The Pennsylvania State University

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INFERENCES CONCERNING BIPEDAL LOCOMOTION FROM THE
INTERNAL STRUCTURE OF THE BAR 1002’00 AND BAR 1003’00
FEMORAL FRAGMENTS

A Dissertation in
Kinesiology

by

Adam J. Kuperavage

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The dissertation of Adam J. Kuperavage was reviewed and approved* by the following:

Robert B. Eckhardt  
Professor of Developmental Genetics and Evolutionary Morphology  
Dissertation Advisor  
Co-Chair of Committee

John H. Challis  
Professor of Kinesiology  
Graduate Program Director  
Co-Chair of Committee

Stephen J. Piazza  
Associate Professor of Kinesiology

H. Joseph Sommer III  
Professor of Mechanical Engineering

*Signatures are on file in the Graduate School
ABSTRACT

The fossil evidence pertinent to the reconstructing the origins of human bipedal locomotion generally is sparse and fragmentary. Prior to four million years ago the record is nearly nonexistent. Among the very limited earlier remains are those from several sites in the Tugen Hills of Kenya, dated to approximately six million years ago. These remains have been assigned by their discoverers to the taxon *Orrorin tugenensis*.

The hypodigm of *Orrorin tugenensis* includes two partial proximal femora, specimens BAR 1002’00 and BAR 1003’00. The external and internal morphological features of these specimens have been described multiple times by their discoverers and others over the last eight years. Studies of the internal properties of these specimens are extended here. These additional studies include measurement of the geometric cross-sectional properties in the femoral diaphyses of BAR 1002’00 and BAR 1003’00, and comparison of these data with those of several samples of earlier hominids and extant humans; measurement of the cortical bone distributions in the femoral neck using moment coefficients of skewness, and comparison of these to samples of chimpanzees and extant humans; and measurement of the calcar femorale in BAR 1003’00, with comparisons to chimpanzee and human specimens.

It was found that total cross-sectional area is markedly smaller for BAR 1002’00 and BAR 1003’00 than for either early or extant hominid proximal femora. The percent cortical areas of the two Kenyan fossil femora are comparable to other fossil hominids. With regard to moment coefficients of skewness, BAR 1002’00 exhibits cortical bone
distributions more similar to chimpanzees than to humans. The calcar femorale was found to be present in chimpanzees as well as in humans. BAR 1003’00 appears to have a calcar femorale more similar to that of extant humans than to chimpanzees. All of these findings, taken together, provide evidence bearing on the status of *Orrorin tugenensis* as a basal hominid.
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CHAPTER 1
INTRODUCTION

1.1 FORM AND FUNCTION IN HOMINID FEMORA

The modern human skeleton is the cumulative result of several million years of ongoing evolution since the separation of our ancestors into an independent lineage. During life bones are extraordinarily adaptive in responding to mechanical requirements, whether through changes in geometry or by the addition of new material. As part of this dynamic system, bone cells may respond to a variety of possible mechanical stimuli, such as strain energy, rate, duration, frequency, peak strain, or minimal strain, although the exact stimuli and regulatory scheme remain unknown.

Many studies have demonstrated the plasticity and sensitivity of long bone diaphyses to applied mechanical loadings (King et al., 1969; Ruff et al., 1984; Trinkaus et al., 1994). It follows that the preserved bone distribution of skeletal or fossil remains should reflect, at least partially, the mechanical loadings imposed during life. This assumption allows us to examine patterns of change in long-bone geometry throughout the human lineage and, therefore, to examine patterns of change in the evolution of human locomotor behavior. The study of bone geometric cross-sectional properties in physical anthropology dates back to the 1970s, when Lovejoy et al. (1976) showed that the principles of structural analysis could be applied to the study of long bone strength.
Significant changes in the long-bone morphology occurred to members of the genus *Homo* throughout the Pleistocene. Over this period, both mid-shaft femoral torsional and compressive strength exhibited significant declines (Ruff, 2006). The most parsimonious explanation for the increasing gracility of the human skeleton is a decline in mechanical loads it endured over that time. Unfortunately, the amount of fossilized postcranial material in which the internal structure is discernible is scant, particularly at the beginning of the human lineage. However, a fortuitous find that has recently become available may allow us to examine the phylogenetic questions fundamental to understanding human origins through functional morphology.

### 1.2 BACKGROUND AND PURPOSE

Over the last half century, dates for the first appearance of a human lineage have been posited from as early as 14-15 million years ago to as recent as 2-3 million years ago (Eckhardt, 2000). In 2000, Pickford and Senut discovered several fossils which they designated as belonging to the taxon *Orrorin tugenensis* (Senut et al., 2001). Dated at 6 million years, the *Orrorin* material possesses several anatomical characteristics indicative of upright posture. The specimen BAR 1002’00 is a partially preserved left femur with an intact head, femoral neck and the proximal two thirds of the shaft. In comparison, BAR 1003’00 is a partially preserved diaphysis with the distal portion of the femoral neck and the proximal one-third of the shaft. Analyses of the external anatomy in the form of both traditional anthropological descriptions (Pickford et al., 2002, Senut et al., 2001) and multivariate analysis (Richmond and Jungers, 2008), support the conclusion
that *Orrorin* was bipedal, even though the incomplete nature of both of these fossils does not allow for a definitive determination of the primary locomotor behavior. Therefore further insight into its locomotor behavior must be gained by also examining the internal anatomy.

The internal structures of BAR 1002’00 and BAR 1003’00 are discernible through computerized tomography (CT), a very uncommon situation since the majority of fossilized post-cranial specimens are completely mineralized. The difference in cortical bone distribution at the neck-shaft junction between extant apes and later hominids is the result of dramatic muscle allocation shifts resulting from a change to upright posture (Lovejoy, et al., 2002). If the internal femoral structure of these femora could be found to more consistent with that of modern humans, this would add additional support to the conclusion that *Orrorin* was bipedal. CT scans at the neck-shaft junction of BAR 1002’00 reveal that the cortical bone that it is markedly thinner superiorly than inferiorly, differing from the approximately equal cortical thicknesses observed in extant African apes, approaching the condition in later hominids, thus providing strong evidence for bipedal locomotion (Galik, et al., 2004).

Despite the significance of this find, more studies are needed, since the analyses performed in Galik et al. (2004) were limited to superior/inferior thickness ratios along the femoral neck of BAR 1002’00. Geometric characteristics that take into account all of the cortical bone in a given cross-section, such as third moment of area, were not considered. In addition, the internal structures of the proximal diaphyses of both femora
are discernable. This provides a unique opportunity to measure the internal anatomical features of two 6 million year old femora pertinent to reconstructing the evolution of bipedal locomotion. These specimens antedate by approximately two million years any other specimen pertinent to direct studies of bipedal locomotion. In the following studies more extensive analyses of the internal structural characteristics of BAR 1002’00 and BAR1003’00 were performed.

BAR 1002’00 and BAR 1003’00 were scanned using computerized tomography (CT) at 1 millimeter increments down their lengths. In Amira 4.1 (Visage Imaging) software, three-dimensional reconstructions of BAR 1002’00 and BAR 1003’00 were generated. Based on these reconstructions, various internal anatomical structures were measured. In the first study cross-sectional geometric properties of the femoral diaphyses of BAR 1002’00 and BAR 1003’00 were compared with an extant human sample and two partial Australopithecine femurs. The second study reexamines the cortical bone distribution in the femoral neck of BAR 1002’00 using normalized third moment of area. The last study explores the significance of an internal anatomical feature of the proximal known as the calcar femorale and its significance in inferring bipedal locomotion.

1.3 SPECIFIC AIMS

The specific aims of this work are the following:
1. To measure the geometric cross-sectional properties in the femoral diaphysis of BAR 1002’00 and BAR 1003’00 and compare these values found in the background literature on extant humans and SK 82 and SK 97.

2. To measure cortical bone distribution in femoral necks of BAR 1002’00 and BAR 1003’00 using normalized third moment of area and to compare these to a sample of human and chimpanzee femora.

3. To measure the calcar femorale in human and chimpanzee samples in order to determine if functions as a diagnostic characteristic of bipedal locomotion.

From these internal anatomical features, I will draw inferences about the locomotor behavior of *Orrorin tugenensis* in particular, as a basis for understanding the origin of human bipedal locomotion.

1.4 OVERVIEW OF STUDIES

The first study (Chapter 3) examines the geometric cross-sectional properties, including second moment of area, of the femoral diaphyseal cross-sections of BAR 1002’00 and BAR 1003’00. Previous research (Galik et al., 2004), has shown that the cortical bone distribution within the femoral neck of BAR 1002’00 to by more like a human than ape. However, more mechanically relevant properties, including third moment of area, were not measured. Therefore the second study (Chapter 4) examines these mechanical properties in the femoral neck cross-sections of BAR 1002’00. CT images of the internal structure of BAR 1002’00 and BAR 1003’00 reveal a long vertical ridge of dense bone...
superior to the lesser trochanter, known as the calcar femorale. The presence of a well-developed calcar femorale has been taken as an indicator of bipedal locomotion (White, 1984), even though no systematic attempt to measure this feature has been made. The third study (Chapter 5) will test this hypothesis by measuring the calcar femorale in a human and chimpanzee sample.

1.5 OVERVIEW OF DISSERTATION

This dissertation is presented in six chapters. Chapter 2 reviews the relevant literature concerning *Orrorin tugenensis* the biomechanical implications of femoral diaphysis and neck shape, the relevant mechanical properties measured, and scanning and image processing techniques. The three studies are contained in chapters 3, 4 and 5, and a general discussion of the findings from these studies is presented in chapter 6.

1.6 REFERENCES


CHAPTER 2
LITERATURE REVIEW

2.1 INTRODUCTION

This chapter reviews the literature on the discovery and significance of the fossilized specimens BAR 1002’00 and BAR 1003’00 assigned to the taxon *Orrorin tugenensis*, the use of the geometric cross-sectional shape analysis performed on the femoral diaphyses of these specimens (including the rationale and limitations of these analyses), the mechanical significance of the differing cortical bone distributions in the femoral necks of humans and apes, the history of the study of the calcar femorale and the methods of CT scanning and image processing.

2.2 OGORIN TUGENENSIS AND THE DAWN OF THE HUMAN LINEAGE

Fossil and molecular evidence are converging on a consensus that the humans diverged from chimpanzees between ~6 and 8 Ma (Begun, 2004; Eckhardt, 2000). Consequently the *Orrorin tugenensis* fossils are believed to represent some of the earliest known hominids that are securely dated biostratigraphically, geologically, radiometrically and paleomagnetically to the Late Miocene, approximately 6 million years ago (Ma) (Senut et al., 2001; Sawada et al., 2002). Samples are derived from four localities in the Lukeino Formation (Aragai, Cheboit, Kapcheberek and Kapsomin), along the eastern approach to the Tugen Hills in the Baringo District, Kenya. The original twelve fossils representing
at least five individuals have been discovered there (a list and description of these fossils is given in Table 2.1).

Table 2.1. Hypodigm of Orrorin tugenensis. Source: Senut et al. (2000).

<table>
<thead>
<tr>
<th>Catalogue No.</th>
<th>Locality</th>
<th>Specimen</th>
<th>Collector</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>KNM LU 335</td>
<td>Cheboit</td>
<td>lower molar</td>
<td>Martin Pickford</td>
<td>1974</td>
</tr>
<tr>
<td>BAR 349'00</td>
<td>Kapcheberek</td>
<td>manual phalanx</td>
<td>Evalyne Kiptalam</td>
<td>13-Oct-00</td>
</tr>
<tr>
<td>BAR 1000'00</td>
<td>Kapsomin</td>
<td>2 mandible fragments</td>
<td>Kiptalam Cheboi</td>
<td>25-Oct-00</td>
</tr>
<tr>
<td>BAR 1002'00</td>
<td>Kapsomin</td>
<td>left femur</td>
<td>Martin Pickford</td>
<td>4-Nov-00</td>
</tr>
<tr>
<td>BAR 1004'00</td>
<td>Kapsomin</td>
<td>right humeral shaft</td>
<td>Brigitte Senut</td>
<td>5-Nov-00</td>
</tr>
<tr>
<td>BAR 1003'00</td>
<td>Kapsomin</td>
<td>proximal left femur</td>
<td>Dominique Gommery</td>
<td>5-Nov-00</td>
</tr>
<tr>
<td>BAR 1001'00</td>
<td>Kapsomin</td>
<td>upper central incisor</td>
<td>Samuel Chetalam</td>
<td>10-Nov-00</td>
</tr>
<tr>
<td>BAR 1215'00</td>
<td>Aragai</td>
<td>proximal right femur</td>
<td>Martin Pickford</td>
<td>11-Nov-00</td>
</tr>
<tr>
<td>BAR 1390'00</td>
<td>Kapsomin</td>
<td>lower fourth premolar</td>
<td>Samuel Chetalam</td>
<td>13-Nov-00</td>
</tr>
<tr>
<td>BAR 1425'00</td>
<td>Kapsomin</td>
<td>upper right canine</td>
<td>Kiptalam Cheboi</td>
<td>16-Nov-00</td>
</tr>
<tr>
<td>BAR 1426'00</td>
<td>Kapsomin</td>
<td>upper left third molar</td>
<td>Evalyne Kiptalam</td>
<td>17-Nov-00</td>
</tr>
<tr>
<td>BAR 1900'00</td>
<td>Kapsomin</td>
<td>upper right third molar</td>
<td>Joseph Chebet</td>
<td>23-Nov-00</td>
</tr>
</tbody>
</table>

The Tugen Hills material is temporally intermediate between two other finds that have yielded the potential earliest hominids. The oldest are the partial cranium (the “Chad cranium”) and fragmentary lower jaws (*Sahelanthropus tchadensis*) from the Toros-Menalla locality (Brunet et al., 2002), estimated to be between 6 to 7 Ma from faunal correlations with East African sites (mainly Lothagam in Kenya). The youngest are fossil hominid teeth (*Ardipithecus kadabba*) from Ethiopia’s Middle Awash valley, which are dated more securely than those from Chad by biostratiographic, paleomagnetic, and radioisotopic techniques to a narrower range of 5.2 to 5.8 Ma (Haile-Selassie et al., 2004). The incomplete nature of these finds makes clear determination of their locomotor behavior difficult. The hominid status of both *Sahelanthropus tchadensis* and *Ardipithecus kadabba* has been criticized (Wolpoff et al. 2006, Begun, 2004, Rose, 1986). The Tugen Hills material is the only find among the three that includes femoral fragments, a part of the postcranium useful for determining primary locomotor behavior.
2.3 EXTERNAL DESCRIPTION OF *ORRORIN TUGENENSIS* FEMORA

Of the twenty fossils discovered at the Lukeino Formation, three are partial femora (Figure 2.1). BAR 1215’00 is a small fragment of a proximal right femur lacking the neck, head and greater trochanter. Only about 20 mm of the upper shaft is preserved below the base of the missing greater trochanter. This specimen is too incomplete for the analyses performed in the following studies and therefore is not considered further. BAR 1002’00, the most complete of the three femoral fragments, includes about 200 mm of shaft and an intact head that is connected to the shaft by an elongated neck. The third partial femur, BAR 1003’00, comprises approximately half of a proximal left femur, including the entire lesser trochanter but lacking both the greater trochanter and the femoral head. Complete anatomical descriptions of BAR 1002’00 and BAR 1003’00 can be found in Senut et al. (2001) and Pickford et al. (2002).
Figure 2.1: The three Orrorin tugenensis femurs. BAR 1002’00 (a), BAR 1003’00 (b), BAR 1215’00 (c). The left image in each panel represents the posterior view of each bone. Source: Nakatsukasa et al. (2007).

BAR 1002’00 has several external morphological attributes that are characteristic of Plio-Pleistocene through later hominids that distinguish them from African apes: a shallow trochantric fossa, an obturator externus groove, and a long femoral neck (Pickford et al., 2002; Begun, 2004). The presence of a large trochanteric fossa demarcates chimpanzee femora from those of most past and present hominids, although its developmental genesis and functional consequences are as yet incompletely understood. In chimpanzees, the central portion of the trochanteric fossa commonly includes a cavity that extends deeply into the diaphyseal shaft, approaching the medullary canal in some specimens (Lovejoy, et al., 2002). In BAR 1002’00 as well as the other two partial femora attributed to Orrorin tugenensis, in common with South African Plio-Pleistocene hominids, there is no
evidence of deep penetration by the trochanteric fossa into the shaft, in contrast with the usual morphology observed in the genus Pan. The obturator externus muscle is an adductor, flexor and external rotator of the thigh. One of primary functions of this muscle is to shorten the distance between the pelvis and the femur, consequently stabilizing the hip joint. The obturator externus groove, present in BAR 1002’00, is believed to result from bone remodeling to accommodate the direct, although passive, contact of the obturator externus tendon with the dorsal surface of the femoral neck at full extension of the femur. A sample of 155 African apes did not include a single example of an obturator externus groove (Lovejoy et al., 2002), while this feature is present in early fossilized remains attributed to early hominids, including OH 20 from Tanzania, SK 82 and SK 97 from south Africa, and AL-333-95, AL 288-1 and MAK-VP-1/1 from Ethiopia (Pickford et al., 2001, Lovejoy et al., 2002). Femoral neck length establishes the moment arm of the anterior gluteal muscles (gluteus minimus, gluteus medius, and tensor fasciae) in the single leg stance phase of bipedal locomotion. Therefore, a long femoral neck, which implies a reorientation of the line of action of the anterior gluteals, is strongly indicative of habitual hominid locomotion (Lovejoy et al., 2002). In BAR 1002’00, the femoral neck length exceeds that of Miocene hominoid fossils attributed to Afropithecus, Dryopithecus, Kenyapithecus, Nacholapithecus, Oreopithecus, and Ugandapithecus (Pickford and Senut, 2001). Among Plio-Pleistocene hominids, a long femoral neck recently has been reconstructed for the partial MAK-VP-1/1 femur (Lovejoy et al., 2002).
Intact hominoid femora allow for a simple determination of primary locomotor pattern. The distal portion of the human femur is characterized by rounded condyles that protrude posteriorly while ape distal femurs are characterized by somewhat square-shaped condyles that do not protrude posteriorly. This occurs because the ape femora have less range of motion at the knee in comparison to humans and their knees also do not enter the locked position during gait. The angle that the femur articulates with tibia also is a distinguishing characteristic in humans. The human femur angles inferiomedially in order to reduce lateral displacement of the pelvis during gait (Whittle, 1996), while apes, being quadrupeds, have no such anatomical adaptation. Unfortunately the distal portion is absent on all three fossilized femurs belonging to *Orrorin tugenensis*.

### 2.4 GEOMETRIC CROSS-SECTIONAL ANALYSIS OF LONG BONES

Bone is shaped by many factors throughout life. Genetic factors are especially important in early development (Murray, 1936). Non-genetic factors include both those that affect the entire skeleton and those that have more localized influences. A fracture is an example of a localized influence. Hormonal effects, nutritional deficits, and various disease states are examples of influences that can affect the whole skeleton (Jowsey, 1977). Mechanical influences also have a systemic effect on growth of the skeleton, particularly on long bone diaphyses, even though the control mechanism remains poorly understood. Evaluating mechanical influences on bone form could be carried out on various different scales, including osteonal and trabecular architecture (Agarwal and Stout, 2003; Rafferty et al., 1998). On a larger scale, the primary response on long bone
diaphyses to mechanical loading is through alteration in the diaphyseal geometry, rather than through alteration of material properties (Woo et al., 1981). Long bone cross-sectional geometry can provide insights into the past mechanical environment of that bone, which can then be related to the behavior of that individual.

Earlier (Pliocene through Pleistocene) humans have more robust postcranial skeletons in comparison to modern populations. “Robusticity” refers to strengthening of a skeletal element through addition of bone tissue, usually assumed to be in response to higher mechanical loading. While the general consensus is that early Homo exhibited greater robusticity than recent Homo, how best to quantify this robusticity remains unresolved. The use of cortical thickness measurements as a measure of mechanical strength can be misleading. For example, thinning of the diaphyseal cortex with aging is interpreted by clinicians as increased fragility. This interpretation is valid only if the diameter of the bone had not increased. If it had increased, as has been observed in elderly populations, then it is possible to maintain the bending rigidity with the lower percentage of cortical thickness. Therefore it is important to examine more mechanically relevant properties than simply cortical thickness.

Throughout the physical anthropology literature, geometric cross-sectional properties are often used to test hypotheses about mechanical adaptations of long bones (Lieberman et al., 2004). Analysis of cortical bone distributions within long bone cross-sections is believed to be of greater relevance than traditional methods that rely on external measurements (Lovejoy et al. 1976). It has been demonstrated experimentally that long
bone diaphyses can be successfully modeled as rigid beams (Huiskes, 1982). In a beam analysis performed on femoral diaphyses, the cross-sectional properties are used to estimate its strength under particular loading situations. The two most important measures of bone strength are cortical bone area (CA) and second moment of area (SMA). CA is a measure of resistance to axial loading, but is a poor measure of resistance to non-axial loading, since resistance to bending depends on both the amount of material and on its distribution about the axis of bending. SMA is the resistance to bending about a specified axis referred to as the neutral axis (NA) (Ruff, 2000). SMA is the squared perpendicular distance of the area from the NA.

\[ \text{SMA} = \int_{y_{\text{min}}}^{y_{\text{max}}} y^2 \, dA \]

where \( A \) represents area and \( y \) is the perpendicular distance from the NA.

Most cross-sectional properties are measured from digital images, therefore SMA is approximated in non-integral form by dividing the cross-sections into many squares of dimension \( x^2 \) (in the following studies, these squares are pixels) each located a distance, \( y \), from the NA (Lieberman et al., 2004).

\[ \text{SMA} = \sum_{i=1}^{n} x_i^2 \cdot y_i^2 \]
SMA (designated “I”) is usually calculated about anatomically defined axes ($I_{xx}$ and $I_{yy}$) or the principal axes ($I_{\text{max}}$ and $I_{\text{min}}$) through the centroid. Polar moment of inertia ($J$) is the resistance to torsion and is calculated as the sum of any two perpendicular measures of SMA (i.e., $I_{xx} + I_{yx}$, $I_{\text{max}} + I_{\text{min}}$) (Ruff and Hayes, 1983). These properties are strongly related to the lifestyle and activity level of the individual. For example, significant declines in the magnitude of these geometric properties were found as a result of the transition from pre-agriculture to agriculture lifestyle among Native Americans (Ruff et al., 1984). Also, significant changes in the long-bone morphology occurred to members of the genus *Homo* throughout the Pleistocene. Over this period, both mid-shaft femoral torsional and compressive strength exhibited significant declines (Ruff, 2006). The most probable explanation for such examples of increasing gracility is the decline in mechanical work loads.

### 2.5 BIOMECHANICAL SIGNIFICANCE OF THE FEMORAL NECK

Among the most important morphological changes that occurred as a result of the shift to upright posture were those changes to the human pelvis. Figure 2.2 shows a superior view of the *Pan troglodytes* and *Homo sapiens* pelvises.
Figure 2.2: Comparison of *Pan troglodytes* (superior) and *Homo sapiens* (inferior) pelvises. This figure is not to scale. Source: Lovejoy (1988).

The most noticeable difference between the two is that the human pelvis is deeper anterior-posteriorly in order to expand the width of the birth canal and thus accommodate the passage of a large brained infant. The second is the relative orientation of the iliac crests. In chimpanzees the iliac crest is oriented posteriorly while in humans it is oriented laterally. In chimpanzees the muscles that originate on the flared iliac crest are known as the anterior gluteal muscles (*gluteus minimus, gluteus medius, tensor fasciae*), function as leg extensors. The lateral orientation of this ilium in humans causes these same muscles to function as abductors. This new function is necessary in order to maintain hip stability during upright gait. This orientation of the iliac blade also puts the femoral neck under a unique type of mechanical load (Lovejoy, 1988). Figure 2.3 illustrates that the combined influences of the ground reaction force, the weight of the
upper body and the force generated by the abductor muscles causes the femoral neck to be in low compression superiorly and high compression inferiorly.

Figure 2.3: Mechanical loading of the femoral neck in humans as a result of the human abductor apparatus. Source: Lovejoy (1988).

The external attributes of bipedal locomotion summarized here have developmentally determined internal structural correlates. A cross section in the region of the neck-shaft junction (which biomechanically is the most relevant section) includes a central marrow cavity surrounded by trabecular bone extending outward toward the surface, which in turn is characterized by a relatively uniform dense ring of cortical bone. The outer cortical bone is thickened inferiorly due to compressive forces. Also, because cortical bone is weaker under tension than under compression, bone in the superior margin of the femoral neck is thickened as well, attaining dimensions that actually exceed those of the inferior margin in nearly half of *Pan troglodytes* observed by Ohman et al. (1997) (46.2%, N=17). In contrast, among past and present hominids the femoral neck exhibits cortical bone that is much thinner superiorly than inferiorly (Lovejoy et al., 2002, Ohman et al., 1997). This reduction in superior cortical thickness is chiefly due to the altered
functional demands of hominid bipedal locomotion, which over time has modified the action of the abductor muscles (*gluteus medius* and *minimus*). In hominids, these muscles are aligned approximately parallel to the femoral neck so that their contraction compresses the bone, balancing the tension that produced the thickening of the superior cortex in apes. The result is that in hominids, cortical thickening is greatest along the inferior margin of the neck-shaft junction. At this point of highest bending stress, in extant humans, superior cortical thickness approximates one-quarter of inferior cortical thickness or less; in extant African apes, superior and inferior cortical thicknesses approximate a 1:1 ratio (See Figure 2.5) (Ohman et al., 1997; Rafferty, 1998).

Figure 2.4: Mechanical implications of femoral neck length. Source: Lovejoy, (1988).
Figure 2.5: Box and whisker plot of the cortical bone superior/inferior thickness ratios at the neck/shaft junction in *Homo sapiens*, A.L. 128-1, and three hominid species. Note the significantly lower thickness ratios in *Homo sapiens*. Source: Ohman et al., (1997)

Galik et al. (2004) used CT scanning to display the interior structure of the more complete Tugen left femur, BAR 1002’00, which comprises the head, neck, and proximal shaft. The results show that the internal distribution of cortical bone in the femoral neck of BAR 1002’00 to constitute direct evidence for frequent bipedal posture and locomotion in this Late Miocene ancestor. In internal and external features BAR 1002’00 exhibits a total morphological pattern distinct from African apes, diagnostic of bipedal locomotion, and appropriate for a population standing at the dawn of the human lineage.
A highly informative historical overview treating representations and conceptions of the calcar femorale was provided by Newell (1997), who emphasized the importance of appreciating the complex three-dimensional nature of this structure. Newell also pointed out an error made by many orthopedic surgeons that leads to a misidentification of structures in the proximal femur that are of critical importance in surgical repair and replacement of the human femoral neck: confusion of the complex internal plate of bone that constitutes the true internal calcar femorale with a simple thickening of cortical bone nearby, at the juncture of the femoral neck and diaphysis.

As noted by Newell, the first anatomist to use the term calcar femorale to describe a bony spur projecting into the cancellous tissue near the base of the femoral neck appears to have been Merkel (1874), though he was anticipated in recognition of the structure by other anatomists. According to Glinkowski and Ciszek (1989), the structure corresponding to the calcar femorale first was illustrated in Pirogov’s *Anatomia Topographica* in 1852, and soon afterward by Humphry (1858) and others.

In a modernized translation of the description provided more than a century ago by Wolff (1869), the calcar femorale can be envisioned as the compact tissue underlying the lesser trochanter. A related and more informative three-dimensional conception of this region
that can be traced to the work of Bigelow (1875) among others, is that the “true neck” of the femur is continuous with the proximal femoral diaphysis, such that these structural elements form cylinders of cortical bone that are moderately compressed anterio-posteriorly and overlain by the irregular trochanteric surfaces. Subsequently, Dixon (1910) made an explicit identification of the calcar femorale as the more or less vertical plate formed by the bony lamina that run beneath the lesser trochanter, rendering it clear that this plate, when seen in cross section, corresponded to Merkel’s “spur.”

The structural and topographical confusions noted by Newell (1997), following Griffin (1982), appear to be perpetuated in the orthopedic surgical literature, where anatomical details concerning the region of the femoral neck take on considerable practical importance in the context of hip fractures, their repair, and their prevention by the use of hip implant devices. Horsman et al. (1982) performed radiographic assessments and measurements on the femora of 58 women who had fractures in the neck of this bone, as well as on 58 age-matched controls. The measurements included total width and medullary width, both near the midshaft of the femur, where the cortical width is maximal; lateral cortical width near the level of the lesser trochanter; and “width of the calcar femorale just above the lesser trochanter.” Regarding the last of these measurements, the text and the caption of their Fig. 1 indicate that what they measured was what Newell referred to as the “orthopaedic calcar” representing a thickening of the cortical wall of the femur rather than the internal plate of the actual calcar femorale. Similarly, Cooper et al. (1986), carried out a study designed to assess the relationship between directly assayed bone mass and radiological measures used to estimate this
mass. In addition to using the method of Singh et al. (1970) to grade the trabecular bone content of the femoral neck, Cooper and colleagues employed the same incorrect measurement of cortical bone thickness in the region of the calcar femorale, but not the true internal calcar femorale itself, thus continuing along the same erroneous path previously followed by Horsman et al. (1982). A complete review of all of the publications that generate data and analyses that are based on an erroneous definition of the calcar femorale is beyond the scope of this paper. However, it should be noted that this tradition continues even within the last several years, in publications that otherwise employ experimental designs and methods that appear to be sophisticated (Peacock et al., 1998; Koller et al., 2001; Peacock et al., 2002). The distinction, between the misnamed orthopaedic “calcar femorale” or cortical surface thickening and the dense, internal plate of bone deep to the lesser trochanter, takes on surgical significance because, as noted by Harty (1957), in some cases of hip fracture, when a longitudinal split occurs on the lateral side of the femoral diaphysis and the lesser trochanter breaks off as a separate fragment attached to the psoas major, the true calcar femorale that remains continuous with the distal portion of the femoral neck can act as a spike that is driven into the upper portion of the femoral shaft, acting as a wedge (Fig. 8 in Harty, 1957). Such an outcome is not possible for the so-called “orthopedic calcar,” so that any measurements of that structure are not pertinent to understanding hip fracture risks, outcomes, preventions and surgical repairs.

There have been some relatively recent attempts to characterize more accurately the three-dimensional structure of the calcar femorale. Adam et al. (2001) carried out a
combined anatomical and radiological study in which thirty human cadaveric femora of central European origin were analyzed by computerized tomography (CT) to produce high resolution thin slices. The CT images then were processed with thresholding to distinguish regions of high density bone in two and three dimensions. In addition, three macerated femur specimens were cut to correspond to the CT slices for validation purposes. Their results confirmed the occurrence of the calcar femorale as a regularly occurring structure (which they characterized as a septum) within the proximal femur, and noted its potential importance for metaphyseal fitting of an endoprosthetic stem.

The preceding year, Wroblewski et al. (2000) had provided extensive data quantifying the actual importance. These researchers accurately described the calcar femorale as a vertical plate of bone lying deep to the lesser trochanter, separating the femoral cortex into two distinct layers, the calcar femorale per se and the medial femoral cortex, these fusing proximally to form the medial femoral neck. The practical application of their work was demonstration that placement of an arthroplastic appliance without removal of the calcar femorale yielded a rate of failure (aseptic loosening of the stem) of 4.8% in 330 patients, versus a failure rate of 0.9% in 111 patients in which the calcar was cleared prior to implantation.

Taken together, these studies provide a context for the broad observation by Griffin (1982), that “[E]very femur with an ossified lesser trochanter has a calcar femorale.” Of course, this hypothesis concerning the occurrence of the calcar femorale was made in the context of a discussion of the extant, human femur, for which the expression of a well
developed calcar femorale is an expected, normative feature, though one that is not invariant. Commenting on the general belief “[T]hat the ‘calcar’ is said to disappear in old age, Thompson (1907) summarized the data then available to him. He reported that the calcar femorale persisted in several males aged 67, 70, 71, 80, and 87, as well as in two females aged 65 and 83. Proceeding through younger ages, he reported the absence of a calcar femorale in a female aged 21 and a male aged 27, as well as in three male subjects each 3 years of age, plus one female aged 6. He did not find this structure develops in very young infants or fetuses. Thus, for more than a century it has been known that the calcar femorale shows considerable individual variation in its expression, and that one component of this variation is developmental age.

More recently these data have been updated and expanded as part of a comprehensive and authoritative study of skeletal development through the lifespan (Blake et al., 1999). These data indicate that the earliest signs of the calcar femorale are bony lamellae that begin to form in the region at the base of the lesser trochanter at about 3 years of age.

Comparative data on the occurrence of the calcar femorale are sparse and, due again to the rather widespread use of an incorrect definition of the calcar femorale, not generally reliable. As one example of this problem, Radin et al. (1982) used domestic sheep (Ovis domesticus) as experimental organisms in which to study loosening of cemented metal femoral components in total hip replacement. They reported that “[T]he resorption of the calcar femorale away from the collar became evident and progressed with time in all animals.” However, their Figure 3 shows that their conception of the calcar femorale is
simply the so-called “orthopedic calcar,” or thickening of the cortical bone in the proximal
diaphysis at the juncture of the femoral neck. Regardless of the value of their
experimental surgical studies, they provide no pertinent comparative data on the
occurrence of the calcar femorale in a species other than our own; indeed, their
contribution to the scientific literature discussing the occurrence of a “calcar femorale” in
domestic sheep is seriously misleading to anyone attempting to review the comparative
functional anatomy of this region.

Among the very few cross-species studies on distribution of the calcar femorale is that of
Glinkowski and Ciszek (1989). Their comparative sample included 10 femoral
specimens each from domestic hens (*Gallus domesticus*), dogs (*Canis lupus familiaris*),
pigs (*Sus scrofa domesticus*), and rhesus monkeys (*Macaca mulatta*), and 52 humans
(*Homo sapiens*, age at death 40 to 80 years). In the femoral bones of all of the nonhuman
specimens, no compact bone was found resembling the calcar femorale present in X-rays
or physical cross sections of the humans (in which the X-rays showed clear presence of a
calcăr shadow in lateral projection on 75% of the specimens, with the text indicating that
this was a minimum estimate). This comparative anatomical perspective should be borne
in mind when evaluating statements that have been made about the significance of the
calcăr femorale in fossil hominids (this term being used here to include all upright and
bipedal ancestors of our own species, and excluding extant chimpanzees in the genus
*Pan*).
Figure 2.6: The calcar femorale (F) in left femur. The calcar femorale is superior to the lesser trochanter (LT). Source: Harty (1957).

2.7 COMPUTERIZED TOMOGRAPHY AND IMAGE PROCESSING

Computerized tomography is a well-established technique for nondestructive determination of internal fossil morphology in paleoanthropology. CT scanners work by passing X-ray beams through a specimen that is scattered or absorbed by through the specimen. In medical CT scanners an x-ray source and an array of detectors rotate about the specimen and measure the attenuation within the confines of a slice-shaped volume in a great number of directions using a fan beam. This resulting attenuation, or decrease radiation intensity due to interaction with the matter, is recorded. Attenuation can be roughly translated roughly into an expression of density, in that on any given image a higher attenuation value corresponds to higher density. However caution should be used...
in the interpretation of attenuation values between images and especially those composed of different materials, due to varying proportion of the photoelectric interaction. This interactions account for less than 5% of the attenuation that occurs in soft organic tissues such as muscle, while greater than 20% of the attenuation that occurs in bone can be attributed to the photoelectric interaction.

Differences in attenuation are expressed in Hounsfield units (HUs), each of which corresponds to 0.1% of the attenuation coefficient difference between water and air. The range of HU unit values is defined by effects representing the attenuation of air (-1000 HU) and that of water (0 HU). A mathematical filter known as a convolution filter is used to reconstruct the CT image. The resulting reconstructed CT image is a matrix composed attenuation values over the area scanned (the diameter of this area is known as the field of view: FOV). The matrix is composed of a set number of elements, usually either \((256)^2\) or \((512)^2\) for a medical scanner. The number of elements is fixed independent of the scanned area. Each attenuation value is stored on a 2-dimensional picture element, or pixel. The length of a pixel, known as the pixel size, can be calculated by dividing the FOV by the number of rows (or columns) of the matrix.

Spatial resolution, referring to the smallest distance between two structures that can be distinguished, should not be confused with pixel size. The conventional usage is that “high” spatial resolution refers to a relatively short distance between two objects and “low” resolution refers to a high distance. Spatial resolution is compromised only when it is lower than pixel size. The best possible spatial resolution for medical CT scanners is
around .3-.5mm (Spoor et al., 2000). The actual spatial resolution obtained, however, is likely to be less than this if the pixel size is large relative to the FOV.

Of critical importance in this study is the determination of accurate air-cortical and cortical-trabecular boundaries. These boundaries are determined by selection of the appropriate attenuation values, known as the threshold. To determine these thresholds Hounsfield plots (HP), which are plots of the attenuation values of along the line passing through the specimen on a CT image, were used. In the following explanation of the issues involved in thresholding, the easiest guide to comprehension is to imagine that we are scanning a cylinder of uniform material and density in a plane orthogonal to the long axis of the cylinder. Two imaging artifacts can normally be observed on a HP. The first is the beam hardening artifact, which is a dip in the attenuation values in the center of material. This artifact illustrates why interpreting attenuation values as density should be done with caution; although the material may be of a constant density, somewhat different attenuation can values result. The second is edge artifact, which is a narrow region with a steep slope of attenuation values at the edge of a specimen (Spoor et al., 1993). The location of real boundary between materials can be determined through the full width half maximum principle (FWHM). FWHM states that the true boundary of the material occurs at halfway between the minimum and maximum attenuation values in the edge effect (Figure 2.7). The error of FWHM determinations is limited to ± 0.1 mm as along as the accuracy is limited only by spatial resolution (Spoor et al., 1993), providing that the planar resolution is one-half the spatial resolution or less.
Figure 2.7: Illustration of the FWHM. Source: Ohman, et al. (1997).

2.8 REFERENCES


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CHAPTER 3
DIAPHYSEAL CROSS-SECTIONAL PROPERTIES OF
BAR 1002’00 AND BAR 1003’00

3.1 ABSTRACT

Reported here are the diaphyseal cross-sectional geometrical properties of two fossilized femora from Kenya dated at 6 Ma (million years ago), designated as the taxon *Orrorin tugenensis*. These femora are sampled at a temporal level near the divergence of ape and human lineages. The geometric properties of the bones are compared with previous findings from SK 82 and SK 97, hominid fossils from two million years later, and a sample of extant humans from Pecos Pueblo, New Mexico. The *Orrorin* femoral specimens BAR 1002’00 and BAR 1003’00 are notably robust, exhibiting cross-sectional areas with relatively high percentages of cortical bone in comparison to a contemporary sample. Total cross-sectional area (TA) is markedly smaller for BAR 1002’00 and BAR 1003’00 than for either of the Swartkrans early hominid proximal femora or the Pecos Pueblo sample, but %CA of the two Kenyan fossil femurs are comparable to those from Swartkrans and one-third higher than the modern sample. Despite their relatively thicker cortical areas BAR 1002’00 and BAR 1003’00 do not exhibit higher bending resistance (Imax and Imin) or torsional rigidity (J) compared with a modern human sample. These findings extend our knowledge of internal femoral structure related to the origins of human locomotion.
3.2 INTRODUCTION

Our human lineage has been separate from other nonhuman primates (extant apes in the genera Gorilla, Pan, Pongo, and their fossil predecessors such as Dryopithecus) for approximately 6 to 8 Ma (Eckhardt, 1972; see also Begun, 2004). Following broad general usage, humans are defined here in terms of their characteristic use of upright posture and bipedal locomotion; other hominoids may employ upright posture and bipedal locomotion as part of their behavioral repertoires, but not in an exclusive or obligate sense. Over the time period during which humans have existed as a separate lineage, populations have shown a mosaic pattern of evolution. The parts of what now seems to be a unitary character complex did not necessarily arise all at the same time. Changes in certain anatomical regions have been much more rapid and extensive than in others. For example, taken in isolation, some human elements (such as molar tooth crowns and the distal humerus) are difficult to distinguish from comparable anatomical parts of chimpanzees, which are our closest living relatives although the respective lineages have been separated for 6 to 8 Ma. In contrast, many components of the human femur are strikingly different from those of all extant apes. These differences reflect changes that have accrued during the evolution of our uniquely human forms of posture and locomotion.

Structurally the human femur serves multiple biomechanical functions, as a link (connecting the tibia with the os coxa), lever (a semi-rigid bar activated by muscles,
especially by those used in bipedal locomotion), and support (a beam bearing the weight of the trunk, head, and forelimbs). Compromises among these various overlapping and competing functional requirements theoretically could be resolved through adjustments in material as well as geometric properties. Currey, (1979), in fact, has demonstrated the wide range of differences in energy absorption and stiffness of various types of bone; clearly, investigation of potentially adaptive adjustments in material properties of bone merits great attention. However, much evidence indicates that within the postcranial skeleton, the primary response to biomechanical demands is through change in diaphyseal geometric properties (Woo, et al., 1981). In an extensive series of papers published over several decades beginning in 1981, Ruff and his colleagues (e.g. Ruff et al. 1993) have shown that in the lineage leading to extant humans, average bone strength (as measured by geometric cross-sectional properties of the femoral diaphysis) has been declining for the past two to three million years. Most of their data comprise populations and individual specimens sampled from the genus Homo; however, a few specimens such as AL 288-1 (“Lucy”) trace a thin line of human ancestry back to as much as four million years ago (Ruff, 2006).

In this paper we present data that extend the comparison back by yet another two million years, or 50% more than the previously documented material evidence that bears on the evolution of upright posture and bipedal locomotion. The *Orrorin tugenensis* femora represent the oldest femoral fragments pertinent to reconstructing posture and locomotion, at a temporal point near the divergence of a human lineage from its more ape-like ancestors. The *Orrorin* femora form part of a sample of fossilized skeletal
remains derived from four localities in the Lukeino Formation (Aragai, Cheboit, Kapcheberek, and Kapsomin), that are arrayed along the eastern approach to the Tugen Hills in the Baringo District of Kenya, securely to the Late Miocene, approximately 6 million years ago (Ma; dating references are summarized in Galik et al., 2004). The unusually favorable conditions of fossilization have retained internal structural features, thus allowing imaging of the diaphyseal cross-sections through computerized tomography (CT). We describe here the geometric properties of the diaphyseal cross-sections of the two partially intact fossilized femora, BAR 1002’00 and BAR1003’00, designated as the taxon *Orrorin tugenensis*.

### 3.3 MATERIALS AND METHODS

The *Orrorin tugenensis* specimens comprise more than twenty fossils representing at least five individuals. Three of these fossils are portions of femurs (See Figure 3.1). BAR 1002’00, the most complete, comprises about 200 mm of left femoral shaft plus a complete head that is connected to the shaft by an intact neck; its anatomical features have been described fully and compared in detail with extant African apes and humans, as well as with Plio-Pleistocene hominids (Galik, et al., 2004). BAR 1003’00 comprises approximately half of a proximal left femur, including the entire lesser trochanter but lacking both the greater trochanter, most of the neck, and the femoral head. The third partial femur, BAR 1215’00, is a small fragment consisting of the proximal portion of a right femur lacking neck and head and preserving only about 20 mm of the upper
diaphysis below the base of the greater trochanter, which also is missing. It is too incomplete for the analyses performed here and will therefore not be considered further.

Figure 3.1. *Orrorin tugenensis* femora. Left: BAR 1002’00, Upper Right: BAR 1003’00, Lower Right: 1215’00. The white bars indicate 1 cm scale.
In their baseline methodology paper, Ruff and Hayes (1983) established the femoral orientation for measuring diaphyseal cross-sections. Ruff and Hayes (1983) placing the bone, dorsal side down, on a flat surface, then elevating the proximal end until the A-P midpoints of two locations on the shaft (just distal to the lesser trochanter and just proximal to the femoral condyles) were equidistant from the supporting surface. So oriented, the centers of articulation of the femoral condyles establish the most distally projecting points of the condylar surfaces. The frontal plane is then defined as the plane parallel to the supporting surface and equidistant between the A-P positions of the condylar centers. The sagittal plane of the femur is perpendicular to the frontal plane, and includes both the deepest point in the intercondylar notch and the M-L midpoint of the shaft at the same proximal location used in establishing the frontal plane. The longitudinal axis of the diaphysis is established by the intersection of these two planes (See their Fig. 2b and Fig. 3). They then measured diaphyseal cross-sections at 20%, 35%, 50%, 65%, and 80% of diaphyseal length, proceeding from the distal to the proximal end of the bone. Because the specimens analyzed in this paper, BAR 1002’00 and BAR 1003’00, both lack the distal diaphyses and condyles, they posed challenges to our ability to generate cross-sectional geometric data comparable with the extensive data base on the cross-sectional geometry of human femora, as well as those of several species of nonhuman primates. In order to establish the locations at which to measure these cross-sections on our incomplete specimens, it was estimated that the femoral diaphysis of BAR 1002’00 was two-thirds complete and that of BAR 1003’00 was half-complete.
(Senut et al., 2001). We were able to measure sections from 35% to 80% for BAR 1002’00 and from 50% to 80% for BAR 1003’00. We also were unable to establish femoral torsion angles on either specimen due to the absence of femoral condyles or well defined linea aspera. This precluded us from measuring second moments of area about the A-P and M-L axes and the orientation angle of the principal second moments of area. In addition, it may be impossible to measure femoral torsion with sufficient accuracy or reproducibility using available methods (Stirland, 1994).

CT was used to image the internal distribution of cortical bone of BAR 1002’00 and BAR 1003’00. Each femur was scanned air helically with a Marconi Twin Flash CT Scanner at 1 mm increments proximally to distally about the long axis of the femur. Instrument settings were 120 kV, table speed of 5 mm/sec; scan angle was 0 degrees (scans were perpendicular to the long axes of the femora). The field of view was (222x222) mm², with a matrix of (512)² pixels yielding planar resolution of 0.434 mm/pixel. The series of CT images for each of the specimens were imported into Amira 4.1.1 software, in which 3D reconstruction of the interior and exterior anatomical features were made. CT images are two-dimensional representations of solid objects consisting of planar arrays of pixels; in Amira 4.1.1 the third dimension slice thickness is added to complete each volume unit (voxel). Since the CT scans were made in 1 mm increments, the resultant in voxel size of 0.434 x 0.434 x 1 mm³. Differences in density are expressed in Hounsfield units (HUs), each of which corresponds to 0.1% of the attenuation coefficient difference between water and air. Each voxel is assigned a numeric value
ranging from -1000 to 3095 HU. Higher HU numbers signify higher density, with water and air having corresponding HU values of zero and –1000. Empirically, bone yields high HU numbers, and fossilized bone usually even higher. At the material boundaries on the CT images the HU values change corresponding to the different attenuation levels. Rather than being abrupt, the change appears on the CT image as a gradient due to the limited spatial resolution of the scanner, resulting in a blurred edge. Accurate measurements of geometric cross-sectional properties depend on determining the true boundary within this blurred region. This is achieved through the Full-Width at Half-Maximum (FWHM) principle. The FWHM principle states that an object’s full width is the distance between the half-maximum attenuation levels at opposing edges (Ohman, et al., 1997). The half-maximum attenuation level is the FWHM threshold used to calculate the potential FWHM threshold error is $< \pm 1$ pixel for each gradient. The determination of distances using FWHM is limited to the minimum thickness measured. Precision of $\pm 0.1$ mm can be achieved for a thickness of 1.1 mm at spatial resolution of 0.5 mm, as long as the planar resolution is half or less the spatial resolution. Fossilization can decrease contrasts between bone and the matrix associated with it, but does not decrease accuracy (Spoor et al., 1993). Since the cortical bone either reached or was only slightly below the maximum of 3095 HU, the threshold for the exterior air to bone (external) perimeter was set to be constant at $([3095 + (-1000)]/2) = 1048$ HU. In BAR 1002’00, the threshold for the cortical-to-trabecular (internal) perimeter was taken as the mean value of 3095 HU and the minimum in the trabecular region, ranging from 1048 to 2870 HU. In BAR 1003’00, the shaft was completely devoid of internal matrix and therefore threshold value of 1048 HU was also used. The external and internal perimeters were combined to form a
single image for each slice. The resultant images have only two possible color values for
each pixel, white for one that is in the cortical bone region and black for one that is not.
These images were imported into MATLAB where a program was written to calculate
the geometric cross-sectional properties. The incomplete nature of the specimens
confined our observations to the following properties: Cortical cross-sectional area (CA)
is a measure of resistance to axial loading. Maximum second moment of area ($I_{\text{max}}$) is the
greatest resistance to bending in the cross-section. Minimum second moment of area
($I_{\text{min}}$) is lowest resistance to bending and occurs about an axis perpendicular to $I_{\text{max}}$.
$I_{\text{max}}/I_{\text{min}}$ ratios close to 1 indicate a more circular biomechanical “shape” that is about
equally resistant to bending in all directions. Ratios substantially greater than 1 indicate
that one axis is significantly more resistant to bending than those of lesser value. The
results were compared with two samples derived from the literature*. Representing
modern humans, the first sample consists of the femora of 135 individuals who lived in
1600 AD in the region of Pecos Pueblo, New Mexico (Ruff and Hayes, 1983). The
second comparative sample consists of the SK 82 and SK 97, dated to 2 Ma and
designated to the taxon *Australopithecus robustus* (Ruff et al., 1999). Prior to the
discovery of the *Orrorin* material these specimens were the earliest known hominid
femora within which the cortical and trabecular bone were discernable.

### 3.4 RESULTS

Ruff and Hayes (1983) measured cross sections at 20%, 35%, 50%, 65%, and 80% of
femoral length, proceeding from the distal end to the proximal end of the bone. We
followed this convention, but due to the incompleteness of our specimens, were able to measure only sections from 35% to 80% for BAR 1002’00 and from 50% to 80% for BAR 1003’00. Note that these section percentages are approximations because of damage to both proximal and distal ends of the bones. At about mid shaft (50% level), BAR 1003’00 exceeds BAR 1002’00 substantially for all of the measurements with one exception: For MA (size of the medullary cavity), BAR 1003’00 values exceed those of BAR 1002’00 only slightly, 121.3 versus 120.3 mm². The overall pattern, other than for MA, is consistent with the external dimensions of the two fossils, with BAR 1003’00 being moderately larger in diameter and appearing generally more robust in its proportions. Since sexual dimorphism is a notable feature of hominoid primates, it is reasonable to hypothesize that BAR 1002’00 may be from a female while BAR 1003’00 is from a male. In any case we are dealing with two adult individuals from the same site (hence same place and approximate time) that differ appreciably in size.

Table 3.1: Summary of BAR 1002’00 and BAR 1003’00 cross-sectional properties.

<table>
<thead>
<tr>
<th>Cross section %</th>
<th>CA</th>
<th>TA</th>
<th>MA</th>
<th>% CA</th>
<th>Imax</th>
<th>Imin</th>
<th>Imax/Imin</th>
<th>J</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR 1002’00</td>
<td>35</td>
<td>263.2</td>
<td>441.4</td>
<td>178.2</td>
<td>59.63</td>
<td>15374</td>
<td>10907</td>
<td>1.41</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>291.4</td>
<td>412.7</td>
<td>121.3</td>
<td>70.61</td>
<td>14443</td>
<td>10603</td>
<td>1.36</td>
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<td></td>
<td>65</td>
<td>257.3</td>
<td>405</td>
<td>147.7</td>
<td>63.53</td>
<td>13164</td>
<td>9764</td>
<td>1.35</td>
</tr>
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<td></td>
<td>80</td>
<td>351.1</td>
<td>439.5</td>
<td>88.4</td>
<td>79.89</td>
<td>19845</td>
<td>11024</td>
<td>1.8</td>
</tr>
<tr>
<td>BAR 1003’00</td>
<td>50</td>
<td>317.8</td>
<td>438.1</td>
<td>120.3</td>
<td>72.54</td>
<td>17913</td>
<td>11076</td>
<td>1.62</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>330</td>
<td>440.5</td>
<td>110.5</td>
<td>74.91</td>
<td>18017</td>
<td>11618</td>
<td>1.55</td>
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<tr>
<td></td>
<td>80</td>
<td>347.3</td>
<td>436.6</td>
<td>89.4</td>
<td>79.55</td>
<td>19122</td>
<td>11086</td>
<td>1.72</td>
</tr>
</tbody>
</table>

The diaphyseal cross-sectional properties measured on BAR 1002’00 and BAR1003’00. See Notation for descriptions of each property.
For comparison, Tables 2 and 3 reproduce the full set of summary data from Ruff and Hayes (1983), including means and standard errors to give an indication of the extent of variation in one extant human population; a more complete overview of patterns in a variety of human populations is given in Ruff (2006). The means from Tables 3.2 and 3.3 then are incorporated into Table 3.4 for comparison with several individual specimens from this study as well as two South African specimens dated to about 1.6 Ma.

Table 3.2: Summary of Pecos Pueblo cross-sectional properties from Ruff and Hayes (1983).

<table>
<thead>
<tr>
<th>Cross section %</th>
<th>CA Mean</th>
<th>S.E.</th>
<th>TA Mean</th>
<th>S.E.</th>
<th>MA Mean</th>
<th>S.E.</th>
<th>% CA</th>
</tr>
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<tbody>
<tr>
<td>20</td>
<td>236.7</td>
<td>3.7</td>
<td>686.3</td>
<td>10.8</td>
<td>449.6</td>
<td>9.7</td>
<td>34.49</td>
</tr>
<tr>
<td>35</td>
<td>284.9</td>
<td>4.4</td>
<td>491.5</td>
<td>7</td>
<td>206.6</td>
<td>5.2</td>
<td>57.97</td>
</tr>
<tr>
<td>50</td>
<td>325.4</td>
<td>4.8</td>
<td>456.3</td>
<td>6</td>
<td>131</td>
<td>4.1</td>
<td>71.31</td>
</tr>
<tr>
<td>65</td>
<td>333.4</td>
<td>5</td>
<td>476.3</td>
<td>6.4</td>
<td>142.9</td>
<td>4.4</td>
<td>70</td>
</tr>
<tr>
<td>80</td>
<td>315.9</td>
<td>4.7</td>
<td>521.9</td>
<td>7.2</td>
<td>206</td>
<td>4.9</td>
<td>60.53</td>
</tr>
</tbody>
</table>

The means and standard errors for the cross-sectional properties measured at each cross-sectional level by Ruff and Hayes (1983). See Notation for descriptions of each property.
Table 3.3: Summary of Pecos Pueblo cross-sectional properties from Ruff and Hayes (1983).

<table>
<thead>
<tr>
<th>Cross section %</th>
<th>Imax</th>
<th>S.E.</th>
<th>Imin</th>
<th>S.E.</th>
<th>Imax/Imin</th>
<th>S.E.</th>
<th>J</th>
<th>S.E.</th>
</tr>
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<td>20</td>
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<td>699</td>
<td>18399</td>
<td>537</td>
<td>1.44</td>
<td>0.02</td>
<td>44363</td>
<td>1198</td>
</tr>
<tr>
<td>35</td>
<td>18293</td>
<td>549</td>
<td>14378</td>
<td>370</td>
<td>1.27</td>
<td>0.02</td>
<td>32671</td>
<td>888</td>
</tr>
<tr>
<td>50</td>
<td>18363</td>
<td>521</td>
<td>13235</td>
<td>315</td>
<td>1.38</td>
<td>0.02</td>
<td>31598</td>
<td>805</td>
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<tr>
<td>65</td>
<td>19047</td>
<td>497</td>
<td>14643</td>
<td>399</td>
<td>1.32</td>
<td>0.02</td>
<td>33690</td>
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<td>80</td>
<td>25559</td>
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<td>388</td>
<td>1.91</td>
<td>0.02</td>
<td>39194</td>
<td>1021</td>
</tr>
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A continuation of the means and standard errors for the cross-sectional properties measured at each cross-sectional level by Ruff and Hayes (1983). See Notation for descriptions of each property.
Table 3.4: Comparisons of cross-sectional properties at 80% of diaphyseal cross-section length.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>CA</th>
<th>TA</th>
<th>MA</th>
<th>%CA</th>
<th>Imax</th>
<th>Imin</th>
<th>Imax/Imin</th>
<th>J</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR 1002’00</td>
<td>351.1</td>
<td>439.5</td>
<td>88.4</td>
<td>80</td>
<td>19845</td>
<td>11024</td>
<td>1.8</td>
<td>30868</td>
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<tr>
<td>BAR 1003’00</td>
<td>347.3</td>
<td>436.6</td>
<td>89.4</td>
<td>80</td>
<td>19122</td>
<td>11086</td>
<td>1.72</td>
<td>30207</td>
</tr>
<tr>
<td>SK 82</td>
<td>490</td>
<td>577</td>
<td>87</td>
<td>84.9</td>
<td>31992</td>
<td>20907</td>
<td>1.53</td>
<td>52899</td>
</tr>
<tr>
<td>SK 97</td>
<td>457</td>
<td>593</td>
<td>136</td>
<td>77.1</td>
<td>34549</td>
<td>20458</td>
<td>1.69</td>
<td>55007</td>
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<tr>
<td>Pecos Means</td>
<td>315.9</td>
<td>521.9</td>
<td>206</td>
<td>60.5</td>
<td>25559</td>
<td>13635</td>
<td>1.91</td>
<td>39194</td>
</tr>
</tbody>
</table>

Comparison of diaphyseal cross-sectional properties of BAR 1002’00 and BAR1003’00 to SK 82 and SK97 (Ruff et al. 1999) and the Pecos Pueblo means (Ruff and Hayes 1983) at 80% diaphyseal cross-sectional length. See Notation for descriptions of each property.

Properties of the SK 82 and SK 97 diaphyses were studied from sections located 1 cm distal to the distal edge of the lesser trochanter, which approximates the “80% of femoral bone length” included in other studies (Ruff and Hayes, 1983; Ruff 1987a, b, 1995) in which length of the femur was measured from the distal end of the femur to the superior surface of the femoral neck. The sections from Pecos Pueblo as well as BAR 1002’00 and BAR 1003’00 also were taken at approximately 80% of femur length.

Total cross sectional area (TA) is markedly smaller for BAR 1002’00 and BAR 1003’00 than for either of the Swartkrans early hominin proximal femora or the Pecos Pueblo sample. Medullary areas (MA) of the two Kenyan partial femora were matched by SK 82 but exceeded by SK 97 and less than half of the Pecos Pueblo mean. Perhaps the most striking comparison, %CA, shows that all of the fossil specimens exhibit high cortical
areas relative to total area. This pattern is particularly notable for BAR 1002’00 and BAR 1003’00 since these two bones have only about 75% as much TA as all of the other femora, ancient or modern. These lower values of TA in BAR 1002’00 and BAR 1003’00 contribute to their values of $I_{\text{max}}$, $I_{\text{min}}$ and $J$ that are much lower than both the Pecos Pueblo means and the Swartkrans early hominid proximal femora. Ruff and Hayes (1983) found that the $I_{\text{max}}/I_{\text{min}}$ ratios were greatest at the proximal and distal ends of the diaphysis and smallest towards the middle region. Absence of the distal diaphyses in BAR 1002’00 and BAR 1003’00 does not allow us to comment on structural properties in that region. However, the $I_{\text{max}}/I_{\text{min}}$ ratios for the available portions of the diaphyses confirm the finding of Ruff and Hayes (1983), in that the ratios that we have determined increase proximally.

3.5 DISCUSSION

There has been consistent decline in diaphyseal robusticity in *Homo* from the early Pleistocene to extant humans (Ruff et al., 1993). The new data reported here on femoral diaphyseal properties of two ancient Kenyan femora extend our knowledge of this temporal trend by a full two million years. The diaphyseal cross-sections of the 6 Ma BAR 1002’00 and BAR 1003’00 exhibit markedly high percentages of cortical area compared to the modern human sample. However, their relatively thicker cortical areas do not translate into higher bending resistance ($I_{\text{max}}$ and $I_{\text{min}}$) or torsional rigidity ($J$) in comparison to modern human sample. This observation about inferred functional
properties probably results from the relatively smaller size of BAR 1002’00 and BAR
1003’00.

Body size is an important consideration when evaluating geometric cross-sectional
properties. Adjusting for factors such as nutrition, physical activity level, ethnicity, etc.,
one would expect a large person to have more robust bones than a smaller person. Size
adjustment of bone geometric cross-sectional properties is generally achieved by dividing
the parameter by femoral length raised to a power. While femoral length estimates of
BAR 1002’00 have been attempted, they have large error terms associated with them,
rendering a size normalization using this dimension untenable. If unbiased estimations
could be made, it might prove that BAR 1002’00 and BAR 1003’00 had relatively higher
bending resistance and torsional rigidity than the modern human sample.

Although more detailed comparative studies of basic diaphyseal properties in hominoid
primates are needed, the high percentages of cortical areas observed in the specimens
reported on here show certain structural resemblances to orangutans (Thorpe et al. 2007),
which exhibit small medullary cavities and therefore larger CA than might be expected
from external dimensions (Ruff, 1987b). Recent suggestions that adaptations for
bipedalism may have arisen in arboreal contexts is directing attention to the locomotor
regimens of these large Asian apes, which, although less closely related to humans than
are chimpanzees, may retain some locomotor patterns from ancestors prior to lineage
division among the African hominoids (O’Higgins and Elton, 2007).
In closing, we wish to note that, despite nearly three decades of intense investigation into the nexus of structure, function, activity levels, environment, and evolution of the human locomotor complex, several large questions remain unresolved. To what extent have trends in internal structural properties of the femur been influenced by changes in bone length, either in absolute terms or relative to body mass? What has been the nature of the feedback relationships among locomotor patterns, changes in masses of the several muscles of the hip complex, and biomechanical properties of the bone? What are the mechanisms by which reductions in activity levels might influence changes in bone mass and distribution during the intertwined timescales of ontogeny and phylogeny? Clearly, there is ample scope for further biomechanical approaches to these important scientific questions.

3.6 NOTATION

The following symbols are used in this paper:
Ma - millions of years ago.
CT – Computerized tomography.
FWHM – Full-Width at Half-Maximum.
CA - the area of the cross section composed of cortical bone (mm²).
TA - the total cross-sectional area (mm²);
MA - the area comprising the medullary cavity (mm²);
% CA - the proportion cortical bone in a cross-section [(CA/TA)* 100] (dimensionless).
Iₘₐₓ, Iₘᵟᵣᵦ - the principal second moments of area, indicating resistance to bending (mm⁴);
I_{max}/I_{min} - Index of biomechanical "shape;” ratios close to 1 indicate a more circular biomechanical “shape” that is about equally resistant to bending in all directions (dimensionless);

J - polar moment of area, reflecting torsional rigidity (mm^4);

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3.7 REFERENCES

Amira 4.1.1, Mercury Computer Systems Inc., Chelmsford, Massachusetts, 01824.


CHAPTER 4

MOMENT COEFFICIENTS OF SKEWNESS IN THE FEMORAL NECK CORTICAL BONE DISTRIBUTION OF BAR 1002’00

4.1 ABSTRACT

The cortical bone distributions in the femoral necks of apes and humans differ as a result of different loading environments caused by the realignment of the hip abductor apparatus. The unique internal anatomy of extant humans allows inferences about primary locomotor from incomplete femora to be made. Here the differences in cortical bone distributions are quantified using moment coefficient of skewness. Skewness coefficients at two locations along the neck of the 6 million year old African femoral specimen BAR 1002’00 were compared to samples of 9 modern humans and 10 chimpanzees. These coefficients indicate that BAR 1002’00 has a femoral neck cortical bone distribution more similar to that of chimpanzees than to humans. This indicates that *Orrorin tugenensis* was either not a full biped or that the human hip abductor apparatus had not yet fully evolved.

4.2 INTRODUCTION

The proximal femur in apes and humans is loaded in a manner similar to a cantilevered beam, with compression on its inferior portion and tension on its superior portion. While the femoral neck of apes exhibits a thick ring of cortical bone, the femoral neck of humans has distinctly thickened cortical bone only at the inferior portion, and exhibits
thin cortical bone at its superior portion (Lovejoy, 1988; Lovejoy et al., 2002; Lovejoy, 2005; Ohman et al., 1997). Since bone is weaker in tension than in compression, the absence of cortical bone in the superior region in the femoral neck of humans may seem puzzling. The most likely answer lies in our unique hip abductor apparatus. The primary abductors, the anterior gluteals, along with the secondary abductors, the pyriformis, gemellis, and obturators, contract in order to prevent pelvic tilt during single limb support (Lovejoy, 2005). Abductor contraction results in progressively decreasing compressive stress along an inferomedial to superolateral transect of the neck/shaft junction (Lovejoy et al., 2002). The thin superior cortical thickness results from insufficient mechanical stimuli to encourage either production or maintenance of bone throughout ontogeny.

This internal anatomical feature unique to the human lineage allows inferences about the primary locomotor from incomplete femora to be made. The fossilized femora A.L. 128-1, A.L. 211-1, and MAK-VP 1/1, all attributed to the taxon *Australopithecus afarensis*, exhibit femoral neck/shaft junction cortical bone distributions indistinguishable from that of modern humans (Ohman et al., 1997). Dated at around 3 to 3.4 million years old (Ma), those specimens were at the time the oldest hominoid femora in which the internal structures were discernible. In 2001, fossilized hominoid materials, including three partial femora, were discovered in Kenya. Designated *Orrorin tugenensis*, the approximately 6 Ma specimens represent the oldest femoral fragments pertinent to reconstructing posture and locomotion, at a temporal point near the divergence of a human lineage from its more ape-like ancestors. The unknown but unusually favorable conditions of fossilization have retained internal structural features of two of the partial
femora, thus allowing imaging of the femoral neck cross-sections through computerized tomography (CT). Galik et al. 2004 measured the cortical bone thickness at the neck/shaft junction of BAR 1002’00, one of the fossilized partial femora, and found that the ratio of superior/inferior cortical thickness is more similar to that of humans than apes. While Galik et al. 2004 provided valuable information about the internal structure of BAR 1002’00, their work has been criticized by Ohman et al. 2005 on various grounds, ranging from the methods of CT imaging and specimen preparation to the inadequacy of simply using thickness ratios to quantify the distribution. Most of these criticisms are beyond the scope of this paper. However, it will address the criticism about measurement technique by using a new method to quantifying the differences in femoral cortical bone distributions between apes and humans.

The cortical bone in a cross-sectional image can be thought of as a bivariate distribution. The third moment of area (TMA) normalized by the standard deviation cubed provides a moment coefficient of skewness of this distribution. Skewness is the degree of asymmetry, or departure from symmetry, of a distribution. This method has the advantage of incorporating all of the cortical area in the cross-section into the measurement, instead of just the superior and inferior thicknesses along the defined anatomical vertical axis. In this study, the skewness values at two locations along the femoral neck of BAR 1002’00 were compared to a sample of humans and chimpanzees using CT imaging. These finding will help us make inferences that place of *Orrorin tugenensis* near the dawn of the human lineage.
4.3 MATERIALS AND METHODS

The *Orrorin tugenensis* specimens comprise more than twenty fossils representing at least five individuals. Three of these fossils are portions of femurs. The subject of this study, BAR 1002’00, the most complete, comprises about 200 mm of left femoral shaft plus a complete head that is connected to the shaft by an intact neck; its anatomical features have been described fully and compared in detail with extant African apes and humans, as well as with Plio-Pleistocene hominids (Galik et al., 2004; Senut et al., 2001). The other femora, BAR 1003’00 and BAR 1215’00, are too incomplete for the analyses performed here. The comparative samples included 9 humans and 10 chimpanzee (*Pan troglodytes*) left femora.

CT was used to image the internal distribution of cortical bone of BAR 1002’00 and the comparative samples. BAR 1002’00 was scanned helically in air with a Marconi Twin Flash CT Scanner at 1.0 mm increments proximally to distally perpendicular to the long axis of the femur. Instrument settings were 120 kV, table speed of 5 mm/sec. Field of view was (222x222) mm$^2$, with a matrix of $(512)^2$ pixels yielding planar resolution of 0.434 mm/pixel. The comparative samples of humans and chimpanzees were scanned using a similar medical scanner as used for BAR 1002’00. The instrument settings used for these were 110 kV, slice increment of 1.0 mm, scan angle of 0 degrees in the transverse plane, and image matrix of $(512)^2$. 
The series of CT images for the specimens were imported into Amira 4.1.1 (Visage Imaging, Richmond, Australia), in which 3D reconstruction of the interior and exterior anatomical features were made (see Figure 2.1). CT images are two-dimensional representations of solid objects consisting of planar arrays of pixels; in Amira the third dimension of slice thickness is added to complete each volume unit (voxel). Since the CT scans were made in 1 mm increments, the resultant in voxel size of 0.434 x 0.434 x 1 mm³. Differences in density are expressed in Hounsfield units (HUs), each of which corresponds to 0.1% of the attenuation coefficient difference between water and air. Each voxel is assigned a numeric value ranging from -1000 to 3095 HU. Higher HU numbers signify higher density, with water and air having corresponding HU values of zero and –1000. Bone yields high HU numbers, and fossilized bone usually even higher.

The original scans were oriented perpendicularly to the shaft and then transformed to be orthogonal to the long axis of the femoral neck by using a Lanczos filter in Amira. Although it is not possible to calculate the resulting error arising from this transformation, it is likely that the planar resolution did not change significantly, since the Lanczos filter performs especially well for small voxel anisotropy (Meijering et al., 2001). The location of each cross-sectional image was defined as percentage of the length of the femoral neck. The point of 0% was defined as the head/neck junction and 100% as the neck/shaft junction. On each specimen six slices were taken from 0% to 100% of the neck, at intervals of roughly 20%.
Figure 4.1: Posterior view of BAR 1002’00 in Amira 4.1.1. Slices corresponding to 60 and 100% of femoral neck length.

At the material boundaries on the CT images the HU values change corresponding to the different attenuation levels. Rather than being abrupt, the change appears on the CT image as a gradient due to the limited spatial resolution of the scanner, resulting in a blurred edge. Accurate measurements of geometric cross-sectional properties depend on determining the true boundary within this blurred edge. This is achieved through the Full-Width at Half-Maximum (FWHM) principle. The FWHM principle states that an object’s full width is the distance between the half-maximum attenuation levels at opposing edges (Ohman et al., 1997). The half-maximum attenuation value is the
FWHM threshold used to calculate the potential FWHM threshold error is < ± 1 pixel for each gradient. Fossilization can decrease contrasts between bone and the matrix associated with it, but does not decrease accuracy (Spoor et al., 1993). In BAR 1002’00 the cortical bone either reached or was only slightly below the maximum of 3095 HU, therefore the threshold for the exterior air to bone (external) perimeter was set to be constant at \( (\frac{3095 + (-1000)}{2}) = 1048 \) HU. The threshold for the cortical-to-trabecular (internal) perimeter was taken as the mean value of 3095 HU and the minimum in the trabecular region. The external and internal perimeters were combined to form a single image for each slice. The resultant images have only two possible color values for each pixel, white for one that is in the cortical bone region and black for one that is not. While there is evidence that trabecular bone does contribute to femoral neck strength (Whitehouse and Dyson, 1974), it was not incorporated into this study because of the difficulty in relating the attenuation values obtained from the CT images for the trabecular bone in BAR 1002’00, a fossil, with that of the human and chimpanzee samples. The images were then imported into MATLAB 2007 (MathWorks, Natick, MA) where a program to calculate the moment coefficients of skewness was used.

TMA is a measure of material distribution about a specific axis, such that

\[
TMA = \int_{r_{\text{min}}}^{r_{\text{max}}} y^3 \, dA \quad (2.1)
\]
where $A$ represents area and $y$ represents the distance from some neutral axis. Since
TMA of the bone cross-section was calculated from digital images, TMA can be
approximated as

$$TMA = \sum_i^n x_i^2 \cdot y_i^3 \quad (2.2)$$

where $x$ is pixel length. TMAs were normalized by the cube of the square root of the
second moment of area (SMA; equivalent to the standard deviation (s.d.) squared) in
order to arrive at the moment coefficient of skewness ($a$).

$$S = \frac{TMA}{s.d.} = \frac{TMA}{3/\sqrt{SMA}} \quad (2.3)$$

TMA was calculated about the anterior-posterior (AP), superior-inferior (SI) anatomical
axes and the major (UU) and minor (VV) principal axes through the centroid. Figure 2.2
shows UU and VV on a human cross-section at 60% of femoral neck length.
Figure 4.2: MATLAB plot of the cross-sectional area of one of the human specimen at the neck/shaft junction. The cross-section is anatomically oriented; such that up is superior, down is inferior, left is posterior and right is anterior. The thick line indicates the major principal axis and the dashed line indicates the minor principal axes. Note the greater concentration of cortical bone below the minor axis. The “tail” of the distribution points in the positive (superior) direction and is therefore positively skewed.

Skewness as calculated about the anatomical axes is invariant to size and skewness calculated about the principal axes is invariant to size and rotation. The sign convention for determining the direction of skewness is that the tail of the distribution points towards the sign. That is, if there is a greater concentration of cortical bone below the AP axis through the centroid, then the “tail” of the distribution would point in the positive (superior) direction and therefore would be skewed positive. Likewise, if there is a greater concentration of cortical bone to the right of the SI axis through the centroid, then
the tail would point towards the positive (posterior) direction and therefore would also be skewed positive. It is expected that the primary difference in cortical skewness will be about the AP and VV axes. Statistical plots for all specimens were generated in Minitab 15.1.3 (Minitab Inc., State College, PA).

4.4 RESULTS

Figures 3.3 through 3.6 show the skewness about the anatomical axes ($S_{AP}$ and $S_{SI}$) and about the principal axes ($S_{VV}$ and $S_{UU}$). For sake of comparison, femoral neck lengths have been standardized such that the base of the head is 0% and the neck-shaft junction is 100%. There were 6 slices at intervals of roughly 20% taken from 0% to 100% of femoral neck length for the human and chimpanzee samples. The slices 0% and 20% were discarded because it was not possible to consistently find appropriate thresholds for determining the interior boundaries. On BAR 1002’00 there were two slices taken at 60% and 100% of the femoral neck. BAR 1022’00 had a crack along its femoral neck and was heavily mineralized in large sections and therefore it was not possible to obtain an acceptably clear image at the 40% level. The primary difference in cortical bone distribution between chimpanzees and humans was in $S_{AP}$ (Figure 3.1) and $S_{VV}$ (Figure 3.2). The slightly rotated principal $S_{VV}$ axis did not change the fundamental pattern. Student t-tests for humans and chimpanzees at the 100% level for both $S_{AP}$ and $S_{VV}$ yielded significant differences ($p<0.001$). The human sample was more skewed along the length of the femoral neck than the chimpanzee sample. BAR 1002’00 falls into the
chimpanzee range for $S_{AP}$. While the human sample tends to have higher $S_{SI}$ (Figure 3.3) the differences disappear when oriented about the principal axis (Figure 3.4).

Figure 4.3: Skewness normalized by standard deviation cubed about the anterior-posterior axis for humans, chimpanzees and BAR 1002’00. The data points corresponding to BAR 1002’00 are offset for clarity.
Figure 4.4: Skewness normalized by standard deviation cubed about the minor axis for humans, chimpanzees and BAR 1002’00. The data points corresponding to BAR 1002’00 are offset for clarity.

Figure 4.5: Skewness normalized by standard deviation cubed about the superior-inferior axis for humans, chimpanzees and BAR 1002’00. The data points corresponding to BAR 1002’00 are offset for clarity.
4.5 DISCUSSION

The loading at the femoral head of humans and apes causes compression at the inferior portion and tension at the superior portion. At some point near the beginning of the human lineage, the posteriorly facing iliac blades externally rotated to face laterally. This converted the muscles that originate on the iliac blades from hip extensors to hip abductors. Strong hip abductors are necessary for human locomotion to prevent pelvic

Figure 4.6: Skewness normalized by standard deviation cubed about the major axis for humans, chimpanzees and BAR 1002’00. The data points corresponding to BAR 1002’00 are offset for clarity.
collapse during the single leg stance phase of walking. In addition to supporting the pelvis, the human abductors cause compression on the femoral neck. The combination of compression and tension at the superior portion of the femoral neck causes a low loading environment. This is reflected in the cortical bone distribution at the neck/shaft junction. The femoral neck of humans exhibit cortical bone distributions characterized by thin superior bone proceeding down the length of the femoral neck. In contrast, African apes have uniformly thick cortical bone along the length of the femoral neck at the neck shaft/junction. Previous researchers have demonstrated that the superior/inferior ratios of cortical thicknesses and areas are significantly lower in humans than in apes and that this trend can be found in the fossil record for humans dating back 3.4 million years (Lovejoy et al., 2002; Ohman et al., 1997).

Galik et al. 2004 extended this comparison back 3 million years by measuring the cortical bone superior/inferior thickness ratios in BAR 1002’00 and found it to be more similar to humans than to apes. This study further examines the cortical bone distributions of the femoral neck of BAR 1002’00 through normalized TMA, which reflects the skewness of its distribution. This method has the advantage of incorporating all of the cortical bone in the cross-section into the measurement, instead of just the bone at a superior/inferior margin. Skewness about the principal axis is also invariant to rotation, decreasing the likelihood that errors in assigning the anatomical axis caused the different values. This is particularly important for fragmentary fossil remain where the assignment of anatomical axis is only a guess.
The human samples had significantly higher $S_{AP}$ and $S_{VV}$ than the chimpanzee samples. Their ranges did not even overlap, except at the 40% length position (where unfortunately, the BAR 1002’00 specimen does not yield a clear image). The low extend of overlap is not surprising, since both human and chimpanzee femoral necks are more circular closer to the femoral head. There appears to have been a slight trend for increasing skewness (more cortical bone distributed inferior to the centroid) in the humans for $S_{AP}$ but this trend disappeared when reoriented to $S_{VV}$. The differing distributions of cortical bone indicate a different load environment for human and chimpanzee femoral necks.

This study, however, is at variance with the results reported by Galik et al. 2004. The cortical bone distribution across the whole neck studied here in BAR 1002’00 fell within the chimpanzee range for $S_{AP}$ and $S_{VV}$. However, for normalized skewness about the major axis BAR1002’00 fell into the middle of the chimpanzee range at the 60% level, but within the lower end of the range at the 100% level. For normalized skewness about the major axis, the chimpanzee and human ranges overlap extensively, with BAR 1002’00 falling into the area of overlap. There are several possible interpretations of this result. The first is that *Orrorin tugenensis* was not bipedal (at least not in an exclusive or obligate sense) and therefore the specimen BAR 1002’00 would be expected to have a femoral neck cortical bone cross-sectional distribution similar to that of apes. However, this interpretation would require us to ignore the independent external anatomical analyses of Senut et al. 2001 and Richmond and Jungers 2008. It is widely noted that the external anatomical features of *Orrorin tugenensis* femora exhibit many indicators of bipedal locomotion, including a long femoral neck and an obturator externus groove. Another other
possibility is that *Orrorin tugenensis* was bipedal but had not yet evolved the uniquely human abductor apparatus among other changes. The latter alternative is compatible with the common inference that in evolution, changes in behavior often precede the evolution of structural modification.

4.6 REFERENCES


CHAPTER 5
THE CALCAR FEMORALE AS A CORRELATE OF BIPEDAL LOCOMOTION

5.1 ABSTRACT

The calcar femorale (CF) is a plate of dense bone internal to the lesser trochanter and continuing to approximately the mid-point of the posterior medial femoral neck wall in humans. It is visible in computerized tomographic images of the 6 million year old femoral fragment BAR 1003’00, among the oldest specimens pertinent to reconstructing the evolution of human bipedal locomotion. A strongly expressed CF has been used as an indicator of bipedality. If true, then there should be a quantifiable difference in the CF among hominoids. The extent of CF expression in apes has not been reported previously. To test the claim that its strong presence is indicative of bipedal locomotion, in this study the normalized CF length was measured from computerized tomographic images at five locations along the proximal portion of BAR 1003’00 plus samples of the 9 human, 10 chimpanzee, and 10 orangutan femora. The human sample exhibited CF lengths that were consistently greater at each location than the chimpanzees. The BAR 1003’00 CF was more similar to humans. Orangutans exhibited variable but generally negligible CF expression. The chimpanzee and human CF ranges overlapped heavily; therefore, if its expression is unquantified, CF presence alone is not suitable as a diagnostic characteristic for bipedality. The chimpanzee femora were more variable both in the occurrence of the trait and, where present, its extent in the proximal femur. A plausible explanation for the
greater CF variation in chimpanzee femora is that they are loaded more variably than in humans.

5.2 INTRODUCTION

Examination of the serial CT scans of the 6 million year old hominid femur BAR 1003’00 revealed a detectable projection of denser material within the trabecular bone of the proximal diaphysis. This projection, known as the “calcar femorale” (CF), is a ridge that originates deep to the lesser trochanter on the posteromedial surface. The CF is a biomechanically important element of the proximal human femur that commonly is overlooked or misunderstood as a component of the structural system which functions in human upright posture and bipedal locomotion. The literature on hominid origins contains sporadic references to the CF as a structure that is diagnostic for the evolution of human upright posture and bipedal locomotion. About the femur fragment from Maka, Ethiopia (circa 4 mya), White (1984) wrote “The internal anatomy of this bone is remarkably well preserved and very clearly visible in all the derived images. In contrast with the typical pongid condition, the ventral portion of the neck in the fossil displays a cortex thickened relative to that through the superior portion of the neck. Both this feature and the strong calcar appear to represent adaptations to a habitually bipedal mode of locomotion.” However, over the succeeding quarter of a century, no evidence in support of the latter statement about the CF has been made available, despite publication of a long and detailed study of this particular specimen (Lovejoy et al., 2002). Other
mentions of the CF in relation to human evolution are sparse, indeterminate, and uninformative.

Grine et al. (1995) described the proximal half of a hominid femur recovered from deep within a paleokarst feature at the Berg Aukus mine in Northern Namibia. It was not possible to place the find in geochronological context, but from the morphology of the specimen they inferred that it finds its closest similarities within archaic *Homo sapiens* and *Homo erectus*. This proximal femoral fragment has more cortical bone at midshaft than any of the more than 700 extant and fossil human specimens with which it was compared. Proximal CT sections are said to have showed a well-defined calcar femorale. This structure is described as having extended from the posteromedial aspect of the diaphysis at the level of the lesser trochanter and then passing anteromedially into the neck. Photographs or CT scans showing the calcar femorale were not shown, however, and no dimensions were provided from which the extent of the feature could be evaluated. Reed et al. (1993) studied a left proximal femur (MLD 46) from Member 4, Makapansgat, South Africa. The specimen consists of the head, neck, and a short portion of the proximal shaft extending to just below the lesser trochanter. The possible presence of a calcar femorale in MLD 46 was studied using computerized axial tomography. However, the heavily mineralized and calcitic interior of the bone precluded identification of a CF.

Because the BAR 1002’00 and BAR 1003’00 specimens, dated to circa six million years ago (Senut et al., 2001) comprise the oldest direct evidence for upright posture and
bipedal locomotion (Galik et al., 2004), this paper provides a comparative context for
documenting the earliest known evolutionary occurrence of the human CF. The claim
that a “strong calcar” is indicative of bipedal locomotion embodies a testable hypothesis.
In this study a simple method for measuring the CF was applied to BAR 1003’00 and
samples of humans and chimpanzees.

5.3 MATERIALS AND METHODS

The specimens that comprise the evidence for what appears to be the earliest known CF
are the proximal femoral fragments BAR 1002’00 and BAR 1003’00. Along with BAR
1215’00, a smaller fragment of proximal femur lacking its head and neck and measuring
only about 20 mm of the upper diaphysis just below the base of the greater trochanter,
which also is missing, these specimens comprise part of the hypodigm (sample from
which the characters of a population are to be inferred) of a hominoid primate taxon
referred to by its discoverers as *Orrorin tugenensis*. The entire sample derives from four
localities (Aragai, Cheboit, Kapcheberak, and Kapsomim) in the Lukeino Formation,
distributed along the eastern approach to the Tugen Hills in the Baringo District of
Kenya. The sample includes more than 20 separate fossil fragments assignable to at least
five individuals. The BAR 1002’00 and BAR 1003’00 specimens are described more
fully in two of our group’s previous publications (Galik et al., 2004; Senut et al., 2001).
The CT scans of the BAR 1002’00 and 1003’00 were compared with a sample supplied
by the Mammalogy Department of the National Museum of Natural History
(Smithsonian) comprising CT scans of 9 extant humans (*Homo sapiens*) and 10
chimpanzees (*Pan troglodytes*). CT scans of 10 orangutans (*Pongo pygmaeus*) were examined but no trace of a CF was found in any of them.

The CF often has been described in the anatomical and anthropological literature, as noted previously, but commonly has not been measured or its extent otherwise quantified (in fact, as noted, we are aware of no specimens for which this previously has been done). A further complication arises from the fact that the single term calcar femorale is used for two different structures in the same anatomical region. As stressed by Newell (1997), following Harty (1957), many orthopedic surgeons continue to apply the term calcar femorale to the thickened, dense cortical bone of the inferomedial neck at its junction with the shaft (illustrated clearly in Newell’s Figure 6; see Chapter 2 here). This unfortunate confusion of fundamentally different structures in the same general region of the proximal femur is understandable, given that the “orthopedic calcar” is an identifiable, thickened region that is concerned with support and the transfer of weight from the femoral neck to diaphysis, and is involved in hip replacement operations.

When the CF is conceived correctly as a three-dimensional internal feature of the proximal femur with variable length, thickness, orientation and composition (in terms of tissue density), difficulty in its quantification becomes understandable. As noted by Li and Aspden (1997), “The calcar is a compact calcified tissue, with a typical thickness of less than 1 mm, which makes difficult the processing of samples for physical measurements using conventional testing machines.” Many studies (including this one) use serial CT sections spaced 1 mm apart, so depending on the orientation of the scan, it
would be possible to miss the occurrence of the CF. However, serial cross-sections largely obviate this problem.

The measurement procedure that we followed was arrived at independently, but resembles that which subsequently was discovered to have been described (albeit somewhat unclearly) by Glinkowski and Ciszek (1989) for use on radiographs. The approach used in the present paper also was similar to some of the simpler techniques employed by Laine et al. (1997) on their sample of 30 axial slices on each of 50 human cadaver femora. These researchers used a variety of image analysis methods ranging from basic thresholding on the more distal femoral shaft, to edge detection operators and finer level local thresholding in the more complex regions of the metaphyseal edge of the femur. When the CT imaging results subsequently were checked by Laine et al. (1997) against caliper-based measurements made on physical sections of bone at ten different levels, the difference between the dimensions from image processing and manual measurements differed by an average of 1.1 mm ± one SD of 0.7 mm. The discrepancies between virtual and physical measurements were lowest (0.9 mm ± 0.6 mm) in the distal slices having highest cortical thicknesses and highest on the proximal slices having the lowest cortical thickness (1.3 mm ± 0.8 mm).

The CT imaging techniques used here were described previously (Galik et al., 2004; Kuperavage and Eckhardt, 2009). The Amira 4.1.1 image processing system was used to take the measurements on the CF in a plane perpendicular to the long axis of the femoral diaphysis. On each femur measurements were taken on five slices: Slice 1 corresponds
to slightly below the mid-point of the femoral neck. Slice 3 corresponds to a position superior to the lesser trochanter. Slice 2 is situated halfway between Slices 1 and 2. Slice 5 corresponds to the widest part of the lesser trochanter, and Slice 4 is midway between Slices 3 and 5 (See Fig. 5.1).

Figure 5.1: The 5 slices locations on BAR 1003’00 using Amira 4.1.1.

The exterior boundary of each image was determined using the “full-width at half-maximum” principle (Ohman et al., 1997). The CF was measured from the tip of the CF, located visually, to the exterior boundary, along a line corresponding to the long axis of the CF (See Figure 5.2). In some specimens the CF was curved slightly, but it is unlikely that the curvature was of an extent that would affect the measurement substantially.
Fig. 5.2: Line drawn over Slice 1 in BAR 1003’00 in order to show the measured length of the CF.

In our work the CF was measured from the visible tip to the external boundary because it was believed that this measurement would be repeatable. The alternative would have been to have measured the CF from its distinguishable tip to its base just within the cortical wall of the femur, but because the CF appears to be relatively continuous in density with the external cortical wall, therefore this approach would have required making an arbitrary assumption about the point at which the CF base begins. With the method employed here it is possible that variability in cortical bone thickness could affect this measurement of the CF length. However, on a subsample of three humans and three
chimpanzees the CF was measured from its tip to the exterior boundary and from the tip to its estimated base, where the base was defined as a point in the middle of the two outer corners of the CF. When the data from the first method was plotted against the data from the sub-samples, the magnitude of the measurements shifted downward, but the pattern itself did not change among specimens. From this pattern it was concluded that potential variations in the juncture of the base with the cortical wall did not introduce any material misrepresentation of the structures being measured. On each femur the widest diameter of the cross-section immediately inferior to the lesser trochanter was used to normalize the data.

5.4 RESULTS

The CF can be seen in the CT scan slices of both BAR 1002’00 and BAR 1003’00, but in the former were considered to be too indistinct to be reliably quantifiable. The BAR 1003’00 specimen preserves the CF with noteworthy clarity. Results from measurements of the CF on BAR 1003’00 are summarized in Table 5.1.

Table 5.1: Absolute and normalized CF length in BAR 1003’00.

<table>
<thead>
<tr>
<th>Level</th>
<th>Length (mm)</th>
<th>Norm. Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.456</td>
<td>0.518</td>
</tr>
<tr>
<td>2</td>
<td>1.552</td>
<td>0.553</td>
</tr>
<tr>
<td>3</td>
<td>1.566</td>
<td>0.557</td>
</tr>
<tr>
<td>4</td>
<td>1.093</td>
<td>0.389</td>
</tr>
<tr>
<td>5</td>
<td>0.583</td>
<td>0.208</td>
</tr>
</tbody>
</table>

Length (mm) and normalized length for BAR 1003’00.
Structures that can be characterized as representing the CF are found consistently in humans, with some variation in expression, as has been known for about a century and a half. Tables 5.2 and 5.3 provide some quantification of that variation in our small sample of specimens. A search of the literature has produced no corresponding previous record of such systematic quantification, however limited.

Table 5.2: Absolute CF length in humans.

<table>
<thead>
<tr>
<th>Slice</th>
<th>Median</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.36</td>
<td>1.51</td>
<td>0.38</td>
<td>1.06</td>
<td>2.05</td>
</tr>
<tr>
<td>2</td>
<td>1.79</td>
<td>1.58</td>
<td>0.38</td>
<td>1.00</td>
<td>1.91</td>
</tr>
<tr>
<td>3</td>
<td>1.56</td>
<td>1.51</td>
<td>0.35</td>
<td>0.95</td>
<td>1.91</td>
</tr>
<tr>
<td>4</td>
<td>1.50</td>
<td>1.45</td>
<td>0.43</td>
<td>0.97</td>
<td>2.06</td>
</tr>
<tr>
<td>5</td>
<td>1.36</td>
<td>1.34</td>
<td>0.27</td>
<td>0.90</td>
<td>1.74</td>
</tr>
</tbody>
</table>

Descriptive statistics of the absolute length (mm) of the CF in humans.

Table 5.3: Normalized CF length in humans.

<table>
<thead>
<tr>
<th>Slice</th>
<th>Median</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.41</td>
<td>0.43</td>
<td>0.09</td>
<td>0.33</td>
<td>0.55</td>
</tr>
<tr>
<td>2</td>
<td>0.48</td>
<td>0.45</td>
<td>0.09</td>
<td>0.31</td>
<td>0.55</td>
</tr>
<tr>
<td>3</td>
<td>0.43</td>
<td>0.43</td>
<td>0.09</td>
<td>0.29</td>
<td>0.55</td>
</tr>
<tr>
<td>4</td>
<td>0.41</td>
<td>0.41</td>
<td>0.10</td>
<td>0.31</td>
<td>0.55</td>
</tr>
<tr>
<td>5</td>
<td>0.39</td>
<td>0.39</td>
<td>0.06</td>
<td>0.30</td>
<td>0.50</td>
</tr>
</tbody>
</table>

Descriptive statistics of the normalized length of the CF in humans.

Tables 5.4 and 5.5 document and quantify the presence of a structure comparable to the CF of extant humans in its approximate location and orientation, though not to the same extent, in chimpanzees as well.
Table 5.4: Absolute CF length in chimpanzees.

<table>
<thead>
<tr>
<th>Slice</th>
<th>Median</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.90</td>
<td>0.91</td>
<td>0.21</td>
<td>0.60</td>
<td>1.11</td>
</tr>
<tr>
<td>2</td>
<td>0.96</td>
<td>0.93</td>
<td>0.23</td>
<td>0.53</td>
<td>1.24</td>
</tr>
<tr>
<td>3</td>
<td>0.81</td>
<td>0.77</td>
<td>0.27</td>
<td>0.34</td>
<td>1.16</td>
</tr>
<tr>
<td>4</td>
<td>0.64</td>
<td>0.64</td>
<td>0.15</td>
<td>0.45</td>
<td>0.82</td>
</tr>
<tr>
<td>5</td>
<td>0.63</td>
<td>0.63</td>
<td>0.37</td>
<td>0.37</td>
<td>0.89</td>
</tr>
</tbody>
</table>

Descriptive statistics of the absolute length (mm) of the CF in chimpanzees.

Table 5.5: Normalized CF length in chimpanzees.

<table>
<thead>
<tr>
<th>Slice</th>
<th>Median</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.36</td>
<td>0.35</td>
<td>0.09</td>
<td>0.24</td>
<td>0.47</td>
</tr>
<tr>
<td>2</td>
<td>0.36</td>
<td>0.36</td>
<td>0.08</td>
<td>0.24</td>
<td>0.49</td>
</tr>
<tr>
<td>3</td>
<td>0.30</td>
<td>0.30</td>
<td>0.09</td>
<td>0.13</td>
<td>0.39</td>
</tr>
<tr>
<td>4</td>
<td>0.27</td>
<td>0.25</td>
<td>0.04</td>
<td>0.19</td>
<td>0.29</td>
</tr>
<tr>
<td>5</td>
<td>0.25</td>
<td>0.25</td>
<td>0.14</td>
<td>0.16</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Descriptive statistics of the normalized length of the CF in chimpanzees.

Both the human and chimpanzee samples exhibited similar variation in the length at each slice. However, CFs in chimpanzees are more variable in their occurrence (presence or absence) and the location at which it begins and ends along the femur. A CF is found in 7 out of 10 chimpanzees, while 9 out of 10 humans had pronounced CFs and all 10 had at least a trace. Concerning its location along the proximal femur, in chimpanzees the CF began and ended at a variety of locations, while in humans it started fairly consistently immediately below the mid-point of the femoral neck and stopped at around or immediately distal to the widest part of the lesser trochanter.
When normalized lengths of the CF are compared, the lengths are seen to be moderately greater in humans than in chimpanzees, but perhaps the most surprising result is the extent of overlap between these hominoid taxa, given the fact that the CF is an internal anatomical feature of the proximal human femur that is encountered so routinely that it has been taken as diagnostic of hominid status; that is, of upright posture and bipedal locomotion, and its presence in fossils is taken as indicative of hominid status (e.g. Reed et al., 1993; and particularly White, 1984). Also of interest is the observation that in the first three slices, values for normalized length of the CF in BAR 1003’00 exceed those of extant humans, although the normalized lengths are lower for the lower two slices in the fossil.

![Calcar Femorale Length (mm)](image)

Figure 5.3: CF length (mm) at each of the slice levels for humans, chimpanzees and BAR 1003’00. Data points corresponding to BAR 1003’00 are offset for clarity.
Figure 5.4: Normalized CF length at each of the slice levels for humans, chimpanzees and BAR 1003’00. Data points corresponding to BAR 1003’00 are offset for clarity.

5.5 DISCUSSION

In this discussion it is assumed that comparability of location and bone composition constitutes evidence for homology of the CF in BAR 1003’00, humans and chimpanzees, though more stringent standards for this assumption should be considered desirable. Scanning electron microscopic studies similar to those carried out by Whitehouse and Dyson (1974) might be useful in this regard.

The presence of a CF in each of the specimens, BAR 1002’00 and BAR 1003’00, assigned to the taxon *Orrorin tugenensis*, is not unexpected given the previous support for this taxon as a hominid (Senut et al., 2001) and the widely held belief that a well developed CF is diagnostic of hominid bipedal locomotion (e.g. White, 1984). In fact,
when our initial observations established the presence of this structure in the fossils, they were taken by us as confirming the initial diagnosis of *Orrorin* as a hominid (Senut et al., 2001) that had been based on the external morphology of the specimens. Although this diagnosis initially was disputed, there has been subsequent independent from an independent using the same external features (Richmond and Jungers, 2008), as well as from our own analysis of CT scans of cortical bone in the femoral neck of BAR 1002’00 (Galik et al., 2004). Against this background, the findings reported in this chapter are novel in two regards: first, the evidence that the BAR 1002’00 and BAR 1003’00 each do show the presence of a CF, and that the BAR 1003’00 specimen shows what appears to be a unique pattern in this structure; and second, that a majority of the chimpanzees in the comparative sample also show some presence of a CF.

In the first regard, the pattern that even one of the specimens, BAR 1003’00, shows is intriguing: nearly hyper-human at the more proximal portion (slices 1 to 3), then tapering to just below the human range in slice 4, and then below the lower end of the chimpanzee distribution in slice 5. There may be functional explanations for such a pattern, but at this point, given the slim evidential base, any detailed hypotheses on this point would be purely speculative.

On the second point, the presence of a clearly expressed CF in the majority of the chimpanzee specimens was unexpected and had not been reported previously in the scientific literature. There is considerable variation in extents and locations of the CF in chimpanzees. A plausible explanation for this variation might be that their proximal
femora are loaded in more variable manners than in humans. This would be consistent with the more evenly thickened cortical bone at the neck/shaft junction in chimpanzees than in humans. This inference may be testable with CT scans of chimpanzees whose femora are known to have been subjected to loading patterns known to have been different, based on behavioral observations in free-ranging and captive chimpanzees.

The literature on behavioral, particularly locomotor, patterns of captive chimpanzees (Elftman, 1944) and their free-ranging conspecifics (Kortlandt, 1962; van Lawick-Goodall, 1968) by now spans more than half a century, and is too extensive to be reviewed here in its entirety, partly because many of the earlier reports are anecdotal and largely unquantified. More recently, however, Hunt (1992) provided a highly quantified, comparative study of the positional and locomotor behavior of chimpanzees (*Pan troglodytes*) in the Mahale Mountains and Gombe Stream Reserve, Tanzania; baboons (*Papio anubis*) at the Gombe Stream Reserve also were included as a comparative/control species of non-hominoid primates. In this study, the most common positional behavior observed was sitting, which comprised 61% of all waking behavior. Knuckle-walking was the second most common positional mode, comprising 15.7%; when periods in stationary positions are excluded, quadrupedal knuckle-walking was the most common mode of locomotion used by chimpanzees when moving between feeding patches and when traveling with no recognized purpose. Progressively less chimpanzee positional modes included lying, arm-hanging with support, standing (in fact, chimpanzees spent lesstime standing than did baboons), climbing, squatting, palm-walking, and suspensory locomotion (brachiation, dropping, clambering, etc.). Bipedal standing, clinging, and
running totaled 0.3% of observed time spent by chimpanzees; bipedal walking was the least common of all the observed categories, at less than 0.1%.

In his study, Hunt (1992) considered these positional mode frequencies to constitute an important consideration in assessing the evolutionary influences on positional anatomy. His argument was that the more frequent a given positional behavior, the greater the need for reinforcing the locomotor apparatus against positional-mode-specific wear and injury; the greater the necessity for shaping bones and muscles to prevent fatigue; and the greater scope for energy conservation if the mode is more efficient.

In this context, Hunt inferred that the distinctiveness of bipedal walking as a chimpanzee behavior pattern is low and the stress that it imposes is medium, factors that he used to argue against any significant anatomical adaptations. In his study, chimpanzees were observed to climb significantly more often than did baboons, and he considered climbing to entail high stress because it involves acceleration directly against gravity. Aside from sitting, the most frequent positional mode used by chimpanzees was knuckle-walking. Since this mode of locomotion is diagnostic of African apes, particularly chimpanzees, perhaps it is toward this mode of locomotion that further structural and functional studies of the CF might be directed.

Another study (Doran, 1993) broaden the comparative perspective on chimpanzee locomotion from *Pan troglodytes* to *Pan paniscus*. Although beyond the scope of this paper, it is likely that observational and experimental studies can be structured to
investigate further the basic observations reported here on the occurrence of CF in chimpanzees.

5.6 REFERENCES


CHAPTER 6

SUMMARY

6.1 INTRODUCTION

This chapter will cover the most significant findings and limitations from the three experimental chapters (Chapters 3 through 5), followed by a general discussion and directions for potential work.

6.2 SUMMARY OF FINDINGS

The specific aims of this work were to:

4. To measure the geometric cross-sectional properties in the femoral diaphysis of BAR 1002’00 and BAR 1003’00 and compare these values found in the background literature on extant humans and SK 82 and SK 97.

5. To measure cortical bone distribution in femoral necks of BAR 1002’00 and BAR 1003’00 using normalized third moment of area and to compare these to a sample of human and chimpanzee femora.

6. To measure the calcar femorale in a human and chimpanzee sample in order to determine if functions as a diagnostic characteristic of bipedal locomotion.
In Chapter 3 geometric cross-sectional properties of the femoral diaphyses of BAR 1002’00 and BAR 1003’00 were measured. Due to the incomplete nature of the fossilized specimens, the specific geometric cross-sectional properties were limited to cortical areas and various derivations of second moment of area. These geometric properties were compared with previous findings from SK 82 and SK 97, hominid fossils from two million years ago, and a sample of extant humans from Pecos Pueblo, New Mexico. The *Orrorin* femoral specimens BAR 1002’00 and BAR 1003’00 both are notably robust, exhibiting cross-sectional areas with relatively high percentages of cortical bone in comparison to a contemporary sample. Total cross-sectional area (TA) is markedly smaller for BAR 1002’00 and BAR 1003’00 than for either of the Swartkrans early hominid proximal femora or the Pecos Pueblo sample, but %CA of the two Kenyan fossil femora are comparable to those from Swartkrans, and one-third higher in percentage of cortical area than the modern sample. The Orrorin femora exhibited low CA and J when compared to the two samples (later fossil and modern), as a result of the smaller sizes of the individuals to which they belonged. It is difficult to find the appropriate size standardization because of the incomplete nature of the material. This chapter addressed the first specific aim.

In Chapter 4, normalized third moment of area was used to quantify the distribution of cortical bone in femoral necks of humans and chimpanzees. As observed by previous researchers (Ohman et al., 1997), humans exhibit femoral neck cortical bone distributions that are distinctly different from apes due to the uniquely human abductor apparatus. Galik et al. (2004) found that superior-inferior thickness ratios of BAR 1002’00 were
more similar to those found in humans. In this study third moment of area was used in place of superior/inferior thickness ratios. It was thought that it would be a more useful way to quantify this distribution than superior/inferior thickness ratios because it incorporates all of the cortical bone in the measurements. This was compared to the normalized third moment of area of cortical bone distribution in the femoral neck of BAR 1002’00. BAR 1002’00 exhibits some cortical bone distributions that are more similar to chimpanzees than to humans, but others that fall within the extant human range.

These findings indicate that either the taxon referred to as *Orrorin tugenensis* was not a biped, at least not in an exclusive or obligate sense of extant humans, or that *Orrorin* was bipedal but had not yet developed all of the uniquely human structural patterns that characterize the uniquely modern human abductor apparatus. This chapter addressed the second specific aim.

In Chapter 5 lengths of the calcar femorale were measured in cross-sections at five locations along the length of the proximal femur in a sample of chimpanzees and humans in order to test the hypothesis that a well-developed calcar femorale is related to upright posture. It was found that the calcar femorale tends to be longer (both in a relative and absolute sense) in humans than in chimpanzees, even though the ranges overlap. Also, its expression in chimpanzees is more variable both in its occurrence (7 out of 10 chimpanzees had calcar femorale while 9 out of 9 humans had visible calcar femorale, even though it was only measurable in 8 out of the 9) and the locations at which it begins and ends. The more variable calcar femorale in chimpanzees is consistent with their
more variable loading patterns in the proximal femur. BAR 1003’00 appears to have a calcar femorale more similar to that of extant humans than to chimpanzees. Wider comparisons were not possible because of the paucity of published findings on this structure in populations other than extant humans, and the further complication that many studies of the calcar femorale in fact present data on an entirely different structure. These findings indicate that the presence of a calcar femorale being taken as a clear indicator of upright posture is unwarranted, even though it tends to be better developed in humans. This chapter addressed the third specific aim.

6.3 LIMITATIONS

The primary limitation of these studies is the number and quality of the CT images of the specimens BAR 1002’00 and BAR 1003’00. To put discussion of these limitations into context, it should be noted that, however imperfect are the CT images analyzed here, there are no data of comparable quality sampled from the human fossil record for at least the succeeding two million years, and after that point very few in any case. Furthermore, even given the limitations of the image qualities for the BAR 1002’00 and BAR 1003’00 specimens, from them it has been possible in this thesis to add structural and functional perspectives that would not have been possible from external surface morphology alone.

In terms of the specific limitations imposed by the study specimens, foremost is their limited number. Although paleoanthropology is a discipline in which elaborate adaptive and phylogenetic single specimens commonly are advanced from single specimens, other
disciplines of functional and population biology are more attentive to considerations of potential sampling bias and resultant limitations to the generality of conclusions drawn. In terms of image qualities, white overflow was noted in a previous study based on these CT images (Galik et al., 2004). White overflow can cause overestimation of thickness of dense material, especially for very dense material such as fossils. A higher resolution CT scanner with appropriate adjustments made for the dense nature of the material would be more appropriate than the medical scanner used. In addition, for examining the cortical bone distribution in BAR 1002’00 it would be more appropriate for the investigators who initially collected the data to have made slices perpendicular to the long axis of the femoral neck, instead of the long axis of the femoral diaphysis. Amira 4.1.1 was used to correct for this problem but the Lanczos filter still introduces an error for which it is difficult to account. The comparative samples (10 for chimpanzees and 9 for humans) are modest in number and may not have been adequate for establishing the frequency and extents of occurrence of the chimpanzees and humans. Finally, the procedural error in selecting the external and internal cortical boundaries using the FWHM principle was not taken into account in these studies. In order to do so would require testing the sensitivity of the properties to the selected threshold settings.

6.4 DISCUSSION

The three studies in this dissertation examined several interrelated internal anatomical features that are pertinent to interpreting the posture and locomotion of the fossilized femora BAR 1002’00 and BAR 1003’00, assigned to the taxon Orrorin tugenensis.
These studies contribute important new data to continuing discussions of several very large questions, though without resolving any of them:

1. The pattern of evolutionary relationships among the large bodied Hominoidea (the African apes including the single species *Gorilla gorilla* and two generally accepted chimpanzee species, the common chimpanzee, *Pan troglodytes* and the pygmy chimpanzee, *Pan paniscus*; and the sole surviving large-bodied Asian ape, the orangutan, *Pongo pygmaeus*).

2. The timing of hominid origins, considered here to be the time of divergence of a human lineage from that of the other African apes, particularly chimpanzee, which abundant data favor as our nearest relative, based on the totality of the morphological and molecular evidence.

3. The nature of the evolutionary changes that transformed the locomotor apparatus characteristic of ancestral African apes to that of extant humans.

4. The interplay of genetic and environmental factors in the development of skeletal, particularly femoral, architecture.

Evolutionary relationships among the large bodied hominoid primates have been discussed at least since the time of Charles Darwin (1859, 1871) and with continuing vigor ever since. The original, largely comparative anatomical, evidence on hominoid phylogenetic patterning first was supplemented by molecular perspectives (Sarich and Wilson, 1966), then largely supplanted by them. In recent years a consensus has emerged and is broadly accepted, that among Old World higher primates, the orangutan (*Pongo pygmaeus*) was first to diverge. Patterns of relationship among the African Hominoidea
still are debated to some extent, though most workers would consider the gorilla (*Gorilla gorilla*) to have diverged next, followed by chimpanzees. The order of splitting among common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*, though this commonly-recognized taxon may not be genetically incompatible with common chimpanzees), and extant humans (*Homo sapiens*) continues as a matter of some dispute (Patterson, et al., 2006; Ebersberger, 2007; Wakely, 2008). However, for the last quarter century there has been one persistent holdout for the orangutan as the nearest relative of extant humans, with the argument having been begun by Schwartz (1984) and continuing to the present (Grehan and Schwartz, 2009). Although this thesis was not designed to analyze the CT scans that are part of our comparative sample, all three of the papers included in this thesis bear to some extent on this point, since they all show how very close all of the anatomical and biomechanical properties measured here for BAR 1002’00 and BAR 1003’00 are to comparable measures on chimpanzees as well as various fossil and extant humans. In particular, the paper on the calcar femorale shows the somewhat unexpected presence of this structure in chimpanzees, but its virtually complete absence in orangutans. Much more work remains to be done in this regard, but it is probable that future studies of this particular feature will contribute more to studies of biomechanical function than primate phylogeny.

With regard to the timing of hominid origins, in the year immediately following their discovery, the *Orrorin tugenensis* fossils were described as hominids dated to approximately 6 million years ago (Senut et al., 2001). In the next year, Brunet et al., (2002) announced the discovery of what they believed to be another hominid up to one
million years older than the finds made by Senut and her colleagues at Baringo, Kenya. Subsequently the finds made by Brunet and his colleagues have been called into question on the grounds that they were unlikely to represent bipedal hominids (Wolpoff et al., 2002; Wolpoff et al., 2006). These developments leave *Orrorin tugenensis* as quite possibly representing the earliest known hominids for which morphological and biomechanical inferences are compatible with an inference of upright posture and bipedal locomotion. The several papers included in this thesis add to our knowledge of the origins of uniquely human posture and locomotion, and at the same time suggest multiple directions for much further work in this area.

Regarding the evolutionary changes that transformed the locomotor apparatus of some African, presumably chimpanzee-like ancestor into that which is recognizably human in numerous details at some time around four million years ago, there is a gap of nearly two million years between the *Orrorin tugenensis* materials analyzed here and those that are known in detail for *Australopithecus afarensis*. See Lovejoy (1988) for an overview of nearly two decades of studies on the Hadar and Laetoli materials attributed to that taxon of undoubted early hominids. Fossils pertinent to the interpretation of hominid posture and locomotion from the intervening temporal gap are known (White et al., 1994; Haile-Selassie, 2001) but remain undescribed. Until that gap has been filled by detailed descriptions and analyses, we must be reliant on what can be inferred from further work on the sample described here, supplemented by analyses of more specimens that might be recovered from further field studies now underway.
The interplay among various genetic and environmental factors in the development of skeletal features across the lifespan is a major topic of current research in many fields of modern biology. For an original contribution and extensive literature review see, for example, Dalou (2007). Efforts also are being made to extend studies of gene-environment interactions during development into studies of human evolution (e.g., Lovejoy, et al., 2003). Among the implications of such an approach is recognition that the proper units of analysis for both function and phylogeny are not arbitrarily defined traits, but rather the morphogenetic fields that underlie them. The view of Lovejoy and his colleagues is that more accurate comprehension of human evolutionary history will lead to rethinking of such problems, dealt with in some of the studies included in this thesis, as the operation of selection on anatomical landmarks and the potential role of homology in phylogenetic reconstruction.

6.5 POTENTIAL FUTURE WORK

What follows is a limited list of specific things that could be accomplished with the data already available.

1. Estimation of body size (mass, stature) means and ranges for members of the taxon that has been designated as *Orrorin tugenensis*. These estimates could be based on femoral head diameter of BAR 1002’00 and possibly diaphyseal diameters of both femoral fragments. With such estimates, further scaling of the various data presented here would be possible. This work would be immediately pertinent to objective 1.
2. Modeling of the effects of changes in hip musculature (e.g. of the adductor apparatus) using SIMM to experimentally alter muscle origins, insertions, and other variables. This research could extend and expand the inferences addressed by objective 2.

3. Assessing the causes of and variations in the loading of proximal femora, in both chimpanzees and orangutans. The finding that chimpanzees exhibit a measurable calcar femorale, the range of expression of which substantially overlaps that of extant humans, calls into question the widespread assumption that a well-developed calcar femorale is indicative of upright posture. Chimpanzees exhibit this structure despite their spending much more time in knuckle-walking quadrupedal locomotion than in bipedal locomotion. At the same time, orangutans, which engage in little or no knuckle-walking (or bipedal locomotion, except limitedly in the forest canopy), exhibit no detectable calcar femorale. These investigations would be pertinent to objective 3.

Among the myriad investigations concerning the origin and evolution of human bipedal locomotion that can be imagined, the ones listed immediately above, while seemingly modest, have reasonable probabilities of being attainable.
6.6 REFERENCES


Cortical bone distribution in the femoral neck of hominoids: Implications for the


APPENDIX A

The original code for calculating moments of area was written by me. The modified version was written by H. Joseph Sommer III (section designated “HJS code”).

% Calculate Centroid and Moments of Area
clc
clear all
close all
data1 = load ('human2_slice3.m');
p = 0.0434; % pixel length (mm)
a = p^2; % pixel area (mm^2)

%%% Slice 3 %%%
D = data1(:,:); D = D'; D = flipud(D);

% HJS code - all computations using mm

% size of image
[ nrow, ncol ] = size(D);
x = p * ones(nrow,1) * (1:ncol);
y = p * (1:nrow)' * ones(1,ncol);

% area and centroid
Dp = D * p^2;
A = sum( sum(Dp) );
xc = sum( sum( Dp .* x ) ) / A;
yc = sum( sum( Dp .* y ) ) / A;

% shift to centroidal coordinates
x = x - xc;
y = y - yc;

% second moments
Iyy = sum( sum( Dp .* x .* x ) );
Ixy = sum( sum( Dp .* x .* y ) );
Ixx = sum( sum( Dp .* y .* y ) );
Imax = .5*(Ixx + Iyy) + (.25*(Ixx-Iyy)^2 + Ixy^2)^.5;
Imin = .5*(Ixx + Iyy) - (.25*(Ixx-Iyy)^2 + Ixy^2)^.5;
J = Ixx + Iyy;
theta = 0.5 * atan( -2*Ixy / (Ixx-Iyy) );

% third moments about X and Y axes
skew_xxx = sum( sum( Dp .* x .* x .* x ) );
skew_xxy = sum( sum( Dp .* x .* x .* y ) );
skew_xyy = sum( sum( Dp .* x .* y .* y ) );
skew_yyy = sum( sum( Dp .* y .* y .* y ) );

skew_norm_yy = skew_xxx / (sqrt(Iyy)^3);
skew_norm_xx = skew_yyy / (sqrt(Ixx)^3);

% second and third moments about principal axes
u = cos(theta)*x  + sin(theta)*y;
v = -sin(theta)*x  + cos(theta)*y;

Ivv = sum( sum( Dp .* u .* u ) );
Iuv = sum( sum( Dp .* u .* v ) );
Iuu = sum( sum( Dp .* v .* v ) );

skew_uuu = sum( sum( Dp .* u .* u .* u ) );
skew_uuv = sum( sum( Dp .* u .* u .* v ) );
skew_uvv = sum( sum( Dp .* u .* v .* v ) );
skew_vvv = sum( sum( Dp .* v .* v .* v ) );

skew_norm_vv = skew_uuu / (sqrt(Ivv)^3);
skew_norm_uu = skew_vvv / (sqrt(Iuu)^3);

Z1 = [xc yc A Ixx Iyy Ixy Imax Imin J skew_norm_xx skew_norm_yy
skew_norm_uu skew_norm_vv theta];

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
CA = a*sum(sum(D)); % total cortical area of the cross-section (mm^2)
%E = slice_area(:,:);
%TA = a*sum(sum(E));

N = size(D); % find image dimensions in number of pixels
m = N(1);
n = N(2);

M = zeros(m,1);  
N = zeros(1,n);

% Calculate Centroid
xa = M;
for i = 1:n
    xa = p*i*a*D(:,i) + xa;
Sigma_xa = sum(xa);
xbar = Sigma_xa/CA;

ya = N;
for i = 1:m
    ya = p*i*a*D(i,:) + ya;
end

Sigma_ya = sum(ya);
ybar = Sigma_ya/CA;
xbar = xbar/p;
ybar = ybar/p;

figure(1)
cif
contour(D,1,'k')
axis equal
grid off

hold on
axis([ 0 ncol 0 nrow ])

r = max([ ncol nrow ]); % convert to radians
theta = thr;
plot([ xbar-r*cos(theta) xbar+r*cos(theta) ], [ ybar-r*sin(theta) ybar+r*sin(theta) ], 'g')
phi = thr + pi/2;
plot([ xbar-r*cos(phi) xbar+r*cos(phi) ], [ ybar-r*sin(phi) ybar+r*sin(phi) ])

end
APPENDIX B

BAR 1002’ 00 and BAR 1003’ 00 were scanned in 2001 by Jacques Treil at the Service du Radiologie in Toulouse, France. The resultant images are available as part of the Supplementary Online Material for the publication by Galik, et al. (2007).

The samples of 10 *Pan troglodytes* and 9 *Homo sapiens* were scanned in 2004 and 10 *Pongo pygmaeus* in 2007 by Bruno Frohlich at the National Museum of Natural History. The femurs were scanned using a medical scanner three at a time. It is our plan that these images, as well as the unpublished ones of BAR 1003’00, also scanned previously by Jacques Treil, will be made available as Supplementary Online Material for a publication now in the form of a partially completed manuscript. In the interim these images could be made available in a file accessible by Committee members.
APPENDIX C

Permission to use comparative data for CHAPTER 3:

John Wiley & Sons, Inc. has no objections to your proposed reuse of this material.
Curriculum Vitae

Adam J. Kuperavage

Education:


Honors:

Sigma Xi Scientific Research Society
American Society of Biomechanics Presidential Award 2005 for abstract presentation “Was the early hominid brain musclebound?”

Articles Published in Referred Journals:


