Although gait kinematics may be similar between chimpanzees and bonobos for a given mode of locomotion, it is also important to stress that kinematics may be similar across modes of locomotion such that mode-specific mechanics may be undetectable in long bone cross-sectional geometries. For instance, D'Août et al. (2004) found overlapping kinesiological characteristics during bipedal and quadrupedal walking in *P. paniscus*, which suggests very subtle kinematic differences in these two locomotor categories. Thus, mechanical similarities within taxa of *Pan* may not necessarily indicate similar locomotor behaviors.

Pan morphology is a compromise between adaptations for arboreal and terrestrial locomotion (Pontzer and Wrangham, 2004). There are slight skeletal differences between chimpanzees and bonobos that may influence locomotion. *P. paniscus* generally has a more gracile upper torso, shorter clavicles, a narrower pectoral girdle, a larger hallux, more curved phalanges, a narrower pelvic girdle, more robust muscular attachments on the femora, relatively shorter arms and longer legs, and smaller articular surfaces compared to chimpanzees (Coolidge, 1933; Roberts, 1974; Zihlman and Cramer, 1978; Corruccini and McHenry, 1979; Susman et al., 1980; Johnson, 1981; McHenry and Corruccini, 1981; Coolidge and Shea, 1982; Doran, 1993a; Doran and Hunt, 1994). One of the most significant morphological differences between chimpanzees and bonobos lies in the shoulder joint. *P. paniscus* is characterized by a long, narrow scapula and an overall scapular shape that resembles the morphology found in *Hylobates* (Coolidge, 1933; Roberts, 1974; Horn, 1976; McHenry and Corruccini, 1981; Susman, 1984; Shea, 1986). Based on these morphological distinctions, some researchers have hypothesized that bonobos should use arboreal locomotor behaviors, especially suspensory behaviors, more frequently than chimpanzees (Roberts, 1974; Johnson, 1981). This has been confirmed by many field observations (e.g. Susman et al., 1980; Hunt, 1991; Doran, 1993a; Doran and Hunt, 1994), but not all (e.g. Horn, 1976, 1979; White, 1992). The morphological distinctions between chimpanzees and bonobos suggest that the latter may resemble the morphology of the *Pan*/hominin last common ancestor more closely since it is more generalized than chimpanzees (Zihlman, 1984; D'Août et al., 2004).

Morphological differences in the postcranial skeleton of *P. troglodytes* ssp. have not been extensively examined, although there are limited data suggesting some morphometric differences among subspecies. Zihlman et al. (2008) found significant differences between Taï (*P. t. verus*) and Gombe (*P. t. schweinfurthii*) communities in iliac breadth, innominate length and acetabular diameter. Differences in humeral, radial and femoral limb lengths were also noted, where Taï chimpanzees were found to have significantly longer bones than Gombe chimpanzees. Limb proportions (e.g. intermembral, humero-femoral, brachial and crural indices), however, were not significantly different (Zihlman et al., 2008).

Given the observational differences in frequencies of specific locomotor behaviors among *Pan* communities in their natural habitat, and the morphological differences between chimpanzees and bonobos that have an affect on locomotion, the following study seeks to examine if such differences significantly influence locomotor behavior to the point where different functional adaptations in bone structure are observed between species of *Pan* and/or among sub-species of *P. troglodytes*.

MATERIALS AND METHODS

Wild-shot *P. troglodytes* ssp. and *P. paniscus* adult skeletal remains housed at the Natural History Museum of Los Angeles County and the Museum of Comparative Zoology (MCZ) at Harvard University were used in this study (Table 1). The right femur was available for all individuals, and was therefore chosen over the left. Since the hindlimbs generally have a single functional role, and since mechanical loading is approximately bilaterally homogeneous in the hindlimbs, only one side was deemed necessary to examine (Ruff and Runestad, 1992; Sarringhaus et al., 2005). The right and left humerus, when available, were examined since the forelimbs have a multifunctional role, some of which may be unrelated to locomotion (Boesch and Boesch, 1990; Ruff and Runestad, 1992; Carlson, 2002, 2005). Age and sex estimates were recorded in the museum catalogs and verified from dental development, and pelvic and cranio-facial morphology, respectively (Anemone et al., 1991; Conroy and Mahoney, 1991; Morbeck et al., 1992; Reid et al., 1998).

Table 1. *Pan* samples.

Specimen	**Species**	**Sex**	**Locality**	**Skeletal Element**
LACM 30545	*P. t. troglodytes*	F	Cameroon	R femur; R/L humerus
LACM 30546	*P. t. troglodytes*	M	Cameroon	R femur; R/L humerus
LACM 30547	*P. t. troglodytes*	F	Cameroon	R humerus
LACM 30548	*P. t. troglodytes*	F	Cameroon	R femur; R/L humerus
MCZ 15312	*P. t. troglodytes*	M	Cameroon, Lolodorf	R femur; R/L humerus
MCZ 19187	*P. t. troglodytes*	M	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 20041	*P. t. troglodytes*	M	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 23163	*P. t. troglodytes*	M	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 23164	*P. t. troglodytes*	F	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 23167	*P. t. troglodytes*	F	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 25950	*P. t. troglodytes*	M	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 26847	*P. t. troglodytes*	F	Cameroon	R femur; R humerus
MCZ 26849	*P. t. troglodytes*	F	Cameroon, Sakbayeme	R femur; R/L humerus
MCZ 48686	*P. t. troglodytes*	M	Equatorial Guinea	R femur; R/L humerus
LACM 51240	*P. t. schweinfurthii*	F	Uganda, Kibale Forest	R femur; R/L humerus
LACM 51239	*P. t. schweinfurthii*	M	Uganda, Kibale Forest	R femur; R/L humerus
BOM 6244	*P. t. verus*	M	West Africa	R femur; R/L humerus
MCZ 38018	*P. paniscus*	M	Dem. Rep. of the Congo	R femur; R/L humerus
MCZ 38019	*P. paniscus*	F	Dem. Rep. of the Congo	R femur; R humerus
MCZ 38020	*P. paniscus*	M	Dem. Rep. of the Congo	R femur; R/L humerus

Samples of chimpanzees were cataloged in museum records as *P. troglodytes* without reference to subspecies. It is well recognized in the primatological literature, however, that there are multiple subspecies of chimpanzees[1], which are largely delimited by geography and confirmed by genetic analyses, superficial morphology (e.g. fur coloring) and cranio-facial morphology (Shea and Coolidge, 1988; Morin et al., 1992; Shea et al., 1993; Morin et al., 1994; Kaessmann et al., 1999; Gonder et al., 2006; Gonder and Disotell, 2006; Zihlman et al., 2008; Oates et al., 2009). Assuming the reported localities of the museum samples are accurate, chimpanzees are allocated to the following subspecies following Gonder and colleagues (1997, 2006): Uganda, Kibale Forest (*P. t. schweinfurthii*), West Africa (*P. t. verus*)[2] and Equatorial Guinea (*P. t. troglodytes*). The samples from Cameroon present with a taxonomic problem since there are potentially two subspecies of *P. troglodytes* in that region—*P. t. vellerosus*[3] in western Cameroon adjacent to Nigeria and *P. t. troglodytes* throughout the rest of the country (Gonder et al., 1997; Gonder et al., 2006). The samples from Lolodorf and Sakbayeme are from southwestern Cameroon. Both localities are south of the Sanaga River, the supposed biogeographic border between *P. t. vellerosus* and *P. t. troglodytes* (Gonder et al., 1997). Thus, they are classified here as *P. t. troglodytes.* The specific localities of five other individuals from Cameroon were not listed in the museum catalogs. They are assumed to be *P. t. troglodytes* since the majority of Cameroon chimpanzees are classified in this taxon (Gonder et al. 2006).

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[1] Although chimpanzee taxonomy is debated, anywhere from three to five subspecies of *P. troglodytes* are recognized (Hill, 1967, 1969; Butynski, 2003; Ely et al., 2005; Groves, 2005, 2006; Inskipp, 2005; Young, 2005; Gonder et al., 2006; Oates et al., 2009).

[2] Morin et al. (1994) have argued that mitochondrial genetic data indicate that *P. t. verus* should be elevated to full species status. Although there is no consensus regarding the taxonomic status of the West African chimpanzee, most researchers consider the West African chimpanzee a subspecies of *P. troglodytes* (e.g. Butynski, 2003; Gonder et al., 2006).

[3] Oates et al. (2009) have argued that *P. t. vellerosus* is a junior synonym of *P. t. troglodytes* since the type specimen was found in Gabon. Therefore, they allocate chimpanzee populations inhabiting the forested areas of Cameroon north and west of the Sanaga River to *P. t. ellioti.*

Locality descriptions

Wild chimpanzees occupy a narrow geographic range that spans discontinuously from western to equatorial central Africa (Kortlandt, 1983; Boesch and Boesch-Achermann, 2000). Wild bonobos occupy an even more restricted territory. They are confined to a ~200,000 km^2 area of primary and secondary forests in the central basin of the Democratic Republic of the Congo (DRC) (Coolidge, 1933; Kano, 1992; White, 1992, 1998; Lacambra et al., 2005) (Fig. 1). Despite their limited geographic distribution, members of the genus *Pan* inhabit a wide variety of environments that range from tropical rain forests to dry savanna-woodlands (Kortlandt, 1962; Reynolds and Reynolds, 1965; Suzuki, 1969; Izawa, 1970; McGrew et al., 1981; Goodall, 1986; Duvall, 2000; Inskipp, 2005; Copeland, 2009).

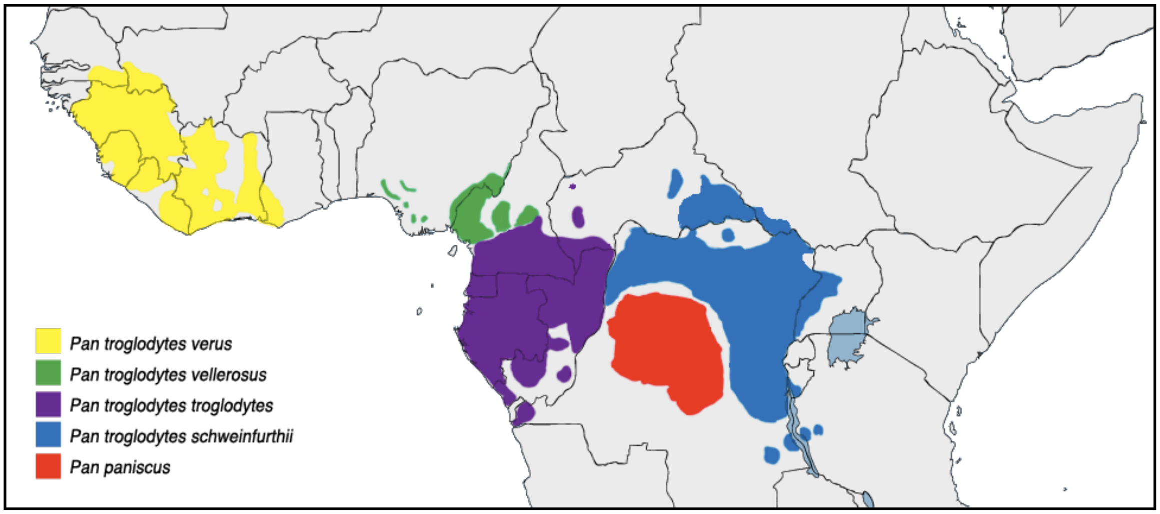


Figure 1. Map of central Africa showing current geographic distributions of *P. troglodytes* ssp. and *P. paniscus*. Adapted from Pope (2006). http://en.wikipedia.org/wiki/File:Pan_spp_range_map.png.

***Uganda, Kibale Forest* (P. t. schweinfurthii).** The Kibale Forest occupies an area of approximately 766 km^2 in southwestern Uganda at an elevation that ranges from 1200 to 1500 m (Chapman et al., 2006). It is a moist, mid-altitude evergreen forest intermixed with lowland rainforest, montane forest, mixed deciduous forest, secondary forest, tall savanna and swamps (Isabirye-Basuta, 1989; Wrangham et al., 1991; Chapman and Wrangham, 1993; Chapman and Lambert, 2000; Carter et al., 2008). The mean annual rainfall is roughly 1475 mm, with rainfall peaks in March-April and September-November (Rode et al., 2003). The average maximum temperature is 24^{o}C and the average minimum temperature is 15.5^{o}C (Rode et al., 2003). There are multiple *P. t. schweinfurthii* communities within the forest (e.g. Kanyawara and Ngogo) (Wrangham et al., 1991; Chapman and Wrangham, 1993; Teelen, 2008). The specific community of the samples in this study is unknown.

***Cameroon* (P. t. troglodytes).** Chimpanzees inhabit several areas in Cameroon including sites near Mount Cameroon, Takamanda Forest Reserve, Korup National Park, Bwombi-Mwo Forest Reserve, Mount Kupe, Douala-Edea Reserve, Campo Reserve and Dja (Sunderland-Groves et al., 2003; Matthews and Matthews, 2004; Deblauwe and Janssens, 2008). One individual in this study is from Lolodorf (3° 14′ N, 10° 44′ E), a small community in the Océan Department of the South Province. Seven individuals are from Sakbayeme (4° 1′ N, 10° 34′ E), a small town just south of the Sanaga River in the Sanaga-Martime Department of the Littoral Province. The climate in southwestern Cameroon (i.e. Lolodorf and Sakbayeme) is tropical with average temperatures between 23 to 27^{o}C and an annual rainfall between 1500 to 2000 mm (van Gemerden et al., 2003). The wet seasons are from March to May, and from August to November (van Gemerden et al., 2003). The exact localities of five other individuals from Cameroon were not listed in the museum catalogs.

The vegetation that covers much of Cameroon is classified as Guineo-Congolian evergreen rainforest (White, 1979; Plana, 2004). This ecosystem covers an area roughly 2.8 million km^2 across equatorial Africa, and is physically divided into two blocks on either side of the Dahomey Gap (White, 2001). The Dahomey Gap is part of the Guinean forest-savanna mosaic that extends to the coasts in Benin, Togo and Ghana (White, 1979) Vegetation within the Guineo-Congolian zone consists mostly of woody plants with forest canopies near 30 m high and emergent trees greater than 60 m high (White, 2001). Altitudinal gradients are typically less than 1000 m nearly everywhere within the Guineo-

Congolian zone (White, 2001). In rare areas with higher altitude, the vegetation becomes Afromontane (White, 2001).

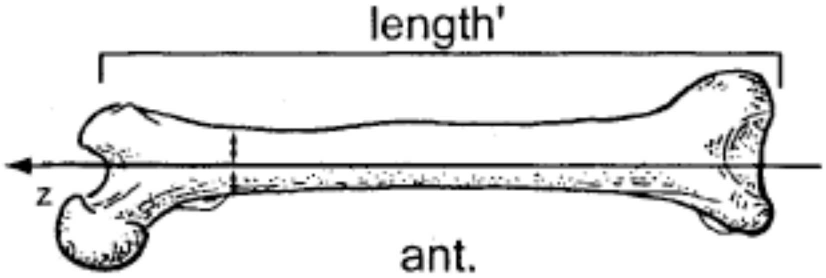
Equatorial Guinea **(P. t. troglodytes).** The single individual from Equatorial Guinea comes from the Great Forest of Ayamiken, which is north of the port city of Bata and south of the Cameroon border. Equatorial Guinea is within the Guineo-Congolian evergreen rainforest zone (Plana, 2004). Temperatures are generally high and constant with an average of 25°C and an annual relative humidity of ~90% (Jones, 1971). Heavy rainfall occurs during the wet seasons, which are from February to June, and from September to December (Jones, 1971). The average annual rainfall around Bata is 2000 mm (Jones, 1971).

West Africa **(P. t. verus).** *P. t. verus* is discontinuously distributed in nine or ten countries from southeastern Senegal east to the Dahomey Gap or the Niger River (Butynski, 2003; Inskipp, 2005). *P. t. verus* occupies a wide range of habitats within West Africa. For instance, the chimpanzees of Mount Assirik in eastern Senegal inhabit a very hot and dry environment dominated by drought-resistant deciduous lowland woodland (37%), plateau (28%) and open grassland (27%) (McGrew et al., 1981; Copeland, 2009). Only 3% of the vegetation is gallery forest and about 5% is bamboo thicket (Copeland, 2009). Chimpanzees at Fongoli, which is 45 km from Mount Assirik, occupy woodland, grassland or plateau habitats (Pruetz, 2006; Copeland, 2009). *P. t. verus* at Bossou, Guinea, occupy secondary and scrub forests, but occasionally traverse through gallery forest corridors to reach areas outside their core home range (Humle and Matsuzawa, 2001). Chimpanzees at Taï National Park, Côte d'Ivoire, inhabit an undisturbed, closed canopy primary rainforest (Boesch and Boesch-Achermann, 2000). The provenience of the single West African chimpanzee individual included in this study is unknown.

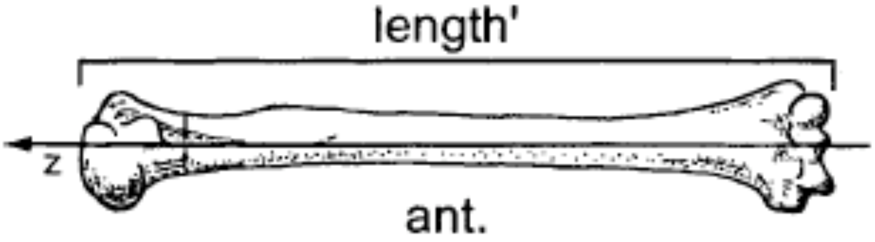
Democratic Republic of the Congo (DRC) **(P. paniscus).** Bonobos are largely restricted to a lowland, primary forest habitat, but may occasionally forage in swampy, seasonally flooded forest environments (e.g. Lake Tumba) (White, 1992; Kortlandt, 1995; Hashimoto et al., 1998; Myers-Thompson, 2003; Reinartz et al., 2006; Inogwabini et al., 2007). Their distribution in the Congo Basin of the DRC is bounded by two river systems: the Congo-Zaire-Walaba River and the Kwa-Kasai-Sankuru River (Kortlandt, 1995). The *P. paniscus* samples in this study are from 25 km south of the town of Stanleyville (now Kisangani) in the Tshopo Province. Kisangani lies just north of the Equator within the Congo Basin along the Congo River in the northwest part of the country. It is surrounded by closed canopy, lush tropical rainforest (Leonard, 2006). The climate for much of the DRC is tropical with an average temperature of 27^{o}C and average annual rainfall between 1500 to 2000 mm (Leonard, 2006).

Osteometrics

Maximum femur and humerus lengths were measured with an osteometric board and recorded to the nearest millimeter. Femur length′ and humerus length′ were measured following Ruff (2002). Femur length′ is defined as the longitudinal length of the diaphysis from just medial to the greater trochanter to the average position of the distal edges of the condyles (Ruff, 2002), and humerus length′ is defined as the longitudinal line from the most proximal point on the humeral head to the lateral lip of the trochlea (Ruff, 2002) (Fig. 2). Cross-sectional locations were taken at 50% (midshaft) and 80% (proximal) of femur length′. To avoid the deltoid tuberosity, humeral cross-sections were taken at 40% of length′ from the distal end.



(a)



(b)

Figure 2. Length′ measurement for the femur (a) and humerus (b). Adapted from Ruff (2002).

Cross-sectional reconstructions

Engineering beam theory predicts that the most mechanically relevant material is located furthest from the section centroid (Ruff and Hayes, 1983; Bertram and Swartz, 1991; Frassica et al., 1997; O'Neill and Ruff, 2004). Therefore, accurate reconstructions of the periosteal surface "should be the most important factor in calculating cross-sectional properties," (Stock, 2002:336). Periosteal and endosteal contours were reconstructed at specified section locations following the latex cast method as described by Stock (2002). Latex casts of the periosteal surface were made using hydrophilic polysiloxane dental impression material (Exaflex®, GC America Inc.). Each cast was marked on its anterior surface, which was oriented perpendicular to the diaphyseal long axis of the bone. The casts were allowed to harden, and then cut from the medial surface. The consistent marking and cutting of the casts ensured that they would be oriented in correct anatomical position during the digitization process.

Endosteal contours were reconstructed from measurements of cortical wall thicknesses, which were derived from bi-planar digital radiographs. Section locations were marked with metal wire prior to x-raying, and a scaling device was included in each shot to correct for magnification[4]. Bones were placed in the x-ray machine in standard

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[4] Magnification factor (z)= y/x where y is the length of the scaling device on the x-rayed image and x is the actual length of the scaling device. A metal bar was used as a scaling device. The measurement on the x-rayed image was divided by z to correct for magnification (Jaundrell-Thompson and Ashworth, 1970).

anatomical position and oriented following Ruff and Hayes (1983) and Ruff (2002). Diaphyses were leveled by placing pieces of clay under the shaft so that the antero-posterior (A-P) midpoints of the proximal and distal ends of the bone were equidistant from the image receptor.

A Faxitron model 43855 C digital x-ray machine was used at the Natural History Museum of Los Angeles County. The source to image distance was 76 cm with a focal spot size of 0.5 mm. The tube current was held constant at 3 mA and the voltage ranged from 60 to 70 kVp. Exposures times ranged from 4 to 8 min depending on the sample. A Thermo Kevex model PXS10-16W digital x-ray machine was used at the MCZ. Source to image distance was 74 cm with a focal spot size of 0.008 mm. The tube current ranged from 34 to 41 mA and the voltage ranged from 70 to 85 kVp depending on the sample. Exposure times varied from 20 to 30 sec.

Digitized radiographic images were enhanced in Adobe Photoshop® and magnified by 300-400% to measure anterior, posterior, medial and lateral cortical thicknesses. Size-adjusted measurements were plotted in correct anatomical position on the periosteal tracings, and the points were connected in an ellipse following the periosteal contours. The reconstructed cross-sectional images were digitized using a Lexmark X 6170 flatbed scanner. Although images were scanned at the same size as the original, a scaling device was included to ensure that the size of the images was not compromised during digitization. Cross-sectional properties were calculated using a Macintosh version of MomentMacro written for ImageJ, which is available courtesy of Dr. Christopher Ruff at http://www.hopkinsmedicine.org/FAE/mmacro.htm.

Cross-sectional properties

The cross-sectional properties calculated in this study are presented in Table 2.

Table 2. Cross-sectional properties.

Symbol	Definition	Mechanical Significance
TA	total subperiosteal area	area within subperiosteal surface
CA	cortical area	axial compressive and tensile strength
%CA	percent cortical area	percentage of cortical bone in the section
$J^{0.73}$	estimates the polar section modulus	torsional and twice average bending strength
Z_x	section modulus about the M-L axis	bending strength in the A-P plane
Z_y	section modulus about the A-P axis	bending strength in the M-L plane
Z_x/Z_y	diaphyseal shape index	ratio of A-P bending strength to M-L bending strength
Z_{max}	maximum section modulus	maximum bending strength
Z_{min}	minimum section modulus	minimum bending strength
Z_{max}/Z_{min}	diaphyseal shape index	ratio of maximum to minimum bending strength

Cortical area (CA) represents the axial compressive and tensile strengths of the section (Ruff et al., 1993; Marchi and Borgognini-Tarli, 2004). Percent cortical area (%CA) is an expression of the relative amount of cortical bone in the cross-section and can be used as a proxy for bone mass (Ruff and Hayes, 1983; Ruff et al., 1993). %CA is calculated as CA/total area (TA) · 100, and does not vary with body size (Ruff et al., 1993). Cross-sectional areas and %CA quantify the absolute and relative amounts, respectively, of bone in a cross-section. CA and TA are reported in mm^2.

The section modulus represents the bending strength[5] of a bone at a measured section (Ruff, 2000, 2008). Section moduli are considered the best estimates of average bending and torsional strength when mechanical loading conditions are unknown (Ruff, 2008). Given locomotor behavioral flexibility in *Pan* and the lack of behavioral data for this sample, specific mechanical loading conditions are deemed uncertain. Z_x (A-P

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[5] Rigidity and strength are often used interchangeably, but they refer to somewhat different, albeit related, structural properties of a material. Rigidity is a measure of the internal resistance of a structure to an externally applied force (or mechanical load), while strength is the maximum stress sustained by a structure before failure (Reilly and Burstein, 1974). Second moments of area measure rigidity, while section moduli measure strength (Ruff, 2008).

bending strength) and Z_y (M-L bending strength) measure the maximum stress in the outermost fiber of the cross-section in the anatomical plane of bending (Ruff and Hayes, 1983; Ruff, 1995, 2008b; Marchi, 2008). Z_{max} (maximum bending strength) is the maximum section modulus about the major principal axis, and Z_{min} (minimum bending strength) is the minimum section modulus about the minor principal axis (Ruff, 2000; Marchi, 2008). Z_{max} and Z_{min} are perpendicular to each other (Ruff and Hayes, 1983; Brock and Ruff, 1988). The polar section modulus, Z_p, is a measure of twice average bending and torsional strength, and can be approximated by taking the polar second moment of area to the power of 0.73 (i.e. $J^{0.73}$) (Ruff, 1995, 2008b; Trinkaus and Ruff, 1999)[6]. Section moduli are reported in mm^3.

Ratios of section moduli (i.e. Z_x/Z_y and Z_{max}/Z_{min}) give an overall indication of diaphyseal shape by comparing the relative distribution of CA along anatomical (Z_x/Z_y) and principal (Z_{max}/Z_{min}) axes (Jungers and Minns, 1979; Ruff, 1987; Carlson, 2002). Bones subjected to bending in a single plane are less circular (i.e. a ratio departing from 1.0) since bending strength is determined by the relative distribution of bone perpendicular to the plane of bending (Ruff and Hayes, 1983; Carlson, 2005). Bones predominately subjected to torsion tend to have a more circular cross-sectional shape (i.e. a ratio approaching 1.0) since torsional strength is determined by the radial distribution of bone about the centroid (Ruff and Hayes, 1983). In addition, diaphyseal circularity is a stable solution when multidirectional loads are experienced because it lessens the susceptibility to failure in a single plane (Biewener, 2003; Carlson, 2005).

Body size standardization

To control for the influence of body size on bone structure, cross-sectional areas are generally standardized to body mass, and section moduli are generally standardized to the product of body mass and maximum bone length (Schaffler et al., 1985; Ruff, 2000). The results presented in this chapter include unstandardized cross-sectional data since

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[6] Section moduli (Z_x, Z_y, Z_{max} and Z_{min}) can also be approximated by taking second moments of area (I_x, I_y, I_{max} and I_{min}) to the power of 0.73. MomentMacro calculates Z_x and Z_y. Maximum (I_{max}) and minimum (I_{min}) bending rigidities were raised to the power of 0.73 to approximate Z_{max} and Z_{min}, respectively.

body mass estimates and maximum bone lengths were not significantly different among the groups.

Statistics

Differences among group medians are examined with non-parametric Median tests with a Monte Carlo resampling method because of the limited sample size. Box-plots are used here to visually examine the data. The box represents the interquartile range, the line across the box represents the sample median and the "whiskers" represent the interquartile range. The location of the box between the "whiskers" and the location of the median within the box describe how the data are distributed. A box in the middle of the "whiskers" suggests an even distribution, a box closer to the upper "whisker" indicates that the data are skewed upwards and a box closer to the lower "whisker" indicates the opposite. Outliers are marked by open circles and extreme outliers are marked by asterisks. Coefficients of variation for each cross-sectional property are calculated (coefficient of variation= standard deviation/mean) to examine the variation within each group. Coefficients of variation express the standard deviation as a percentage of the sample mean. These values are compared to the coefficients of variation for the combined group to determine if combining the groups increases the amount of variation.

Bivariate scatterplots are used to examine axial loading (i.e. CA) relative to average bending and torsional strength (i.e. $J^{0.73}$) in the proximal and midshaft femur, and in the mid-distal right and left humerus. CA is expected to be relatively greater than $J^{0.73}$ in species that emphasize axial loading rather than bending and torsional loading (Ruff and Runestad, 1992). African apes that experience active propulsion in the hindlimbs are generally characterized by a decrease in axial loading relative to average bending and torsional strength (Ruff and Runestad, 1992). Midshaft femoral strength ($J^{0.73}$) relative to humeral strength ($J^{0.73}$) is also examined in order to investigate the relative loading in the hindlimbs compared to the forelimbs. Cross-sectional properties were log-transformed because of differences in scale. Statistical analyses were carried out with *SPSS* 17.0. Statistical significance is $p= 0.05$.

RESULTS

Although sex differences in frequencies of specific locomotor behaviors in *Pan* have been observed in the field (Doran, 1993b, 1996; Doran and Hunt, 1994), combined-sex analyses were conducted here to increase sample size within each group. A limitation to this approach, however, is that sex-differences are ignored and may contribute to group differences if an unequal number of males and females is represented in each group. Sex differences due to size, however, are probably not significant since there is relatively low body size sexual dimorphism in *Pan* compared to other non-human primates (Leutenegger and Kelly, 1977; Mobb and Wood, 1977; Reno et al., 2003). Observable pathology was not noted on any of the femora. However, the right humerus of a male *P. t. troglodytes* individual (MCZ 15312) presented with an unusually robust deltoid tuberosity and evidence of periosteal reaction in the antero-lateral surface of the upper third of the diaphysis. In addition, the diaphysis was slightly twisted longitudinally near the midshaft. Since these irregularities may influence the functional use of the right forelimb, special attention is paid to this individual in the humeral analysis.

Proximal femur

Median cross-sectional properties in the proximal femur are not significantly different among the groups (Table 3).

Table 3. Median test for the proximal femur.

		TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_x/Z_y	Z_{max}	Z_{min}	Z_{max}/Z_{min}
N		19	19	19	19	19	19	19	19	19	19
Median		438.04	273.14	65.28	1630.68	903.94	1098.65	0.81	1111.28	795.10	1.43
Chi-Square		3.98[a]	3.37[a]	5.89[a]	3.98[a]	3.98[a]	3.98[a]	1.36[a]	3.98[a]	3.98[a]	3.98[a]
df		3	3	3	3	3	3	3	3	3	3
Asymp. Sig.		0.26	0.34	0.12	0.26	0.26	0.26	0.72	0.26	0.26	0.26
Monte Carlo Sig.		0.36[b]	0.59[b]	0.12[b]	0.36[b]	0.36[b]	0.36[b]	1.00[b]	0.36[b]	0.36[b]	0.36[b]
99% Conf. Interval	Lo. Bnd.	0.35	0.57	0.11	0.35	0.35	0.35	1.00	0.35	0.35	0.35
	Up. Bnd.	0.37	0.60	0.12	0.37	0.37	0.37	1.00	0.37	0.37	0.37

a. 6 cells (75.0%) have expected frequencies less than 5. The minimum expected cell frequency is .5.
b. Based on 10000 sampled tables with starting seed 2000000.

Ranges of variation in proximal femoral TA and CA overlap extensively among the groups (Fig. 3). Even when the *P. t. troglodytes* outlier is removed from the analysis, median TA values are not significantly different among the groups (p= 0.20).

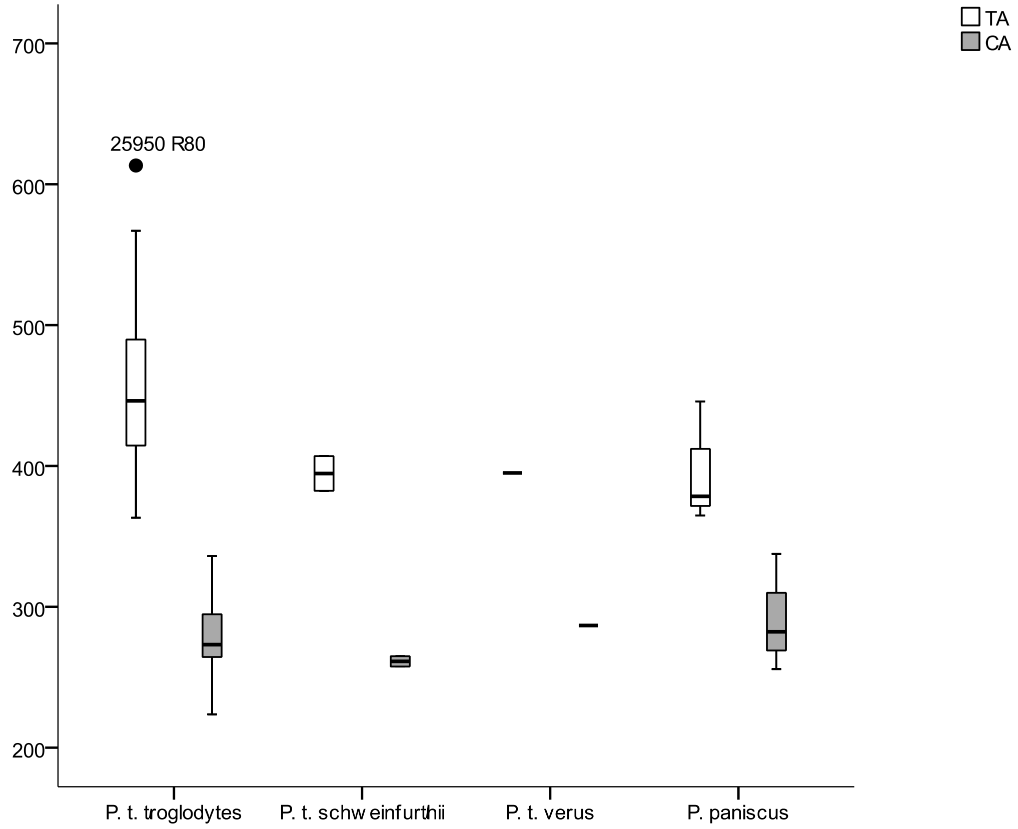

Figure 3. Box-plot of total area (TA) and cortical area (CA) in the proximal femur among the groups.

Ranges of variation in %CA overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. %CA in *P. t. verus* is encompassed within the ranges of variation in *P. t. troglodytes* and *P. paniscus* (Fig. 4). When the two *P. t. troglodytes* outliers are removed from the analysis, median %CA approaches significance (p= 0.06).

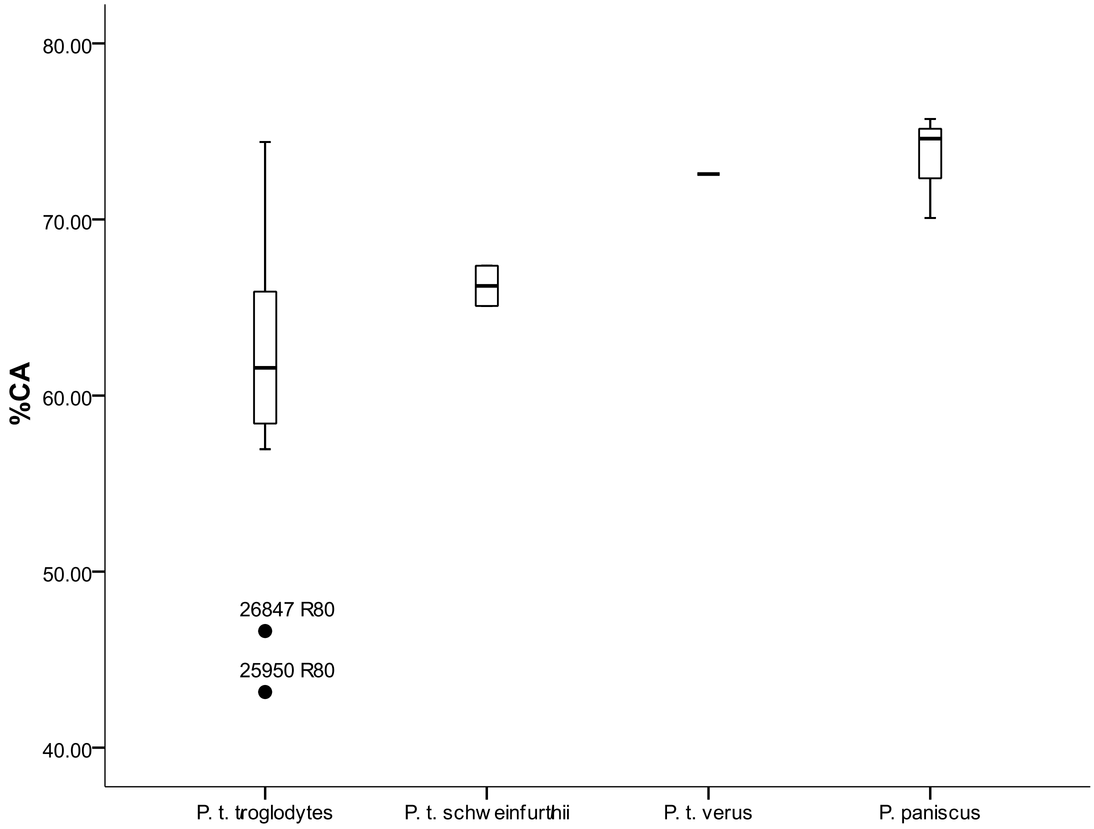

Figure 4. Box-plot of percent cortical area (%CA) in the proximal femur among the groups.

Ranges of variation in $J^{0.73}$ overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. $J^{0.73}$ in *P. t. verus* is encompassed within the ranges of variation in the other three groups (Fig. 5). Thus, average bending and torsional strength in the proximal femur is similar among the taxa.

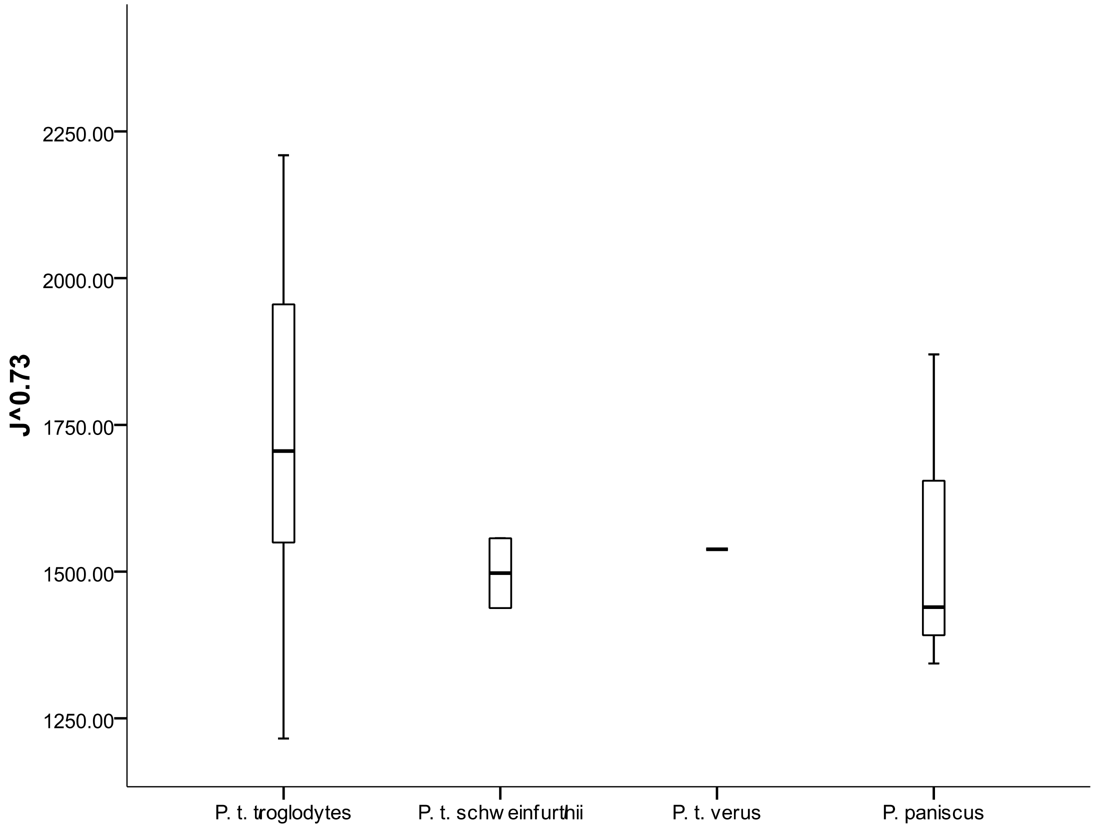

Figure 5. Box-plot of average bending and torsional strength ($J^{0.73}$) in the proximal femur among the groups.

Ranges of variation in Z_x overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. The Z_x value in *P. t. verus* falls within the lower range of variation in *P. t. troglodytes.* Ranges of variation in Z_y overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. The Z_y value in *P. t. verus* falls within the ranges of variation in *P. t. troglodytes* and *P. paniscus* (Fig. 6).

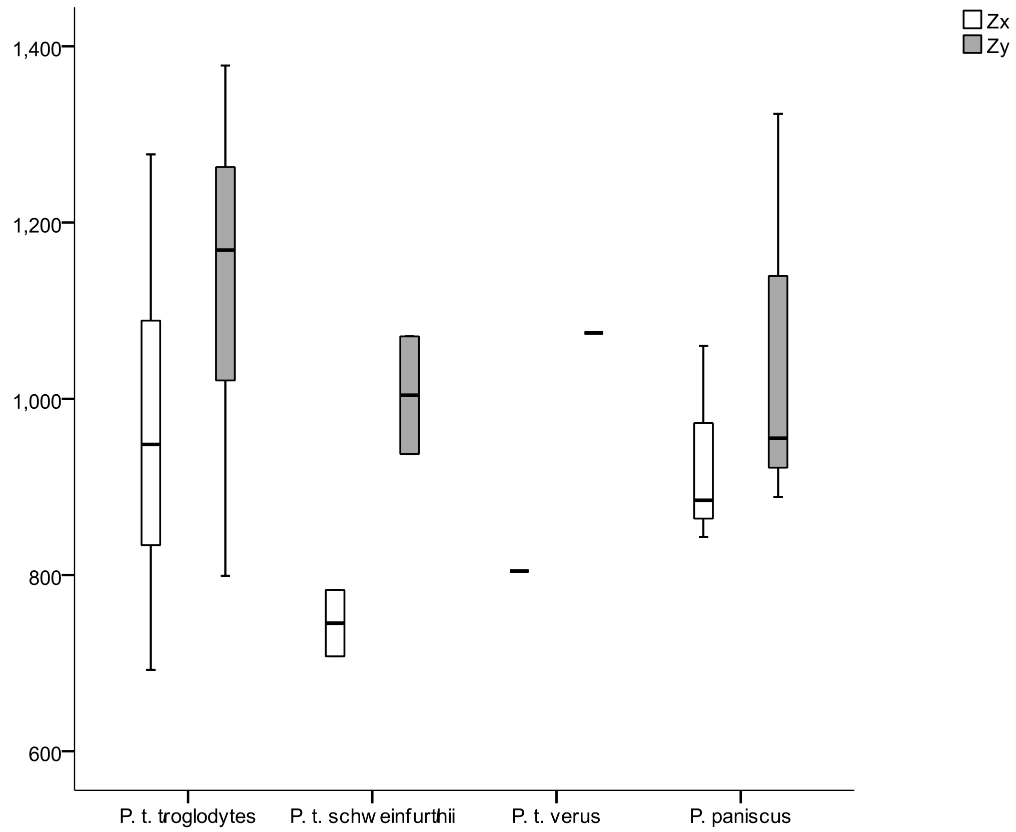

Figure 6. Box-plot of bending strength in the A-P plane (Z_x) and bending strength in the M-L plane (Z_y) in the proximal femur among the groups.

Ranges of variation in Z_x/Zy overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Z_x/Z_y in *P. t. verus* is encompassed within the ranges of variation in the other two chimpanzee subspecies, but not within the range of variation in *P. paniscus* (Fig. 7). All taxa of *Pan* generally show a common pattern in greater bending strength in the M-L plane relative to the A-P plane in the proximal femur (i.e. $Z_x/Z_y < 1.0$), although the range of variation in *P. t. troglodytes* indicates that some individuals show greater bending strength in the A-P plane relative to the M-L plane (i.e. $Z_x/Z_y > 1.0$).

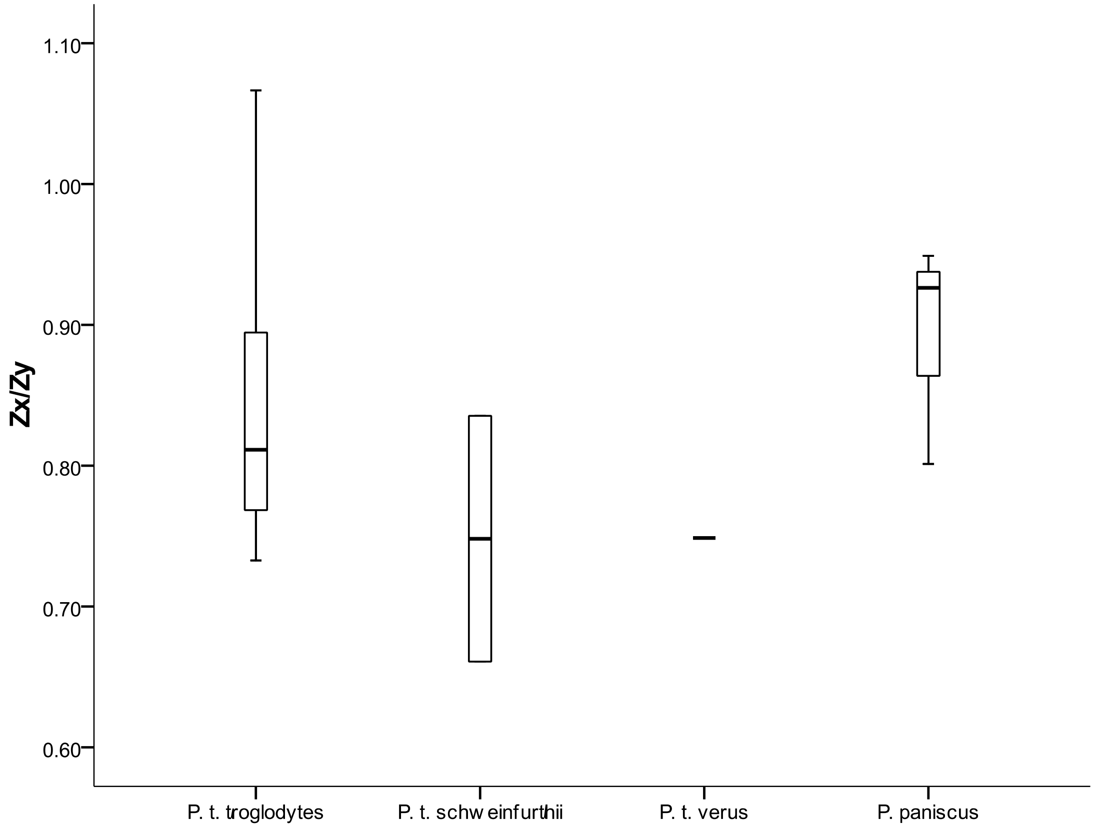

Figure 7. Box-plot of diaphyseal shape (Z_x/Z_y) in the proximal femur among the groups.

Ranges of variation in Z_{max} overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. The Z_{max} value in *P. t. verus* is encompassed within the ranges of variation in the other three groups. Ranges of variation in Z_{min} overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. The Z_{min} value in *P. t. verus* is encompassed within the ranges of variation in *P. t. troglodytes* and *P. t. schweinfurthii* (Fig. 8). When the *P. t. troglodytes* outlier is removed from the analysis, median Z_{min} is still not significantly different among the groups (p= 0.46).

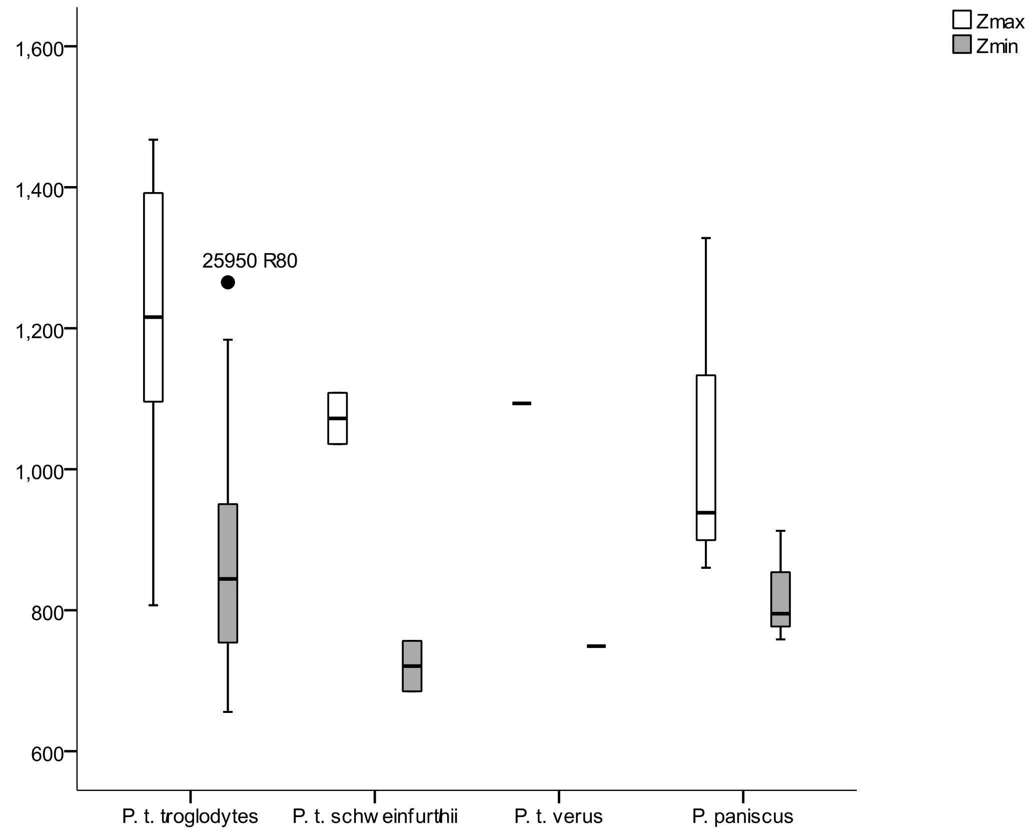

Figure 8. Box-plot of maximum bending strength (Z_{max}) and minimum bending strength (Z_{min}) in the proximal femur among the groups.

Ranges of variation in Z_{max}/Z_{min} overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. Z_{max}/Z_{min} in *P. t. verus* is encompassed within the range of variation in *P. t. troglodytes*, just below the range of variation in *P. t. schweinfurthii* and just above the range of variation in *P. paniscus* (Fig. 9).

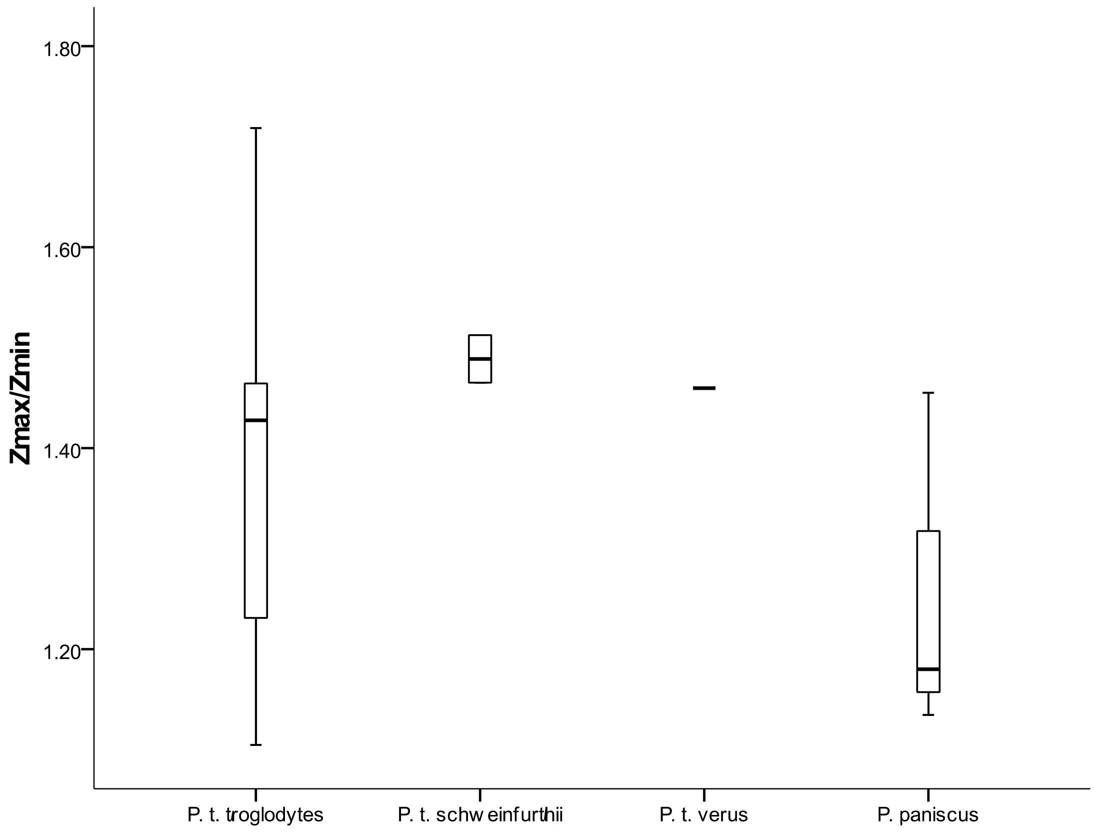

Figure 9. Box-plot of diaphyseal shape (Z_{max}/Z_{min}) in the proximal femur among the groups.

Coefficients of variation for *P. t. troglodytes*, *P. t. schweinfurthii*, *P. paniscus* and the combined sample are presented in Table 4. Coefficients of variation for *P. t. verus* are not calculated since n= 1. There is more variation in *P. t. troglodytes* than in *P. t. schweinfurthii* and *P. paniscus* in TA, %CA, Z_x and Z_{min}. There is more variation in *P. t. schweinfurthii* than in *P. t. troglodytes* and *P. paniscus* in Z_x/Z_y. There is more variation in *P. paniscus* than in the chimpanzee subspecies in CA, $J^{0.73}$, Z_y, Z_{max} and Z_{max}/Z_{min}. When the samples are combined, coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*. Coefficients of variation in Z_y and Z_{max} are slightly greater (1%) in the combined sample than in *P. t. troglodytes*. These results indicate that combining the samples does not significantly increase the variability expressed within *P. t. troglodytes*. These results also suggest that sex differences in proximal femoral cross-sectional properties in *P. t. schweinfurthii*, which is represented by one male and one female, are low. The exception is with regard to diaphyseal shape (Z_x/Z_y), which has a much larger coefficient of variation than any other property in *P. t. schweinfurthii*. Coefficients of variation in *P. paniscus* are high, which may reflect sex differences since two males and one female are sampled.

Table 4. Coefficients of variation in the proximal femur.

	Coefficients of Variation			
	P. t. troglodytes	*P. t. schweinfurthii*	*P. paniscus*	Combined[a]
TA	0.15	0.04	0.11	0.15
CA	0.11	0.02	0.14	0.11
%CA	0.15	0.02	0.04	0.14
$J^{0.73}$	0.16	0.06	0.18	0.16
Z_x	0.18	0.07	0.12	0.18
Z_y	0.14	0.09	0.22	0.15
Z_x/Z_y	0.13	0.16	0.09	0.13
Z_{max}	0.16	0.05	0.24	0.17
Z_{min}	0.21	0.07	0.10	0.19
Z_{max}/Z_{min}	0.13	0.02	0.14	0.13

a. Includes *P. t. verus*.

Summary. Median proximal femoral cross-sectional properties are not significantly different among the groups. Ranges of variation in proximal femoral cross-sectional properties generally overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Although *P. t. veru*s is only represented by a single individual, cross-sectional properties are consistently encompassed within the ranges of variation in *P. t. troglodytes*, and often within the ranges of variation in the other two groups as well. Coefficients of variation generally decrease when the groups are combined compared to the coefficients of variation in the largest group (i.e. *P. t. troglodytes*). This suggests that combining the samples does not increase the variability. The results generally indicate that cross-sectional properties in the proximal femur among these specific samples of *Pan* are not markedly distinct.

Midshaft femur

Median cross-sectional properties are not significantly different among the groups except with regard to %CA (Table 5).

Table 5. Median test for the midshaft femur.

		TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_x/Z_y	Z_{max}	Z_{min}	Z_{max}/Z_{min}
N		19	19	19	19	19	19	19	19	19	19
Median		428.93	272.87	64.22	1612.85	959.47	1040.20	0.86	1062.82	881.16	1.25
Chi-Square		3.98^a	1.36^a	7.89^a	3.98^a	3.98^a	3.98^a	1.36^a	3.98^a	3.98^a	1.98^a
df		3	3	3	3	3	3	3	3	3	3
Asymp. Sig.		0.26	0.72	0.05	0.26	0.26	0.26	0.72	0.26	0.26	0.58
Monte Carlo Sig.		0.36^b	1.00^b	**0.02**^{b}	0.36^b	0.36^b	0.36^b	1.00^b	0.36^b	0.36^b	0.66^b
99% Conf. Interval	Lo. Bnd.	0.35	1.00	0.02	0.35	0.35	0.35	1.00	0.35	0.35	0.65
	Up. Bnd.	0.37	1.00	0.02	0.37	0.37	0.37	1.00	0.37	0.37	0.68

a. 6 cells (75.0%) have expected frequencies less than 5. The minimum expected cell frequency is .5.
b. Based on 10000 sampled tables with starting seed 2000000.
Significance is indicated in bold.

Ranges of variation in TA and CA overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. TA in *P. t. verus* falls within the ranges of variation in the other groups, and CA in *P. t. verus* falls just within the lower range of variation in *P. t. troglodytes* (Fig. 10).

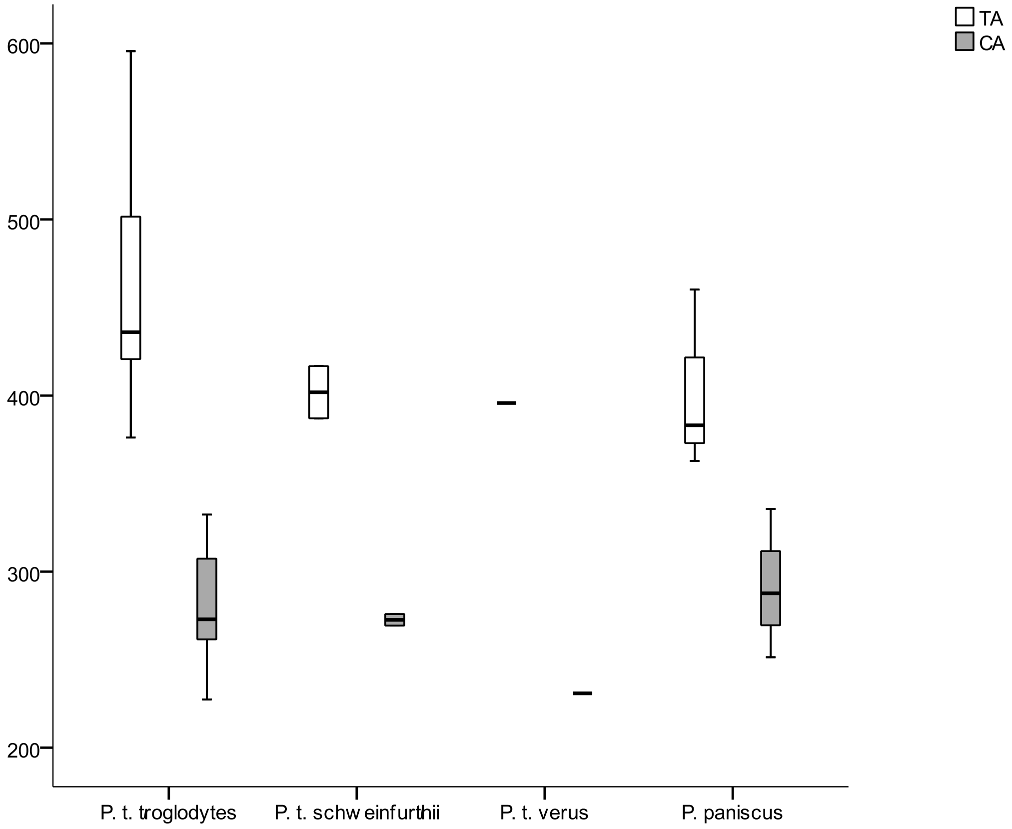

Figure 10. Box-plot of total area (TA) and cortical area (CA) in the midshaft femur among the groups.

Ranges of variation in %CA overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. %CA in *P. t. verus* is encompassed within the lower range of variation in *P. t. troglodytes* (Fig. 11). The Median test indicates that %CA is significantly different among the groups. Significance remains even when the *P. t. troglodytes* outliers are removed from the analysis (p= 0.02).

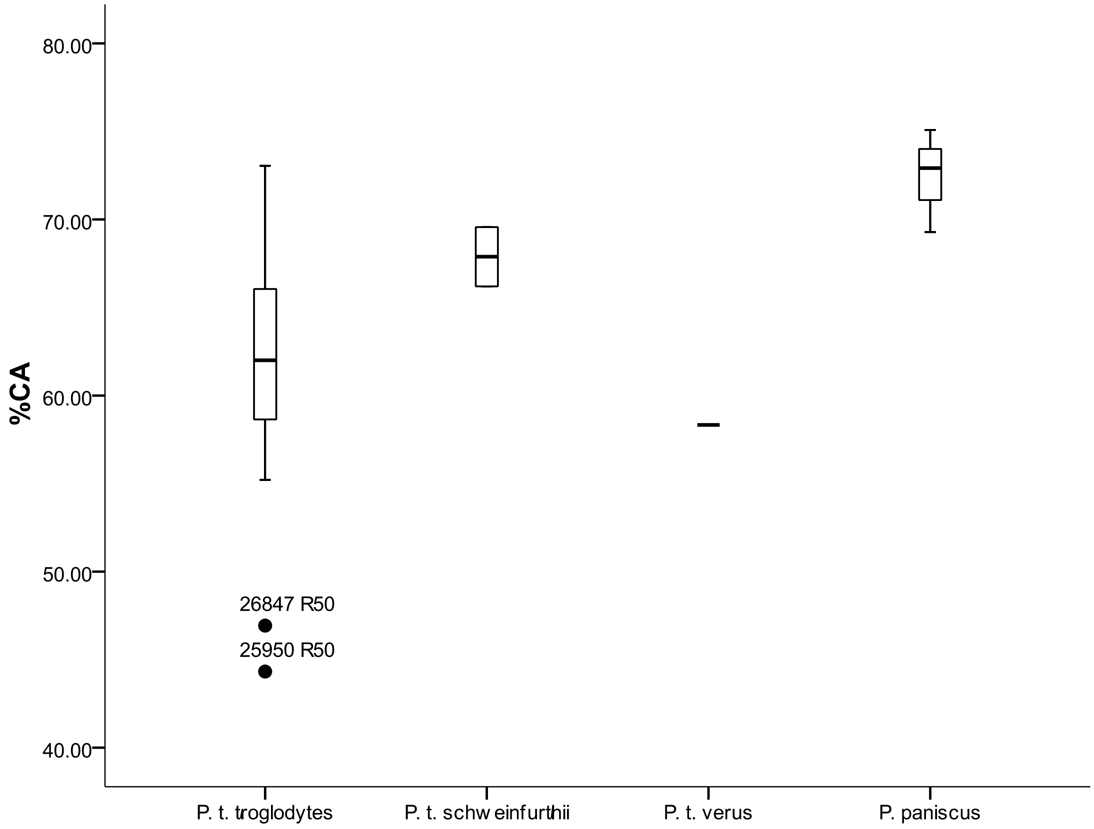

Figure 11. Box-plot of percent cortical area (%CA) in the midshaft femur among the groups.

Ranges of variation in $J^{0.73}$ overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. $J^{0.73}$ in *P. t. verus* is encompassed within the lower ranges of variation in *P. t. troglodytes* and *P. paniscus* (Fig. 12).

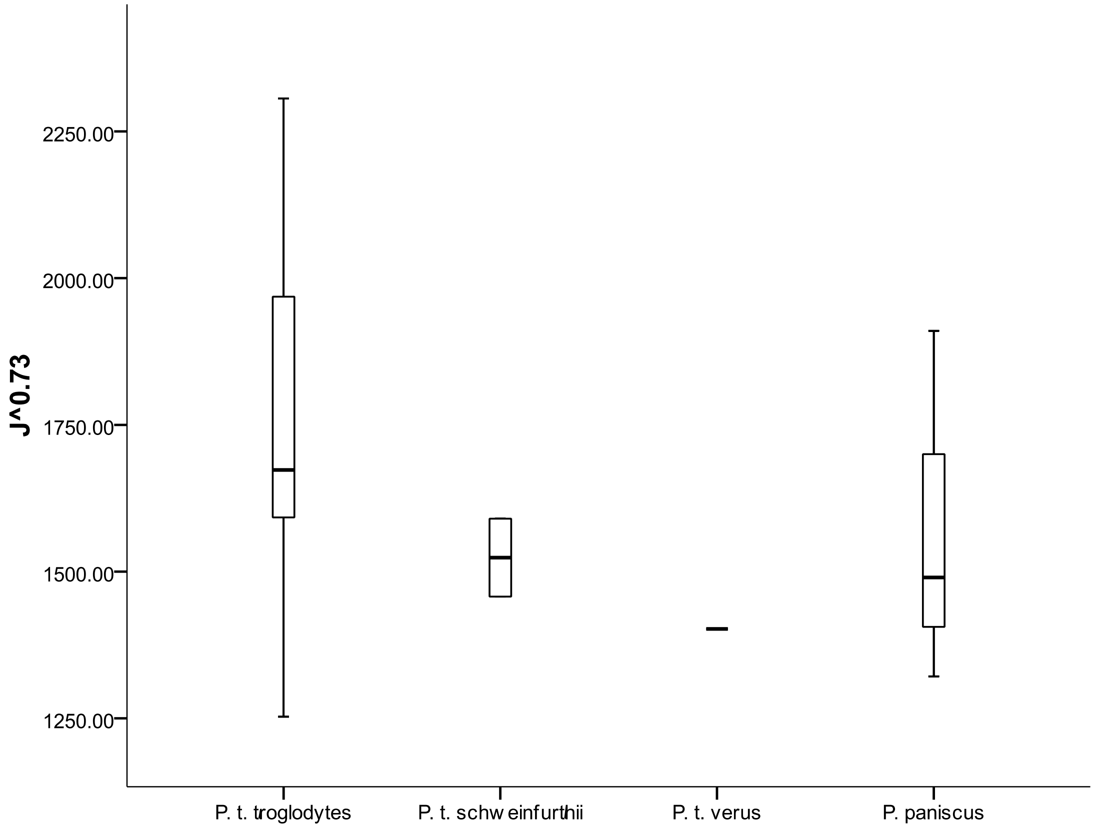

Figure 12. Box-plot of average bending and torsional strength ($J^{0.73}$) in the midshaft femur among the groups.

Ranges of variation in Z_x and Z_y overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Z_x in *P. t. verus* is encompassed within the lower range of variation in *P. t. troglodytes*, and Z_y is encompassed within the ranges of variation in *P. t. troglodytes* and *P. paniscus* (Fig. 13).

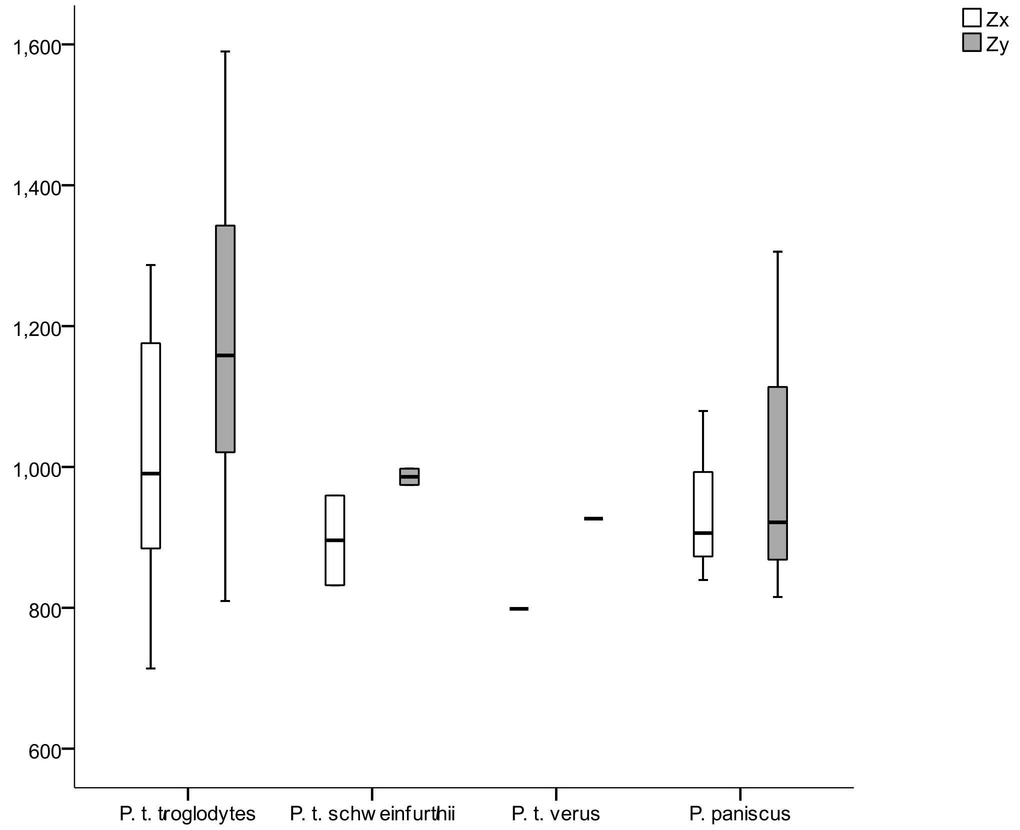

Figure 13. Box-plot of bending strength in the A-P plane (Z_x) and bending strength in the M-L plane (Z_y) in the midshaft femur among the groups.

Diaphyseal shape based on anatomical axes (i.e. Z_x/Z_y) is similar among the groups. Ranges of variation overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*, and the Z_x/Z_y value in *P. t. verus* is encompassed within the ranges of variation in the other groups (Fig. 14). All taxa of *Pan* generally show an increase in bending strength in the M-L plane relative to bending strength in the A-P plane (i.e. $Z_x/Z_y < 1.0$).

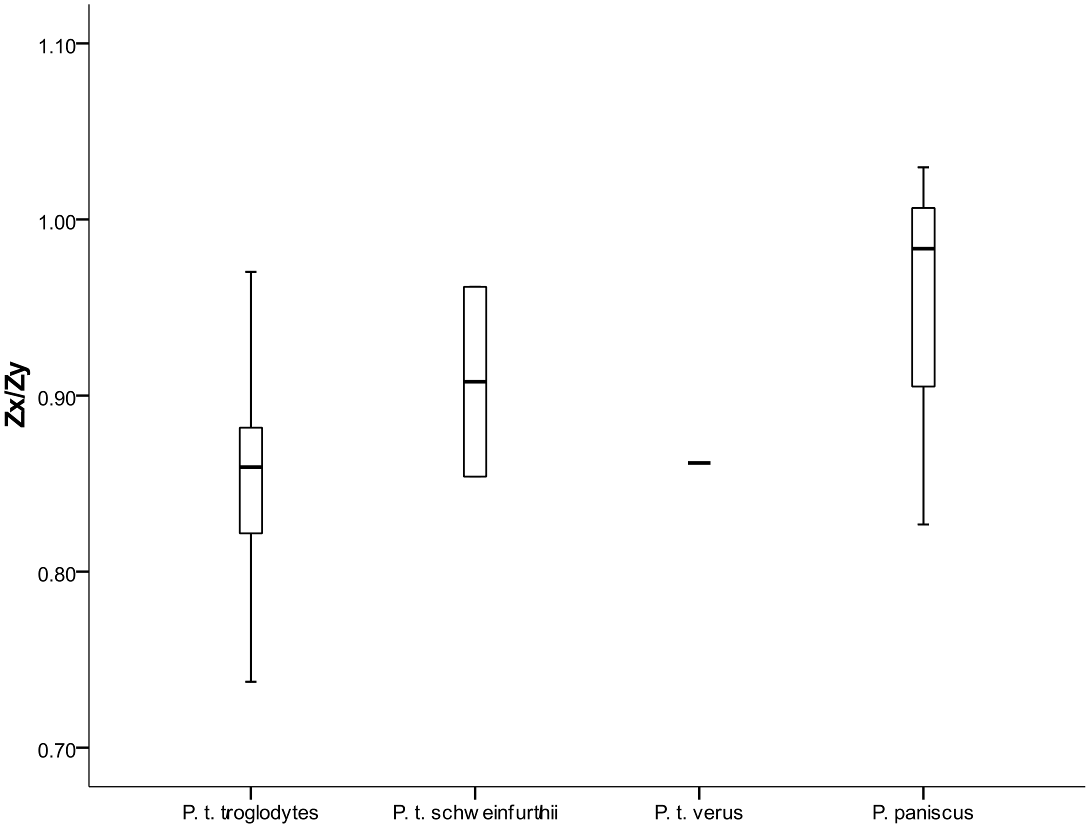

Figure 14. Box-plot of diaphyseal shape (Z_x/Z_y) in the midshaft femur among the groups.

Ranges of variation in Z_{max} and Z_{min} overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Z_{max} and Z_{min} in *P. t. verus* are encompassed within the lower ranges of variation in *P. t. troglodytes* and *P. paniscus* (Fig. 15).

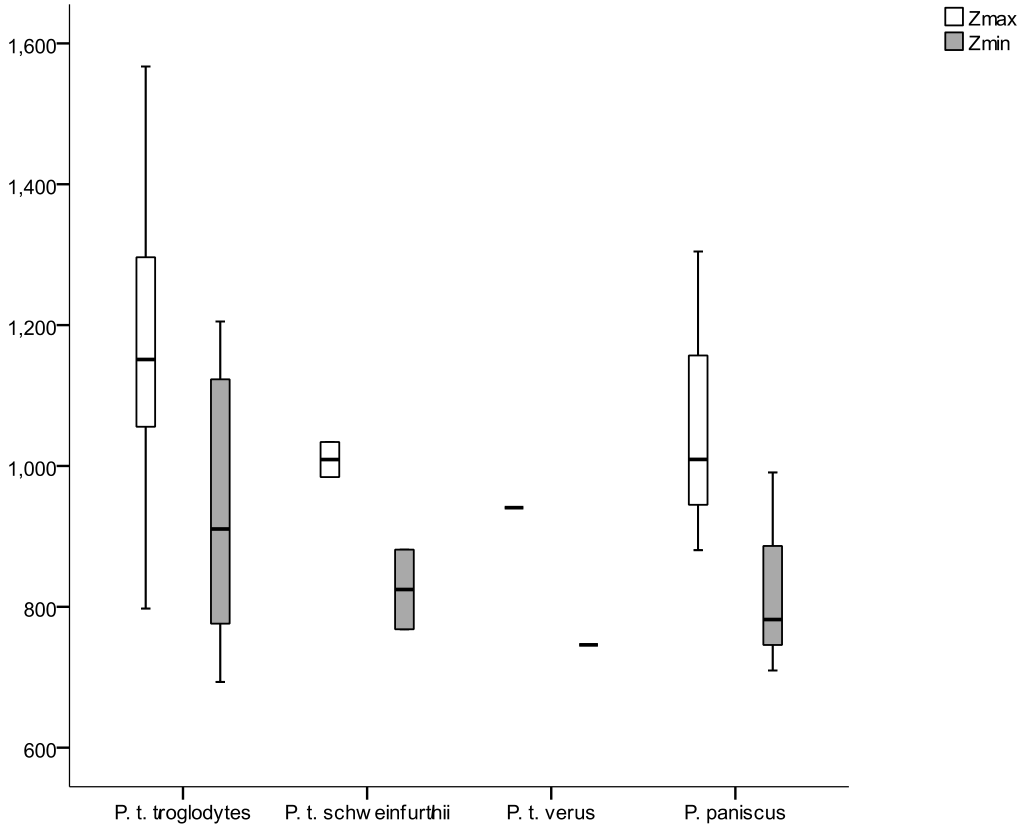

Figure 15. Box-plot of maximum bending strength (Z_{max}) and minimum bending strength (Z_{min}) in the midshaft femur among the groups.

Ranges of variation in Z_{max}/Z_{min} overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Z_{max}/Z_{min} in *P. t. verus* is encompassed within the ranges of variation in the other three taxa (Fig. 16). The Median test indicates that median Z_{max}/Z_{min} is not significantly different among the groups. Median Z_{max}/Z_{min} is still not significantly different among the groups when the *P. t. troglodytes* outlier is removed from the analysis (p= 0.77).

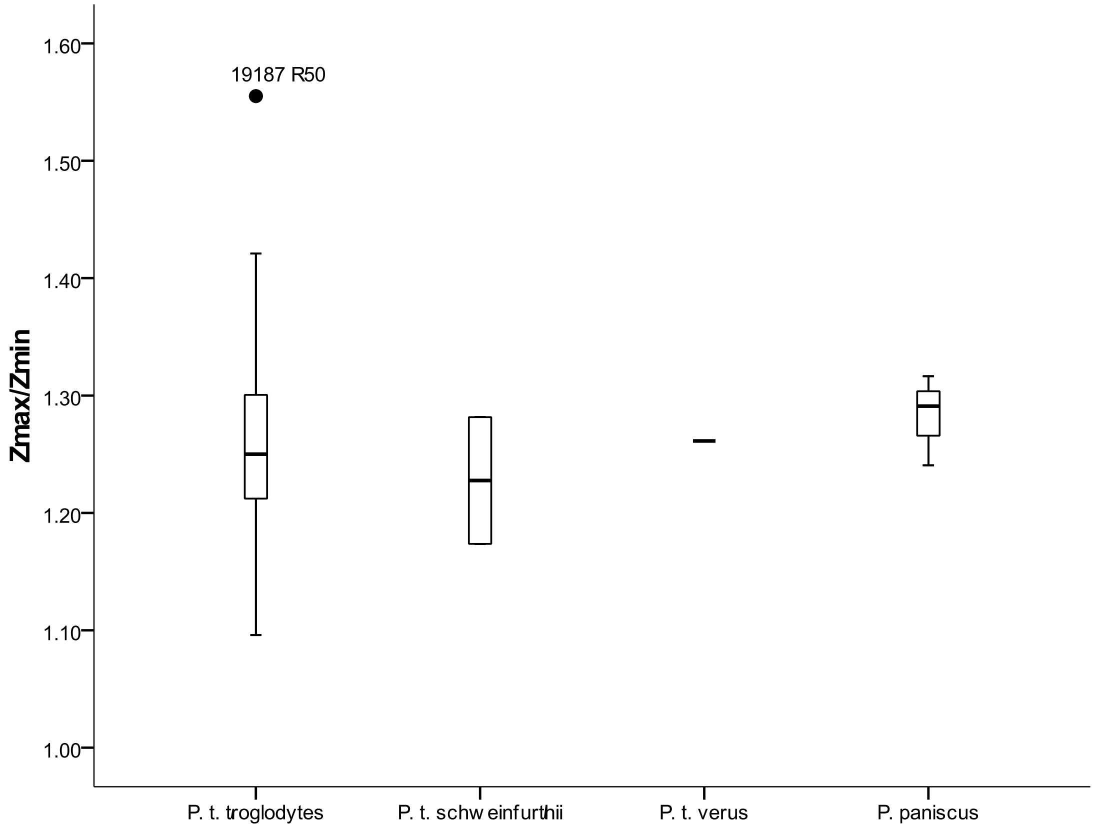

Figure 16. Box-plot of diaphyseal shape (Z_{max}/Z_{min}) in the midshaft femur among the groups.

Coefficients of variation for *P. t. troglodytes*, *P. t. schweinfurthii*, *P. paniscus* and the combined sample are presented in Table 6. Coefficients of variation for *P. t. verus* are not calculated since n= 1. There is more variation in *P. t. troglodytes* than in *P. t. schweinfurthii* and *P. paniscus* in TA, %CA, Z_x, Z_{min} and Z_{max}/Z_{min}, and there is more variation in *P. paniscus* than in *P. t. troglodytes* and *P. t. schweinfurthii* in CA, $J^{0.73}$, Z_y, Z_x/Z_y and Z_{max}. When the samples are combined, most coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*. Coefficients of variation in Z_y and Z_x/Z_y in the combined sample are slightly greater (1%) than coefficients of variation in *P. t. troglodytes*. These results indicate that combining the samples does not significantly increase the variability in *P. t. troglodytes*. Coefficients of variation in all cross-sectional properties in *P. t. schweinfurthii* are lower than in *P. t.*

troglodytes and *P. paniscus*. Since *P. t. schweinfurthii* is represented by one male and one female, the results suggest that sex differences are low. Sex differences appear to be high in *P. paniscus*, which is represented by two males and one female, except with regard to %CA and Z_{max}/Z_{min}.

Table 6. Coefficients of variation in the midshaft femur.

	Coefficients of Variation			
	P. t. troglodytes	*P. t. schweinfurthii*	*P. paniscus*	Combined[a]
TA	0.15	0.05	0.13	0.15
CA	0.12	0.02	0.14	0.12
%CA	0.14	0.04	0.04	0.13
$J^{0.73}$	0.18	0.06	0.19	0.18
Z_x	0.19	0.10	0.13	0.18
Z_y	0.19	0.02	0.25	0.20
Z_x/Z_y	0.07	0.08	0.11	0.08
Z_{max}	0.19	0.03	0.20	0.19
Z_{min}	0.19	0.10	0.18	0.18
Z_{max}/Z_{min}	0.10	0.06	0.03	0.08

a. Includes *P. t. verus*.

Summary. Median midshaft femoral cross-sectional properties are not significantly different among the groups except with regard to %CA. Significant differences in %CA among the groups remain even when the *P. t. troglodytes* outliers are removed from the analysis. Ranges of variation in midshaft femoral cross-sectional properties overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Cross-sectional properties in *P. t. verus* are consistently encompassed within the ranges of variation in *P. t. troglodytes*, and often encompassed within the ranges of variation in *P. t.*

schweinfurthii and *P. paniscus* as well. Coefficients of variation do not increase when the groups are combined, which suggests that variation is not introduced. The general overlapping ranges of variation in midshaft femoral cross-sectional properties among the taxa, and the low coefficients of variation when the groups are combined suggest that mechanical loading in the femoral midshaft of the *Pan* samples in this study are similar.

Humerus

Median cross-sectional properties in the right humerus are not significantly different among the groups except with regard to %CA (Table 7).

Table 7. Median test for the right humerus.

		TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_x/Z_y	Z_{max}	Z_{min}	Z_{max}/Z_{min}
N		20	20	20	20	20	20	20	20	20	20
Median		358.81	218.69	63.85	1248.39	740.57	800.11	0.96	806.91	691.15	1.14
Chi-Square		5.14[a]	1.62[a]	7.14[a]	5.14[a]	1.62[a]	1.62[a]	3.62[a]	5.14[a]	1.62[a]	6.00[a]
df		3	3	3	3	3	3	3	3	3	3
Asymp. Sig.		0.16	0.66	0.07	0.16	0.66	0.66	0.31	0.16	0.66	0.11
Monte Carlo Sig.		0.14[b]	0.78[b]	**0.04**[b]	0.14[b]	0.78[b]	0.78[b]	0.47[b]	0.14[b]	0.78[b]	0.10[b]
99% Conf. Interval	Lo. Bnd.	0.13	0.77	0.03	0.13	0.77	0.77	0.46	0.13	0.77	0.09
	Up. Bnd.	0.15	0.79	0.04	0.15	0.79	0.79	0.48	0.15	0.79	0.11

a. 6 cells (75.0%) have expected frequencies less than 5. The minimum expected cell frequency is .5.
b. Based on 10000 sampled tables with starting seed 2000000.
Significance is indicated in bold.

Median cross-sectional properties in the left humerus are not significantly different among the groups except with regard to %CA (Table 8).

Table 8. Median test for the left humerus.

		TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_x/Z_y	Z_{max}	Z_{min}	Z_{max}/Z_{min}
N		17	17	17	17	17	17	17	17	17	17
Median		347.02	228.16	62.02	1218.45	763.47	760.48	0.96	814.58	666.42	1.21
Chi-Square		2.95[a]	0.94[a]	6.30[a]	3.29[a]	0.94[a]	3.29[a]	4.99[a]	2.95[a]	3.29[a]	5.29[a]
df		3	3	3	3	3	3	3	3	3	3
Asymp. Sig.		0.40	0.82	0.10	0.35	0.82	0.35	0.18	0.40	0.35	0.15
Monte Carlo Sig.		0.72[b]	1.00[b]	**0.05**[b]	0.57[b]	1.00[b]	0.57[b]	0.23[b]	0.72[b]	0.57[b]	0.15[b]
99% Conf. Interval	Lo. Bnd.	0.71	1.00	0.05	0.56	1.00	0.56	0.22	0.71	0.56	0.14
	Up. Bnd.	0.73	1.00	0.06	0.59	1.00	0.59	0.24	0.73	0.59	0.16

a. 6 cells (75.0%) have expected frequencies less than 5. The minimum expected cell frequency is .5.
b. Based on 10000 sampled tables with starting seed 2000000.
Significance is indicated in bold.

Ranges of variation in TA in the right and left humerus overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. TA in the right and left humerus of *P. t. verus* is encompassed within the ranges of variation in the other chimpanzee taxa. Ranges of variation in CA in the right and left humerus overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. CA in the right humerus of *P. t. verus* is encompassed within the range of variation in *P. t. troglodytes* and in the lower range of variation in *P. t. schweinfurthii*. CA in the left humerus is encompassed within the ranges of variation in the other three taxa (Fig. 17). The Median test indicates that TA in the left humerus is not significantly different among the groups. Median TA is still not significantly different among the groups when the *P. t. troglodytes* outlier is removed from the analysis (*p*= 0.71).

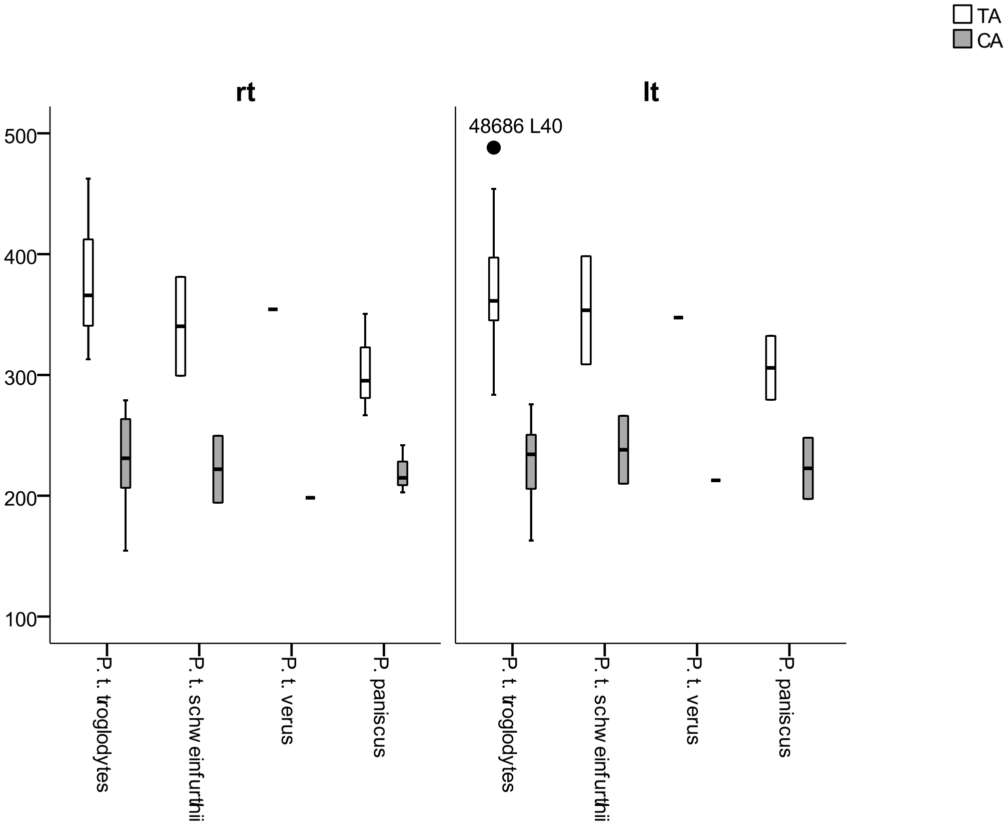

Figure 17. Box-plot of total area (TA) and cortical area (CA) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in %CA in the right and left humerus overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. %CA in the right and left humerus of *P. t. verus* is encompassed with the range of variation in *P. t. troglodytes* (Fig. 18).

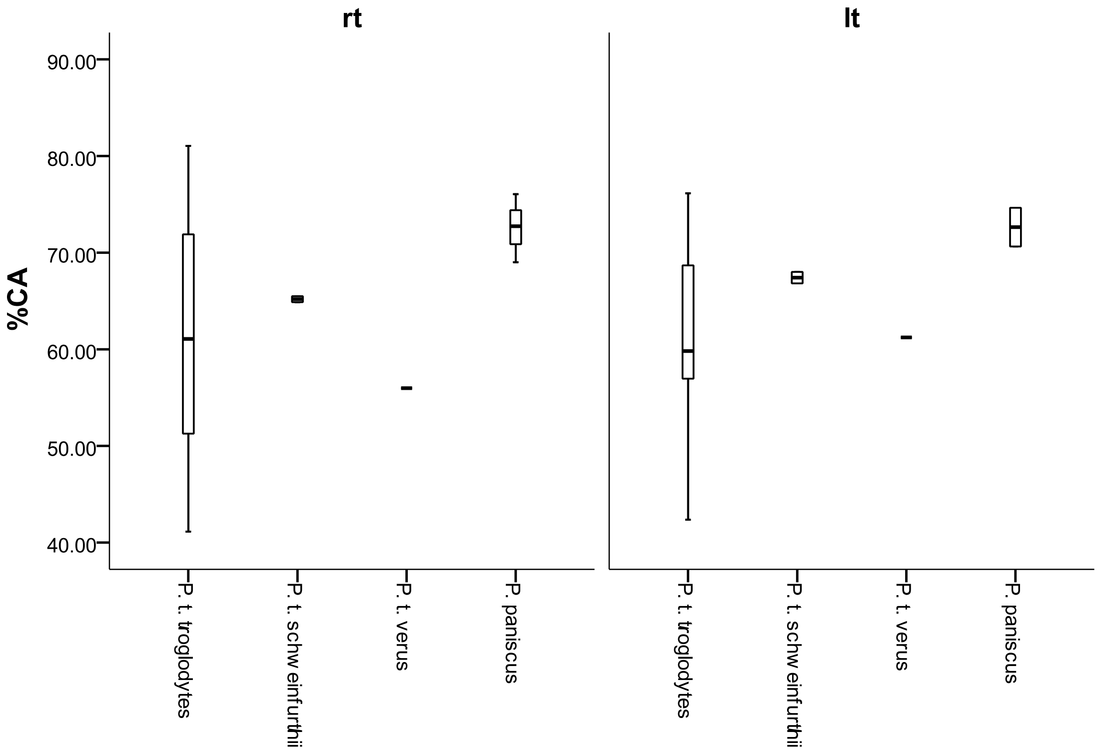

Figure 18. Box-plot of percent cortical area (%CA) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in $J^{0.73}$ in the right and left humerus overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. $J^{0.73}$ in the right humerus of *P. t. verus* is encompassed within the ranges of variation in the other three taxa, and in the left humerus it is encompassed within the ranges of variation in *P. t. troglodytes* and *P. t. schweinfurthii* (Fig. 19). The Median tests indicated that $J^{0.73}$ in the left humerus is not significantly different among the groups. $J^{0.73}$ is still not significantly different among the groups when the *P. t. troglodytes* outliers are removed from the analysis (p= 0.55).

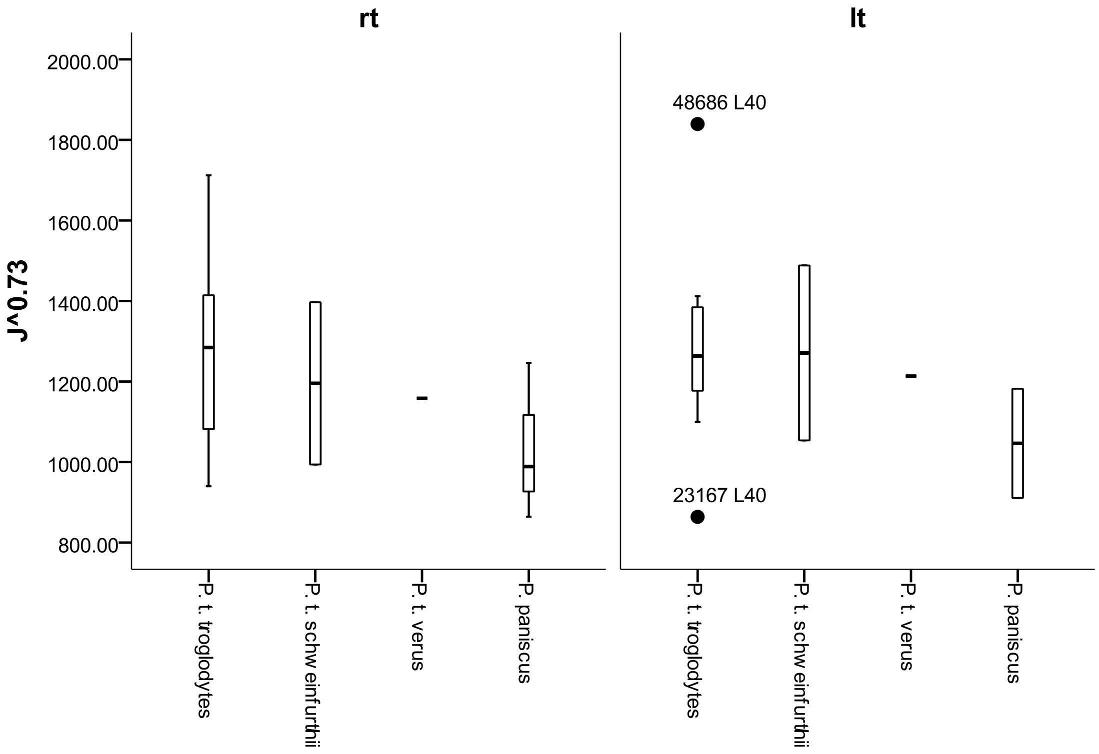

Figure 19. Box-plot of average bending and torsional strength ($J^{0.73}$) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in Z_x and Z_y in the right and left humerus overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Z_x in the right humerus of *P. t. verus* falls within the lower ranges of variation in the other three groups, and Z_y falls within the ranges of variation in the other three groups. Z_x in the left humerus of *P. t. verus* falls within the ranges of variation in the other three groups, and Z_y falls within the ranges of variation in the other chimpanzee taxa (Fig. 20). The Median tests indicated that Z_x and Z_y in the left humerus are not significantly different among the groups. Median Z_x (p= 1.00), and median Z_y (p= 0.56) are still not significantly different among the groups when the *P. t. troglodytes* outliers are removed from the analysis.

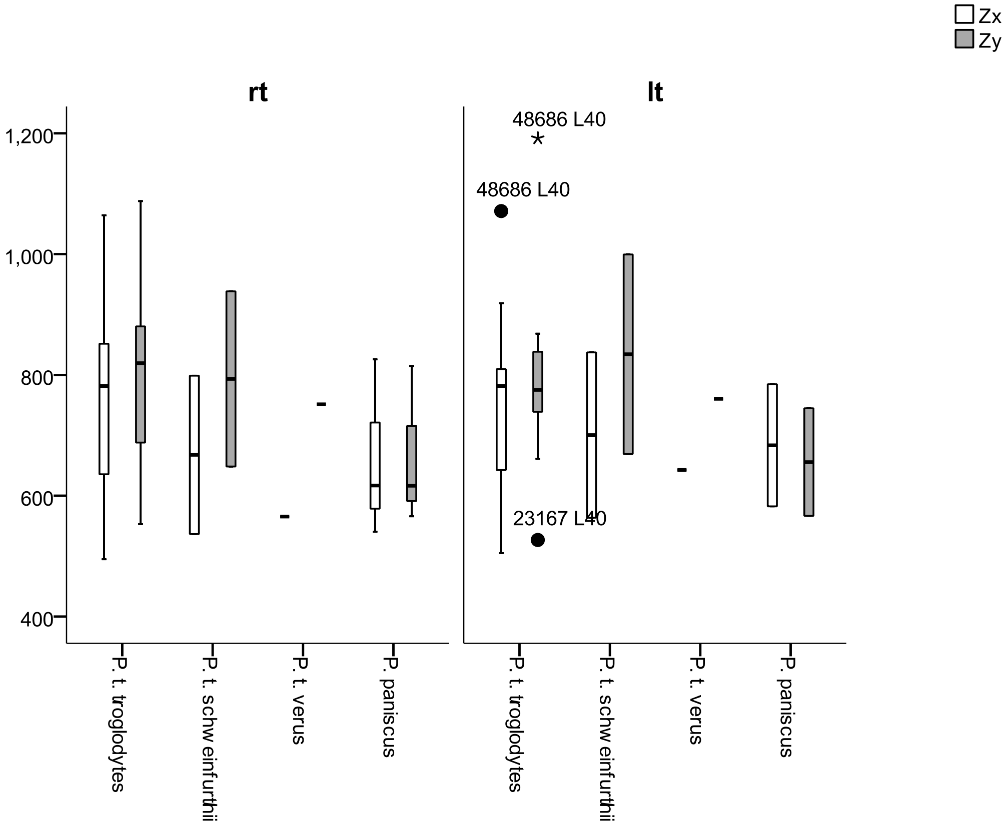

Figure 20. Box-plot of bending strength in the A-P plane (Z_x) and bending strength in the M-L plane (Z_y) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in Z_x/Z_y in the right humerus overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus.* The Z_x/Z_y value in the right humerus of *P. t. verus* is not encompassed within the ranges of variation in any of the other groups. Ranges of variation in Z_x/Z_y in the left humerus only overlap between *P. t. troglodytes* and *P. paniscus*. The range of variation in Z_x/Z_y in *P. t. schweinfurthii* falls below the ranges of variation in *P. t. troglodytes* and *P. paniscus*. The Z_x/Z_y value in *P. t. verus* falls near the range of variation in *P. t. schweinfurthii* (Fig. 21). Group differences in median Z_x/Z_y remain insignificant when the *P. t. troglodytes* outlier is removed from the analysis (p= 0.22). *P. t. schweinfurthii* and *P. t. verus* tend to show significantly greater M-L bending strength relative to A-P bending strength in the right and left humerus (i.e. $Z_x/Z_y < 1.0$) compared to *P. t. troglodytes* and *P. paniscus.*

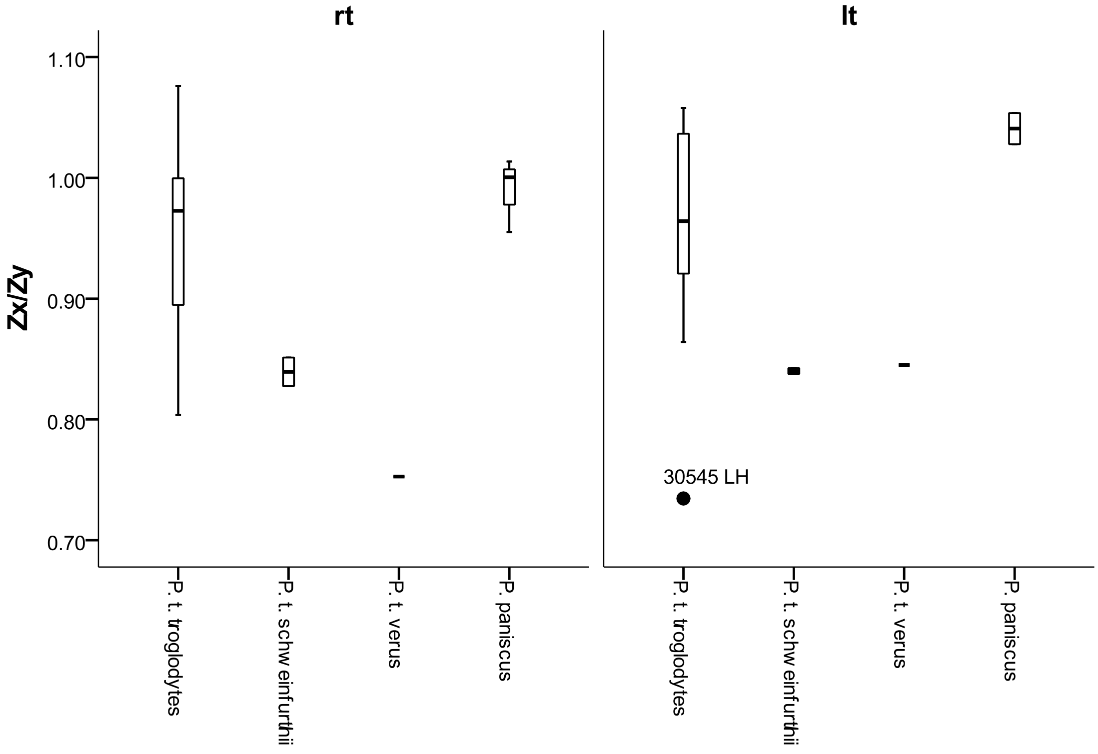

Figure 21. Box-plot of diaphyseal shape (Z_x/Z_y) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in Z_{max} in the right and left humerus overlap between *P. t. troglodytes* and *P. t. schweinfurthii.* The range of variation in Z_{max} in the right and left humerus of *P. paniscus* falls within the lower ranges of variation in *P. t. troglodytes* and *P. t. schweinfurthii.* Z_{max} in the right and left humerus of *P. t. verus* is encompassed within the ranges of variation in the other chimpanzee taxa. Ranges of variation in Z_{min} in the right and left humerus overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P.*

paniscus. Z_{min} in the right and left humerus of *P. t. verus* is encompassed within the ranges of variation in the other three groups (Fig. 22). The Median test indicates that Z_{max} is not significantly different among the groups. Median Z_{max} is still not significantly different among the groups when the *P. t. troglodytes* outliers are removed from the analysis (p= 0.72).

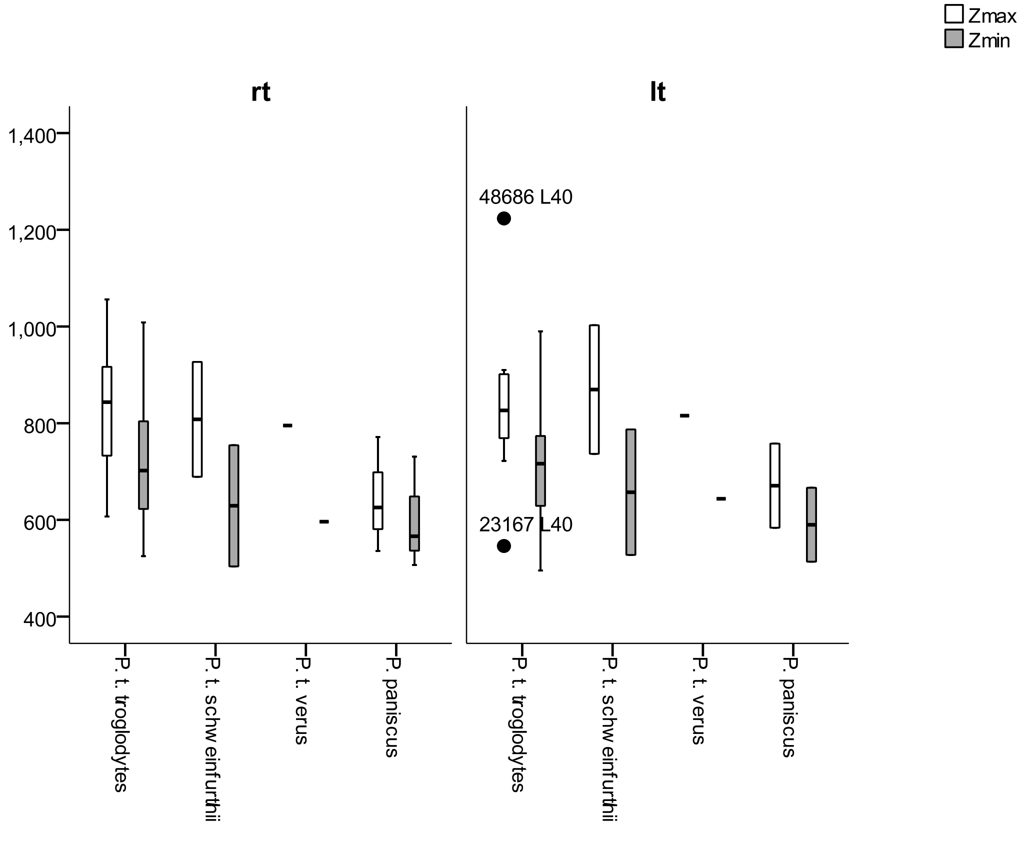

Figure 22. Box-plot of maximum bending strength (Z_{max}) and minimum bending strength (Z_{min}) in the right (rt) and left (lt) humerus among the groups.

Ranges of variation in Z_{max}/Z_{min} in the right and left humerus overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. Z_{max}/Z_{min} in the right humerus of *P. t. verus* is encompassed within the ranges of variation in the other two chimpanzee taxa. Z_{max}/Z_{min} in the left humerus is only encompassed within the range of variation in *P. t. troglodytes,* and falls just below the range of variation in *P. t. schweinfurthii* (Fig. 23).

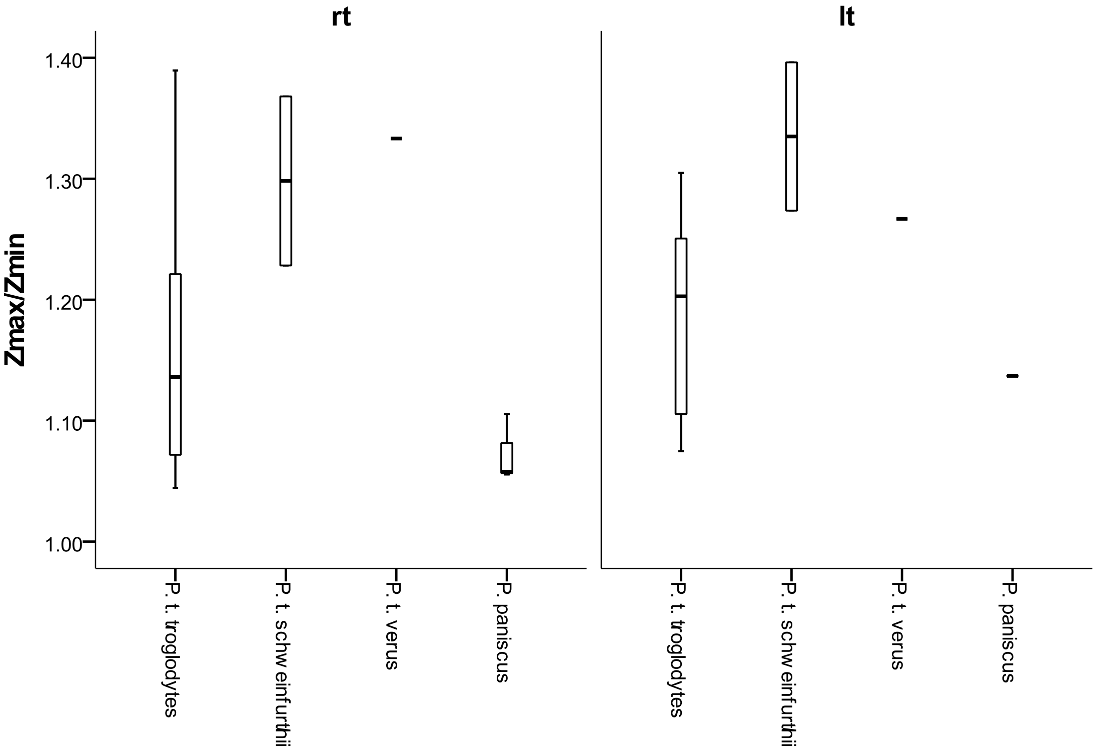

Figure 23. Box-plot of diaphyseal shape (Z_{max}/Z_{min}) in the right (rt) and left (lt) humerus among the groups.

Right humeral coefficients of variation for *P. t. troglodytes*, *P. t. schweinfurthii*, *P. paniscus* and the combined sample are presented in Table 9. Coefficients of variation for *P. t. verus* are not calculated since n= 1. There is more variation in *P. t. schweinfurthii* than in *P. t. troglodytes* and *P. paniscus* for most cross-sectional properties. There is more variation in *P. t. troglodytes* than in *P. t. schweinfurthii* and *P. paniscus* in %CA, Z_x/Z_y

and Z_{max}/Z_{min}. When the samples are combined, coefficients of variation increase in TA, $J^{0.73}$, Z_x, Z_y, Z_x/Z_y, Z_{max} and Z_{min} compared to the coefficients of variation in the largest group, *P. t. troglodytes*. However, the increases are very moderate (1-2%). The coefficients of variation in CA and %CA in the combined sample decrease by 1-2% compared to the coefficients of variation in *P. t. troglodytes*. The coefficient of variation in Z_{max}/Z_{min} in the combined sample is the same as in *P. t. troglodytes*. These results indicate that combining the samples introduces some variability, particularly in TA, $J^{0.73}$, Z_x, Z_y, Z_x/Z_y, Z_{max} and Z_{min}, but the small increase (1-2%) is likely negligible. In general, the results indicate that combining the samples does not increase the variability.

Table 9. Coefficients of variation in the right humerus.

	Coefficients of Variation			
	P. t. troglodytes	*P. t. schweinfurthii*	*P. paniscus*	Combined[a]
TA	0.12	0.17	0.14	0.14
CA	0.17	0.18	0.09	0.16
%CA	0.19	0.01	0.05	0.17
$J^{0.73}$	0.16	0.24	0.19	0.17
Z_x	0.21	0.28	0.22	0.22
Z_y	0.17	0.26	0.20	0.18
Z_x/Z_y	0.08	0.02	0.03	0.09
Z_{max}	0.15	0.21	0.18	0.17
Z_{min}	0.19	0.28	0.19	0.20
Z_{max}/Z_{min}	0.11	0.08	0.03	0.11

a. Includes *P. t. verus*.

Left humeral coefficients of variation for *P. t. troglodytes*, *P. t. schweinfurthii*, *P. paniscus* and the combined sample are presented in Table 10. Coefficients of variation for

P. t. verus are not calculated since n= 1. There is more variation in *P. t. schweinfurthii* than in *P. t. troglodytes* and *P. paniscus* for most cross-sectional properties. There is more variation in *P. t. troglodytes* than in *P. t. schweinfurthii* and *P. paniscus* in %CA, Z_x/Z_y and Z_{max}/Z_{min}. When the samples are combined, coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*. These results indicate that combining the samples does not increase the variability.

Table 10. Coefficients of variation in the left humerus.

	Coefficients of Variation			
	P. t. troglodytes	*P. t. schweinfurthii*	*P. paniscus*	Combined[a]
TA	0.15	0.18	0.12	0.15
CA	0.14	0.17	0.16	0.13
%CA	0.15	0.01	0.04	0.14
$J^{0.73}$	0.18	0.24	0.18	0.18
Z_x	0.20	0.28	0.21	0.19
Z_y	0.20	0.28	0.19	0.20
Z_x/Z_y	0.10	0.00	0.02	0.10
Z_{max}	0.19	0.22	0.18	0.19
Z_{min}	0.18	0.28	0.18	0.18
Z_{max}/Z_{min}	0.07	0.06	0.00	0.07

a. Includes *P. t. verus*.

Summary. As previous mentioned, the right humerus of MCZ 15312 has an unusually robust deltoid tuberosity, periosteal reaction in the antero-lateral surface of the upper third of the diaphysis and a longitudinally twisted diaphysis near the midshaft[7]. This individual, however, never presented as an outlier in the analyses.

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[7] The cross-sectional location examined and the location of bony reaction do not overlap.

Median %CA in the right and left humerus represents the only humeral cross-sectional property to be significantly different among the groups. Ranges of variation in most right and left humeral cross-sectional properties generally overlap among the groups. Diaphyseal shape along the anatomical axes (i.e. Z_x/Z_y) is the most distinguishing cross-sectional property among the taxa. Z_x/Z_y in the right humerus of *P. t. verus* is not encompassed within the ranges of variation in the other three groups. The very low Z_x/Z_y value in the right humerus of *P. t. verus* indicates extreme M-L buttressing compared to the other groups. The Z_x/Z_y values in the left humerus of *P. t. schweinfurthii* and *P. t. verus* are significantly lower than in *P. t. troglodytes* and *P. paniscus*. Moderate increases or decreases in the coefficients of variation when the samples are combined suggest that combining the samples does not increase the variability compared to the variation in the largest group, *P. t. troglodytes.*

Sex differences in humeral cross-sectional properties in *P. t. schweinfurthii*, as represented by one male and one female in the comparative sample set, are greater than sex differences in femoral cross-sectional properties. Coefficients of variation in right and left humeral %CA and diaphyseal shape (Z_x/Z_y and Z_{max}/Z_{min}), however, are low in *P. t. schweinfurthii*. Sex differences in the right humerus of *P. paniscus*, which is represented by two males and one female, are lower than in *P. t. schweinfurthii*. Coefficients of variation in the left humerus of *P. paniscus*, which is represented by two males, are generally lower or match the coefficients of variation in the right humerus. This suggests that sex differences in humeral cross-sectional properties in *P. paniscus* are low.

Mechanical loading patterns

A bivariate scatterplot of CA versus $J^{0.73}$ in the proximal femur suggests little difference in loading preference among this sample of *Pan* largely because of the variation in *P. t. troglodytes* (Fig. 24).

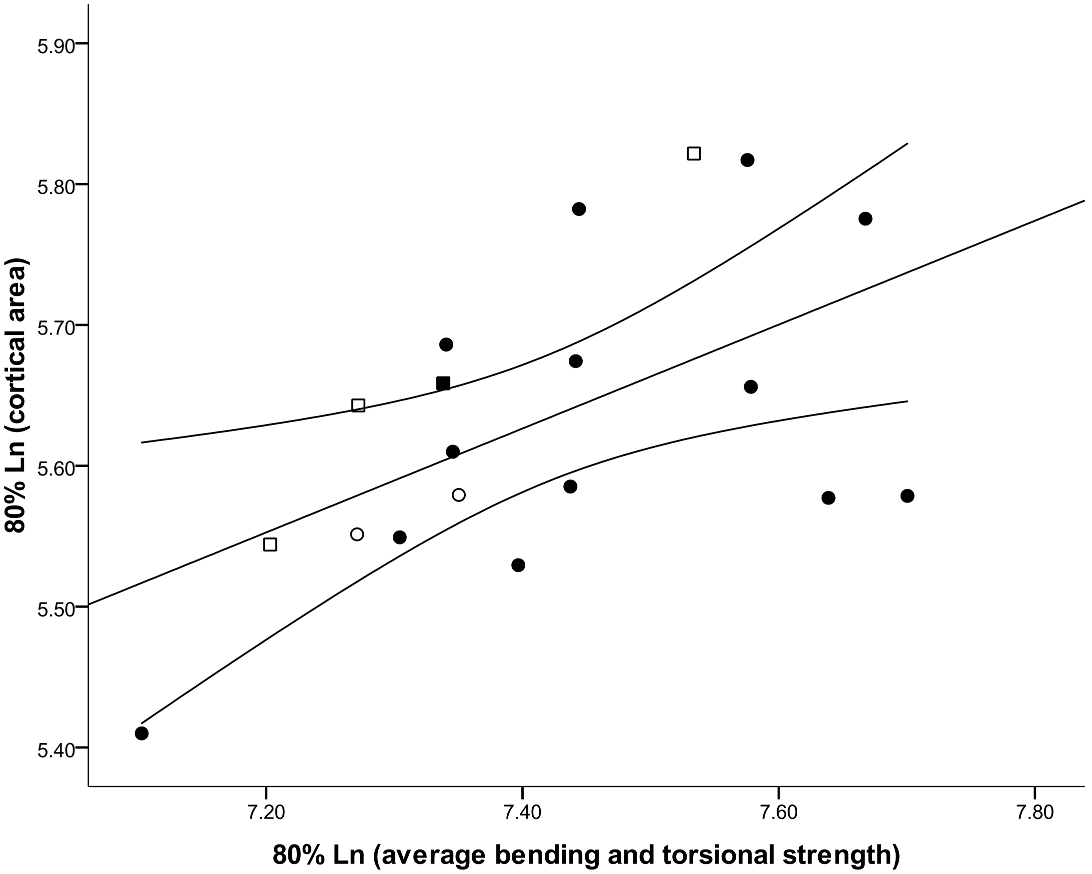

Figure 24. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the proximal femur. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. $R^2 = 0.31$.

A bivariate scatterplot of CA versus $J^{0.73}$ in the midshaft femur suggests little difference in loading preference among this sample of *Pan* largely because of the amount of variation in *P. t. troglodytes* (Fig. 25). A comparison of CA relative to $J^{0.73}$ in the proximal and midshaft femur of *P. paniscus* indicates that the two male bonobos show preferential axial loading relative to average bending and torsional loading compared to the single bonobo female. The *P. t. schweinfurthii* sexes do not show preferential loading differences between each other. Given the small sample size, it is unclear if these differences reflect real sex differences or the lack of sex differences in hindlimb loading in *P. paniscus* and *P. t. schweinfurthii*, respectively. Axial loading is greater relative to average bending and torsional loading in the proximal femur of the *P. t. verus* individual, but this pattern is reversed in the femoral midshaft.

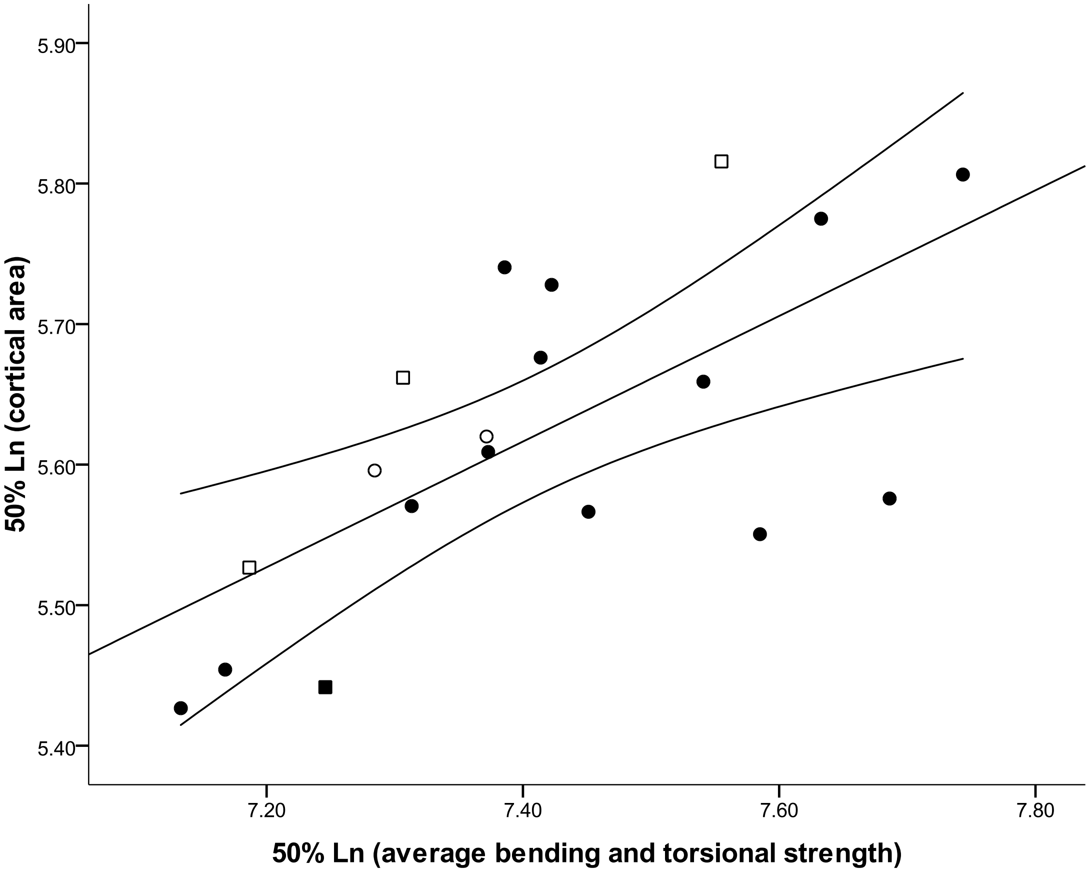

Figure 25. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the midshaft femur. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. R^2= 0.45.

Axial loading is elevated relative to average bending and torsional loading in the right humerus of *P. paniscus* compared to chimpanzee subspecies, but this pattern is not exclusive to bonobos since some *P. t. troglodytes* individuals also present with this loading pattern (Fig. 26). Variation in *P. t. troglodytes* subsumes group differences. Sex differences in *P. paniscus* and in *P. t. schweinfurthii* are not apparent.

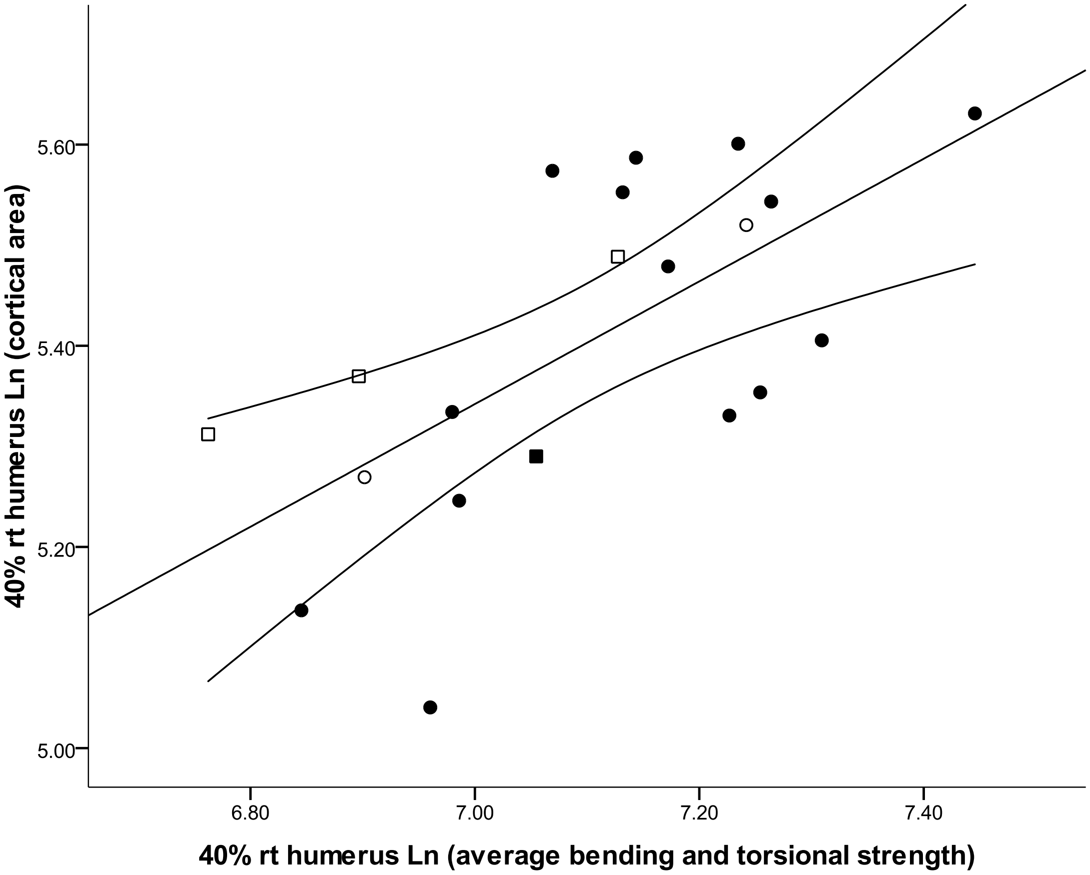

Figure 26. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the right humerus. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. $R^2= 0.43$.

Differences among the groups in axial loading relative to average bending and torsional loading in the left humerus are not evident (Fig. 27). The *P. t. schweinfurthii* sexes do not show markedly different loading patterns.

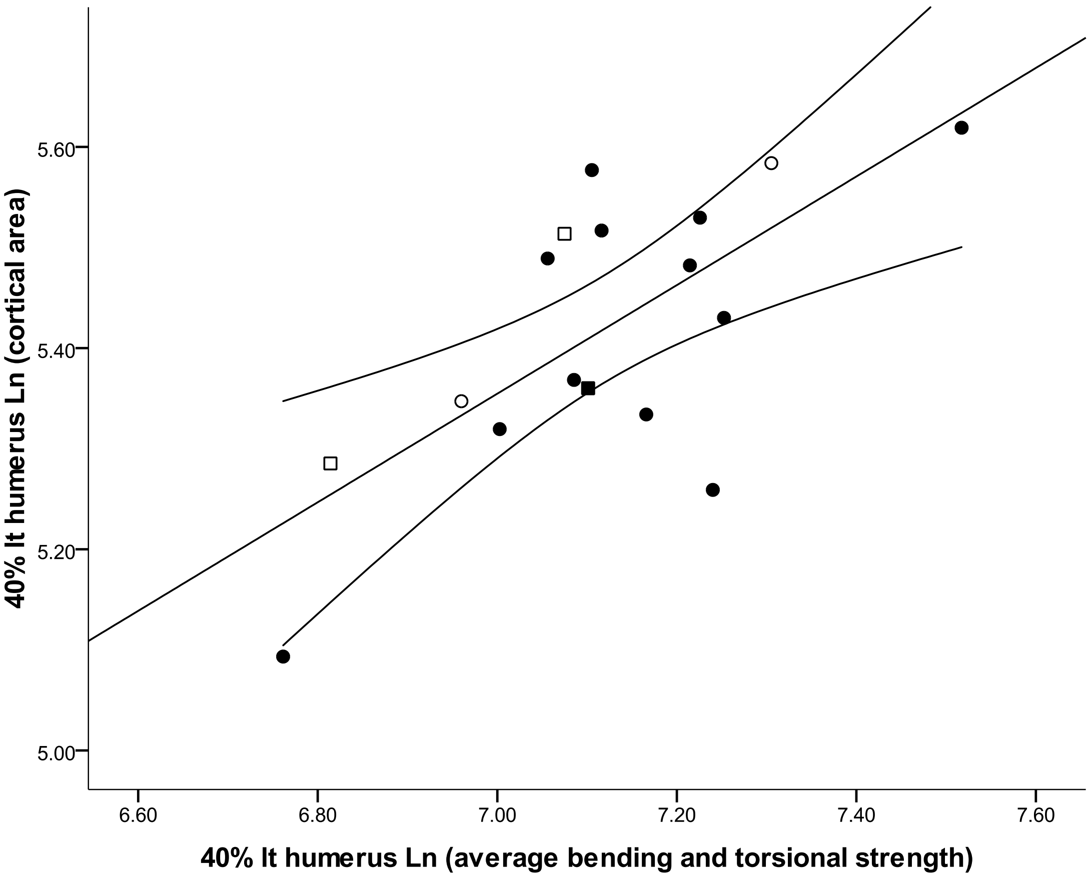

Figure 27. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the left humerus. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. R^2= 0.49.

The highest bending stresses in the femur occur at the midshaft (Demes et al., 1991). Therefore, $J^{0.73}$ in the femoral midshaft was examined relative to $J^{0.73}$ in the humerus to investigate inter-limb differences in strength. Group differences in femoral strength versus right humeral strength (Fig. 28) and femoral strength versus left humeral strength (Fig. 29) are not evident largely because of the amount of variation in *P. t. troglodytes*. Although femoral strength is relatively greater than humeral strength in *P. paniscus* compared to *P. troglodytes* ssp., this pattern is not exclusive to bonobos since some *P. t. troglodytes* individuals also show this pattern.

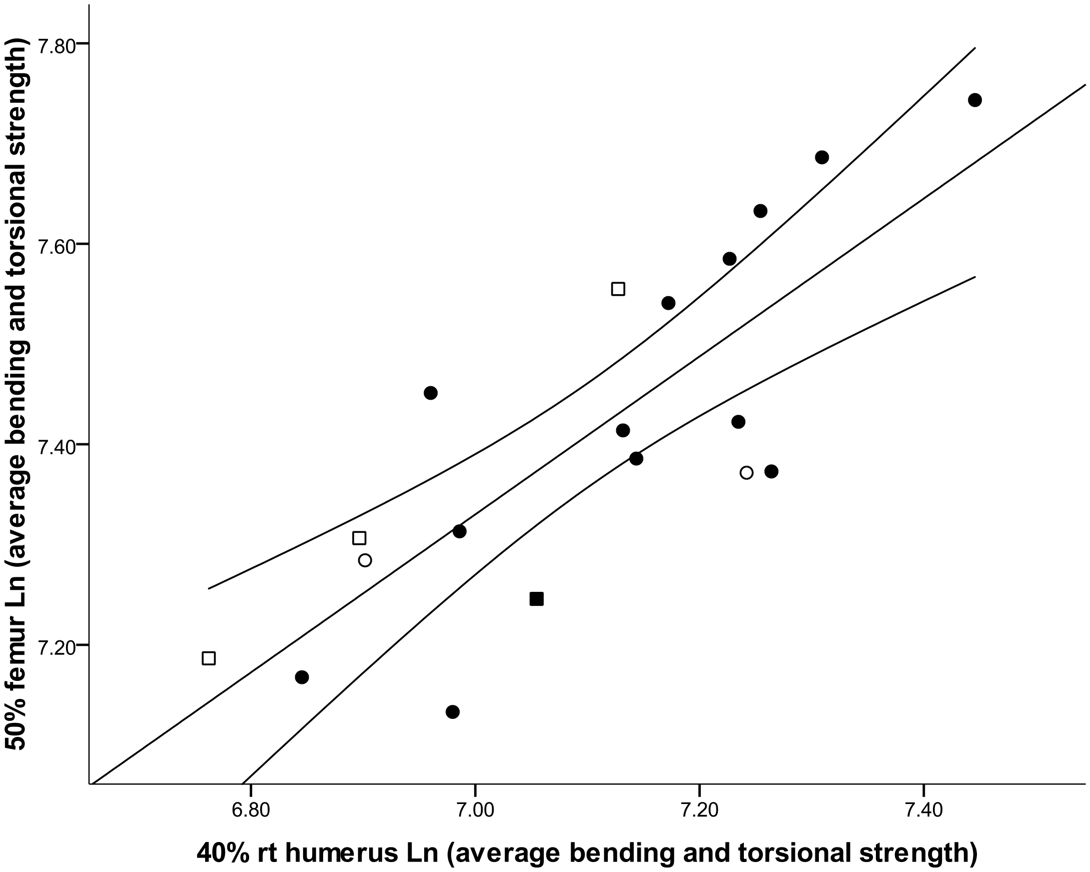

Figure 28. Bivariate scatterplot of log-transformed average bending and torsional strength ($J^{0.73}$) in the midshaft femur on log-transformed average bending and torsional strength ($J^{0.73}$) in the right humerus. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. R^2= 0.65.

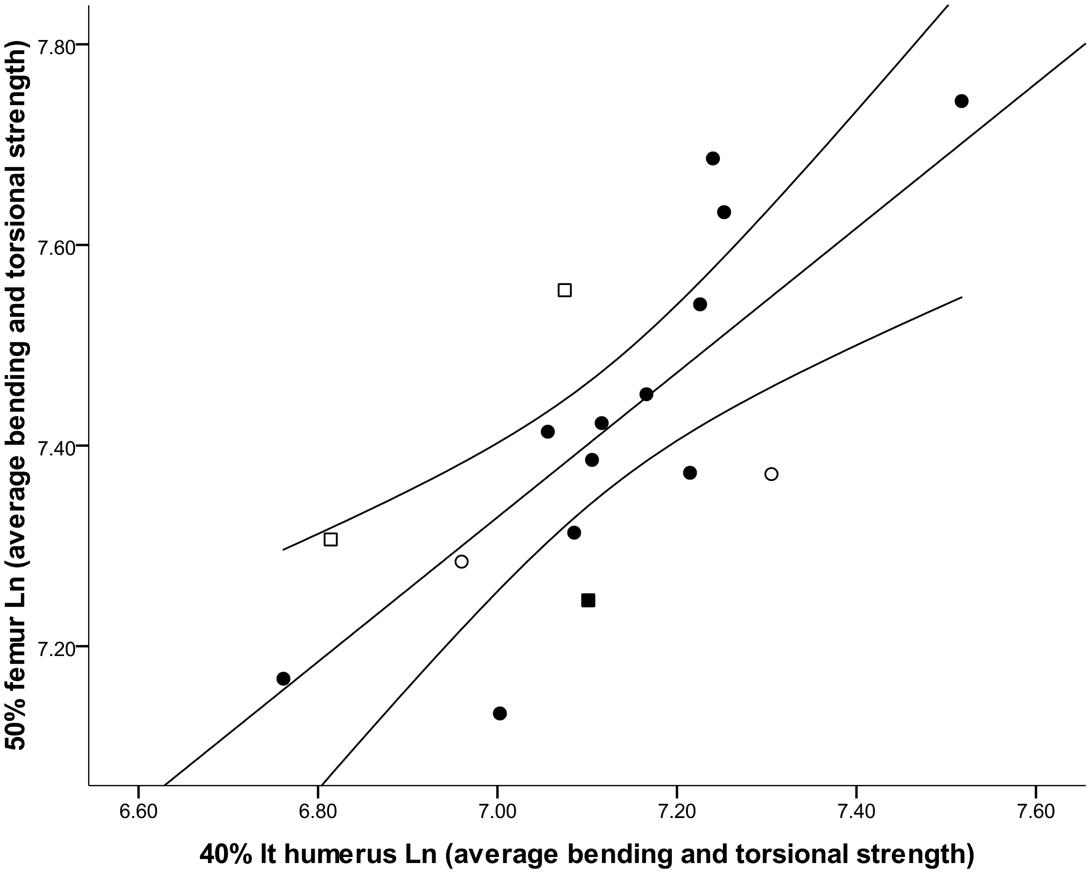

Figure 29. Bivariate scatterplot of log-transformed average bending and torsional strength ($J^{0.73}$) in the midshaft femur on log-transformed average bending and torsional strength ($J^{0.73}$) in the left humerus. *P. t. troglodytes* is represented by closed circles, *P. t. schweinfurthii* is represented by open circles, *P. t. verus* is represented by a closed square and *P. paniscus* is represented by open squares. The fit line with 95% confidence intervals around the mean is plotted for the total sample. R^2= 0.56.

Bivariate scatterplots of axial loading relative to average bending and torsional loading in the proximal and midshaft femur, and in the right and left humerus, and bivariate scatterplots of inter-limb strength suggest little mechanical loading differences among these taxa of *Pan*.

DISCUSSION

Since mechanical loading in the proximal femur is influenced by hip morphology (e.g. Lovejoy, 1988; Ruff, 1995), chimpanzees and bonobos may differ in cross-sectional properties at the 80% section because of phylogenetic differences related to the pelvis rather than strictly behavioral differences reflective of locomotion. It has been argued that the pelvis of *P. paniscus* is smaller and more primitive than that of chimpanzees, with a shorter ilium, a shorter pubis and a narrower pelvic girdle than any of the chimpanzee subspecies (Coolidge, 1933; Zihlman and Cramer, 1978; Jungers and Susman, 1984). Despite the reported morphological differences in the pelvis between chimpanzees and bonobos, overall similarities in proximal femoral cross-sectional properties among these taxa of *Pan* suggest that morphological differences around the hip joint may be insufficient to affect loading in the proximal femur.

There is a wide range of variation in all cross-sectional properties in *P. t. troglodytes* in the proximal and midshaft sections. This variation may reflect sex differences since the sample consists of seven males and six females. Ranges of variation in proximal femoral TA, CA, $J^{0.73}$, Z_y, Z_x/Z_y, Z_{max} and Z_{min} all overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus.* Ranges of variation in %CA, Z_x and Z_{max}/Z_{min} do not overlap between *P. t. schweinfurthii* and *P. paniscus*, but their ranges of variation are encompassed within the respective ranges of variation in *P. t. troglodytes*. Although *P. t. verus* is only represented by one individual, all cross-sectional properties fall within the range of variation in at least one of the other taxa. Coefficients of variation in proximal femoral cross-sectional properties are generally lowest in *P. t. schweinfurthii*, which is represented by one male and one female. When the samples are combined, coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*. Coefficients of variation in Z_y and Z_{max} are slightly greater in the combined sample than in *P. t. troglodytes*. These results indicate that combining the taxa does not increase the degree of variability, and therefore, the species-specific samples can be treated as a single sample set.

In the midshaft femur, median %CA is significantly different among the groups. Significance remains even when the *P. t. troglodytes* outliers are removed from the analysis. Ranges of variation in all cross-sectional properties overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Values in *P. t. verus* are encompassed with the ranges of variation in *P. t. troglodytes* and often within the ranges of variation in all three other taxa. Coefficients of variation in midshaft femoral cross-sectional properties are generally lowest in *P. t. schweinfurthii*. When the samples are combined, coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*. Coefficients of variation in Z_y and Z_x/Z_y in the combined sample are slightly greater than coefficients of variation in *P. t. troglodytes*. These results indicate that combining the taxa does not increase the variability.

M-L bending strength (Z_y) in the femur is relatively greater than A-P bending strength (Z_x) in the proximal and midshaft sections across *Pan* taxa. This trend was previously noted in *Pan* femora, but its significance is unclear (Carlson, 2002; Carlson et al., 2008). Non-human primates that habitually engage in turning behaviors are often exposed to increased M-L forces on their limb bones (Demes et al., 2006; Carlson and Judex, 2007). Carlson et al. (2008) found an increase in M-L bending strength in *P. t. verus* from Taï relative to *P. t. schweinfurthii* from Gombe and Mahale. The dense, closed forest environment at Taï potentially offers more obstacles than in the more open environments at Gombe and Mahale, which may result in a higher frequency of turning behavior among Taï chimpanzees compared to Gombe and Mahale chimpanzees (Carlson et al., 2008).

The humerus was included in this study to examine if there were species-specific and/or subspecies-specific differences in humeral loading within this *Pan* sample. Median cross-sectional properties in the right humerus are not significantly different among the groups except with regard to %CA. Median cross-sectional properties in the left humerus are not significantly different among the groups. Ranges of variation in right and left humeral TA, CA, $J^{0.73}$, Z_x, Z_y, Z_{max} and Z_{min} all overlap among *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Ranges of variation in right and left %CA and Z_{max}/Z_{min}

and right Z_x/Z_y overlap between *P. t. troglodytes* and *P. t. schweinfurthii*, and between *P. t. troglodytes* and *P. paniscus*. Ranges of variation in left Z_x/Z_y only overlap between *P. t. troglodytes* and *P. paniscus*. Cross-sectional properties in *P. t. verus* are often encompassed within the ranges of variation in *P. t. troglodytes,* and often within the ranges of variation in all three other taxa. The exception is with regard to diaphyseal shape assessed along the anatomical axes. Z_x/Z_y in the right humerus of *P. t. verus* is not encompassed within the range of variation in any other group. Z_x/Z_y in the left humerus falls just above the range of variation in *P. t. schweinfurthii* and well below the ranges of variation in *P. t. troglodytes* and *P. paniscus*.

Coefficients of variation in right and left humeral cross-sectional properties are generally highest in *P. t. schweinfurthii* compared to *P. t. troglodytes* and *P. paniscus*. The opposite pattern was found in the proximal and midshaft femur (i.e. coefficients of variation were lowest in *P. t. schweinfurthii* compared to *P. t. troglodytes* and *P. paniscus*). Since *P. t. schweinfurthii* is represented by one male and one female, these results may indicate that sex differences in mechanical loading are more pronounced in the forelimbs rather than the hindlimbs in this subspecies.

In the right humerus, when the samples are combined coefficients of variation increase in TA, $J^{0.73}$, Z_x, Z_y, Z_x/Z_y, Z_{max} and Z_{min} compared to the coefficients of variation in the largest group, *P. t. troglodytes*. However, the increases are very moderate (1-2%). The coefficients of variation in CA and %CA in the combined sample decrease by 1-2% compared to the coefficients of variation in *P. t. troglodytes*. The coefficient of variation in Z_{max}/Z_{min} in the combined sample is the same as in *P. t. troglodytes*. These results indicate that combining the samples introduces some variability, particularly in TA, $J^{0.73}$, Z_x, Z_y, Z_x/Z_y, Z_{max} and Z_{min}, but the small increase (1-2%) is negligible. In the left humerus, when the samples are combined coefficients of variation either match or are lower than the coefficients of variation in the largest group, *P. t. troglodytes*.

Carlson et al. (2008) found that chimpanzees generally show greater M-L bending strength relative to A-P bending strength in the humeral diaphysis, albeit this pattern is not consistent among chimpanzees. In the current study, chimpanzee subspecies show greater M-L bending strength relative to A-P bending strength in the right and left humerus, but *P. paniscus* shows slightly greater A-P bending strength relative to M-L bending strength in the humerus. The results from this study support the findings by Carlson et al. (2008) that chimpanzee humeri are buttressed in the M-L plane relative to the A-P plane, but this pattern may not characterize *Pan* humeri in general since bonobos showed the opposite pattern.

Sarringhaus et al. (2005) examined bilateral asymmetry in the humeral midshaft of wild-shot adult *P. troglodytes*. TA was used as a proxy for bone strength. Directional asymmetry in humeral TA was found where values on left-sided humeri were significantly greater than values on right-sided humeri. The greater mechanical loading on the left forelimb among chimpanzees is contrary to behavioral studies which suggest right-sided bias or unlateralized hand preference in captivity and in nature, respectively (e.g. McGrew and Marchant, 2001; Humle and Matsuzawa, 2009). Sarringhaus et al. (2005) hypothesized that left forelimb dominance may result from supporting a larger portion of body weight with the left forelimb while leaving the right forelimb to manipulate objects. Based on a visual examination of the data presented in the box-plot, *Pan* taxa in the current study do not show remarkable directional asymmetry in humeral TA, which alludes to unlateralized forelimb use in accordance with behavioral observations of many wild and semi-free-ranging *Pan* communities (Marchant and McGrew, 1996, 2005: McGrew and Marchant, 2001). The discordance between Sarringhaus et al. (2005) and the current study may reflect sample bias or variation in directional asymmetry in forelimb strength among different *Pan* communities.

Differences in shoulder joint morphology are commonly cited between chimpanzees and bonobos. *P. paniscus* has a long, narrow scapula and an overall scapular shape that resembles the morphology found in *Hylobates* (Coolidge, 1933; Roberts, 1974; Horn, 1976; McHenry and Corruccini, 1981; Susman, 1984; Shea, 1986). Based on this morphology, as well as other aspects of the postcranial skeleton (e.g. small body size, curved phalanges), many researchers have hypothesized that bonobos should use arboreal locomotor behaviors, especially suspensory behaviors, more frequently than chimpanzees

(Roberts, 1974; Johnson, 1981). This has been confirmed by some field observations (e.g. Susman et al., 1980; Hunt, 1991; Doran, 1993a; Doran and Hunt, 1994), but not all (e.g. Horn, 1979; White, 1992). Ranges of variation in right and left humeral cross-sectional properties in *P. paniscus* are encompassed within the ranges of variation in *P. t. troglodytes*, and often within the ranges of variation in *P. t. troglodytes* and *P. t. schweinfurthii*. Mechanical analyses presented in this study therefore suggest similar forelimb loading regimes among these specific taxa of *Pan*. However, since similar loading may result from different locomotor behaviors (e.g. D'Août et al., 2004), it is not possible to conclude, especially in the absence of behavioral data, that chimpanzees and bonobos use their forelimbs in a similar manner.

The humerus has a multifunctional role in locomotion and non-locomotor behaviors (e.g. tool-use). Thus, it is not possible to interpret mechanical similarities and differences in the forelimbs from a purely locomotor perspective. Carlson (2005) suggested, however, that because mechanical loadings from non-locomotor behaviors are generally static, they are less likely to influence cross-sectional geometries. Overall similarities in humeral cross-sectional geometries in this sample of *Pan* suggest general similarities in mechanical loading in the forelimbs, which may reflect similar forelimb use, or different forelimb use with overlapping mechanical signals.

Axial strength relative to average bending and torsional strength in the proximal and midshaft femur is not remarkably different among the groups largely because of the amount of variation in *P. t. troglodytes*. Although *P. paniscus* males show an increase in CA relative to $J^{0.73}$ compared to most *P. troglodytes* ssp., this pattern is not exclusive to bonobos since some *P. t. troglodytes* individuals also show an increase in CA relative to $J^{0.73}$. Axial strength relative to average bending and torsional strength in the right and left humerus is not exceedingly different among the groups. Bonobos show an increase in CA relative to $J^{0.73}$ compared to many chimpanzees, but this pattern does not strictly characterize *P. paniscus* since some *P. t. troglodytes* individuals show the same pattern. Group differences are not apparent in average bending and torsional strength in the femur relative to the right and left humerus.

A considerable amount of primatological research has focused on the relationship between habitat and locomotion (e.g. Doran and Hunt, 1994; Garber and Pruetz, 1995; Gebo and Chapman, 1995; McGraw, 2000; Garber and Leigh, 2001; Kimura, 2003; Bitty and McGraw, 2007; Wright, 2007). For instance, *P. t. verus* at Mt. Assirik, Senegal and conspecifics at Taï Forest, Côte d'Ivoire have been observed to engage in different frequencies of specific locomotor behaviors (Hunt and McGrew, 2002). Intra-species behavioral variation in *P. t. verus* may reflect contrasting habitats, where the open grassland setting at Mt. Assirik offers more opportunities for terrestrial bipedalism while the primary rainforest habitat at Taï does not (Hunt and McGrew, 2002). Since the habitats that these samples were drawn from are very similar, with the possible exception of *P. t. verus*, it is possible that similarities in forelimb and hindlimb loading reflect similar locomotor behavior due to comparable habitats. A larger sample size and the inclusion of *Pan* taxa from diverse habitats are needed to verify if observational differences in locomotor behavior due to environment transcend into mechanical differences in the long bones.

CONCLUSION

Ranges of variation in cross-sectional properties in the forelimbs and hindlimbs, and inter-limb and intra-limb mechanical loading patterns are very similar among all four of the *Pan* taxa examined in this study. It is possible that slight morphological differences observed between chimpanzees and bonobos are not functionally significant enough to affect locomotor behavior, at least as registered in cross-sectional geometries, that variation in locomotor behaviors overlap among groups such that a dominant loading regime is not detectable, or that locomotor behavior is simply not distinct within this sample of *Pan*. Indeed, it is also quite possible that sample sizes are too small for pronounced differences among the taxa to be apparent. Undoubtedly, a larger sample size is needed to substantiate the patterns found in this study. Since cross-sectional geometric properties in the forelimbs and hindlimbs of the specific *P. troglodytes* ssp. and *P.*

paniscus samples in this study are similar, it should not be detrimental to combine these taxa in future biomechanical analyses.

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CHAPTER III

CROSS-SECTIONAL MORPHOLOGY IN PLIO-PLEISTOCENE HOMININS AND ITS RELEVANCE TO TAXONOMIC ASSIGNMENTS

More than a century ago, Darwin suggested that bipedalism arose when our arboreal ancestors expanded their ecological niche to include life on the ground possibly because of "a change in [their] manner of procuring subsistence, or to a change in the conditions of [their] native country," (1872:135). Since then, the origin and evolution of human locomotion has been an important topic of inquiry (e.g. Morton, 1926; Gregory, 1928; Napier, 1964; Robinson, 1972; McHenry, 1975a; McHenry and Temerin, 1979; Rodman and McHenry, 1980; Stern and Susman, 1983; Latimer et al., 1987; Tuttle et al., 1991; Richmond and Strait, 2000; Harcourt-Smith and Aiello, 2004; Crompton et al., 2008; Richmond and Jungers, 2008). Despite the plethora of research on the subject, debate continues regarding the mode of locomotion before hominin[1] bipedalism, when and how bipedalism first emerged and how much locomotor variability may have been expressed in early hominins (e.g. Lovejoy et al., 1973; Fleagle, 1976; Fleagle et al., 1981; Tuttle, 1981; Gebo, 1992, 1996; Berge, 1994; Hunt, 1996; Crompton et al., 1998; Corruccini and McHenry, 2001; Richmond et al., 2001; Ward, 2002; McHenry and Jones, 2006; Wallace et al., 2008).

A major hurdle that has hindered analyses of locomotion among several hominin groups is the disconnect between the evidence used to identify species in the fossil record and the evidence used to reconstruct locomotor behavior. Species recognition of fossil hominins is traditionally based on craniodental morphology since several traits in the maxillofacial region, cranium and dentition are believed to be genetically and developmentally conserved (e.g. Leakey, 1959; Wood, 1993; Lieberman, 1995; Grine et al., 1996; Lieberman et al., 1996; Rightmire, 1998; Wood and Lieberman, 2001; Strait and Grine, 2004; Wood and Lonergan, 2008; but see Scott and Lockwood, 2004).

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[1] Hominin is defined as species that postdate the separation of African apes and the lineage that led to modern humans (Delson, 1981).

Although cranial evidence can give some insight into posture (e.g. Dean and Wood, 1981; Dean and Wood, 1982; Spoor et al., 1997), interpretations of locomotor behavior are largely based on postcranial remains, which are often not associated with diagnostic craniodental material (e.g. Day and Napier, 1964; Tobias, 1965; Day and Wood, 1968; Leakey, 1972; McHenry, 1975a, b; Latimer and Lovejoy, 1989; Gebo and Schwartz, 2006; McHenry et al., 2007; Drapeau, 2008; Ruff, 2009).

Taxonomic uncertainty, propelled by the lack of associated skeletons and the fragmentary nature of many postcranial elements, has hampered analyses of locomotion among early hominins because it is unclear if reconstructed locomotor behaviors, which are primarily based on isolated postcranial remains, are actually valid for a species largely identified craniodentally. This is particularly the case for *Paranthropus* and early *Homo*[2]. Similarities between corresponding postcranial elements attributed to early *Homo* and those attributed to *Paranthropus* have challenged the taxonomic assignments of many fossils. For instance, based on comparisons of corresponding skeletal elements in KNM-ER 1500 (*P. boisei*) and OH 8 and OH 35 (*H. habilis*), Grausz et al. (1988) suggested that the Olduvai samples should be attributed to *P. boisei* rather than *H. habilis*, or that the lower limb skeletons of *P. boisei* and *H. habilis* are almost indistinguishable. The former suggestion echoes previous concerns doubting the taxonomic allocations of OH 8 and OH 35 to the genus *Homo* (Day, 1976a; Wood, 2000; but see Susman, 2008). If OH 8 and OH 35 are not representatives of early *Homo*, then inferences of locomotor behavior gleaned from them may not be valid for the earlist members of the genus *Homo*.

The purpose of this study is to examine the relationship between cross-sectional morphology and taxonomy (or presumed taxonomy) in Plio-Pleistocene hominin groups. If members of a genus are expected to occupy the same or similar adaptive zone, then, at the very least, locomotor behavior should be relatively homogeneous among its species, and somewhat different from species of another genus (Mayr, 1950; Wood and Collard,

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[2] In this study, early *Homo* refers to members of the genus *Homo* that predate *H. erectus*, but whose species identification is uncertain or unknown (e.g. KNM-ER 1472), and *H. habilis* (i.e. OH 62). Although it has been suggested that the allocation of OH 62 to the genus *Homo* may not be valid, it is included in the early *Homo* group since it is generally referred to as *H. habilis* in the literature (but see Wood, 1992a; Wood and Collard, 1999a, b).

1999b; Cela-Conde and Ayala, 2003). The cross-sectional properties of a long bone at a given section describe the structural modifications that the bone has endured as a result of mechanical loading history, and therefore provide clues into the habitual functional usage of skeletal elements (Enlow, 1963; Frost, 1964, 1988; Huiskes, 1982; Martin and Burr, 1989; Rubin et al., 1990; Ruff et al., 2006). While long bone cross-sectional morphology by itself is inappropriate for taxonomic identification, given its plasticity and our incomplete knowledge of the relationship between mechanical loading and resultant cross-sectional morphology, inferences of locomotion that can be gleaned from them have significance for taxonomy. The most widespread application of long bone cross-sectional geometric investigations among fossil hominins is in reconstructing broad locomotor behavior (e.g. Ruff et al., 1993; Ohman et al., 1997; Trinkaus et al., 1998; Ruff et al., 1999; Trinkaus et al., 1999; Ruff, 2009; Kuperavage and Eckhardt, 2009). Locomotor behavior can be used to reconstruct general models regarding hominin behavioral ecology, which bear directly on food procurement strategies, physical and physiological adaptations and interspecific relationships within an ecological community. Thus, there is certainly value in exploring the relationship between cross-sectional morphology (and hence locomotion) and taxonomy.

The first hominin to display anatomical traits fully consistent with the modern human form of obligate terrestrial bipedalism was *H. erectus* nearly 1.8 mya (Walker and Leakey, 1993; McHenry and Coffing, 2000; Antón, 2003; Bramble and Lieberman, 2004; Polk, 2004; Lordkipanidze et al., 2007; Ruff, 2008), and most certainly by ~1.5 mya (Bennett et al., 2009). Modes of locomotion in *Paranthropus* and early *Homo*, however, are less conclusive. Although most researchers agree that pre-*H. erectu*s hominins were capable of bipedalism, there are differences of opinion on the degree of terrestrial bipedalism (i.e. facultative or obligate), gait kinematics (i.e. modern human-like or *Pan*-like bipedalism) and whether traits indicative of arborealism are primitive, nonfunctional retentions or functionally significant (Leakey et al., 1964; Davis, 1964; Day and Napier, 1964; Lewis, 1972; McHenry, 1975a, b; Susman and Stern, 1979, 1982; Oxnard and Lisowski, 1980; Susman et al., 1984; Kidd et al., 1996; McHenry and Berger, 1998;

Aiello and Andrews, 2000; Richmond et al., 2002; Haeusler and McHenry, 2004; Gebo and Schwartz, 2006; Ruff, 2009). Moreover, while it was initially argued that postcranial morphological differences between *Paranthropus* and early *Homo* suggested that at least two patterns of locomotion, which were evolving in parallel, were in existence around the same time (Davis, 1964; Day, 1976a, b; Wood, 1976; Wood, 1978), recent evidence and reevaluation of previous data indicate that the locomotor repertoire in early *Homo* likely included an arboreal component, and in this way was more similar to *Paranthropus* than to later *Homo* (Oxnard and Lisowski, 1980; Richmond et al., 2002; Gebo and Schwartz, 2006; Haeusler and McHenry, 2007).

Cross-sectional geometries in the proximal femur have been shown to follow taxonomy more closely than in the femoral midshaft likely because of the mechanical roles of a suite of phylogenetically constrained morphological traits around the hip joint (e.g. pelvis, femoral neck length), which affect loading in the proximal femur (Ruff, 1987, 1995, 2000; Ruff et al., 1993; Ruff et al., 1999; Trinkaus et al., 1999; Lovejoy et al., 2002). Thus, it is expected that groups should be readily distinguished based on proximal femoral cross-sectional geometries if there are distinct locomotor differences between *Paranthropus* and *Homo*. *Paranthropus* femora are expected to be more similar among each other than to *Homo*, both modern and fossil, and fossil *Homo* proximal femora are expected to be more similar to modern human femora than to *Paranthropus*.

Mechanical loading on the lower limbs due to habitual activity is best examined at the femoral midshaft because of the combined effects of the hamstring (posterior thigh muscles) and quadriceps (anterior thigh muscles) muscle groups, which are highest in the region around the knee (i.e. between the femoral midshaft and tibial midshaft) (Morrison, 1969, 1970; Carter, 1984; Ruff, 1987, 1995). If all members of the genus *Homo* are committed to terrestrial bipedalism, as suggest by Leakey et al. (1964), then fossil *Homo* femora should be mechanically similar both among each other and to modern human femora. Fossil *Homo* femora that are distinct may either represent a non-*Homo* species, or suggest variability in the locomotor behavior of fossil *Homo*. Since the kinematics of paranthropine bipedalism suggest a bipedal gait somewhat different from modern humans, and since there is evidence suggesting that *Paranthropus* was not fully detached from arborealism (Robinson, 1972; McHenry, 1978; Macchiarelli et al., 1999; Ruff et al., 1999; Susman and deRuiter 2004; Patel, 2005; Gebo and Schwartz, 2006; McHenry et al., 2007; Richmond and Jungers, 2008), *Paranthropus* femora should be mechanically distinct from modern and fossil *Homo*.

Cross-sectional geometries are phenotypically plastic and are also influenced by non-mechanical factors such as genetics, pathology and age (Ruff, 2000a; Lovejoy et al., 2002; Lovejoy et al., 2003; Volkman et al., 2003). Moreover, although several studies have shown that long bones do indeed remodel to accommodate to mechanical loading during life (e.g. Jones et al., 1977; Martin and Burr, 1989; Biewener et al., 1996; Sumner and Andriacchi, 1996; Frost et al., 1998; Shaw and Stock, 2009), the relationships among behavior, external loading and resultant cross-sectional geometries are not completely understood (Bertram and Swartz, 1991; Pearson and Lieberman, 2004; Lieberman et al., 2004). Therefore, it is important to emphasize that this study is not suggesting that cross-sectional geometries in and of themselves be used for taxonomic identification. Rather, the goal is to examine how well cross-sectional geometries, which can yield insights into locomotor behavior, reflect current and generally accepted taxonomies. If cross-sectional geometries are commensurate with locomotor expectations given taxonomic identities, a biomechanical approach may be useful in helping to taxonomically identify isolated fossil hominin femora, at least to the genus level.

MATERIALS AND METHODS

A selection of fossil hominin femora[3] housed at the National Museums of Kenya in Nairobi was included in this study (Table 1). Samples were chosen if length estimates were available so that properties could be size standardized, if enough of the diaphysis

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[3] Taxonomic assignments of several samples are tentative and/or controversial (e.g. KNM-ER 736, KNM-ER 1500d, OH 62). Taxonomic attributions are based on the original descriptions of the material, but other taxonomic assignments are listed followed by a question mark. Original taxonomic assignments to *Australopithecus* (robust) are replaced with the genus name "*Paranthropus*" following Robinson (1972), Wood and Constantino (2007) and Wood and Lonergan (2008).

was preserved so that proximal or midshaft section locations could be estimated and if at least one natural break in the subtrochanteric and/or estimated midshaft regions of the diaphysis perpendicular to the long axis was present so that cortical wall thicknesses could be measured.

Table 1. Fossil samples.

Sample[a]	**Section**	**Side**	**Est. age (mya)**	**Taxonomic attribution**	**Reference**[b]
KNM-ER 736	midshaft	L	1.5-1.7	*P.* (cf. *boisei)*/*Homo*/*H. erectus*?	1
KNM-ER 738	proximal	L	~1.8	*Paranthropus*/*Homo*?	1
KNM-ER 999a	proximal	L	~0.75 ± 0.02 ~0.1-0.5	*Homo* sp. indet./*H. erectus*?/ late archaic *H. sapiens*?	2, 3, 4
KNM-ER 1472	midshaft	R	1.89 ± 0.05	*Homo* sp.	5
KNM-ER 1481a	proximal	L	1.89	*Homo* sp./*H.* (cf. *erectus*?)/ *H. habilis*?/*H. rudolfensis?*	5, 6, 7, 8, 9
KNM ER 1500d	proximal	R	1.88-2.2	*P. boisei*	9, 10
KNM-ER 1592	midshaft	R	1.85	*Paranthropus*?	11
KNM ER 1807	midshaft	R	1.5-1.6	*H.* (cf. *erectus*)?/*P. boisei*?	10
KNM-ER 1808	midshaft	L	1.69	*H. erectus*	11
KNM-WT 15000	midshaft	R/L [c]	1.53-1.65	*H. erectus*	12
OH 34	midshaft	L	0.8-1.15	*Homo* sp. indet./*H. erectus*?	13, 14
OH 62	midshaft	L	1.75-1.85	*H. habilis*	15
SK 82	proximal	R	1.6-1.8	*P. robustus*	16
SK 97	proximal	R	1.6-1.8	*P. robustus*	16

[a] Data for all samples are from this study except KNM-WT 15000 and KNM-ER 1808 (Ruff, 2008), OH 62 (Ruff, 2009) and SK 82 and SK 97 (Ruff et al., 1999).

[b] 1. Leakey et al. (1972); 2. Day and Leakey (1974); 3. Bräuer et al. (1997); 4. Trinkaus (1993); 5. Day et al. (1975); 6. Wood (1992b); 7. Trinkaus (1984); 8. Kennedy (1983); 9. Leakey (1973b); 10. Day et al., (1976); 11. Leakey and Walker (1985); 12. Brown et al. (1985); 13. Day and Molleson (1976); 14. Leakey (1978); 15. Johanson et al. (1987); 16. Napier (1964).

[c] Cross-sectional data are averaged from the right and left femora as reported by Ruff (2008).

Hominin proximal femora

Proximal fossil femora examined in this study include KNM-ER 738, KNM-ER 1500d, KNM-ER 999a and KNM-ER 1481a, all of which were analyzed directly. Cross-sectional properties for SK 82 and SK 97 were taken from the published literature.

Paranthropus. The head, neck, lesser trochanter and approximately 88 mm of the diaphysis below the distal margin of the lesser trochanter is preserved in KNM-ER 738. It was recovered from the KBS Channel Complex within the KBS Member at Koobi Fora, Area 105, and was initially described as a robust australopithecine (Leakey et al., 1972; Feibel et al., 1989). Its taxonomic status has been referred to in the published literature as *Homo*/*A*. (*P.*) *boisei*? (e.g. Day, 1986; Geissmann, 1986; McHenry, 1988, 1991; Jungers, 1988; Ruff et al., 1999). KNM-ER 1500d is part of an associated skeleton recovered from the Upper Burgi Member below the KBS Tuff at Koobi Fora, Area 130 (Leakey, 1973a; Feibel et al., 1989). It was initially allocated to the *Australopithecus* (robust) genus and is generally regarded as the only associated skeleton of *P. boisei* (Leakey, 1973a; Grausz et al., 1988; McHenry, 1994; but see Wood, 2005 and Wood and Constantino, 2007). SK 82 and SK 97 are proximal right femora recovered from the Hanging Remnant of Member 1 at Swartkrans, South Africa, and are attributed to *P. robustus* (Napier, 1964; Robinson, 1972). According to Grine (1989), more than 95% of the craniodental material in Member 1 can be attributed to *P. robustus*, albeit *Homo* material has also been recovered from the site (Susman, 1993; Grine et al., 1996; Susman et al., 2001). Thus, although SK 82 and SK 97 could potentially represent members of the genus *Homo*, it is unlikely given their lack of morphological resemblance to *Homo* femora (Day, 1969; McHenry and Corruccini, 1976; Wood and Constantino, 2007; Harmon, 2009). Cross-sectional properties for SK 82 and SK 97 were taken from Ruff et al. (1999).

Homo *sp.* KNM-ER 999a is an almost complete left femur recovered at Ileret, Koobi Fora, Area 6a (Day and Leakey, 1974). The femur is believed to have derived from 9-11 m from the base of the Guomde Formation (now part of the Chari Formation) (Leakey et al., 1978; Brown and Feibel, 1986). The Silbo Tuff, which lies within the Guomde Formation, has been dated at 0.74 ± 0.01 mya (McDougall, 1985) and 0.75 ±

0.02 mya (McDougall and Brown, 2006). Since these later deposits are undifferentiated, it is possible that KNM-ER 999a is of Middle or initial Late Pleistocene age, or even early Holocene age (Feibel et al., 1989). Feibel et al. (1989:614) suggested that KNM-ER 999a was derived from "undifferentiated later deposits, *probably* in the time span 0.5 to 0.1 my." Bräuer et al. (1997) suggested that KNM-ER 999a was from the Galana Boi Formation, and, based on gamma ray spectroscopy, may be as young as 301,000 ± 96,000 BP. The uncertain stratigraphic provenience of the femur has confounded its taxonomic affiliation. Day and Leakey (1974) attributed KNM-ER 999a to *Homo* sp. indet., and Wolpoff (1980) allocated it to *H. erectus.* According to Trinkaus (1993), KNM-ER 999a is morphologically aligned with early modern humans, particularly from the Levant. Uranium-series dating suggests that the femur may be as young as 300 kya, thus making it either an early representative of a near-modern transitional or late archaic *H. sapiens* (Bräuer et al., 1997). KNM-ER 1481a is part of a well-preserved left femur recovered from the Upper Burgi Member at Koobi Fora, Area 131 (Leakey, 1973a, b; Day et al., 1975; Feibel et al., 1989). Leakey (1973) initially attributed it to *Homo* sp. It has since been suggested to represent *H. erectus* (Kennedy, 1983), *H. habilis* (Trinkaus, 1984) and *H. rudolfensis* (Wood, 1992b). In this study, KNM-ER 999a and KNM-ER 1481a are considered to be representatives of *Homo* sp.

Hominin midshaft femora

Midshaft fossil femora examined in this study include KNM-ER 1592, KNM-ER 736, KNM-ER 1472, KNM-ER 1807 and OH 34. Data for OH 62, KNM-ER 1808 and KNM-WT 15000 were derived from the published literature.

Paranthropus. KNM-ER 1592 is the distal half of a robust right femur, which preserves a strong pilaster and the distal articulation (Leakey and Walker, 1985). The femoral fragment is approximately 200 mm in length. It was recovered from the lower KBS Member of the Koobi Fora Formation below the Ileret Tuff in Area 12, and initially assigned to the robust australopithecine genus (Leakey, 1973a; Howell, 1978; Leakey and Walker, 1985). McHenry (1992), however, suggested that KNM-ER 1592 should be left unclassified since there are no diagnostic morphological characteristics present on the femur.

Homo *sp*. KNM-ER 736 is a shaft fragment of a large left femur recovered from the Upper Member of the Koobi Fora Formation roughly 2-4 m below the projected level of the base of the Koobi Fora Tuff in Area 103 (Leakey et al., 1978). Leakey et al. (1972) described the specimen and tentatively assigned it to the *Australopithecus* (robust) genus. Day (1978) and Ruff and Walker (1993) advocated for its reassignment to the genus *Homo*, while others referred to it as a possible representative of *H. erectus* (McHenry, 1991; Franciscus and Holliday, 1992; Grine et al., 1995; Antón, 2003). KNM-ER 1472 is a well-preserved complete right femur recovered below the KBS Tuff at Koobi Fora, Area 131 (Leakey, 1973a, b; Day et al., 1975). Its taxonomic status as *Homo* sp. has not been challenged. KNM-ER 1807 is a right femoral diaphysis, which is broken into two fragments approximately near the midshaft. It was recovered from the Okote Member above the Black Pumice Tuff at Koobi Fora, Area 103 (Feibel et al., 1989). It has been allocated to both *Homo* and *Paranthropus* (Day et al., 1976; McHenry, 1991). OH 62 is a partial skeleton attributed by its discoverers to *H. habilis* (Johanson et al., 1987), albeit its allocation to the genus *Homo* has not been unanimously supported (Wood, 1992a, b, 1996; Wood and Collard, 1999a, b). Several lines of indirect evidence suggest that it derives from lower Bed I below Tuff ID and likely from the sand lens below Tuff IC, which would make it contemporary with material from the FLK (*Zinjanthropus*) level (~1.8 mya) (Johanson et al., 1987). OH 62 was not available for study at the time of data collection. Cross-sectional properties for the left femoral midshaft are taken from Ruff (2009). Scaled, digital photographs of the OH 62 femoral cast were used to measure section contours at a transverse natural break along the femoral diaphysis, which roughly corresponds to the 50-65% section location of bone length′ from the distal end (Ruff, 2009). In this study, KNM-ER 736, KNM-ER 1472, KNM-ER 1807 and OH 62 are referred to as early *Homo* without species designations.

H. erectus. *H. erectus* femora were included to represent Plio-Pleistocene obligate terrestrial bipeds. OH 34 is a left femoral diaphysis recovered from Bed III at the

JK 2 West site (Day and Molleson, 1976; Hay, 1976; Leakey, 1978). The head is abraded, and the greater and lesser trochanters and distal condyles are missing. The diaphysis is broken near the approximated midshaft (Day and Molleson, 1976). Although Day and Molleson (1976) and Leakey (1978) attributed the specimen to *Homo* sp. indet., it is often regarded as a representative, or tentative representative, of *H. erectus* (Howell, 1978; Tobias, 1991; Wood, 1992a, b; Antón, 2003; Steudel-Numbers, 2006; but see Haeusler and McHenry, 2004). It has been argued that the femoral diaphysis is so abraded that its taxonomic affiliation and the reconstruction of its original diaphyseal breadth and shape must remain uncertain (Leakey, 1978; Ruff, 1995; but see Day and Molleson, 1976 and Haeusler and McHenry, 2004). KNM-WT 15000 is a well-preserved associated skeleton of a male juvenile recovered in West Lake Turkana from the Natoo Member of the Nachukui Formation, and is dated between ~1.53-1.65 mya (Brown et al., 1985; Feibel et al., 1989; Walker and Leakey, 1993). KNM-ER 1808, recovered from the KBS Member at Koobi Fora, Area 103, is an adult, possibly female, associated skeleton dated to ~1.69 mya (Walker et al., 1982; Leakey and Walker, 1985; Feibel et al., 1989). It has been suggested that KNM-ER 1808 suffered from a systemic pathology since most long bone surfaces are covered with coarse-woven bone (Walker et al., 1982). The pathological bone deposits and the original periosteal surface are readily discernible on broken sections, such that the amount of bone added by the pathological lesions can be separated from the true bone surface (Ruff, 2008). Cross-sectional properties for KNM-WT 15000 and KNM-ER 1808 are taken from Ruff (2008) since the samples were not available at the time of data collection. Multi-planar radiography was used to reconstruct endosteal contours (Ruff, 2008). Cross-sectional properties of the right and left femora of KNM-WT 15000 were averaged, and the right femur was analyzed for KNM-ER 1808 (Ruff, 2008).

Modern human comparative sample

A well-preserved sample of modern human adults (n= 31), housed in the Department of Anthropology at the University of Western Ontario, is included in this study to serve as a referential obligate bipedal sample (Table 2). There are two caveats with this sample. First, there is a sex bias towards males (n= 26 males, n= 5 females). Second, the sample is not from a single population and many of the individuals are of unknown provenience. However, since the purpose for including the modern human data is to have a comparative obligate bipedal sample, mechanical loading in the femur should reflect patterns consistent with a commitment to bipedalism despite the heterogeneous nature of the collection. The right femur was preferentially chosen over the left, but the latter was included if the right was absent. Sexes were combined in the analyses.

Table 2. Modern human samples.

Sample	Sex	Provenience	Side
Stirrup Court 3	F	19th century peri-urban settlement	R
Stirrup Court 10	M	19th century peri-urban settlement	R
Stirrup Court 14	M	19th century peri-urban settlement	R
Stirrup Court 17	M	19th century peri-urban settlement	R
Stirrup Court 20	M	19th century peri-urban settlement	R
Odd Fellows 1	M	unknown	R
Odd Fellows 2	M	unknown	R
Odd Fellows 3	M	unknown	R
Odd Fellows 4	M	unknown	R
Odd Fellows 6	M	unknown	R
Odd Fellows 7	M	unknown	R
Odd Fellows 8	M	unknown	R
Odd Fellows 9	M	unknown	L
Odd Fellows 10	M	unknown	R
Odd Fellows 11	M	unknown	R
Odd Fellows 12	M	unknown	R
Odd Fellows 13	F	unknown	R

Sample	Sex	Provenience	Side
Odd Fellows 14	M	unknown	R
Odd Fellows 17	F	unknown	R
Odd Fellows 19b	M?	unknown	R
Odd Fellows 20	M	unknown	R
Birkette	F	Grand River Valley, Ontario	R
Breslau 1	M	19th century Kitchener, Ontario	R
Breslau 2	F	19th century Kitchener, Ontario	R
Downham Nursery	M?	Ontario Iroquoian village, Dutton	R
Orangeman’s Lodge	M?	unknown	L
H. Helmuth donation	M?	unknown	L
N. Halbert donation	M?	unknown	R
Van Oordt 10	M	15th century Waterloo, Ontario	R
Peterborough Jail 2	M	Russian immigrant to Canada	R
Peterborough Jail 3	M	Austrian immigrant to Canada	R

The Stirrup Court cemetery series, excavated in 1982 in London, Ontario, Canada, consists of residents of a historic peri-urban settlement area (Parish, 2000). The cemetery was in use between 1828 to 1890 (Parish, 2000). The individuals interred in Stirrup Court belong to one of two faiths—Primitive Methodist or Anglican (Church of England) (Parish, 2000). The former was layperson-centered, and therefore likely appealed to farmers and those of lower socio-economic status (Parish, 2000). Multiple lines of evidence on the skeletal remains of many of the Stirrup Court individuals in the current study suggest cyclical systemic stress (e.g. linear enamel hypoplasia and Harris lines) and poor general health (e.g. lytic lesions throughout the skeleton, porotic hyperostosis, cribra orbitalia) (Parish, 2000).

The Independent Order of Odd Fellows, a men’s fraternal organization, used human skeletal remains in various ceremonies for symbolic and ritual purposes (Ginter, 2001). The series consists of human remains from several lodges across Ontario, Canada, which were donated to the Department of Anthropology at the University of Western Ontario. The exact provenience of the samples is unknown, but it is believed that the majority of lodges received their human remains between 1860 to 1880 from medical schools (Ginter, 2001).

The Birkette burial was excavated in the Grand River Valley near Brantford, Ontario, Canada (Bull and Spence, 1988). The burial context is unknown since it was not excavated properly by trained archaeologists (Bull and Spence, 1988). Cultural material was not recovered in subsequent excavations by professional archaeologists (Bull and Spence, 1988). Multiple lines of skeletal and dental evidence suggest that the Birkette individual was an Iroquoian female in her late 20s to early 30s (Bull and Spence, 1988).

The Breslau burials are from a small burial plot near Kitchener, Ontario, Canada (Spence, 1985). The burials likely date to the 19th century (Spence, 1985). Pelvic traits using the Phenice method suggest that Breslau 1 is a probable male and Breslau 2 is a probable female (Spence, 1985). Numerous dental cavities suggest a heavily-based agricultural diet (Spence, 1985). A coin beneath the head of Breslau 1 implies that the burial probably took place between 1831-1833 (Spence, 1985).

The Downham Nursery burial derives from an Early Ontario Iroquoian village near Dutton (Spence, 1994). Early Ontario Iroquoian life emerged *circa* 1000 AD, and people relied on corn agriculture, hunting and fishing (Ferris, 1999).

The Van Oordt 10 individual is from a small 15th century burial site near Waterloo, Ontario, Canada, and may have been an Iroquoian warrior (Molto et al., 1986). Pelvic traits using the Phenice method suggest a probable male, and public symphysis morphology based on the McKern and Stewart method suggests an estimated age between 20 to 24 years-old (Molto et al., 1986). Projectile points made from Onondaga chert were found embedded in several locations throughout the body, and there is skeletal evidence for dismemberment and beheading (Molto et al., 1986).

The Peterborough Jail sample consists of two male inmates executed in Peterborough, Ontario, Canada in 1920 (Spence et al., 1999).

Cross-sectional reconstructions

The reconstruction of diaphyseal cross-sectional geometries and the calculation of cross-sectional parameters are based on accurate determinations of periosteal and endosteal contours at specified section locations. Traditionally, these sections are taken at 50% and 80% of femoral length′ measured from the distal end of the bone (Ruff and Hayes, 1983; Ruff, 1995, 2000a, 2002). Femur length′ is defined as the longitudinal length of the diaphysis from the average distal projection of the condyles to the superior surface of the femoral neck at its most distal point (Ruff, 2002) (see Fig. 2 in Chapter II). In the current study, section locations could not be taken at traditional percentages of bone length′ for the fossil samples due to technological limitations (see below). Instead, section locations were taken at natural breaks estimated to be in the proximal (~70-80%) or midshaft (~40-50%) region of the femoral diaphysis. Reconstructing cross-sections under these circumstances will still allow one to compare results from this study with those from other studies, particularly those involving fragmentary fossil material, since traditional section locations are approximated from estimated maximum bone length (e.g. Ruff et al., 1999; Kuperavage and Eckhardt, 2009). Sládek et al. (2010) found that femoral bending strength, and to some degree cortical area, in the midshaft femur of modern humans were accurately estimated even when the section location was inaccurately located (midshaft was considered being anywhere from 40-60% of bone length). Proximal and midshaft section locations were taken at 80% and 50% of bone length′, respectively, for the modern human sample.

Since engineering beam theory predicts that the most mechanically relevant material is located furthest from the section centroid (Ruff and Hayes, 1983; Bertram and Swartz, 1991; Ruff et al., 1993; Frassica et al., 1997; O’Neill and Ruff, 2004), accurate reconstructions of the periosteal surface “should be the most important factor in calculating cross-sectional properties,” (Stock, 2002:336). Periosteal and endosteal contours were reconstructed following the latex cast method as described by Stock (2002) (see Chapter II). Although latex casting is a non-destructive technique, there is potential for the casting material to leave traces of residue on the bone. In an effort to preserve the integrity of the fossil material, casting was done on casts provided by the National Museums of Kenya in Nairobi. Periosteal casts for the modern human sample were made directly on the bone.

Due to technological limitations, endosteal contours could not be reconstructed using bi-planar radiography for the hominin femora. Instead, anterior, posterior, medial and lateral cortical thicknesses, and antero-posterior (A-P) and medio-lateral (M-L) bone diameters were measured directly on the fossil material at natural breaks with digital calipers to the nearest 0.01 mm. Previous studies have reconstructed cross-sectional geometries at natural breaks in a similar manner (e.g. Ruff et al., 1993; Carretero et al., 2009). Thus, this method is considered acceptable when technological equipment (e.g. x-ray, computer tomography) is unavailable.

Endosteal contours for the modern human sample were reconstructed from measurements of cortical wall thicknesses, which were derived from traditional bi-planar radiographs using a Faxitron model 43855A x-ray machine in the Department of Anthropology at the University of Western Ontario. Section locations were marked with metal wire prior to x-raying, and a scaling device was included in each shot to correct for magnification[4]. Bones were placed in the x-ray machine in standard anatomical position and oriented following methods described by Ruff and Hayes (1983). Diaphyses were leveled by placing pieces of clay under the shaft so that the A-P midpoints of the proximal and distal ends of the bone were equidistant from the image receptor.
Kodak T-Mat film was used in Kodak Lanex regular and fast screens. The source to film distance was 61 cm with a focal spot size of 0.5 mm. The tube current ranged from 2 to 3 mA and the voltage ranged from 60 to 70 kVp depending on the sample. Exposure times varied from 3 to 5 sec. Films were manually processed using Pro Plus® developing and fixing solutions.

Periosteal casts were traced on graph paper with a 2 mm square grid. For hominin samples, measurements of cortical wall thicknesses were plotted onto the A-P and M-L

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[4] Magnification factor (z)= y/x where y is the length of the scaling device on the x-rayed image and x is the actual length of the scaling device. A metal bar was used as the scaling device. The measurement on the x-rayed image was divided by z to correct for magnification (Jaundrell-Thompson and Ashworth, 1970).

axes of the periosteal tracings. Cortical wall thicknesses for the modern human samples were measured directly on the radiographic film using digital calipers and a light box. A magnifying lens was used to aid in finding endosteal contours. Size-adjusted measurements were plotted in correct anatomical position on the periosteal tracings. Plotted points were connected in an ellipse for all samples.

The reconstructed cross-sections were digitized using a Lexmark X 6170 flatbed scanner. Although images were scanned at the same size as the original, a scaling device was included to ensure that the size of the images was not compromised during digitization. Cross-sectional properties were calculated using a Macintosh version of MomentMacro written for ImageJ, which is available courtesy of Dr. Christopher Ruff at http://www.hopkinsmedicine.org/FAE/mmacro.htm. Cross-sectional properties were calculated three times and the average was recorded.

A methodological concern in cross-sectional geometric reconstruction involves the axis where cross-sectional properties are calculated. In straight, symmetrical beams under uniform bending, the neutral axis passes through the geometric centroid of a section and is therefore also known as the centroidal axis (Lieberman et al., 2004). However, since long bones are subjected to a combination of bending and axial loads, and since long bones are neither entirely straight nor symmetrical, the neutral axis may not always pass through the centroid of a section (Demes et al., 2001; Lieberman et al., 2004). Experimental studies have confirmed that under varied loading regimes, the neutral axis shifts away from the centroid and towards the cortex under tension (Carter et al., 1981; Demes et al., 1998; Lieberman et al., 2004). Although the neutral axis can be experimentally determined *in vivo*, this is not possible with skeletal material. In this study, cross-sectional properties are calculated with reference to a neutral axis assumed to run through the cross-sectional area centroid "with the understanding that these [cross-sectional properties] are only approximations of true bending rigidity and strength *in vivo*," (Ruff et al., 2006:490).

Cross-sectional properties

The cross-sectional properties calculated in this study are presented in Table 3.

Table 3. Cross-sectional properties.

Symbol	Definition	Mechanical Significance
TA	total subperiosteal area	area within the subperiosteal surface
CA	cortical area	axial compressive and tensile strength
%CA	percent cortical area	percentage of cortical bone in the section
Z_x	section modulus about the M-L axis	bending strength in the A-P plane
Z_y	section modulus about the A-P axis	bending strength in the M-L plane
$J^{0.73}$	estimates the polar section modulus	torsional and twice average bending strength
Z_x/Z_y	diaphyseal shape index	ratio of A-P to M-L bending strength

Cortical area (CA) reflects the axial compressive and tensile strengths of the section (Ruff and Hayes, 1983; Ruff, 1994; Stock and Pfeiffer, 2004). Percent cortical area (%CA) is an expression of the relative cortical thickness of the cross-section and can be used as a proxy for bone mass (Ruff and Hayes, 1983; Ruff et al., 1993). %CA is calculated as CA/total area (TA) · 100, and does not vary with body size (Ruff et al., 1993). CA and %CA quantify the absolute and relative amounts, respectively, of bone in a cross-section. CA and TA are reported in mm^2.

Section moduli estimate the average bending and torsional strength[5] of a section (Ruff, 2008). They are less dependent than second moments of area on the precise orientation of the section along the A-P and M-L axes, and are preferred when anatomical axes are imprecisely determined as is the case when using x-rays (Ruff, 2009).

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[5] Rigidity and strength are often used interchangeably, but they refer to somewhat different, albeit related, structural properties of a material. Rigidity is a measure of the internal resistance of a structure to an externally applied force (or mechanical load), while strength is the maximum stress sustained by a structure before failure (Reilly and Burstein, 1974).

Furthermore, section moduli are a more direct measure of bending strength than second moments of area since “they compensate for the distance from the neutral axis to the bone’s outer perimeter (where the highest bending stresses occur),” (Demes et al., 1991:540). Z_x and Z_y are used to calculate the maximum stress in the outermost fiber of the cross-section in the anatomical plane of bending, which is proportional to cross-sectional bending strength (Ruff and Hayes, 1983; Ruff, 1995). Z_x corresponds to bending strength in the A-P plane measured about the M-L axis (*x*-axis), and Z_y corresponds to bending strength in the M-L plane measured about the A-P axis (*y*-axis) (Ruff, 2002, 2009). Z_x and Z_y in the proximal femur are interpreted with caution because the antetorsion angle of the femoral neck makes it challenging to correctly orient the bone along anatomical axes (Ruff and Hayes, 1983; Ruff, 1987). The polar section modulus is a measure of twice average bending and torsional strength, and can be approximated by taking the polar second moment of area[6] to the power of 0.73 (i.e. $J^{0.73}$)[7] (Ruff, 1995; Trinkaus and Ruff, 1999; Ruff, 2002). Section moduli are reported in mm^3.

Ratios of section moduli (i.e. Z_x/Z_y) give an overall indication of diaphyseal shape (Jungers and Minns, 1979; Ruff, 1987). Bones subjected to bending in a single plane are less circular (i.e. a ratio departing from 1.0) since bending strength is determined by the relative distribution of bone perpendicular to the plane of bending (Ruff and Hayes, 1983; Carlson, 2005). Bones predominately subjected to torsion tend to have a more circular cross-sectional shape (i.e. a ratio approaching 1.0) because torsional strength is determined by the radial distribution of bone about the centroid (Ruff and Hayes, 1983).

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[6] The polar second moment of area, J, measures torsional rigidity and average bending rigidities in all planes of a section. It is the sum of any two perpendicular second moments of area (i.e. $I_x + I_y$ or $I_{max} + I_{min}$) (Ruff and Hayes, 1983; Ruff et al., 1993; Ruff, 2000a; Stock, 2002).

[7] Z_x and Z_y can also be approximated by taking second moments of area (i.e. I_x and I_y) to the power of 0.73. This was not done for the samples analyzed in the current study since MomentMacro calculates Z_x and Z_y. Z_x and Z_y were published for KNM-WT 15000, KNM-ER 1808 and OH 62 (Ruff, 2008, 2009). Only second moments of area were reported for SK 82 and SK 97 (Ruff et al., 1999). Thus, Z_x and Z_y were estimated as $I_x^{0.73}$ and $I_y^{0.73}$, respectively, for the Swartkrans femora.

Body size standardization

It is necessary to control for the effects of body size on cross-sectional properties before comparing groups. To avoid circular reasoning, it is better to use a non-mechanical method to estimate body size (Ruff, 2000b). However, this may not always be possible given the limitations associated with fossil material (Kuperavage and Eckhardt, 2009). Cross-sectional properties have been shown to scale with appropriate powers of bone length (Ruff et al., 1993). Powers of bone length rather than body mass and maximum bone length were used to standardize cross-sectional properties since this method only relies on one variable (i.e. maximum bone length) rather than two (i.e. maximum bone length and body mass). Since maximum bone length and body mass are often estimated for fossil samples, standardizing by powers of bone length was deemed more appropriate than standardizing by body mass and maximum bone length since only one variable is used in the former technique. Area was standardized by dividing by bone length^{3} then multiplying by 10^{8}, and section moduli were standardized by dividing by bone length$^{5.33}$ then multiplying by 10^{12} following Ruff et al. (1993) and Trinkaus and Ruff (1996). Femoral length estimates for all fossil samples were taken from McHenry (1991), except KNM-ER 999a (Geissmann, 1986), KNM-WT 15000 (Ruff and Walker, 1993) and OH 62 (Richmond et al., 2002). *Pan* was excluded from this study since standardizing by powers of bone length is not applicable to chimpanzees and bonobos.

Statistics

Agglomerative hierarchical cluster analysis using the unweighted pair-group average method (UPGMA) is used to identify homogeneous groups based on all cross-sectional properties (i.e. TA, CA, %CA, $J^{0.73}$, Z_x, Z_y and Z_x/Z_y) (Aldenderfer and Blashfield, 1984). The distance between two clusters is calculated as the average distance between all pairs of cases in the two different clusters (Aldenderfer and Blashfield, 1984). Euclidean distance is used to measure distances between samples.

Stepwise discriminant function analysis (DFA) is conducted to investigate which cross-sectional properties best discriminate among the groups[8] (Field, 2009). At each step in this analysis, the variable that maximizes the Mahalanobis distance between the two closest groups is entered. The process continues until a variable is selected that does not significantly increase the R-squared value (Manly, 2005). Since the stepwise method capitalizes on chance associations, significance levels may be higher than the real alpha (Kachigan, 1991; Manly, 2005). It is therefore necessary to run the statistics multiple times and include a cross-validation test (Manly, 2005). Cross-sectional properties were transformed into z-scores prior to analysis because of differences in scale (Aldenderfer and Blashfield, 1984).

Two assumptions about the data that should be investigated prior to cluster analysis and DFA are normality and homogeneity of the variance (homoscedasticity). Normality and homogeneity of the variances are examined with Kolmogorov-Smirnov tests with Lilliefors correction and Levene's tests, respectively (Lilliefors, 1967; Thode, 2002; Field, 2009). Statistical analyses were carried out with *SPSS* version 17.0 with p= 0.05.

RESULTS

In the proximal femur, all cross-sectional properties except %CA and Z_x/Z_y violate the assumption of normality based on the combined sample mean and sample variance (Table 4). $J^{0.73}$, Z_x and Z_y violate the assumption of homogeneity of the variances (Table 5).

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[8] In the proximal femur, "group" refers to *Paranthropus*, fossil *Homo* sp. and *H. sapiens*. In the midshaft femur, "group" refers to *Paranthropus*, fossil *Homo* sp., *H. erectus* and *H. sapiens*.

Table 4. Normality test for the proximal femur.

	Kolmogorov-Smirnov[a]		
	Statistic	df	Sig.
TA	0.18	37	**0.00**
CA	0.21	37	**0.00**
%CA	0.10	37	0.20*
$J^{0.73}$	0.30	37	**0.00**
Z_x	0.28	37	**0.00**
Z_y	0.25	37	**0.00**
Z_x/Z_y	0.10	37	0.20*

a. Lilliefors Significance Correction.
*. This is a lower bound of the true significance.
Significance is indicated in bold.

Table 5. Levene's test for the proximal femur.

	Levene Statistic	df1	df2	Sig.
TA	1.03	2	34	0.37
CA	0.33	2	34	0.72
%CA	1.03	2	37	0.37
$J^{0.73}$	28.12	2	34	**0.00**
Z_x	4.47	2	34	**0.02**
Z_y	12.01	2	34	**0.00**
Z_x/Z_y	1.00	2	34	0.38

Significance is indicated in bold.

In the midshaft femur, TA, $J^{0.73}$, Z_x and Z_y violate the assumption of normality (Table 6). $J^{0.73}$, Z_x and Z_y violate the assumption of homogeneity of the variances (Table 7).

Table 6. Normality test for the midshaft femur.

	Kolmogorov-Smirnov[a]		
	Statistic	df	Sig.
TA	0.15	39	**0.02**
CA	0.13	39	0.13
%CA	0.07	39	.200*
$J^{0.73}$	0.32	39	**0.00**
Z_x	0.21	39	**0.00**
Z_y	0.19	39	**0.00**
Z_x/Z_y	0.13	39	0.08

a. Lilliefors Significance Correction.
*. This is a lower bound of the true significance.
Significance is indicated in bold.

Table 7. Levene's test for the midshaft femur.

	Levene Statistic	df1	df2	Sig.
TA	1.65	2	35	0.21
CA	2.93	2	35	0.07
%CA	0.23	2	35	0.80
$J^{0.73}$	33.14	2	35	**0.00**
Z_x	17.90	2	35	**0.00**
Z_y	16.34	2	35	**0.00**
Z_x/Z_y	0.54	2	35	0.59

Significance is indicated in bold.

Although the data violate assumptions of normality and homogeneity of the variances, cluster analysis and DFA are robust to such violations (Aldenderfer and Blashfield, 1984; Manly, 2005). Nevertheless, results are interpreted cautiously.

Proximal femur

Cluster analysis. The proximity matrix for the fossil samples is presented in Table 8. Among all pairs, KNM-ER 1500d and SK 82 share the closest proximity (1.21). KNM-ER 999a and KNM-ER 1481a are also close (1.61). Paranthropine femora are more similar among each other than to fossil *Homo* sp. femora. The closeness between East and South African paranthropines suggests spatio-temporal continuity in paranthropine proximal femoral cross-sectional morphology. KNM-ER 999a and KNM-ER 1481a are more similar to KNM-ER 738 (4.93 and 3.46, respectively) than to any other paranthropine femur. It should be noted, however, that the taxonomic identity of KNM-ER 738 as a *Paranthropus* is uncertain.

Table 8. Proximity matrix for the proximal femur.

	KNM-ER 738	KNM-ER 1500d	SK 82	SK 97	KNM-ER 999a	KNM-ER 1481a
KNM-ER 738 (P)	0.00	3.03	2.48	2.73	4.93	3.46
KNM-ER 1500d (P)		0.00	1.21	3.44	7.58	6.27
SK 82 (P)			0.00	3.57	7.23	5.86
SK 97 (P)				0.00	4.96	4.09
KNM-ER 999a (H)					0.00	1.61
KNM-ER 1481a (H)						0.00

(P) after sample indicates *Paranthropus* and (H) after sample indicates *Homo* sp.

Two main clusters are formed based on proximal femoral cross-sectional properties. The first cluster includes modern humans and fossil *Homo*, and the second cluster consists of *Paranthropus* (Fig. 1). The taxonomically uncertain KNM-ER 738 femur is grouped with *Paranthropus* to the exclusion of modern and fossil *Homo*.

```
                  0         5        10        15        20        25
                  +---------+---------+---------+---------+---------+
H. sapiens        -+
H. sapiens        -+---+
H. sapiens        -+    +-+
H. sapiens        -----+ |
H. sapiens        -+-+   +---+
H. sapiens        -+ +-+ |   |
H. sapiens        ---+ +-+   |
H. sapiens        -----+     +-+
H. sapiens        -+---+     | |
H. sapiens        -+   +---+ | |
H. sapiens        -----+   | | |
H. sapiens        -----+-+ +-+ |
H. sapiens        -----+ | |   |
H. sapiens        ---+-+ | |   |
H. sapiens        ---+ +-+-+   |
H. sapiens        -+-+ | |     +---+
H. sapiens        -+ +-+ |     |   |
H. sapiens        -+-+   |     |   |
H. sapiens        -+ |   |     |   |
H. sapiens        -------+     |   |
H. sapiens        -+---+       |   +---+
H. sapiens        -+   +---+   |   |   |
H. sapiens        -+---+   +---+   |   |
H. sapiens        -+       |       |   |
H. sapiens        ---------+       |   +-----+
H. sapiens        ---+---+         |   |     |
H. sapiens        ---+   +---------+   |     |
H. sapiens        -------+             |     +---------------------+
H. sapiens        ---------------------+     |                     |
KNM-ER 999a (H)   -----------+-----+         |                     |
KNM-ER 1481a (H)  -----------+     +---------+                     |
H. sapiens        -----------------+                               |
KNM-ER 1500d (P)  -------+---------------+                         |
SK 82 (P)         -------+               +-------------------------+
KNM-ER 738 (P)    -------------------+---+
SK 97 (P)         -------------------+
```

Figure 1. Dendrogram from the UPGMA cluster analysis of the proximal femur. (P) after fossil samples indicates *Paranthropus*, and (H) indicates *Homo* sp.

DFA. All cross-sectional properties (i.e. TA, CA, %CA, $J^{0.73}$, Z_x, Z_y and Z_x/Z_y) were initially entered into a stepwise DFA to determine which variables contribute most to group differences. CA is entered in the first step, Z_x/Z_y is entered in the second step, Z_x is entered in the third step and $J^{0.73}$ is entered in the fourth step. Pairwise group comparisons suggest that distances between group means are significantly different at each step in the analysis (Table 9).

Table 9. Pairwise group comparisons for the proximal femur.

Step	Species		*H. sapiens*	*Paranthropus*	*Homo* sp.
1	*H. sapiens*	F		148.55	15.86
		Sig.		**0.00**	**0.00**
	Paranthropus	F	148.55		17.00
		Sig.	**0.00**		**0.00**
	Homo sp.	F	15.86	17.00	
		Sig.	**0.00**	**0.00**	
2	*H. sapiens*	F		72.37	19.30
		Sig.		**0.00**	**0.00**
	Paranthropus	F	72.37		14.72
		Sig.	**0.00**		**0.00**
	Homo sp.	F	19.30	14.72	
		Sig.	**0.00**	**0.00**	
3	*H. sapiens*	F		54.85	14.24
		Sig.		**0.00**	**0.00**
	Paranthropus	F	54.85		17.71
		Sig.	**0.00**		**0.00**
	Homo sp.	F	14.24	17.71	
		Sig.	**0.00**	**0.00**	
4	*H. sapiens*	F		133.96	27.78
		Sig.		**0.00**	**0.00**
	Paranthropus	F	133.96		18.79
		Sig.	**0.00**		**0.00**
	Homo sp.	F	27.78	18.79	
		Sig.	**0.00**	**0.00**	

1, 34 degrees of freedom for step 1.
2, 33 degrees of freedom for step 2.
3, 32 degrees of freedom for step 3.
4, 31 degrees of freedom for step 4.
Significance is indicated in bold.

$J^{0.73}$ is associated with the first function, which explains 94% of the variance, and Z_x/Z_y is associated with the second function (Table 10). Wilks' λ is significant for both functions (Table 11). For the first function, the *Paranthropus* and fossil *Homo* sp. group centroids are negative and the modern human group centroid is positive. These results indicate that modern humans and fossil hominins are discriminated by $J^{0.73}$. The first function discriminates most between modern humans and *Paranthropus*. Fossil *Homo* falls intermediate. For the second function, the modern human and *Paranthropus* group centroids are negative and the fossil *Homo* sp. group centroid is positive. These results indicate that fossil *Homo* is discriminated from modern humans and *Paranthropus* by Z_x/Z_y (Table 12).

Table 10. Structure matrix for the proximal femur.

	Function	
	1	2
$J^{0.73}$	0.69*	-0.50
Z_y[a]	0.57*	-0.52
Z_x	0.52*	-0.30
CA	0.50*	-0.12
TA[a]	0.42*	-0.32
Z_x/Z_y	0.04	0.72*
%CA[a]	0.19	0.28*

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions.
Variables ordered by absolute size of correlation within function.
*. Largest absolute correlation between each variable and any discriminant function.
a. This variable not used in the analysis.

Table 11. Wilks' lambda for the proximal femur.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 2	0.02	121.45	8.00	**0.00**
2	0.47	24.37	3.00	**0.00**

Significance is indicated in bold.

Table 12. Functions at groups centroids for the proximal femur.

Species	Function	
	1	2
H. sapiens	-1.76	-0.12
Paranthropus	11.08	-1.09
Homo sp.	5.13	4.05

Unstandardized canonical discriminant functions evaluated at group means.

The canonical plot for the DFA is displayed in Figure 2. Of particular note is the low scatter among modern humans despite the heterogeneity of the sample. These results are a good indication of homogeneity in cross-sectional properties in the proximal femur of the modern human sample. It is evident from the canonical plot that modern human, fossil *Homo* and *Paranthropus* proximal femora are distinct from one another based on cross-sectional properties.

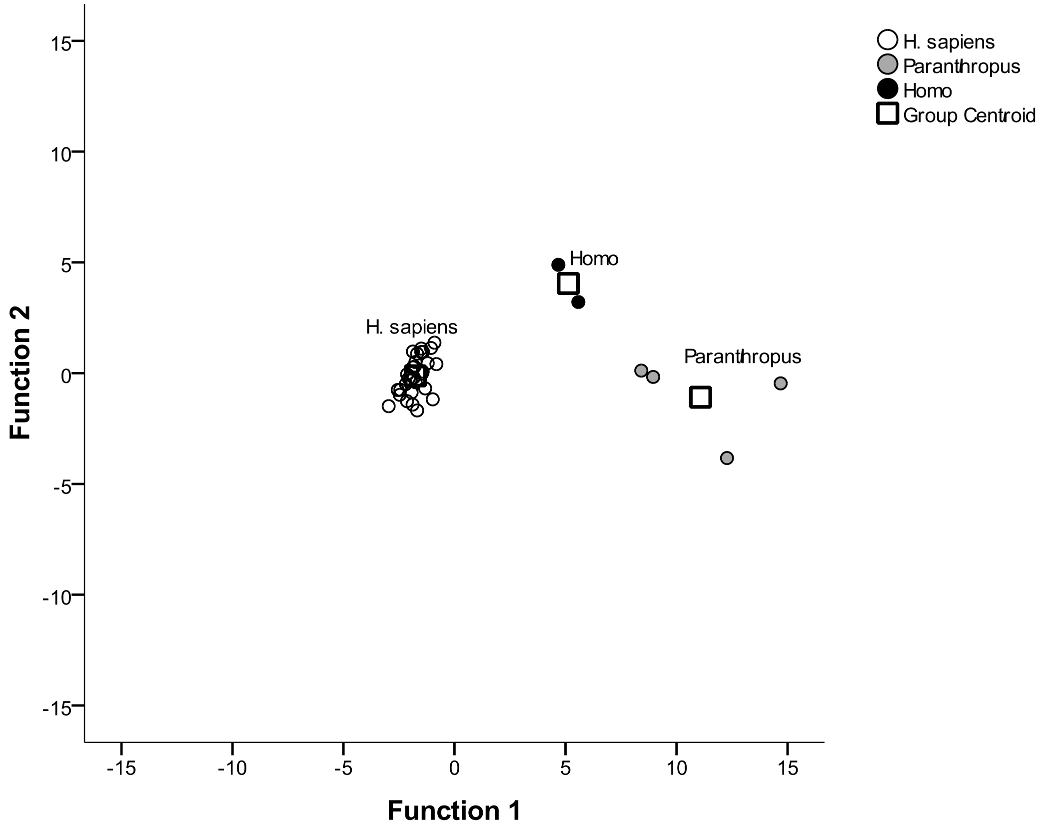

Figure 2. Canonical plot for the proximal femur. $J^{0.73}$ is associated with the first function and Z_x/Z_y is associated with the second function. *Homo*= KNM-ER 999a and KNM-ER 1481a. *Paranthropus*= KNM-ER 738, KNM-ER 1500d, SK 82 and SK 97.

All original grouped cases are correctly classified, and 97% of cross-validated grouped cases are correctly classified (Table 13). Only one *Paranthropus* femur (KNM-ER 738) was misclassified as fossil *Homo*. The classification results suggest that $J^{0.73}$, and to some extent Z_x/Z_y, are valid discriminators among modern human, fossil *Homo* and *Paranthropus* proximal femora.

Table 13. Classification results for the proximal femur.

		Species	Predicted Group Membership			Total
			H. sapiens	*Paranthropus*	*Homo* sp.	
Original	Count	*H. sapiens*	31	0	0	31
		Paranthropus	0	4	0	4
		Homo sp.	0	0	2	2
	%	*H. sapiens*	100.0	0.0	0.0	100.0
		Paranthropus	0.0	100.0	0.0	100.0
		Homo sp.	0.0	0.0	100.0	100.0
Cross-validated[a]	Count	*H. sapiens*	31	0	0	31
		Paranthropus	0	3	1	4
		Homo sp.	0	0	2	2
	%	*H. sapiens*	100.0	0.0	0.0	100.0
		Paranthropus	0.0	75.0	25.0	100.0
		Homo sp.	0.0	0.0	100.0	100.0

[a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
100.0% of original grouped cases correctly classified.
97.3% of cross-validated grouped cases correctly classified.

Summary. The cluster analysis suggests that fossil *Homo* and modern human proximal femora are more similar among each other than they are to *Paranthropus* femora. East and South African *Paranthropus* femora are more similar among each other than they are to *Homo*, which supports the long held view of morphological spatial and temporal continuity among paranthropine proximal femora (Ruff et al., 1999; Harmon, 2009). The results from the DFA suggest that group differences are mainly due to $J^{0.73}$, and to some extent Z_x/Z_y. Modern humans and fossil hominins are discriminated along the first function, which is associated with $J^{0.73}$. Fossil *Homo* is discriminated from modern humans and *Paranthropus* along the second function, which is associated with Z_x/Z_y. Results support the taxonomic allocations of KNM-ER 999a and KNM-ER 1481a to the genus *Homo*, albeit their species designations cannot be resolved. In addition, results support the taxonomic assignments of KNM-ER 1500d, SK 82 and SK 97 to a non-*Homo* genus. The taxonomic assignment of KNM-ER 738 is ambivalent. The results cannot definitively confirm or refute the taxonomic status of KNM-ER 738 as a paranthropine, although in terms of its cross-sectional morphology it is closer to paranthropine femora than to modern and fossil *Homo* femora based on the cluster analysis. It was, however, (mis)classified as fossil *Homo* in the cross-validation classification in the DFA.

Midshaft femur

Cluster analysis. The proximity matrix for the fossil samples is presented in Table 14. Of particular interest is the closeness among all fossil femora (i.e. low distance measures), excluding OH 62, which is the most distant individual. OH 62 is particularly distant from *H. erectus* femora (i.e. OH 34, KNM-WT 15000 and KNM-ER 1808). The *H. erectus* femora share a close proximity among each other. KNM-ER 1808 also shares a close proximity to KNM-ER 1592 (2.97), a purported paranthropine. The taxonomically debatable KNM-ER 1807 femur is closest to KNM-ER 1592 (2.02), while the other taxonomically debatable femur, KNM-ER 736, is closest to KNM-ER 1472 (2.10), a likely representative of the genus *Homo*. The proximity of KNM-ER 1592 to all *Homo* and/or possible *Homo* sp. femora, excluding OH 62, challenges its taxonomic status as a paranthropine, or suggests that midshaft cross-sectional morphology in *Paranthropus* and fossil *Homo* is similar.

Table 14. Proximity matrix for the midshaft femur.

	KNM-ER 1592	KNM-ER 736	KNM-ER 1472	KNM-ER 1807	OH 62	KNM-ER 1808	KNM-WT 15000	OH 34
KNM-ER 1592 (P)	0.00	3.66	2.08	2.02	9.18	2.97	4.50	4.73
KNM-ER 736 (H)		0.00	2.10	2.98	8.77	4.89	4.11	5.61
KNM-ER 1472 (H)			0.00	2.72	9.51	3.11	3.16	4.00
KNM-ER 1807 (H)				0.00	7.70	4.53	5.36	6.24
OH 62 (H)					0.00	11.80	12.10	13.20
KNM-ER 1808 (He)						0.00	2.80	2.29
KNM-WT 15000 (He)							0.00	2.18
OH 34 (He)								0.00

(P) after sample indicates *Paranthropus*, (H) after sample indicates *Homo* sp. and (He) after sample indicates *H. erectus*.

Cluster formations are not very distinct, which suggests overall homogeneity in midshaft cross-sectional properties among the groups. KNM-ER 1592 and all fossil *Homo* femora, except OH 62, cluster with modern humans (Fig. 3). The distinctiveness of OH 62 compared to other fossil *Homo* femora is evidenced by its lone clustering.

```
                  0         5        10        15        20        25
                  +---------+---------+---------+---------+---------+
H. sapiens        -+
H. sapiens        -+-+
H. sapiens        -+ +-+
KNM-WT 15000 (He) ---+ +-+
H. sapiens        -+-+ | |
H. sapiens        -+ +-+ |
H. sapiens        ---+   +-+
H. sapiens        -+-+   | |
H. sapiens        -+ +-+ | |
H. sapiens        ---+ +-+ |
H. sapiens        -----+   +-+
H. sapiens        -+---+   | |
H. sapiens        -+   +-+ | |
H. sapiens        ---+-+ | | |
KNM-ER 1472 (H)   ---+   +-+ |
H. sapiens        ---+   |   |
H. sapiens        ---+-+ |   |
H. sapiens        ---+ +-+   |
H. sapiens        ---+-+     +-+
H. sapiens        ---+ |     | |
H. sapiens        -+-+ |     | |
H. sapiens        -+ +-+     | |
H. sapiens        -+-+       | |
H. sapiens        -+ |       | |
H. sapiens        ---+       | +-+
H. sapiens        -----+     | | |
H. sapiens        -----+-----+ | |
OH 34 (He)        -----+     | | |
KNM-ER 1808 (He)  -----------+ | |
H. sapiens        ---+---+     | +---------------------------------+
H. sapiens        ---+   +---+ | |                                 |
H. sapiens        -------+   +-+ |                                 |
H. sapiens        -----------+   |                                 |
H. sapiens        ---+-----+     |                                 |
KNM-ER 1592 (P)   ---+     +---+ |                                 |
H. sapiens        -------+-+   +-+                                 |
KNM-ER 1807 (H)   -------+     |                                   |
KNM-ER 736 (H)    -------------+                                   |
OH 62 (H)         -------------------------------------------------+
```

Figure 3. Dendrogram from the UPGMA cluster analysis of the midshaft femur. (P) after fossil samples indicates *Paranthropus*, (H) after fossil samples indicates *Homo* sp. and (He) indicates *H. erectus.*

DFA. All cross-sectional properties (i.e. TA, CA, %CA, $J^{0.73}$, Z_x, Z_y and Z_x/Z_y) were entered into a stepwise DFA to determine which variables contribute most to group differences. CA is entered in the first step, %CA is entered in the second step, $J^{0.73}$ is entered in the third step, Z_x is entered in the fourth step and Z_y is entered in the fifth step.

Pairwise group comparisons are presented in Table 15. In the final step, which includes all five variables entered into the analysis, distances between group means are significantly different between modern humans and fossil *Homo* sp., modern humans and *H. erectus*, *Paranthropus* and fossil *Homo* sp. and fossil *Homo* sp. and *H. erectus*. Distances between group means are not significantly different between modern humans and *Paranthropus*, and *Paranthropus* and *H. erectus*.

Table 15. Pairwise group comparisons for the midshaft femur.

Step	Species		*H. sapiens*	*Paranthropus*	*Homo* sp.	*H. erectus*
1	*H. sapiens*	F		3.17	26.11	3.15
		Sig.		0.08	**0.00**	0.09
	Paranthropus	F	3.17		0.66	6.23
		Sig.	0.08		0.42	**0.02**
	Homo sp.	F	26.11	0.66		24.60
		Sig.	**0.00**	0.42		**0.00**
	H. erectus	F	3.15	6.23	24.60	
		Sig.	0.09	**0.02**	**0.00**	
2	*H. sapiens*	F		3.24	14.18	5.01
		Sig.		**0.05**	**0.00**	**0.01**
	Paranthropus	F	3.24		3.44	3.05
		Sig.	**0.05**		**0.04**	0.06
	Homo sp.	F	14.18	3.44		17.37
		Sig.	**0.00**	**0.04**		**0.00**
	H. erectus	F	5.01	3.05	17.37	
		Sig.	**0.01**	0.06	**0.00**	

3	*H. sapiens*	F		2.28	12.29	7.80
		Sig.		0.10	**0.00**	**0.00**
	Paranthropus	F	2.28		2.43	2.53
		Sig.	0.10		0.08	0.07
	Homo sp.	F	12.29	2.43		11.45
		Sig.	**0.00**	0.08		**0.00**
	H. erectus	F	7.80	2.53	11.45	
		Sig.	**0.00**	0.07	**0.00**	
4	*H. sapiens*	F		2.19	14.81	7.36
		Sig.		0.09	**0.00**	**0.00**
	Paranthropus	F	2.19		2.01	1.84
		Sig.	0.09		0.12	0.15
	Homo sp.	F	14.81	2.01		8.76
		Sig.	**0.00**	0.12		**0.00**
	H. erectus	F	7.36	1.84	8.76	
		Sig.	**0.00**	0.15	**0.00**	
5	*H. sapiens*	F		2.16	30.41	8.80
		Sig.		0.08	**0.00**	**0.00**
	Paranthropus	F	2.16		3.64	1.53
		Sig.	0.08		**0.01**	0.21
	Homo sp.	F	30.41	3.64		9.46
		Sig.	**0.00**	**0.01**		**0.00**
	H. erectus	F	8.80	1.53	9.46	
		Sig.	**0.00**	0.21	**0.00**	

1, 35 degrees of freedom for step 1.
2, 34 degrees of freedom for step 2.
3, 33 degrees of freedom for step 3.
4, 32 degrees of freedom for step 4.
5, 31 degrees of freedom for step 5.
Significance is indicated in bold.

$J^{0.73}$ is associated with the first function, which explains 84% of the variance, CA is associated with the second function, which explains 14% of the variance and %CA is associated with the third function (Table 16). Wilks' λ is significant for the first two functions (Table 17). The modern human group centroid is negative for the first function, and all fossil hominin group centroids are positive for the first function. These results indicate that fossil hominins, as a group, are discriminated from modern humans by $J^{0.73}$. These results mirror those found in the proximal femoral analysis. The first function discriminates most between modern humans and fossil *Homo* sp. Given the results of the cluster analysis, it is unclear if the separation of modern humans from fossil *Homo* is due to fossil *Homo* as a group or to the distinctiveness OH 62. *Paranthropus* and *H. erectus* group centroids are negative, and modern human and fossil *Homo* group centroids are positive for the second function. These results indicate that CA discriminates between *Paranthropus* and *H. erectus*, and modern humans and fossil *Homo* sp. (Table 18).

Table 16. Structure matrix for the midshaft femur.

	Function		
	1	2	3
$J^{0.73}$	0.44^*	0.33	0.15
TA^a	0.30	0.87^*	0.20
CA	0.33	0.62^*	0.62
Z_x	0.33	0.56^*	0.24
Z_y	0.33	0.53^*	0.33
%CA	0.15	-0.14	0.95^*
Z_x/Z_y^a	-0.01	0.03	-0.26^*

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions.

Variables ordered by absolute size of correlation within function.

*. Largest absolute correlation between each variable and any discriminant function.

a. This variable not used in the analysis.

Table 17. Wilks' lambda for the midshaft femur.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	0.07	87.14	15	**0.00**
2 through 3	0.47	25.60	8	**0.00**
3	0.87	4.51	3	0.21

Significance is indicated in bold.

Table 18. Functions at groups centroids for the midshaft femur.

Species	Function	
	1	2
H. sapiens	-1.00	0.17
Paranthropus	1.67	-0.55
Homo sp.	5.91	0.98
H. erectus	1.92	-2.92

Unstandardized canonical discriminant functions evaluated at group means.

The canonical plot for the DFA is displayed in Figure 4. Despite the heterogeneous nature of the modern human sample, the data are not dispersed. They are, however, more scattered compared to the results for the proximal section. Although groups are separated from each other, it is clear from the canonical plot that they are not as separated as in the proximal femoral analysis.

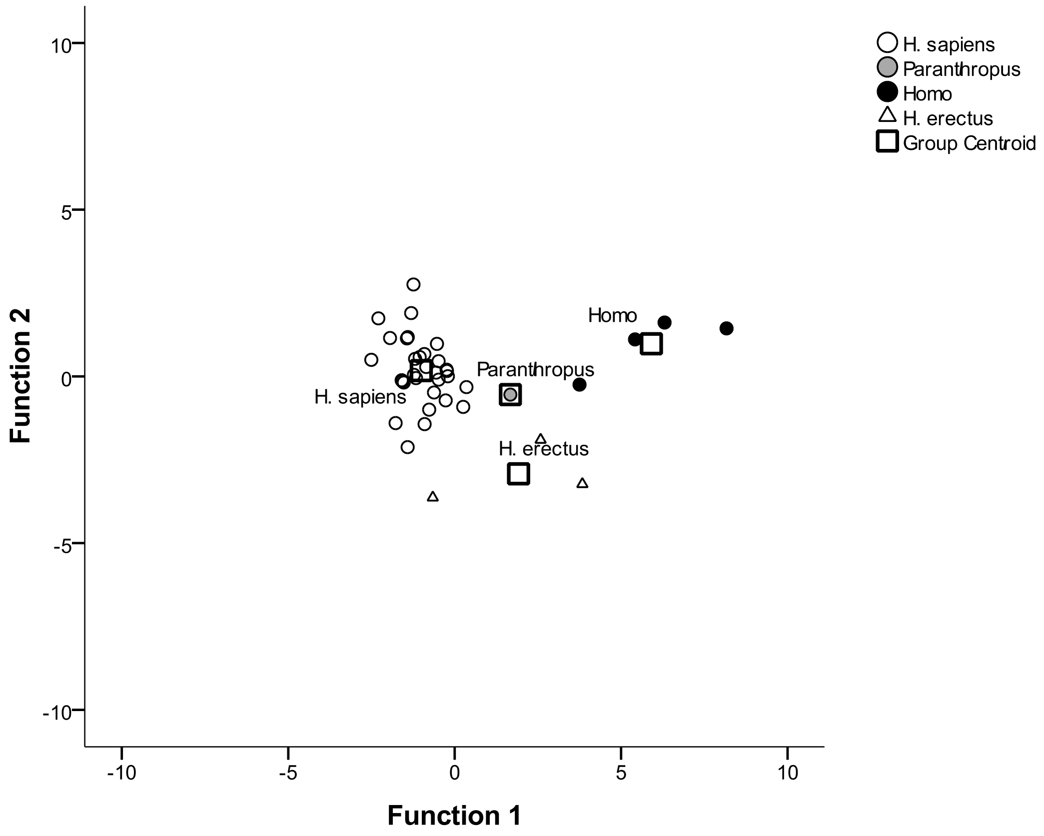

Figure 4. Canonical plot for the midshaft femur. $J^{0.73}$ is associated with the first function and CA is associated with the second function. *Paranthropus*= KNM-ER 1592. *Homo*= KNM-ER 736, KNM-ER 1472, KNM-ER 1807 and OH 62. *H. erectus*= KNM-ER 1808, KNM-WT 15000 and OH 34.

All of the original grouped cases are correctly classified, and 92% of the cross-validated grouped cases are correctly classified. KNM-ER 1592 was misclassified as modern human, one fossil *Homo* sp. Femur (OH 62) was misclassified as *H. erectus* and one *H. erectus* femur (KNM-WT 15000) was misclassified as modern human (Table 19).

Table 19. Classification results for the midshaft femur.

			Predicted Group Membership				Total
		Species	*H. sapiens*	*Paranthropus*	*Homo* sp.	*H. erectus*	
Original	Count	*H. sapiens*	31	0	0	0	31
		Paranthropus	0	1	0	0	1
		Homo sp.	0	0	4	0	4
		H. erectus	0	0	0	3	3
	%	*H. sapiens*	100.0	0.0	0.0	0.0	100.0
		Paranthropus	0.0	100.0	0.0	0.0	100.0
		Homo sp.	0.0	0.0	100.0	0.0	100.0
		H. erectus	0.0	0.0	0.0	100.0	100.0
Cross-validated[a]	Count	*H. sapiens*	31	0	0	0	31
		Paranthropus	1	0	0	0	1
		Homo sp.	0	0	3	1	4
		H. erectus	1	0	0	2	3
	%	*H. sapiens*	100.0	0.0	0.0	0.0	100.0
		Paranthropus	100.0	0.0	0.0	0.0	100.0
		Homo sp.	0.0	0.0	75.0	25.0	100.0
		H. erectus	33.3	0.0	0.0	66.7	100.0

[a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
100.0% of original grouped cases correctly classified.
92.3% of cross-validated grouped cases correctly classified.

Summary. Two main clusters are formed based on midshaft femoral cross-sectional properties. One cluster includes modern humans and all fossil femora, except OH 62, and the other cluster includes OH 62. Results from the DFA suggest that $J^{.073}$ primarily contributes to group differences. However, it only accounts for 84% of the variance among groups. This may reflect general similarities in average bending and torsional strength among the groups. Results suggest that KNM-ER 1592, based on midshaft femoral cross-sectional morphology, may not be a representative of *Paranthropus*, or that the single sample cannot be differentiated from the *Homo* groups. The cluster analysis indicates that OH 62 is the most distinct individual, which suggests that midshaft femoral cross-sectional properties in OH 62 are not consistent with its taxonomic allocation to the genus *Homo* if all members of the genus *Homo* are expected to be committed bipeds (Leakey et al., 1964; Wood and Collard, 1999b). However, results from the DFA, based on $J^{0.73}$ and CA, suggest that OH 62 is not atypical from other *Homo* sp. femora. Since the number of variables entered into the analysis can affect the results, it is possible that when all variables are considered (i.e. in the cluster analysis) real differences among the groups cannot be elucidated because of the effects of less discriminating variables. This may explain the distinctiveness of OH 62 in the cluster analysis, but its similarity to other *Homo* sp. femora in the DFA. A summary of the relationship between cross-sectional morphology and taxonomy is presented in Table 20.

Table 20. Summary of the results.

	Sample	**Genus**	**Taxonomic support based on cross-sectional morphology**
Proximal			
	KNM-ER 738	*Paranthropus*/*Homo*	uncertain, but cannot be excluded from *Paranthropus*
	KNM-ER 1500d	*Paranthropus*	yes
	SK 82	*Paranthropus*	yes
	SK 97	*Paranthropus*	yes
	KNM-ER 999a	*Homo*	yes
	KNM-ER 1481a	*Homo*	yes
Midshaft			
	KNM-ER 1592	*Paranthropus*[*]	uncertain, but similar to *Homo*
	KNM-ER 736	*Paranthropus*/*Homo*	uncertain, but similar to *Homo*
	KNM-ER 1472	*Homo*	yes
	KNM-ER 1807	*Paranthropus*/*Homo*	uncertain, but similar to *Homo*
	OH 62	*Homo*[*]	uncertain
	KNM-ER 1808	*H. erectus*	yes
	KNM-WT 15000	*H. erectus*	yes
	OH 34	*H. erectus*	yes

[*] Indicates uncertain genus.

DISCUSSION

Loading in the proximal femur cannot be understood in isolation since a suite of morphological traits around the hip joint (e.g. pelvic orientation, morphology and proportions, hip musculature and femoral neck length) influence biomechanical loading in the subtrochanteric region of the femur (Lovejoy, 1988; Ruff, 1995; Trinkaus and Ruff, 1999; Lovejoy et al., 2002; Richmond and Jungers, 2008). Previous research has yielded conflicting interpretations of morphological and functional similarities and differences between and among paranthropine pelves, and their morphological similarities and differences from *Homo* pelves (McHenry, 1975a, b, c; McHenry and Corruccini, 1975; Steudel, 1978; Berge, 1984; Berge and Kazmierczak, 1986). While a detailed analysis of Plio-Pleistocene hominin hip morphology is beyond the scope of this study, there are a few defining characteristics of the paranthropine pelvis that differentiate it from *Homo*.

Although rare and fragmentary, paranthropine pelves are generally characterized by a low, broad ilium, laterally splayed iliac blades and small acetabulae (Lovejoy et al., 1973; McHenry, 1975c). These traits, in addition to a relatively long femoral neck, act to increase M-L bending strength in the proximal femur (Lovejoy, 1988; Ruff et al., 1999). A decrease in the lateral flare of the greater trochanter in *Paranthropus* relative to *Homo* and the A-P compressed femoral neck characteristic of paranthropines are additional traits which likely have a functional role with implications for locomotion (Lovejoy, 1988; Harmon, 2009; Holliday et al., 2010). Fossil *Homo* pelves are distinguished from modern human pelves in having extremely robust iliac pillars, laterally flared iliac blades, relatively wide biacetabular breadths, large and laterally facing ischial tuberosities and relatively small auricular surfaces (i.e. fossil hominin pelves are generally more platypelloid than modern human pelves) (Ruff, 1995, 2005). Indeed, the primary selective pressures on pelvic morphology ultimately derive from obstetrical constraints rather than locomotion, and therefore reflect evolutionary changes in encephalization rather than locomotor behavior (McHenry, 1976; Berge et al., 1984; Tague and Lovejoy, 1986; Ruff, 1995; McHenry and Coffing, 2000; Simpson et al., 2008). However, the consequences of such morphological differences among *Paranthropus*, fossil *Homo* and modern humans have an effect on posture and locomotion. Since the suite of morphological traits influencing the hip joint are thought to be phylogenetically stable (Ruff, 1995; Ruff et al., 1999; Trinkaus et al., 1999; Lovejoy et al., 2002; Harmon, 2009), it is expected that proximal femoral cross-sectional geometry should reflect phylogeny to a greater degree than midshaft femoral cross-section geometry.

Differences among modern human, fossil *Homo* and *Paranthropus* proximal femora are largely due to differences in $J^{0.73}$, and to a lesser degree Z_x/Z_y. Average bending and torsional strength discriminates most between modern humans and *Paranthropus*, while diaphyseal shape discriminates fossil *Homo* from modern humans and *Paranthropus*. KNM-ER 999a and KNM-ER 1481a are more similar to each other than either one is to paranthropine femora, and both fossil *Homo* femora cluster with modern humans to the exclusion of *Paranthropus*. Based on proximal femoral cross-sectional properties, the taxonomic assignment of KNM-ER 999a and KNM-ER 1481a to the genus *Homo* is supported, although their species designations cannot be elucidated.

KNM-ER 738, KNM-ER 1500d, SK 82 and SK 97 are closer among each other than they are to fossil *Homo* femora, and cluster together to the exclusion of modern humans and fossil *Homo*. KNM-ER 1500d, SK 82 and SK 97 are generally regarded as members of the *Paranthropus* genus (but see Wood, 2005 and Wood and Constantino, 2007 regarding KNM-ER 1500d), albeit their taxonomic identifications are not based on craniodental features. However, morphological and morphometric analyses suggest affiliations for all three femora to a non-*Homo* genus (Day, 1969; McHenry and Corruccini, 1976; Grausz et al., 1988; Wood and Constantino, 2007; Harmon, 2009). Proximal femoral cross-sectional properties in KNM-ER 1500d, SK 82 and SK 97 support their non-*Homo* status. KNM-ER 738 was initially allocated to the robust australopithecine group, but subsequent analyses and comparisons with other femora suggest an ambiguous classification (Leakey et al., 1972; Walker, 1973; Day, 1986; McHenry, 1988; Susman et al., 2001). While KNM-ER 738 shares an almost similar proximity to KNM-ER 1500d (3.03) and KNM-ER 1481a (3.46), it is closer still to SK 82 (2.48) and SK 97 (2.73), and is therefore more similar to *Paranthropus* femora as a group than to modern and fossil *Homo* femora. Results from this study cannot definitively exclude KNM-ER 738 from the *Paranthropus* genus. However, until a larger sample size of definite paranthropine proximal femora is available, KNM-ER 738 may tentatively and conservatively be regarded as Hominidae gen. et. sp. indet. following McHenry (1994).

Differences among groups in the femoral midshaft are best attributed to differences in $J^{0.73}$, which discriminates most between modern humans and fossil *Homo* sp., and CA, which discriminates *H. erectus* from the other groups. *H. erectus* femora are more similar among each other than they are to other fossil *Homo* femora. Although it has been argued that OH 34 is so abraded that its taxonomic affiliation and the reconstruction of its original diaphyseal breadth and shape will remain uncertain (Leakey, 1978; Ruff, 1995; but see Day and Molleson, 1976), it is still closer to other *H. erectus* femora than to *Homo* sp. and KNM-ER 1592. KNM-ER 736, which was initially described as an australopithecine (Leakey et al., 1972), but subsequently considered a member of the genus *Homo* (e.g. Day, 1976a, b; Ruff and Walker, 1993), shares a close proximity to KNM-ER 1472, a likely member of the genus *Homo*. Although it has also been suggested that KNM-ER 736 may represent *H. erectus* (McHenry, 1991; Franciscus and Holliday, 1992; Grine et al., 1995; Antón, 2003), results from this study cannot confirm or refute the species status of KNM-ER 736. It is, however, closer to KNM-ER 1592, a purported paranthropine, than to *H. erectus* femora. Ruff (1995) found that the proximal femoral cross-sectional morphology of KNM-ER 736 was similar to early *Homo*, which suggests an affinity with *Homo* rather than with *Paranthropus*. McHenry (1994) suggested a taxonomic allocation of KNM-ER 736 to Hominidae gen. et. sp. indet. Results from this study support a likely allocation of KNM-ER 736 to the genus *Homo* based on midshaft femoral cross-sectional properties, which supports the proximal femoral analyses by Ruff (1995).

KNM-ER 1807 has been allocated to both *Homo* and *Paranthropus* (Day et al., 1976; McHenry, 1991). Its closest affinity is with KNM-ER 1592, a possible paranthropine. Since no definitive paranthropine midshaft femora were examined, it is not possible to conclude with confidence that KNM-ER 1807 is closer to *Paranthropus* than to *Homo*. KNM-ER 1807 is also close to KNM-ER 736 and KNM-ER 1472, both, especially the latter, considered likely members of the genus *Homo*. The taxonomic identity of KNM-ER 1807 cannot be resolved with confidence based on midshaft femoral cross-sectional morphology, but given its clustering with modern and fossil *Homo*, and the results from the DFA, it may tentatively be considered as *Homo* sp., or, more conservatively, as Hominidae gen. et. sp. indet.

KNM-ER 1472 is generally regarded as a member of the genus *Homo*. Like KNM-ER 1807, however, its closest proximity is with KNM-ER 1592, but it is also close to KNM-ER 736. Howell (1978) suggested that KNM-ER 1472 may represent *H. habilis sensu lato*, and Wood (1992a) suggested an affinity with *H. rudolfensis*. Since femora confidently attributed to these taxa are not well-represented in the fossil record, it is not possible to determine if the femoral cross-sectional morphology of KNM-ER 1472 is *H. habilis*-like or *H. rudolfensis*-like. However, *if* OH 62 is indeed representative of *H. habilis*, it is unlikely that KNM-ER 1472 is also representative of that species based on cross-sectional morphology, although it is possible that there is locomotor behavioral variability within *H. habilis* as potentially represented by KNM-ER 1472 and OH 62. The results from this study suggest an attribution of KNM-ER 1472 to the genus *Homo*, but its species designation is unclear.

It is possible that KNM-ER 1592 is not a representative of *Paranthropus*, at least as reflected by its midshaft femoral cross-sectional properties. Its stratigraphic location is not useful for taxonomic purposes since *Homo* and non-*Homo* species are found in the KBS Member of the Koobi Fora Formation in East Lake Turkana (Leakey, 1973a; Leakey and Walker, 1985; Feibel et al., 1989). Its closest proximity is to KNM-ER 1807, a possible *Homo*, and KNM-ER 1472, a likely *Homo*. Moreover, like the other *Homo*/ *Homo*(?) femora, KNM-ER 1592 is most distant from OH 62. Pairwise group comparisons for the last step are not significantly different between KNM-ER 1592 and modern humans, and KNM-ER 1592 and *H. erectus*. Finally, KNM-ER 1592 was misclassified as modern human in the DFA cross-validation classification. The cluster analysis and DFA strongly suggest that KNM-ER 1592 may not be a representative of *Paranthropus*, or that midshaft femoral cross-sectional properties in *Paranthropus*, at least as represented by KNM-ER 1592, and *Homo* are similar. It is important to note that the section location for KNM-ER 1592 was taken at ~43% of the diaphysis based on an estimated femur length of 470 mm by McHenry (1991). It is therefore possible that incompatible section locations may be contributing to the seemingly *Homo*-like cross-sectional morphology in KNM-ER 1592. However, Sládek et al. (2010) found that femoral bending strength, and to some degree cortical area, in the midshaft femur of modern humans were accurately estimated even when the section location was inaccurately located (midshaft was considered being anywhere from 40-60% of bone length). Since definite paranthropine midshaft femora were not examined in the current study, it is not possible to exclude KNM-ER 1592 from *Paranthropus* with confidence. KNM-ER 1592 may be best left unclassified until it can be compared with taxonomically secure specimens.

The cluster analysis indicates that OH 62 is the most distinct femur compared to the other fossil femora. Its closest proximity is to KNM-ER 1807, but it is still more distant from KNM-ER 1807 than any other fossil femur is from each other. While all fossil femora clustered with modern humans, OH 62 was the only femur to form a cluster on its own. Results from the DFA, however, do not suggest that OH 62 is particularly aberrant from *Homo*. Since the full range of variation in Plio-Pleistocene hominin midshaft femoral cross-sectional geometry is currently unknown, it is possible that OH 62 may be a *Homo* outlier, may not be a representative of *Homo*, or may indeed be a representative *Homo*, but of a species that was not an obligate terrestrial biped. Unlike many of the fossil samples in this study, OH 62 is an associated skeleton and its allocation to the genus *Homo* was partly based on craniodental evidence (Johnson et al., 1987), albeit this assignment has been questioned (Wood, 1992a, b, 1996; Wood and Collard, 1999a, b). If OH 62 is to remain in the genus *Homo*, then the behavioral attributes of its members, at least in terms of locomotion, may need to be redefined to possibly include non-committed bipeds.

CONCLUSION

The findings from this study are summarized as follows: (1) proximal femoral cross-sectional properties in KNM-ER 999a and KNM-ER 1481a are consistent with their taxonomic allocations to the genus *Homo*; (2) proximal femoral cross-sectional properties in KNM-ER 1500d, SK 82 and SK 97 are consistent with their taxonomic allocations to a non-*Homo* genus; (3) proximal femoral cross-sectional properties in KNM-ER 738, which is taxonomically ambiguous, are more similar to *Paranthropus* femora (i.e. KNM-ER 1500d, SK 82 and SK 97) than to modern and fossil *Homo* femora, although its taxonomic status cannot be definitively resolved based on its proximal femoral cross-sectional properties because it also shares a close similarity to KNM-ER 1481a (*Homo* sp.); (4) the spatio-temporal continuity among paranthropine proximal femora with regard to external morphology is also found with regard to proximal femoral cross-sectional morphology; (5) midshaft femoral cross-sectional properties in *H. erectus* femora are more similar among each other than to other fossil *Homo* sp. femora; (6) midshaft femoral cross-sectional properties in KNM-ER 1472 are consistent with its taxonomic allocation to the genus *Homo*; (7) midshaft femoral cross-sectional properties in OH 62 are not consistent with its taxonomic assignment to the genus *Homo* based on the cluster analysis, but are not atypical of *Homo* based on the DFA, which either indicates that the species represented by OH 62 (i.e. *H. habilis*) is not a representative of *Homo* or that there is a lot of variability in early *Homo* midshaft femoral cross-sectional morphology, and in turn, locomotor behavior; (8) midshaft femoral cross-sectional properties in KNM-ER 736 and KNM-ER 1807, which are taxonomically debatable, are consistent with modern and fossil *Homo* (excluding OH 62); and (9) midshaft femoral cross-sectional properties in KNM-ER 1592, a purported paranthropine, are similar to those in modern and fossil *Homo* (excluding OH 62), which either suggests that it is not a representative of *Paranthropus*, that midshaft femoral cross-sectional properties in *Paranthropus* and fossil *Homo* are similar or that the single paranthropine individual is not distinguished from *Homo* based on midshaft femoral cross-sectional morphology. As more fossil femora become available for analyses, cross-sectional morphological comparisons between taxonomically secure samples and taxonomically ambiguous samples may help lend insight into the taxonomic identities of the latter, as well as support or challenge the results presented in the current study.

Revelations from the hominin fossil record are made piecemeal. In turn, the taxonomic shuffling and reshuffling of fossil material has almost become a common practice. The disconnect between taxonomically classifying a hominin species largely by craniodental morphology, but interpreting mode of locomotion from postcranial elements, which are often fragmentary and isolated, has hindered reconstructions of locomotor behavior in several hominin groups. As many researchers have noted, some corresponding postcranial elements attributed to *Paranthropus* and early *Homo*, including *H. habilis,* are morphologically similar, and morphological resemblance has been used to cast doubt on the taxonomic status or justify the taxonomic reshuffling of certain postcranial fossils (e.g. Day, 1976a; Grausz et al., 1988; Lague and Jungers, 1996; Wood, 2000; Gebo and Schwartz, 2006). Wood and Constantino (2007) have suggested a more conservative approach with regard to the taxonomic affinities of several isolated postcranial remains. They argued that the *Australopithecus*-like postcranial material from Olduvai Gorge and Koobi Fora (e.g. OH 62 and KNM-ER 1500) should, for the time being, be classified simply as Hominini gen. et sp. indet. instead of arbitrarily attempting to classify them, which only propels taxonomic confusion.

Locomotion is the primary means by which a species interacts with its environment, and thus, it is an invaluable attribute for reconstructing and defining the adaptive zone of a genus (Mayr, 1950). If members of a genus are expected to occupy the same or similar adaptive zone, then, at the very least, locomotor behavior should be relatively homogeneous among its species, and somewhat different from species of another genus (Wood and Collard, 1999b; Cela-Conde and Ayala, 2003). The degree of locomotor behavioral difference between and among genera, however, is vulnerable to subjective interpretation (Cela-Conde and Ayala, 2003). Wood and Collard (1999b:71) argued that members of the genus *Homo* should have “a postcranial skeleton whose functional morphology is consistent with modern human-like obligate bipedalism and limited facility for climbing.” The definition of “limited”, however, is unclear.

While cross-sectional morphology by itself is inappropriate for taxonomic identification, the information that can be cautiously gleaned from it with regard to broad locomotor behavior has taxonomic relevance. The use of cross-sectional morphology with other lines of morphological and behavioral evidence may help elucidate the taxonomic status, at least to the genus level, of many isolated fossil hominin femora.

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CHAPTER IV

FEMORAL CROSS-SECTIONAL MORPHOLOGY AND MECHANICAL LOADING IN PLIO-PLEISTOCENE HOMININS: IMPLICATIONS FOR LOCOMOTION

The first hominin to display anatomical traits fully consistent with the modern human form of obligate terrestrial bipedalism was *Homo erectus* nearly 1.8 mya (Walker and Leakey, 1993; McHenry and Coffing, 2000; Antón, 2003; Bramble and Lieberman, 2004; Polk, 2004; Lordkipanidze et al., 2007), and most certainly by ~1.5 mya (Bennett et al., 2009). Pre-*H. erectus* hominins retain some anatomical evidence of ancestral adaptations to arborealism with increasing adaptations to terrestrial bipedalism over time (Robinson, 1972; Susman and Creel, 1979; Oxnard and Lisowski, 1980; Susman and Stern, 1982; Stern and Susman, 1983; Susman et al., 1984; Susman and Brain, 1988; Duncan et al., 1994; Clarke and Tobias, 1995; Leakey et al., 1995; Berger and Tobias, 1996; Asfaw et al. 1999; Kidd, 1999; Aiello and Andrews, 2000; Pontzer et al., 2010). The amalgamation of ancestral and derived traits, and the mosaic nature of human evolution, have made reconstructing locomotor behavior difficult among early hominin groups since it is challenging to tease apart morphological traits of functional significance from those that are vestigial and non-functional.

A biomechanical approach may help clarify questions regarding the locomotor behavior of early hominin groups (e.g. Ruff et al., 1993; Grine et al., 1995; Ohman et al., 1997; Ruff et al., 1999; Ruff, 2009; Kuperavage and Eckhardt, 2009; Pontzer et al., 2010). Since osseous tissue responds to habitual, dynamic mechanical loading throughout life, the functional usage of skeletal elements is essentially recorded in bone structure (Enlow, 1963; Frost, 1964, 1988, 1998; Huiskes, 1982; Currey, 1984; Martin and Burr, 1989; Rubin et al., 1990; Turner, 1998; Skerry, 2000; Ruff et al., 2006). Dynamic mechanical loading, particularly in weight-bearing bones, stimulates bone modeling and remodeling, which subsequently influences the cross-sectional geometry of a bone (Frost, 1964; Woo et al., 1981; Lanyon and Rubin, 1984; Lanyon, 1987; Martin and Burr, 1989; Biewener et al., 1996; Sumner and Andriacchi, 1996). Long bone cross-sectional properties can be examined to reconstruct mechanical loading patterns, which can then be used to yield insight into broad locomotor behaviors. There certainly is value in exploring locomotion and locomotor variability in the hominin fossil record since locomotor behavior can be used to construct general models regarding hominin behavioral ecology, which bear directly on food procurement strategies, physical and physiological adaptations and interspecific relationships within an ecological community.

This study investigates cross-sectional properties in the femoral diaphysis of Plio-Pleistocene hominins to determine if mechanical loading patterns are consistent with modern human-like locomotion, *Pan*-like locomotion or intermediate locomotor behavior. A wide range of variation in cross-sectional morphology and loading patterns may be associated with a single broad locomotor category, or the biomechanics of different modes of locomotion may vary little from each other such that mechanical signals overlap (e.g. D'Août et al., 2004; Preuschoft, 2004). However, given what is known about loading patterns in modern humans and *Pan*, expectations can be proposed for fossil hominins.

Quadrupedal knuckle-walking is the primary mode of locomotion in *Pan*, but acrobatic arm-swinging, arm-hanging, suspension, vertical climbing and quadrumanous climbing are also part of the *Pan* locomotor repertoire (Hunt, 1991, 1992; Schmitt, 2003). Quadrupedal walking in *Pan* involves a diagonal footfall sequence, diagonal couplets gait where a forelimb footfall follows the contralateral hindlimb footfall such that contralateral forelimb-hindlimb pairs are related in time (Schmitt, 2003; D'Août et al., 2004). Chimpanzees and bonobos tend to gallop quadrupedally at high velocities rather than trot (Schmitt, 1999; D'Août et al., 2004; Preuschoft 2004). Trotting may be an energetically inefficient gait since it leads to high peak stresses on the limbs and high moments of inertia about the hip (D'Août et al., 2004).

Although chimpanzees and bonobos frequently engage in short bouts of bipedal locomotion (e.g. Van Lawick-Goodall, 1968; Susman et al., 1980; McGrew et al., 1981; Stanford, 2002), there are significant biomechanical contrasts that differentiate modern human and *Pan* bipedalism, which mainly arise from morphological differences between the two groups[1] (e.g. Thorpe et al., 2004). Members of the genus *Pan* are unable to fully extend the lower limb (i.e. simultaneously extend the hip and knee) and stabilize the knee joint when standing erect (Berge, 1994; Li et al., 1996; Crompton et al., 1998; D'Août et al., 2002; Schmitt, 2003; Sockol et al., 2007). The flexed knee position in *Pan* precludes toe-off and heel-strike during the swing phase of the gait cycle, which results in a "shuffling" movement (Schmitt, 2003; Lewin, 2005; Harcourt-Smith, 2007). Since the lower limbs are flexed and the trunk is bent forward, the center of mass in *Pan* is placed anterior to the hip joint, which increases the moment arm of the ground reaction force and subsequently generates large external flexion moments (Preuschoft, 2004; Sockol et al., 2007). Body posture generally remains stable in *Pan* during bipedal gait because the center of mass is in a relatively constant position (Schmitt, 2003; Skoyles, 2006). The inclined position of the pelvis and the convex-curved vertebral column, as opposed to the S-shaped spine in modern humans, also constrains fully erect body posture, and thus fully erect bipedalism, in *Pan* (D'Août et al., 2002).

Modern human bipedal gait is characterized by two distinct phases: the stance phase and the swing phase (Lewin, 2005; Harcourt-Smith, 2007) (Fig. 1). Humans are able to fully extend the lower limb and stabilize the knee joint when standing erect, which minimizes the amount of muscle force acting on the lower limbs to support the body and allows toe-off and heel-strike during the swing phase of the gait cycle (Alexander and Jayes, 1978; Lovejoy, 1988; Bramble and Lieberman, 2004; Skoyles, 2006; Sockol et al., 2007; Richmond and Jungers, 2008). The total weight of the upper body (i.e. the head, trunk and arms) is transmitted throughout the vertebral column and pelvis onto the lower limbs when standing erect (Volpato et al., 2008). The center of mass alternately shifts towards the supporting leg in human bipedalism, which creates cyclical periods of instability (Cavagna et al., 1977; Lewin, 2005). However, the center of mass does not need to laterally shift a great distance during alternating swing- and stance-phases since the feet are placed almost directly beneath the body at midline because of the femoral

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[1] There are also minor kinesiological differences between chimpanzee and bonobo bipedalism (e.g. *P. paniscus* takes smaller strides at higher frequencies than *P. t. troglodytes*), but limited studies preclude any attempt to quantify the significance (if any) of these differences (Aerts et al., 2000; D'Août et al., 2004).

valgus angle (Tardieu and Trinkaus, 1994; Lewin, 2005; Harcourt-Smith, 2007; Richmond and Jungers, 2008). Contraction of the gluteal abductors on the hip entering the stance phase counteracts collapse during the single-support phase (Duda et al., 1997; Bramble and Lieberman, 2004). Experimental evidence suggests that during the single-support phase of human walking, contraction of the abductor complex generates strong axial compression in the femoral neck, which is subsequently transferred to the proximal femur and down the femoral diaphysis (Carter et al., 1989; Duda et al., 1997; Kalmey and Lovejoy, 2002).

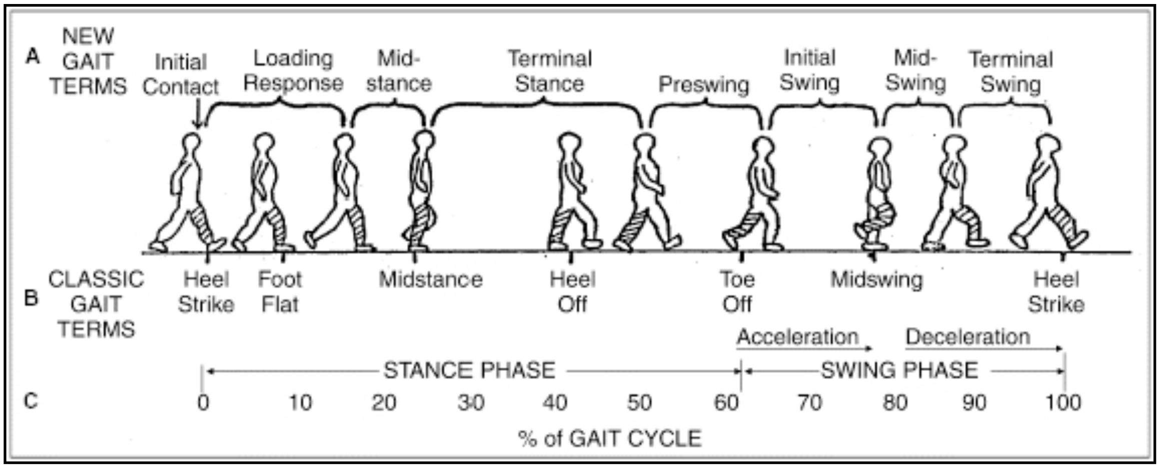

Figure 1. Human gait cycle at normal walking speed (~4.8 km/hr). Adapted from Uustal and Baerga, 2009. Illustration by Carson Schneck, M.D. http://www.ncbi.nlm.nih.gov/bookshelf/br.fcgi book=physmedrehab&part=A8414.

These kinesiological contrasts result in the characterization of modern human bipedalism as an energy-efficient inverted pendulum motion and *Pan* bipedalism as a compliant, “bent-hip, bent-knee” gait (Cavagna et al., 1977; Alexander, 1991; Li et al., 1996; Crompton et al., 1998; D’Août et al., 2002; Schmitt, 2003; Bramble and Lieberman, 2004; Skoyles, 2006). The inverted pendulum motion in modern humans refers to the up and down movement of the center of mass, which is highest at midstance and lowest at double support (D’Août et al., 2002; Schmitt, 2003; Bramble and Lieberman, 2004; Skoyles, 2006). As the center of mass vaults over the extended leg during the stance phase, potential and kinetic energy are exchanged. Forward kinetic energy is exchanged for gravitational potential energy between heel-strike and mid-stance, and gravitational potential energy is exchanged for forward kinetic energy between mid-stance and toe-off (Bramble and Lieberman, 2004; Kuo et al., 2005; Skoyles, 2006). In compliant gait, the center of mass is maintained in a fixed position because of the bent-hip and bent-knee posture, and kinetic and potential energies are not exchanged (D'Août et al., 2002; Schmitt, 2003; Skoyles, 2006). In addition, compliant walking in *Pan* requires hindlimb muscles to exert larger moments at the joints for the same ground reaction force as in modern human bipedalism (Thorpe et al., 2004). Despite the mechanical differences between modern human and *Pan* bipedalism, spatio-temporal bipedal gait characteristics (e.g. step length, stride length, stride frequency), are very similar between the groups at comparable speeds (Aerts et al., 2000).

Given the biomechanical differences in bipedal gait between modern humans and *Pan*, expectations about loading patterns can be predicted. Axial strength is expected to be greater relative to bending and torsional strength in modern human femora compared to *Pan* femora because of the reaction forces experienced during fully-extended erect posture and gait, and because of the muscle actions, particularly of the abductor complex, around the hip joint. *Pan* femora are expected to be characterized by a decrease in axial strength relative to average bending and torsional strength since multi-oriented bending loads, and dynamic and propulsive movements tend to be associated with quadrupedal locomotion and arborealism (Ruff and Runestad, 1992; Kimura, 1995; Demes et al., 2001; Kalmey and Lovejoy, 2002; Carlson, 2005; Marchi, 2007). In addition, the flexed hindlimb in *Pan* should act to increase bending moments, particularly at the femoral midshaft (Polk et al., 2000).

Femoral neck length determines the moment arm of the anterior gluteal muscles during the pelvic support phase of bipedal gait (Lovejoy et al., 2002). A long femoral neck acts to decrease hip joint and abductor loading because to maintain equilibrium during the single-support phase of modern human gait, the two moments about the hip (i.e. body weight times body weight moment arm, and abductor force times abductor moment arm) must cancel each other out (Ruff, 1995). At the same time, however, an increase in bending moments along the femoral diaphysis occurs because as neck length increases, the femoral diaphysis is moved more laterally relative to the center of the femoral head (Lovejoy, 1988; Ruff, 1995). As a result, the iliotibial band (i.e. the lateral tension band of the knee that extends along the lateral femoral diaphysis) must exert a force to maintain equilibrium about the knee joint (Lovejoy, 1988; Ruff, 1995). In addition, more laterally flared ilia and greater biacetabular breadth in modern humans compared to *Pan* leads to an increase in bending strength in the medio-lateral (M-L) plane of the femoral diaphysis since it is laterally displaced (Lovejoy et al., 1973; Ruff, 1995). Thus, modern humans should show greater bending strength in the M-L plane relative to the antero-posterior (A-P) plane along the femoral diaphysis compared to *Pan* since modern humans have relatively longer femoral necks and more platypelloid pelves than *Pan*.

Many researchers have interpreted the primitive retention of ape-like traits in *Paranthropus* as functionally significant (Jungers and Stern, 1983; Stern and Susman, 1983; Susman et al., 1984; Grine and Susman, 1991; Ward, 2002). Conversely, Lovejoy et al. (1973:778) argued that paranthropine proximal femoral morphology indicated biomechanical patterns "fully commensurate with erect striding as is that of modern man." While debate continues regarding the nature and degree of paranthropine bipedalism and the significance of arborealism in their locomotor repertoire, several lines of evidence suggest that the mode of locomotion in *Paranthropus* included both a rudimentary form of terrestrial bipedalism as well as a strong arboreal component (Day, 1969; Jolly, 1970; Leakey, 1971, 1972; Robinson, 1972; McHenry, 1975a, b; Grine, 1988; Susman and Brain, 1988; Susman, 1989; Harcourt-Smith and Aiello, 2004; Susman and deRuiter 2004; Gebo and Schwartz, 2006). If femoral cross-sectional morphology in *Paranthropus* is more human-like than *Pan*-like, then it is likely that their mode of locomotion was kinematically more akin to our own, as some researchers have suggested for the earliest hominins (e.g. McHenry, 1975a, b; Lovejoy, 1988; Latimer and Lovejoy, 1989; Latimer, 1991; Lovejoy et al., 2001; Ward, 2002; Nagano et al., 2005). If femoral cross-sectional morphology in *Paranthropus* is more *Pan*-like than human-like, then their mode of locomotion was probably kinematically distinct from ours (e.g. Oxnard, 1975; Stern and Susman, 1983; Susman et al., 1984; Ruff et al., 1999; Stern, 2000). In laboratory studies, modern humans who engaged in compliant bipedalism (i.e. *Pan*-like bipedalism) showed longer stride lengths, faster maximum walking speeds, lower peak vertical forces and improved impact shock attenuation relative to controls who engaged in normal walking (Yaguramaki et al., 1995; Schmitt et al., 1996). Thus, it has been argued that compliant bipedalism may have been advantageous for small-bodied Plio-Pleistocene hominins (Schmitt, 2003).

The mode of locomotion in members of the genus *Homo* is defined as obligate terrestrial bipedalism (Leakey et al., 1964; Wood and Collard, 1999a, b). It has been suggested, however, that early *Homo* (i.e. pre-*H. erectus*) shares several postcranial morphological traits with pre-*Homo* hominins which do not indicate a commitment to terrestrial bipedalism (Day and Wood, 1968; Day, 1976a, b; Oxnard and Lisowski, 1980; Susman and Brain, 1988; Clark and Tobias, 1995; Kidd et al., 1996; McHenry and Coffing, 2000; Gebo and Schwartz, 2006; Harcourt-Smith, 2007; Pontzer et al., 2010). For instance, Gebo and Schwartz (2006:510) proposed that the well-curved medial trochlear rims of the OH 8 foot, which is attributed to *H. habilis*, indicated an adaptation to “movements or postures, such as those used during arboreal activities”, and further suggested that its closest functional morphological affinities were with tali attributed to *Paranthropus*.

Limb proportions in more complete early *Homo* skeletons may not indicate a commitment to terrestrial bipedalism (e.g. McHenry and Berger, 1998a, b; Richmond et al., 2002). Haeusler and McHenry (2004:460) suggested “the earliest species of the genus *Homo* [OH 62 and KNM-ER 3735] possessed an elongated hindlimb relative to that of *Australopithecus africanus* and *A. afarensis*, whereas the forelimb probably retained brachial proportions with long forearms.” Relatively long hindlimbs may have been an adaptation to more energy efficient long distance terrestrial travel, whereas long forelimb proportions and the shoulder joint morphology, particularly in KNM-ER 3735, may indicate adaptations to arborealism (Haeusler and McHenry, 2004; Haeusler and McHenry, 2007). According to Harcourt-Smith (2007:1504), the most "conservative estimate of the locomotor behavior of *H. habilis* would place it between the habitual bipedalism of the australopiths and the obligate bipedalism of *H. ergaster* [*H. erectus*] and later species of *Homo*."

If femoral cross-sectional morphology in early *Homo* and *Homo* sp. femora is more similar to patterns in modern human femora than to patterns in *Pan* femora, then it is likely that their mode of locomotion was kinematically commensurate with human-like bipedalism. However, if femoral cross-sectional morphology in early *Homo* femora is more similar to patterns in *Pan* femora than to patterns in modern human femora, then it is possible that their mode of locomotion was kinematically distinct from ours. This may indicate that the sample is misclassified as *Homo* or that all members of the genus *Homo* cannot be characterized as committed bipeds per Leakey et al. (1964) because there is variation in locomotor behavior in the *Homo* lineage.

A final consideration is that human-like gait characteristics may be accomplished without phylogenetic morphological modifications. An important study by Hirasaki et al. (2004) demonstrated that the kinematics of human bipedalism could be attained, to a certain degree, in Japanese macaques trained to stand and walk bipedally. Wild macaques occasionally walk bipedally, but, as with *Pan*, their bipedal gait is mechanically different from that in modern humans (Hirasaki et al., 2004). Compared to the control group, the trained macaques were able to walk with longer, less-frequent strides primarily because of the adoption of a relatively more extended hindlimb (i.e. extended hip and knee) (Hirasaki et al., 2004). Most importantly, the bipedally trained macaques were able to efficiently transfer potential and kinetic energy (i.e. inverted pendulum mechanics), which is one of the key characteristics of human bipedalism (Hirasaki et al., 2004; Kuo et al., 2005). In a related study, Volpato et al. (2008) found that the characteristics of the trabecular bony network in the ilia and proximal femora of a bipedally trained Japanese macaque were consistent with functional adaptations to an increase in compressive loads compared to non-bipedal, wild macaques. These loads were transmitted back and forth along the axis from the sacro-iliac joint towards the coxo-femoral joint (Volpato et al., 2008). Thus, while anatomical adaptations for bipedalism would likely be selected only if that behavior was consistently employed (Lovejoy, 1988), it is possible that the earliest hominins without the suite of morphological traits indicative of a full commitment to terrestrial bipedalism (i.e. modern human-like bipedalism) were able to walk, at least on occasion, in a similar mechanical fashion as modern humans. Evidence for this should be recognizable in the femoral cross-sectional geometry since bone tissue responds to habitual, mechanical loading throughout life.

MATERIALS AND METHODS

A selection of fossil hominin femora housed at the National Museums of Kenya in Nairobi were included in this study (Table 1)[2]. Samples were chosen if enough of the diaphysis was preserved so that proximal or midshaft section locations could be approximated based on estimated maximum femur length and/or morphological landmarks, and if at least one natural break in the subtrochanteric and/or estimated midshaft region of the diaphysis perpendicular to the longitudinal axis was present so that cortical wall thicknesses could be directly measured on the fossil.

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[2] Taxonomic assignments of several samples are tentative and/or controversial (e.g. KNM-ER 736, KNM-ER 1500d, OH 62). Taxonomic attributions are based on the original descriptions of the material, but other taxonomic assignments are listed followed by a question mark. Original taxonomic assignments to *Australopithecus* (robust) are replaced with the genus name “*Paranthropus*” following Robinson (1972), Wood and Constantino (2007) and Wood and Lonergan (2008).

Table 1. Fossil samples.

Sample[a]	**Section**	**Side**	**Est. age (mya)**	**Taxonomic attribution**	**Reference**[b]
KNM-ER 736	midshaft	L	1.5-1.7	*P.* (cf. *boisei)*/*Homo*/ *H. erectus*?	1
KNM-ER 738	proximal	L	~1.8	*Paranthropus/Homo*?	1
KNM-ER 815	proximal	L	1.77 > 0.10	*Paranthropus*?	18
KNM-ER 999a	proximal	L	~0.75 ± 0.02 ~0.5-0.1	*Homo* sp. indet./*H. erectus*?/ late archaic *H. sapiens*?	2, 3, 4
KNM-ER 1472	midshaft	R	1.89 ± 0.05	*Homo* sp.	5
KNM-ER 1481a	proximal	L	1.89	*Homo* sp./*H.* (cf. *erectus*?)/ *H. habilis*/*H. rudolfensis*	5, 6, 7, 8, 9
KNM ER 1500d	proximal	R	1.88-2.2	*P. boisei*	9, 10
KNM-ER 1592	midshaft	R	1.85	*Paranthropus*?	11
KNM ER 1807	midshaft	R	1.5-1.6	*H.* (cf. *erectus*)?/*P. boisei*?	10
KNM-ER 1808	midshaft	L	1.69	*H. erectus*	11
KNM-WT 15000	midshaft	R/L [c]	1.53-1.65	*H. erectus*	12
OH 20	proximal	L	1.66-1.79	*P. boisei*	14, 17
OH 34	midshaft	L	0.8-1.15	*Homo* sp. indet./*H. erectus*?	13, 14
OH 62	midshaft	L	1.75-1.85	*H. habilis*	15
SK 82	proximal	R	1.6-1.8	*P. robustus*	16
SK 97	proximal	R	1.6-1.8	*P. robustus*	16

[a] Data for all samples are from this study except KNM-WT 15000, KNM-ER 1808, OH 62, SK 82 and SK 97 (Ruff et al., 1999; Ruff, 2008, Ruff, 2009).

[b] 1. Leakey et al. (1972); 2. Day and Leakey (1974); 3. Bräuer et al. (1997); 4. Trinkaus (1993); 5. Day et al. (1975); 6. Wood (1992b); 7. Trinkaus (1984); 8. Kennedy (1983a); 9. Leakey (1973); 10. Day et al., (1976); 11. Leakey and Walker (1985); 12. Brown et al. (1985); 13. Day and Molleson (1976); 14. Leakey (1978); 15. Johanson et al. (1987); 16. Napier (1964); 17. Day (1969); 18. Leakey (1972).

[c] Cross-sectional data are averaged from the right and left femora as reported by Ruff (2008).

Hominin proximal femora

Proximal hominin femora examined in this study include KNM-ER 738, KNM-ER 1500d, KNM-ER 815, OH 20, SK 82, SK 97, KNM-ER 999a and KNM-ER 1481a. The former six are representatives of *Paranthropus*, and the latter two are considered *Homo* sp.

Paranthropus. The head, neck, lesser trochanter and approximately 88 mm of the diaphysis below the distal margin of the lesser trochanter is preserved in KNM-ER 738. It was recovered from the KBS Channel Complex within the KBS Member of the Koobi Fora Formation in Area 105, and was initially attributed to the robust australopithecines (Leakey et al., 1972; Feibel et al., 1989). However, its taxonomic status has been referred to in the published literature as *Homo*/*A*. (*P.*) *boisei*?, *Australopithecus*?, *P. boisei*, *Australopithecus* (robust) sp. (e.g. Geissmann, 1986; McHenry, 1988, 1991; Jungers, 1988; Ruff et al., 1999). KNM-ER 1500d is part of an associated skeleton recovered from the Upper Burgi Member of the Koobi Fora Formation below the KBS Tuff in Area 130 (Leakey, 1973a; Feibel et al., 1989). It was initially allocated to the robust *Australopithecus* genus and is generally regarded as the only associated skeleton representative of *P. boisei* (Leakey, 1973a; Day, 1976b; Grausz et al., 1988; McHenry, 1994; but see Wood and Constantino, 2007). KNM-ER 815 is a left femur lacking the femoral head (Leakey, 1972). It was recovered from the KBS Member of the Koobi Fora Formation in Area 10, but its exact stratigraphic position within the member cannot be made more precisely (Leakey, 1972; Feibel et al., 1989). It was initially attributed to the robust australopithecine genus (Leakey, 1972; Leakey and Walker, 1973; Howell, 1978).

OH 20 is a proximal left femur lacking the femoral head and the tips of the greater and lesser trochanters (Day, 1969). It was recovered at the HWK site at Olduvai Gorge, and its inferred stratigraphic position is from lower Bed II (Leakey, 1978). OH 20 was assigned to the robust australopithecines (*Paranthropus* cf. *boisei*) largely because of its morphological affinities to SK 82 and SK 97 (Day 1969, 1976a; Leakey, 1978; Wood and Constantino, 2007).

SK 82 and SK 97 are proximal right femora recovered from the Hanging Remnant of Member 1 at Swartkrans, and are attributed to *P. robustus* (Napier, 1964; Robinson, 1972; McHenry, 1988). The date of the Hanging Remnant deposit, based on bovid and suid correlations from East African sites, is estimated to be ~1.5 to 1.8 mya (Brain, 1988; Grine, 1988) or ~1.0-1.8 mya (Brain, 1993). However, because local carnivores could have used the cave site as a lair or den for hundreds or thousands of years, and because the chronology of the site is not well understood, it may be misleading to assume that the faunal and hominin assemblages were deposited simultaneously and thus associated (Broom and Schepers, 1978; Brain, 1988). According to Grine (1989), more than 95% of the craniodental material in Member 1 can be attributed to *P. robustus*, albeit *Homo* material has also been recovered from the site (Susman, 1993; Grine et al., 1996; Susman et al., 2001). Thus, although SK 82 and SK 97 could potentially represent members of the genus *Homo*, it is unlikely given their lack of morphological resemblance to *Homo* femora (Day, 1969; McHenry and Corruccini, 1976; Wood and Constantino, 2007; Harmon, 2009). Cross-sectional properties for SK 82 and SK 97 are taken from Ruff et al. (1999).

Homo *sp.* KNM-ER 999a is an almost complete left femur recovered in Area 6a at Ileret, East Lake Turkana (Day and Leakey, 1974) The femur is believed to have derived from 9-11 m from the base of the Guomde Formation (now part of the Chari Formation) (Leakey et al., 1978; Brown and Feibel, 1986). The Silbo Tuff, which lies within the Guomde Formation, has been dated to 0.74 ± 0.01 mya (McDougall, 1985) and 0.75 ± 0.02 mya (McDougall and Brown, 2006). Since these later deposits are undifferentiated, it is possible that KNM-ER 999a is of Middle or initial Late Pleistocene age, or even early Holocene age (Feibel et al., 1989). Bräuer et al. (1997) suggested that KNM-ER 999a was from the Galana Boi Formation, and, based on gamma ray spectroscopy, may be as young as 301,000 ± 96,000 BP. The uncertain stratigraphic provenience of the femur has confounded its taxonomic affiliation. Day and Leakey (1974) attributed KNM-ER 999a to *Homo* sp. indet., and Wolpoff (1980) allocated it to *H. erectus.* According to Trinkaus (1993), KNM-ER 999a is morphologically aligned with early modern humans, particularly from the Levant. Based on uranium-series dating, which suggests that the femur may be as young as 300 kya, Bräuer et al. (1997) argued that KNM-ER 999a may be an early representative of a near-modern transitional or late archaic *H. sapiens.* KNM-ER 1481a is part of a well-preserved left femur recovered from the Upper Burgi Member of the Koobi Fora Formation in Area 131 (Day et al., 1975; Feibel et al., 1989). Leakey (1973) initially attributed it to *Homo* sp., but it has also been suggested to represent *H. erectus* (Kennedy, 1983a), *H. habilis* (Trinkaus, 1984; Pontzer et al., 2010) and *H. rudolfensis* (Wood, 1992a, b). In this study, KNM-ER 999a and KNM-ER 1481a are simply considered as fossil *Homo* sp.

Hominin midshaft femora

Midshaft hominin femora examined in this study include KNM-ER 736, KNM-ER 1472, KNM-ER 1592, KNM-ER 1807, OH 62, OH 34, KNM-ER 1808 and KNM-WT 15000. KNM-ER 1592 is considered a representative of *Paranthropus*, KNM-ER 736, KNM-ER 1472, KNM-ER 1807 and OH 62 are considered representatives of *Homo* sp. and OH 34, KNM-WT 15000 and KNM-ER 1808 are considered representatives of *H. erectus*.

Paranthropus. KNM-ER 1592 is the distal half of a robust right femur, which preserves a strong pilaster and the distal articulation (Leakey and Walker, 1985). The femoral fragment is approximately 200 mm in length. It was recovered from the lower KBS Member of the Koobi Fora Formation below the Ileret Tuff in Area 12, and initially assigned to the robust australopithecus genus (Leakey, 1973a; Howell, 1978; Leakey and Walker, 1985; but see McHenry, 1992).

Homo *sp.* KNM-ER 736 is a shaft fragment of a large left femur recovered from the Upper Member of the Koobi Fora Formation roughly 2-4 m below the projected level of the base of the Koobi Fora Tuff in Area 103 (Leakey et al., 1978). Leakey et al. (1972) described the specimen and tentatively assigned it to the *Australopithecus* (robust) genus. Day (1978) and Ruff and Walker (1993) advocated for its reassignment to the genus *Homo*, while others referred to it as a possible representative of *H. erectus* (McHenry, 1991; Franciscus and Holliday, 1992; Grine et al., 1995; Antón, 2003). KNM-ER 1472 is a well-preserved complete right femur recovered at Koobi Fora, Area 131 below the KBS Tuff (Leakey, 1973a, b; Day et al., 1975). Its preserved femoral morphology taxonomically aligns it with *Homo* (Leakey, 1973a, b; Day et al., 1975). KNM-ER 1807 is a right femoral diaphysis, which is broken into two fragments approximately near the midshaft (Day et al., 1976). It was recovered from the Okote Member of the Koobi Fora

Formation above the Black Pumice Tuff in Area 103 (Feibel et al., 1989). It has been allocated to both *Homo* and *Paranthropus* (Day et al., 1976; McHenry, 1991).

OH 62 is a partial skeleton attributed by its discoverers to *H. habilis* (Johanson et al., 1987), albeit its allocation to the genus *Homo* has not been unanimously supported (e.g. Wood, 1992a, b, 1996; Wood and Collard, 1999a, b). Several lines of indirect evidence suggest that it derives from lower Bed I below Tuff ID and likely from the sand lens below Tuff IC, which would make it contemporary with material from the FLK (*Zinjanthropus*) level (~1.8 mya) (Johanson et al., 1987). Cross-sectional properties for the left femoral midshaft are taken from Ruff (2009). Scaled, digital photographs of the OH 62 femoral cast were used to measure section contours at a transverse natural break in the diaphysis, which roughly corresponds to the 50-65% section location of bone length′ from the distal end (Ruff, 2009).

H. erectus. *H. erectus* femora were included to represent Plio-Pleistocene obligate terrestrial bipeds. KNM-WT 15000 is a well-preserved associated skeleton of a male juvenile recovered in West Lake Turkana from the Natoo Member of the Nachukui Formation, and is dated between ~1.53-1.65 mya (Brown et al., 1985; Feibel et al., 1989; Walker and Leakey, 1993). KNM-ER 1808, recovered from the KBS Member of the Koobi Fora Formation in Area 103, is an adult, possibly female, associated skeleton dated to ~1.69 mya (Walker et al., 1982; Leakey and Walker, 1985; Feibel et al., 1989). It has been suggested that KNM-ER 1808 suffered from a systemic pathology since most long bone surfaces are covered with coarse-woven bone (Walker et al., 1982). Although the exact diagnosis of the pathology is unknown, Walker et al. (1982) suggested that the bony reactions could have resulted from hypervitaminosis A. It is unclear if movement (e.g. locomotion) in KNM-ER 1808 was restricted and/or irregular because of the pathology. The pathological bone deposits and the original periosteal surface are readily discernible on broken sections, such that the amount of bone added by the pathological lesions can be separated from the true bone surface (Ruff, 2008). Cross-sectional properties for KNM-WT 15000 and KNM-ER 1808 are taken from Ruff (2008). Multi-planar radiography was used to reconstruct endosteal contours (Ruff, 2008). Cross-sectional properties of the right and left femora of KNM-WT 15000 were averaged, and the right femur was analyzed for KNM-ER 1808 (Ruff, 2008). It should be noted that KNM-WT 15000 is the only juvenile individual examined in this study. Since cross-sectional properties follow non-linear trajectories during growth and development, mechanical interpretations for this individual are interpreted in light of his age (Ruff et al., 1994).

OH 34 is a left femoral diaphysis recovered from Bed III at the JK 2 West site (Kleindienst, 1973; Day and Molleson, 1976; Leakey, 1978). The head is abraded, and the greater and lesser trochanters and distal condyles are missing (Day and Molleson, 1976). The diaphysis is broken near the approximated midshaft (Day and Molleson, 1976). Day and Molleson (1976) and Leakey (1978) attributed the specimen to *Homo* sp. indet., but it is now generally regarded as a likely representative of *H. erectus* (Tobias, 1991; Wood, 1992a, b; Antón, 2003).

Comparative samples

To provide a comparative framework for the fossil samples, cross-sectional data were collected on samples of *Pan* and modern humans. The *Pan* sample consists of wild-shot, adult males (n= 11) and females (n= 8) housed at the Natural History Museum of Los Angeles County and the Museum of Comparative Zoology (MCZ) at Harvard University (Table 2). Taxa were combined since it was previously shown that femoral cross-sectional properties were generally homogeneous among the groups (see Chapter II). Data from right femora were included in the analysis and the sexes were combined.

Table 2. *Pan* samples.

Sample[a]	Sex	Locality	Species
LACM 30545	F	Cameroon	*P. t. troglodytes*
LACM 30546	M	Cameroon	*P. t. troglodytes*
LACM 30548	F	Cameroon	*P. t. troglodytes*
MCZ 15312	M	Cameroon	*P. t. troglodytes*
MCZ 19187	M	Cameroon	*P. t. troglodytes*
MCZ 20041	M	Cameroon	*P. t. troglodytes*
MCZ 23163	M	Cameroon	*P. t. troglodytes*
MCZ 23164	F	Cameroon	*P. t. troglodytes*
MCZ 23167	F	Cameroon	*P. t. troglodytes*
MCZ 25950	M	Cameroon	*P. t. troglodytes*
MCZ 26847	F	Cameroon	*P. t. troglodytes*
MCZ 26849	F	Cameroon	*P. t. troglodytes*
MCZ 48686	M	Equatorial Guinea	*P. t. troglodytes*
LACM 51240	F	Uganda	*P. t. schweinfurthii*
LACM 51239	M	Uganda	*P. t. schweinfurthii*
BOM 6244	M	West Africa	*P. t. verus*
MCZ 38018	M	DRC[b]	*P. paniscus*
MCZ 38019	F	DRC	*P. paniscus*
MCZ 38020	M	DRC	*P. paniscus*

[a] LACM= Natural History Museum of Los Angeles County, BOM and MCZ= Museum of Comparative Zoology, Harvard University.
[b] Democratic Republic of the Congo.

A sample of modern human adults (n= 31), housed in the Department of Anthropology at the University of Western Ontario, serves as a comparative obligate bipedal sample (Table 3). The right femur was preferentially chosen over the left, but the latter was included if the right was absent. The sexes were combined in the analyses. There are two caveats with this sample. First, there is a sex bias towards males (n= 26 males, n= 5 females). Second, the sample is not from a single population, but rather is composed of individuals from either archaeological excavations or unknown provenience (see Chapter III for sample descriptions). Despite the heterogeneous nature of the collection, mechanical loading in the lower limbs should reflect patterns consistent with committed bipedalism.

Table 3. Modern human samples.

Sample[a]	**Sex**	**Provenience**	**Side**
Stirrup Court 3	F	19th century peri-urban settlement	R
Stirrup Court 10	M	19th century peri-urban settlement	R
Stirrup Court 14	M	19th century peri-urban settlement	R
Stirrup Court 17	M	19th century peri-urban settlement	R
Stirrup Court 20	M	19th century peri-urban settlement	R
Odd Fellows 1	M	unknown	R
Odd Fellows 2	M	unknown	R
Odd Fellows 3	M	unknown	R
Odd Fellows 4	M	unknown	R
Odd Fellows 6	M	unknown	R
Odd Fellows 7	M	unknown	R
Odd Fellows 8	M	unknown	R
Odd Fellows 9	M	unknown	L
Odd Fellows 10	M	unknown	R
Odd Fellows 11	M	unknown	R
Odd Fellows 12	M	unknown	R
Odd Fellows 13	F	unknown	R
Odd Fellows 14	M	unknown	R
Odd Fellows 17	F	unknown	R
Odd Fellows 19b	M?	unknown	R

Sample[a]	Sex	Provenience	Side
Odd Fellows 20	M	unknown	R
Birkette	F	Grand River Valley, Ontario	R
Breslau 1	M	19th century Kitchener, Ontario	R
Breslau 2	F	19th century Kitchener, Ontario	R
Downham Nursery	M?	Ontario Iroquoian village, Dutton	R
Orangeman's Lodge	M?	unknown	L
H. Helmuth donation	M?	unknown	L
N. Halbert donation	M?	unknown	R
Van Oordt 10	M	15th century Waterloo, Ontario	R
Peterborough Jail 2	M	Russian immigrant to Canada	R
Peterborough Jail 3	M	Austrian immigrant to Canada	R

Cross-sectional reconstructions

The reconstruction of diaphyseal cross-sectional geometries and the calculation of cross-sectional properties are based on accurate determinations of periosteal and endosteal contours at specified section locations. Traditionally, these sections are taken at 20%, 50% and 80% of femoral length′ measured from the distal end of the bone (Ruff and Hayes, 1983; Ruff, 1995, 2000, 2002a). Femur length′ is defined as the longitudinal length of the diaphysis from the average distal projection of the condyles to the superior surface of the femoral neck at its most distal point (Ruff, 2002) (see Fig. 2 in Chapter II). In the current study, section locations could not be taken at traditional percentages of bone length′ for the fossil samples due to technological limitations (see below). Instead, section locations were taken at natural breaks estimated to be at the proximal (~70-80%) or midshaft (~40-50%) section. Reconstructing cross-sections under these categories will still allow one to compare results from this study with other studies involving fragmentary fossil material since traditional section locations are routinely approximated from estimated maximum bone length (e.g. Ruff et al., 1999; Kuperavage and Eckhardt, 2009). In addition, Sládek et al. (2010) found that femoral bending strength, and to some degree cortical area, in the midshaft femur of modern humans were accurately estimated even when the section location was inaccurately located (midshaft was considered being anywhere from 40-60% of bone length). Proximal and midshaft section locations were taken at 80% and 50% of bone length′, respectively, for the *Pan* and modern human samples.

Periosteal and endosteal contours were reconstructed following the latex cast method as described by Stock (2002) (see Chapter II). Although latex casting is a non-destructive technique, there is potential for the casting material to leave traces of residue on the bone. In an effort to preserve the integrity of the fossil material, casting was done on casts provided by the National Museums of Kenya. Periosteal casts for the *Pan* and modern human samples were made directly on the bone.

Due to technological limitations, endosteal contours for the fossil hominin femora could not be reconstructed using bi-planar radiography. Instead, anterior, posterior, medial and lateral cortical thicknesses, and A-P and M-L diameters were measured directly on the fossil material at natural breaks with digital calipers to the nearest 0.01 mm. Previous studies have reconstructed cross-sectional geometries at natural breaks in a similar manner (e.g. Ruff et al., 1993; Carretero et al., 2009). Thus, this method is considered acceptable when technological equipment (e.g. x-ray, computer tomography) is unavailable.

Endosteal contours for the *Pan* and modern human samples were reconstructed from measurements of cortical wall thicknesses, which were derived from bi-planar radiographs. Section locations were marked with metal wire and a scaling device was included in each shot to correct for magnification[3]. Bones were placed in the x-ray machine in standard anatomical position and oriented following methods described by Ruff and Hayes (1983). Diaphyses were leveled by placing pieces of clay under the shaft so that the A-P midpoints of the proximal and distal ends of the bone were equidistant

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[3] Magnification factor (z)= y/x where y is the length of the scaling device on the x-rayed image and x is the actual length of the scaling device. A metal bar was used as the scaling device. The measurement on the x-rayed image was divided by z to correct for magnification (Jaundrell-Thompson and Ashworth, 1970).

from the image receptor. The specific techniques for reconstructing the endosteal contours for the *Pan* sample via digital bi-planar radiography are found in Chapter II, and the specific techniques for reconstructing endosteal contours for the modern human sample via traditional bi-planar radiography are found in Chapter III.

Periosteal casts were traced on graph paper with a 2 mm square grid. For fossil samples, measurements of cortical thicknesses were plotted onto the A-P and M-L axes of the periosteal tracings. For *Pan* samples, digitized radiographic images were enhanced in Adobe Photoshop® and magnified by 300-400% to measure anterior, posterior, medial and lateral cortical wall thicknesses. Size-adjusted measurements were plotted in correct anatomical position on the periosteal tracings. Cortical wall thicknesses for the modern human samples were measured directly on the radiographic film using digital calipers and a light box. A magnifying lens was used to aid in finding endosteal contours. Size-adjusted measurements were plotted in correct anatomical position on the periosteal tracings. Plotted points were connected in an ellipse for all samples.

The reconstructed cross-sections were digitized using a Lexmark X 6170 flatbed scanner. Although images were scanned at the same size as the original, a scaling device was included to ensure that the size of the images was not compromised during digitization. Cross-sectional properties were calculated using a Macintosh version of MomentMacro written for ImageJ, which is available courtesy of Dr. Christopher Ruff at http://www.hopkinsmedicine.org/FAE/mmacro.htm. Cross-sectional properties were calculated three times and the average was recorded.

A methodological concern in cross-sectional geometric reconstruction involves the axis where cross-sectional properties are calculated. In straight, symmetrical beams under uniform bending, the neutral axis passes through the geometric centroid of a section and is therefore also known as the centroidal axis (Lieberman et al., 2004). However, since long bones are subjected to a combination of bending and axial loads, and since long bones are neither entirely straight nor symmetrical, the neutral axis may not always pass through the centroid of a section (Lieberman et al., 2004; Ruff et al., 2006). Experimental studies have confirmed that under varied loading regimes, the neutral axis shifts away from the centroid and towards the cortex under tension (Carter et al., 1981; Demes et al., 1998; Lieberman et al., 2004). Although the neutral axis can be experimentally determined, this is not possible with skeletal material. Lieberman et al. (2004) have shown that *patterns* in cross-sectional properties are not affected when assumed centroidal axes are chosen over experimentally derived ones. In this study, cross-sectional properties are calculated with reference to a neutral axis assumed to run through the cross-sectional area centroid "with the understanding that these [cross-sectional properties] are only approximations of true bending rigidity and strength *in vivo*," (Ruff et al., 2006:490).

Cross-sectional properties

The cross-sectional properties calculated in this study are presented in Table 4.

Table 4. Cross-sectional properties.

Symbol	Definition	Mechanical Significance
TA	total subperiosteal area	area within the subperiosteal surface
CA	cortical area	axial compressive and tensile strength
%CA	percent cortical area	percentage of cortical bone in the section
Z_x	section modulus about the M-L axis	bending strength in the A-P plane
Z_y	section modulus about the A-P axis	bending strength in the M-L plane
$J^{0.73}$	estimates the polar section modulus	torsional and twice average bending strength

Cortical area (CA) reflects the axial compressive and tensile strength of the section (Ruff and Hayes, 1983; Stock and Pfeiffer, 2004). An increase in the relative amount of CA (i.e. %CA) in a cross-section could result from a relatively narrow medullary canal, a relatively expanded periosteal surface or both. The relative amount of CA in proximal and midshaft sections of the femur varies significantly among different modern human groups, and has generally declined over time within the genus *Homo* as part of an overall evolutionary trend in decreased robusticity (Ruff et al., 1993; Ruff, 1994; Trinkaus, 1997; Trinkaus and Ruff, 1999). The relative amount of cortical bone in a section does not have an intrinsic biomechanical significance, but it can be informative when examined in conjunction with other cross-sectional properties, and it can be useful as a simple morphological trait (Ruff et al., 1993; Ruff et al., 1984; Sládek et al., 2006). Total area and CA are reported in mm^2.

Section moduli are considered the best estimates of average bending and torsional strength[4] when mechanical loading conditions are unknown (Ruff, 2008). In addition, they are less dependent on the precise orientation of the section along the A-P and M-L axes, and are therefore preferred for use with fragmentary fossil remains which are often difficult to orient in correct anatomical position (Ruff, 2009). Thus, section moduli were examined in this study rather than second moments of area.

Patterns of variation in section moduli should correspond to patterns of variation in second moments of area since they are derived from them (Ruff and Hayes, 1983; Marchi, 2008). Z_x and Z_y are used to calculate the maximum stress in the outermost fiber of the cross-section in the anatomical plane of bending, which is proportional to cross-sectional bending strength (Ruff and Hayes, 1983; Ruff, 1995). Z_x corresponds to bending strength in the A-P plane measured about the M-L axis (x-axis), and Z_y corresponds to bending strength in the M-L plane measured about the A-P axis (y-axis) (Ruff, 2002, 2009). Z_x and Z_y in the proximal femur are interpreted with caution because the antetorsion angle of the femoral neck makes it challenging to correctly orient the bone along anatomical axes (Ruff and Hayes, 1983; Ruff, 1987). The polar section modulus, Z_p, is a measure of twice average bending and torsional strength, and can be

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[4] Rigidity and strength are often used interchangeably, but they refer to somewhat different, albeit related, structural properties of a material. Rigidity is a measure of the internal resistance of a structure to an externally applied force (or mechanical load), while strength is the maximum stress sustained by a structure before failure (Reilly and Burstein, 1974).

approximated by taking the polar second moment of area to the power of 0.73 (i.e. $J^{0.73}$) (Ruff, 1995; Trinkaus and Ruff, 1999)[5]. Section moduli are reported in mm^3.

Body size standardization

It is generally thought to be necessary to control for the influence of body size on cross-sectional properties before comparing groups (Ruff et al., 1993; Ruff, 2000). However, cross-sectional properties were not standardized in the current study since relationships between cross-sectional properties are examined among groups rather than a comparison of absolute values among samples. In the regression analysis (see below), smaller-bodied individuals tend to fall towards the bottom left corner of the plot while larger-bodied individuals tend to fall towards the upper right corner of the plot.

Statistics

Regression analysis is used to investigate relationships between cross-sectional properties. CA is plotted against TA to examine the relative amount of cortical bone in the cross-section, CA is plotted against $J^{0.73}$ to examine if bones are preferentially adapted for axial strength or bending and torsional strength and Z_y is plotted against Z_x to examine bending preferences in the anatomical axes, which give an overall indication of diaphyseal shape. The two major assumptions of regression analysis are equal variances (i.e. homoscedasticity), and normal distribution of the data (Kachigan, 1991). Homoscedasticity in the modern human and *Pan* sample is examined with the Levene test, and normality is examined with the Kolmogorov-Smirnoff test with a Lilliefors correction.

Correlation (R) between the observed and predicted values of the dependent variable and the coefficient of determination (R^2), which is a measure of the variance in the dependent variable that is explained by the independent variable, are presented. An

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[5] Z_x and Z_y can also be approximated by taking second moments of area (i.e. I_x and I_y) to the power of 0.73. This was not done for the samples analyzed in the current study since MomentMacro calculates these properties. Z_x and Z_y were published for KNM-WT 15000, KNM-ER 1808 and OH 62. Only second moments of area were reported for SK 82 and SK 97. Thus, Z_x and Z_y were estimated as $I_x^{0.73}$ and $I_y^{0.73}$, respectively, for these two femora.

expression of the regression analysis as an analysis of variance in the dependent variable is presented in an ANOVA. The F ratio is used to determine if the independent variable explains a significant amount of variation in the dependent variable, and is therefore a test of the significance of the regression model as a whole (Kachigan, 1991; Madrigal, 2000). The coefficients table presents the regression coefficient (b), which is equal to the slope of the regression line, the y-intercept of the regression line and their associated significance levels (Kachigan, 1991). If the slope of the line is not significantly different from zero, then the independent variable does not explain or predict the dependent variable (i.e. there is no significant association between the variables) (Kachigan, 1991; Madrigal, 2000).

The slopes and y-intercepts for the modern human and *Pan* regression lines are compared to determine if the lines differ in slope, y-intercept or both. Differences between the sample slopes are tested following equations from Kleinbaum et al., 2008. The test statistic is:

$$[1]\ t = \frac{\beta_{1H} - \beta_{1P}}{S_{(\beta 1H - \beta 1P)}}$$

where β_{1H} and β_{1P} are the slopes of the modern human and *Pan* samples, respectively and $S_{(\beta 1H - \beta 1P)}$ is an estimate of the standard error of the estimated differences between the sample slopes, which is equal to the square root of:

$$[2]\ S^2_{(\beta 1H - \beta 2P)} = S^2_{P,\ Y|X}\left[\frac{1}{(n_H - 1)(S^2_{XH})} + \frac{1}{(n_P - 1)(S^2_{XP})}\right]$$

Differences between the sample y-intercepts are tested following equations from Kleinbaum et al., 2008. The test statistic is:

$$[3]\ t = \frac{\beta_{0H} - \beta_{0P}}{S_{(\beta 0H - \beta 0P)}}$$

where β_{0H} and β_{0P} are the intercepts for the modern human and *Pan* samples, respectively, and $S_{(\beta 0H - \beta 0P)}$ is an estimate of the variance of the estimated difference between the sample intercepts by means of the square root of :

$$[4]\ S^2_{(\beta 0H - \beta 0P)} = S^2_{P,\,Y|X} \left[\frac{1}{(n_H)} + \frac{1}{(n_P)} + \frac{X^2_H}{(n_H - 1)\,S^2_{XH}} + \frac{X^2_P}{(n_P - 1)\,S^2_{XP}} \right]$$

The degrees of freedom (df) for both test statistics is $n_H + n_P - 4$.

Analysis of residual errors were plotted to examine if the assumptions of the regression model are valid. Statistical analyses were carried out with *SPSS* 17.0 with a significance level of $p = 0.05$.

RESULTS

The Levene test indicates that homogeneity is not met in any of the proximal femoral cross-sectional properties, and in CA, Z_x and Z_y in the midshaft femur in modern humans and *Pan* (Table 5). TA in the proximal femur is not normally distributed in the *Pan* sample (Table 6). Weighted least squares (WLS) regression is used since the assumption of homoscedasticity has been violated. Cross-sectional properties are log-transformed to correct for heteroscedasticity (unequal variance) and violations of normality in the data.

Table 5. Test of homogeneity of the variances for modern human and *Pan* data.

		Levene Statistic	df1	df2	Sig.
Proximal					
	TA	5.90	1	48	**0.02**
	CA	18.91	1	48	**0.00**
	$J^{0.73}$	8.03	1	48	**0.01**
	Z_x	13.06	1	48	**0.00**
	Z_y	19.18	1	48	**0.00**
Midshaft					
	TA	3.36	1	48	0.07
	CA	10.03	1	48	**0.00**
	$J^{0.73}$	3.25	1	48	0.08
	Z_x	15.51	1	48	**0.00**
	Z_y	10.17	1	48	**0.00**

Significance is indicated in bold.

Table 6. Test of normality for modern human and *Pan* data.

		Kolmogorov-Smirnov[a]		
	Species	Statistic	df	Sig.
Proximal				
TA	*H. sapiens*	0.15	31	0.07
	Pan	0.24	19	**0.01**
CA	*H. sapiens*	0.12	31	0.20^{*}
	Pan	0.16	19	0.20^{*}
$J^{0.73}$	*H. sapiens*	0.13	31	0.20^{*}
	Pan	0.15	19	0.20^{*}
Z_x	*H. sapiens*	0.09	31	0.20^{*}
	Pan	0.15	19	0.20^{*}
Z_y	*H. sapiens*	0.10	31	0.20^{*}
	Pan	0.10	19	0.20^{*}
Midshaft				
TA	*H. sapiens*	0.11	31	0.20^{*}
	Pan	0.18	19	0.11
CA	*H. sapiens*	0.07	31	0.20^{*}
	Pan	0.11	19	0.20^{*}
$J^{0.73}$	*H. sapiens*	0.13	31	0.20^{*}
	Pan	0.14	19	0.20^{*}

Z_x	*H. sapiens*	0.12	31	0.20[*]
	Pan	0.13	19	0.20[*]
Z_y	*H. sapiens*	0.09	31	0.20[*]
	Pan	0.15	19	0.20[*]

a. Lilliefors Significance Correction.
*. This is a lower bound of the true significance.
Significance is indicated in bold.

Proximal section

Relative cortical bone. CA is increased relative to TA in modern human and fossil hominin proximal femora compared to *Pan* (Fig. 2 and Table 7). The correlation between the observed and predicted values of CA is higher in modern humans (R= 0.82) than in *Pan* (R= 0.29), and there is a much tighter relationship between CA and TA in modern humans (R^2= 0.68) than in *Pan* (R^2= 0.08) (Table 8). TA explains a significant part of the variation in CA in modern humans, but not in *Pan* (Table 9). The y-intercept is significantly different from zero in both groups, but the slope is significantly different from zero only in modern humans (Table 10). There is no statistical inference for a significant linear relationship between CA and TA in the proximal femur of *Pan*. The modern human and *Pan* y-intercepts are not significantly different from each other (t= -0.59, df=46), but the slopes are significantly different from each other (t= 2.70, df= 46). *Paranthropus* and fossil *Homo* have relatively greater CA versus TA compared to modern humans, which is in accordance with previous studies that have found a general increase in relative CA in Plio-Pleistocene hominins compared to modern humans (Ruff et al., 1993; Ruff, 1994; Trinkaus, 1997; Ruff et al., 1999; Trinkaus and Ruff, 1999).

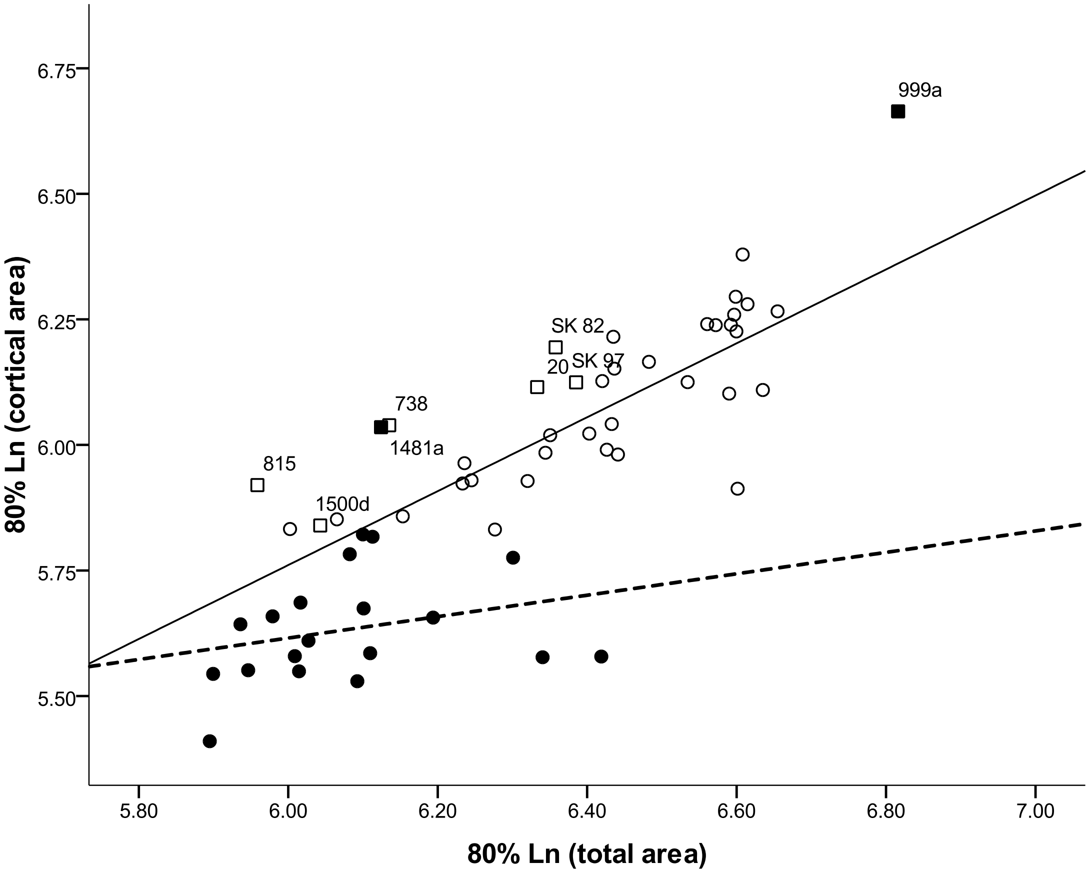

Figure 2. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed total area (TA) in the proximal femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares and fossil *Homo* is represented by closed squares. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.68. R^2 linear for *Pan*= 0.08.

Table 7. Relative amount of cortical bone in the proximal femur.

Sample	**%CA**
Modern human average	70.53
Pan average	64.46
KNM-ER 999a	85.90
KNM-ER 1481a	91.50
KNM-ER 738	90.85
KNM-ER 1500d	81.61
KNM-ER 815	96.20
OH 20	80.00
SK 82	84.92
SK 97	77.07

Table 8. Model summary for CA relative to TA in the proximal femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	0.82[a]	0.68	0.66	0.56	31.10
Pan		0.29[a]	0.08	0.03	0.02	16.61

a. Predictor: TA, dependent: CA.

Table 9. ANOVA for CA relative to TA in the proximal femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	18.65	1	18.65	60.12	**0.00**[a]
		Residual	9.00	29	0.31		
		Total	27.64	30			
Pan		Regression	0.00	1	0.00	1.57	0.23[a]
		Residual	0.01	17	0.00		
		Total	0.01	18			

a. Predictor: TA, dependent: CA.
Significance is indicated in bold.

Table 10. Coefficients for CA relative to TA in the proximal femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	1.28	0.62		2.06	**0.05**
		TA	0.75	0.10	0.82	7.75	**0.00**
Pan		(Constant)	4.32	1.04		4.14	**0.00**
		TA	0.22	0.17	0.29	1.25	0.23

Predictor: TA, dependent: CA.
Significance is indicated in bold.

Residual plots of CA versus TA for modern humans and *Pan* are presented in Figures 3 and 4, respectively.

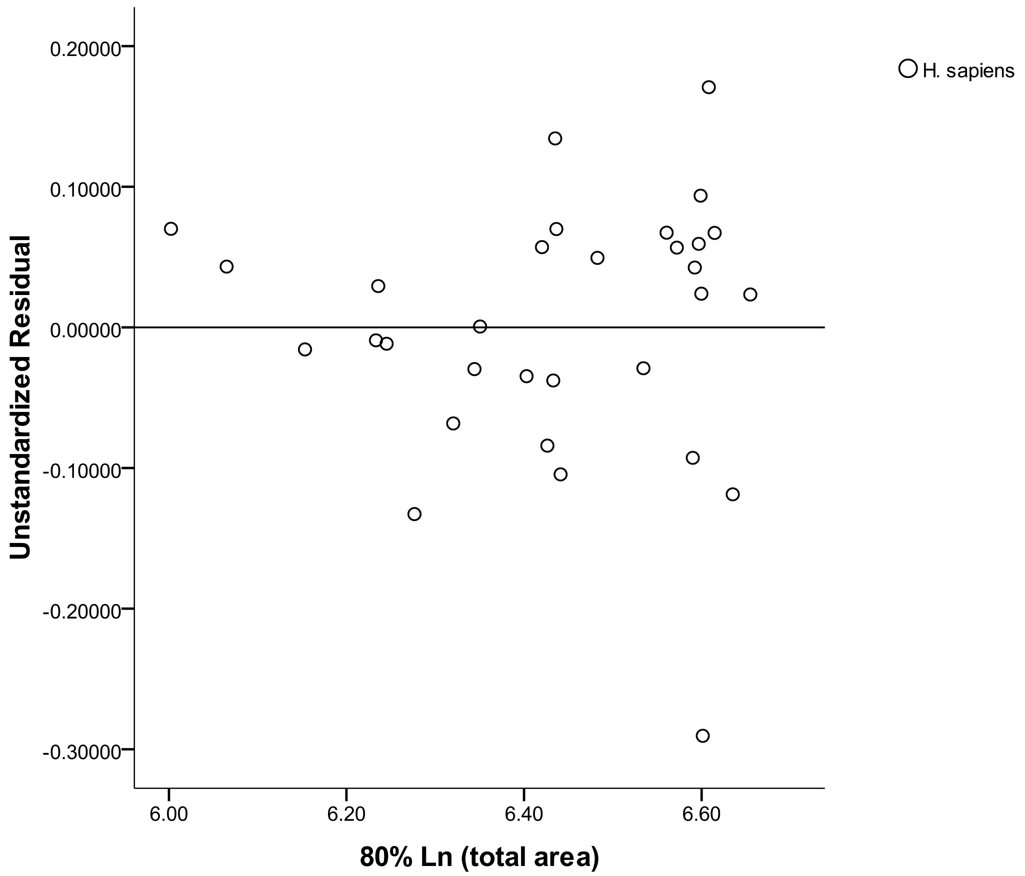

Figure 3. Scatterplot of the residuals for CA relative to TA in the proximal femur of modern humans.

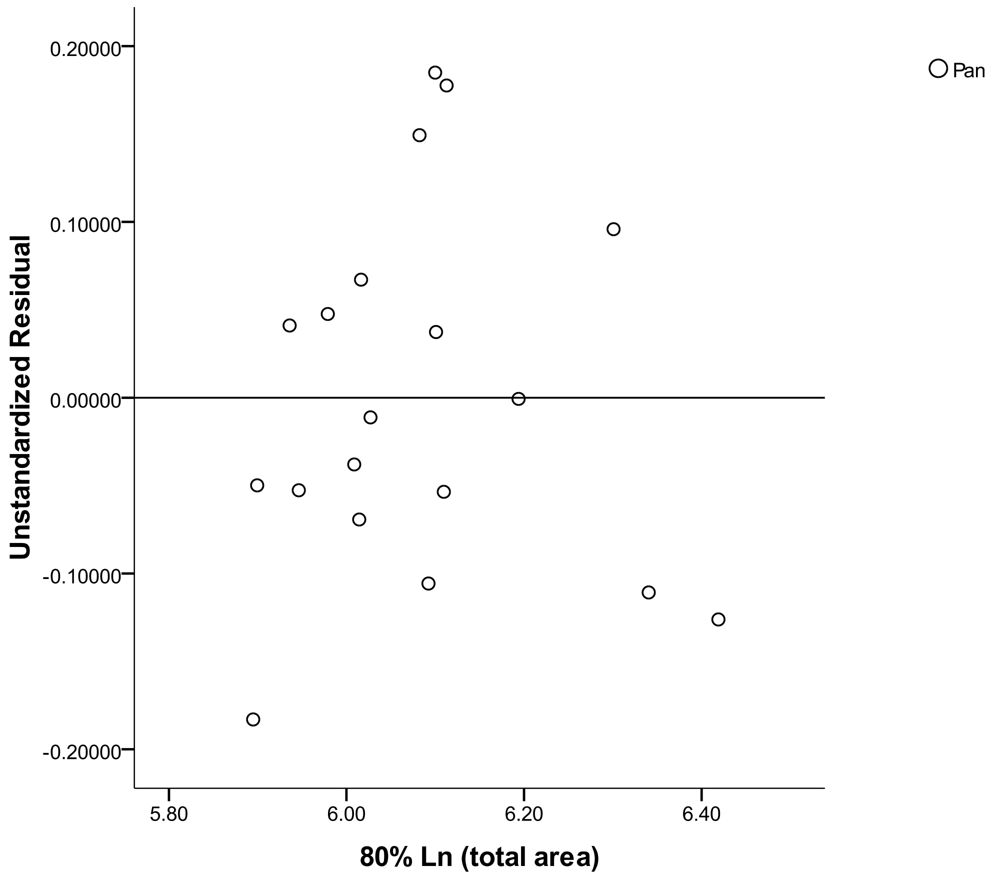

Figure 4. Scatterplot of the residuals for CA relative to TA in the proximal femur of *Pan*.

Axial strength relative to average bending and torsional strength. CA is increased relative to $J^{0.73}$ in modern humans compared to *Pan* (Fig. 5). The correlation between the observed and predicted values of CA is higher in modern humans (R= 0.88) than in *Pan* (R= 0.56), and there is a tighter relationship between CA and $J^{0.73}$ in modern humans (R^2= 0.78) than in *Pan* (R^2= 0.31) (Table 11). $J^{0.73}$ explains a significant part of the variation in CA in both groups (Table 12). The y-intercept and slope are significantly different from zero in both groups (Table 13). The modern human and *Pan* y-intercepts are significantly different from each other (t= -2.17, df= 46), but the slopes are not (t= 1.54, df=46). Fossil *Homo* follows the modern human-like pattern more than the *Pan*-like pattern, which suggests an increase in axial strength relative to average bending and torsional strength. This loading regime is commensurate with the kinematics of human-like bipedalism. *Paranthropus* also displays the human-like pattern compared to *Pan*, but shows a slight decrease in CA relative to $J^{0.73}$ when compared to modern and fossil *Homo*. Moderate differences in axial strength relative to average bending and torsional strength between *Paranthropus* and *Homo* may reflect anatomical contrasts in the pelvis and/or joint structures, which subsequently alter mechanical loading, albeit slightly, between the two genera.

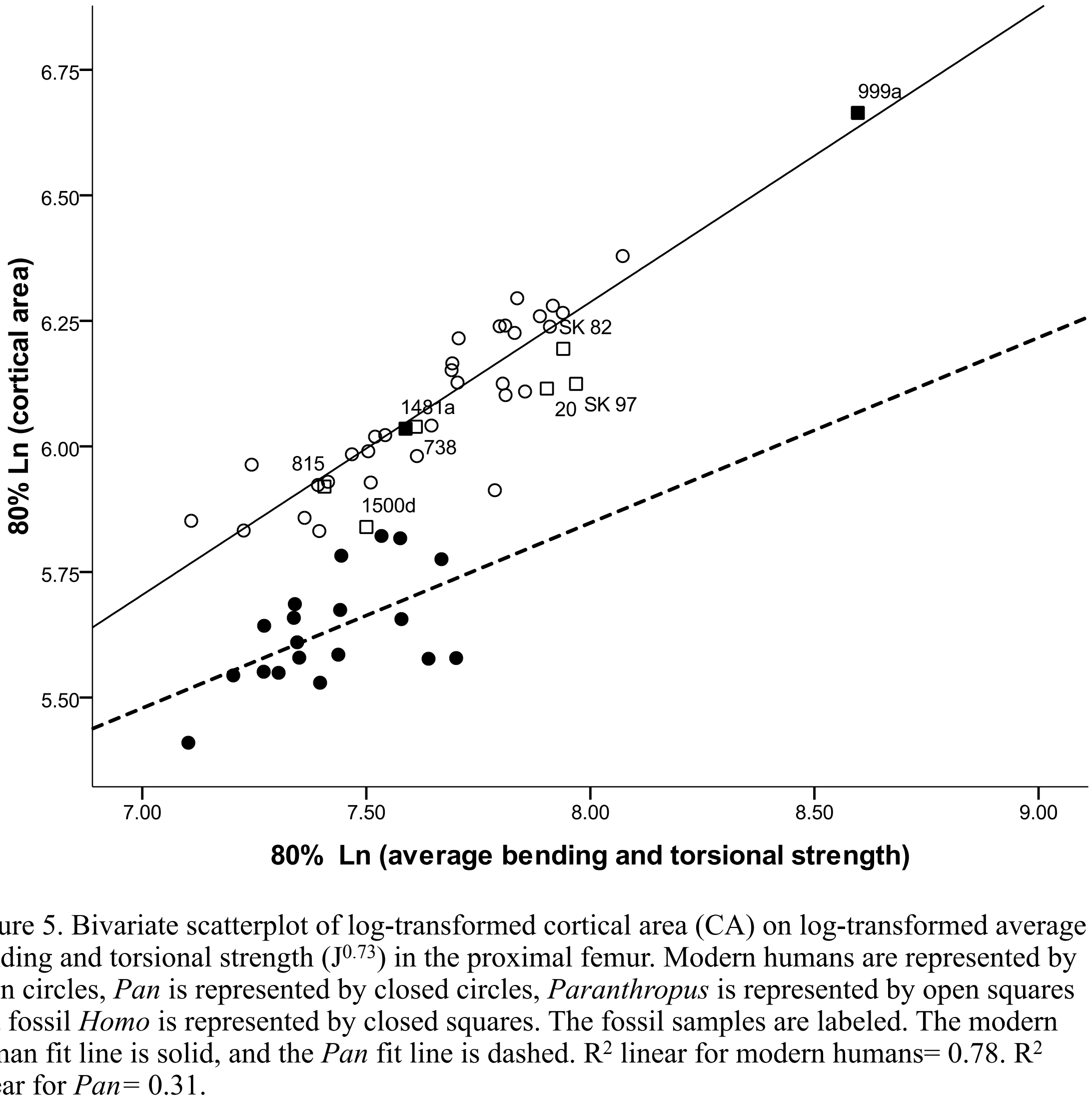

Figure 5. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the proximal femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares and fossil *Homo* is represented by closed squares. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.78. R^2 linear for *Pan*= 0.31.

Table 11. Model summary for CA relative to $J^{0.73}$ in the proximal femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	0.88[a]	0.78	0.77	0.46	36.99
Pan		0.56[a]	0.31	0.27	0.02	19.31

a. Predictor: $J^{0.73}$, dependent: CA.

Table 12. ANOVA for CA relative to $J^{0.73}$ in the proximal femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	21.49	1.00	21.49	101.25	**0.00**[a]
		Residual	6.16	29.00	0.21		
		Total	27.64	30.00			
Pan		Regression	0.00	1.00	0.00	7.68	**0.01**[a]
		Residual	0.01	17.00	0.00		
		Total	0.01	18.00			

a. Predictor: $J^{0.73}$, dependent: CA.
Significance is indicated in bold.

Table 13. Coefficients for CA relative to $J^{0.73}$ in the proximal femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	1.58	0.45		3.54	**0.00**
		$J^{0.73}$	0.59	0.06	0.88	10.06	**0.00**
Pan		(Constant)	2.91	0.98		2.97	**0.01**
		$J^{0.73}$	0.37	0.13	0.56	2.77	**0.01**

Predictor: $J^{0.73}$, dependent: CA.
Significance is indicated in bold.

Residual plots of CA versus $J^{0.73}$ for modern humans and *Pan* are presented in Figures 6 and 7, respectively.

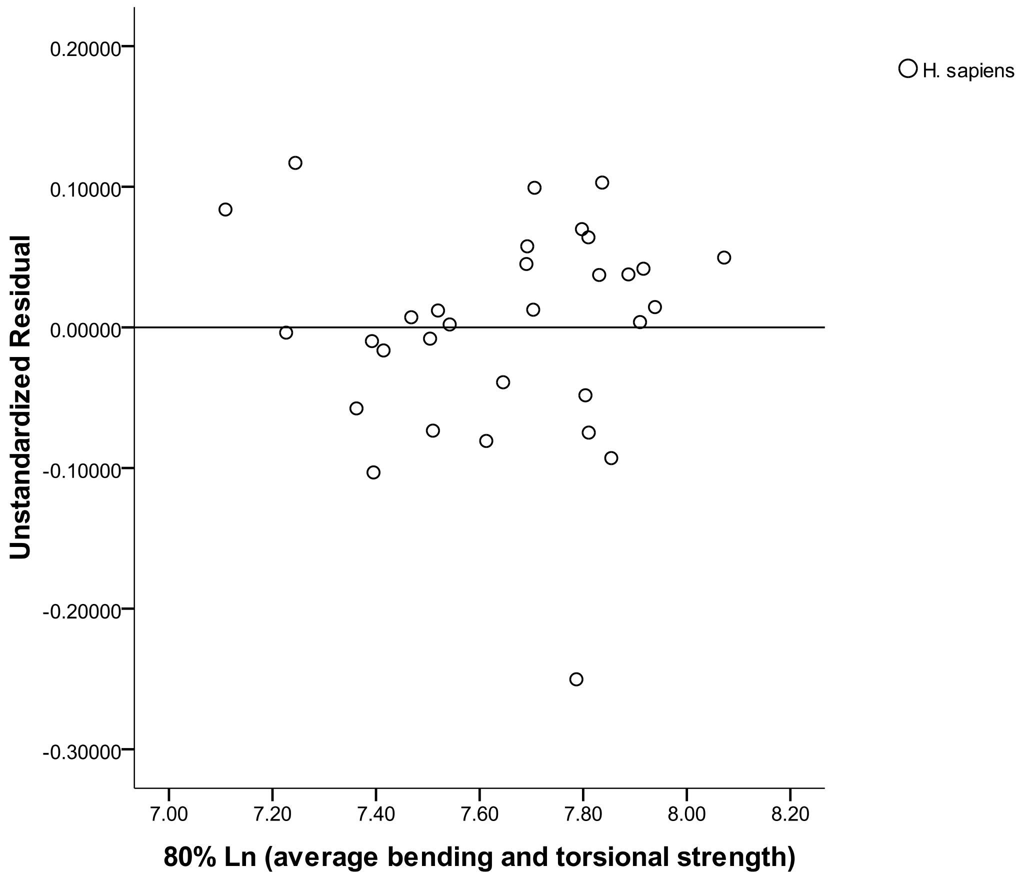

Figure 6. Scatterplot of the residuals for CA relative to $J^{0.73}$ in the proximal femur of modern humans.

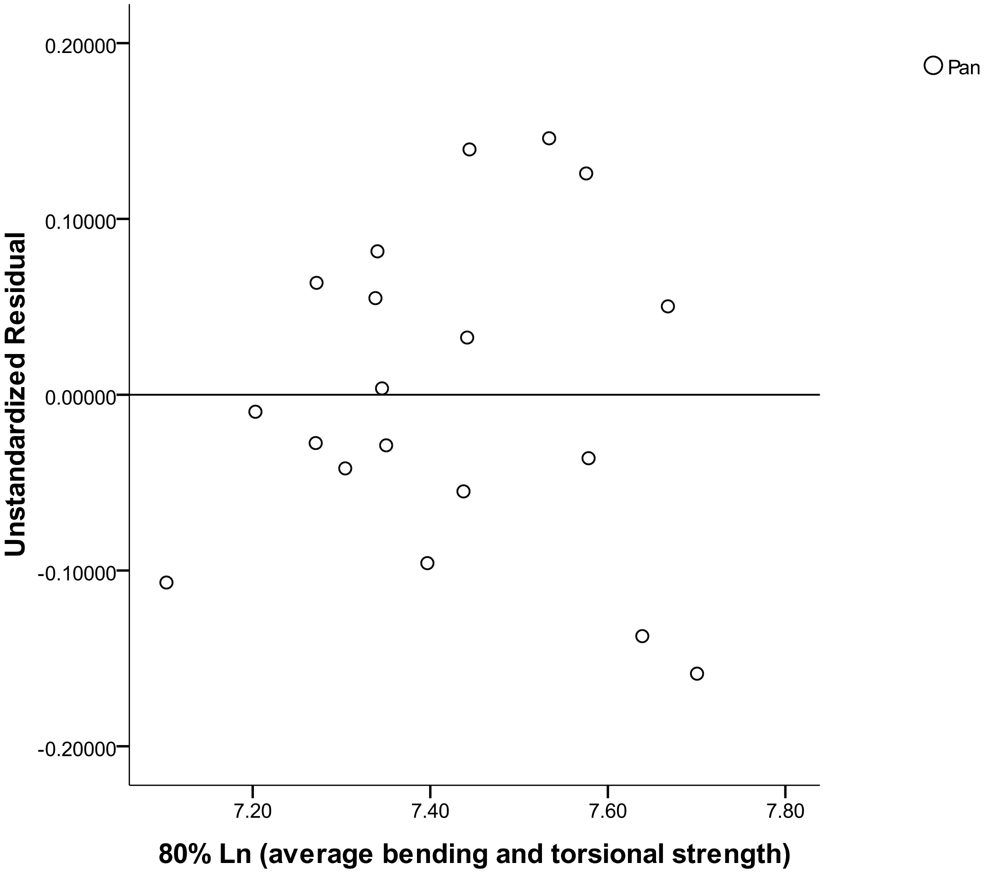

Figure 7. Scatterplot of the residuals for CA relative to $J^{0.73}$ in the proximal femur of *Pan*.

Diaphyseal shape. Bending strength in the M-L plane is greater relative to bending strength in the A-P plane in modern human proximal femora compared to *Pan* (Fig. 8). The correlation between the observed and predicted values of Z_y is higher in modern humans (R= 0.93) than in *Pan* (R= 0.73), and there is a tighter relationship between Z_y and Z_x in modern humans (R^2= 0.87) than in *Pan* (R^2= 0.53) (Table 14). Z_x explains a significant part of the variation in Z_y in both groups (Table 15). The y-intercept and slope are significantly different from zero in both groups (Table 16). The modern human and *Pan* y-intercepts and slopes are not significantly different from each other (t= -1.86, df= 46 and t= 1.65, df=46, respectively). Most fossil femora show the modern human pattern rather than the *Pan* pattern, but only KNM-ER 1500d and SK 97 fall above, albeit slightly, the fit line for the modern human sample. KNM-ER 1481a shows decreased bending strength in the M-L plane relative to the A-P plane compared to modern humans and other fossil hominin femora.

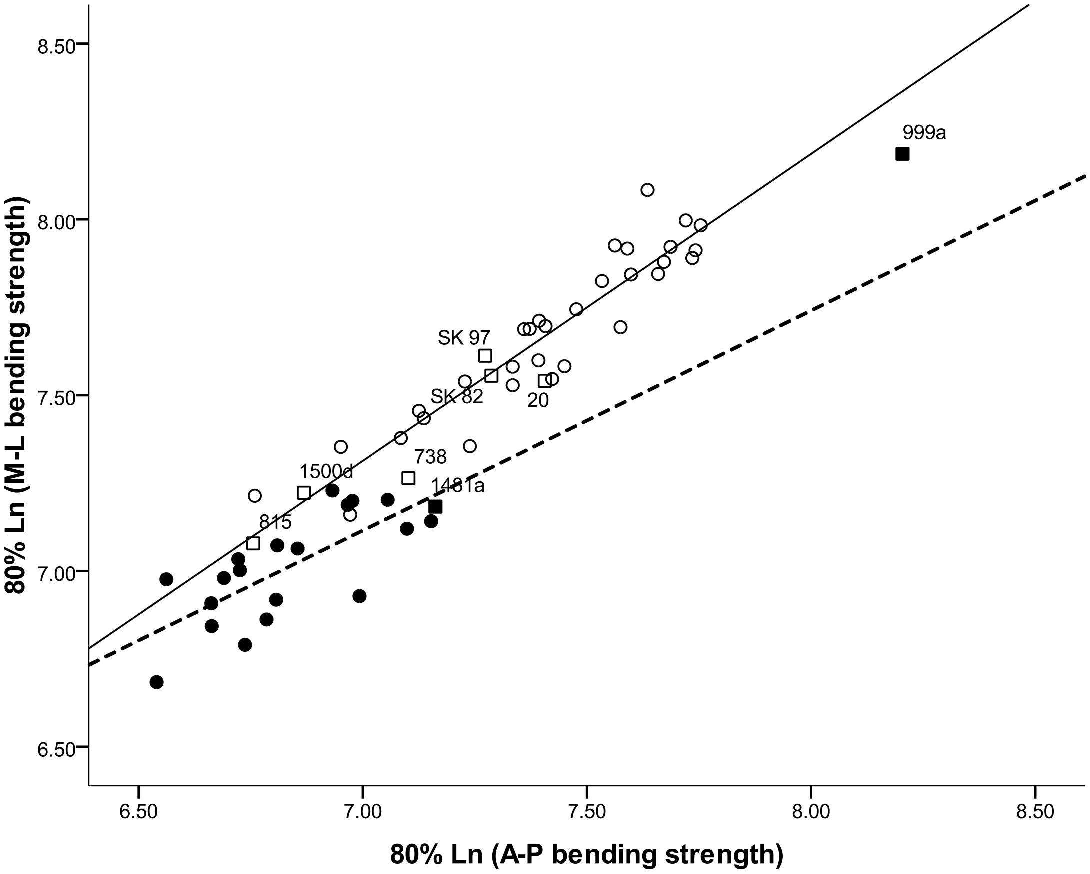

Figure 8. Bivariate scatterplot of log-transformed bending strength in the M-L plane (Z_y) on log-transformed bending strength in the A-P plane (Z_x) in the proximal femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares and fossil *Homo* is represented by closed squares. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.87. R^2 linear for *Pan*= 0.53.

Table 14. Model summary for Z_y relative to Z_x in the proximal femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	0.93[a]	0.87	0.87	0.40	32.86
Pan		0.73[a]	0.53	0.50	0.75	16.44

a. Predictor: Z_x, dependent: Z_y.

Table 15. ANOVA for Z_y relative to Z_x in the proximal femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	31.68	1.00	31.68	198.81	**0.00**[a]
		Residual	4.62	29.00	0.16		
		Total	36.30	30.00			
Pan		Regression	10.80	1.00	10.80	19.08	**0.00**[a]
		Residual	9.62	17.00	0.57		
		Total	20.42	18.00			

a. Predictor: $J^{0.73}$, dependent: CA.
Significance is indicated in bold.

Table 16. Coefficients for Z_y relative to Z_x in the proximal femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	1.18	0.46		2.55	**0.02**
		Z_x	0.88	0.06	0.93	14.10	**0.00**
Pan		(Constant)	2.77	0.97		2.85	**0.01**
		Z_x	0.62	0.14	0.73	4.37	**0.00**

Predictor: Z_x, dependent: Z_y.
Significance is indicated in bold.

Residual plots of Z_y versus Z_x for modern humans and *Pan* are presented in Figures 9 and 10, respectively.

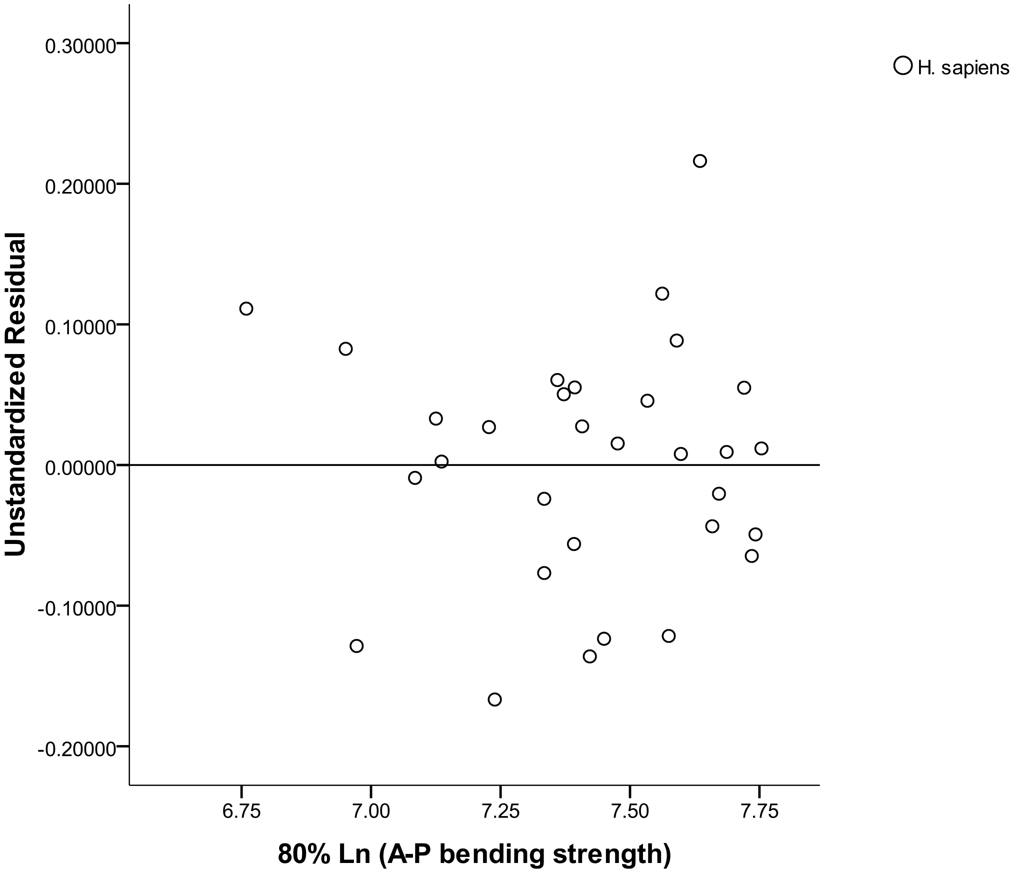

Figure 9. Scatterplot of the residuals for Z_y relative to Z_x in the proximal femur of modern humans.

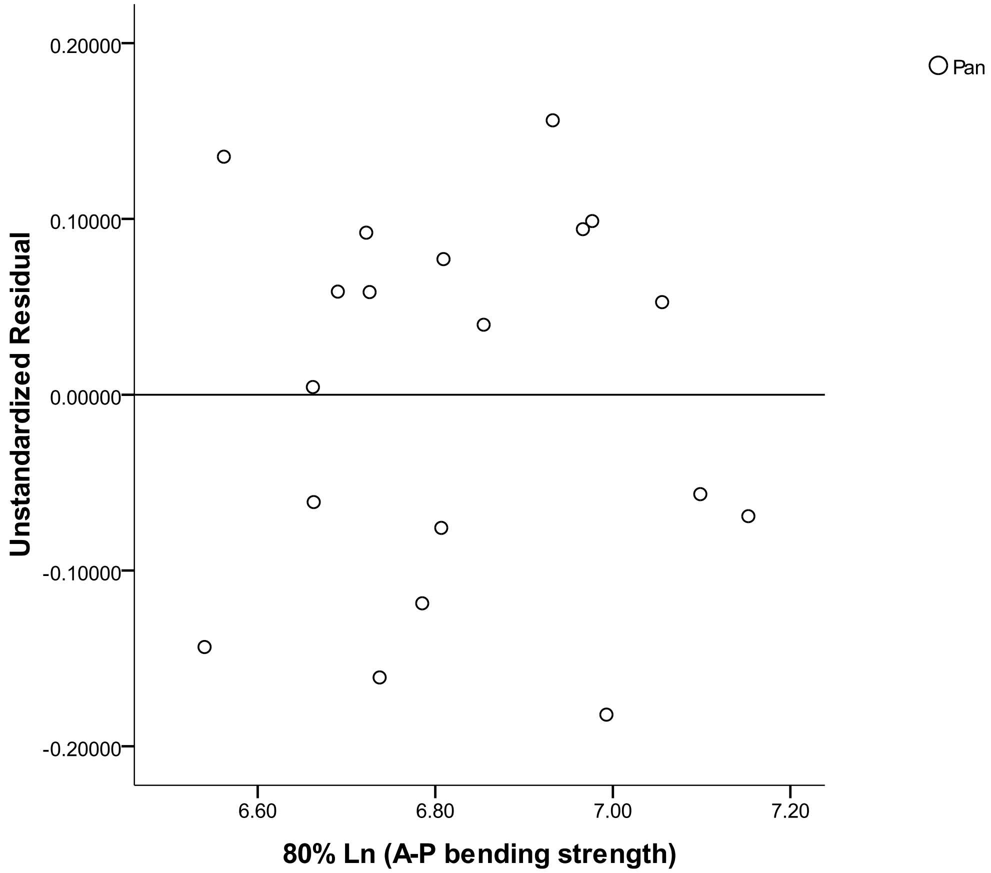

Figure 10. Scatterplot of the residuals for Z_y relative to Z_x in the proximal femur of *Pan*.

Summary. There is a tighter relationship between CA and TA in modern humans than in *Pan* (i.e. CA increases more steadily with TA in modern humans). The relationship between CA and TA is not significant in *Pan*. The relative amount of cortical bone in the proximal femora of modern humans, *Paranthropus* and fossil *Homo* is greater than in *Pan*. The relative amount of cortical bone in the proximal femora of fossil hominins is greater than in modern humans. Previous studies have shown an increase in relative femoral cortical area among fossil hominins compared to modern humans, which may reflect a reduction in overall mechanical loading on the modern human skeleton (Kennedy, 1983b; Ruff et al., 1993; Ruff, 1995; Ruff et al., 1999; Trinkaus and Ruff, 1999; Ruff, 2009). This idea is supported by the results of CA relative to $J^{0.73}$ since $J^{0.73}$ explains a significant amount of variation in CA in modern humans. An increase in average bending and torsional strength in fossil hominins versus modern humans may also explain their increase in relative CA compared to modern humans.

Axial strength is greater relative to average bending and torsional strength in modern humans, *Paranthropus* and fossil *Homo* compared to *Pan*. The increase in CA versus $J^{0.73}$ in the proximal femur of modern humans reflects structural reinforcement from an increase in axial loading relative to bending and torsional loading, which is commensurate with the kinematics of modern human-like bipedalism (Cristofolini et al., 1995; Aamodt et al., 1997; Duda et al., 1997). Fossil *Homo* is most similar to modern humans in this regard, which supports a mode of locomotion comparable with modern human-like bipedalism. *Paranthropus* displays the modern human-like pattern more than the *Pan*-like pattern when compared to *Pan*, but shows a decrease in CA relative to $J^{0.73}$ when compared to *Homo*, both modern and fossil. These results suggest a moderately different mechanical loading pattern in the proximal femur of *Paranthropus* compared to *Homo*, which may reflect slight differences in pelvic and hip morphology, and subsequently different locomotor kinematics, albeit within a generally more human-like pattern rather than *Pan*-like pattern.

Modern humans and most fossil femora display greater M-L bending strength relative to A-P bending strength in the proximal femur compared to *Pan*, but the modern human and *Pan* lines are not significantly different from each other in y-intercept and slope. M-L buttressing in the proximal femoral diaphysis is a widely recognized trait among modern humans and fossil hominins, which likely stems from a laterally displaced proximal femoral diaphysis (Lovejoy et al., 1973; Lovejoy, 1988; Ruff, 1995; Richmond and Jungers, 2008). A relatively long femoral neck and greater biacetabular breadth in modern humans and fossil hominins compared to *Pan* contribute to this lateral displacement of the femoral diaphysis. Greater bending strength along the M-L plane relative to the A-P plane in the proximal femur of *Pan* taxa was previously noted by Carlson (2002) and Carlson et al. (2008), but its significance is unclear. Non-human primates that habitually engage in turning behaviors, however, are often exposed to increased M-L forces on their limb bones (Demes et al., 2006; Carlson and Judex, 2007).

Since the modern human and *Pan* regression lines are not significantly different from each other, the results suggest that similar diaphyseal shapes may result from contrasting loading patterns.

Midshaft section

Relative cortical bone. CA is increased relative to TA in modern human midshaft femora compared to *Pan*, although the pattern is reversed at smaller sizes (Fig. 11 and Table 17). The correlation between the observed and predicted values of CA is higher in modern humans (R= 0.82) than in *Pan* (R= 0.43), and there is a much tighter relationship between CA and TA in modern humans (R^2= 0.67) than in *Pan* (R^2= 0.19) (Table 18). TA explains a significant part of the variation in CA in modern humans, but not in *Pan* (Table 19). In modern humans, the y-intercept is not significantly different from zero, but the slope is significantly different from zero. In *Pan*, the y-intercept is significantly different from zero, but the slope is not (Table 20). These results suggest that TA does not significantly explain or predict CA in the midshaft femur of *Pan*. The y-intercepts of the two groups are not significantly different from each other (t= -0.49, df= 46), but the slopes are significantly different from each other (t= 2.48, df= 46). KNM-ER 1592, KNM-ER 736, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472 follow the modern human-like pattern. OH 62 and OH 34 also follow the modern human-like pattern, but their low positions on the scatterplot may reflect their slender diaphyses and overall smaller size compared to the other samples (Day and Molleson, 1976; Johnson et al., 1987: Haeusler and McHenry, 2004). KNM-WT 15000 falls with *Pan* in having reduced CA relative to TA, but this may be an artifact of his juvenile status. Modern human children tend to have relatively thin cortical walls relative to TA because net endosteal resorption outweighs net endosteal deposition (Ruff et al., 1994; Schoenau et al., 2001; Ruff, 2005). This process is reversed during mid-adolescence (Ruff, 2005). In addition, modern human children (i.e. before mid-adolescence) experience more periosteal responses to mechanical loading than endosteal responses, which partially explains the larger medullary cavities in children compared to young adults and adults (Ruff, et al., 1994; Ruff, 2000). Assuming modern human-like growth patterns in *H. erectus* (Clegg and Aiello, 1999), the low CA relative to TA in KNM-WT 15000 may be a product of his age. Ruff et al. (1994:48) compared %CA in modern human children from Pecos Pueblo (8- to 13-year olds) with KNM-WT 15000 and found that "when placed into proper developmental context his [KNM-WT 15000] %CA is fairly high," in accordance with higher CA relative to TA in Plio-Pleistocene adult hominins.

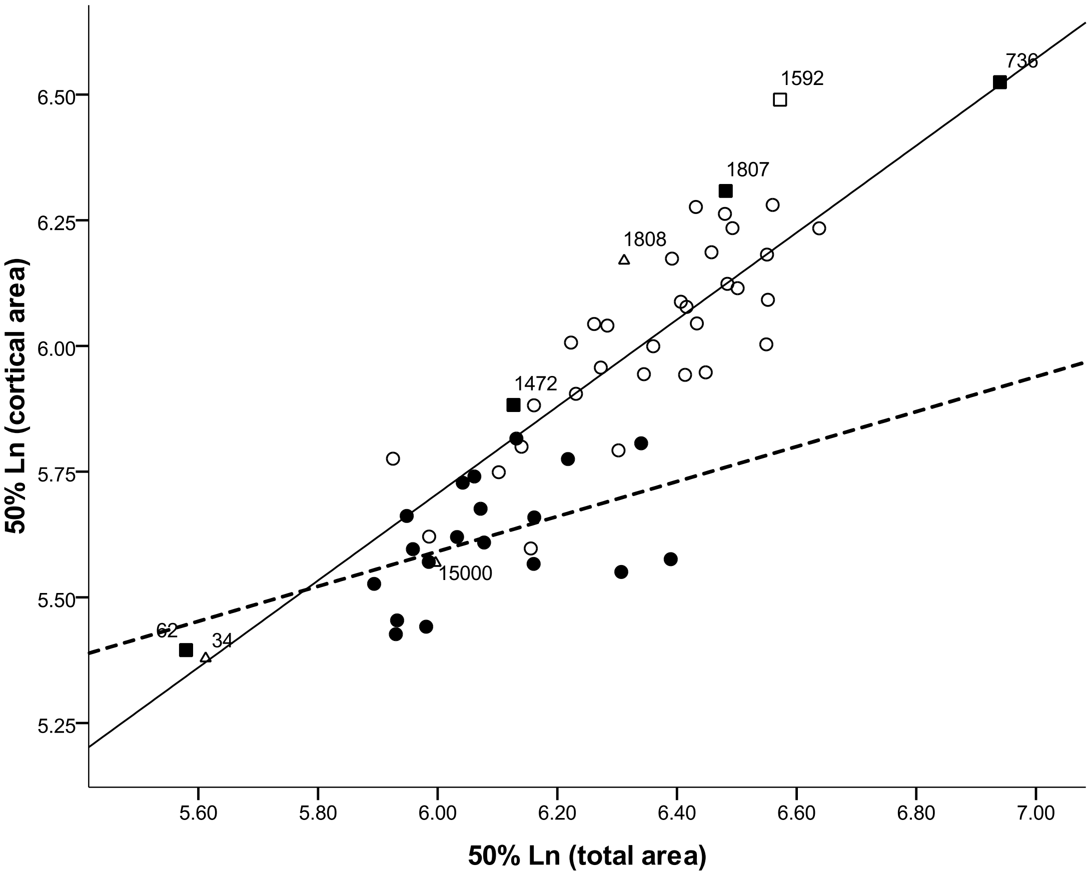

Figure 11. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed total area (TA) in the midshaft femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares, *Homo* sp. is represented by closed squares and *H. erectus* is represented by open triangles. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.67. R^2 linear for *Pan*= 0.19.

Table 17. Relative amount of cortical bone in the midshaft femur.

Sample	**%CA**
Modern human average	71.48
Pan average	63.43
KNM-ER 1592	92.08
KNM-WT 15000	65.17
KNM-ER 1808	86.75
OH 34	79.16
KNM-ER 736	66.01
KNM-ER 1472	78.33
KNM-ER 1807	84.10
OH 62	83.16

Table 18. Model summary for CA relative to TA in the midshaft femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	0.82[a]	0.67	0.66	0.64	26.42
Pan		0.43[a]	0.19	0.14	0.02	16.19

a. Predictor: TA, dependent: CA.

Table 19. ANOVA for CA relative to TA in the midshaft femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	23.80	1.00	23.80	58.04	**0.00**[a]
		Residual	11.89	29.00	0.41		
		Total	35.70	30.00			
Pan		Regression	0.00	1.00	0.00	3.91	0.06[a]
		Residual	0.01	17.00	0.00		
		Total	0.01	18.00			

a. Predictor: TA, dependent: CA.
Significance is indicated in bold.

Table 20. Coefficients for CA relative to TA in the midshaft femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	0.53	0.72		0.75	0.46
		TA	0.86	0.11	0.82	7.62	**0.00**
Pan		(Constant)	3.51	1.07		3.29	**0.00**
		TA	0.35	0.18	0.43	1.98	0.06

Predictor: TA, dependent: CA.
Significance is indicated in bold.

Residual plots of CA versus TA for modern humans and *Pan* are presented in Figures 12 and 13, respectively.

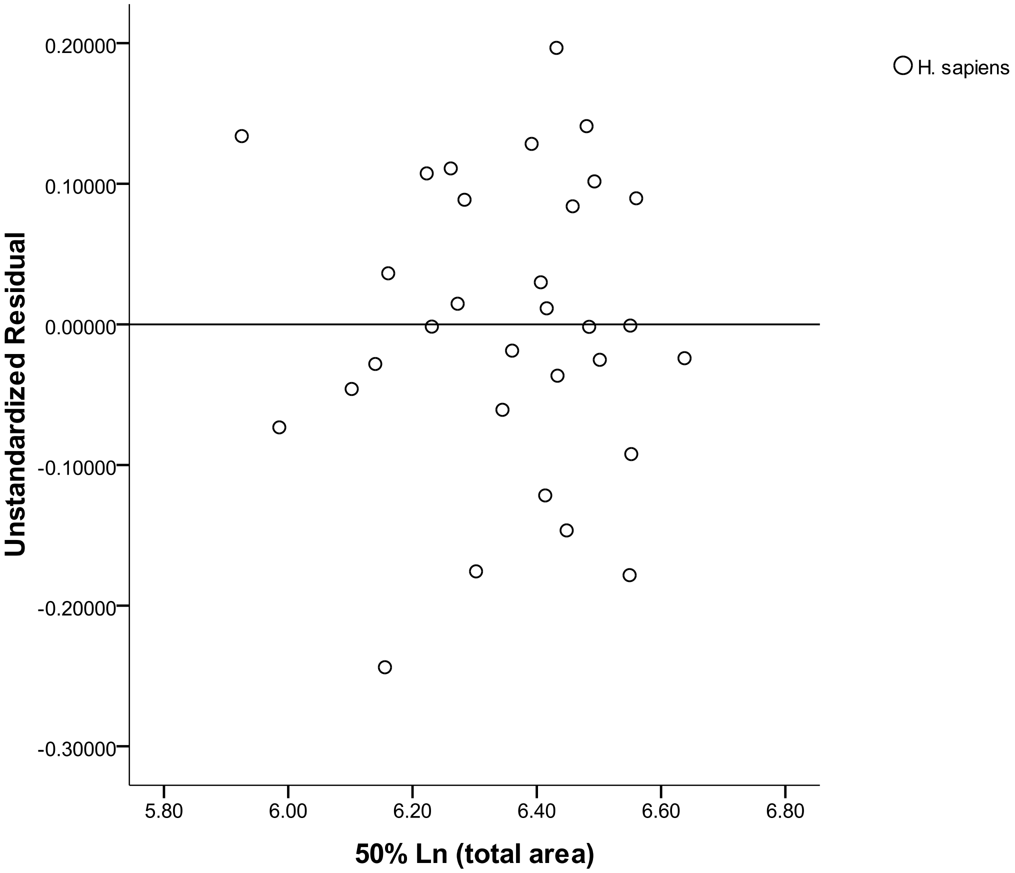

Figure 12. Scatterplot of the residuals for CA relative to TA in the midshaft femur of modern humans.

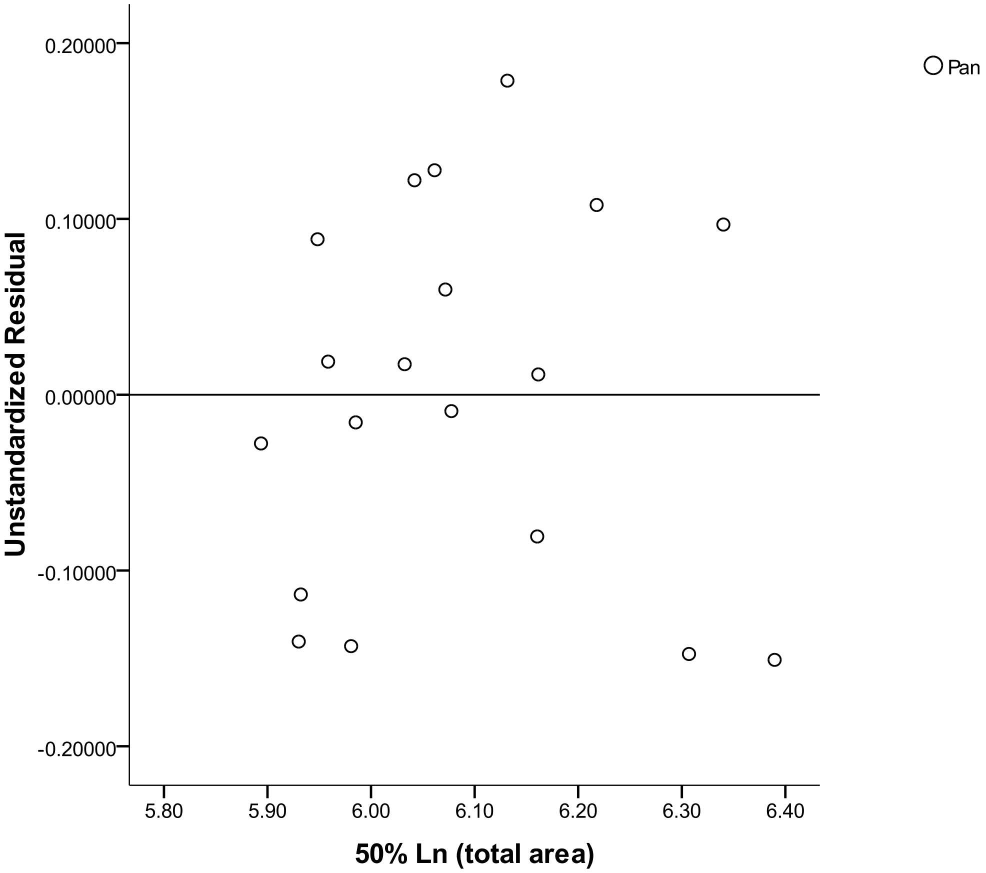

Figure 13. Scatterplot of the residuals for CA relative to TA in the midshaft femur of *Pan*.

Axial strength relative to average bending and torsional strength. Modern human midshaft femora are adapted to withstand greater axial loading relative to average bending and torsional loading compared to *Pan* midshaft femora (Fig. 14). The correlation between the observed and predicted values of CA is higher in modern humans (R= 0.84) than in *Pan* (R= 0.67), and there is a tighter relationship between CA and $J^{0.73}$ in modern humans (R^2= 0.70) than in *Pan* (R^2= 0.45) (Table 21). $J^{0.73}$ explains a significant part of the variation in CA in both groups (Table 22). The modern human and *Pan* y-intercepts and slopes are significantly different from zero (Table 23). The modern human and *Pan* y-intercepts are significantly different from each other (t= -5.02, df= 46), but the slopes are not (t= 1.00, df= 46). KNM-ER 1592, KNM-ER 736, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472 follow the modern human-like pattern compared to

Pan, but CA is decreased relative to average bending and torsional strength in these fossil femora compared to modern humans. These results suggest that while mechanical loading patterns are similar among modern humans, KNM-ER 1592, KNM-ER 736, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472, the fossil femora are mechanically stronger than modern human femora. KNM-WT 15000, OH 62 and OH 34 follow the *Pan*-like pattern compared to modern humans. As previously discussed, the relatively low CA in KNM-WT 15000 is likely a reflection of his juvenile age, which may explain his “similarity” to *Pan*. Loading patterns in OH 62 are more similar to patterns in *Pan* than to patterns in modern humans and fossil *Homo*. Johanson et al. (1987) observed slight abrasion of the femoral diaphysis of OH 62. Thus, it is possible that OH 62 follows the *Pan*-like pattern because of preservation bias. However, since the femoral diaphysis of OH 62 is not as severely eroded as in OH 34, and because the two femora are very similar in size (Haeusler and McHenry, 2004), low CA relative to $J^{0.73}$ in OH 62 may suggest that preservation bias is not contributing to the *Pan*-like pattern. A decrease in CA relative to $J^{0.73}$ in OH 62 may indeed reflect a different mechanical loading pattern in the species represented by this femur compared to other members of the genus *Homo*, both modern and fossil.

Leakey (1978) and Ruff (1995) argued that the femoral diaphysis of OH 34 is so abraded that the reconstruction of its original diaphyseal breadth and shape will remain uncertain. Although Day and Molleson (1976) did not believe severe erosion markedly affected the femoral diaphyseal circumference of OH 34, they did suggest that the original midshaft cortical thickness may have been ~6 mm more than at present. It is possible that the very moderate increase in CA relative to $J^{0.73}$ in OH 34 is an artifact of the imprecise reconstruction of its true diaphyseal shape and size.

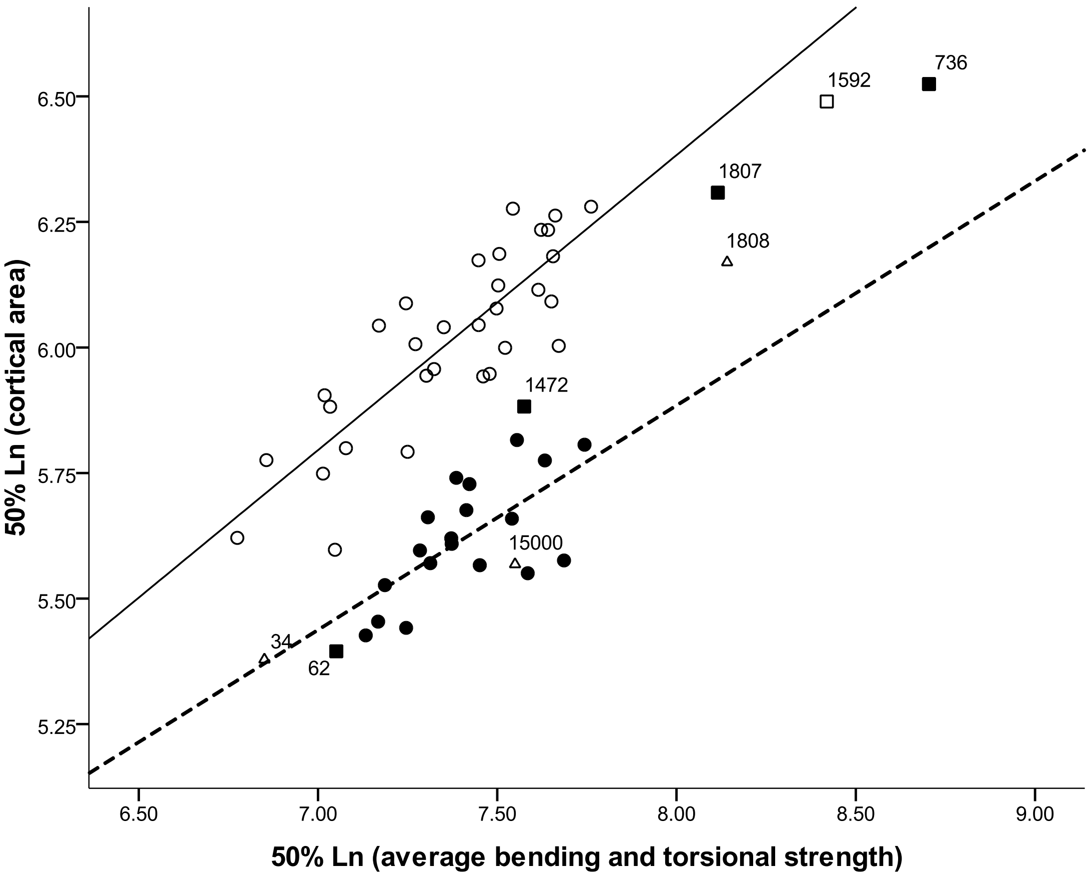

Figure 14. Bivariate scatterplot of log-transformed cortical area (CA) on log-transformed average bending and torsional strength ($J^{0.73}$) in the midshaft femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares, *Homo* sp. is represented by closed squares and *H. erectus* is represented by open triangles. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.70. R^2 linear for *Pan*= 0.45.

Table 21. Model summary for CA relative to $J^{0.73}$ in the midshaft femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	.084[a]	0.70	0.69	0.61	28.06
Pan		0.67[a]	0.45	0.42	0.02	19.92

a. Predictor: $J^{0.73}$, dependent: CA.

Table 22. ANOVA for CA relative to $J^{0.73}$ in the midshaft femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	0.72	1.00	0.72	69.22	**0.00**[a]
		Residual	0.30	29.00	0.01		
		Total	1.02	30.00			
Pan		Regression	0.00	1.00	0.00	13.99	**0.00**[a]
		Residual	0.00	17.00	0.00		
		Total	0.01	18.00			

Predictor: $J^{0.73}$, dependent: CA.
Significance is indicated in bold.

Table 23. Coefficients for CA relative to $J^{0.73}$ in the midshaft femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	1.70	0.53		3.24	**0.00**
		$J^{0.73}$	0.59	0.07	0.84	8.23	**0.00**
Pan		(Constant)	2.32	0.88		2.62	**0.02**
		$J^{0.73}$	0.45	0.12	0.67	3.74	**0.00**

Predictor: $J^{0.73}$, dependent: CA.
Significance is indicated in bold.

Residual plots of CA versus $J^{0.73}$ for modern humans and *Pan* are presented in Figures 15 and 16, respectively.

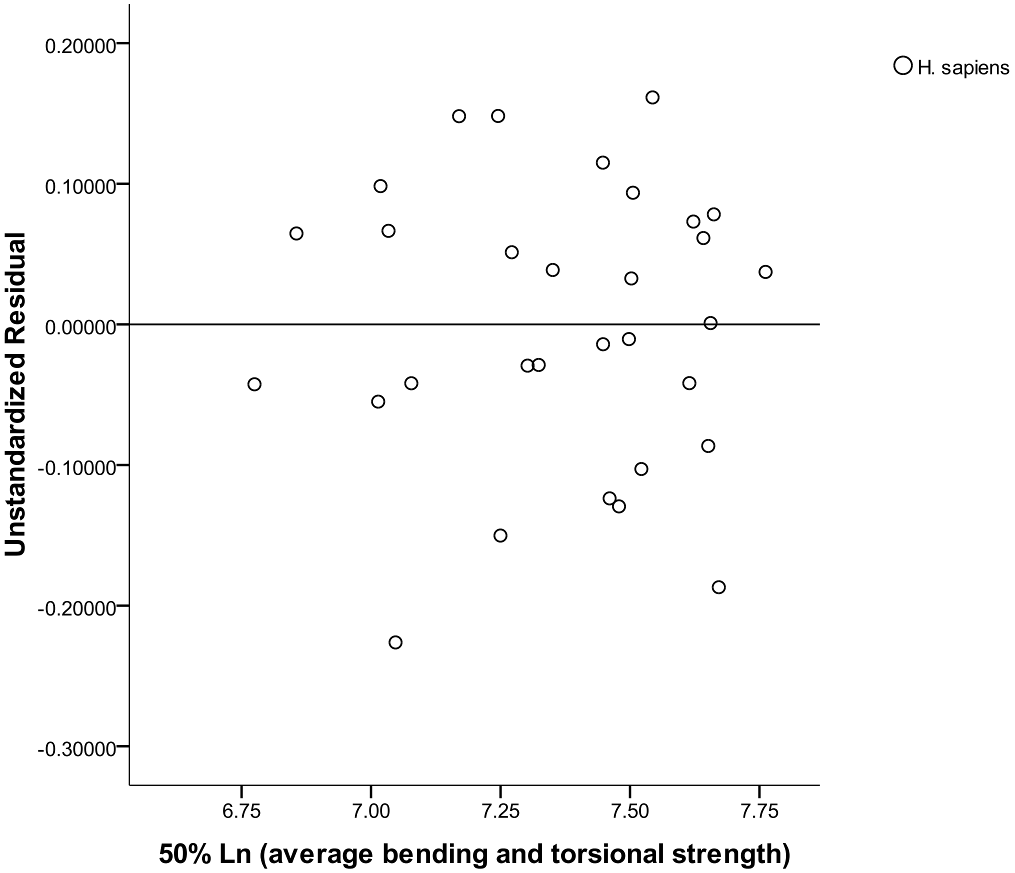

Figure 15. Scatterplot of the residuals for CA relative to $J^{0.73}$ in the midshaft femur of modern humans.

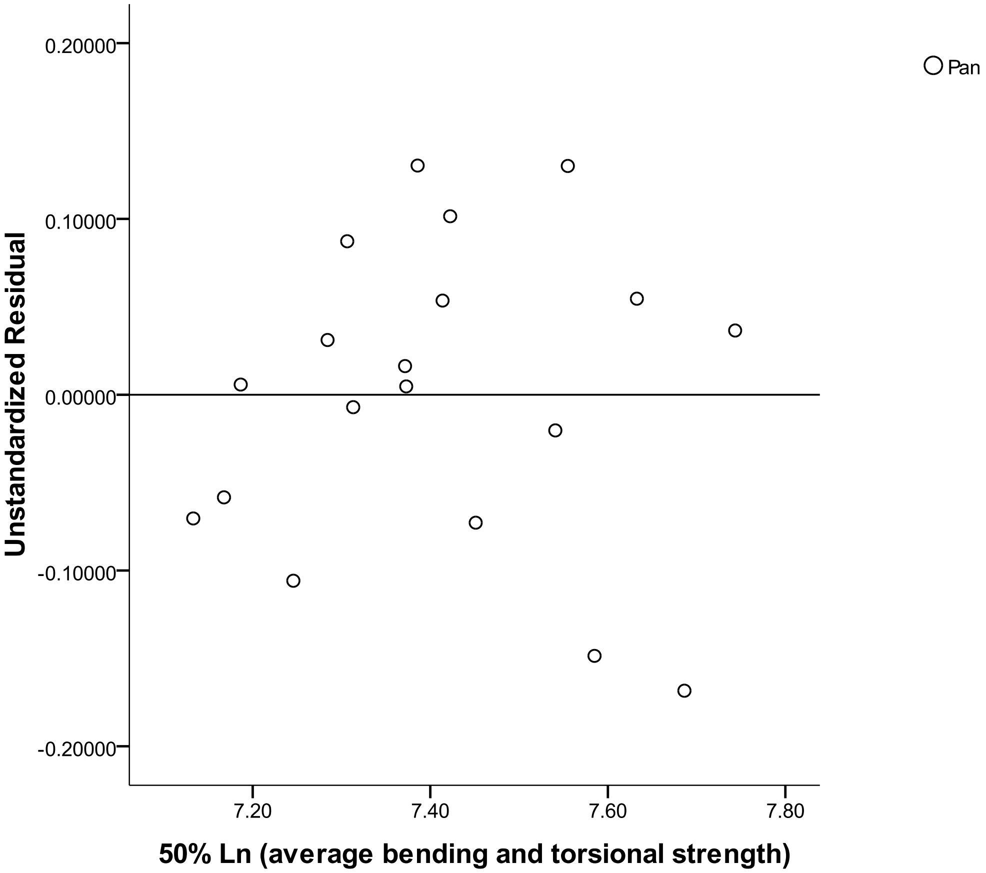

Figure 16. Scatterplot of the residuals for CA relative to $J^{0.73}$ in the midshaft femur of *Pan*.

Diaphyseal shape. Bending strength in the M-L plane is slightly decreased relative to bending strength in the A-P plane in modern humans compared to *Pan*, but the difference is probably not significant since the modern human and *Pan* y-intercepts and slopes are not significantly different from each other (t= 0.50, df= 46 and t= -0.73, df= 46, respectively) (Fig. 17). The correlation between the observed and predicted values of Z_y is slightly lower in modern humans (R= 0.88) than in *Pan* (R= 0.91), and there is a moderately weaker relationship between Z_y and Z_x in modern humans (R^2= 0.77) than in *Pan* (R^2= 0.82) (Table 24). Z_x explains a significant part of the variation in Z_y in both groups (Table 25). The y-intercept is not significantly different from zero, but the slope is significantly different from zero in modern humans and in *Pan* (Table 26). KNM-ER 1808, KNM-ER 1807 and KNM-ER 1592 show the *Pan*-like pattern in greater bending strength in the M-L plane relative to the A-P plane compared to modern humans. KNM-ER 736, KNM-WT 15000 and KNM-ER 1472 show the modern human-like pattern in lower bending strength in the M-L plane relative to the A-P plane compared to *Pan*. OH 62 and OH 34 fall very close to the intersection of the modern human and *Pan* lines, with little preference for bending strength in either plane. Since the modern human and *Pan* lines are not significantly different from each other in y-intercept and slope, the distribution of the fossils likely reflects variation rather than statistically significant differences in diaphyseal shape related to locomotor behavior.

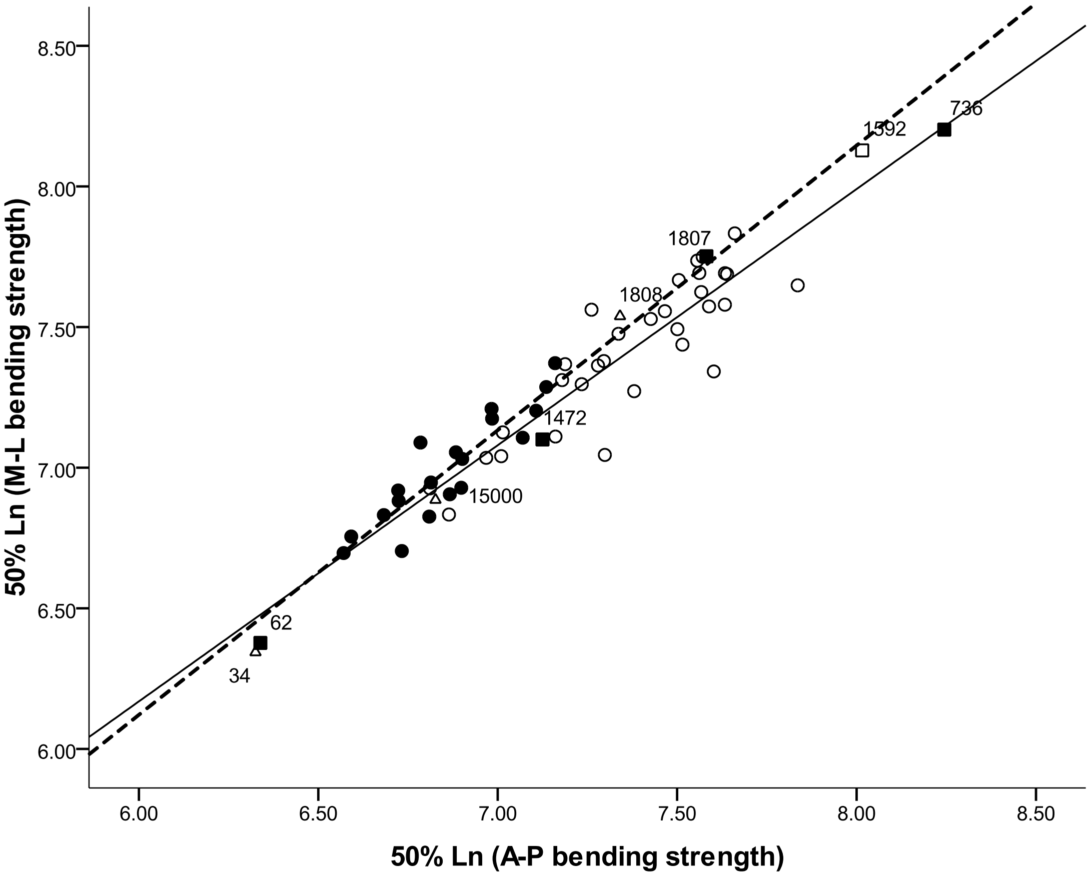

Figure 17. Bivariate scatterplot of log-transformed bending strength in the M-L plane (Z_y) on log-transformed bending strength in the A-P plane (Z_x) in the midshaft femur. Modern humans are represented by open circles, *Pan* is represented by closed circles, *Paranthropus* is represented by open squares, *Homo* sp. is represented by closed squares and *H. erectus* is represented by open triangles. The fossil samples are labeled. The modern human fit line is solid, and the *Pan* fit line is dashed. R^2 linear for modern humans= 0.77. R^2 linear for *Pan*= 0.82.

Table 24. Model summary for Z_y relative to Z_x in the midshaft femur.

	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	Log-likelihood Function Value
Modern human	1	0.88[a]	0.77	0.76	0.95	20.58
Pan		0.91[a]	0.82	0.81	0.60	20.76

a. Predictor: Z_x, dependent: Z_y.

Table 25. ANOVA for Z_y relative to Z_x in the midshaft femur.

Model			Sum of Squares	df	Mean Square	F	Sig.
Modern human	1	Regression	86.09	1.00	86.09	94.58	**0.00**[a]
		Residual	26.40	29.00	0.91		
		Total	112.49	30.00			
Pan		Regression	28.22	1.00	28.22	78.87	**0.00**[a]
		Residual	6.08	17.00	0.36		
		Total	34.30	18.00			

a. Predictor: Z_x, dependent: Z_y.
Significance is indicated in bold.

Table 26. Coefficients for Z_y relative to Z_x in the midshaft femur.

Model			Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Modern human	1	(Constant)	0.74	0.69		1.07	0.29
		Z_x	0.91	0.09	0.88	9.73	**0.00**
Pan		(Constant)	0.04	0.79		0.05	0.97
		Z_x	1.01	0.11	0.91	8.88	**0.00**

Predictor: Z_x, dependent: Z_y.
Significance is indicated in bold.

Residual plots of Z_y versus Z_x for modern humans and *Pan* are presented in Figures 18 and 19, respectively.

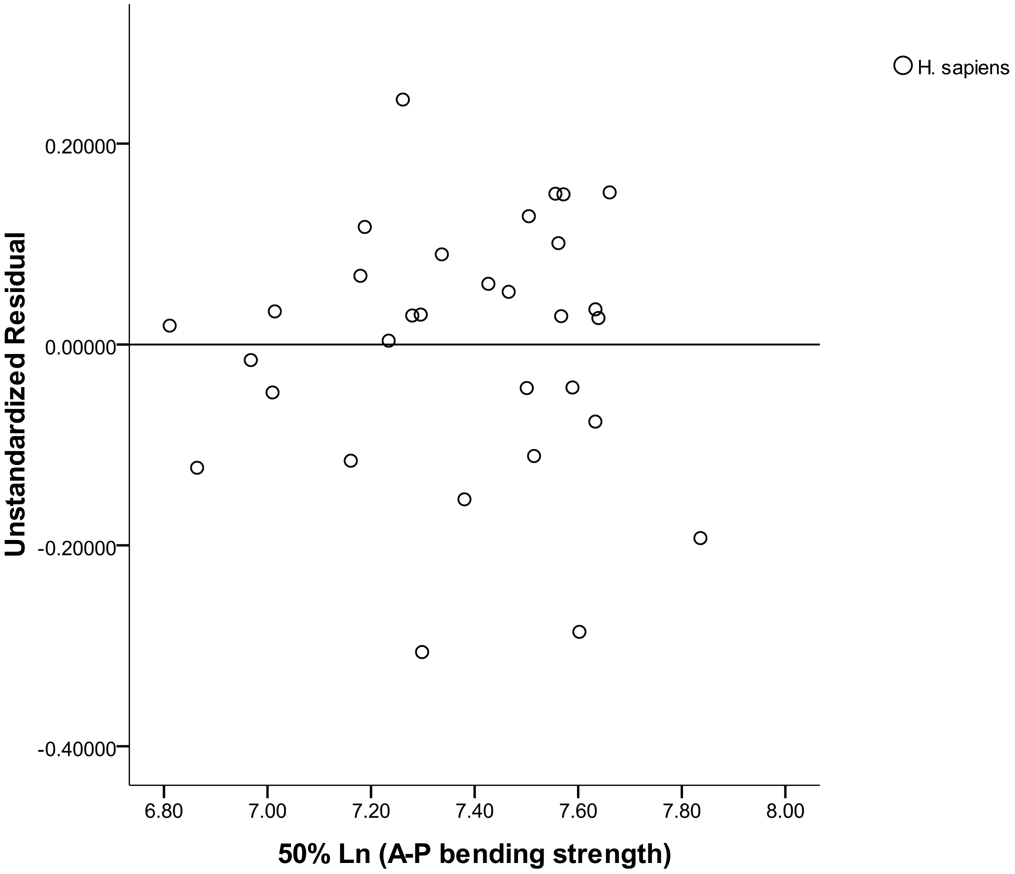

Figure 18. Scatterplot of the residuals for Z_y relative to Z_x in the midshaft femur of modern humans.

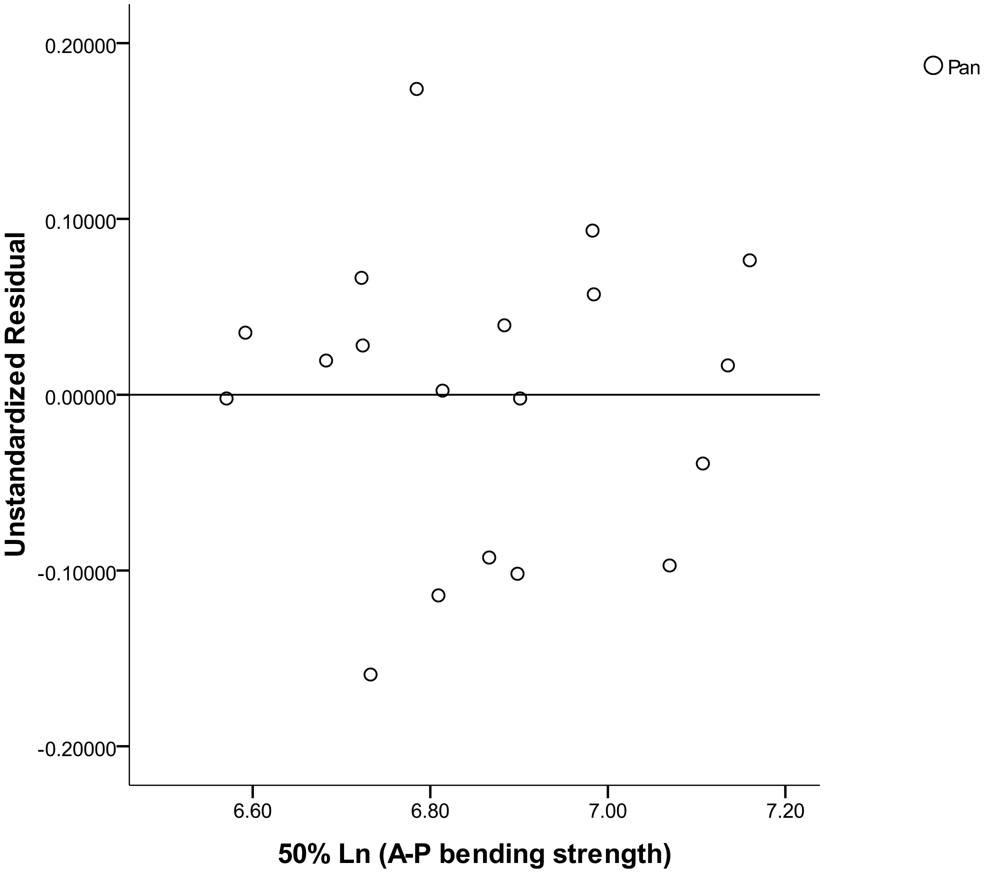

Figure 19. Scatterplot of the residuals for Z_y relative to Z_x in the midshaft femur of *Pan*.

Summary. The relative amount of cortical bone in the midshaft femur of modern humans is greater than in *Pan*. All fossil femora, except KNM-WT 15000, follow the modern human-like pattern. The low relative amount of CA in KNM-WT 15000 may be a product of his age, assuming a modern human-like growth pattern in *H. erectus* (Clegg and Aiello, 1999). TA explains a significant amount of variation in CA in modern humans, but not in *Pan*.

Modern human midshaft femora are structurally adapted for greater axial strength relative to average bending and torsional strength, which is in accordance with the kinematics of modern human bipedalism (Alexander and Jayes, 1978; Cristofolini et al., 1995; Aamodt et al., 1997; Duda et al., 1997; Sockol et al., 2007). *Pan* femora are characterized by a decrease in axial strength relative to bending and torsional strength, which is likely a mechanical adaptation to multi-oriented bending loads, and dynamic and propulsive movements associated with quadrupedal locomotion and arborealism (Ruff and Runestad, 1992; Demes et al., 2001; Kalmey and Lovejoy, 2002; Carlson, 2005; Marchi, 2007). $J^{0.73}$ explains a significant amount of the variation in CA in both modern humans and *Pan*. KNM-ER 1592, KNM-ER 738, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472 show the modern human-like pattern compared to *Pan*, albeit they are stronger than modern human femora. The *Homo*-like loading pattern in KNM-ER 1592 suggests either a kinematically similar mode of bipedalism between *Homo* and *Paranthropus*, as represented by KNM-ER 1592, or that KNM-ER 1592 is not representative of *Paranthropus* (see Chapter III). OH 34 displays a moderate increase in axial strength relative to average bending and torsional strength. The low CA relative to $J^{0.73}$ in KNM-WT 15000 may be an artifact of his age. OH 62 follows the *Pan*-like pattern in decreased CA relative to $J^{0.73}$, which may indicate a non-modern human-like mode of bipedalism.

Bending strength in the M-L plane is relatively lower than bending strength in the A-P plane in modern human midshaft femora compared to *Pan* midshaft femora, but there is overlap as size decreases. The modern human and *Pan* y-intercepts and slopes are not significantly different from each other, which suggests that the relationship between M-L bending strength relative to A-P bending strength is not significantly different between the two groups. Thus, the dispersion of the fossil data along the modern human and *Pan* lines likely reflects variation rather than real, significant differences in diaphyseal shape.

DISCUSSION

Loading in the proximal femur is influenced by a suite of morphological traits around the hip joint (e.g. pelvic orientation, morphology and proportions, hip musculature and femoral neck length) (Lovejoy et al., 1973; McHenry, 1976; Ruff and Hayes, 1983; Ruff, 1995; Ruff et al., 1999; Trinkaus and Ruff, 1999; Lovejoy et al., 2002;

Ruff, 2005; Richmond and Jungers, 2008). Previous research has yielded conflicting interpretations of morphological and functional similarities and differences between and among paranthropine pelves (e.g. McHenry, 1975c; McHenry and Corruccini, 1975; Steudel, 1978; Marchal, 2000). While a detailed analysis of Plio-Pleistocene hominin, *Pan* and modern human hip morphology is beyond the scope of this study, there are a few defining characteristics that deserve attention. Although rare and fragmentary, paranthropine pelves are generally characterized by a low, broad ilium, laterally splayed iliac blades and small acetabulae (Lovejoy et al., 1973; McHenry, 1975c, 1976). Fossil *Homo* pelves are distinguished from modern human pelves in having extremely robust iliac pillars, laterally flared iliac blades, relatively wide biacetabular breadths, large and laterally facing ischial tuberosities and relatively small auricular surfaces (i.e. fossil hominin pelves are generally more platypelloid than modern human pelves) (Ruff, 1995, 2005). Indeed, the primary selective pressures on pelvic morphology ultimately derive from obstetrical constraints rather than locomotion, and therefore reflect evolutionary changes in encephalization rather than locomotor behavior (McHenry, 1976; Berge et al., 1984; Tague and Lovejoy, 1986; Ruff, 1995; McHenry and Coffing, 2000; Simpson et al., 2008). However, the consequences of such morphological differences among *Paranthropus*, *Homo*, modern human and *Pan* pelves have an effect on posture and locomotion.

Several traits in the modern human proximal femur have been linked to bipedal locomotion. The relatively large femoral head and shorter greater trochanter in modern humans help to resist ground reaction forces about the hip, and the superior position of the femoral head relative to the supero-inferiorly oriented and medio-laterally expanded greater trochanter provides additional leverage for the hip stabilizers (i.e. the anterior gluteals) (McHenry and Corruccini, 1976; Lovejoy, 1988; Lovejoy et al., 2002; Harmon, 2007). The relatively long femoral neck in modern humans also helps to provide leverage for the anterior gluteal muscles during the pelvic support phase of bipedal gait (Lovejoy, 1988; Lovejoy et al., 2002). The relationship between proximal femoral morphology and locomotion in *Pan* is not well documented, but Harmon (2007) found that the relatively small femoral head, shorter femoral neck and supero-inferiorly long greater trochanter in African apes are, as a complex, commensurate with greater hip joint stability and muscle leverage associated with knuckle-walking quadrupedalism.

The function of the anterior gluteals in *Pan* is very different from that in modern humans largely because of differences in pelvic orientation and proximal femoral bone morphology. In *Pan*, the anterior gluteals stretch from the superior margin of the ilium to the greater trochanter, which extends above the femoral head and is superio-inferiorly elongated (Lovejoy, 1988). The position of the gluteus medius and gluteus minimus enables them to act as hip extensors during quadrupedalism (Lovejoy, 1988). Since the ilium is relatively long in *Pan*, these muscles have a large range of contraction (Lovejoy, 1988). Conversely, the forward rotation of the ilia, the relatively long femoral neck and the relatively high femoral neck angle in modern humans laterally repositions the anterior gluteals away from the hip (Lovejoy, 1988). Thus, the anterior gluteals serve as stabilizing abductors in modern humans, which act to support the body during the single-support phase of the bipedal gait cycle (Lovejoy, 1988; Duda et al., 1997; Harcourt-Smith, 2007).

Harmon (2007) found striking similarities in proximal femoral morphology between modern humans and orangutans, which result from different functional requirements associated with clearly different locomotor behaviors. This shared proximal femoral morphology between *Homo* and *Pongo* may be an example of homoplasy, and therefore highlights the necessary caution needed when attempting to link morphology with function. It is also important to to be conscious of the fact that morphological traits around the hip act as a complex, that their functional roles are not strictly related to posture and locomotion and that a change in one structure may or may not lead to a change in another structure.

As is the case with Plio-Pleistocene hominins in general, relative CA in the proximal and midshaft femur is elevated in *Paranthropus*, fossil *Homo* sp. and *H. erectus* compared to modern humans and *Pan*. The functional significance of the relative amount of cortical bone in a cross-section can be difficult to interpret because this property is related to different aspects of bone morphology and does not have an intrinsic biomechanical significance (Ruff et al., 1993; Ruff, 1994; Sládek et al., 2006; Carlson et al., 2007). However, it has been suggested that the relatively thick femoral cortex in Plio-Pleistocene hominins may reflect a general increase in mechanical loading from greater musculature and activity levels compared to modern humans (Kennedy, 1983b; Ruff et al., 1993; Trinkaus and Ruff, 1999; Ruff, 2005). This suggestion is supported by evidence that $J^{0.73}$ significantly contributes to variation in CA in the proximal and midshaft femur of modern humans. An increase in $J^{0.73}$ in fossil hominins compared to modern humans may also partially explain their increase in CA relative to modern humans. At the very least, the greater CA relative to TA in the proximal and midshaft femur of Plio-Pleistocene hominins is a morphologically diagnostic trait that distinguishes *Paranthropus*, fossil *Homo* sp. and *H. erectus* from modern humans and *Pan*.

Cross-sectional morphology in the proximal and midshaft femur are distinct between modern humans and *Pan*. The former generally have greater axial strength relative to bending and torsional strength, while *Pan* shows lower axial strength relative to bending and torsional strength. The increase in axial strength relative to average bending and torsional strength in modern humans likely results from the actions of the abductor complex in the hip, which generates strong axial compression in the femoral neck, particularly during the single-support phase of human walking, that is subsequently transferred to the proximal femur and down the femoral diaphysis (Cristofolini et al., 1995; Aamodt et al., 1997; Duda et al., 1997). Stereotypical compressive and tensile loading characteristic of habitual erect posture and bipedalism also leads to greater axial strength relative to average bending and torsional strength in the modern human proximal femur (Carter et al., 1989; Duda et al., 1997; Kalmey and Lovejoy, 2002). Conversely, an increase in bending and torsional strength relative to axial strength in the proximal and midshaft femur in *Pan* likely reflects the dynamic, non-stereotypical, propulsive movements characteristic of arboreal locomotion (Ruff and Runestad, 1992; Carlson, 2005; Marchi, 2007). Moreover, bending moments in *Pan* are increased because of the varus position of the hindlimb (Marchi, 2007).

CA relative to $J^{0.73}$ in the proximal femur of fossil *Homo* is commensurate with loading patterns consistent with modern human-like locomotion. *Paranthropus* shows the modern human-like pattern in greater CA relative to $J^{0.73}$ compared to *Pan*, but the *Pan*-like pattern in lower CA relative to $J^{0.73}$ compared to modern humans and fossil *Homo*. These results indicate a mode of locomotion in *Paranthropus* that is not *Pan*-like, but instead kinematically more similar to, albeit still distinct from, that in *Homo*, both modern and fossil. Macchiarelli et al. (1999) examined the architecture of cancellous bone in the ilia of South African gracile and robust australopithecines, and found that the structure of the trabecular network indicated a loading regime commensurate with a bipedal gait somewhat different from modern humans. The results from this study support trabecular bone structural analyses indicating a rudimentary mode of bipedalism in *Paranthropus*.

CA relative to $J^{0.73}$ in the midshaft femur of *Paranthropus*, fossil *Homo* sp. and *H. erectus* generally conform to modern human-like patterns rather than *Pan*-like patterns, albeit fossil hominin femora are stronger than modern human femora. *Pan*-like loading patterns in KNM-WT 15000 most likely reflect the overall decrease in CA because of his juvenile age. Growth patterns in CA in modern human children and adolescents tend to follow body weight (Sumner and Andriacchi, 1996). Therefore, it is presumed that CA in KNM-WT 15000 is lower than expected given that he has not yet attained full adult size. In addition, modern human children tend to have relatively thin cortical walls because net endosteal resorption outweighs net endosteal deposition (Ruff et al., 1994; Schoenau et al., 2001; Ruff, 2005). Modern human children (i.e. before mid-adolescence) also experience more periosteal responses to mechanical loading than endosteal responses, which partially explains the larger medullary cavities in children compared to young adults and adults (Ruff, et al., 1994). Assuming modern human-like growth patterns in *H. erectus* (Clegg and Aiello, 1999), the low CA in KNM-WT 15000, which is likely a product of his age, may be contributing to the aberrant pattern in CA relative to $J^{0.73}$. There is no morphological or functional morphological evidence to suggest that KNM-

WT 15000 was not a committed biped (e.g. Brown et al., 1985; Ruff and Walker, 1993; Walker and Leakey, 1993; Wood and Collard, 1999b).

CA is slightly elevated relative to $J^{0.73}$ in OH 34 compared to *Pan*, but not nearly on the same magnitude as in KNM-ER 1592, KNM-ER 736, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472. It is possible that the apparently non-*Homo*-like loading pattern in OH 34 reflects taxonomic bias. OH 34 is generally considered a representative of *H. erectus*, or *Homo* sp. indet., but its taxonomic status is not secure (Day and Molleson, 1976; Howell, 1978). OH 34 could be allocated to either *H. erectus* or *P. boisei* based on its inferred stratigraphic position from Bed III at Olduvai Gorge (0.8-1.15 mya) (Hay, 1976). The gracile shaft and the well-developed femoral pilaster suggest an affinity with *Homo* rather than with *Paranthropus* (Howell, 1978; Haeusler and McHenry, 2004). However, the M-L buttressing of the proximal femoral diaphysis in OH 34 is not as pronounced as in other early *Homo* femora, and proximal femoral cross-sectional shape differences between OH 34 and KNM-ER 737 (*H. erectus*), and between OH 34 and OH 28 (*H. erectus*) exceed differences found in extant hominoids (Haeusler and McHenry, 2004). According to Haeusler and McHenry (2004), OH 34 is unique because its external femoral morphology is statistically significantly different from that in *P. boisei* and *H. erectus*. Based on morphology and size, OH 34 is most closely matched with OH 62, and therefore may best be regarded as *Homo* sp. indet. as suggested by Day and Molleson (1976) (Haeusler and McHenry, 2004). Size-standardized midshaft femoral cross-sectional geometry in OH 34, however, has been shown to be most similar to KNM-WT 15000 and KNM-ER 1808, and quite distinct from OH 62 (see Chapter III).

A second possibility is that the low CA relative to $J^{0.73}$ in OH 34 reflects preservation bias. As previously suggested by Leakey (1978) and Ruff (1995), the reconstruction of the original diaphyseal breadth and shape of OH 34 may be uncertain because of extensive weathering (but see Day and Molleson, 1976). Thus, the moderate amount of CA relative to $J^{0.73}$ may reflect error in the reconstruction of the true diaphysis.

It is unclear if preservation bias in OH 62 is contributing to *Pan*-like patterns in CA relative to $J^{0.73}$. Although Johanson et al. (1987:208) observed “slight exfoliation of the OH 62 femur", Haeusler and McHenry (2004:438) described the external appearance of it as "rugged" with "the loss of surface detail" undoubtedly resulting from heavy abrasion. However, it should be noted that abrasion in OH 34 is more severe than in OH 62 (Haeusler and McHenry, 2004), yet they show similar relative CA values. This suggests that the pattern in OH 62 is not reflective of error in diaphyseal reconstruction due to poor preservation. Instead, the results indicate a mode of locomotion in OH 62 that is mechanically different from that in *Homo* in having decreased CA relative to $J^{0.73}$.

Femoral neck length determines the moment arm of the anterior gluteal muscles during the pelvic support phase in bipedal gait (Lovejoy et al., 2002). The relatively long femoral neck in Plio-Pleistocene hominins, both *Paranthropus* and *Homo*, acts to increase M-L bending strength in the proximal femur because it laterally displaces the femoral diaphysis relative to the femoral head center (Ruff et al., 1999; Ruff, 2005; Richmond and Jungers, 2009). As a result, the iliotibial band (i.e. the lateral tension band of the knee) must exert a force to maintain equilibrium about the knee joint (Lovejoy, 1988; Ruff, 1995). An increase in biacetabular breadth leads to an increase in abductor and joint reaction force, which further increases M-L bending in the proximal femoral diaphysis (Ruff, 1995).

In the proximal femur, modern humans show greater bending strength in the M-L plane relative to the A-P plane compared to *Pan*, which likely reflects the generally longer femoral neck, more laterally flared ilia and greater biacetabular breadth in the former compared to the latter. Conversely, in the midshaft femur *Pan* shows a moderate increase in bending strength in the M-L plane relative to the A-P plane compared to modern humans, particularly as size increases. The relationship between M-L bending strength relative to A-P bending strength in the proximal and midshaft femur*,* however*,* is not significantly different between modern humans and *Pan* since y-intercepts and slopes are not significantly different between the two groups. This finding supports the statement by Lieberman et al. (2004:169) that "the lack of any simple, predictable relationship between bone function and midshaft shape complicates interpretations of shape, and potentially invalidates comparisons between species."

Most Plio-Pleistocene hominins examined here show an increase in M-L bending strength relative to A-P bending strength in the proximal femur compared to *Pan*, and are similar to modern humans in this regard. These results support previous findings characterizing proximal fossil hominin femora as medio-laterally expanded (e.g. Lovejoy and Heipel, 1972; Kennedy, 1983b; Ruff, 1995; Grine et al., 1995; Ruff et al., 1999; Richmond and Jungers, 2008; Holliday et al., 2010). In the current study, *Paranthropus*, fossil *Homo* and modern humans are similar in M-L bending strength relative to A-P bending strength. Ruff (1995) and Ruff et al. (1999), however, found that bending strength in the M-L plane relative to bending strength in the A-P plane was greatest in fossil *Homo*, least in modern humans and intermediate in *Paranthropus.* Since bending strength in the M-L plane relative to the A-P plane is highly variable across modern human populations, it is possible that conflicting results between the current study and Ruff (1995) and Ruff et al. (1999) may reflect slight differences in the modern human comparative sample[6].

In the femoral midshaft, modern humans show a slight decrease in bending strength in the M-L plane relative to the A-P plane compared to *Pan*, but the difference between the two groups is very small, especially as size decreases. Moreover, y-intercepts and slopes are not significantly different between modern humans and *Pan*, which suggests that the relationship between M-L and A-P bending strengths is similar between the groups. Fossil hominins generally show greater bending strength in the M-L plane relative to the A-P plane compared to modern humans. The increase in midshaft femoral M-L buttressing relative to A-P buttressing in fossil *Homo*, especially in *H. erectus,* and *Paranthropus* has been previously noted (e.g. Ruff, 1995, 2005, 2009; Antón, 2003).

KNM-ER 1472 fell within the modern human sample distribution, but slightly below the modern human regression line, and below many other fossil samples. Ruff

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[6] The modern human comparative sample in Ruff (1995) and Ruff et al. (1999) consisted of prehistoric and protohistoric Pecos Pueblo Amerindians from New Mexico, and East Africans from Uganda ("Nilotics") and Kenya (Bantu). The Pecos Pueblo inhabitants were horticulturalists with a rigorous lifestyle (Ruff and Hayes, 1983). The East African sample has been described as tall, relatively thin individuals with relatively long limbs (Ruff, 1995). Occupational information is unavailable, but since the samples were collected prior to 1960 "most of the individuals would not have been highly urbanized" and likely engaged in some manual labor without reliance on mechanized transport (Ruff, 1995:530).

(1995) found similar results with regard to the latter observation. However, when compared to Amerindians from Pecos Pueblo and East Africans from Uganda and Kenya, KNM-ER 1472 fell within the modern human sample distribution and above the modern human least squares regression line (Ruff, 1995). The diaphysis surrounding the natural break near the midshaft of KNM-ER 1472 showed evidence of abrasion. In the current study, the missing bone, mainly on the lateral side, was conservatively estimated based on the contours of the diaphysis above and below the natural break. Ruff (1995) estimated the missing bone in a similar manner and used a combination of methods to reconstruct the cross-sectional geometry of KNM-ER 1472 at the same section location. The somewhat contrasting results between Ruff (1995) and the current study may reflect inherent complications in biomechanical analyses of poorly preserved fossil remains, differences in modern human reference samples and/or methodological differences.

M-L bending strength is slightly decreased relative to A-P bending strength in KNM-ER 736 compared to other fossil *Homo* samples (e.g. KNM-ER 1807 and KNM-ER 1808). Ruff (1995) found similar results (fossil *Homo* samples included KNM-ER 737, KNM-ER 803a, KNM-ER 1481a, KNM-ER 1808 and OH 28). In the current study, however, KNM-ER 736 also fell slightly below *Paranthropus*, as represented by KNM-ER 1592, but Ruff (1995) found that it fell moderately above paranthropines as represented by KNM-ER 1463, KNM-ER 1822 and KNM-ER 993. The section location for KNM-ER 1592 in this study was taken at ~43% of the femoral diaphysis based on an estimated femur length of 470 mm from McHenry (1991). An artificial increase in M-L bending strength may be a consequence of the more distal section location since M-L breadth increases as the condyles are approached. In addition, although KNM-ER 1592 is often referred to in the published literature as *Paranthropus* sp. or *P*. cf. *boisei*, its taxonomic status is contentious (McHenry, 1992; see Chapter III). It is possible that differences in results between KNM-ER 736 and *Paranthropus* in the current study versus Ruff (1995) may reflect error due to section location, variation in relative bending strength along the anatomical planes in *Paranthropus* or taxonomic uncertainty with KNM-ER 1592 (see Chapter III).

CONCLUSION

Paranthropus proximal femora are generally characterized by relatively thick cortices, a modern human-like pattern in greater CA relative to $J^{0.73}$ compared to *Pan*, but the *Pan*-like pattern in decreased CA relative to $J^{0.73}$ compared to modern humans and fossil *Homo*, and greater bending strength in the M-L plane relative to the A-P plane. Of particular note are the mechanical similarities among OH 20, SK 82 and SK 97, which complements previous observations of their external morphological similarities (e.g. Day, 1969, 1976a; Leakey, 1978; Wood and Constantino, 2007; Harmon, 2009). Fossil *Homo* proximal femora are characterized by relatively thick cortices and a modern human-like pattern in greater CA relative to $J^{0.73}$ compared to *Pan*. KNM-ER 999a shows greater bending strength in the M-L plane relative to the A-P plane compared to *Pan*, but KNM-ER 1481a shows slightly lower bending strength in the M-L plane relative to the A-P plane.

The *Paranthropus* midshaft femur, based on KNM-ER 1592, is characterized by a relatively thick cortex compared to modern humans and *Pan*, a mechanical loading pattern more similar to *Homo*, both modern and fossil, than to *Pan* and greater bending strength in the M-L plane relative to the A-P plane compared to modern humans. Fossil *Homo* midshaft femora are generally characterized by relatively thick cortices, mechanical loading patterns more similar to modern humans than to *Pan* with an increase in M-L bending strength relative to A-P bending strength.

Mechanical loading patterns in the proximal and midshaft femur in *Paranthropus* suggest a mode of locomotion mechanically more similar to human-like locomotion than *Pan*-like locomotion in accordance with many functional morphological interpretations of paranthropine postcranial anatomy (Napier, 1964; Day, 1969; McHenry, 1976; Robinson, 1972; Grausz et al., 1988; Susman, 1988, 1989; Susman and Brain, 1988; Harcourt-Smith and Aiello, 2004; Richmond and Jungers, 2008). As a group, *Paranthropus* proximal femora display mechanical similarities among each, which supports previous assertions of morphological continuity among paranthropine proximal femora from Olduvai Gorge, Koobi Fora and Swartkrans (e.g. Walker, 1973; Day, 1976b; McHenry and Corruccini, 1978; Harmon, 2009; Holliday et al., 2010).

The *Homo*-like patterns in the midshaft femur of KNM-ER 1592 suggest mechanically similar loading patterns between *Homo* and *Paranthropus*, or that KNM-ER 1592 is misclassified as a paranthropine (see Chapter III). Midshaft femoral cross-sectional properties in KNM-ER 1592 should be compared with known, or reasonably ascribed *Paranthropus* samples to better understand its mechanical significance.

Mechanical loading patterns in the proximal and midshaft femur in *Homo* sp. and *H. erectus* are generally mechanically very similar to modern humans, which indicates a mode of locomotion commensurate with modern human-like bipedalism. The artificial peculiarities of KNM-WT 15000 compared to modern humans and fossil *Homo* may be an artifact of his immature age. It is unclear if the reconstructed cross-sections in OH 34 and OH 62 are accurate given their preservation (Leakey, 1978; Ruff 1995; but see Haeusler and McHenry, 2004). Both femora are mechanically very similar to each other and distinct from other fossil *Homo* samples. Since the taxonomic status of OH 34 and especially OH 62 are uncertain, it is also possible that they are representatives of a species not fully committed to terrestrial bipedalism. If OH 34 and OH 62 are indeed members of the genus *Homo* (see Chapter III), there is the possibility that locomotor behavior in *Homo* is more variable than generally thought.

The expectation of greater CA relative to TA in the proximal and midshaft femur of modern humans compared to *Pan*, and greater CA relative to TA in the proximal and midshaft femur of fossil hominins compared to modern humans is supported. Although the mechanical significance of an increase in CA relative to TA in Plio-Pleistocene hominin femora compared to modern human femora is unclear, it has been suggested that it may reflect an increase in overall mechanical loading among early hominins relative to modern humans (Kennedy, 1983b; Ruff et al., 1993; Ruff, 1995; Ruff et al., 1999; Trinkaus and Ruff, 1999; Ruff, 2009). Since $J^{0.73}$ explains a significant amount of the variation in CA among modern humans, and since $J^{0.73}$ is lower in modern human femora compared to fossil hominin femora, it is possible that a decrease in average bending and torsional strength in modern humans may also explain a decrease in relative CA.

The expectation of greater axial strength relative to average bending and torsional strength in the proximal and midshaft femur of modern humans compared to *Pan* is supported. Fossil *Homo* is most similar to modern humans in this regard, albeit their femora are stronger than modern human femora. *Paranthropus* is more similar to modern humans than to *Pan* in proximal femoral axial strength relative to average bending and torsional strength, which suggests a loading pattern similar to modern humans, albeit still distinct. The single midshaft *Paranthropus* femur shows an increase in CA relative to $J^{0.73}$, which is more similar to the modern human-like pattern than the *Pan*-like pattern. However, since the taxonomic status of this individual (i.e. KNM-ER 1592) is uncertain, it is unclear if *Paranthropus* indeed follows the human-like pattern in increased CA relative to $J^{0.73}$ in the femoral midshaft, or if KNM-ER 1592 is misclassified as *Paranthropus*.

The expectation of significantly greater M-L bending strength relative to A-P bending strength in the proximal and midshaft femur or modern humans compared to *Pan* is not supported. Although modern humans show an increase in proximal femoral M-L bending strength relative to A-P bending strength, the regression line is not significantly different from the *Pan* regression line. Modern human midshaft femora show slightly lower M-L bending strength relative to A-P bending strength compared to *Pan*. Like the proximal femur, however, the regression line is not significantly different from the *Pan* regression line. These results indicate that the relationship between M-L bending strength and A-P bending strength is similar in modern humans and *Pan* despite obvious locomotor differences between the two groups. Relative bending strength along the anatomical axes is highly variable among modern human populations, which has been particularly well-demonstrated among archeological samples specifically in relation to subsistence economy (e.g. Ruff and Hayes, 1983; Ruff, 1987, 1999; Bridges, 1995; Stock and Pfeiffer, 2004; Marchi et al., 2006; Sládek et al., 2006; Sparacello and Marchi, 2008). Therefore, the results presented in this study with regard to relative M-L and A-P bending strength should be taken with caution given the nature of the modern human reference sample. Finally, several factors (e.g. velocity, directional change, terrain, bi-iliac breadth) influence bending strength in the M-L plane relative to the A-P plane in the femoral diaphysis, especially in the midshaft section (Ruff, 1994, 1999, 2000; Demes et al., 2006; Marchi et al., 2006; Carlson et al., 2007; Carlson et al., 2008; Shaw and Stock, 2010). The relationship between many of these factors and their influence on diaphyseal shape, however, is unclear (Lieberman et al., 2004). It is therefore possible that different mechanical demands could potentially yield similarities in the relationship between M-L bending strength and A-P bending strength in modern humans and *Pan* in much the same way that external proximal femoral morphologies are similar between *Homo* and *Pongo* despite distinctly different postural and locomotor behaviors (Harmon, 2007). Further investigation of the relationship between mechanical loading and diaphyseal shape are warranted to better understand the link between relative bending strength in the anatomical axes of the femur.

The results from this study are summarized as follows: (1) cross-sectional morphologies in the proximal and midshaft femur of fossil *Homo* sp. and *H. erectus* are generally commensurate with modern human-like patterns; (2) cross-sectional morphology in the proximal femora of *Paranthropus* is more similar to modern human-like patterns than to *Pan*-like patterns, which suggests a mode of locomotion kinematically more akin to *Homo* than to *Pan*; (3) cross-sectional morphology in the midshaft femur of *Paranthropus*, represented by KNM-ER 1592, is very similar to modern human-like patterns, which either indicates that locomotor behavior in *Paranthropus* was commensurate with modern human-like locomotion or that KNM-ER 1592 is not a representative of *Paranthropus*; and (4) cross-sectional morphologies in OH 34 and OH 62 are similar to each other, similar to modern humans in CA versus TA, but more similar to *Pan* than to modern humans in CA versus $J^{0.73}$. It is unclear if preservation bias is influencing the results of the latter, particularly in OH 34, or if OH 34 and OH 62 had a mode of locomotion somewhat distinct from *Homo*. If OH 34 and OH 62 are indeed representative of *Homo*, and if preservation bias is not significantly altering their femoral diaphyses, then the results from this study support the idea of locomotor variability in fossil *Homo*.

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CHAPTER V

SUMMARY OF CONCLUSIONS, CONTRIBUTIONS AND FUTURE DIRECTIONS

The major goal of this dissertation was to examine locomotion and locomotor variability in the Plio-Pleistocene hominin fossil record from a biomechanical perspective. The three primary objectives were to investigate: (1) if femoral cross-sectional morphology reflects current taxonomic assignments of isolated fossil femora; (2) if mechanical loading patterns in *Paranthropus* suggest human-like locomotion, *Pan*-like locomotion or intermediate locomotor behavior; and (3) if mechanical loading patterns in early *Homo* and *Homo* sp. are consistent with locomotor behavior in later *Homo* (i.e. *H. erectus*) and modern humans. The following sections describe the major findings of this study.

TAXONOMY AND LOCOMOTION

A major hurdle that has hindered analyses of locomotion among several fossil hominin groups is the disconnect between the evidence used to diagnose/identify species in the fossil record (i.e. craniodental remains) and the evidence used to reconstruct locomotor behavior (i.e. postcranial remains). Thus, it is often unclear if reconstructed locomotor behaviors, which are primarily based on isolated postcranial elements, are actually valid for a species largely identified craniodentally. Members of the same genus are expected to occupy the same adaptive zone (Mayr, 1950; Cela-Conde and Ayala, 2003), and members of an adaptive zone are expected to share similar posture and locomotor behavior (Wood and Lonergan, 2008). This hypothesis was tested by examining how fossil hominin groups were differentiated based on cross-sectional properties, and which cross-sectional properties best discriminate among the groups. A modern human sample was used for comparative purposes.

All modern human femora clustered together in the proximal and midshaft femoral analyses. In the proximal femur, KNM-ER 999a and KNM-ER 1481a, which are attributed to *Homo* sp., were closer to each other than either one was to *Paranthropus,* and clustered with modern humans to the exclusion of *Paranthropus*. KNM-ER 1500d, SK 82 and SK 97, which are allocated to *Paranthropus*, shared a close proximity among each other and formed a cluster to the exclusion of modern and fossil *Homo*. KNM-ER 738, which has been allocated to both *Paranthropus* and *Homo*, was closest to SK 82 and SK 97 and clustered with *Paranthropus*. The DFA for the proximal section indicated that CA, Z_x/Z_y, Z_x and $J^{0.73}$, which were entered in the first through fourth steps, respectively, were the most important properties contributing to group differences. Pairwise group differences between modern humans and *Paranthropus*, and between modern humans and fossil *Homo* were significantly different in all four steps of the analysis. $J^{0.73}$, which accounts for most of the variation among groups, was associated with the first function and Z_x/Z_y was associated with the second function. Both functions were significant based on Wilks' lambda. Modern humans were discriminated from *Paranthropus* and fossil *Homo* along the first function, and from fossil *Homo* along the second function. All originally grouped and cross-validated grouped modern human femora were correctly classified. All originally grouped fossil femora were correctly classified. Of the cross-validated grouped cases, only one paranthropine femur was misclassified as fossil *Homo*. The results from the DFA suggest that the clustering of proximal femora was largely due to differences in average bending and torsional strength.

Cluster analysis for the midshaft femur revealed that OH 62 was clearly the most distant sample compared to modern humans and fossil hominins. However, it is unclear if its distinctiveness is due to taxonomic and/or preservation bias. *H. erectus* femora (i.e. KNM-WT 15000, KNM-ER 1808 and OH 34) were closer among each other than either one was to non-*erectus* samples. KNM-ER 1807 and KNM-ER 736, which are taxonomically debatable, were close to KNM-ER 1472, a likely representative of *Homo*. KNM-ER 1592, a purported paranthropine, was close to KNM-ER 1807, KNM-ER 1472 and KNM-ER 1808. KNM-ER 1592 was as distant from OH 62 as were the other fossil femora. KNM-ER 1592, fossil *Homo* and *H. erectus* femora clustered with modern humans. OH 62, however, formed a cluster to the exclusion of all other samples. The DFA for the midshaft section indicated that CA, %CA, $J^{0.73}$, Z_x and Z_y, which were entered in the first through fifth steps, respectively, were the most important properties contributing to group differences. Pairwise group comparisons indicated that modern humans were not significantly different from *Paranthropus*, as represented by KNM-ER 1592, and *H. erectus* in step 1, and from *Paranthropus* in steps 2 through 5. $J^{0.73}$ was associated with the first function, CA was associated with the second function and %CA was associated with the third function. Only the first two functions were significant based on Wilks' lambda. Modern humans were discriminated from all fossil hominin groups along the first function, and from *Paranthropus* and *H. erectus* along the second function. All originally grouped and cross-validated grouped modern human femora were correctly classified. All originally grouped fossil femora were correctly classified. Of the cross-validated grouped cases, KNM-ER 1592 and one *H. erectus* femur were misclassified as *H. sapiens*, and one fossil *Homo* sp. femur was misclassified as *H. erectus*. These results suggest that the clustering of midshaft femora was primarily due to differences in $J^{0.73}$ and CA.

Based on proximal femoral cross-sectional morphology, the current taxonomic status of KNM-ER 999a and KNM-ER 1481a as representatives of *Homo* is supported, albeit their species designations within that genus cannot be resolved. The taxonomic status of KNM-ER 1500d, SK 82 and SK 97 as non-*Homo* hominins is supported. The taxonomic status of KNM-ER 738 based on proximal femoral cross-sectional morphology cannot be confidently determined, but results tentatively suggest that it cannot be excluded from the *Paranthropus* genus.

Cluster analysis based on midshaft femoral cross-sectional properties suggest that OH 62 may not be a representative of *Homo*, or that there is a high degree of cross-sectional morphological variation in the midshaft femur of early *Homo*. Results from the DFA, however, do not indicate that midshaft femoral cross-sectional properties in OH 62 are particularly aberrant from other early fossil *Homo* sp. Since results from a cluster analysis vary depending on the number of variables examined, it is possible that the inclusion of several cross-sectional properties falsely contributed to the distinctiveness of OH 62. The DFA extracted the most important variables discriminating among the groups, and in this analysis, OH 62 was not separated from other fossil *Homo* sp. Although it has been argued that preservation bias may be contributing to the distinctiveness of OH 62, it is important to note that the preservation of OH 34 is worse than in OH 62 (Haeusler and McHenry, 2004). However, OH 34 still fell with other fossil *Homo* samples. Thus, it is doubtful if preservation bias in OH 62 is contributing to its distinctiveness from other *Homo* femora. If OH 62 is to remain in the genus *Homo*, then the behavioral attributes of its members, at least in terms of locomotion, may need to be redefined to possibly include non-committed bipeds.

KNM-ER 1592 clustered with modern and fossil *Homo*, and was most similar to KNM-ER 1807, a possible member of the genus *Homo*, and KNM-ER 1472, a likely member of the genus *Homo*. This finding does not support functional morphological and biomechanical interpretations of paranthropine locomotor behavior suggesting a significant arboreal component in conjunction with a kinematically non-human-like form of terrestrial bipedalism (e.g. Robinson, 1972; McHenry, 1978; Grausz et al., 1988; Spoor et al., 1994; Aiello et al., 1999; Macchiarelli et al., 1999; Ruff et al., 1999; Gebo and Schwartz, 2006). It is therefore possible that KNM-ER 1592 is not a representative of *Paranthropus*, at least as indicated by its midshaft femoral cross-sectional morphology. Certainly, comparisons with definitive paranthropine femora are needed to substantiate this claim.

KNM-ER 736 and KNM-ER 1807 have been allocated to both *Homo* and *Paranthropus* (Leakey et al., 1972; Day, 1976; Day et al., 1976; McHenry, 1991; Grine et al., 1995). Midshaft femoral cross-sectional morphology suggests that both femora cannot be excluded from the genus *Homo*. Since no definitive paranthropine midshaft femora were examined, it is not possible to exclude KNM-ER 736 and KNM-ER 1807 from *Paranthropus*, but given their similarity to modern and fossil *Homo*, it is also not possible to exclude them from the genus *Homo*. A summary of the relationship between cross-sectional morphology and taxonomy among the fossil hominin samples examined in this study is presented in Table 1.

Table 1. Summary of the relationship between cross-sectional morphology and taxonomy.

	Sample	**Genus**	**Taxonomic support based on cross-sectional morphology**
Proximal			
	KNM-ER 738	*Paranthropus*/*Homo*	uncertain, but cannot be excluded from *Paranthropus*
	KNM-ER 1500d	*Paranthropus*	yes
	SK 82	*Paranthropus*	yes
	SK 97	*Paranthropus*	yes
	KNM-ER 999a	*Homo*	yes
	KNM-ER 1481a	*Homo*	yes
Midshaft			
	KNM-ER 1592	*Paranthropus**	uncertain, but similar to *Homo*
	KNM-ER 736	*Paranthropus*/*Homo*	uncertain, but similar to *Homo*
	KNM-ER 1472	*Homo*	yes
	KNM-ER 1807	*Paranthropus*/*Homo*	uncertain, but similar to *Homo*
	OH 62	*Homo**	uncertain
	KNM-ER 1808	*H. erectus*	yes
	KNM-WT 15000	*H. erectus*	yes
	OH 34	*H. erectus*	yes

* Indicates uncertain genus.

Cross-sectional geometries are phenotypically plastic and are also influenced by non-mechanical factors such as genetics, pathology and age (Ruff, 2000; Lovejoy et al., 2002, 2003; Volkman et al., 2003). Moreover, the relationships among behavior, external loading and resultant cross-sectional geometries are not completely understood (Bertram and Swartz, 1991; Pearson and Lieberman, 2004; Lieberman et al., 2004). Despite these caveats and limitations, several studies have shown that long bones do indeed remodel to accommodate to mechanical loading during life (Jones et al., 1977; Ruff and Hayes, 1983; Ruff, 1987, 1994; Martin and Burr, 1989; Biewener et al., 1996; Sumner and Andriacchi, 1996; Frost et al., 1998; Shaw and Stock, 2009). Therefore, while cross-sectional morphology by itself should not be used for direct taxonomic identification, it can lend insight into taxonomy since locomotor behavior is an important aspect of the adaptive zone of a genus. The findings from this study suggest that femoral cross-sectional morphology in fossil hominins generally support current taxonomic identities at least to the genus-level. The broader implication of these results is that biomechanical analyses may aid in the taxonomic identification of isolated femora, which abound in the hominin fossil record.

MECHANICAL LOADING PATTERNS IN MODERN HUMANS AND *PAN*

Modern human and *Pan* referential models are often used to infer locomotor behavior in fossil hominins. The former serves as the preeminent model for obligate terrestrial bipedalism, while the latter serves as a model for the possible ancestral condition since there is a close phylogenetic relationship between *Pan* and the lineage that led to modern humans (Rogers, 1993; D'Aoút et al., 2004; Crompton et al., 2008; Tocheri et al., 2008; Pontzer et al., 2009). Thus, modern humans and *Pan* represent the two extremes of the locomotor continuum of modern human ancestors.

Analyses of mechanical loading patterns in the proximal and midshaft femora of modern humans and *Pan* have revealed many important findings. The relative amount of cortical bone in modern human femora was greater than in *Pan* femora, and TA explained a significant amount of the variation in CA in modern humans, but not in *Pan*. These results indicate that there is not a linear relationship between TA and CA in *Pan* femora. The functional significance of the relative amount of cortical bone in a cross-section can be difficult to interpret because this property is related to different aspects of bone morphology and does not have an intrinsic biomechanical significance (Ruff et al., 1993; Ruff, 1994; Sládek et al., 2006). At the very least, however, the relative amount of cortical bone in the femoral diaphysis serves as a morphological trait to distinguish modern humans from *Pan*.

Modern human femora were shown to be structurally adapted for greater axial strength relative to average bending and torsional strength compared to *Pan* femora. The increase in CA relative to $J^{0.73}$ in modern humans reflects the actions of the abductor complex in the hip, which generates strong axial compression in the femoral neck, particularly during the single-support phase of human walking, that is subsequently transferred to the proximal femur and down the femoral diaphysis (Cristofolini et al., 1995; Aamodt et al., 1997; Duda et al., 1997). *Pan* femora are characterized by a decrease in axial strength relative to average bending and torsional strength. This loading pattern likely reflects the multi-oriented bending loads, and dynamic and propulsive movements associated with quadrupedal locomotion and arborealism (Ruff and Runestad, 1992; Demes et al., 2001; Kalmey and Lovejoy, 2002; Carlson, 2005; Marchi, 2007). This mechanical adaptation is also reflected in cortical bone distribution in the femoral neck of *Pan*, which is characterized by a uniformly thick circumferential cortical shell (Lovejoy et al., 2002). The advantage of this morphology is that the femoral neck is better able to withstand strong bending moments and resist torsional loads in multiple planes (Lovejoy et al., 2002).

Bending strength in the M-L plane was relatively greater than bending strength in the A-P plane in modern human proximal femora compared to *Pan*, while bending strength in the M-L plane was relatively greater than bending strength in the A-P plane in *Pan* midshaft femora compared to modern humans. The y-intercepts and slopes of the regression lines, however, were not significantly different between the two groups in the proximal and midshaft femur, which suggests that the relationship between M-L and A-P bending strengths are not significantly different between modern humans and *Pan*. Although *Pan* femora are typically characterized as being M-L buttressed (Carlson, 2002, 2005; Carlson et al., 2008), relative M-L to A-P bending strength in modern human femora, especially in the midshaft, is highly variable depending on activity levels and terrain (e.g. Ruff, 1987, 2005; Bridges, 1995; Stock and Pfeiffer, 2004; Marchi et al., 2006; Sládek et al., 2006; Sparacello and Marchi, 2008). Therefore, the results from this study should be interpreted cautiously given the nature of the modern human reference sample.

It is also possible that different mechanical demands and morphological complexes could potentially yield similarities in the relationship between M-L bending strength and A-P bending strength. For instance, M-L buttressing in the proximal femoral diaphysis is a widely recognized trait among modern humans and fossil hominins, which likely stems from a laterally displaced proximal femoral diaphysis (Lovejoy et al., 1973; Lovejoy, 1988; Ruff, 1995; Richmond and Jungers, 2008). A relatively long femoral neck and greater biacetabular breadth in modern humans and fossil hominins contribute to this lateral displacement of the femoral diaphysis. Greater M-L bending strength relative to A-P bending strength in the femoral diaphysis of *Pan* may be brought about by an increase in turning behaviors and directional changes during locomotion (Demes et al., 2006; Carlson et al., 2008). The results indicate that diaphyseal shape may be a poor indicator of locomotor behavior, and is probably not useful for identifying broad locomotor categories in the hominin fossil record. These findings support the claim by Lieberman et al. (2004) that the lack of a predictable relationship between bone function and diaphyseal shape complicates interpretations of shape, and possibly negates comparisons between species.

While diaphyseal shape, or the relationship between M-L bending strength relative to A-P bending strength, is not clearly distinct between modern humans and *Pan*, the relationship between axial strength relative to average bending and torsional strength, and the relative amount of cortical bone in the cross-section relative to total area, easily differentiate modern human femora from *Pan* femora.

LOCOMOTION AND LOCOMOTOR VARIABILITY IN FOSSIL HOMININS

Analyses of mechanical loading patterns in the proximal and midshaft femora of Plio-Pleistocene hominins have revealed several important findings regarding the nature of locomotion and the degree of locomotor variability in early hominin groups. As is the case with Plio-Pleistocene hominins in general, the relative amount of CA in the proximal and midshaft femoral sections was shown to be elevated in *Paranthropus* and fossil *Homo* compared to modern humans and *Pan*. It has been suggested that the relatively thicker femoral cortices in Plio-Pleistocene hominins may reflect a general increase in mechanical loading from greater musculature and activity levels compared to modern humans (Kennedy, 1983; Ruff et al., 1993; Trinkaus and Ruff, 1999; Ruff, 2005). This suggestion is supported by evidence that $J^{0.73}$ significantly contributes to variation in CA in the proximal and midshaft femur of modern humans. An increase in $J^{0.73}$ in fossil hominins compared to modern humans may also explain their increase in CA relative to modern humans. At the very least, an increase in CA relative to TA in the proximal and midshaft femur of Plio-Pleistocene hominins is a morphologically diagnostic trait that distinguishes them from modern humans and *Pan*.

Axial strength relative to average bending and torsional strength in the proximal femora of fossil *Homo* is commensurate with loading patterns indicative of modern human-like locomotion. *Paranthropus* shows the modern human-like pattern in greater CA relative to $J^{0.73}$ compared to *Pan*, but the *Pan*-like pattern in lower CA relative to $J^{0.73}$ compared to modern humans and fossil *Homo*. These results indicate a form of locomotion in *Paranthropus* that is not *Pan*-like, but instead kinematically more similar to, albeit distinct from, that in *Homo*, both modern and fossil. Axial strength relative to average bending and torsional strength in the midshaft femur of *Paranthropus*, fossil *Homo* sp. and *H. erectus* generally conform to modern human-like patterns rather than *Pan*-like patterns, albeit fossil hominin femora are stronger than modern human femora. The *Homo*-like loading pattern in KNM-ER 1592 suggests either a kinematically similar mode of locomotion between *Homo* and *Paranthropus*, or that KNM-ER 1592 is not representative of *Paranthropus*. A decrease in CA relative to $J^{0.73}$ in KNM-WT 15000 most likely reflects the overall decrease in CA because of his juvenile age. Growth patterns in CA in modern human children and adolescents follow body weight (Sumner and Andriacchi, 1996). Therefore, it is presumed that CA in KNM-WT 15000 is lower than expected given that he has not yet attained full adult size. Assuming modern human-like growth patterns in *H. erectus* (Tardieu, 1998; Clegg and Aiello, 1999; Smith, 2004; but see Smith, 1993; Thompson and Nelson, 2000; Graves et al., 2010), the low CA in KNM-WT 15000, which is likely a product of his age, may be contributing to the aberrant pattern in CA relative to $J^{0.73}$.

CA is slightly elevated relative to $J^{0.73}$ in OH 34 compared to *Pan*, but not nearly to the same degree as in KNM-ER 1592, KNM-ER 736, KNM-ER 1807, KNM-ER 1808 and KNM-ER 1472. It is possible that the apparently non-*Homo*-like loading pattern in OH 34 reflects taxonomic and/or preservation bias (Day and Molleson, 1976; Leakey, 1978; Ruff, 1995; Haeusler and McHenry, 2004). It is unclear if taxonomic and/or preservation bias in OH 62 contributes to *Pan*-like patterns in CA relative to $J^{0.73}$. Although Johanson et al. (1987:208) observed “slight exfoliation of the OH 62 femur”, Haeusler and McHenry (2004:438) described the external appearance of it as “rugged” with “the loss of surface detail” undoubtedly resulting from heavy abrasion. However, it should be noted that abrasion in OH 34 is more severe than in OH 62 (Haeusler and McHenry, 2004), yet they show similar relative CA values. This suggests that the pattern in OH 62 is not reflective of error in diaphyseal reconstruction due to poor preservation. Instead, the results indicate a mode of locomotion in OH 62 that is mechanically different from that in *Homo*. If the taxonomic allocation of OH 62 is correct, these results suggest a moderate degree of locomotor variability in the early *Homo* lineage. It is also possible that the current taxonomic allocation of OH 62 to the genus *Homo* is incorrect, which would explain its non-*Homo*-like loading patterns.

Most Plio-Pleistocene hominins examined here show an increase in M-L bending strength relative to A-P bending strength in the proximal femur compared to *Pan*, and are similar to modern humans in this regard. These results support previous findings characterizing proximal fossil hominin femora as medio-laterally expanded (e.g. Lovejoy and Heipel, 1972; Ruff, 1995; Grine et al., 1995; Ruff et al., 1999; Richmond and Jungers, 2008; Holliday et al., 2010). Fossil hominins generally show greater bending strength in the M-L plane relative to the A-P plane in the midshaft femur compared to modern humans. However, given the lack of significant differences in M-L relative to A-

P bending strength in modern humans compared to *Pan*, it is difficult to interpret the significance of diaphyseal shape among fossil hominins. Further investigation of the relationship between M-L and A-P bending strength is warranted to better understand the link between mechanical loading and diaphyseal shape.

The results from this study cautiously support the use of cross-sectional morphology as a tool to infer the taxonomic identity of isolated fossil femora, assuming that members of the same genus engage in similar locomotor behavior. Mechanical loading patterns in the proximal and midshaft femora of fossil *Homo,* except OH 62, are similar to patterns in modern humans and distinct from patterns in *Pan*. Proximal femoral mechanical loading patterns in *Paranthropus* are more similar to patterns in modern humans than to patterns in *Pan*, which supports the view that locomotor behavior in *Paranthropus* included a mode of bipedalism similar to, albeit distinct from, modern human-like bipedalism. Mechanical loading patterns in the midshaft femur of *Paranthropus*, as represented by KNM-ER 1592, suggest similar locomotor behavior between *Paranthropus* and *Homo*, or that KNM-ER 1592 is not a paranthropine. Finally, midshaft femoral cross-sectional properties and loading patterns in OH 62 suggest a different mode of locomotion in the species represented by OH 62 compared to modern and fossil *Homo*. This either indicates a wide degree of variation in locomotor behavior in the *Homo* lineage and that all individuals currently assigned to the genus *Homo* cannot be identified as committed bipeds, or, as suggested by Wood and colleagues, that OH 62 is not a member of the genus *Homo* (Wood, 1993, 2000, 2005; Wood and Collard 1999a, b).

FUTURE DIRECTIONS

Future research will include: (1) an examination of ranges of variation in cross-sectional properties and loading pattens in *Ardipithecus* and *Australopithecus* to further survey locomotor behavioral variability among pre-*H. erectus* hominins; (2) an analysis of bone structure in Plio-Pleistocene hominins through the use of other methodologies (e.g. finite element analysis) to gain a higher-resolution of bone functional adaptation; (3)

further investigation of the relationship between mechanical loading and cross-sectional geometry to better understand the link between function and morphology; (4) an examination of the relationship between cross-sectional morphology in the femoral neck and cross-sectional morphology in the proximal femur; and (5) an examination of the role of the environment in influencing locomotor behavior.

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APPENDICES

Appendix A — Raw cross-sectional properties in *Pan* proximal femora (right)

Specimen	Species	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
LACM 30545	Ptt	F	295	451.60	336.00	74.40	1950.02	1024.90	1378.34	1467.41	853.83
LACM 30546	Ptt	M	298	489.73	286.03	58.40	1955.27	1071.46	1338.27	1391.84	950.43
LACM 30548	Ptt	F	299	450.17	266.46	59.19	1698.37	1088.74	1020.77	1111.28	933.78
MCZ 15312	Ptt	M	273	414.50	273.14	65.90	1549.46	833.85	1098.65	1094.00	763.46
MCZ 19187	Ptt	M	285	410.09	294.73	71.87	1541.52	782.23	1000.05	1095.88	750.96
MCZ 20041	Ptt	M	292	446.23	291.28	65.28	1705.43	948.16	1168.70	1215.74	826.97
MCZ 23163	Ptt	M	312	438.04	324.50	74.08	1709.89	906.20	1179.26	1205.59	844.42
MCZ 23164	Ptt	F	312	409.27	257.03	62.80	1486.57	903.94	1010.48	1030.48	754.11
MCZ 23167	Ptt	F	293	363.18	223.62	61.57	1215.39	692.38	799.16	807.05	655.58
MCZ 25950	Ptt	M	302	613.33	264.70	43.16	2209.39	1277.43	1263.01	1397.65	1265.23
MCZ 26847	Ptt	F	306	567.01	264.33	46.62	2077.26	1159.20	1342.48	1415.94	1080.49
MCZ 26849	Ptt	F	281	442.48	252.00	56.95	1630.68	830.69	1133.72	1218.63	724.32
MCZ 48686	Ptt	M	320	545.03	322.29	59.13	2138.12	1210.18	1236.41	1391.25	1183.81
LACM 51240	Pts	F	272	382.35	257.58	67.37	1437.90	782.96	937.25	1035.75	684.81
LACM 51239	Pts	M	286	406.96	264.89	65.09	1556.71	707.62	1070.78	1108.33	756.46
BOM 6244	Ptv	M	317	395.05	286.74	72.58	1537.96	804.54	1074.62	132.14	163.24
MCZ 38018	Pp	M	288	378.41	282.26	74.59	1439.33	884.75	955.11	938.27	795.10
MCZ 38019	Pp	F	290	364.83	255.72	70.09	1343.53	843.32	888.59	860.40	758.45
MCZ 38020	Pp	M	304	445.81	337.54	75.71	1870.30	1060.26	1323.37	1328.16	912.81

Appendix B — Raw cross-sectional properties in *Pan* midshaft femora (right)

Specimen	Species	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
LACM 30545	Ptt	F	295	420.70	307.33	73.05	1673.06	993.44	1131.28	1103.57	910.39
LACM 30546	Ptt	M	298	501.59	322.14	64.23	2064.65	1255.40	1460.85	1362.33	1122.98
LACM 30548	Ptt	F	299	474.11	286.86	60.51	1883.47	1077.89	1351.78	1296.38	965.77
MCZ 15312	Ptt	M	273	397.50	262.56	66.05	1500.00	830.95	1011.24	1055.69	742.96
MCZ 19187	Ptt	M	285	433.42	291.81	67.33	1658.81	884.21	1199.06	1206.83	776.03
MCZ 20041	Ptt	M	292	435.96	272.87	62.59	1592.28	910.37	1040.20	1062.82	852.91
MCZ 23163	Ptt	M	312	428.93	311.18	72.55	1612.85	990.57	1020.90	1034.37	908.92
MCZ 23164	Ptt	F	312	376.22	227.39	60.44	1252.68	713.74	809.49	797.38	712.22
MCZ 23167	Ptt	F	293	376.98	233.72	62.00	1296.80	729.05	858.61	866.74	693.38
MCZ 25950	Ptt	M	302	595.61	263.98	44.32	2178.13	1220.51	1342.68	1479.18	1139.04
MCZ 26847	Ptt	F	306	548.34	257.36	46.93	1968.48	1175.69	1219.92	1240.60	1132.10
MCZ 26849	Ptt	F	281	473.63	261.50	55.21	1721.92	976.01	1158.41	1151.15	920.39
MCZ 48686	Ptt	M	320	566.88	332.42	58.64	2306.30	1286.79	1590.12	1567.17	1205.03
LACM 51240	Pts	F	272	416.72	275.88	66.20	1590.21	959.47	997.62	1034.07	881.16
LACM 51239	Pts	M	286	387.05	269.29	69.58	1457.27	832.08	974.42	984.24	768.01
BOM 6244	Ptv	M	317	395.73	230.82	58.33	1402.23	798.45	926.59	940.78	745.87
MCZ 38018	Pp	M	288	383.11	287.68	75.09	1489.89	906.15	921.44	1009.33	781.84
MCZ 38019	Pp	F	290	362.76	251.32	69.28	1321.47	839.46	815.30	880.40	709.64
MCZ 38020	Pp	M	304	460.18	335.55	72.92	1910.20	1079.48	1305.59	1304.48	990.93

Appendix C — Raw cross-sectional properties in *Pan* humeri (right)

Specimen	Species	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
LACM 30545	Ptt	F	292	366.68	270.64	73.81	1386.65	851.68	899.53	965.57	698.53
LACM 30546	Ptt	M	302	412.25	211.37	51.27	1414.19	812.58	840.19	871.09	834.00
LACM 30547	Ptt	F	283	325.06	263.46	81.05	1175.10	750.55	750.86	358.24	334.68
LACM 30548	Ptt	F	298	365.15	239.57	65.61	1302.75	831.15	813.11	818.76	751.58
MCZ 15312	Ptt	M	259	340.73	189.79	55.70	1081.60	635.58	668.68	754.71	543.11
MCZ 19187	Ptt	M	293	358.71	257.89	71.89	1251.02	632.67	787.12	867.24	634.57
MCZ 20041	Ptt	M	297	406.76	255.52	62.82	1428.08	908.51	904.41	916.61	804.02
MCZ 23163	Ptt	M	322	358.91	266.90	74.37	1265.97	730.58	852.40	819.68	705.24
MCZ 23164	Ptt	F	308	335.30	207.30	61.82	1074.72	678.25	688.05	673.01	622.52
MCZ 23167	Ptt	F	290	312.95	170.19	54.38	939.57	494.85	552.98	606.97	524.87
MCZ 25950	Ptt	M	319	444.44	222.59	50.08	1493.95	947.42	880.38	923.86	877.33
MCZ 26847	Ptt	F	306	416.24	206.56	49.63	1375.85	818.51	825.90	880.31	777.51
MCZ 26849	Ptt	F	275	375.68	154.54	41.13	1053.87	510.82	604.79	697.35	571.09
MCZ 48686	Ptt	M	317	462.45	278.93	60.32	1712.35	1064.11	1087.73	1056.06	1008.51
LACM 51240	Pts	F	245	381.14	249.62	65.49	1396.82	798.86	938.45	926.63	754.40
LACM 51239	Pts	M	285	299.45	194.28	64.88	993.95	536.62	648.43	689.31	503.86
BOM 6244	Ptv	M	310	354.31	198.35	55.98	1158.27	565.62	751.41	795.06	596.34
MCZ 38018	Pp	M	278	295.26	214.78	72.74	988.85	616.86	616.54	625.71	566.11
MCZ 38019	Pp	F	273	266.55	202.75	76.07	864.64	540.54	565.93	535.86	506.58
MCZ 38020	Pp	M	297	350.46	241.89	69.02	1245.75	825.78	814.81	771.24	730.69

Appendix D — Raw cross-sectional properties in *Pan* humeri (left)

Specimen	Species	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
LACM 30545	Ptt	F	291	340.28	248.84	73.13	1231.66	616.71	839.58	838.08	642.27
LACM 30546	Ptt	M	315	396.29	228.16	57.57	1411.63	803.65	837.37	898.49	802.67
LACM 30548	Ptt	F	300	375.54	252.04	67.11	1374.45	918.73	868.47	904.42	750.24
MCZ 15312	Ptt	M	271	345.88	214.50	62.02	1194.45	706.61	749.62	797.03	640.08
MCZ 19187	Ptt	M	291	344.47	242.03	70.26	1159.90	644.72	746.18	777.18	618.08
MCZ 20041	Ptt	M	298	396.22	240.38	60.67	1359.03	810.93	795.23	910.19	724.63
MCZ 23163	Ptt	M	320	347.02	264.26	76.15	1218.45	763.47	731.97	760.88	707.98
MCZ 23164	Ptt	F	309	346.44	204.27	58.96	1099.61	640.50	661.32	722.18	601.72
MCZ 23167	Ptt	F	290	283.57	162.92	57.45	863.87	505.13	526.80	546.01	495.19
MCZ 25950	Ptt	M	307	453.99	192.29	42.36	1394.20	808.16	773.89	883.28	797.04
MCZ 26849	Ptt	F	276	397.97	207.26	52.08	1294.61	800.09	776.76	814.58	745.91
MCZ 48686	Ptt	M	315	488.19	275.63	56.46	1839.47	1071.28	1191.83	1223.48	990.00
LACM 51240	Pts	F	271	398.25	266.10	66.82	1488.15	837.22	999.46	1002.53	787.10
LACM 51239	Pts	M	287	308.80	210.01	68.01	1053.61	563.61	669.04	736.55	527.50
BOM 6244	Ptv	M	312	347.47	212.74	61.23	1213.35	642.69	760.48	815.54	643.79
MCZ 38018	Pp	M	277	279.46	197.41	70.64	910.63	582.49	566.71	583.76	513.45
MCZ 38020	Pp	M	300	332.30	248.04	74.64	1181.96	784.61	744.67	757.72	666.42

Appendix E — Raw cross-sectional properties in modern human proximal femora (right)

Specimen	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
Stirrup Court 3	F	444	509.39	373.59	73.34	1623.09	1193.77	1600.28	1646.76	1053.26
Stirrup Court 10	M	425	572.78	411.28	71.80	1843.81	1531.95	1960.40	1875.23	1324.13
Stirrup Court 14	M	478	776.52	526.37	67.79	2803.19	2253.78	2972.17	2865.59	2003.49
Stirrup Court 17	M	487	569.15	397.17	69.78	1751.00	1531.99	1859.65	1758.36	1356.75
Stirrup Court 20	M	476	734.24	541.91	73.81	2531.56	2303.80	2729.61	2532.02	2056.78
Odd Fellows 1	M	465	714.88	512.09	71.63	2723.50	1978.67	2743.33	2734.32	1719.40
Odd Fellows 2	M	407	555.72	375.45	67.56	1825.81	1377.00	1879.52	1829.31	1176.22
Odd Fellows 3	M	448	627.14	395.79	63.11	2023.95	1622.58	1996.12	2049.26	1445.04
Odd Fellows 4	M	449	706.69	513.18	72.62	2465.01	2146.87	2641.81	2476.91	1863.81
Odd Fellows 6	M	427	623.32	500.33	80.27	2221.68	1571.51	2181.22	2268.54	1393.79
Odd Fellows 7	M	491	761.35	450.06	59.11	2576.37	1924.07	2767.82	2662.10	1784.67
Odd Fellows 8	M	411	653.71	475.99	72.81	2190.50	1948.54	2193.87	2193.02	1669.35
Odd Fellows 9	M	440[a]	624.17	469.59	75.23	2186.91	1648.28	2200.31	2219.58	1411.80
Odd Fellows 10	M	438	736.05	369.73	50.23	2408.54	1765.56	2308.14	2416.27	1587.23
Odd Fellows 11	M	449	531.96	340.87	64.08	1627.92	1256.58	1693.14	1627.89	1122.11
Odd Fellows 12	M	463	515.54	375.99	72.93	1659.72	1242.92	1729.11	1678.42	1103.97
Odd Fellows 13	F	408	510.70	389.02	76.17	1399.86	1392.52	1563.76	1474.21	1227.41
Odd Fellows 14	M	472	729.47	512.44	70.25	2434.46	2287.23	2671.17	2452.62	2023.21
Odd Fellows 17	F	441	727.82	446.83	61.39	2466.92	1994.58	2548.42	2496.17	1783.11
Odd Fellows 19b	M?	482	617.87	399.55	64.66	1815.76	1719.49	1962.96	1841.22	1557.13
Odd Fellows 20	M	445	430.53	347.86	80.80	1223.20	1066.42	1286.81	1275.00	893.00

Appendix E — continued

Specimen	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
Birkette	F	423	470.25	349.97	74.42	1575.20	1044.26	1560.67	1586.90	898.84
Breslau 1	M	480	745.93	533.93	71.58	2741.39	2330.22	2930.77	2759.54	1946.03
Breslau 2	F	380	404.36	341.22	84.39	1375.19	861.84	1358.05	1382.78	715.31
Downham Nursery	M?	516	732.73	522.87	71.36	2663.13	2119.10	2552.22	2773.56	1835.82
Orangeman's Lodge	M?	489	688.46	457.14	66.40	2451.11	1869.80	2501.55	2510.55	1607.46
H. Helmuth donation	M?	466	614.14	458.09	74.59	2215.93	1625.01	2234.13	2241.59	1369.91
N. Halbert donation	M?	456	741.06	589.37	79.53	3203.72	2069.47	3241.57	3218.60	1736.98
Van Oordt 10	M	473	621.97	420.54	67.61	2090.80	1591.14	2182.86	2091.13	1443.51
Peterborough Jail 2	M	463	734.89	505.75	68.82	2517.03	2178.88	2756.88	2520.98	1958.88
Peterborough Jail 3	M	480	603.56	412.61	68.36	1885.91	1673.12	1892.79	1886.38	1481.68

Appendix F — Raw cross-sectional properties in modern human midshaft femora (right)

Specimen	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
Stirrup Court 3	F	444	471.38	269.68	57.21	1149.69	1061.91	1135.62	1197.66	1037.81
Stirrup Court 10	M	425	504.16	406.09	80.55	1439.05	1312.10	1497.50	1439.16	1293.91
Stirrup Court 14	M	478	699.58	483.79	69.15	2112.39	1911.97	2289.82	2242.49	1943.10
Stirrup Court 17	M	487	464.10	330.12	71.13	1185.32	1112.27	1243.42	1278.62	1075.56
Stirrup Court 20	M	476	621.15	531.84	85.62	1888.52	1933.47	2047.78	2017.84	1731.27
Odd Fellows 1	M	465	637.60	486.04	76.23	1818.32	1976.10	1945.59	1993.43	1802.95
Odd Fellows 2	M	407	473.87	358.50	75.65	1134.16	1288.05	1224.86	1549.53	1005.26
Odd Fellows 3	M	448	622.20	421.86	67.80	1716.36	1834.74	1698.52	1795.24	1699.94
Odd Fellows 4	M	449	578.41	403.17	69.70	1848.08	1424.25	1923.18	1849.04	1355.30
Odd Fellows 6	M	427	529.89	386.42	72.92	1515.75	1323.27	1584.31	1544.59	1352.33
Odd Fellows 7	M	491	611.53	436.00	71.30	1804.21	1747.15	1913.02	1807.16	1655.99
Odd Fellows 8	M	411	596.86	479.90	80.40	1715.72	1809.21	1794.39	1778.16	1712.51
Odd Fellows 9	M	440[a]	535.75	420.06	78.41	1557.45	1474.13	1601.97	1635.82	1288.35
Odd Fellows 10	M	438	610.05	380.86	62.43	1738.16	1535.43	1765.32	1747.54	1635.16
Odd Fellows 11	M	449	569.48	381.39	66.97	1483.57	1450.30	1576.90	1530.11	1328.31
Odd Fellows 12	M	463	545.80	327.73	60.05	1407.87	1385.78	1475.42	1474.86	1295.97
Odd Fellows 13	F	408	508.30	366.77	72.15	1116.90	1478.07	1147.57	1589.34	1112.00
Odd Fellows 14	M	472	698.74	404.70	57.92	2146.27	1816.49	2136.99	2147.21	1768.64
Odd Fellows 17	F	441	666.03	452.52	67.94	2027.55	1923.10	2191.41	2031.71	1864.02
Odd Fellows 19b	M?	482	605.74	440.49	72.72	1401.40	2002.54	1544.03	2214.35	1401.00
Odd Fellows 20	M	445	397.69	276.11	69.43	875.58	957.29	928.21	996.13	844.74

Appendix F — continued

Specimen	Sex	Max. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
Birkette	F	423	446.80	313.82	70.24	1111.88	1107.38	1142.39	1127.42	1074.81
Breslau 1	M	480	706.24	534.00	75.61	2348.97	2123.14	2522.38	2358.81	2027.00
Breslau 2	F	380	374.39	322.37	86.11	949.52	907.95	1018.98	950.39	834.65
Downham Nursery	M?	516	763.35	509.77	66.78	2083.15	2529.88	2097.35	2659.29	2045.85
Orangeman's Lodge	M?	489	660.34	509.94	77.22	2043.25	2065.81	2189.83	2043.61	1924.47
H. Helmuth donation	M?	466	654.75	456.46	69.72	1812.66	2065.11	1957.65	2113.69	1688.15
N. Halbert donation	M?	456	652.03	524.60	80.46	2125.55	1941.86	2321.01	2128.21	1835.35
Van Oordt 10	M	473	524.02	421.39	80.41	1299.75	1604.07	1439.43	1634.61	1259.68
Peterborough Jail 2	M	463	700.65	442.14	63.10	2102.80	2077.71	2182.44	2118.47	1946.18
Peterborough Jail 3	M	480	631.46	382.76	60.61	1769.98	1679.94	1860.55	1815.96	1626.63

Appendix G — Raw cross-sectional properties in Plio-Pleistocene hominin proximal femora

Specimen	Species	Est. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
KNM-ER 738	*Paranthropus*/ *Homo*?	335	461.80	419.56	90.85	2018.90	1214.13	1427.68	1324.57	1106.20
KNM-ER 815	*Paranthropus*?	NA	387.10	372.39	96.20	1646.66	859.01	1185.94	1236.47	724.25
KNM-ER 999a	*Homo* sp. indet./ *H. erectus*?/ late archaic *H. sapiens*?	482	912.51	783.83	85.90	5414.52	3654.62	3592.67	3499.65	3022.77
KNM-ER 1481a	*Homo* sp./ *H.* (cf. *erectus*?)/ *H. habilis*/ *H. rudolfensis*	369	456.74	417.91	91.50	1973.60	1289.40	1316.75	1216.47	1163.09
KNM-ER 1500d	*P. boisei*	310	421.05	343.62	81.61	1808.10	961.74	1369.66	1341.61	814.73
SK 82[a]	*P. robustus*	337	577.00	490.00	84.92	2806.00	1461.15	1911.40	1943.93	1424.99
SK 97[a]	*P. robustus*	367	593.00	457.00	77.07	2887.00	1440.93	2022.61	2056.16	1402.59
OH 20	*P. boisei*	NA	562.90	452.66	80.42	2704.85	1645.80	1883.32	1948.30	1288.31

[a] Data from Ruff et al. (1999). Z_x, Z_y, Z_{max} and Z_{min} derived from second moments of area to the power of 0.73.
All estimated femur length estimates from McHenry (1991) except KNM-ER 999a (Geissmann, 1986).
Z_{max} and Z_{min} not used in the analysis.
Area in mm^2. Section moduli in mm^3.

Appendix H — Raw cross-sectional properties in Plio-Pleistocene hominin midshaft femora

Specimen	Species	Est. length	TA	CA	%CA	$J^{0.73}$	Z_x	Z_y	Z_{max}	Z_{min}
KNM-ER 736	*P.* (cf. *boisei)*/ *Homo*/ *H. erectus*?	482	1032.63	681.68	66.01	6028.98	3806.69	3648.29	3761.40	3506.75
KNM-ER 1472	*Homo* sp.	401	457.94	358.71	78.33	1949.04	1242.39	1212.13	1273.45	1073.57
KNM-ER 1592	*Paranthropus*?	470	714.96	658.38	92.09	4533.20	3028.03	3388.81	2944.27	2515.66
KNM-ER 1807	*H.* (cf. *erectus*)?/ *P. boisei*?	420	652.92	549.08	84.10	3345.36	1961.69	2325.51	2163.41	1866.39
KNM-ER 1808[a]	*H. erectus*	485	551.00	478.00	86.75	3433.00	1542.00	1879.00	NA	NA
KNM-WT 15000[a]	*H. erectus*	432	402.00	262.00	65.17	1900.00	922.00	978.00	NA	NA
OH 34	*Homo* sp. indet./ *H. erectus*?	432	273.74	216.69	79.16	944.38	558.32	568.74	659.38	473.73
OH 62[b]	*H. habilis*	280	264.90	220.30	83.16	1154.00	566.00	588.00	NA	NA

[a] Data from Ruff (2008).

[b] Data from Ruff (2009).

All estimated femur length estimates from McHenry (1991) except KNM-WT 15000 (Ruff and Walker, 1993) and OH 62 (Richmond et al., 2002).

Z_{max} and Z_{min} not used in the analysis.

Area in mm^2. Section moduli in mm^3.

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