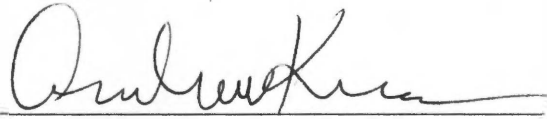


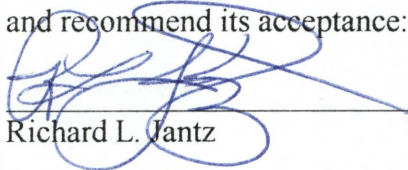
To the Graduate Council:

I am submitting herewith a thesis written by Adam D. Sylvester entitled "Joint Surface Area Proportions and Articular Curvature In AL 288-1: A Functional Interpretation." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Art, with a major in Anthropology.

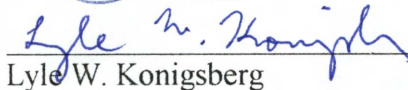


Andrew Kramer, Major Professor

We have read this thesis
and recommend its acceptance:



Richard L. Jantz



Lyle W. Konigsberg

Accepted for the Council:



Associate Vice Chancellor and
Dean of The Graduate School

Joint Surface Area Proportions and Articular Curvature
In AL 288-1: A Functional Interpretation

A Thesis
Presented for the
Master of Arts Degree
The University of Tennessee, Knoxville

Adam David Sylvester

August 2000

Abstract

Body size has been recognized by several authors as one of the most important parameters affecting the biology of an organism. It has been argued that body size plays roles in metabolic cost, mobility, thermoregulation, and foraging strategy. For extinct species body masses can only be estimated using fossil remains and extant reference samples. To accurately estimate body mass the reference sample must have the same relationship between body mass and skeletal elements. Establishing a reference sample with similar body proportions as the fossil species is imperative.

The purpose of this study is to investigate forelimb to hindlimb joint surface area proportions and articular surface curvature in the *Australopithecus afarensis* specimen AL 288-1 “Lucy”. This specimen is compared to reference samples of humans, African apes, and orangutans to determine which most accurately reflects the joint surface area proportions and joint curvature observed in “Lucy”. Joint surface area and articular surface curvature are known to be related to body mass and locomotor repertoire and hence provide clues about body proportions, locomotor and postural behaviors. Findings in this analysis indicate that “Lucy” is a mosaic of human and pongid postcranial joint features. Analyses of joint surface area reveal proportions intermediate between apes and humans but which suggest heavy reliance on the hindlimbs for locomotion. Analyses of joint curvature reveal highly curved joint surfaces consistent with high mobility and multidirectional stability indicative of an arboreal component to Lucy’s locomotor repertoire.

Dedication

To rock climbers everywhere: Who prove that humans have never become *obligate* terrestrial bipeds.



Acknowledgements

I would foremost like to thank my committee members for their valuable guidance and advice. To my committee chair Dr. Andrew Kramer whose ability to direct research makes his deep understanding of scientific investigations obvious. To Dr. Richard Jantz whose perception and insight into the issues of this project were of the greatest assistance. And to Dr. Lyle Konigsberg whose endless statistical knowledge is exceeded only by his patience in explaining it. Thanks are also due to Linda Gordon and Helen Kafka in the Department of Vertebrate Zoology at the National Museum of Natural History for the use of the great ape skeletons. Also at the National Museum of Natural History, I would like to thank David Hunt for arranging my use of the Terry Collection. At the Cleveland Museum of Natural History I would like to thank Lyman Jellema for arranging my visit and Dr. Bruce Latimer for the use of the primate skeletons and fossil cast specimens. Finally I would like to thank my parents for providing the funding for this project and to Angi Christensen for her suggestions and support.

Table of Contents

Chapter 1: Introduction.....	1
Australopithecine Locomotion and the Origins of Bipedality.....	1
Cranially Based Phylogenies.....	7
Joint Function.....	9
Australopithecine Proportions: Functional and Phylogenetic Importance...	10
Chapter 2: Material and Methods.....	20
Sample.....	20
Measurements.....	22
Analyses.....	40
Chapter 3: Results.....	43
Chapter 4: Discussion.....	52
Chapter 5: Conclusion.....	57
References	60
Vitae.....	69

List of Plates

Plate 1: Triangle Digitizer Pattern.....	31
Plate 2: Digital Coordinate Calipers with Accessory Kit.....	39

List of Tables

Table 1: Skeletal Size and Body Mass Correlation	17
Table 2: Analysis of Covariance.....	23
Table 3: G. gorilla / Pan Comparison.....	24
Table 4: Combined African Ape / Human Comparison	25
Table 5: Combined African Ape / P. pygmaeus Comparison.....	26
Table 6: Surface Area Estimation.....	29
Table 7: RMA Regression Formulae for Surface Area and Curvature	44
Table 8: Analysis of AL288-1 Joint Proportions and Curvature.....	47

List of Figures

Figure 1: Relative Mobility.....	11
Figure 2: Latex Casting Method.....	28
Figure 3: Relative Curvature of Joint Surfaces.....	33
Figure 4: Femur Head Measurements.....	35
Figure 5: Acetabulum Measurements.....	36
Figure 6: Humerus Head Measurements.....	37
Figure 7: Scapula Measurements.....	38
Figure 8: Acetabulum on Femur.....	45
Figure 9: Scapula on Humerus.....	45
Figure 10: Humerus on Acetabulum.....	46
Figure 11: Humerus on Femur.....	46
Figure 12: Scapula on Acetabulum.....	48
Figure 13: Scapula on Femur.....	48
Figure 14: Acetabular Shape.....	49
Figure 15: Femur Head Shape.....	49
Figure 16: Humeral Head Shape.....	50

Chapter 1

Introduction

Australopithecine Locomotion and the Origins of Bipedality

In 1925 Raymond A. Dart reported the discovery of a fossilized face and cranial endocast removed from a limestone quarry at Taung in South Africa. Dart recognized this find as representing a juvenile individual of an extinct primate species. In the Taung child Dart observed a mosaic of human and ape characteristics and felt this fossil represented a “creature well advanced beyond modern anthropoids in just those characters, facial and cerebral...” but that “a creature with anthropoid brain capacity and lacking the distinctive, localized temporal expansion which appear to be concomitant with and necessary to articulate man, is no true man.” (Dart 1925, p.198). As a result Dart proposed the creation of a new taxon, *Australopithecus africanus*, to accommodate this individual (Dart, 1925). The proposed taxon was positioned as an extinct species of primate, an intermediate form, linking anthropoids and humans (Dart, 1925). However, Dart’s evolutionary positioning of the Taung Child was disputed by the paleoanthropologists of his day (Grine, 1993). Due in part to the Piltdown hoax, more than thirty years would pass before Dart’s assessment of the fossil was fully accepted.

In Dart’s assessment of the fossil’s characteristics he notes one feature, which, although it has bearing on the phylogeny, also allowed him to consider the locomotor repertoire of this species. An index of cranial measurements indicated the position of the skull on the vertebral column. In the Taung child the index suggested to Dart a posture

more erect than extant anthropoids; that in this creature the hindlimbs were the main limbs of locomotion, or that *A. africanus* was bipedal (Dart, 1925). However, as with his phylogenetic assessment, Dart's suggestion that australopithecines were bipedal would wait more than twenty years for confirmation (see historical overview in McHenry and Berger, 1998).

In 1947 Dart's contention that *A. africanus* was bipedal was confirmed with the discovery of pelvic remains from Sterkfontein (Broom and Robinson, 1947). Since the 1947 discoveries, these and other researchers have emphasized the human appearance of the pelvis, suggesting a human-like gait (Broom and Robinson, 1947; Lovejoy et al., 1973; and Robinson, 1972). While not all investigators shared the bipedal interpretations of this material (Zuckerman et al. 1973), new fossils from the Hadar and Laetoli formations discovered during the 1970's strengthened the argument for bipedality (Johanson et al., 1978; Leakey et al., 1976). The discovery of footprints in the Laetoli Beds made by hominids solidified the notion of australopithecine bipedality (Leakey and Hay, 1979; White, 1980). Analyses of the *A. afarensis* knee and reconstructed pelvis revealed to some researchers that *A. afarensis* was adapted to full and complete bipedality (Lovejoy, 1979; Johanson et al., 1976; Johanson et al., 1982). This belief was further substantiated by a series of analyses focusing on the foot and ankle (Latimer and Lovejoy, 1989; Latimer and Lovejoy, 1990a; Latimer and Lovejoy, 1990b; Latimer et al. 1987). The human-like gait of *A. afarensis* was also emphasized by detailed analyses of the pelvis, proximal femur, and reconstructed musculature (Lovejoy, 1988).

Although several authors have forcefully argued that the australopithecine hip had fully realized terrestrial bipedal features, others note deviations from the modern human

condition that suggest compromised bipedality. It has been demonstrated that the hips of *A. afarensis* are extraordinarily wide (Rak, 1991). Some contend that the wider hip conferred an energetically more efficient form of bipedality (Lovejoy, 1988). Others believe that when compared to femoral neck length, the relatively wider hip reduces the mechanical advantage of the hip abductors. This would require greater muscular action potentials in the gluteals compared to humans in order to prevent the hip from collapsing when the other foot is off the ground (Jungers, 1991). Thus this would require a more robustly built hip joint and stronger hip abductors. The wider hip also increases the moment arm of stress on the diaphyseal/femoral neck junction requiring a more robust juncture (Hunt, 1994). Further, it has been demonstrated that compared to modern humans, the hip joint of *A. afarensis* is small and has reduced in its capacity to sustain endurance bipedalism (Jungers, 1991). The wide australopithecine hip, with all of its disadvantages, appears poorly adapted to powerful and sustained bouts of bipedalism. It has been proposed that the wide hip, with its many bipedal features, evolved as part of a bipedal postural, and not locomotor, adaptation (Hunt, 1994). Wide hips increase the base of support, an advantage in a postural adaptation of this kind. Further postural bipedalism does not create the stresses produced by bipedal locomotion.

Arguments that support the notion of an australopithecine locomotor repertoire fundamentally different from that of modern humans are also grounded in interpretations of the *A. afarensis* hand, shoulder, hip, knee, and foot. These interpretations work to create a picture of a hominid with a significant arboreal component in its locomotor repertoire. The humero-femoral index of Lucy, intermediate between apes and humans, is believed to have facilitated climbing activities but increased the energetic cost of

terrestrial bipedalism (Stern and Susman, 1983). Analysis of pedal phalanx length to femoral head diameter to assess relative toe length indicates that the Hadar fossils are intermediate between bonobos and humans (Stern and Susman, 1983). Further analysis of the foot of Lucy reveals a skeletal foot length compared to hindlimb length well outside the range of human variation (Susman et al., 1984). Additionally, the Hadar fossils were shown to have toes as long as the fingers of a 2-year old human. Thus, if there were no restrictions on flexion, these hominids would have been able to grab with their feet as well as young children do with their hands (Susman et al., 1985). However, if the Hadar fossil were straight, this would have been an indication that these hominids did not use their feet for climbing. Investigation seeking to quantify pedal phalanx curvature of the Hadar fossils demonstrates a considerable degree of curvature in these bones consistent with an arboreal component (Stern and Susman, 1983).

The forelimb anatomy also portrays a hominid adapted to life in the trees. The torso of *A. afarensis* is both shallow and funnel-shaped, moving the shoulder joint closer to the midline making one arm hanging more efficient (Hunt, 1994). The cranially oriented glenoid fossa, a highly mobile wrist, and long and ventrally curved fingers have all been cited as arboreal adaptations present in *A. afarensis* (McHenry, 1991; Stern and Susman, 1983). Further, the hand morphology indicates a powerful chimpanzee-like grasping ability well suited to grasping branches and sustaining body weight (Stern and Susman, 1983).

The lumbar vertebrae and lumbrosacral articular surface of *A. afarensis* has been shown to be smaller than expected using a human model (Jungers, 1988a; McHenry, 1991; Rak, 1991). Since the torso of australopithecines is large compared to humans,

more weight resides in the upper portion of the body. During bipedal locomotion the lumbar vertebrae would then be under greater stress than is the case with modern humans, and therefore are expected to be larger (Jungers, 1988).

As a whole, the postcranium of *A. afarensis* appears not to reflect a hominid obligated to terrestrial bipedal locomotion as once thought, and certainly less adapted than modern humans. Even for a hominid in transition between ecological niches, the exceptionally wide hips that generate greater stresses seem poorly adapted to the demands of bipedal locomotion. The small hip joint and small diameter spine are not expected from a bipedal hominid with a relatively large torso. Further, the numerous climbing and grasping adaptations still present in the australopithecines seem to indicate a large arboreal component.

Beyond functional interpretation made from fossil material other arguments have been made that reinforce the picture of *A. afarensis* taking advantage of both the terrestrial and arboreal worlds. While body size estimates for *A. afarensis* have varied, there is little doubt that these creatures were relatively small and it is not clear how such diminutive hominids could have survived while living solely on the ground. Even chimpanzees that range in size up to 70 kg require the use of trees for sleep and as refuge from predators (Susman et al., 1985). *A. afarensis* possessed neither the large canine size nor the overall body size of chimpanzees and hence it is hard to imagine how these hominids could have fared better on the ground compared to extant primates which must rely on trees (Susman et al., 1985). Although this line of evidence is at best circumstantial, it does lend support to an arboreal component.

Theories about the selective pressures leading to the origin of bipedality are more diverse than those about australopithecine locomotor patterns. Several have been offered and include increased viewing distance (Dart, 1959; Day, 1977, 1986), food/tool transport (Bartholomew and Birdsell, 1953; Etkins, 1954; Hewes, 1961; Lovejoy, 1981; Washburn, 1967), tool use (Washburn, 1960), more efficient long distance travel for hunting or scavenging purposes (Carrier, 1984; Shipman, 1986b; Sinclair et al., 1986), and thermal radiation enhancement (Wheeler 1991a; 1991b). Lovejoy (1981, 1993) argues that bipedalism evolved as a way for males to provision females and their young. This leaves the female more energy to expend in reproduction and caring for offspring thereby increasing reproductive success and creating the selective pressure for bipedality. It has also been suggested that bipedalism emerged as a large branch locomotor mode and an arboreal feeding posture (Tuttle, 1975). The forelimbs of the proto-hominids were poorly suited for quadrupedalism when terrestrial locomotion became advantageous and hence lead to frequent and then exclusive bipedality. Others have offered that bipedalism arose as a product of the demands of collecting small evenly distributed food sources at or near ground level (Jolly, 1970; Wrangham, 1980). However neither of these hypotheses can account for the mosaic of arboreal and bipedal features present in the australopithecines. The well-developed australopithecine bipedal features are hard to explain given an exclusively arboreal setting. The persistence of arboreal features is difficult to account for given evolution in a terrestrial setting. The combination of arboreal and bipedal traits is consistent with one theory. A terrestrial bipedal feeding posture supported by arm hanging in the low branches of trees can account for both the derived hip morphology and the persistent arboreal features (Hunt, 1994).

Cranially Based Phylogenies

As already noted, the postcrania have been used in a multitude of studies focused on functional morphology that strive to reconstruct behavioral patterns. In contrast, when attempts have been made to elucidate evolutionary relationships and phylogenies, the postcranium is often abandoned for cranial analyses (Pilbeam 1997). Dart was able to make his initial assessment of the Taung child as intermediate in form between apes and humans based on several cranial characteristics (Dart 1925). As additional australopithecine species have been discovered and recognized, they have often been situated in the hominid lineage based on cranial features. The most recent additions of early hominid species, *Ardipithecus ramidus* and *Australopithecus anamensis*, have not changed the picture of early hominid phylogeny significantly. *A. ramidus*, which is both the oldest and most primitive, is placed ancestrally to all other australopithecine species (White et al., 1994,1995). *A. anamensis*, another recent discovery, is less primitive and slightly later in time than the Aramis fossils but is interpreted as ancestral to *A. afarensis* (Leakey et al., 1995).

Not all discoveries fit as nicely into established phylogenies. In 1985 the discovery of the specimen KNM-WT 17000 (The Black Skull), attributed to a new taxon *A. aethiopicus*, required the reevaluation of the early hominid phylogeny (Walker et al., 1986; Skelton and McHenry, 1990). While some researchers felt this specimen could be incorporated into existing theoretical frameworks (Clark, 1988; Eckhardt, 1986; Falk, 1986), the prevailing opinion was that all previous hypotheses about relationships among the Plio-Pleistocene hominids were invalid and needed to be replaced by completely new hypotheses (Delson, 1986, 1987; Lewin, 1986; Shipman, 1986a; Vrba, 1988). One

hypothesis as advanced by Walker et al. (1986) and, in part, by Kimbel et al. (1988) held *A. afarensis* as the root to all other hominids from which evolved one branch that lead to the east African “robust” (*A. aethiopicus* and *A. boisei*) and another lineage to *Homo* through *A. africanus* and *A. robustus*. This phylogeny interprets the shared morphology of *A. boisei* and *A. robustus* as the product of functional convergence. However, some of the similarities between these two “robust” species such as the pattern of the venous drainage from the endocranium are difficult to attribute to a functional cause and hence make this phylogeny difficult to defend (Grine, 1993).

Other hypotheses promoted, including one advocated by Grine (1988a, 1988b) and to some extent by Kimbel et al. (1988), recognized all “robust” forms as representing a monophyletic clade. *A. afarensis* was suggested to be the last common ancestor of the “robust” lineage and the branch that leads to *Homo* through *A. africanus* (Grine 1988a, 1988b; Kimbel et al. 1988). This phylogeny is based on the mosaic pattern of primitive and derived features present in the “Black Skull” that suggest strongly that *A. aethiopicus* is evolutionary between the other “robust” forms and *A. africanus*. A phylogeny put forth by Skelton and McHenry (1990) based on cladistic analysis of seventy-seven traits grouped separately by anatomical region and function revealed a different evolutionary picture. This analysis placed *A. afarensis* at the base of the hominid phylogeny. *A. aethiopicus* is seen as a sister clade to all later hominids branching off from a hypothetical ancestor which also gave rise to *A. africanus*. From *A. africanus* comes another hypothetical form that gives rise to a “robust” lineage and a branch leading to *Homo* (Skelton and McHenry, 1990).

Joint Function

It is suspected that the size and shape of joints in the postcranium are linked biomechanically to habitual postures and locomotor repertoires (Jungers, 1988a). Joint morphology is a reflection of the specific movements required and the necessity of sustaining repetitive loads and the resultant stresses (Kapandji, 1970; MacConaill and Basmajian, 1969; Norkin and Levangie, 1983). Joint surface architecture reflects design constraints and requirements for joint strength, mobility and stability (Hamrick, 1996a). Joint strength is proportional to the magnitude and frequency of loading that can be supported by the epiphysis without suffering cartilage degeneration or trabecular damage (Hamrick, 1996a). Joint mobility is the potential range of limb movement in a given plane without causing joint displacement (Hamrick, 1996a). Joint stability refers to the ability of the joint to resist dislocation in a given loading direction (Hamrick, 1996a). Features of external joint architecture that have been argued to affect joint strength, mobility and stability are joint surface area (Currey, 1984; Godfrey et al., 1991, 1995; Jungers, 1988a; Ruff, 1988; Swartz, 1989; Wainwright et al., 1982) and joint curvature (MacConaill, 1950, 1966; Hamrick, 1996b; Sarmiento, 1988; Yalden, 1972).

It has been proposed that the surface areas of animal joints are proportional to body mass (Alexander, 1980). Swartz (1989) argues that joint sizes scale to body mass with positive allometry. However, these findings are confounded by the varied locomotor and postural repertoires of the animals examined. Other researchers have found that both the male (convex) and female (concave) joint surfaces scale at or near isometry (Godfrey et al., 1991; Jungers, 1988a; Ruff and Runestad, 1992). Loading is not the only parameter that will affect joint surface area. It has also been shown that joint

surface area is related to joint mobility. If all other aspects of joint mobility are held constant, increasing the size of the male joint surface will result in increases in potential range of motion. In Figure 1 the male and joint surfaces are enlarged isometrically while the diaphysis size is held constant, and the results is an increased range of motion. Thus animals of similar body size that differ in limb mobility should be also expected to vary in joint surface area.

Another important determinant of joint mobility is relative joint surface curvature. Male joint surfaces that are more tightly curved compared to relative joint size are known to allow for greater range of motion (Hamrick, 1996a). Hence, animals that differ in the degree of mobility would also be expected to differ in the degree of male joint surface curvature. The curvature of the female joint mating surface is an important stability determinant (Hamrick, 1996a). Tightly curved female mating surfaces allow for variably directed compressive loads without displacement, while flatter surfaces are only stable in more unidirectional loading (Yalden, 1972; Sarmiento, 1988). Joint surfaces can provide significant information about the locomotor and postural repertoire of an organism as well as providing clues to body size and body proportions (Jungers, 1988a).

Australopithecine Proportions: Functional and Phylogenetic Importance

It has long been noted that humans and apes differ in forelimb to hindlimb proportions (Shultz, 1930). In apes, the forelimb is large relative to the hindlimb, while

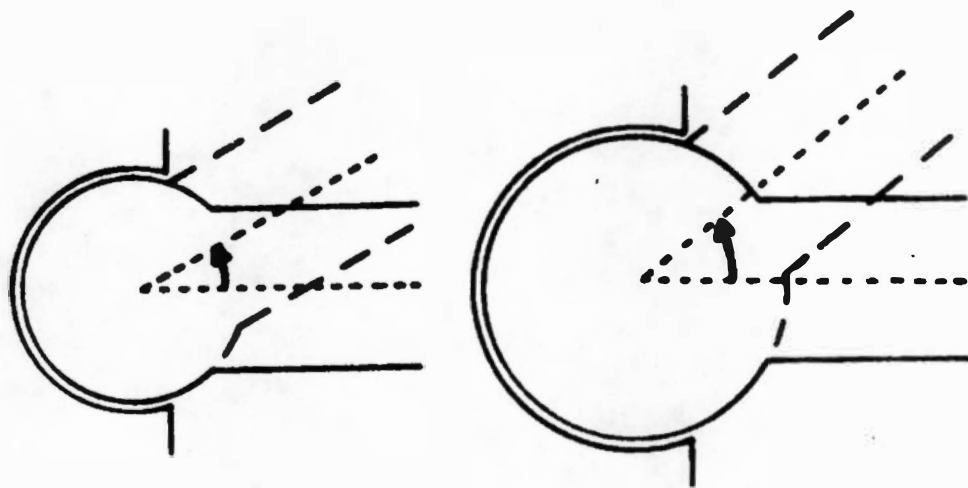


Figure 1. Relative Mobility. (Ruff 1988)

in humans it is the hindlimb that is relatively large. Early in hominid studies, limb proportions were the subject of great interest and suggested that australopithecines had limb proportions unlike humans (Coon, 1962). However, early estimates of limb proportions were viewed with caution since they were not based on limbs associated with the same individual (McHenry, 1974). Until 1971, only one fossil hominid from the early Pleistocene was known with associated fore and hindlimbs (McHenry, 1978). This specimen from Kromdraai (TM 1517), attributed to *A. robustus*, allowed for initial comparison of relative proportions of associated limbs (Hamilton, 1972; McHenry, 1974). The comparison of the TM1517 distal humerus to talus indicated that the humerus was proportionately much larger than would be expected by human standards, but smaller than expected by pongid standards (McHenry, 1974). In the early 1970s other australopithecine specimens with associated fore and hindlimbs were discovered. R.E.F. Leakey led expeditions in 1971 and 1972 during which three skeletons with associated limbs were found on the east shore of Lake Turkana in northern Kenya (Leakey, 1972, 1973). Two years later, D.C. Johanson discovered the 40% complete remains of the skeleton commonly known as Lucy (AL 288-1) (Johanson and Taieb, 1976). These remains allowed for more direct comparison of limb proportions.

The fossils attributed to the *Australopithecus* genus substantiate earlier claims that these species were intermediate between apes and humans with respect to limb proportions. It was demonstrated that Lucy had a humerofemoral index of 83.9, a value almost exactly between the averages for small statured humans ($X = 73.7$) and small bodied African apes ($X = 97.8$) (Hens, 1998; McHenry, 1978; Susman et al. 1985). This intermediate position was further corroborated by relative size of Lucy's hindlimb joint.

Jungers (1988a) demonstrates that Lucy had some modest degree of hindlimb enlargement, compared to modern non-human hominoids. However, this australopithecine had not yet achieved the highly derived enlarged hindlimb joint size as seen in modern humans (Jungers, 1988a).

While the body proportions of *A. afarensis* revealed a relatively simple human evolutionary history, other fossil hominid proportions depicted a more complex scenario. Studies by some researchers proposed that *A. afarensis* was more derived in body proportions than some later fossil hominids (Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998). An analysis of OH62, a *Homo habilis* skeleton, revealed body proportions that more closely resemble modern apes than does the chronologically earlier and cranially more primitive *A. afarensis* (Hartwig-Scherer and Martin, 1991). These findings complicate the previously held evolutionary sequence in which *H. habilis*, shown to be postcranially primitive, is an evolutionary intermediate between a postcranially more human-like *A. afarensis* and a fully bipedal *H. erectus* (Hartwig-Scherer and Martin, 1991). If OH 62 is representative of the species to which it is attributed, then it may require that *H. habilis* be omitted from the lineage leading to humans (Hartwig-Scherer and Martin, 1991). Alternatively, this scenario would require multiple episodes of bipedal evolution.

McHenry and Berger (1998) review joint size proportions in *A. afarensis* and *A. africanus* comparing them to extant large bodied hominoids. They use joint size as a reflection of phylogeny, and the idea that joint morphology may be influenced by phylogenetic history has received support from other researchers (Rafferty and Ruff, 1994). These researchers have argued that the external morphology of joint surfaces is

primarily constrained by its phylogenetic history and by mobility requirements (Ruff and Runestad, 1992). The morphology of the internal trabecular bone, they suggest, which responds to changes in loading requirements without creating joint incongruence, is a better reflection of mechanical loading (Ruff and Runestad, 1992; Singh, 1978).

As more australopithecine remains were discovered and body proportions analyzed, the evolutionary picture became more complex. The analysis of a considerable amount of new material from Sterkfontein, especially the skeleton with associated fore and hindlimbs (Sts 431), complicates currently held views about human evolution. Analysis of joint surface areas revealed unexpected findings about body proportions of *A. africanus*. *A. africanus* has been shown to have more ape-like forelimb to hindlimb joint size proportion than does the earlier *A. afarensis* (McHenry and Berger, 1998). This is surprising in light of the fact that *A. afarensis* is cranially and dentally more primitive than the later *A. africanus* (McHenry and Berger, 1998). *A. africanus* is known to share a number of derived craniodental features with early species of *Homo* including reduced canines, expanded brains, shortened muzzles, deepened tempromandibular joint, more bicuspid lower third premolars, and mandibular symphyses that are more vertical.

Along with those findings of Hartwig-Scherer and Martin (1991), the work of McHenry and Berger (1998) contradict the cranial evidence and imply to McHenry and Berger an evolutionary history complicated by homoplasy. They suggest two scenarios to account for the contradictory cranial and postcranial evidence. One possible explanation is that *A. africanus* and *H. habilis* may have evolved craniodental characteristics in parallel with the lineage leading to later *Homo*. Alternatively, the fore-

to hindlimb proportions of *A. africanus* evolved independently of the lineage leading to *Homo* and does not imply a close phylogenetic link (McHenry and Berger, 1998).

McHenry and Berger's study of joint size casts serious doubt on a cranially based australopithecine phylogeny. The two possible phylogenies leave the question: Which is more phylogenetically important, the crania or the postcrania? While postcranial analyses have primarily been focused on functional interpretations, crania have been the center of taxonomic and phylogenetic inquiries. A recent investigation, however, reveals that phylogenies based solely on craniodental evidence may be poor reflections of evolutionary relationships (Collard and Wood, 2000). Collard and Wood (2000) suggest the use of postcranial features in concert with cranial evidence to increase the power of analyses to resolve evolutionary relationships. Additionally, studies of function can strengthen phylogenetic analyses by discriminating between phylogenetically informative and phylogenetically misleading behaviorally induced morphologies (Collard and Wood, 2000).

While functional interpretations of body proportions will undoubtedly aid in future phylogenetic assessments, these analyses are also important in making assessments of locomotion, posture, and body mass. The importance of assessing body size is becoming obvious through research demonstrating the central role body size plays in the biology of an animal (Jungers, 1985; Schmidt-Nielson, 1984). Body size has been used to determine degree of encephalization and sexual dimorphism and has been related to numerous variables including metabolic cost, mobility, thermoregulation, diet, and foraging strategy (Foley, 1987; Hartwig-Scherer, 1993; Hofman, 1983; McHenry, 1988, 1992; Ruff, 1993). Body weight estimates for fossil hominids have been made based on

regression formulae that relate some osteological measurement to body weight.

Estimates for *A. afarensis* have varied from 26 to 99 kg depending on the specimen (Hartwig-Scherer, 1993). Even for the same specimen, estimates have ranged by as much as 15 kg (McHenry, 1982; 1988).

Reliable body weight estimates for fossil hominids are difficult to establish. These estimates are based on body weights of extant primates. By necessity, samples of humans, gorillas, and chimpanzees are used to attain a relationship between body weight and some measure of a skeletal element. This relationship is then used to reach a body weight estimate for the fossil specimen. The underlying assumption is that the extinct forms had the same relationship of skeletal measurement to body weight, as do the reference samples. Studies have shown that body weight and skeletal size are highly correlated (Table 1)(Godfrey et al. 1991; Ruff, 1988, 1990) and scale very near isometry in both mammals generally and anthropoids specifically (Aiello, 1981; Alexander, 1980; Godfrey et al. 1991, 1995; Ruff, 1984, 1988, 1990). However, deviations from the general pattern of interspecific isometry have also been noted and have been attributed to differences in joint function, a product of locomotor and postural adaptations (Godfrey et al. 1991, 1995; Ruff and Runestad, 1992). Body weight estimates for fossil specimens thus need to be based on reference samples that are behaviorally similar. These species need to have carried and supported their weight in a similar manner to the reference sample. However, evidence strongly supports the picture of australopithecines as unique with respect to locomotor system as indicated by body proportions not comparable to extant hominoids. When postcranial evidence is used to make either functional assessments of behavioral patterns or phylogenetic appraisals of evolutionary histories,

Table 1. Skeletal Size and Body Mass Correlations

Skeletal Element	Sample	Correlation Coefficient
Femoral head surface area ¹	Human	0.983
	Pan, Gorilla, Pongo, and Macaca	0.997
Femoral condyles medial and lateral ¹	Pan, Gorilla, Pongo, and Macaca	0.998
Tibial plateaus medial and lateral ¹	Pan, Gorilla, Pongo, and Macaca	0.995
Tibiotalar ¹	Pan, Gorilla, Pongo, and Macaca	0.996
Humeral head surface area ²	24 species of Anthroidea	0.920
Femur midshaft cross-sectional cortical area ³	Human, Great Apes, and Macaca	0.994
	Great Apes	0.973
Femur length ³	Human, Great Apes, and Macaca	0.864
	Great Apes	0.960
Tibia midshaft cross-sectional cortical area ³	Human, Great Apes, and Macaca	0.978
	Great Apes	0.945
Tibia length ³	Humans, Great Apes, and Macaca	0.900
	Great Apes	0.948

Ruff (1988)¹; Godfrey et al., (1991)²; Ruff (1990)³

these analyses should attempt to model the skeletal elements in terms that reflect the actual morphology.

In the past, joint sizes have been estimated by the simple product of linear measurements (Jungers, 1988a, 1988b; McHenry, 1974, 1992; McHenry and Berger, 1998). For certain joint surfaces this may actually approximate the surface area of the joint and hence, for flatter joints such as the glenoid fossa, be a realistic reflection of the joint surface area. Accurate estimates of surface area, along with surface curvature, are important because these are the two main joint attributes that have been argued to have influence on joint function and morphology (Wainwright et al., 1982; Currey, 1984; Jungers, 1988a; Ruff, 1988; Swartz, 1989; Godfrey et al., 1991, 1995. MacConnail, 1950, 1966; Yalden, 1972; Sarmiento, 1988; Hamrick, 1996b). As such, models that represent the actual joint surface area are important. The simple product of linear measurements may indeed reflect some flatter joint surfaces, but it has been established that attempts to model surface areas of other joints by such measurements lead to erroneous estimates of surface area (Godfrey, 1991). Such estimates assume universal joint morphology and introduce errors in surface area estimation that most certainly become greater the more the joint diverges from flat and rectangular. These models are especially poor estimators of joints such as the femoral and humeral heads and the acetabulae.

Joint surfaces are complex structures and are the product of both articular surface area and joint curvature. Simple products of linear dimensions have been employed to evaluate surface area but tend to be poor estimators. To gain a more accurate estimate of these surfaces more complex models must be employed. Models of these joints as partial

spheres have been employed by some researchers and appear to give accurate estimates of surface areas (Godfrey et al. 1995; Ruff, 1998). Only with accurate estimates of surface area can well-grounded functional and phylogenetic assessments be made. The intent of this investigation is to examine joint surface area proportions in the *A. afarensis* specimen AL 288-1 (Lucy), using more accurate estimates of the heads of the femur and humerus and the acetabulum based on partial sphere models. Joint curvature will also be investigated as another important factor influencing joint architecture. This more detailed and accurate modeling of joint surfaces will allow for better assessment of the body proportions of this species. In conjunction with joint mobility and stability evaluations based on relative joint curvature, the body proportions will be used to consider the locomotor repertoire and postural behaviors of this species.

Chapter 2

Material and Methods

Sample

The species included as reference samples in this analysis included *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, and *Pongo pygmaeus*. The human sample of 37 males and 4 females are part of the William M. Bass Donated Skeletal Collection housed at the Department of Anthropology at the University of Tennessee, Knoxville. Individuals between the ages of 20 and 55 were selected based on the presence of associated body masses. The bias of the human sample towards males is a reflection of the demographics of the collection and could not be controlled. This sex difference may make this sample poorly suited for examining AL 288-1, a presumed female. Without knowing if and how sex differences effects joint surface area and curvature it is impossible to estimate the effect the bias will have. Some researchers suggest wider hips are less efficient for bipedal locomotion (Susman et al., 1985). If this were the case then human females would be expected to have larger hip joint components than males. Lucy, with a small hip joints is more likely to resemble the human condition if the sample is biased towards males than if there were equal sex ratio in this sample. The bias in this sample is regarded as a potential source of error, however as the differences between the sexes are unknown it is impossible to correct for them.

Measurements on the 29 *Pongo pygmaeus* (9 males and 20 females) specimens were taken in part at the Department of Mammalogy at National Museum of Natural History, Washington D.C., and additional specimens were measured at the Cleveland

Museum of Natural History in the Department of Anthropology. The sample of 16 *Pan* (6 males and 10 females) and 18 *Gorilla gorilla* (11 males, 6 females, and 1 unknown) specimens are housed at the Department of Mammalogy in the National Museum of Natural History. The sample of African apes was supplemented with an additional 14 *Pan* (7 males and 7 females) specimens from the Department of Anthropology at the Cleveland Museum of Natural History. All measurements of australopithecine fossil casts were taken in the Department of Anthropology at the Cleveland Museum of Natural History.

All measurements of joint surfaces were taken on the right side. If one of the right elements was missing or damaged the left was used in its place. When this was the case, the measurements on the bone that constitutes the other half of the joint were also taken on the left side. All measurements were taken by the author except those taken to investigate inter-observer error.

For this study, the *G. gorilla* and *Pan* species were combined into a single sample of African apes. The African apes were combined into a single group to increase the sample size. Other researchers have used a combined sample of African apes to investigate questions of both function and phylogeny (Hartwig-Scherer, 1992; McHenry and Berger, 1998). However, to ensure that this grouping was appropriate, the gorillas and chimpanzee were compared using four skeletal proportions. The combined sample was then compared to both humans and orangutans. The samples were compared using analysis of covariance for proportion of femoral to humeral surface area, femoral to acetabular surface area, acetabular height to acetabular radius, and femoral head height to femoral head radius. Analysis of covariance examines two regression lines and

determines the probability of agreement for the slopes of the lines. If the slopes are equivalent, the regression lines are then analyzed for agreement of the intercept. If the intercepts are also found to agree then the lines are regarded as the same (Tatsuoka, 1971). The dependent and independent variables and the covariant for each analysis are given in Table 2.

Probabilities for agreement of regression lines were obtained using analysis of covariance in SAS. Gorilla and chimpanzee were found to be similar with respect to the four skeletal proportions investigated, and probabilities are given in Table 3. Humans were compared to the African ape sample on each of the four skeletal proportions. Probabilities of agreement for these analyses are given in Table 4. Orangutans were also compared to the African ape sample and probabilities on the four skeletal proportions are given in Table 5.

Measurements

Several methods for determining joint surface area were investigated to determine which one produces accurate estimates of surface area. The standard by which all other methodologies were judged was a latex cast methodology. This method is used and described by Swartz (1989). Joint surface areas were covered in a high resolution nil shrinkage latex casting compound. Dow Corning J RTV *Silastic Rubber* © was employed for this as recommended by Swartz (1989). The latex base and catalyst were mixed as per the instructions included in the latex kit. The latex components were weighed using a sliding arm balance. The *Silastic Rubber* © was then applied to five human femoral heads and allowed to fully vulcanize for twenty-four hours. Despite results from Swartz (1989), it was found that one coating was not sufficient to create a

Table 2. Analysis of Covariance

Skeletal Proportion	Independent Variable	Dependent Variable	Covariant
Area of femur head to area of humerus head	Femur head surface area	Humerus head surface area	Species
Area of femur head to area of acetabulum	Femur head surface area	Acetabulum surface area	Species
Height of femur head to radius of femur head	Height of femur head	Radius of femur head	Species
Height of acetabulum to radius of acetabulum	Height of acetabulum	Radius of acetabulum	Species

Table 3. *G. gorilla* / *Pan* Comparison

Skeletal Proportion	Slope Probability	Intercept Probability
Area of femur head to area of humerus head	0.7942	0.5118
Area of femur head to area of acetabulum	0.0539	0.0705
Height of femur head to radius of femur head	0.3575	0.1696
Height of acetabulum to radius of acetabulum	0.635	0.3091

Table 4. Combined African Ape / Human Comparison

Skeletal Proportion	Slope Probability	Intercept Probability
Area of femur head to area of humerus head	<0.0001	<0.0001
Area of femur head to area of acetabulum	0.0002	0.0321
Height of femur head to radius of femur head	<0.0001	0.0001
Height of acetabulum to radius of acetabulum	<0.0001	0.1152

Table 5. Combined African Ape / *P. pygmaeus* Comparison

Skeletal Proportion	Slope Probability	Intercept Probability
Area of femur head to area of humerus head	0.3564	0.0655
Area of femur head to area of acetabulum	<0.0001	<0.0001
Height of femur head to radius of femur head	0.0018	<0.0001
Height of acetabulum to radius of acetabulum	0.0025	.1060

thick and durable cast of the femur heads and a second coat was added to each joint surface. After fully vulcanized, the latex casts were trimmed using a scalpel well below the joint capsule to remove excess latex and facilitate the removal of the cast. The casts were then peeled away from the joint surfaces. The latex casts were then turned inside out and the edge of the joint surface was drawn in using a permanent magic marker. In most cases the high-resolution nature of this latex compound made for easy identification of the articular area. In places where it was difficult to identify the edge of the articular surface the original bone was referenced. The casts were then trimmed around the joint surface leaving a latex cast of the articular area. These casts were then slit to allow the cast to be pressed into a two dimensional shape with minimal distortion (Figure 2).

The latex shapes were then traced on to 0.10-inch thick acetate film and outlines were then carefully cut out. The acetate film templates were weighed on an electronic scale to the one-ten thousandths of a gram. Known area reference squares of acetate film were also weighed on the same scale. Acetate film is of uniform density and thickness and thus provides a constant relationship between weight and surface area. The acetate film joint shapes can easily be converted from weights into surface area using the relationship established by the reference squares. The acetate film methodology was followed as described by Swartz (1989). All Human femur head acetate shapes were converted to surfaces and are provided in Table 6. These surface areas were the standard by which all other methodologies investigated were judged. This method itself was not employed for the study for two reasons. The first was that calculating joint surface area with this methodology is both laborious and tedious. In addition, there was concern that

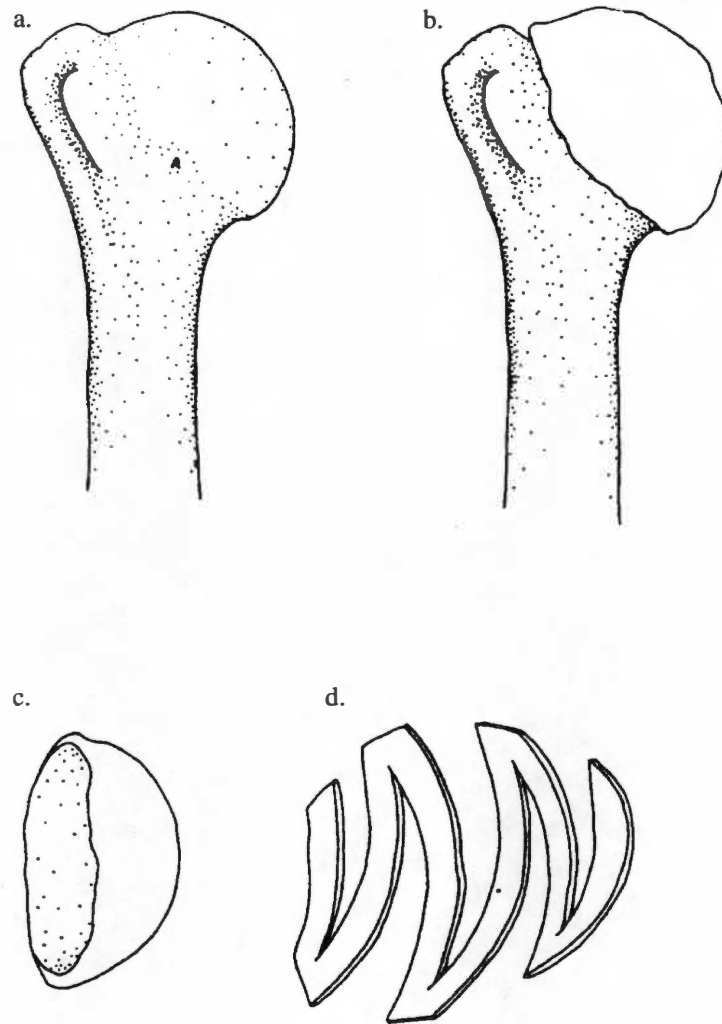


Figure: a. Proximal humerus; b. Humerus covered in latex casting compound; c. Latex cast of humeral head trimmed to edge of joint capsule; d. Latex cast slit to allow the latex to be pressed into a 2D surface. (Swartz, 1989).

Figure 2. Latex Casting Method

Table 6. Surface Area Estimation

Specimen	Latex Cast (mm ²)	Digitized Points (mm ²)	Curved Triangle (mm ²)	Partial Sphere Model (mm ²)
A	3508.580	2081.52	2217.50	3580.838
B	3604.438	2421.322	2652.35	3575.417
C	4200.888	3068.279	3165.68	4312.929
D	4307.101	3366.615	3415.15	4238.579
E	4233.136	3164.947	3196.68	4278.443

the latex casting material may cause damage to the plaster fossil casts (B. Latimer, personal communication).

Three other methods for calculating surface area were investigated as possible avenues for estimating joint surface area. One method involved the use of a 3D digitizer to collect data points on the joint surface. A sixteen point pattern was developed that could be reproduced on any femur head and was drawn on the joint surface with pencil (Plate 1). This pattern creates 20 flat triangles from the sixteen points. A 3D digitizer was then used to collect X,Y,Z coordinate data for each of the sixteen data points. These points were loaded into an Excel routine that first calculated the length of each line and then from the length of these lines calculated and summed the surface area of the 20 triangles. Each of the five human femora was digitized and surface areas were calculated. This method was found to produce gross underestimation of the actual surface area. The flat triangles represent the smallest surface area bound by three points and hence do not reflect the additional surface area included by a curved surface. Comparisons of the surface areas estimated by this method to those established by the latex cast methodology are presented in Table 6.

The second methodology investigated as a possible means for estimating surface area was to divide the joint surface into eight curved triangles. The triangles were produced by drawing eight equally spaced points along the edge of the joint capsule and a single point roughly in the middle of the joint surface and then connecting each edge point to its closest neighbors and to the point in the middle. The length of each arc was measured by first laying dental floss over the arc and marking the endpoints of the arc on

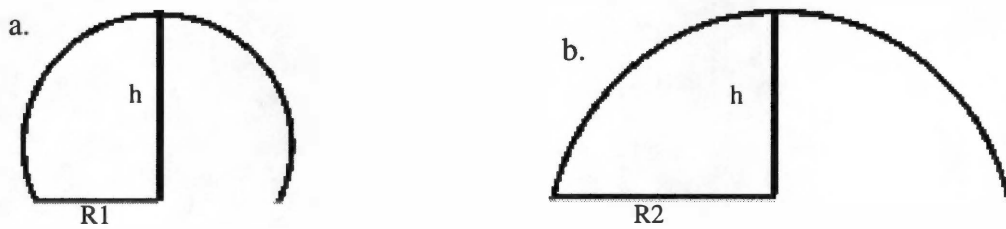
Plate 1: Triangle Digitizer Pattern



the floss. Then the length of floss was measured with calipers. Surface areas estimated with this method and were found to be below latex cast values (Table 6).

The third method, and the one used for this analysis, is to model the joint surfaces as geometric shapes. The glenoid is modeled as a flat rectangle and surface areas are given as the product of length (superior /inferior) and breadth (anterior/ posterior). Measurements were taken using digital calipers and measured to the nearest 0.01mm. The other three surfaces investigated in this study, the head of the femur and humerus and the acetabulum, were all modeled as partial spheres as described by Ruff (1988). The surface area of a partial sphere is given as a proportion of the surface area of a total sphere. The surface area of a partial sphere is given by $A = 4\pi R^2(h/2R)$, where R is the radius of the whole sphere and h is the maximal height of the partial sphere (Ruff, 1988). This formula, however, assumes that the radius of the partial sphere can be measured, that is that the height is greater than radius. However, if the height is not greater than the radius of the complete sphere then the radius of the whole sphere cannot be measured. This is the case when calculating the surface area of the head of the humerus. The formula of the surface area of a partial sphere with height less than the radius of the whole sphere is $A = \pi (h^2 + r^2)$, where h is the height and r is the maximal radius of the partial sphere (Harris and Stocker, 1998).

Joint curvature was evaluated by examining the relationship between the height and radius of the joint surface. Joint surfaces that vary in the their ratio of height to radius have different degrees of curvature. If the height of a joint surface is held constant and the radius of the joint is increased the curvature of the joint surface will decrease (Figure 3).



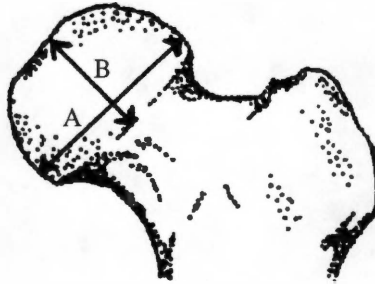
a. Joint surface with height “h” and radius “R1” is tightly curved relative to joint surface in b. which has the same height “h”, but has a larger radius “R2”.

Figure 3: Relative Curvature of Joint Surfaces

Four measurements were taken on each of these joint surfaces to estimate the surface area. Since none of the joint surfaces are perfect spheres, two separate measurements were taken for both the radius and the height. The radius was determined as half the average of two diameter measurements. These diameters were taken as the maximal superior /inferior and anterior/posterior distances for each articular surface. Although Ruff (1988) takes the height using one measurement, other researchers have noted that two measurements provide better estimates of surface area (Godfrey et al., 1991, 1995). Following this procedure, the height was taken as the average of two separate measurements. The heights were taken as the maximal distance perpendicular to the superior/inferior and anterior/posterior diameters. Measurements are illustrated for the femur head, acetabulum, humerus head, and scapula in Figures 4,5,6 and 7. The heights were taken using digital coordinate calipers fitted with an accessory kit that allowed for the arms of the coordinate calipers to reach the edge of the joint capsule and were measured to the nearest 0.1 mm (Plate 2). Diameter measurements were taken using digital calipers and were taken to the nearest 0.01 mm. The surface areas of the five human femora were calculated using this model and were compared to areas derived from latex casts. The partial sphere model was found to provide accurate estimates of joint surface area and was employed for this study.

Values for each of the surface area estimate techniques and for the latex cast technique are given in Table 6. The partial sphere model produced the best estimates of surface area as judged against the latex cast technique. The worst estimate of surface area using the partial sphere model produced an estimate 3% greater than the latex cast (Specimen C). Regression of partial sphere areas on the latex cast areas yield a slope of

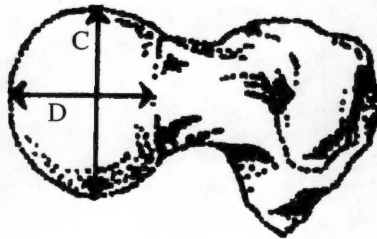
a.



Measurement A – Maximum superior-inferior diameter

Measurement B – Maximum depth taken perpendicular to anterior-posterior diameter

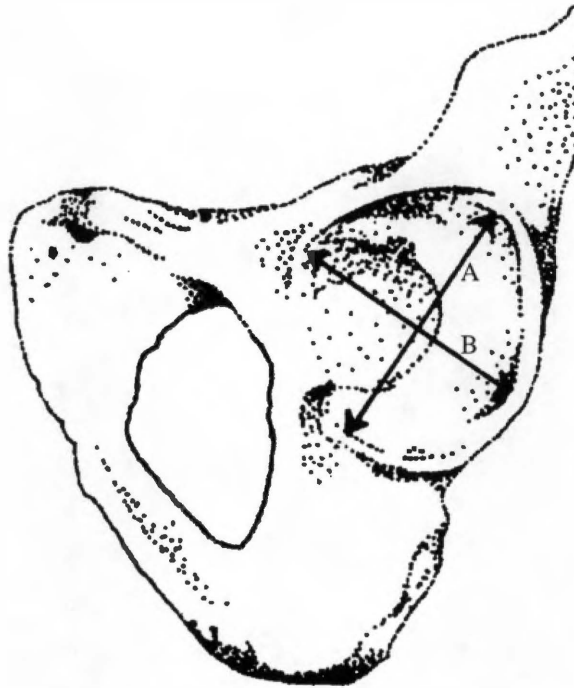
b.



Measurement C – Maximum anterior-posterior diameter

Measurement D – Maximum depth taken perpendicular to superior-inferior diameter

Figure 4: Femur Head Measurements



Measurement A – Maximum superior-inferior diameter

Measurement B – Maximum anterior- posterior diameter

Measurements C and D (not pictured) – The two depth measurements for the acetabulum were taken as the maximum distances perpendicular to the two diameters from the rim to the acetabular fossa. The acetabular fossa was used instead of approximating the lunate surface to provide a consistent methodology for depth.

Figure 5: Acetabulum Measurements

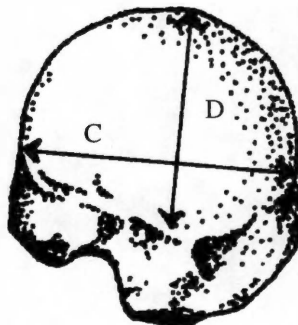
a.



Measurement A – Maximum superior-inferior diameter

Measurement B – Maximum depth taken perpendicular to anterior-posterior diameter

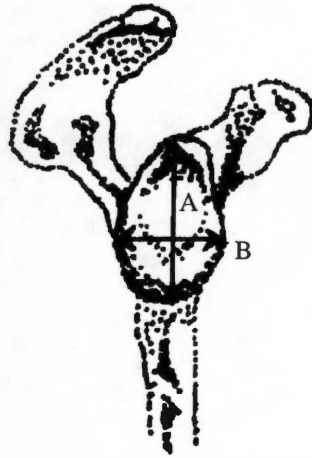
b.



Measurement C – Maximum anterior-posterior diameter

Measurement D – Maximum depth taken perpendicular to superior-inferior diameter

Figure 6: Humerus Head Measurements

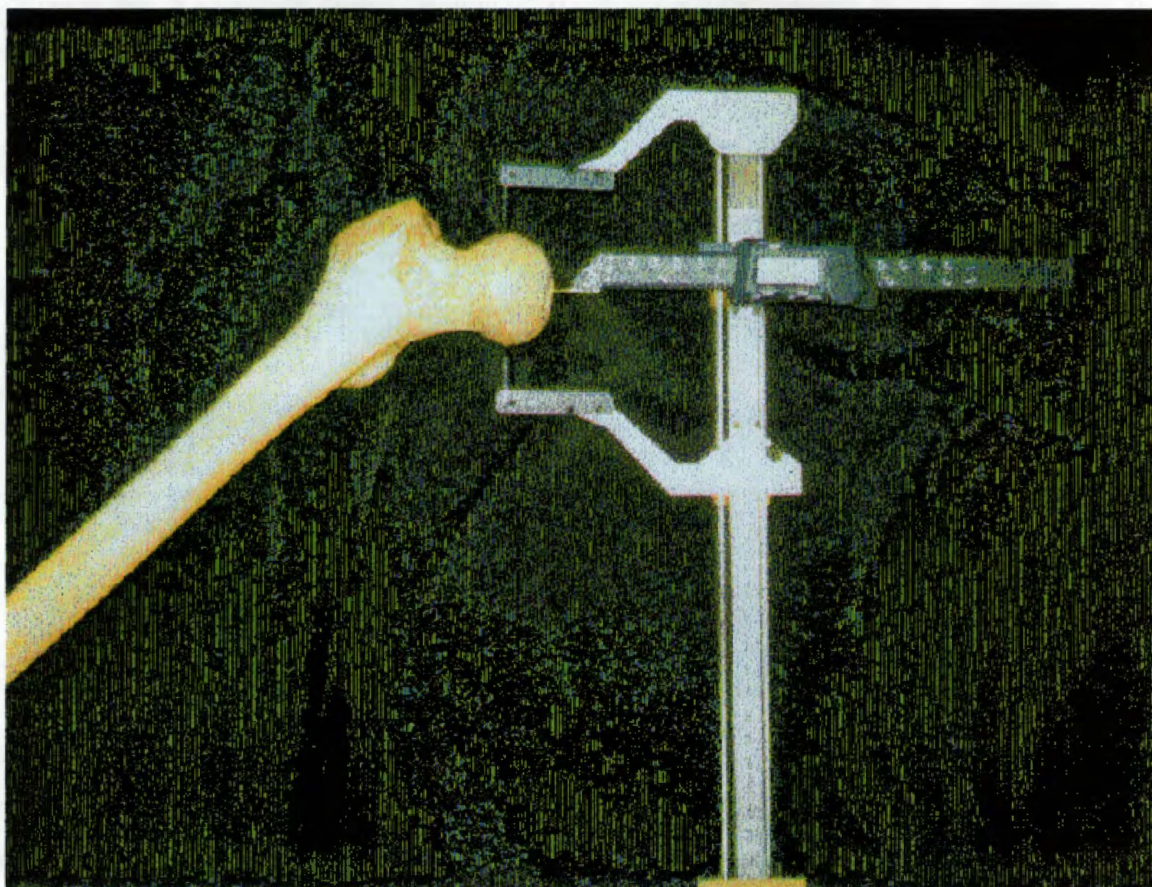


Measurement A – Maximum superior-inferior distance

Measurement B – Maximum anterior-posterior distance

Figure 7: Scapula Measurements

Plate 2: Digital Coordinate Calipers with Accessory Kit



0.98601, an intercept of 81.9458, and an r^2 of 0.963. Other researchers testing the partial sphere model against the latex cast standard also confirm the accuracy of this model. These researchers report a regression slope of 0.96 and an r^2 of 0.994 (Godfrey et al., 1995). The curved triangle method produced a slope of 1.232, an intercept of -1966.9363, and an r^2 of 0.9354 while the digitized method produced a slope of 1.405, an intercept of -2759.25 and an r^2 of 0.9721. Although the digitized point method produced a higher correlation, it was not significantly higher than the partial sphere model. Further the partial sphere model did not require a correction factor to provide an accurate surface area estimate.

A two sample paired t-test was performed on areas produced by the latex method and the partial sphere model. This analysis reveals a probability of 0.4692 that the between group difference is zero. The differences between the latex cast technique and the partial sphere model are small and allow for confidence in this model.

Analyses

Intra-observer Error: To investigate the influence of intra-observer error in the estimation of surface area and joint curvature ten percent of the measurements for the reference sample were retaken. This included four human specimens, eight of the combined African ape sample (5 chimpanzee and 3 gorilla) and three orangutans. The measurements for diameter and those for depths were analyzed separately. The measurements were compared using two analyses. Measurements were first compared using a two sample paired T-test for means. Also the two sets of measurements were used to perform a linear regression to determine the correlation and slope of the regression line.

All analysis for intra-observer error indicates that this did not play a significant role in the estimation of joint surface area or articular curvature. Regression of the two data sets reveals a slope of 0.98273 and a correlation coefficient of .9946 for the diameter measurements. Additionally, the two sample paired t-test for the mean gave a probability of 0.2364 consistent with the null. The analysis for the depth showed that measurements were also reproducible. The regression analysis produced a slope of 0.99469 and a correlation coefficient of 0.9885. The two sample paired t-test furnished a probability of 0.7344 consistent with the null.

Inter-observer Error: To investigate the influence of inter-observer error on surface area estimates and articular curvature, measurements were taken on four of the human specimens by another researcher. The researcher was provided with measurement descriptions and figures from the Materials and Methods section of this thesis. Measurements were compared using a two sample t-test for the mean. The correlation and slope of a regression line was determined by performing a linear regression using the two data sets. Analyses for diameter and depth measurements were performed separately.

Analysis of inter-observer error revealed that these measurements were replicable by other researchers. Regression analysis of diameter measurements produced a slope of 1.00524 and a correlation coefficient of 0.9834. Further, the T-test revealed a probability of 0.273 that the difference in means is zero. The regression analysis of depth measurements gave a slope of 0.97969 and a correlation coefficient of 0.9811. The probability from the two sample T-test was 0.2064.

Australopithecine Proportion Analysis: To evaluate australopithecine forelimb to hindlimb proportions, the specimen AL 288-1, an individual with associated fore- and hindlimbs, was compared to the regression lines of the three reference samples. Each of the four joint surfaces estimated was compared to the other three surfaces used in this study. Articular surface curvature for the humeral head, acetabulum, and femur head was also investigated and was done by regressing joint radius on joint height. Reduced Major Axis (RMA) regression formulae were calculated for each extant primate joint surface comparison. The method of RMA had advantages over least squares because the slope is independent of the correlation coefficient and it gives the best relationship estimate in cases where the error variance is not known (Aiello, 1992). RMA regression formulae were derived as described in Konigsberg et al. (1998). The slope of the regression line was calculated as the ratio of the standard deviation of the dependent and independent variables. The intercept was calculated as the difference between the mean of the independent variable and the product of the slope and the mean of the dependent variable. Residuals from AL 288-1 to each of the regression lines were calculated and converted to z-scores. To convert Lucy's residuals to z-scores, her residuals were divided by the standard deviation of the residuals of each individual in the sample groups to its group regression line. These z-scores were then converted to probabilities (tail-areas) and represent consistency of Lucy with each of the sample group regression lines. The method, however, does have the disadvantage of assuming no error variance in the reference samples. It assumes the slope and intercept are known and hence produces some illegitimate explanatory power.

Chapter 3

Results

Nine regression formulae were determined for each of the three reference samples. This included six surface area comparisons and three comparisons for articular surface curvature the formulae for which are given in Table 7. These formulae were used to calculate residuals and probabilities for AL 288-1. In three of the nine comparisons AL 288-1 was within two standard deviations of all three reference samples. However, in two of these comparisons, femur to acetabulum (Figure 8) and scapula to humerus (Figure 9), AL 288-1 is closest to the orangutan. In the third comparison, humerus to acetabulum (Figure 10), the specimen is most like the African ape model and is furthest from the human regression line. The other analyses of proportions and the curvature analyses eliminate at least one of the three reference samples. The relationship between femur head surface area and humeral head surface area (Figure 11) reveal probabilities that Lucy was most like humans with respect to this body proportion. AL 288-1 is outside the ninety-five percent confidence interval of both orangutans and the African apes. AL 288-1 is however well within the confidence interval in comparison to the human regression line (Table 8). In the remaining two surface area comparison, scapula to acetabulum (Figure 12) and scapula to femur head (Figure 13), AL 288-1 falls outside two standard deviations for orangutans. In both these proportions AL 288-1 is closest to African apes, but still well within the human range of variation.

The remaining three comparison analyzed acetabulum (Figure 14), femur head (Figure 15), humerus head (Figure 16), and for surface curvature. In these analyses AL 288-1,

Table 7. RMA Regression Formulae for Surface Area and Curvature

Comparison (y on x)	Reference Group	Formulae
Humerus on Femur	African Ape	$h = 0.926*f + 74.23$
	Orangutan	$h = 0.976*f + 152.62$
	Human	$h = 0.625*f - 201.52$
Acetabulum on Femur	African Ape	$a = 1.043*f - 39.63$
	Orangutan	$a = 0.692*f + 367.67$
	Human	$a = 0.966*f + 408.60$
Humerus on Acetabulum	African Ape	$h = 0.887*a + 109.39$
	Orangutan	$h = 1.144*a - 366.24$
	Human	$h = 0.648*a - 466.13$
Scapula on Acetabulum	African Ape	$s = 0.437*a - 278.56$
	Orangutan	$s = 0.434*a + 16.80$
	Human	$s = 0.216*a + 8.25$
Scapula on Femur	African Ape	$s = 0.456*f - 295.88$
	Orangutan	$s = 0.330*f + 95.57$
	Human	$s = 0.222*f + 28.39$
Scapula on Humerus	African Ape	$s = 0.493*h - 322.43$
	Orangutan	$s = 0.338*h + 44.04$
	Human	$s = 0.355*h + 99.99$
Acetabular Shape (radius on depth)	African Ape	$r = 0.863*d + 2.26$
	Orangutan	$r = 1.065*d + 0.15$
	Human	$r = 0.503*d + 12.10$
Femoral Head Shape (radius on depth)	African Ape	$r = 0.767*d + 1.15$
	Orangutan	$r = .612*d + 3.16$
	Human	$r = 0.513*d + 9.34$
Humeral Head Shape (radius on depth)	African Ape	$r = 1.106*d + 1.55$
	Orangutan	$r = 0.915*d + 3.07$
	Human	$r = 1.05*d + 4.90$

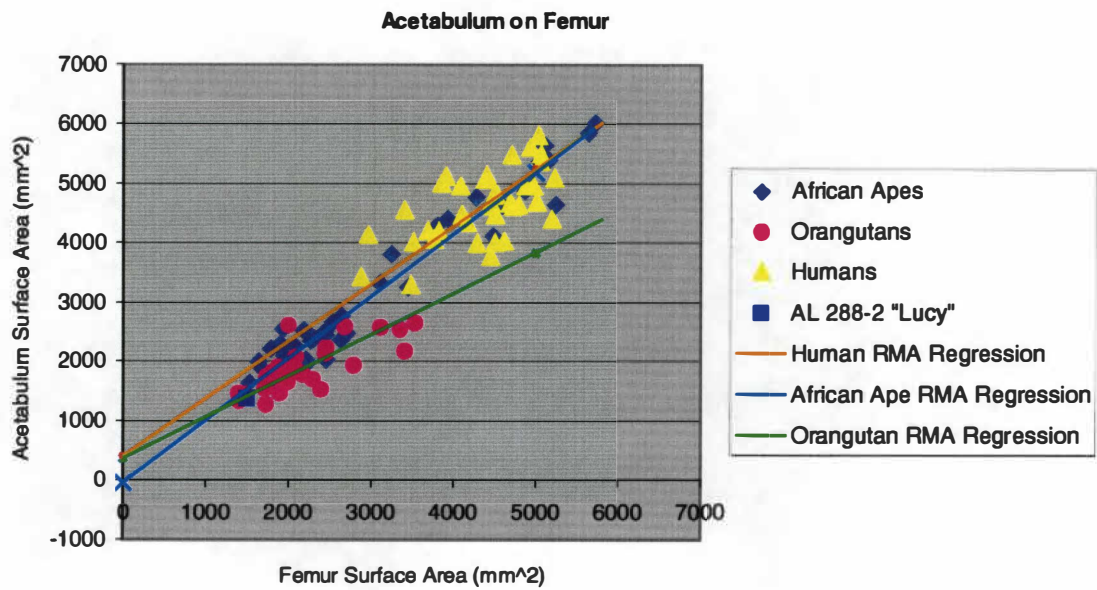


Figure 8:

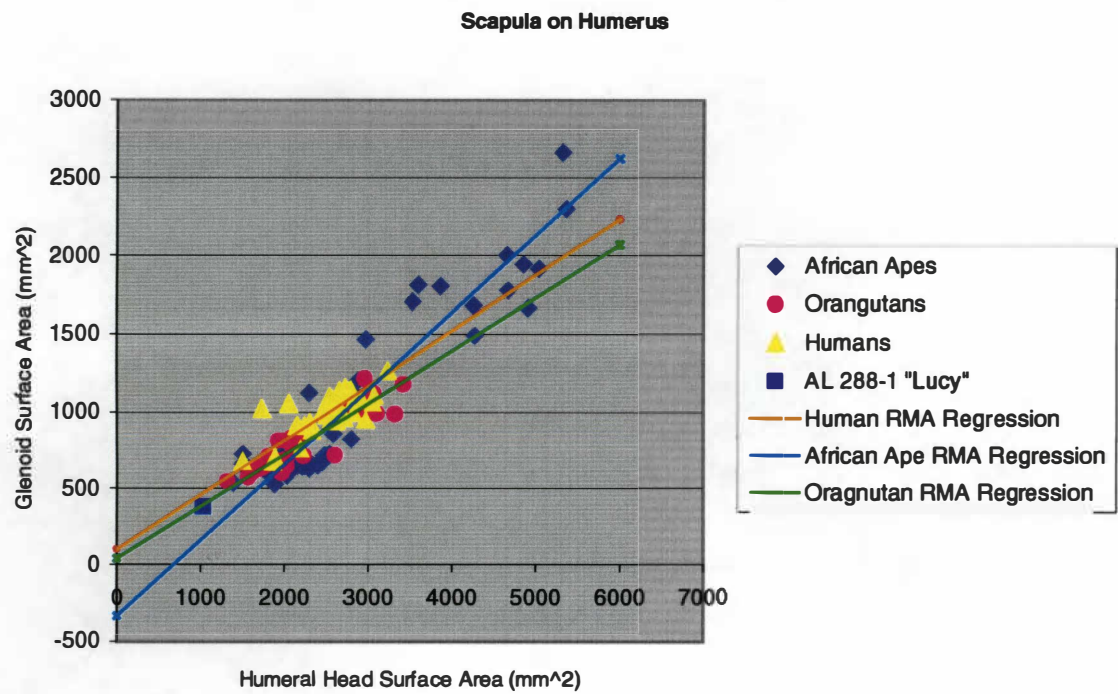


Figure 9:

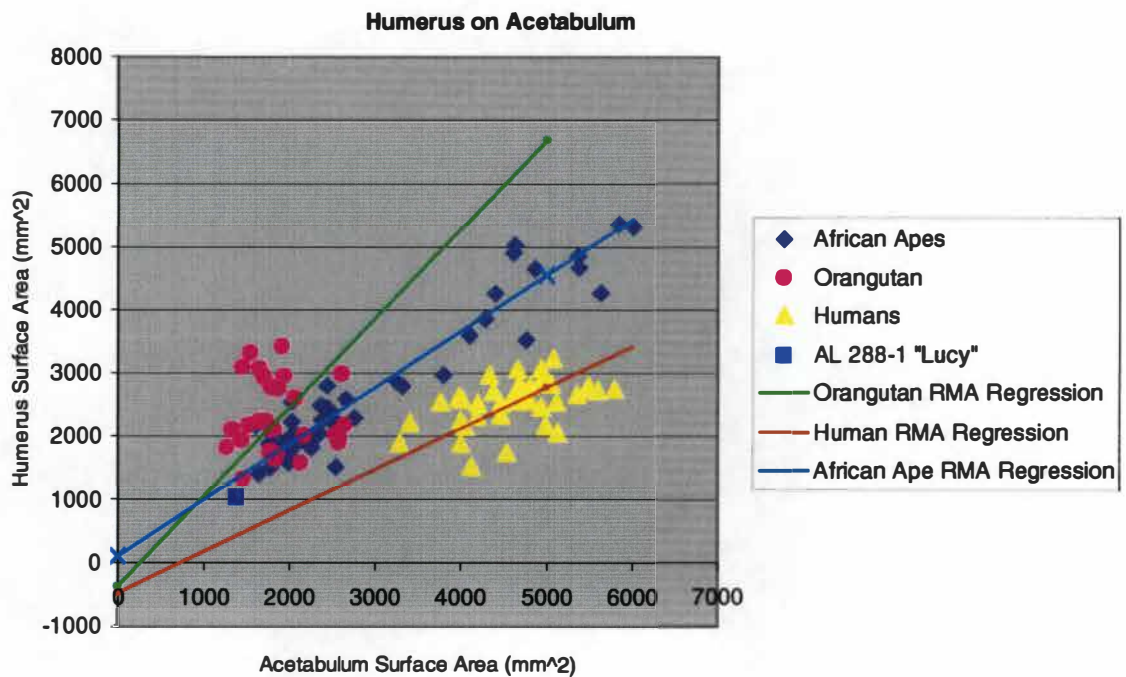


Figure 10:

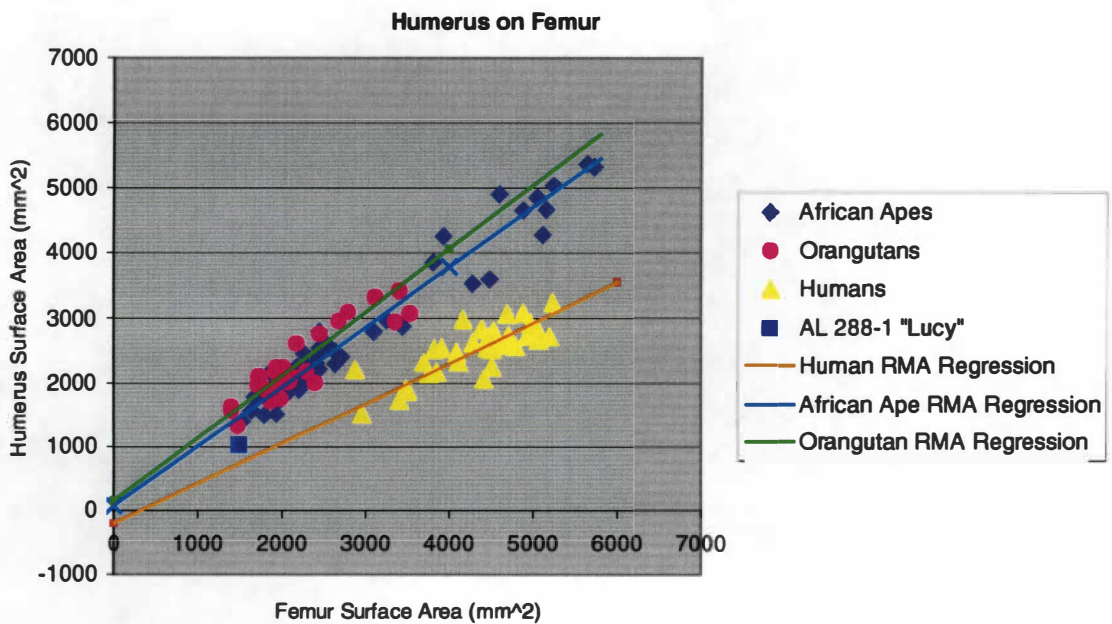


Figure 11:

Table 8. Analysis of AL 288-1 Joint Proportion and Curvature

Comparison / Sample*		Reference Residual Standard Deviation	AL 288-1 Residual	Probability
Humerus on Femur	AA	257.7375	-423.068	0.04683
	Oran	286.7224	-586.188	0.02045
	Hum	240.9661	295.5174	0.11003
Acetabulum on Femur	AA	284.8715	150.787	0.27653
	Oran	274.0701	-29.0578	0.45778
	Hum	508.7292	-481.64	0.17188
Humerus on Acetabulum	AA	358.0193	298.302	0.20237
	Oran	360.0152	545.183	0.06497
	Hum	382.0193	607.427	0.056
Scapula on Acetabulum	AA	162.3253	60.43354	0.35652
	Oran	116.2999	-231.445	0.02329
	Hum	100.4044	78.32755	0.21766
Scapula on Femur	AA	163.6584	-5.44545	0.48673
	Oran	109.6559	-206.906	0.02959
	Hum	89.97816	21.76364	0.40444
Scapula on Humerus	AA	191.0511	207.3497	0.1389
	Oran	83.24622	-8.9361	0.4503
	Hum	96.11036	-83.2479	0.1932
Acetabulum Shape	AA	1.207016	1.765694	0.07175
	Oran	2.473211	1.10153	0.32802
	Hum	1.450494	-3.13794	0.01526
Femoral Head Shape	AA	1.153923	-0.04344	0.48498
	Oran	1.725581	0.588879	0.35284
	Hum	1.559231	-3.91816	0.01158
Humeral Head Shape	AA	1.837137	-1.21491	0.25421
	Oran	1.191458	-0.43806	0.35656
	Hum	2.079965	-3.89002	0.03073

*Sample abbreviation: AA – African apes; Oran – Orangutans; Hum - Humans

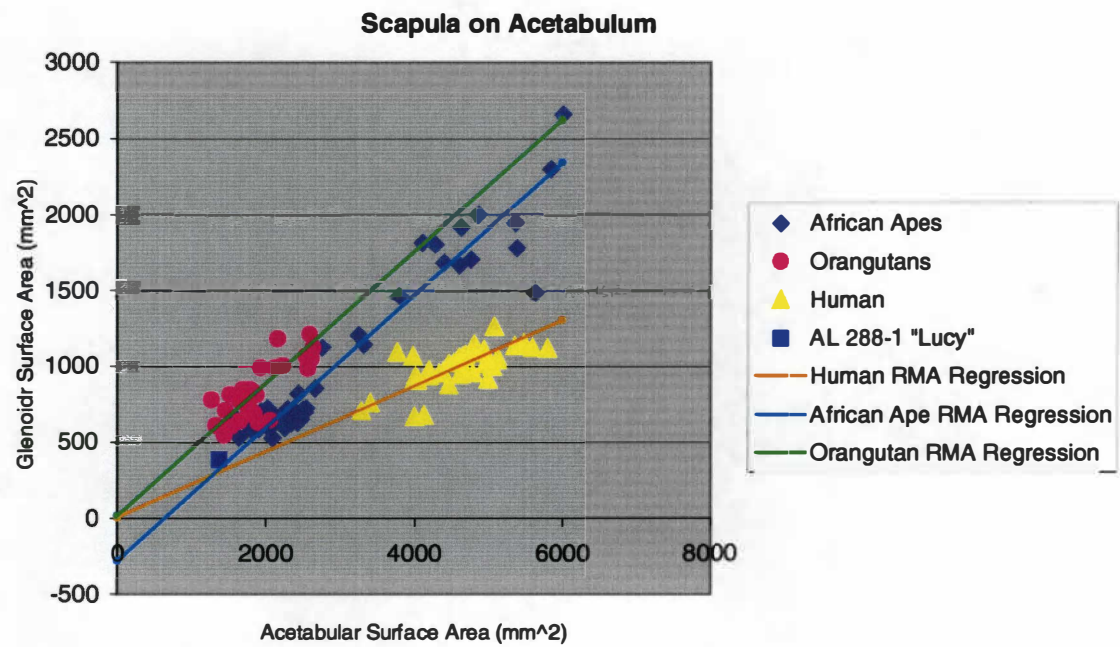


Figure 12:

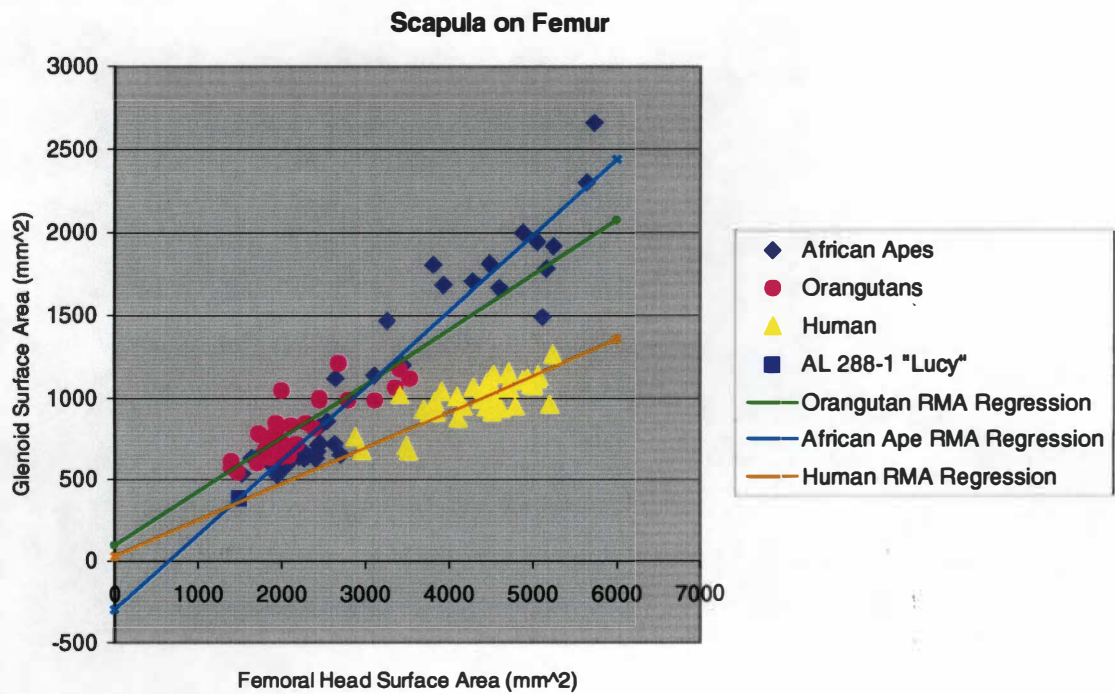


Figure 13:

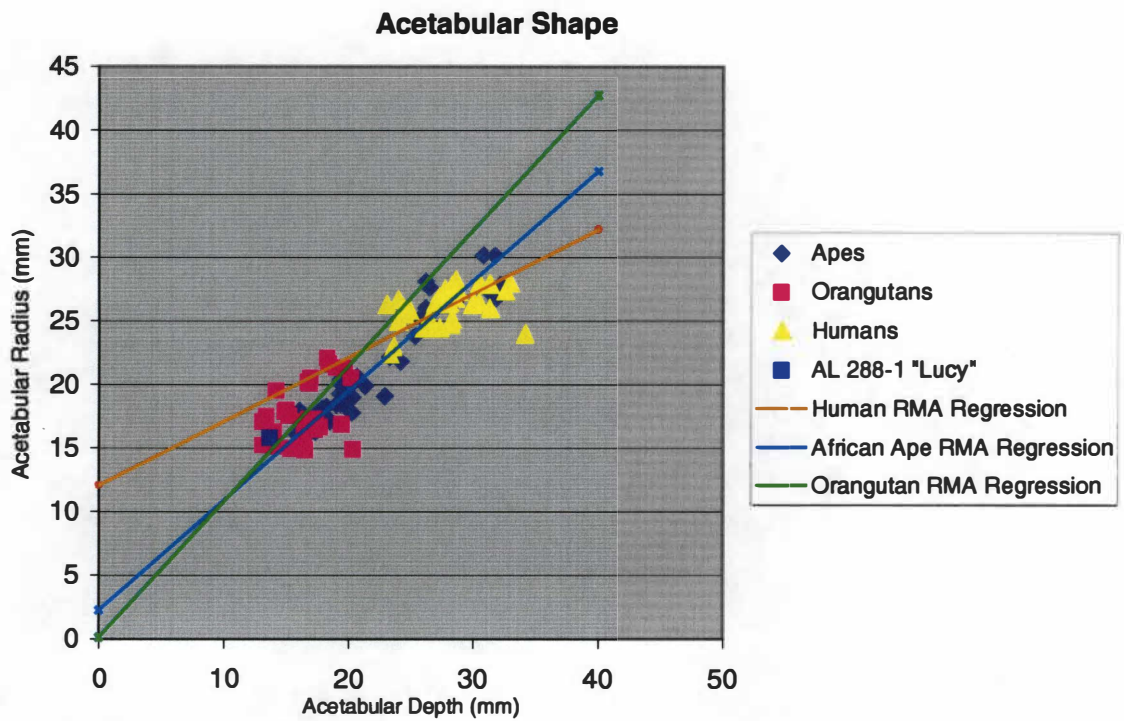


Figure 14:

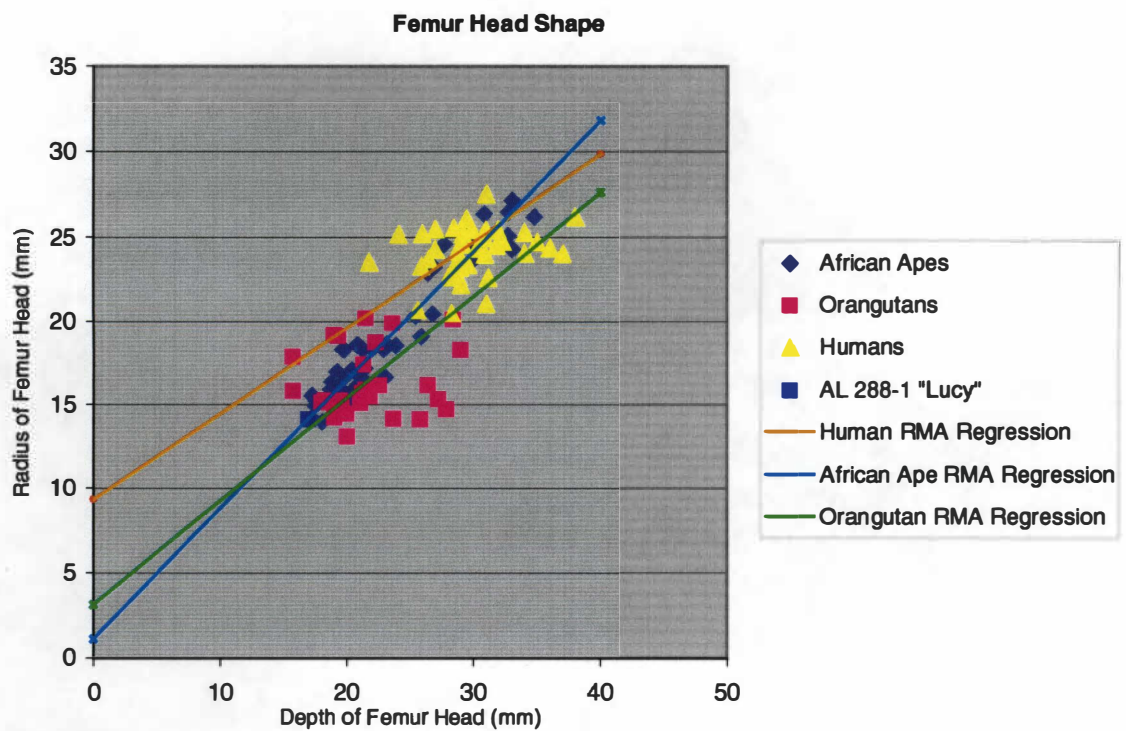


Figure 15:

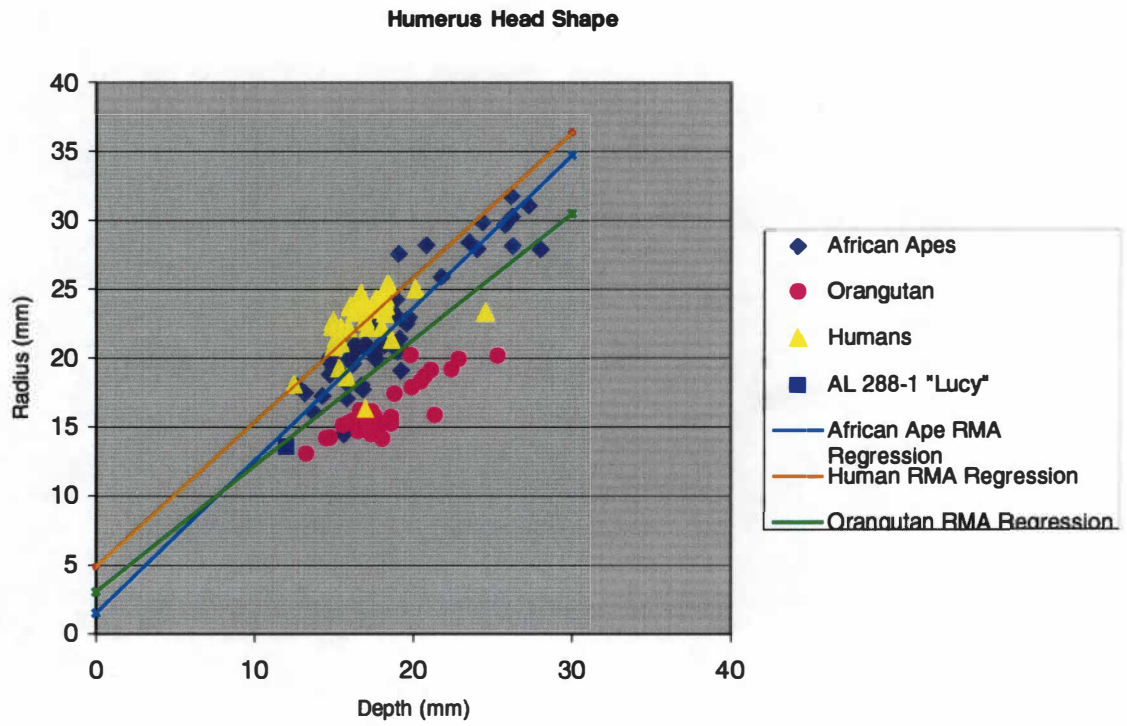


Figure 16:

was outside the range of variation for human joint curvature, but with that for both orangutans and the African apes.

Chapter 4

Discussion

The nine regression analyses of AL 288-1 body proportions reveal a pattern in this specimen not seen in extant primate forms. This is not surprising as many researchers have argued that australopithecines utilized their own unique locomotor repertoire. Even those that have argued for obligate bipedalism have suggested that it was fundamentally different than that of modern humans. However, the results from this study suggest an organism that took advantage of both terrestrial and aboreal worlds. One of the most telling results is the forelimb to hindlimb proportions as represented by humerus to femur surface area regression. The proportions of these surfaces exhibited by Lucy are intermediate between the humans and the large bodied hominoids. However, Lucy's proportions more closely resemble those of modern humans and are further removed from the condition seen in both the African apes and orangutans. The relatively large femur and small humerus surface areas of Lucy suggest an organism whose hindlimbs were the primary organs of locomotion freeing the forelimbs from load bearing requirements. The heavy dependency on hindlimbs does not appear to be reflected in other hindlimb to forelimb proportions. Comparison of the acetabulum to the glenoid fossa does not reveal a pattern in Lucy that most closely resembles the human condition. Although well within both human and African ape distributions, Lucy lies closer to the African ape regression line, with a relatively small acetabulum and large glenoid fossa. One would expect the lower limb dominance to be reflected in acetabulum to glenoid proportion as it is in humerus to femur proportion. Some contend that a small acetabulum may be expected even in a fully bipedal australopithecine because of a more efficient hip

stabilizing morphology (Lovejoy, 1988). However, the work of other researchers suggests the australopithecine hip was poorly adapted for frequent bipedalism (Hunt, 1994; Jungers, 1991; Rak, 1991). AL 288-1 would require a larger more robust acetabulum to sustain the larger reaction forces created by wider hips and the associated musculature necessary to stabilize this joint. However a large acetabulum would not be expected if bipedalism was not a locomotor adaptation, but rather a postural adaptation as suggested by Hunt (1994). In this scenario, bipedality first evolved as a part of a feeding posture. To increase feeding efficiency, long bouts of terrestrial and arboreal postural bipedalism is sustainable because weight is supported by both hindlimbs with the assistance of hanging from one forelimb, while the other forelimb is left unhindered to forage. This would produce minimal loads on the hindlimb in comparison to bipedal locomotion and would require a relatively small acetabulum.

The small size of the acetabulum is reflected in other surface area proportions. Comparison of acetabulum to femur head surface area reveals a proportion in AL 288-1 more similar to African apes and orangutans than humans. This proportion speaks to the relative degree of mobility in the joint. If the difference in size between the male and female joint surfaces is great this is indicative of a joint with high mobility. In the hip joint, a small acetabulum relative to femur head is the high mobility condition. This is seen in both the African apes and orangutans and is absent in the human hip joint. The hip joint of AL 288-1 is found to have a small acetabulum when compared to femur head size relative to humans. This proportion indicates that Lucy may have had a high degree of hip mobility, comparable to the modern great apes. While it has already been noted that the small size in the acetabulum is likely the result of reduced loading compared to

fully bipedal locomotive requirements, the australopithecine hip almost certainly attained a higher degree of mobility than modern humans. This high mobility is necessary in an arboreal setting. The small acetabulum indicating both lower loading and higher mobility are consistent with Hunt's postural model.

In the analysis of humerus head to glenoid fossa surface areas, Lucy exhibits a pattern that is similar to both orangutans and humans but removed from the African ape condition. The resemblance to the human and orangutan condition is due to the similar use of this limb. Humans and orangutans both use this joint for tensile loading, although orangutans use the forelimb for suspending body weight while humans generally use their forelimbs for carrying objects. In both of these groups the shoulder joint is most commonly loaded by tensile stresses. This results in little pressure produced between joint surfaces as soft tissue is the primary load support structure. In the African ape group, a much larger glenoid fossa compared to humerus size is the result of compressive loading during habitual terrestrial knuckling walking. Lucy has a humerus to glenoid surface area ratio within the range of all three reference groups but most removed from the African ape model. Lucy's shoulder joint meets expectations for a shoulder generally used in tensile loading situations and renders a terrestrial quadrupedal component very unlikely in the *A. afarensis* locomotor repertoire.

The other two surface area comparisons are difficult to interpret as they do not compare two surfaces from a single joint nor do they compare functionally similar surfaces from different joints. In the comparison of humerus to acetabulum surface areas Lucy is within the ninety-five percent confidence limits of all three reference groups, but is closest to the African ape regression line. When the femur head is compared to the

glenoid fossa only orangutans are excluded and AL 288-1 is intermediate between African ape and humans.

The skeletal proportions of AL 288-1 are consistent with Hunt's bipedal posture model. The large femur head and small humerus relative to the human condition indicates a heavy reliance on the hindlimbs as weight bearing structures. However the presence of the small acetabulum in a wide hip that would generate greater forces seems difficult to explain if this species were fully bipedal. Instead, the small acetabulum is expected in the postural bipedal model.

Analyses of articular surface curvature present information about joint mobility and provide the opportunity to distinguish between the two possibilities. While Lucy did show intermediate forelimb to hindlimb proportions, single joint surface comparisons analyses of joint curvature reveal a very different picture. Joint surface curvature has been related to joint mobility and joint stability. More tightly curved male joint surfaces are associated with higher mobility joints. Tight curvature in female joint surfaces is associated with stability requirement from multidirectional loading while flatter female surfaces are only stable under unidirectional loads. In the three curvature analyses performed (femur head, humerus head, and acetabulum) Lucy fell well outside articular surface curvature for all human joint surfaces. The tightly curved humerus and femur heads of Lucy are well within the range of both orangutans and the African ape sample and suggest high degree of mobility in these joints relative to humans.

The shape of the acetabulum is the product of stability requirements. This is a function of both the amount of loading the joint is subjected to and the variability of direction of these stresses. Without looking at other variables such as midshaft cortical

area that speak only to joint loading and not mobility, these two factors are difficult to tease apart. Interpretation of AL 288-1 acetabulum reveals a shape on par with the great apes and reinforces the picture of an australopithecine hip joint that has similar mobility capabilities and stability requirements of these primates. The australopithecine acetabulum is thus smaller and shallower than would be expected for a human. The human acetabulum appears to be shaped fundamentally differently from other primates. Humans have relatively deep acetabulua compared to the other groups. This is most certainly due to the stresses of fully modern bipedalism.

Chapter 5

Conclusion

The analysis of Lucy's joint surface area proportions and articular surface curvature reveal a hominid with a mosaic of bipedal and arboreal adaptations. The australopithecine humerus head to femur head surface area proportion as represented by Lucy is more like the human condition and is far removed from the other primates investigated. This depicts an animal that often relied on its hindlimbs as weight bearing structures. However, this relationship is not mirrored in the acetabulum to glenoid fossa proportion. This is apparently the result of a small acetabulum as compared to the human condition. The relatively small acetabulum is also apparent in proportion to femur head size. If the australopithecine hip is reflective of a more efficient bipedality, the small acetabulum may reflect the lower forces generated at this joint. If the wide hip is poorly suited for bipedal locomotion the small acetabulum is still consistent with the bipedal postural feeding model proposed by Hunt (1994). In this feeding model body weight is sustained by both hindlimbs and one forelimb during early bipedal events. Such posturing would produce low stresses in the hip joint and would allow for the persistence of a small acetabulum. Those features argued by some to indicate an australopithecine hip poorly adapted to bipedal locomotion are expected if bipedality evolved as a postural adaptation.

The scapula to humerus analysis shows Lucy to most closely resemble humans and orangutans. Both of these groups primarily stress their shoulder joints with tensile loads, and differentiates them from the African ape which introduce heavy compressive

loads to the shoulder joint with frequent terrestrial quadrupedal locomotion. This proportion in Lucy suggests that the forelimb of this hominid was loaded similarly to humans or orangutans. However, it cannot differentiate between carrying objects and supporting body weight. The curvature of the humeral head, however, completes the functional picture of the shoulder joint. The tightly curved humeral head in Lucy is a morphology associated with high mobility. Although it could be argued that this morphology is retained from the ancestral condition, it seems difficult to defend this position in light of the size changes occurring at the shoulder joint. The relatively high degree of curvature present after changes in proportional size are likely the result of selection to retain this morphology. The highly mobile shoulder joint would not greatly benefit a hominid long confined to the terrestrial world, but one that still or in its immediate evolutionary past took advantage of an aboreal environment. This again dovetails well with the bipedalism evolving from a postural adaptation. An aboreal component to australopithecine locomotion has been argued by several authors and comes from several lines of evidence (Susman et al., 1985 and all references there in). The high mobility requirements of the australopithecine hip are also reflected in the curvature of the femur head. The retention of a tightly curved femur head concurrent with the changes required by bipedality strongly suggest selection for retention of this feature. A high mobility hip joint would only be necessary of a hominid still taking advantage of the trees.

The mosaic of aboreal and terrestrial features present in the australopithecine postcrania as represented by Lucy strongly suggest either a hominid in an adaptive transition or one that evolved bipedality as a postural adaptation. Humerus to femur

proportions are consistent with expectations about an australopithecine form of bipedality and closely resemble the modern human condition. However, tightly curved joint surfaces out of the human range of variation but similar to those of the great ape suggest selection for the retention of this morphology. High mobility, not only in the hip but especially in the shoulder, is of the greatest benefit to the groups that frequently take advantage of an arboreal environment. This implies that australopithecines were spending a significant proportion of their time in trees. If the hip were the product of a more efficient bipedality and one that obligated this hominid to the terrestrial realm, then it is difficult to explain the persistence of a high mobility shoulder and other features related to supporting body weight with the forelimb. Instead these features are consistent with bipedalism as a postural adaptation. The retention of a highly mobile shoulder would be necessary to aid in support of body weight if hips were only suited to postural bipedalism.

The analyses presented here are most compatible with the evolution of bipedality as a feeding posture. The surface area proportions indicate that a great deal of the body mass was supported by the hindlimbs. However, the acetabulum seems to be suited to either a more efficient form of bipedal locomotion that creates lower stresses on the joint, or postural bipedalism where weight is supported by the forelimbs and movement stresses are limited. The degree of curvature retained in the humerus head suggests a highly mobile joint, one not retained for terrestrial bipedalism, but rather to support the body by hanging from the forelimb.

References

References

- Aiello LC. 1981. The allometry of primate body proportions. *Symposia Zoological Society of London* 48:331-358.
- Aiello LC. 1992. Allometry and the analysis of size and shape in human evolution. *Journal of Human Evolution* 22:127-147.
- Alexander R McN. 1980. Forces in animal joints. *Engineering Medicine* 9:93-97.
- Bartholomew GA, Birdsell JB. 1953. Ecology and the protohominids. *American Anthropologist* 55:481-498.
- Broom R and JT Robinson. 1947. Further Remains of the Sterkfontein Ape-Man, *Plesianthropus*. *Nature* 160:430-431.
- Carrier DR. 1984. The energetic paradox of human running and hominid evolution. *Current Anthropology* 25: 483-495.
- Clark GA. 1988. Some thoughts on the Black Skull: an archeologist's assessment of WT-17000 A. *boisei* and systematics in human paleontology. *American Anthropologist* 90:357-371.
- Collard M, Wood B. 2000. How reliable are human phylogenetic hypotheses? *Proceedings of the National Academy of Science* 97:5003-5006.
- Coon CS. 1962. *The Origin of Races*. New York.
- Currey J. 1984. *The Mechanical Adaptation of Bone*. Princeton:Princeton University Press.
- Dart RA. 1925. *Australopithecus africanus*: The Man-Ape of South Africa. *Nature* 115:195-199.
- Dart RA. 1959. *Adventures with the Missing Link*. New York: Harper
- Day MH. 1977. Locomotor adaptations in man. *Biology of Human Affairs* 42:149-151.
- Day MH. 1986. Bipedalism: pressures, origins and modes. In Wood B, Martin L, Andrews, P editors. *Major Topics in Primate and Human Evolution*. Cambridge: Cambridge University Press. p. 188-202.
- Delson E. 1986. Human phylogeny revised again. *Nature* 322:496-497.
- Delson E. 1987. Evolution and paleobiology of robust *Australopithecus*. *Nature* 327:654-655.

- Eckhardt RB. 1986. Hominid evolution. *Science* 234:11.
- Ethkin W. 1954. Social behavior and evolution of man's mental faculties. *American Naturalist* 88: 129-143.
- Falk D. 1986. Hominid evolution. *Science* 234:11.
- Foley R. 1987. *Another Unique Species: Patterns of Human Evolutionary Ecology*. Harlow: Longman Scientific and Technical.
- Godfrey L, Sutherland M, Boy D, Gomberg N. 1991. Scaling of limb joint surface areas in anthropoid primates and other mammals. *Journal of Zoology* 223:603-625.
- Godfrey L, Sutherland M, Paine R, Williams F, Boy D, Vuillaume-Randriamianatena. 1995. Limb joint surface areas and their ratios in Malagasy lemurs and other mammals. *American Journal of Physical Anthropology* 97:11-36.
- Grine FE. 1988a. Evolutionary history of the "robust" australopithecines: a summary and historical perspective. In Grine FE, editor. *Evolutionary History in the "Robust" Australopithecines*. New York: Aldine de Gruyter. p 509-519.
- Grine FE. 1988ba. New craniodental fossils of *Paranthropus* from Swartkrans Formation and their significance in "robust" australopithecine evolution. In Grine FE, editor. *Evolutionary History in the "Robust" Australopithecines*. New York: Aldine de Gruyter. p.223-244.
- Grine FE. 1993. Australopithecine Taxonomy and Phylogeny: Historical Background and Recent Interpretation. In Ciochon RL, Fleagle JG editors. *The Human Evolution Source Book*. Englewood, NJ: Prentice Hall. p 198-210.
- Hamilton ME. 1972. Australopithecine limb proportions. *American Journal of Physical Anthropology* 37:439.
- Hamrick MW. 1996a. Articular Size and Curvature as Determinants of Carpal Joint Mobility and Stability in Strepsirrhine Primates. *Journal of Morphology* 23:113-127.
- Hamrick MW. 1996b. Locomotor adaptations reflected in the wrist joints of early tertiary primates (Adapiformes). *American Journal of Physical Anthropology* 100:585-604.
- Harris JW, Stocker H. 1998. *Handbook of Mathematics and Computational Science*. New York: Springer. p. 107.

- Hartwig-Scherer S. 1993. Body Weight Prediction in Early Fossil Hominids: Towards a Taxon-“Independent” Approach. *American Journal of Physical Anthropology* 92:17-36.
- Hartwig-Scherer S, Martin RD. 1991. Was “Lucy” more human than her “child”? Observations on early hominid postcranial skeletons. *Journal of Human Evolution* 21:439-449.
- Hens S. 1998. Stature Estimation in Fossil Hominids. PhD Dissertation. University of Tennessee, Knoxville.
- Hewes GW. 1961. Food transport and the origin of hominid bipedalism. *American Anthropologist* 63:687-710.
- Hofman MA. 1983. Encephalization in himinids: Evidence for the model of punctualism. *Brain Behavior Evolution* 22:102-117.
- Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. *Journal of Human Evolution* 26:183-202.
- Johanson DC, Lovejoy CO, Burstein AH, Heiple KG. 1976. Functional Implications of the Afar knee joint. (Abstract) *American Journal of Physical Anthropology* 44:188.
- Johanson DC, Taieb M. 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260:293-297.
- Johanson DC, Taieb M, Coppens Y, Roche Y. 1978. A new speices of the genus *Australopithecus* (Primate Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28: 1-14.
- Johanson DC, Tiaeb M, and Coppens Y. 1982. Pliocene Hominids From the Hadar Formation, Ethiopia (1973-1977): Stratigraphic, Chronologic, and Paleoenvironmental Context, With Notes on Hominid Morphology and Systematics. *American Journal of Physical Anthropology* 57:373-402.
- Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5:1-26.
- Jungers WL. 1985. *Size and Scaling in Primate Biology*. New York: Plenum.
- Jungers WL. 1988a. Relative joint size and hominid locomotor adaptations with implications for the evolution of hominid bipedalism. *Journal of Human Evolution* 17:247-265.

- Jungers WL. 1988b. New Estimates of Body Size in Australopithecines. In Grine FE, editor. *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter. p 115-125.
- Jungers WL. 1991. A pygmy perspective on body size and shape in *Australopithecus afarensis* (AL 288-1, "Lucy"). . In Coppens Y, Senut B, editors. *Origine de la Bipedie chez les Hominides*, Cah. Paleoanthrop. Paris:CNRS. p 215-224.
- Kapandji IA. 1970. *The Physiology of the Joints*. New York: Churchill Livingstone.
- Kimbel WH, White TD, Johanson DC. 1988. Implications of KNM-WT 17000 for the evolution of "robust" *Australopithecus*. In Grine FE, editor. *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter. p 259-268.
- Konigsberg LW, SH Hens, LM Jantz, WL Jungers. 1998. Stature Estimation and Calibration: Bayesian and Maximum Likelihood Perspectives in Physical Anthropology. *Yearbook of Physical Anthropology* 41:65-92.
- Latimer B, Ohman JC, Lovejoy CO. 1987. Talocrual Joint in African Hominoids: Implications for *Australopithecus afarensis*. *American Journal of Physical Anthropology* 74:155-175.
- Latimer B, Lovejoy CO. 1989. The Calcaneus of *Australopithecus afarensis* and Its Implications for the Evolution of Bipedality. *American Journal of Physical Anthropology* 78:369-386.
- Latimer B, Lovejoy CO. 1990a. Metatarsophalangeal Joints of *Australopithecus afarensis*. *American Journal of Physical Anthropology* 83:13-23.
- Latimer B, Lovejoy CO. 1990b. Hallucal Tarsometatarsal Joint in *Australopithecus afarensis*. *American Journal of Physical Anthropology* 82: 125-133.
- Leakey REF. 1972. Further evidence of Lower Pleistocene hominids from East Rudolf, Northern Kenya, 1971. *Nature* 231:241-245.
- Leakey REF. 1973. Further evidence of Lower Pleistocene hominids from East Rudolf, Northern Kenya, 1972. *Nature* 242:170-173.
- Leakey MD, Hay RL, Curtis GH, Drake RE, Jakes MK, White TD. 1976. Fossil hominids from the Laetolil Beds. *Nature* 262:460-466.
- Leakey MD, Hay RL. 1979. Pliocene footprints in the Laetolil Beds at Laetoli, North Tanzania. *Nature* 278:317-323.

- Leakey MG, Reibel CS, McDougall I, Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565-571.
- Lewin R. 1986. New fossil upsets human family. *Science* 333:720-722.
- Lovejoy CO. 1979. A reconstruction of the pelvis of A.L.288 (Hadar Formation, Ethopia). *American Journal of Physical Anthropology* (Abstract) 50:454.
- Lovejoy CO. 1981. The origin of man. *Science* 211:341-350.
- Lovejoy CO. 1988. Evolution of Human Walking. *Scientific American* 259:118-125.
- Lovejoy CO. 1993. Modeling human origins: Are we sexy because we're smart or smart because we're sexy?. Rasmussen TD, editor. *The Origin and Evolution of Humans and Humanness*. Boston: Jones and Barlett. p 1-28.
- Lovejoy CO, KG Keiple, AH Burstein. 1973. The gait of *Australopithecus*. *American Journal of Anthropology* 38:757-780.
- MacConnaill MA. 1950. The movements of bones and joints: The synovial fluid and its assistants. *Journal of Bone and Joint Surgery* 32B:244-252.
- MacConnaill MA. 1966. The geometry and algebra of articular kinematics. *Biomedical Engineering* 1:205-212.
- MacConnaill MA, Basmajian JV. 1969. *Muscles and Movement: A Basis for Human Kinesiology*. Baltimore: Williams and Watkins.
- McHenry HM. 1974. How large were the Australopithecines? *American Journal of Physical Anthropology* 40:329-340.
- McHenry HM. 1978. Limb Proportions in Early Hominids. *American Journal of Physical Anthropology* 49:15-22.
- McHenry HM. 1982. The pattern of human evolution: Studies on bipedalism, mastication, and encephalization. *Annual Review of Anthropology* 11:151-173.
- McHenry HM. 1988. New Estimates of body weight in early hominids and their significance to encephalization and megadontia in "robust" australopithecines. In Grine FE, editor. *The Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter. p 133-148.
- McHenry HM. 1991. First step? Analyses of the postcranium of early hominids. In Coppens Y, Senut B, editors. *Origine de la Bipedie chez les Hominides*, Cah. Paleoanthrop. Paris:CNRS. p 133-141.

- McHenry HM. 1992. Body size and proportions in early hominids. *American Journal of Physical Anthropology* 87:407-431.
- McHenry HM, LR Berger. 1998. Body Proportions in *A. afarensis* and *A. africanus* and the Origin of the Genus *Homo*. *Journal of Human Evolution* 35: 1-22.
- Norkin C, Levangie P. 1983. *Joint Structure and Function: A Comprehensive Analysis*. Philadelphia: F.A. Davis.
- Pilbeam D. 1997. Research on Miocene Hominoids and Hominid Origins. In Begun DR, Ward CV, Rose MD, editors. *Function, Phylogeny, and Fossils: Miocene Hominoids Evolution and Adaptation*. New York: Plenum Press. p 13-28.
- Rafferty KL, Ruff CB. 1994. Articular Structure and Function in *Hylobates*, *Colobus*, and *Papio*. *American Journal of Physical Anthropology* 94:395-408.
- Rak Y. 1991. Lucy's pelvic anatomy; its role in bipedal gait. *Journal of Human Evolution* 20:283-290.
- Robinson JT. 1972. *Early Hominid Posture and Locomotion*. Chicago: University of Chicago Press.
- Ruff CB. 1984. Allometry Between Length and Cross-Sectional Dimensions of Femur and Tibia in *Homo sapiens sapiens*. *American Journal of Physical Anthropology* 65:347-358.
- Ruff CB. 1987. Structural allometry of the femur and tibia in Hominoidea and *Macaca*. *Folia Primatologica* 48:9-49.
- Ruff CB. 1988. Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphysis scaling. *Journal of Human Evolution* 17:687-714.
- Ruff CB. 1990. Body mass and hindlimb cross-sectional and articular dimensions in anthropoid primates. In Damuth J, McFadden B, editors. *Body Size in Mammalian Paleobiology*. Cambridge: Cambridge University Press. p 41-62.
- Ruff CB. 1993. Climatic adaptation and hominid evolution; the thermoregulatory imperative. *Evolutionary Anthropology* 3:52-60.
- Ruff CB, Runestad JA. 1992. Primate limb bone structural adaptations. *Annual Review of Anthropology* 21:407-433.
- Sarmiento EE. 1988. Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. *International Journal of Primatology* 9:281-345.

- Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. *Human Biology* 2:303-438.
- Schmidt-Nielsen K. 1984. *Scaling: Why is Animal Size So Important?* Cambridge: Cambridge University Press.
- Shipman P. 1986a. Baffling limb on the family tree. *Discover* 7:86-93.
- Shipman P. 1986b. Scavenging or hunting in early hominids: theoretical framework and tests. *American Anthropologist* 88:27-43.
- Sinclair A, Leakey RE and Norton-Griffiths MD. 1986. Migration and hominid bipedalism. *Nature* 324:307-308.
- Singh I. 1978. The architecture of cancellous bone. *Journal of Anatomy* 127:305-310.
- Skelton RR, McHenry HM. 1990. Evolutionary relationships among early hominids. *Journal of Human Evolution* 23:309-349.
- Stern JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology* 60:279-318.
- Susman RL, Stern JT, Jungers WL. 1984. Arboreality and Bipedality in the Hadar Hominids. *Folia Primatologica* 43:113-156.
- Susman RL, Stern JT, Jungers WL. 1985. Locomotor Adaptations in the Hadar Hominids. In Delson E, editor. *Ancestors: the Hard Evidence*. New York City: Liss. p 184-192.
- Swartz SM. 1989. The functional morphology of weight-bearing: Limb joint surface area allometry in anthropoid primates. *Journal of Zoology* 218:441-460.
- Tatsuoka MM. 1971. *Multivariate Analysis: Techniques for Educational and Psychological Research*. New York: John Wiley and Sons. p 39-48.
- Tuttle RH. 1975. Parallelism, brachiation and hominoid phylogeny. In Luckett WP Szalay FS, editors. *The Phylogeny of the Primates: A Multidisciplinary Approach*. New York: Plenum. p 447-480.
- Vrba ES. 1988. Late Pliocene climatic events and hominid evolution. In Grine FE, editors. *Evolutionary history of the "Robust" Australopithecines*. New York: Aldine di Gruvier. p 247-258.
- Wainwright SA, Biggs W, Currey J, Gosline J. 1982. *Mechanical Design in Organisms*. Princeton: Princeton University Press.

- Walker A, Leakey RE, Harris JM and Brown FH. 1986. 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* 322:517-522.
- Washburn SL. 1960. Tools and human evolution. *Scientific American* 203:63-75.
- Washburn SL. 1967. Behavior and the origin of man. *Proceedings of the Royal Anthropological Society* 3:21-27
- Wheeler PE. 1991a. The thermoregulatory advantages of hominid bipedalism in open equatorial environments, body form and bipedality. *Journal of Human Evolution* 14:23-28.
- Wheeler PE. 1991b. The influence of bipedalism on the energy and water budgets of early hominids. *Journal of Human Evolution* 21:117-136.
- White TD. 1980. Evolutionary Implications of Pliocene Hominid Footprints. *Science* 208: 175-176.
- White TD and Suwa C. . Hominid footprints at Laetoli: Facts and interpretations. In Johanson DC, editor. *The Origin of Human Locomotion*. San Diego: Academic.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306-312.
- White TD, Suwa G, and Asfaw B. 1995. Corrigendum: *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 375:88.
- Wrangham RW. 1980. Bipedal locomotion as a feeding adaptation in Gelada baboons, and its implications for hominid evolution. *Journal of Human Evolution* 9:329-331.
- Yalden DW 1972. The form and function of the carpal bones in some arboreally adapted mammals. *Acta Anatomica* 82:383-406.
- Zuckerman SS, Ashton EH, Flinn RM, Oxnard CE. 1973. Some locomotor features of the pelvic girdle in primates. *Symposia of Zoological Society of London* 33: 71-165.

Vitae

Adam David Sylvester was born and raised in Teaneck, New Jersey. After graduating high school he attended undergraduate school at the University of Tennessee in Knoxville, receiving his Bachelors of Science, Magna Cum Lauda, in Zoology in May of 1996. In the spring of 1998 he returned to the University of Tennessee to complete undergraduate work in Anthropology with the intent of continuing onto graduate school. He was accepted to the Masters program in Anthropology at the University of Tennessee, Knoxville for the fall of 1998 with a concentration in paleoanthropology. In August of 2000 he was awarded his Masters Degree in Anthropology.