Summer 2010

Three-dimensional morphometrics of the proximal metatarsal articular surfaces of Gorilla, Pan, Hylobates, and shod and unshod humans

Daniel Jason Proctor
University of Iowa

Recommended Citation

Proctor, Daniel Jason. "Three-dimensional morphometrics of the proximal metatarsal articular surfaces of Gorilla, Pan, Hylobates, and shod and unshod humans." PhD (Doctor of Philosophy) thesis, University of Iowa, 2010.
http://ir.uiowa.edu/etd/725.

THREE-DIMENSIONAL MORPHOMETRICS OF THE PROXIMAL METATARSAL ARTICULAR SURFACES OF *GORILLA*, *PAN*, *HYLOBATES,* AND SHOD AND UNSHOD HUMANS

by

Daniel Jason Proctor

An Abstract

Of a thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Anthropology
in the Graduate College of
The University of Iowa

July 2010

Thesis Supervisor: Professor Russell Ciochon

ABSTRACT

There is debate about how fossil hominin pedal morphology relates to terrestrial habits. Were early hominins adapted to a bipedal lifestyle with a significant arboreal component, or were they more dedicated to a terrestrial lifestyle? The proximal articular surfaces of the metatarsals (MT) are examined in *Gorilla*, *Pan*, *Hylobates*, and habitually shod and unshod *Homo* using three-dimensional morphometrics. The results for MT 1 show three trends. OH 8 (*Homo habilis*) is indistinguishable from humans, specimens SKX 5017 and SK 1813 (*Paranthropus robustus*) are apelike, and all other fossil 1st metatarsals are intermediate in shape between humans and apes.

The MT 2 and MT 3 analyses show that humans have a narrower surface that is expanded in the plantar aspect relative to apes. These features increase joint stability for the human longitudinal arch. The MT 2 fossils for Stw 573d (Little Foot) and OH 8 are humanlike. The MT 2 specimen of SKX 247 (possibly *Paranthropus*) is apelike, while all other MT 2 fossils are intermediate between humans and apes. In the MT 3 analysis, Stw 387, Stw 496, Stw 388, and OH 8 metatarsals are humanlike in shape, while Stw 435 and Stw 477 are intermediate between humans and apes. The MT 3 surface of *Hylobates* is markedly convex, suggesting that the midfoot break in gibbons extends to include this joint in addition to the MT 4 and MT 5 tarsometatarsal joints.

The results of the MT 4 analysis show a highly convex surface in apes, with *Hylobates* extending further to the dorsal aspect of this metatarsal, with a greater range of motion at the midfoot break compared to the African apes. The MT 4 specimens of OH 8 and Stw 628 show greater morphological affiliation with humans.

The MT 5 analysis shows that *Pan* and *Hylobates* have a medio-laterally extended and concave articular surface that is convex in the dorso-plantar plane. The two human groups are narrower and flatter in the medio-lateral plane, with a little dorso-plantar convexity. There is overlap in shape patterns between groups in the MT 5 analysis.

Greatest similarity is between humans and *Gorilla*. The MT 5 fossil specimens tend to show closer affiliation to humans and *Gorilla*.

Abstract Approved: _______________________________________

Thesis Supervisor

____

Title and Department

____

Date

THREE-DIMENSIONAL MORPHOMETRICS OF THE PROXIMAL METATARSAL ARTICULAR SURFACES OF *GORILLA*, *PAN*, *HYLOBATES,* AND SHOD AND UNSHOD HUMANS

by

Daniel Jason Proctor

A thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Anthropology
in the Graduate College of
The University of Iowa

July 2010

Thesis Supervisor: Professor Russell Ciochon

Graduate College
The University of Iowa
Iowa City, Iowa

CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

Daniel Jason Proctor

has been approved by the Examining Committee
for the thesis requirement for the Doctor of Philosophy
degree in Anthropology at the July 2010 graduation.

Thesis Committee: ______________________________
Russell Ciochon, Thesis Supervisor

____
Robert Franciscus

____
Nelson Ting

____
Daniel Gebo

____
Christopher Brochu

To my family

ACKNOWLEDGMENTS

I want to thank my dissertation committee for their input and support over the last several years. Thanks to my advisor and committee chair Russ Ciochon, and the following committee members who helped at various stages of exams and proposals: Bob Franciscus, Jim Enloe, Dan Gebo, Chris Brochu, and Nelson Ting. I owe the Departments of Anthropology at both the University of Iowa and Florida Atlantic University for support and providing teaching and funding opportunities throughout my graduate student career, without which it would not have been possible for me to complete my degree.

I have received grant funding from various sources over the course of my graduate degree. I thank the Department of Anthropology at Florida Atlantic University for the Morrow Research Assistantship, and a grant from the Department of Biomedical Science at Florida Atlantic University, both which were instrumental in supporting my master’s thesis. I thank the Department of Anthropology at the University of Iowa for a Summer Research Fellowship that helped me to conduct my pilot study for this dissertation. In addition, I thank the Graduate College at the University of Iowa for the T. Anne Cleary International Dissertation Research Fellowship, the Stanley Graduate Award for International Research, and the Graduate College Summer Fellowship.

A great debt is owed to many people and institutions for allowing me to study their collections: The Cleveland Museum of Natural History, Yohannes Haile-Selassie and Lyman Jellema; The Museum of Comparative Zoology and Judith Chupasko; The National Museum, Bloemfontein, and James Brink; The South African Museum, Cape Town, Sarah Wurz and Wilhelmina Seconna; the Transvaal Museum, Francis Thackery and Stephany Potze; and the University of Witwatersrand, Bernhard Zipfel and Ron Clarke. I need to particularly thank Lyman for his hard work in making the collections at Cleveland so easy to navigate. Lyman always provides great discussion and I enjoy my visits with him very much. I thank Judy at Harvard for going out of her way to help me organize my visit. Stephany and Francis in Pretoria were very helpful and generous in their time. Bernhard and Ron in Johannesburg were extremely generous in allowing me to examine so many fossil specimens, and Bernhard was very helpful and giving of his time. James in Bloemfontein went out of his way to make me feel at home during my visit, and helped make my stay at Florisbad very productive. Finally I have to offer special recognition to Sarah and Wilhelmina in Cape Town, who were very gracious when I showed up at the museum very unexpectedly due to an inadvertent miscommunication.

My stay in Johannesburg was safe and fun very much due to the efforts of Alison Groves and Andrew “Maggie” Thatcher. I thank them both so much for great conversations and the opportunity to stay with a family from South Africa. My stay in Cape Town was splendid, and the view of Table Mountain was spectacular. I thank Pennie Dobbie for that opportunity and for the hospitality.

I have established friendships with several colleagues over the course of my research. I offer very special thanks to Bernhard Zipfel for his discussion and insights. Bernhard provided expert feedback and helped me to think about issues in different ways. Many thanks go to Jerry DeSilva, another expert in the “elite” field of pedal evolution, whose generosity in providing laser scans and photos of OH 8 helped me profoundly. I’m very grateful to Dan Gebo, who has given me helpful professional feedback on various manuscripts and helped me to improve my writing. I thank Will Harcourt-Smith for his guidance, particularly at a very formative stage of my research. An immeasurable debt is owed to Ron Clarke for his generosity in allowing me to examine a number of fossil specimens that are unpublished or currently under study. This opportunity has contributed greatly to the importance of my research, and I can’t emphasize my gratitude enough.

I’m grateful for the support of my family, including my mom, Betsy, my dad, Jerry, my sister, Julie, and my brother, Kris. It has been a very long journey with many ups and downs, but I appreciate all of the support through all of the good, bad, and crazy times. All I can say is it's a good thing we're Proctors. Of course I need to thank one family member who has probably borne the brunt of the stress and manic moments, my wife Lavanya Murali Proctor. I have drawn a great deal of strength and stability from Lavanya, sometimes like a vampire at her emotional expense, I'm sure! I couldn't have gotten through this without her support.

When writing something like this it is hard to account for all of the little things that add up to a lot by so many people. However, I think many of us who go through this education process can think of people who were very instrumental early on. I owe a debt to the Department of Anthropology at Eastern Washington University, where I earned my undergraduate degree. I have to thank Fred Strange for shaking up my assumptions and making me think in different ways. I thank Jerry Galm for his advice and for a quote I've never forgotten, "In graduate school you'll learn a lot, not just about what to do but what *not* to do." Finally, I must especially offer sincere gratitude to Sarah Keller. As my undergraduate advisor, she helped me build an academic and intellectual foundation that I have relied on through all of my graduate student experiences. Without that solid basis I don't think I would have been able to take on the challenges of graduate school. As my friend, Sarah has provided unique, practical, and dare I say at times shrewd, insights that I have benefited from and will continue to find valuable into the future.

ABSTRACT

There is debate about how fossil hominin pedal morphology relates to terrestrial habits. Were early hominins adapted to a bipedal lifestyle with a significant arboreal component, or were they more dedicated to a terrestrial lifestyle? The proximal articular surfaces of the metatarsals (MT) are examined in *Gorilla*, *Pan*, *Hylobates*, and habitually shod and unshod *Homo* using three-dimensional morphometrics. The results for MT 1 show three trends. OH 8 (*Homo habilis*) is indistinguishable from humans, specimens SKX 5017 and SK 1813 (*Paranthropus robustus*) are apelike, and all other fossil 1st metatarsals are intermediate in shape between humans and apes.

The MT 2 and MT 3 analyses show that humans have a narrower surface that is expanded in the plantar aspect relative to apes. These features increase joint stability for the human longitudinal arch. The MT 2 fossils for Stw 573d (Little Foot) and OH 8 are humanlike. The MT 2 specimen of SKX 247 (possibly *Paranthropus*) is apelike, while all other MT 2 fossils are intermediate between humans and apes. In the MT 3 analysis, Stw 387, Stw 496, Stw 388, and OH 8 metatarsals are humanlike in shape, while Stw 435 and Stw 477 are intermediate between humans and apes. The MT 3 surface of *Hylobates* is markedly convex, suggesting that the midfoot break in gibbons extends to include this joint in addition to the MT 4 and MT 5 tarsometatarsal joints.

The results of the MT 4 analysis show a highly convex surface in apes, with *Hylobates* extending further to the dorsal aspect of this metatarsal, with a greater range of motion at the midfoot break compared to the African apes. The MT 4 specimens of OH 8 and Stw 628 show greater morphological affiliation with humans.

The MT 5 analysis shows that *Pan* and *Hylobates* have a medio-laterally extended and concave articular surface that is convex in the dorso-plantar plane. The two human groups are narrower and flatter in the medio-lateral plane, with a little dorso-plantar convexity. There is overlap in shape patterns between groups in the MT 5 analysis.

Greatest similarity is between humans and *Gorilla*. The MT 5 fossil specimens tend to show closer affiliation to humans and *Gorilla*.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

Background

There are two primary areas of broad concern in studies of the evolution of bipedalism. The first area concerns the origins of bipedalism. Questions surrounding this area center primarily on when bipedalism first emerges, the reasons for its emergence, and how we detect it in the skeletal anatomy of fossils. The second area is the subsequent adaptation of bipedalism. Questions in this area focus on how the anatomy of early hominins changes through natural selection until it resembles the form of bipedalism demonstrated in modern humans. This area of concern interprets the mosaic evolution of human evolution for insights into how early hominins walked, and whether different hominin lineages exhibit different modes of bipedalism. For example, there is considerable debate on the significance of fossil hominin pedal morphology and how it relates to terrestrial habits (e.g., Harcourt-Smith and Aiello, 2004; Ward, 2002; Stern, 2000; Latimer, 1991; Susman and Stern, 1991; Latimer and Lovejoy, 1990a, 1990b; Susman et al., 1984; Stern and Susman, 1983; Susman, 1983). Were early hominins adapted to a bipedal lifestyle that contained a significant arboreal component, or is there is evidence indicating a more dedicated terrestrial lifestyle? Recently Harcourt-Smith and Aiello (2004, pg. 413) raised the question of whether pedal anatomy, as represented in currently available fossil hominin specimens, could represent a “mosaic [of ape-like and human-like anatomical traits] in their adaptations, but, critically, may have been mosaic in different ways to each other.” In short, although bipedalism may have a single origin in the evolutionary line leading to *Homo sapiens*, it is possible that adaptations to a bipedal lifestyle in different hominin lineages may follow different anatomical paths. We might not expect, for instance, that the finer points of bipedal anatomy in the foot are the same in *Homo habilis* as they are in *Paranthropus robustus*, where each hominin dealt with different ecological niches.

This topic is one of the most contentious in the field of physical anthropology, and was clearly summarized by Stern (2000) ten years ago. It still accurately represents the state of affairs today. The primary issue is largely theoretical. Stern (2000) identifies two schools of thought about how to interpret mosaic anatomical traits in fossil hominins. The first is that mosaic traits are mostly irrelevant to interpreting hominin behavior and to some extent function of skeletal anatomy. Early hominins are dedicated to habitual bipedal behavior, even though their anatomy preserves plesiomorphic traits that are apelike or primitive traits that do not reflect any ape-like function. From this point of view apomorphic traits are the most important for the interpretation of functional anatomy.

The second theoretical perspective is that some plesiomorphic traits may not be "vestigial." This approach interprets fossil anatomy is in fossil hominins as adaptations for that species' current form of locomotion or other functions. The anatomy represents adaptations to current behavior, at a moment in evolutionary time, not necessarily a step to something else. In other words, plesiomorphic and apomorphic anatomy represent an organism's most efficient (mosaic) adaptation to the selective pressures in the environment at that moment in time (see Rose, 1991; Hunt 1994, 1996). This is an important point of view. These two theoretical views are important even though they may seem subtle. Both views have profound implications for how we interpret hominin anatomy and develop evolutionary models for the emergence and subsequent adaptation of bipedalism.

The research presented in this dissertation follows the latter theoretical perspective and builds upon previous anatomical observations for the evolution of the hominin foot. This research investigates Harcourt-Smith and Aiello's (2004) idea that mosaic evolution in fossil hominin lineages is mosaic in lineages. The specific hypotheses tested are discussed in Chapter 4. However, one broad area of interest is whether there is evidence for alternative modes of bipedalism between the hominin lineages. The specific hypotheses add insight to the view that the hominin foot develops "modernity," in this context meaning anatomical stability for a rigid longitudinal arch, beginning on the lateral side of the foot earlier in evolution and progressing medially later. The implication of this idea is that plesiomorphic traits in the medial foot, especially in the hallux, may maintain functional significance as the foot is adapting to more efficient bipedalism. As early hominins become completely dependent on a habitually terrestrial form of bipedalism, the medial foot presumably develops a stable longitudinal arch as well. Although this model is supported by other anatomical observations of the foot, it is not very well supported in terms of proximal metatarsal articular surface shape.

Methodological Importance

In recent years three-dimensional morphometrics has become increasingly important in the analysis of complex anatomical shapes (Adams et al., 2004). The use of a microscribe has perhaps became the most common tool in three-dimensional studies. However, laser scanners are becoming increasingly more common, primarily due to availability of relatively inexpensive portable laser scanners. Microscribes remain useful for larger structures. However, laser scanners do provide advantages over other technology in the study of small structures, such as articular surfaces, as well as the amount of data that can be sampled.

One disadvantage to a microscribe is that the stylus only samples one point in a three-dimensional space, or at best a series of points on a line or curve. A laser scanner can record surface topography at a resolution of hundreds of dots per square inch, with fine resolution depending on the needs of the project. The end result is that a complete 3D structure can be modeled, manipulated, and subjected to a variety of analyses whereas landmarks selected with a microscribe may only be useful in one study or context. This reduces errors during data collection. In contrast, if errors with a microscribe are discovered after leaving the field, entire specimens may be useless. If one ensures that a laser scan is complete in the field, landmarks can be sampled later. Another advantage to a laser scanner is that a delicate fossil can be sampled with very little physical manipulation. Although a microscribe can be less damaging than calipers, it still requires contact with a specimen that often occurs via a metal stylus tip. Additionally, a laser scan can be revisited any number of times for later additional studies without having to submit a fossil specimen to additional handling. Laser scans can potentially be shared between researchers to reduce wear and tear on invaluable specimens, not to mention reducing the costs involved in traveling the world to examine a few specimens.

Laser scanners have been used successfully in previous studies on articular surfaces (Tocheri, 2007; DeSilva, 2010). However, laser scans have not yet been used for initial data collection in landmark-based studies of articular surfaces. This dissertation expands on the study by Proctor et al. (2008) in which the proximal MT 1 articular surface was analyzed with a landmark scheme collected by a microscribe. It was the first study of its kind on the first metatarsal, but due to the difficulty in collecting landmarks on small articular surfaces, a laser scanner was employed for this dissertation. The New York Consortium in Evolutionary Primatology (NYCEP) collaborated with the Institute of Data Analysis and Visualization at the University of California, Davis, to produce the software Landmark for the application of landmarks on laser scans. Small objects can be expanded in size on a computer monitor to allow greater control over placement of landmarks. This dissertation successfully combines the use of a laser scanner and the program Landmark for analyzing joint surface shape with a landmark-based methodology for the first time.

Dissertation Structure

This dissertation is divided into eleven chapters. Chapter 1 is the introduction. Chapter 2 provides a discussion and overview of the theories on the origin of bipedalism, in order to present the broader theoretical bases from which interpretation of fossil anatomy originates. Chapter 3 presents a discussion of human and ape comparative evolutionary anatomy, with particular emphasis on the foot. In addition, this chapter presents a discussion about the differences in foot anatomy between shod and unshod human populations, and the fossil evidence for the emergence and subsequent evolution of bipedalism.

Chapter 4 presents the materials and methods of this dissertation. In addition to a detailed list of the specimens in this study, there is an in-depth discussion of the specific hypotheses tested and their functional bases. Here is a discussion and definition of the landmarks used in these analyses, and how the data collected is analyzed. Chapter 5 assesses the influence of observation error on these analyses. This is important in all research studies; however, it is particularly important for the studies presented here because the methodology is new in terms of the combination of technologies used and the methodology of landmark application on joint surfaces.

Chapter 6 presents the results of the analysis of the first metatarsal (MT 1) proximal joint surface morphology, and this chapter sets the pattern for which all remaining metatarsal analyses will be presented. Chapters 7, 8, 9, and 10 present the results of the analyses of MT 2, MT 3, MT 4, and MT 5, respectively. At the end of each analysis chapter there is a discussion section that synthesizes the results of the analysis, with particular emphasis on the most important morphological findings. The dissertation concludes with discussion and conclusions in Chapter 11, with particular emphasis on integrating the results of all of the metatarsal analyses to address the implications of these results and how the analyses relate to each other. This chapter also discusses future research.

CHAPTER 2: MODELS FOR THE ORIGIN OF BIPEDALISM

Models Explaining the Origin of Bipedalism

This chapter is a discussion of the major theories relating to the origin of hominin bipedalism. A broad perspective is important to establish the basis from which anatomical interpretations of the hominin fossil record draw. Many theories overlap in their discussion of evolutionary pressures and early hominin behaviors. The following theories are divided in traditional categories, with recognition that in some cases there is a fine line between them.

The Seed-eating Hypothesis

The seed-eating hypothesis proposed by Jolly (1970) provides a model that draws parallels between early hominin anatomy and *Theropithecus gelada* (gelada baboon) anatomy. Jolly uses behaviorally observations of *Theropithecus*, along with these anatomical parallels, to draw inferences about early hominin behavior and the origin of bipedalism. This model attempts to answer one of the “whys” of bipedalism, not just the “how.”

A few of the important anatomical parallels from the postcranial skeleton include a reduced hallux and a dexterous hand capable of a precision grip. Further, the pedal phalanges of rays 2 to 4 are reduced in both groups. A few of the important cranial parallels include a prominent mastoid process, a vertical ascending mandibular ramus, a robust mandibular corpus, and reduced anterior teeth.

The significance of the reduced hallux is that early hominins are evolving a terrestrial bipedal lifestyle and gelada baboons have a terrestrial quadrupedal lifestyle, with both evolutionary pressures favoring a shorter hallux that does not interfere with locomotion. The importance of shared manual dexterity relates to an increased evolutionary pressure to harvest foods that require greater dexterity to manipulate.

The significance of the cranial parallels is related to diet and posture. The increased size of the mastoid process is related to larger sternocleidomastoid muscles, needed for erect walking in hominins and a tendency in erect sitting posture among gelada baboons. The vertical ascending ramus is in part related to this erect posture, as well as to greater dependence on processing harder foods with their molars. The orientation of the ramus and the corpus assumes a position closer to 90 degrees, offering a more efficient moment arm for mastication. The significance offered for the parallel condition of reduced anterior teeth is that in gelada baboons reduced anterior teeth, particularly the canines, could facilitate grinding motions ("rotary chewing") of the molars during mastication, which would otherwise be impeded by large, locking canine teeth. Presumably in this model, this is the same explanation for why early hominins have a trend for reduced anterior teeth.

The seed-eating model itself is outlined as follows: a Miocene ape, likely a dryopithecine*,* shifts from a diet high in fruit to a diet consisting more of grains requiring finer manual dexterity to harvest, as well as more time sitting in a vertical position during feeding. This shift in diet is related to a changing climate, in which increased seasonality leads to larger areas of grasslands, thereby reducing availability of some fruits and other foods requiring high amounts of rainfall. Jolly refers to these beginnings of this shift in behavior as Phase I. In Phase II, what used to be opportunistic hunting practices become more premeditated and diet shifts to include a higher proportion of meat. Due to the preadapted condition of reduced anterior teeth from seed eating, early hominins are required to innovate with tools in order to process food.

One of the big themes with this model is "preadaptation," or certain traits that evolve for one reason happen to be useful for other purposes. Jolly attributes much of human evolution that takes place after the emergence of the first hominins as resulting from characteristic's attained for seed-eating that are preadapted to later behaviors. Examples include having a larger tongue for manipulating food being useful for later vocalization and then speech. Another is the increased reliance on hunting creates more labor divisions between the sexes. This leads to a delay of food consumption, provisioning, and long term planning for acquiring food that requires cooperation between separate bands of early humans.

Part of the problem with the seed-eating hypothesis is that despite the perceived parallels offered between hominin and gelada baboon behavior and anatomy, there are several questions left unanswered by this model. If bipedalism is a logical evolutionary path based on this lifestyle, why are gelada baboons quadrupeds? Why are they a good parallel to begin with? Wrangham (1979) attempts to address this issue when he reports that gelada baboons often move very short distances bipedally when feeding so that they continue to feed using two hands. This does not provide a convincing possibility for selective pressures however since when gelada baboons move any longer distance between feeding areas they rely on quadrupedal walking. Wrangham addresses this potential criticism by suggesting that early hominins would have been feeding on closely grouped feeding bushes in a semi-forested environment. In this case, early hominins would not have been traveling great distances for food, but instead would be constantly feeding with two hands and moving bipedally between closely grouped feeding bushes.

The reduction of the hallux shared by hominins and gelada baboons, reported by Jolly (1970), is not very revealing since the hallux becomes a weight-bearing structure in humans but is only reduced in gelada baboons. Essentially, it gets out of the way when baboons walk on the heads of their metatarsals. One potential issue we do not know from Wrangham's work is if geladas, when they walk bipedally, walk in a digitigrade fashion or whether they have a tendency for plantigrade movement. Another interesting point is that gelada baboons are apparently able to evolutionarily develop considerable manual dexterity of the hands while maintaining the use of their forelimbs in efficient quadrupedal locomotion. This is not the case in hominins. This seems to be a case in point of why bipedalism might not be favored solely to allow freeing of the hands for manual dexterity.

The Thermoregulation Hypothesis

The Thermoregulation Hypothesis is put forth by Wheeler (1984, 1985, and 1991) as a means of explaining one evolutionary selective pressure for bipedalism and the relative lack of long, thick body hair in humans compared to other mammals and primates. Wheeler lays out the argument that hominins need an efficient whole-body cooling mechanism because they are less efficient at cooling their bodies through other means, including air flow through the nasal sinuses and brain cooling through venous blood flow (a carotid rete), compared to other mammals. These relative inefficiencies are present in other hominoids as well, but Wheeler argues that hominins are a special case in that they travel for extensive amounts of time in open savannah exposed to heat. This extra exposure to heat, according to this model, favors bipedalism as a cooling mechanism for animals that have diurnal foraging habits.

Wheeler (1984) argues that one of the evolutionary pressures that may have provided a selective advantage to bipedalism is heat gain through exposure to the sun. He explains that a biped only exposes about 40% of the body surface area to the sun relative to a quadruped. In this model, the hominin ancestor develops a bipedal posture first to reduce body heat. He additionally argues that an upright posture exposes more of the body to wind, aiding in cooling (Wheeler 1984, 1991). Subsequently, bipedal locomotion as a body cooling strategy is further refined by the loss of body hair shielding the skin and by additional capacity to store subcutaneous fat (Wheeler, 1984).

By reducing body hair, skin does not have the layer of insulation provided by hair and skin is more directly exposed to wind (Wheeler, 1991). Wind and moisture from sweat glands provide evaporative cooling (that would not be possible to the same degree if wind cannot reach the skin) (Wheeler 1984). Wheeler (1984) suggests that the addition of subcutaneous fat storage is not a cooling mechanism, but a method of staying warm during the cold nights of the savannah, which hominins would be more susceptible to due to hair loss. He argues that the addition of body fat does not affect the efficiency of evaporative cooling. Other adaptations explained through this model include the retention of head hair, which maintains a shield between the scalp and the direct rays of the sun. Head hair potentially covers 40% of exposed skin surfaces for a biped but only grows on about 10% of a biped's total skin surface (Wheeler, 1985). This layer of insulation, though obstructing evaporative cooling to some degree, provides a layer of protection from increased direct heat gain to the brain from solar exposure. Wheeler (1984) further suggests that all of these adaptations relieve constraints on brain size. Larger brains produce more heat, but due to an overall more efficient body cooling mechanism, brains may have been able to expand and stay cool with these bipedal adaptations.

Chaplin et al. (1994) offer considerable criticism of Wheeler's ideas. They point out that although Wheeler's explanation for the evolution of reduced body hair in humans may hold truth, it is a bit of a stretch to extend the selective pressures in the thermoregulation model to the primary evolutionary pressure for the development of habitual bipedalism. Experimental work in this article retests some of the work done by Wheeler (1991). They examine the fundamental assumption that the thermoregulation model makes, that a hominin can withstand longer foraging times than a quadruped in a hot savannah environment due to bipedalism. Chaplin et al. (1994) find that at best, under varying conditions from relative inactivity to high activity, a biped will maintain a cooler body than a quadruped from about 15 to 30 minutes longer. They argue that these small time differences would not provide a strong evolutionary pressure for bipedalism.

Wheeler (1994) counters this claim by explaining that in the model Chaplin et al. use to calculate the potential extra time bipedalism grants for foraging, they only used maximum noon temperatures rather than varying temperatures of the morning or afternoon. When taking this into account, Wheeler (1994) argues that hominins would actually have as much as three extra hours of foraging time per day due to the benefits of bipedalism and evaporative cooling relative to hair-covered quadrupeds.

One of the problems with the thermoregulation model, in terms of the evaporative cooling element, is that we do not know when hominins lost their thick body hair. However, all hominoids rely on sweating for thermoregulation, so in some sense hominins would be preadapted to this strategy (Carrier, 1984). The question still remains whether bipedalism evolved as a response to body-cooling evolutionary pressure, or whether it evolved for other reasons and some of the other evolutionary responses, such as reduced body hair, followed later from preadaptations bipedalism offered.

Hand-freeing Hypotheses

Many ideas on the origin of bipedalism share at least one component in common. Whether it is for transporting food or using weapons, the central focus is on the idea that bipedal locomotion evolves from evolutionary pressure to free the hands for tasks other than locomotion. This section deals with several of these ideas.

Bipedalism as an Adaptation for Provisioning

Lovejoy (1981) makes the argument that bipedalism is selected for as an adaptation to provisioning behavior. It is important to make a distinction here between provisioning and tool use. Lovejoy does not argue that bipedalism is an adaptation to using tools, since as he points out there is no evidence for complex tool use by the earliest hominins.

Lovejoy’s model for the development of bipedalism is as follows. During the Miocene, ecological conditions for hominin ancestors encouraged a diverse diet. This diverse diet required foraging over long distances. Two kinds of behavior result from this situation. The first is monogamy and the second is male provisioning. Lovejoy proposes that in an environment requiring a great deal of travel time to acquire food, natural selection would favor limited mobility for females, due to reduced exposure to predators and less stress on infants. Females who maintained a smaller range would be able to devote more attention to their young and decrease infant mortality. This behavior, Lovejoy argues, goes hand-in-hand with monogamy. Males would need to travel further to acquire food while females stayed closer to a home base. The males would acquire food, likely from hunting and scavenging meat, and bring it back to their mates and offspring.

Lovejoy argues that monogamy is a key aspect to this strategy because otherwise males have little incentive to share food with others. An interesting question to address in this model is if monogamy and reduced female range is more advantageous in primates that have wide feeding ranges, why do we not see more monogamous primates? Why is monogamy so uncommon? One might argue that the key to this model is the combination of these pressures with the threat of predators. Is it more advantageous to have females confined to a narrow range, burdened with infants, while half of their group (the males) are away gathering meat? Would predators actually have better success attacking females in this situation?

Lovejoy argues for this kind of model because Jolly's (1970) seed-eating hypothesis does not explain why, if bipedalism is important to foraging behavior, his primate example retains an efficient quadrupedal mechanism of locomotion. Lovejoy is of the opinion that distance traveling for food is not enough to explain the key evolutionary pressure for bipedalism. Rather, distance traveling combined with a consistent need to free the hands for carrying food is required. Lovejoy makes a valid argument that although chimpanzees do walk bipedally over very short distances when carrying objects, behavior like this would need to be more consistent and over greater distances in order to provide an evolutionary advantage toward bipedal skeletal adaptations.

One area, which Lovejoy does not expand upon, is how he sees the relationships between males in this scenario. Although Lovejoy does not emphasize hunting, Etkin (1954) makes the suggestion that early hominins were cooperative hunters. Since chimpanzees are cooperative hunters, this idea has some basis in extant primate behavior (Stanford, 1998). If there is heavy selection for monogamy and male provisioned females, there must be some further system governing how males split up resources among themselves before it is redistributed among females. This "male sharing" need not be constrained to meat since territory would also be valuable when foraging for other resources.

The Food Transport Hypothesis *and* The Food Sharing Hypothesis

Some have hypothesized that the major evolutionary selective factor in the development of bipedalism is the need to transport scavenged or hunted meat on a savannah to a safe location for consumption (Hewes, 1964; Isaac, 1978). Hewes suggests that early hominins would have had to compete with other hunters and scavengers at a kill site. Rather than lose their food to other animals or become food for other animals, they would carry food back to a "home base" or other safe location.

This idea makes habitual bipedalism a necessity. Hewes creates an image of early quadrupedal apes, like chimpanzees, carrying food and likely stopping for frequent rests. In time, apes with a more efficient bipedal anatomy would be evolutionarily selected for, presumably because those apes who either could not keep food effectively or who are less energetically efficient will reproduce less frequently.

This model differs from Lovejoy's (1981) provisioning model in that Hewes' model is a model for transporting food for the sake of transporting it. Transportation itself is a strategy for keeping food, whereas Lovejoy does not see transporting food in and of itself as the prime mover of selection for bipedalism. Implicit in Hewes' model is also a high emphasis on meat in the diet of early hominins. Lovejoy (1981) does not stress any particular food for provisioning. Hewes' central focal point is the idea that meat must be defended and the defense of this resource is the primary behavioral impetus for habitual bipedalism. Hewes (1964) recognized that his emphasis on meat could be overstated.

However, through his own observations of a macaque, as well as other researchers' observation of primate food transport, Hewes stresses that whichever foods might have been most important to hominin ancestors, it was the need to transport this food to a safe location for consumption that drove our early ancestors toward a habitually bipedal lifestyle.

Issac (1978) places more emphasis on food sharing than on carrying food for the sake of it or specifically provisioning females. Isaac argues that the behavior that favors selection for bipedalism is sharing food between hominins, thus increasing everyone's access to resources and developing a social network, which leads to more complex social capability in later hominin evolution.

Even though Hewes acknowledges a problem in assuming our ancestors ate high quantities of meat, he does not explain why there is such a strong pressure to take food to a safe location. Presumably if we remove meat as the primary food, early hominins do not need to defend fruits and seeds or other vegetable foods from predators. In the instances Hewes cites for evidence of primate food carrying, primates are trying to defend their food from others of their kind or other primates. This leaves the question of what force would drive consistent long-distance food transport beyond that which most primates already engage in.

The Postural Feeding Hypothesis

Hunt's (1994, 1996) postural feeding hypothesis is based on data collected on chimpanzee feeding habits. Hunt observed a group of 21 chimpanzees in Tanzania for 700 hours. During this time, he noted that chimpanzees would take on a bipedal posture in an arboreal situation more often than on the ground. Chimpanzees were found to take a bipedal posture when on the ground most often when feeding on fruit from short trees. Bipedalism also occurred while feeding in trees on small or terminal branches and while hanging vertically from the branches. In both cases this behavior is required to increase reach for harvesting fruit. Similar observations were made by Stanford (2002, 2006), showing that chimpanzees engage in a wide range of position behavior while feeding.

Central to Hunt's model for the origin of bipedalism is a comparison of chimpanzee and *Australopithecus afarensis* skeletal anatomy. Hunt (1994, 1996) makes the argument that while *A. afarensis* is well adapted for suspensory behavior, the species is not as well equipped for terrestrial bipedal walking. Hunt (1994, 1996) cites examples, including curved phalanges in the hands and robust muscle attachments for flexor muscles as indicative of suspensory behavior, as well as the angle of the glenoid relative to the scapula being similar to apes. Hunt argues that *A. afarensis* is not as well adapted to bipedal locomotion as modern humans (australopith hips are relatively wider than in humans, with a small acetabulum and femoral head, coupled with a more coronal orientation of the ilium). *A. afarensis* would have been energetically less efficient than modern humans at terrestrial bipedalism. Further, Hunt argues that the greater posterior orientation of the ilium places the gluteal muscles in an orientation more like that of apes, which function to extend the legs and flex the trunk in arboreal locomotion. Hunt further argues that *A. afarensis* was adapted to gripping branches to some extent with its feet, by having pedal phalanges that curve, and the third ray longer than either the second or first.

This host of adaptations, while being intermediate between humans and chimpanzees, provides the bulk of Hunt's argument that early hominins evolve bipedalism not due to evolutionary pressure for terrestrial bipedalism but due to collecting small fruits while vertically clinging in the trees and standing bipedally on branches. This idea is in many ways not unlike the seed-eating hypothesis by Jolly (1970), but Hunt makes a detailed anatomical comparison that seems more relevant than the comparison to gelada baboons. The important difference between these two theories is that while Jolly places importance on terrestrial movement, Hunt places importance on bipedal posture in an arboreal setting. The question Hunt does not address is what pressure would have brought *A. afarensis* out of the trees to take on a fully terrestrial bipedal lifestyle.

Rose (1991) relates a hypothesis that is in support of Hunt's ideas. Rose suggests that there may not have been one sudden selective pressure for bipedalism and that instead selection was a gradual process. Since primates have several positional behaviors, Rose presents the hypothesis that it would only be a matter of increasing the tendency for bipedalism in a primate group, not making it exclusive, which would create selective pressures for anatomical change. Rather than one particular pressure, several possible factors would contribute to an overall increase in the proportion of bipedal behavior, marginalizing other forms. In this model, early hominins would become less efficient quadrupeds but not necessarily lose efficiency at arboreal activity at the same magnitude. Hunt's analysis of *A. afarensis* does seem to fit Rose's model.

The Threat Display Hypothesis

The threat display hypothesis, presented by Jablonski and Chaplin (1993), suggests that bipedalism evolved in two phases. The first phase is the most important, in which a tendency for bipedal standing is selected for, and this phase preadapts an early hominin species for complete habitual bipedal locomotion. Jablonski and Chaplin (1993) argue that the selective pressure for a bipedal stance occurs through bipedal threat displays, charges, and "mock fights" between proto-hominins. They claim that in some way this kind of behavior can be seen in modern humans. We allegedly value being tall and when someone physically cowers it is a sign of submissiveness. Further, they claim that conditions in the Miocene would have made intergroup and intragroup confrontations between males more frequent due to groups overlapping when seeking resources, and that the display behaviors mentioned provide a relatively peaceable way of establishing group order, mate selection, and conflict resolution between groups. They cite evidence that extant primates, including apes, do engage in bipedal displays of aggression and that it is this behavior that is evolutionarily elaborated upon in proto-hominins. In addition, they present this hypothesis as a way of explaining sexual dimorphism in humans and early hominins, that differential body size is not accompanied by increased tooth size because the primate displays are related to becoming “better at bipedalism” (Jablonski and Chaplin, 1993).

Freeing the Hands for Hunting

Some scholars have hypothesized that the primary evolutionary pressure for the development of bipedalism is to free the hands for hunting (Darwin, 1871; Dart, 1953; Dart, 1972; Etkin, 1954; Washburn, 1967; Washburn and Lancaster, 1968; Hill, 1982). Dart (1953) envisioned early hominins as aggressive flesh eaters, and that humans had a very bloody, violent past. To him, it seemed logical that walking upright in order to use weapons would be natural, because it could make early hominins more effective killers. Dart is making inferences from observed carnivorous baboon behaviors, but he is also amplifying and projecting his perception of the potential for violence in modern humans onto humanity’s past. Merker (1984) takes a slightly different approach. To him, bipedality involves weapon use, but he also sees the evolution of the human foot as an effective stalking mechanism. He envisions early hominins crouching and moving slowly on two feet, sneaking up on prey. Washburn and Lancaster (1968) see hunting in apes and early hominins as only the beginning of behavior that becomes more elaborate over the course of human evolution, from which stems human social and intellectual evolution.

Hill (1982) argues that hominin hunting was very important for the development of bipedalism. According to Hill, modern foragers consume more meat than omnivorous primates, including chimpanzees and baboons. In many ways, Hill’s model on the development of bipedalism is similar to Lovejoy’s (1981). However, where these two ideas differ is that Hill does not see monogamous pair bonding as important, but does see provisioning as important. In this case, the selective pressure is not to allow females to take care of young but for males to collect meat to carry back and trade for sex with females. The pressure for bipedalism would also lead to preadaptation not just for carrying meat, but also for carrying other tools as they are developed for acquiring meat. Hill hypothesizes that this situation is tied into human females being sexually receptive at all times, so that they can receive meat at all times rather than only when in estrus.

Freeing the Hands for Tools Use

The idea that humans evolved bipedalism to free the hands for tools was strongly supported by Darwin (1871). Washburn (1960) argued that humans evolved bipedalism first for bursts of bipedal running, but not for efficient habitual walking. These bursts of running are important in Washburn's model because it is during these bursts that early hominins would have their hands occupied with tools as they run toward prey. Washburn also argues that freeing the hands and increasing manual dexterity has an impact on the brain. He suggests that, as bipedalism evolves first due to the demand for having hands free for tool use, increasing intelligence also demands a large birth canal and infants that are born less developed, because of increasing brain size. Washburn argues that by the time this occurs hominins are preadapted to hold and carry infants that are born helpless and developmentally immature.

Ardrey (1961) proposes a hypothesis that is somewhere between Washburn's perception of the importance of tool use and Dart's "murderous ape" model for the emergence of bipedalism (Dart, 1953). For Ardrey, hominin ancestors do not simply have an innate desire for hunting; they also have the urge to commit violence against each other. Put simply, hominins have a predisposition for fabricating weapons of war. In this model, hunting or tool use is concomitant with interpersonal violence as an evolutionary driving force for the development of bipedalism, in order to free the hands to make weapons.

Freeing the Hands for Carrying Infants and Food

The hypothesis that early hominins were under selective pressure to free the hands for carrying items has been proposed in different forms by many authors, and this general hypothesis has been covered in some of the more discrete theories laid out above. This section will cover some more loosely connected theories that fall under this theme. They differ in emphasis over how and why certain items will be carried, but they all share the idea that either food or infants, when carried, provide a selective advantage to bipedalism.

Day (1977) commented that bipedalism probably evolved as a response to evolutionary pressure for carrying food and infants. Etkin (1954) argued for bipedal origin in a model not unlike Lovejoy's (1981). He argues for a monogamous hominin family structure in which men hunt and women forage. In this situation, females carry infants and gather food while males hunt. This relationship combines to create evolutionary pressure for freeing the hands through bipedalism. Sinclair (1986) hypothesized that humans followed ungulates through their migration patterns, and that one selective pressure to do this would be in freeing the hands for carrying infants over these great distances. This idea centers on the concept that the entire hominin group is on the move, scavenging carcasses opportunistically.

Long-Distance Walking Hypothesis

Rodman and McHenry (1980) provide evidence and argument for adaptive selection favoring bipedalism from an energetic perspective. They argue that in order to estimate the efficiency of hominin locomotion, proper comparisons must be made. Previous work by Taylor et al. (1970) provided energetic costs for several quadrupedal hominins while running. Rodman and McHenry point out that chimpanzees have an energy cost during quadrupedal locomotion of about 150% of what they call "true" quadrupedal mammals of similar size. This means that although chimpanzees are quadrupeds, they are expensive quadrupeds from an energetic perspective and if we compare human efficiency to quadrupeds we must compare them to chimpanzees, not other quadrupeds. This comes from the underlying assumption that the hominin ancestor is a knuckle-walking quadruped.

Day (1986) called Carrier's (1984) article a presentation of the "endurance-hunting hypothesis," which is in some ways a variation of the Long-Distance Walking Hypothesis (Rodman and McHenry, 1980). Carrier (1984) reports that hominins are efficient bipedal walkers because they are able to "mechanically recover" energy during locomotion due to a pendulum motion of the body during strides. Further, they make an argument that bipedalism may have an advantage, even in running, despite being energetically more costly than in quadrupeds. They state that quadrupeds have breathing constraints when running, such that they cannot vary their breathing and they can only breathe once per stride, due to flexion of the spine and compression of the abdominal and thoracic cavities during locomotion. As a consequence, quadrupeds have an optimum running speed, and when the speed gets higher running is more costly and cannot be sustained. In contrast, hominins do not have these constraints because the abdomen and thorax are not compressed during locomotion. This allows hominins to alter their breathing to account for greater oxygen needs at greater speeds, making hominin running equally as efficient at all speeds. Carrier argues that this is an advantage because hominins have a wide range of running speeds at their disposal. Due to breathing and sweating capability, despite the relative inefficiency in running, hominins have great running endurance. Carrier argues that this greater endurance allows hominins to run for longer, uninterrupted periods, which is more efficient than bursts of running with rest in between. This would mean that hominin hunters could run after wounded prey and beat them in endurance where they can't beat them in speed.

Rodman and McHenry (1980) find that hominin bipedalism is actually more efficient at walking speeds than "typical" quadrupedalism, and is far more efficient than chimpanzee quadrupedalism (see Steudel-Numbers, 2003 for a different view). They do not argue in terms of the factors that encouraged bipedal behavior, but instead argue for bipedalism as an effective evolutionary response to pressure for long distance walking, no matter which needs this behavior fulfills. In the end, many ideas about behavior relating to habitual bipedalism amount to evolutionary pressure for extensive time walking on two legs. These ideas have been discussed extensively above. Sinclair (1986) and Shipman (1986) offer another specific behavior for this pressure. Sinclair suggested that early hominins were scavengers, and they followed ungulate herds in order to opportunistically scavenge those that die. This kind of walking, Sinclair argues, would require free hands for carrying infants but also an efficient form of bipedalism. Shipman (1986) has a slightly different take on this. She argues that long distance walking is important, but freeing the hands is necessary to carry meat back to a home base.

This view may be supported by Steudel-Numbers (2003), in which she found that primate quadrupedalism is not less efficient than generalized endotherms. The implications of this are that hominin ancestors would not have evolved bipedalism as a solution to inefficient quadrupedalism. Instead, there must be another pressure for bipedalism. Evolving more efficient bipedalism in hominins relative to the inefficiency of a quadrupedal primate walking bipedally would be favored by natural selection.

The Visual Surveillance Hypothesis

One idea on the origin of bipedalism focuses on the notion that bipedalism evolved as a defense mechanism for seeing over tall grasses or seeing longer distances by being able to stand higher than a quadruped (Dart, 1959; Day, 1977; Howells, 1959; Ravey, 1978). Selective pressure for bipedalism, following this model, would favor individuals who could stand more frequently and for longer periods of time. This behavior would not be entirely self-serving, as individuals would spot predators and warn the group.

Summary

This chapter has presented the primary models on the origin of bipedalism. Many of these models present an argument that identifies one or a few selective pressures as the most important in making bipedalism evolutionarily advantageous. One can create a synthesis from which to interpret evolutionary anatomy (from many of these theories). It is likely that no single proposed idea alone answers the riddle of “why” natural selection worked to favor bipedalism. It is more productive to view these ideas as interacting components. The next chapter provides a review of human and ape comparative anatomy, with reference to fossil hominin evidence.

CHAPTER 3: HUMAN AND APE EVOLUTIONARY PEDAL ANATOMY

Introduction

This chapter contains an overview of observed human and ape osteological differences, with particular attention to the foot. With few exceptions, which will be noted below, all observed adaptations to bipedalism are explained by any model of the origin of bipedalism. No matter which environmental or behavioral pressures existed to select for habitual bipedalism, they all share bipedalism as the evolutionary solution. Therefore, each model equally explains the observed morphologies. However, it must be noted that this applies only when comparing modern human anatomy and extant ape anatomy. There is debate about how to interpret transitional anatomy, such as that observed in *A. afarensis*, and this will be addressed below in the discussion of the fossil evidence.

Cranial Skeleton

The single trait in the cranium most indicative of a bipedal posture is the position of the foramen magnum (Dart, 1925; Ashton and Zuckerman 1952, 1956; Schultz, 1955; Le Gros Clark, 1971; Day, 1977; Dean and Wood, 1981, 1982; Aiello and Dean, 1990; Ahern, 2005). In humans, the foramen magnum is in a more anterior position, and in apes it is more posterior, as it is in other quadrupeds. The significance of the position of the foramen magnum in humans is that the forward position allows the head to balance on the spine, rather than project beyond it, facilitating an erect stance by reducing tension and stress on the neck and back (Dart, 1925; Broom, 1938, Le Gros Clark 1954).

The Post Cranial Skeleton

Neck

Apes have large spinous processes relative to humans in the cervical vertebrae, a fact related to apes having larger neck muscles than humans (Aiello and Dean, 1990). Large neck muscles are necessary for quadrupedalism in apes to support the cranium

(Aiello and Dean, 1990). In addition, the longer spinous processes of apes limits extension of the neck (Schultz, 1961).

Spine and Sacrum

Humans have a convex curve in the cervical region of the spine, kyphosis in the thoracic region, and lordosis in the lumbar region. Apes lack the cervical curvature, but do exhibit limited curvatures in the thoracic and lumbar regions, and the exaggerated curvature in humans serves to distribute weight through the spine during bipedal locomotion (Schultz, 1961, Aiello and Dean, 1990). Human ribs differ from ape ribs in that the human spinal column is located relatively more ventral, creating greater rib curvature at the dorsal aspect and changing the center of gravity by shifting the spine into a relatively more central location (Schultz, 1961).

Humans have a relatively wide sacrum compared to apes, which is related to changes in the pelvis to accommodate bipedalism (discussed below) and, as a result, human lumbar vertebrae are progressively larger as they approach the sacrum distally (Aiello and Dean, 1990). In contrast, the lumbar vertebrae, although they do enlarge slightly as they approach the sacrum, are closer in size to one another (Aiello and Dean, 1990). Further, the lumbar vertebrae are more robust in humans, reflecting the increased burden of body weight bipedalism imposes on these vertebrae (Schulz, 1961). Humans have a wider promotorium than apes, or a wider angle between the sacrum and the fifth vertebrae (Aiello and Dean, 1990). This increased angle in humans is related to bipedal posture and orientation of the pelvis, but also related to an increased size of the birth canal (Aiello and Dean, 1990; Abitbol, 1987).

Shoulder

The human shoulder differs from apes in that the acromial and coracoid processes project further beyond the glenoid fossa than in apes, providing additional support of the rotator cuff but also limiting the human range of motion in the arm relative to apes (Aiello and Dean, Ciochon and Corruccini, 1977). A greater range of motion in apes reflects a brachiating lifestyle, which is no longer habitual in modern humans (Aiello and Dean, 1990). Further, the scapula in apes is oriented to a greater degree in the sagittal plane than in humans, which also makes the lateral aspect of the clavicle positioned ventrally in apes, and this reflects the use of the upper limbs for support in locomotion in apes (Schultz, 1950; Aiello and Dean, 1990). Also connected to this idea, Schultz (1930) reported that the scapula is elongated in the posteriomedial aspect in apes, whereas the medial border in humans is closer to 90 degree to the spin in humans.

Forelimb

Humans have shorter arms relative to trunk size when compared to apes (Aiello and Dean, 1990). In addition, humans exhibit slightly more humeral head torsion than apes, which relates to arm flexion that occurs more in a sagittal plane (Evans and Krahl, 1945; Knussman, 1967). The distal humerus is different in humans than in apes, which is related to the fact that human arms are no longer involved in locomotion. Apes have a deeper olecranon fossa, which facilitates hyperextension of the ulna for supporting weight (Knussman, 1967; Tuttle and Basmajian, 1974; Senut, 1981).

Hands

Although not directly related to bipedal locomotion, there are differences between the hands of humans and apes. This topic is particularly relevant since many theories on the origin of bipedalism focus on freeing the hands for various tasks. Apes use their hands for locomotion in addition to manipulating objects, whereas human hands have few other tasks than handling objects. Napier (1960, 1980) analyzed human and ape hand movements and identified four main kinds of grips that the human hand is capable of, the hook grip, scissor grip, precision grip, and power grip.

Apes and humans both use the hook grip. This grip involves only rays 2-4, and they hook around objects such as carrying something attached to a strap, or hanging from a branch in the case of apes (Napier 1960, 1980; Aiello and Dean, 1990). Apes are more efficient with the hook grip than humans because apes have longer lateral digits and can lock the tips of their fingers in a more effective grip around smaller items (Napier, 1960). The scissor grip is also used by apes and humans, and simply utilizes the intrinsic adductor muscles of the hand to adduct rays 2, 4, and 5 toward ray 3 (Napier 1960, 1980; Aiello and Dean, 1990). This is a weaker grip used to pinch small objects between the fingers. The precision grip involves making contact between the palmer side of the tips of the fingers with the tip of the thumb. This is possible with human hands for delicate manipulation of objects, but is not possible with apes because their thumbs are relatively shorter and fingers are relatively longer than those of humans' (Napier 1960, 1980; Aiello and Dean, 1990). Finally, the power grip involves several different more descriptive grips, but as a whole it involves gripping with rays 2-5 while the thumb also grips for support. This is only effectively possible in the human hand due to the longer thumbs of humans (Napier 1960, 1980; Aiello and Dean, 1990). The question does remain as to whether the human hand has evolved for manipulation of objects in general, or if it has evolved for the express purpose of tool using.

Pelvis

Besides the location of the foramen magnum on the cranium, the other "smoking gun" indicating a biped is the overall morphology of the pelvis. The fundamental difference of the architecture of the pelvis in humans and apes is in the fact that apes are quadrupedal, with only occasional bipedal behavior, while humans are habitually bipedal.

There are a number of differences between the pelvis of apes and humans, and a few of the more important differences are discussed below. The human pelvis is shorter, wider, and "basin shaped" compared to apes (Aiello and Dean, 1990). The human ilium is oriented in a more sagittal plane, while the ape ilium is oriented in more of a coronal plane (Schultz, 1969; Aiello and Dean, 1990). The significance of this adaptation is that the gluteal and iliacus muscles have become abductors and adductors of the leg in humans, to facilitate efficient bipedal locomotion, but they are primarily flexors and extensors of the trunk in apes (Stern and Susman, 1981, 1983). One important point made by Susman and Stern (1981) is that when a chimpanzee walks bipedally, these muscles are involved in the same tasks with which they are involved when humans walk bipedally. However, humans have osteological adaptations (the orientation of the ilium, already mentioned) that make these muscle movements more effective and efficient for maintaining a bipedal stance.

The sacrum is wider and more robust in humans than in apes (Aiello and Dean, 1990). This difference is related to two major factors. A wider sacrum increases the overall width of the pelvis, and reduces the amount that the pelvis twists during locomotion. These factors reduce stress on the pubic symphyses as well as provide larger muscle attachment areas for back muscles in order to help balance the trunk over the pelvis during bipedal locomotion (Leutenegger, 1977; Aiello and Dean, 1990). In addition, the sacrum is more robust because it bears considerable body weight (Leutenegger, 1977; Aiello and Dean, 1990).

Hindlimb

There are many differences between the femora of apes and humans, but only a few of the more important ones are discussed here. The femur in humans is longer relative to body size (and absolutely) than in apes (Jungers and Stern, 1983; Jungers 1984; Aiello and Dean, 1990). In addition, the distal end of the femur is angled toward the medial aspect of the body in humans, creating a valgus angle to redirect the center of gravity for bipedal locomotion (Walmsley, 1933; Aiello and Dean, 1990). In addition, a sign of bipedalism is a well-developed linea aspera on the posterior aspect of the femur, which is the location for the attachment of gluteus maximus at the proximal aspect, and abductor muscles of the thigh below (Hrdlicka, 1937; Aiello and Dean, 1990). Another very important difference between humans and apes is in cortical bone thickness of the femoral neck. Humans have thick cortical bone at the inferior aspect of the neck and thinner cortical bone at the superior aspect, while apes have cortical bone thickness that is much more uniform around the circumference of the neck (Lovejoy, 1988; Ohman et al., 1997). This difference is related to greater consistent tension at the inferior aspect of the femoral neck in humans, due to a habitual bipedal stance (Ohman et al. 1997).

The proximal tibia in humans is more robust than apes, and has larger articular surfaces for the condyles of the femur (Thompson, 1889; Martin and Saller, 1959; Spencer, 1989; Aiello and Dean, 1990). This is directly related to the greater weight burden human knees are exposed to (Aiello and Dean, 1990). The distal tibia in humans differs from apes in that the articular surface is positioned in a perpendicular plane to the tibial shaft, granting greater stability to the articulation of the tibia with the talus (Latimer et al. 1987). In addition, the distal end of the tibia exhibits lateral torsion, so that the foot articulates with the tibia in such a way as to be angled slightly with the phalanges pointing in the lateral direction (Elftman and Manter, 1935b; Lewis, 1981a; Aiello and Dean, 1990). This adaptation probably reflects the human use of the foot in human locomotion, where the foot bears body weight as it shifts from lateral to medial at toe-off (Elftman and Manter, 1935b; Lewis, 1981a; Aiello and Dean, 1990).

Functional and Gross Anatomy of the Foot

The following section outlines the most relevant gross functional comparative anatomical work that has been done comparing human feet to ape feet, with primary emphasis on an African ape comparison.

Arches and Gross Structure of the Foot

The most dramatic differences between the human and non-human primate foot are related to the longitudinal arch and permanently adducted human hallux. A transverse arch is present in varying degrees in all primates (Sarmiento, 1994; Weidenreich, 1923). However, the longitudinal arch is only present in the human foot and functions as a fulcrum to transfer weight directly from the calcaneus to the metatarsal heads and phalanges (Leardini et al., 2007; Sharkey and Hamel, 1998; Gebo, 1992; Jones, 1944; MacConaill and Basmajian, 1969; Morton, 1924; Weidenreich, 1923, 1940). Berillon (2003) analyzed joint articulation angles in humans, chimpanzees, gorillas, *A. afarensis* and *H. habilis*. He reported that *H. habilis* had articular joint angles consistent with modern humans, and from this he inferred that *H. habilis* probably had a longitudinal arch. In contrast, Berillon (2003) found that the joint angles of *A. afarensis*, particularly at the medial aspect of the foot, most closely resemble apes. From this he inferred that *A. afarensis* probably did not have a modern longitudinal arch of the foot. Berillon's (2003) study conflicts with Oxnard and Lisowski's (1980) study in that Oxnard and Lisowski reconstructed the OH 8 foot bones and concluded that *H. habilis* would have had a more flat ape-like foot lacking a longitudinal arch.

The permanently adducted hallux is a derived trait in humans, not shared by the other primates that use the foot as a grasping organ (Elftman and Manter, 1935b; Weidenreich, 1923). However, Schultz (1924) notes that until late in fetal development the human hallux is abducted.

The entire human leg and foot is in a fixed pronated condition relative to the upper limbs (MacConaill, 1945). In contrast, the general anatomical position of the foot in non-human primates is supinated with the sole in a medial position (Morton, 1924; Weidenreich, 1923). Humans exhibit pronation early in fetal development (Schultz, 1923). Further, the human trait seems to be shared by *Homo habilis* (Susman and Stern, 1982).

The longitudinal arch is divided into medial and lateral pillars; the medial pillar that is formed by the first metatarsal, medial cuneiform, navicular and calcaneus is higher than the lateral arch formed by the fifth metatarsal, cuboid, and calcaneus (Jones, 1944). Hicks (1955) argued that there are actually five longitudinal arches, one for each metatarsal. In defining the longitudinal arch of the human foot, Hicks (1955) makes a distinction between a true arch and a beam. An arch, he argues, does not allow movement at either end. However, a curved beam does allow bending forces and allows some movement at either end. In this regard the longitudinal arch in the foot should be structurally compared to an arch when the metatarsophalangeal joints are hyperextended during toe off, but as a beam when the foot is flat on the ground as occurs when standing or at the midstance phase of walking. As a beam the metatarsal bones undergo bending forces. As an arch the plantar aponuerosis tightens, causing the calcaneus to shift forward, creating a stable arch as weight is transferred to the metatarsal heads and the phalanges at toe off (Hicks, 1955). Importantly, during hyperextension of the metatarsophalangeal joints (especially MT 1) the plantar aponuerosis is tightened, which causes the posterior portion of the calcaneus to shift anteriorly, thus raising the longitudinal arch of the foot (Hicks, 1954). This occurs during the walking phase when the foot is rising onto the toes, and the toes are hyperextending. The plantar aponuerosis absorbs 60% of the stress while walking, and the metatarsals themselves absorb the remaining stress (Hicks, 1954).

Although there is some debate in the literature regarding whether it is primarily ligaments or muscles that support the longitudinal arch, they both make contributions to the stability of the arch. There are three primary ligaments that facilitate arch support: the plantar calcaneoligament (spring ligament), the short plantar ligament, and the long plantar ligament (Aiello and Dean, 1990). The spring ligament runs from the sustantaculum tali to the navicular, supporting the talar head. The short planar ligament stretches from the anterior of the calcaneus at the plantar aspect to the proximal cuboid. The long plantar ligament runs from the plantar calcaneus to the bases of metatarsals two to five. Additionally, plantar interosseous ligaments attach the metatarsals to one another.

Muscle action provides additional support to the longitudinal arch (Keith, 1928 Thordarson et al., 1995; Erdemir et al. 2004). The plantar aponuerosis provides the greatest proximo-distal longitudinal arch stability (Thordarson et al., 1995; Erdemir et al. 2004). Keith (1928) reports that tibialis anterior helps hold up the longitudinal arch in humans, in addition to everting the foot. Additionally, tibialis posterior inverts and plantar flexes the foot, and in humans by its insertion on the navicular tuberosity also helps support the arch of the foot. In apes it inserts at the bases of the second, third, and fourth metatarsals (Keith, 1928). Peroneus longus inserts on the base of the first metatarsal and medial cunieform in humans (Keith, 1928). In apes the muscle strengthens the stability of the grip of the hallux, but for humans where the first metatarsal is permanently adducted, the muscle acts to support the arch of the foot (Keith, 1928; Thordarson et al., 1995).

The Foot During Bipedal Locomotion

A great deal has been said about the action of the foot during locomotion (Aiello and Dean, 1990; D'Aout et al., 2002; Elftman, 1969; Elftman and Manter, 1935a; Gebo, 1992; Hicks, 1953; Hicks, 1954; Hicks, 1955; Kidd, 1999; MacConaill and Basmajian, 1969; Nawoczenski et al., 1999; Schultz, 1963; Shereff et al., 1986; Susman, 1983; Susman, 1989). One characteristic that humans and African great apes share is that of plantigrady, or locomotion that involves the heel touching the substrate (Gebo, 1992; Morton, 1924; Morton, 1935).

One of the earliest explanations of the action of the human foot is given in comparison to the action of the chimpanzee foot during bipedal locomotion (Elftman and Manter, 1935a). During bipedal locomotion, the human foot first absorbs ground reaction forces at the heel or calcaneus, and the subcalcaneal fat pad deforms and is able to return about 70% of the force it is subjected (Elftman and Manter, 1935a; Bennett and Ker, 1990). Weight is then transferred from the heel to the metatarsal heads, shifting medially, and toe off occurs with the final burden of weight on the distal phalange of the hallux (Leardini et al., 2007; D’Août et al. 2002; Chen et al., 2001; Gefen et al., 2000; Kidd, 1999, Nawokzenski, 1999; Scott and Winter, 1993; Gebo, 1992; Aiello and Dean, 1990; Susman, 1989; Shereff et al., 1986; Susman, 1983; Elftman, 1969; MacConaill and Basmajian, 1969; Schultz, 1963; Hicks 1953, 1954, 1955; Elftman and Manter 1935a). In contrast, the chimpanzee foot initially absorbs ground reaction forces on the heel and the posterio-lateral portion of the foot simultaneously. Weight primarily transfers along the lateral border of the foot, with some support on the posteriomedial aspect. In the final phase of walking, the greatest weight burden is on the second and fifth metatarsal heads due to the presence of a transverse arch (D'Août et al., 2004; Vereecke et al., 2003; D'Août et al., 2002; Susman, 1983; Elftman and Manter, 1935a).

Elftman and Manter (1935a) divide the weight transfer sequence in the foot into six arbitrary segments during the heel strike, midstance, and toe off phases. See Figures 3.1 and 3.2. The six-segment weight distribution is a reflection of the center of weight over the foot during locomotion. In the human foot, pressure follows a trajectory down the center of the foot over the third metatarsal before veering medially over the phalanx of the hallux for toe off (Elftman and Manter, 1935a). In chimpanzees, weight follows a curved path that angles laterally once passed the tarsals and then medially over the head of the third metatarsals, until finally over the phalanges of the second digit.

Figure 3.1 Foot pressure in the human foot from heel strike to toe off. Adapted from Elftman and Manter (1935a).

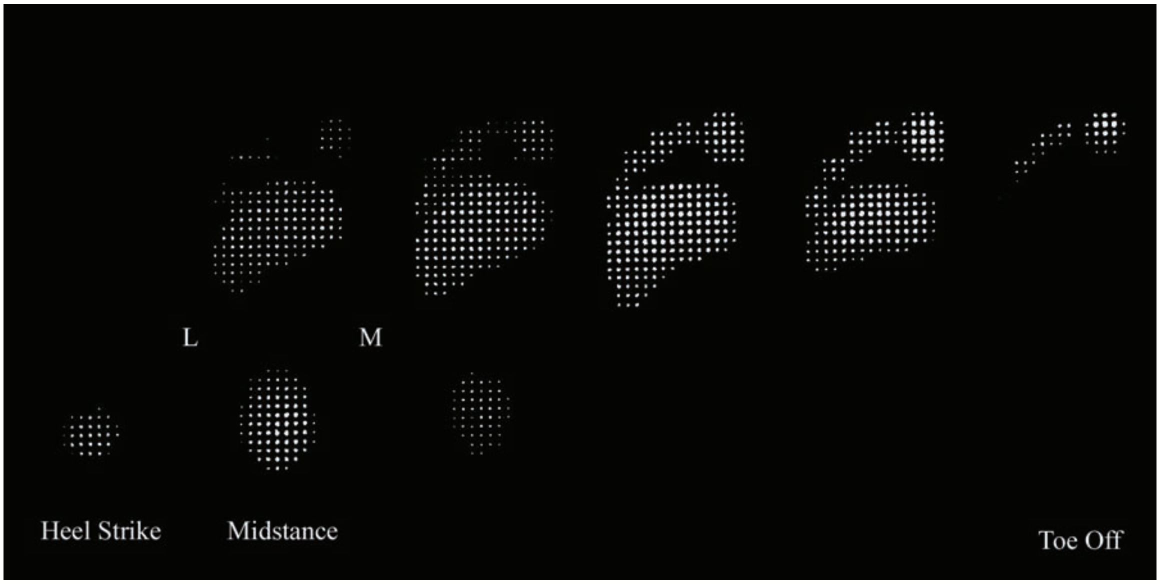


Figure 3.2 Foot pressure in the chimpanzee foot during bipedal locomotion. Adapted from Elftman and Manter (1935a).

Stress on bones of the human foot during locomotion has the following pattern. At heel strike, compression forces are directed primarily at the plantar aspect of the calcaneal tuberosity and the tibio-talar joint. At midstance, the greatest compression forces are exhibited on the calcaneus, talus, and metatarsals 1-4, with higher compression on the medial aspect of the cuboid across the tarsometatarsal joint of MT 4, and higher compression on the third cuneiform and across the tarsometarsal joint of MT 3. At push-off, higher compression exists in MT 3, and is distributed throughout the metatarsal heads at toe-off (Chen et al., 2001; Gefen et al., 2000; Giacomozzi et al., 2000; Scott and Winter, 1993; Manter, 1946).

As cited above, studies have captured relative foot pressures in chimpanzees during locomotion, but to date no detailed compression studies exist for examining how they differ in specific bones of the ape foot during locomotion. Vereeke et al. (2003) have the most revealing results to date for *Pan paniscus* foot pressures during locomotion. Their results reveal that during both bipedal and quadrupedal locomotion, considerable pressure exists on the lateral aspect of the foot, with flexion at the tarsometatarsal joint of

MT 5, associated with a mid-tarsal break. During bipedal locomotion, high forces exist on the heel, but during bipedal locomotion less weight is on the heel and pressure is transferred to the lateral aspect of the foot more quickly. There is greater pressure on the hallux during quadrupedal walking than bipedal walking, where forces are distributed on the metatarsal heads of MT 2-4 and the lateral phalanges, with more of the plantar aspect of the foot making contact with the substrate when compared to quadrupedal walking. The apes from the study by Vereeke et al. (2003) showed greater pressure on the MT 4 and 5 heads, compared to the other MT heads, due to the primary compression forces during locomotion transferring across the lateral aspect of the foot. High forces are exhibited on the distal phalanx of the hallux at toe off, but not on the MT 1 head as is the case in humans.

Evolutionary Osteology of the Foot

Most comparative work on human and ape feet has been in the context of interpreting fossil hominin anatomy. For this reason, the most logical way to discuss the comparative human and ape pedal anatomy is along with the evolutionary anatomy of fossil hominins, and how they relate to this comparative study. This is the approach the following section takes.

Many scholars have noted that the proportions of the human foot to the ape foot are different (Elftman and Manter, 1935b; Jones, 1944; Keith, 1928; Lessertisseur and Jouffroy, 1973; Morton, 1924; Morton, 1926; Olson and Seidel, 1983; Schultz, 1923; Schultz, 1930; Susman, 1983). Collectively, the tarsals are longer in the human foot than in other primates (Schultz, 1930). Additionally, the adult human metatarsal length formula is commonly 2>1>3>4>5, whereas in apes it is 2>3>4>5>1 (Jones, 1944). Though during human fetal development prior to the fourth month the formula is often 3>2>1>4>5 (Jones, 1944). The phalanges of humans and apes differ in length as well, with humans having shortened phalanges (Elftman, 1969; Midlo, 1934; Schultz, 1930; Weidenreich, 1923). However, early in fetal development humans share with apes a long third toe, and in many ways the human foot in early fetal development resembles the apes (Schultz, 1923; Schultz, 1924).

The Transverse Tarsal Joint

The transverse tarsal joint consists of the joints between the talus and navicular and the distal calcaneus and the cuboid; this joint exhibits many differences between apes and humans (Aiello and Dean, 1990; Bojsen-Moller, 1979; Conroy and Rose, 1983; Elftman, 1960; Elftman, 1969; Elftman and Manter, 1935a; Elftman and Manter, 1935b; Gebo, 1992; Kidd, 1999; Lewis, 1981; Lewis, 1989; Weidenreich, 1923). This joint is primarily involved in eversion and inversion of the foot (Lewis, 1981). The human calcaneocuboid joint has a convexity at the superior aspect (Elfman, 1969; Lewis, 1981; Aiello and Dean, 1990). When in anatomical position, the joint is perpendicular to the ground and creates a locking mechanism for the use of the foot as a fulcrum (Elfman, 1969; Lewis, 1981; Aiello and Dean, 1990). The joint is essentially immobile in humans (Bojsen-Moller, 1979; Elftman, 1969; Kidd, 1999). Elftman (1960) reports that there is some movement in the human calcaneocuboid joint at the plantar aspect, which serves to slightly elevate the arch. In apes, the surface of the calcaneocuboid joint is concave centrally and allows movement, or a midtarsal break, during locomotion (Aiello and Dean, 1990; Bojsen-Moller, 1979; Conroy and Rose, 1983; Elftman and Manter, 1935a; Weidenreich, 1923). Gebo (1992) reports that the calcaneocuboid joint of *A. afarensis* exhibits mobility somewhere in between humans and apes.

The Talus

The talus head is angled to a greater degree medially with greater talar head torsion in apes, and the neck is shorter in humans (Lewis, 1980b; Aiello and Dean, 1990; Kidd et al. 1996). However, before the fourth month in human fetal development the neck of the talus is longer and more medially oriented (as in adult apes) than the adult human condition (Jones, 1944). The human talar head is dorsiflexed relative to apes (Susman, 1983). The groove for the flexor hallucis longus tendon, on the posterior aspect of the talus, is obliquely positioned in apes but vertical in humans; the orientation indicates the angle of motion for the tendon. (Latimer et al., 1987). During locomotion, then, the human foot moves in more sagittally oriented plane, and the ape foot swings laterally.

The articular surface of the talar head of chimpanzees is extended more posteriorly on the lateral side, a reflection of talo-navicular movement (Elftman and Manter, 1935b). Further, the trochlea of the talus in humans has rotated medially to be more in line with the neck (Elftman and Manter, 1935b). The medial aspect of the trochlea is elevated in relation to this area in chimpanzees (Elftman and Manter, 1935b). The medial portion of the trochlea is anterior-posteriorly shorter in apes than in modern humans, early *Homo*, and *A. afarensis*, which have medial and lateral portions of the trochlea of similar anterio-posterior length (Leakey and Wood, 1974; Johanson et al., 1982; Latimer et al., 1987).

The subtalar joint is partly responsible for inversion and eversion as the talus moves on an axis on the calcaneus, and the talar head articulates with a concavity on the calcaneus (Lewis, 1980b; Lewis, 1981; Aiello and Dean, 1990). At the same time, the concave posterior surface of the talus moves on a convex surface of the calcaneus (Lewis, 1980b; Lewis, 1981; Aiello and Dean, 1990). The subtalar joint in humans has a lesser degree of transverse angulation than that seen in African apes and OH 8. This means the human talar head is more in line with the hallux (Lewis, 1980b).

Multivariate analyses of the tali by Lisowski et al. (1974, 1976) found that *H. habilis* and *Paranthropus* more closely resemble more arboreal primates, such as *Pongo* and *Hylobates*, rather than humans, chimpanzees or gorillas. This observation led Lisowski et al. to suggest that these two early hominin species may have had a form of bipedal locomotion unlike humans. One further implication is that the last common ancestor of humans and African apes may not have been a knuckle walker. An earlier study by Day and Wood (1968) revealed a similar relationship between the talus of *H.*

habilis and *Paranthropus*. In terms of tali dimensions this study found that these fossil hominins are closer in resemblance to African apes than to modern humans. In another study by Kidd et al. (1996), it was reported that *H. habilis* (OH 8) has talar head torsion greater than humans but less than in apes, and medial deviation of the talar neck more similar to apes as well. Gebo and Schwartz (2006) have recently suggested that the OH 8 tali is *P. boisei* rather than *H. habilis*. A Neanderthal talus was reported to be essentially indistinguishable from that of a modern human talus, implying similar locomotion between these two groups and establishing antiquity of human talar anatomy (Rhoads and Trinkaus, 1977).

The Calcaneus

The human calcaneus is more robust and wider than in non-human primates (Aiello and Dean, 1990; Elftman and Manter, 1935b; Kidd, 1999; Latimer and Lovejoy, 1989; Latimer et al., 1982; Morton, 1924; Morton, 1926; Sarmiento, 1994; Stern and Susman, 1983; Weidenreich, 1923; Weidenreich, 1940). In addition, humans possess a lateral process at the posterior aspect of the calcaneal tuberosity (Aiello and Dean, 1990; Deloison, 1985; Elftman and Manter, 1935b; Gebo, 1992; Latimer and Lovejoy, 1989; Trinkaus, 1983; Weidenreich, 1923; Weidenreich, 1940). The significance of this process is that it provides stability to the heel during bipedal locomotion. Although gorillas lack this process, they are sufficiently large and terrestrial to have a robust calcaneus more similar to humans than to other primates (Sarmiento, 1994). There is some confusion in the literature as to whether the lateral process is present in *A. afarensis*. Deloison (1985) reported a complete absence of the calcaneal lateral process in *A. afarensis*, which was disputed by Latimer and Lovejoy (1989).

The human calcaneus is elevated at the anterior aspect, which is directly related to the longitudinal arch that is present in humans but absent in non-human primates (Gebo, 1992; Weidenreich, 1923; Weidenreich, 1940). Although it has been mentioned that the calcaneus is longer in humans than in apes, it is interesting to note that in the human fetus it is shorter in relation to the rest of the foot compared to an adult (Jones, 1944). It is therefore possible that the differences in the foot proportions between humans and apes are due to differing rates and duration of fetal development.

The Cuboid

All of the human tarsals, including the cuboid, are longer than in apes (Elftman and Manter, 1935b). The proximal aspect of the cuboid has a "beak" that articulates with the superior distal calcaneus (Jones, 1944). This beak is larger in humans than in apes, and the larger beak in humans contributes to stability of the longitudinal arch (Bojsen-Moller, 1979; Lewis, 1980b, 1981; Kidd et al. 1996). Kidd et al. (1996) reported that the OH 8 cuboid beak is larger and human-like. The distal aspect of the cuboid articulates with the proximal articular surfaces of metatarsals four and five, of which the cuboid articulation for metatarsal five is convex (Aiello and Dean, 1990; Lewis, 1980a; Lewis, 1989).

The Navicular

The navicular articulates proximally with the head of the talus and distally with the first, second, and third cuneiform bones. The navicular overall is larger in humans than in apes, but apes have a larger navicular tuberosity (Aiello and Dean, 1990; Elftman and Manter, 1935b; Kidd, 1999; Susman, 1983). The large navicular tuberosity in apes is a trait shared by *A. afarensis* (Latimer et al., 1982). *Homo habilis* exhibits a smaller human-like navicular tuberosity (Susman, 1982). In humans the navicular does not articulate with the cuboid as it does in apes (Aiello and Dean, 1990).

The Cuneiform Bones

The cuneiform bones articulate proximally with the navicular and distally with the proximal articular surfaces of metatarsals one, two, and three respectively. Like other tarsals, the cuneiforms are longer in humans than in apes (Elftman and Manter, 1935b). The second cuneiform is shorter than the first and third cuneiforms (Jones, 1944). The lateral aspect of the medial cuneiform has an "L" shaped articular surface for articulation with the middle cuneiform, rather than two joint surfaces as in apes (Clarke and Tobias, 1995).

The medial cuneiform bone, especially the distal orientation and articular surface morphology, has gotten a lot of attention in the literature (Berillon, 1999; Elftman and Manter, 1935b; Latimer and Lovejoy, 1990a; Latimer et al., 1982; Lewis, 1989; Morton, 1922; Morton, 1924; Schultz, 1930; Susman, 1989). The distal articular surface of the medial cuneiform faces more medially in apes than in humans (Berillon, 1999; Elftman and Manter, 1935b; Latimer and Lovejoy, 1990a; McHenry and Jones, 2006; Schultz, 1930). Latimer and Lovejoy (1990) reported that *A. afarensis* has a human-like distal medial cuneiform orientation. The medial cuneiform of the OH 8 foot, *Homo habilis*, is also reported to have a human-like distal orientation (Susman, 1982). This claim is disputed by Kidd et al. (1996), who remark that the distal orientation of OH 8 appears to deviate medially, thus presenting the possibility that *H. habilis* has a partially abductable hallux. The medial cuneiform distal articular surface is also reported to be more flat in humans than in apes, which is an indication of opposability or lack thereof (Latimer and Lovejoy, 1990a; Lewis, 1989; Morton, 1922; Morton, 1924). The surface is reported to be intermediate in curvature to humans and apes in *A. afarensis* (Latimer and Lovejoy, 1990a). Interestingly, the surface is reported to be flat in *P. robustus* (Susman, 1989).

The Metatarsals and Pedal Phalanges

The relative robusticity of the metatarsals have a high degree of variation. Archibald et al. (1972) reported that humans (Amerindians) have a robusticity pattern of 1>5>4>3>2 in 56% of their sample, and a pattern of 1>5>4>2>3 in 20% of their sample. This demonstrated that *Homo habilis*, as observed in the OH 8 foot, has a pattern similar to 20% of humans based on the OH 8 pattern of 1>5>4>2>3 reported by Day and Napier (1964). Archibald et al. (1972) report that this implies *H. habilis* had a gait pattern like modern humans, and its slight deviation from the robusticity pattern of the majority of modern humans is likely due to normal variation rather than variation with a functional significance related to gait.

In contrast, apes have a robusticity pattern that, while highly variable, is quite different from modern humans and OH 8. The first metatarsals of chimpanzees and gorillas are the most robust of the metatarsals, but are followed in robusticity by either MT 2, MT 3, or MT 4. In humans, MT 4 is the second most robust metatarsal in only 8% of the population (Archibald et al. 1972). Archibald et al. (1972) further reported that in apes MT 2 and MT 3 tend to be more robust than in humans, due to high stress during locomotion. In humans, MT 1 bears the greatest burden of weight at toe off, which alleviates this burden from MT 2 and MT 3. In contrast, when apes walk MT 1 is typically in an abducted position, and bears little to no weight, thus shifting the burden to MT 2 and MT 3 (Archibald et al., 1972). As mentioned previously, in chimpanzees a great deal of weight remains on the lateral side of the foot during locomotion, but stress on MT 4 and MT 5. A recent study demonstrated that there is flexibility at the MT 4 and MT 5 tarsometatarsal joints of chimpanzees, contributing lateral foot flexion to what has been called the “mid-tarsal break” (DeSilva, 2010).

The metatarsal proximal articular surfaces, with the exception of the first metatarsal, have not been described at length in the literature. However, in humans the bases of metatarsals two through four are enlarged in the dorso-plantar aspect, and the fifth metatarsal is enlarged medio-laterally (Susman, 1983).

The first metatarsal is more robust in humans than in apes (Aiello and Dean, 1990). In apes the first metatarsal is capable of considerable movement for grasping, whereas in humans the joint is immobile (Berillon, 1999; Elftman and Manter, 1935b; Latimer and Lovejoy, 1990a; Latimer et al., 1982; Lewis, 1989; Morton, 1922; Morton, 1924; Schultz, 1930; Susman, 1989). The proximal articular surface of the first metatarsal is often described as “kidney” or “crescent” shaped (Dykyj et al., 2001; Jones, 1944; Lewis, 1972). This articular surface is also described as “screw shaped” or “ellipsoid shaped," forcing the joint into adduction during plantar flexion of the foot (Reimann and Marlovits, 1992). The human first metatarsal often has an articular facet at the lateral aspect for articulation with the second metatarsal (Jones, 1944; Le Minor and Winter, 2003; Lewis, 1980b; Tuttle, 1984). Le Minor and Winter (2003) report that the frequency of this facet in humans is about 30%, whereas it never appears in non-human primates. This human trait is present on the OH 8 *Homo habilis* first metatarsal (Day and Napier, 1964). It has been suggested that the presence of this articulation rules out opposability of the hallux (Day and Napier, 1964). This assumption is challenged by Lewis (1980b) when he suggests that this joint is a psuedoarthrosis, and a synovial joint capsule bridges the metatarsals. According to Kidd et al. (1996), Lewis' suggestion leaves the possibility open that OH 8 had an opposable hallux.

The proximal articular surface of the first metatarsal is variably divided into dorsal and plantar aspects by an elevated and invaginated region in the medio-lateral central area of the surface (Aiello and Dean, 1990; Clarke and Tobias, 1995; Jones, 1944; Latimer and Lovejoy, 1990a). As to the significance of this elevation, it has been suggested that it is an impediment to rotation and abduction of the hallux (Latimer and Lovejoy, 1990a). The proximal articular surface of the first metatarsal is shallower in humans than in apes (Latimer et al., 1982; Lewis, 1972). The surface is deeper at the dorsal aspect than the plantar aspect in humans (Szalay and Dagosto, 1988). It has been reported that *A. afarensis* has a deeper surface more similar to the apes, but has the characteristic of lateral invagination more similar to humans (Latimer et al., 1982). In contrast, *Homo habilis* is described as having a flat, human-like articular surface (Susman and Stern, 1982). It has been suggested that a flatter articular surface implies reduced mobility of the hallux (Lewis, 1972; Lewis, 1989).

The second metatarsal is indented into the tarsals due to the shorter middle cuneiform, and the metatarsal articulates medially with the medial cuneiform and laterally with the lateral cuneiform (Lewis, 1980a). This configuration stabilizes the base of the second metatarsal (Lewis, 1980a). However, *Pongo* differs in that the lateral cuneiform is not as projecting, and as a result the second metatarsal is not as indented and does not articulate with the lateral cuneiform (Lewis, 1980a).

The lateral cuneiform projects distally further than the cuboid, allowing the base of the fourth metatarsal to articulate with the lateral cuneiform and the third metatarsal (Lewis, 1980a). The fifth metatarsal is curved at the lateral border in humans but straighter in apes; the base is wider in humans, and at a more acute angle (straighter) (Aiello and Dean, 1990).

A dorsal sulcus is present proximal to the dorsal aspect of the metatarsal heads in humans, but is completely absent in non-human primates (Latimer and Lovejoy, 1990b; Latimer et al., 1982; Stern and Susman, 1983; Susman and Brain, 1988). This sulcus is present in *A. afarensis* (Latimer et al., 1982; Stern and Susman, 1983). Similarly, the sulcus is present in *P. robustus* (Susman and Brain, 1988). The presence of a dorsal sulcus is the result of the hyperextension of the phalanges at the dorsal aspect during locomotion (Nawoczenski et al., 1999; Shereff et al., 1986; Susman, 1983; Weidenreich, 1923). *A. afarensis* has a dorsal and plantar phalange range of motion like humans (Latimer and Lovejoy, 1990b).

One striking difference in the heads of the metatarsals between humans and apes is in the fact that the human metatarsal heads lack the same degree of torsion. In non-human primates, the head of the first metatarsal exhibits torsion toward the lateral aspect, while the lateral four metatarsal heads exhibit torsion toward the medial aspect (Aiello and Dean, 1990; Conroy and Rose, 1983; Elftman and Manter, 1935b; Lewis, 1980b; Lewis, 1981; Lewis, 1989; Morton, 1922; Morton, 1935; Olson and Seidel, 1983; Sarmiento, 1994). However, Sarmiento (1994) reports that the degree of torsion in the first metatarsal in gorillas overlaps the range of variation in humans. He indicates that this similarity is due to the increased terrestrial lifestyle of gorillas compared to the other great apes. In light of this it is interesting that *P. robustus* displays greater torsion of the first metatarsal head than in humans, but not as much as that seen in apes (Susman and Brain, 1988). On the grounds of metatarsal torsion Lewis (1980) argues that *H. habilis* (OH 8) is ape-like and likely retained grasping ability in the foot. It is unclear how this was determined by Lewis (1980) since OH 8 lacks metatarsal heads.

In addition to torsion, the metatarsal heads of apes are more round than in humans (Stern and Susman, 1983). Another difference in the metatarsal heads between humans and apes is that the heads are wider in humans; the metatarsal heads of *A. afarensis* and *P. robustus* are narrower than those of humans (Susman and Brain, 1988; Susman et al., 1984). In a multivariate morphometric analysis conducted by Susman and de Ruiter (2004), *Paranthropus* has more affiliation with apes than humans in terms of dorsal head breadth. Finally, the first metatarsal head is narrower at the dorsal aspect in humans than in either apes, *A. afarensis*, or *P. robustus* (Susman and Brain, 1988; Susman et al., 1984). The narrowness in humans is a reflection of the tubercles on the first metatarsal being reoriented to the plantar aspect, thus providing more surface area to the plantar aspect of the first metatarsal for locomotion. The metatarsal bases are elevated relative to the heads in humans, which is a direct reflection of the longitudinal arch (Morton, 1922).

Overall, the phalanges are shortened in humans compared to non-human primates (Elftman, 1969; Elftman and Manter, 1935b; Midlo, 1934; Schultz, 1963; Weidenreich, 1923). The proximal phalanx length range of variation in *A. afarensis* seems to generally be in between humans and gorillas, sometimes overlapping higher extremes of humans and lower extremes of gorillas (Latimer and Lovejoy, 1990b). The proximal articular surfaces of the proximal phalanges are more dorsally located in humans than in apes (Latimer and Lovejoy, 1990b). These articular surfaces are plantarly oriented in apes compared to the dorsal orientation in *Homo* (Duncan et al., 1994). *Pan* and *Gorilla* have articular surface intermediate to these two (Duncan et al., 1994). The articular surface observed in *A. afarensis* is intermediate between *Homo* and the African apes (Duncan et al., 1994). The proximal phalanges are more curved in apes than humans, and *A.*

afarensis has curved proximal phalanges resembling apes (Stern and Susman, 1983; Susman et al., 1984; Tuttle, 1984).

The orientation of the distal hallucal phalanx is different in humans than in non-human primates (Wilkinson, 1954). In humans the distal phalanx of the hallux has a lateral deviation of 8-25° relative to the metatarsal. Wilkinson examined both adults and fetuses, and found that this lateral orientation is present during fetal development. This rules out an environmental ontogenetic influence on bone plasticity, such as wearing shoes. This human trait appears to be shared by the OH 10 distal hallucal phalange, which is contemporary to OH 8 (1.7 mya) but has not been allocated to a particular genus and species (Day and Napier, 1964; Day and Napier, 1966; Day, 1967; Leakey, 1971; Oxnard, 1972; Wood, 1974).

Anatomy and Models on the Origin of Bipedalism

There has been a heated debate in the field of physical anthropology regarding the interpretation of fossil evidence in regard to bipedal locomotion. This argument is summarized in Stern's (2000) review article on the work and opinions to date. As several researchers analyzed *Australopithecus afarensis*, very differing points of view were expressed. In one camp Lovejoy, Latimer, and others chose to see the mosaic of human and ape-like traits apparent in *A. afarensis* as plesiomorphic characters that no longer had any functional significance (Stern, 2000). In the other camp Stern, Susman and others saw the ape-like traits in *A. afarensis* as behaviorally significant (Stern, 2000).

These differing points of view may be related to a way of thinking, on the one hand, that apes ancestral to hominins abruptly started walking exclusively bipedally and did not have any significant climbing behavior. On the other hand, the camp championed by Stern and Susman thought that the shift to bipedalism might have been a gradual adaptation to terrestrial bipedalism that continued to exhibit an important arboreal component (Duncan et al., 1994; Stern and Susman, 1983; Susman et al., 1984). However, despite these differences in opinion, no one disagrees that *A. afarensis* is habitually bipedal when on the ground (Duncan et al., 1994; Latimer and Lovejoy, 1989; Latimer and Lovejoy, 1990a; Latimer and Lovejoy, 1990b; Stern and Susman, 1983; Susman et al., 1984).

When considering the evolutionary anatomy of the foot specifically, Hunt's (1994, 1996) postural feeding hypothesis offers one theoretical model for the initial evolution of bipedalism. Hunt's model is most closely aligned with Stern's position, which reflects an interpretation of the available anatomy as representing a repertoire (as represented by *A. afarensis*) of behavior that is highly reliant on an arboreal component. In this model, there is a point when bipedality becomes the dominant and most evolutionarily significant locomotor behavior, and it is after this transition that modern bipedal anatomy emerges.

When considering the difference between a mosaic of behavior and exclusive terrestrial behavior in relation to the foot, it must be expected that adaptations to make long distance walking more efficient will manifest in the hominin line. The primary two adaptations are the complete absence of an opposable hallux and the presence of a longitudinal arch, both of which are necessary for the pattern of weight transference observed in modern humans (Elftman and Manter, 1935).

Laetoli Prints and Implications of Shod and Unshod Feet

Some evolutionary interest in the anatomical differences that might arise in shod versus unshod modern human populations has its roots in efforts to interpret the discovery of the Laetoli fossil foot prints reported by Leakey and Hay (1979). The stratigraphy bearing the tracks is dated at 2.6 to 3 mya, and based on the interpretation that the tracks reflect a foot with an adducted hallux and a longitudinal arch, it was reported that the prints belong to hominins with a fully modern gait (Leakey and Hay, 1979; Hay and Leakey, 1982). Day and Wickens (1980) corroborated this interpretation with a comparative study examining the depth impressions of the Laetoli prints compared to modern human footprints. White (1980) and White and Suwa (1987) further agreed with this interpretation, and suggested that the fossil footprints belong to the contemporary *A. afarensis*. Stern and Susman (1983) interpret the Laetoli prints in a different way, reporting that the depth pattern has similarities to impressions that can be made by ape feet. In particular, they claim that the appearance of a medial longitudinal arch in the fossil prints can also appear in ape footprints. This is explained partly due to the way weight transfers across the lateral side of the foot in ape locomotion (Elftman and Manter, 1935a). Stern and Susman (1983) interpret the Laetoli prints to indicate a foot with ape-like weight transmission, lacking a shift of weight to the medial forefoot for toe off, evidenced from a lack of a deep print impression in the region corresponding to the location of the MT 1 head. Stern and Susman (1983) acknowledge that the prints are human-like in having an adducted hallux that is more extreme than occurs in ape footprints, but also point out that the variable appearance of the length of the lateral toes in the fossil casts relative to the length of the hallux likely reflects curling the toes under the foot as occurs in chimpanzees during bipedal locomotion (Elftman and Manter, 1935a). In all of these characteristics, Stern and Susman (1983) find it likely that the Laetoli prints represent prints from *A. afarensis*. White and Suwa (1987) disagree with the assessment that the Laetoli prints do not reflect a modern toe-off mechanism, contending that the appearance of a lack of weight transfer to the medial forefoot for toe off is an artifact of the preservation of the footprint and that even in modern humans weight transfer to the medial forefoot in soft substrate has a high degree of variability.

Tuttle et al. (1996) report that in a comparison of prints made from apes, habitually unshod modern humans, and the Laetoli prints, modern unshod human prints very closely resemble the Laetoli prints. With this result, Tuttle et al. (1996) conclude that a hominin other than *A. afarensis* must have made the Laetoli prints, because the mosaic *A. afarensis* pedal morphology would likely not have left prints resembling modern humans in their view.

Charteris et al. (1981, 1982) estimated the stride length of the hominins represented by the Laetoli tracks, and came to the primary conclusion that the hominins were traveling at a slow speed when they were found, based on relative stride length to stature estimates. They state that the less likely interpretation is that the hominins had a "shuffling" gait that was shorter than in modern humans, but based on the previously cited work they conclude that since it appears the prints represent an essentially modern foot this is probably not the case.

One of the underlying assumptions of some of the studies discussed above is that habitually unshod humans have either different pedal anatomy, gait as reflected in the foot, or both. Hilton (1997) examined gait in habitually unshod Venezuelans and in shod Americans from New Mexico. He found that in terms of stride length, the Americans have a longer stride solely due to being larger in body size, overall, compared to the Venezuelan sample. A regression line draws a predictable stride length that does not seem to be affected by the variables of being shod or unshod. Differences in gait between the habitually shod and unshod groups examined by Hilton (1997) are attributed to unshod individuals carrying heavy loads over distances, affecting the gait in a way an unencumbered individual would not be. This has implications for the study of stride length by Charteris et al. (1981, 1982) discussed above. It can be expected that stride lengths can be estimated with body proportions while eliminating shod versus unshod as potential influences if it is assumed that early hominins are not carrying a heavy load. Hilton (1997) reports one significant difference between shod and unshod individuals. This difference is in the angle of the foot when walking. Shod individuals have an increased "hallucal stride width," meaning that the forefoot is angled more laterally as opposed to in unshod individuals where the forefoot is angled more medially, making the feet more parallel to one another.

The possibility must be considered that habitually unshod individuals will exhibit different pedal anatomy from shod individuals. There is sometimes an implication in the literature that the anatomy of an unshod individual will have similarities to ape anatomy not seen in habitually shod individuals. This draws into question any interpretation of arboreal tendencies of early hominins if compared to modern individuals who are habitually shod. These concerns seem to be more relevant in some aspects of anatomy than in others. It has been observed that unshod people have greater mobility of the hallucal phalanges (Shulman, 1945; Sim-Fook et al., 1958). These observations could impact interpretations of the lateral angle of the distal phalange, but only a comparative osteological study of shod and unshod phalanges will be revealing. It is possible that the increased mobility of the hallucal phalanges would be most noticeable in footprints rather than in a quantitative osteological observation. It has also been observed that the entire forefoot is more flexible in unshod populations compared to habitually shod populations (Kadambande et al., 2006). However, maximum forefoot width is unaffected by being habitually shod or unshod (Thompson and Zipfel, 2005). The significance of these last two points should be considered carefully. Greater flexibility in the forefoot has been measured by comparing the forefoot width when weight is applied and when it is relieved. Since maximum width is not affected by being shod or unshod, but having a narrower forefoot in a nonweight-bearing state is related to being unshod, it is unclear if this condition is related to mobility of the phalanges and tarsals or soft tissues, or both (Sim-Fook, 1958). It has been reported that children are developmentally affected by habitually shod lifestyles in that they have collapsed arches and greater incidence of flat foot (Roa and Joseph, 1992). In addition, it has been reported that adults who have been habitually unshod have a well-developed longitudinal arch (Sim-Fook et al, 1958).

Combining the literature discussed above reveals that unshod people have a better-developed longitudinal arch combined with greater overall flexibility of the foot, particularly in the phalanges of the forefoot. This observation does not necessarily suggest how these traits reflect on pedal osteological morphology, particularly in relation to the bony arch. However, Trinkaus (2005) found that the proximal phalanges of the lateral foot of shod individuals are significantly less robust than shod individuals. This shows that reduced ground reaction forces can influence bone thickness. It must be considered that conditions resulting from the shod condition are the “unnatural” conditions. After all, humans did not evolve a longitudinal arch in order to wear shoes. This issue is most relevant to my work in the following ways.

Metatarsal surface morphology should only be primarily affected by being shod or unshod if either condition grants a higher degree of active mobility at the tarso-metatarsal joints. Excessive mobility in this region in modern humans leads to pathology that is reported in reduced frequency in unshod populations (Shulman, 1945; Roa and Joseph, 1992; Kadambande et al., 2006). It could be argued that habitually shod individuals would have to walk a great deal unshod to achieve extra movement at the tarso-metatarsal joints that would leave osteological evidence. The often weakened and flat arch of the shod foot is being supported by an artificial arch in a shoe, but is nonetheless supported. The possibility that unshod individuals might appear more ape-like in pedal morphology should be considered skeptically for several reasons. One reason is that increased mobility of the foot in unshod groups is in the phalanges, not the metatarsals. The hallucal phalanges may be capable of more abduction in unshod groups, but this does not indicate mobility at the hallucal tarso-metatarsal joint. Since unshod groups have a better-developed longitudinal arch, one would not expect any additional movement at the tarso-metatarsal joints that would grant them an ape-like appearance. It is important to note that for most of these joints an “ape-like” appearance has not been described (with the greatest exception being MT1). In addition to the issue of joint mobility, one must ask whether it would be possible for a pathological human foot to appear ape-like. It is likely that increased joint mobility in a pathological human foot would not resemble an ape foot because in addition in increased mobility, ape feet are in a permanently pronated position and have foot proportions different from modern humans. A permanently pronated foot position is partially responsible for the weight transition pattern reported by Elftman and Manter (1935a), in addition to the adducted hallux of modern humans.

Fossil Evidence for the Emergence of Bipedalism

This section contains a brief discussion of current evidence for the emergence of bipedalism, and its subsequent evolution.

Sahelanthropus tchadensis

Some argue that the earliest hominin found to date comes from Chad in Central Africa at the Toros-Menalla locality, from stratigraphy that is biostratigraphically dated to between 6 and 7 mya (Brunet et al. 2001; Vignaud et al. 2002, Guy et al. 2005). Brunet et al. argue that this find, a cranium and other associated teeth designated *Sahelanthropus tchadensis*, is a hominin based on some of the following features: orthognathic face, lack of canine honing complex (apical wear present), foramen magnum oval shaped and anteriorly located, presence of canine fossa, and face below the neurocranium. It is important to note that some of these traits, such as the supraorbital torus, are derived features that do not otherwise appear in the hominin line until the emergence of *Homo erectus* or later *Homo* (Wolpoff et al. 2002). Wolpoff et al. (2002) criticized the initial interpretation of the *Sahelanthropus* find, arguing that the find actually represents a quadrupedal ape with heavy chewing musculature. They also argue that the position of the foramen magnum is no further anterior than that of female gorillas and chimpanzees. They further argue that some of the features cited as indicating hominin affiliation, such as orthognathism and a supraorbital torus, are not relevant because the features that are shared with hominins are features belonging to *Homo* from the Pleistocene, and there is no direct fossil link between these hominins and *Sahelanthropus*. Beauvilain and Le Guellec (2004) have questioned the provenience and accuracy of the estimation of MNI from the finds reported by Brunet et al. (2001). This brings into question the estimated date for *Sahelanthropus*. The recovered cranium was badly distorted, but a virtual reconstruction by Zollikofer et al. (2005) seemingly confirmed the interpretation of

Brunet et al. (2001) that the location of the foramen magnum is in an anterior position. However, Ahern (2005) reported that the position of the foramen magnum, as estimated by landmarks on the basicranium, falls within an area of overlapping variation between humans and chimpanzees.

Orrorin tugenensis

Brigitte Senut, Martin Pickford, and their colleagues reported an early hominin from the Lukeino Formation in Kenya, dated at approximately 6 mya (Senut et al., 2001; Pickford and Senut, 2001). There is strong mounting evidence that this new genus was bipedal. Some of the first bipedal characteristics reported by Senut et al. (2001) included a long femoral neck and a femoral head larger than that of *A. afarensis*. Subsequently, Galik et al. (2004) reported stronger evidence by showing that the cortical bone at the inferior aspect of the femoral neck is thicker than at the superior aspect. This has been shown to be indicative of bipedalism (Ohman et al., 1997). However, the Galik et al. study was criticized by Ohman et al. (2005). Despite the bipedal characteristic described, it is argued that *O. tugenensis* maintained an important arboreal component to its lifestyle, based on humerus morphology and morphology of the distal first phalange (Senut et al., 2001; Gommery and Senut, 2006). Senut et al. (2001) place *O. tugenensis* as a direct ancestor to *Homo*, and place *Australopithecus* as a separate hominin line. Aiello and Collard (2001) believe further evidence should be collected before this claim is made.

Ardipithecus

White et al. (1994, 1995) reported a new species of hominin dated at 4.4 mya from Aramis, Ethiopia, which they ultimately named *Ardipithecus ramidus*. This new genus was initially differentiated from *Australopithecus* in having more ape-like dentition, including having thinner tooth enamel. White et al. (1994) present the anterior position of the foramen magnum as evidence for bipedality in *A. ramidus,* and this claim is supported by Ahern (2005). Until recently, nothing new on the specimens reported by

White et al. (1994, 1995) and further described by Wolpoff (1999) had been published. Then in 2009 a team of researchers released a series of articles simultaneously in a special issue of *Science* (Louchart et al., 2009; Lovejoy, 2009; Lovejoy et al, 2009a, 2009b, 2009c, 2009d; Suwa et al., 2009a, 2009b; White et al., 2009a, 2009b; Woldegabriel et al., 2009). The skull was highly fragmented, but after reconstruction it is described as being similar to *Sahelanthropus* and being unlike *Australopithecus* or extant apes (Suwa, 2009a). It has less facial prognathism than extant African apes, a small brain (300-350 cc), a small canine diastema, and has less dental specialization than later hominins (Suwa et al., 2009a). The pelvis has a shorter ilium relative to apes, the ilium is flared as in other hominins, and it is rotated further to the sagittal plane than it is in apes (Lovejoy et al., 2009c). *A. ramidus* has shorter metacarpals (MC) relative to African apes, with MC heads bearing some similarity to Old World monkeys and to some Miocene apes, suggesting slightly greater dorsiflexion of the phalanges in *A. ramidus* (Lovejoy et al., 2009b, 2009d).

The overall argument presented for the locomotor behavior of *A. ramidus* is that it represents a "careful climber" that walked in trees rather than engaging in suspensory behavior (Lovejoy et al., 2009a, 2009b, 2009d). It had evolved a tendency for arboreal bipedal posture, and was not adapted to knuckle walking. Its foot is argued to have been less flexible in the lateral area as it is in apes (Lovejoy et al., 2009a, 2009b; DeSilva, 2010). One of the most important arguments about the relationship of *A. ramidus* to humans and African apes is that the last common ancestor of human and African apes was not a knuckle walker, and that this mode of locomotion was independently developed in the lineages of *Pan* and *Gorilla* (Lovejoy, 2009b, 2009d). It is argued that the last common ancestor between humans and African apes would have had more in common with more generalized monkey-like Miocene apes (Lovejoy, 2009b).

Other specimens are attributed to the genus and species *Ardipithecus kadabba* have been described by Haile-Selassie (2001) and Haile-Selassie et al. (2004) that are dated at 5.2-5.8 mya from the Middle Awash, Ethiopia. This species of *Ardipithecus* is described as being more primitive overall than *A. ramidus*, and having curvature in the phalanges of the feet that more closely resembles apes than those of *A. afarensis* (Haile-Selassie, 2001). Most of the evidence that associates *Ardipithecus* to *Australopithecus* is related to tooth morphology. An implication is made that there is a natural progression from the older *Ardipithecus* species to *A. afarensis*, which based on morphology would seem to rule out other potential hominin ancestors from being ultimately ancestral to *Homo*, such as *Orrorin tugenensis* (Haile-Selassie et al., 2004).

Subsequent Evolution of Bipedalism

It is uncertain which of the current fossil evidence, if any, represents the "first" hominin ancestor. The earliest australopith that has been found may be *A. anamensis*, which is a likely ancestor of *A. afarensis*, but to date the osteological evidence for its locomotion is sparse (Leakey et al. 1988; Ward et al. 1999; Ward et al. 2001; Kimbel et al. 2006). In addition, the new findings regarding *A. ramidus* present a very different picture of early hominin evolution than what had previously been inferred using extant apes as knuckle walking models for a last common ancestor (Louchart et al., 2009; Lovejoy, 2009; Lovejoy et al, 2009a, 2009b, 2009c, 2009d; Suwa et al., 2009a, 2009b; White et al., 2009a, 2009b; Woldegabriel et al., 2009). Nonetheless, even if the evidence presented regarding *A. ramidus* becomes corroborated by further studies and more fossil finds, there is an abundance of evidence present with the fossil finds of *A. afarensis* as to how more primitive apelike anatomy makes a transition to modern hominin anatomy (Johanson et al. 1982a; White and Johanson, 1989).

An anterior foramen magnum position is observed in *Australopithecus* and *Paranthropus*, and in early *Homo*. (Dart, 1925, 1926; Dean and Wood, 1981, 1982; Aiello and Dean, 1990). Further derived traits observed in *A. afarensis* and later *Australopithecus* and *Paranthropus* indicate that bipedalism includes a short, wide ilium oriented more in a sagittal plane than in a coronal plane (Johanson et al. 1982b, Day, 1973, Aiello and Dean, 1990). However, Stern and Susman (1983) reported that the *A. afarensis* acetabulum is ape-like in that the anterior portion of the lunate surface does not extend inferiorly as far as it does in humans, which might have implications for posture. By the time *A. africanus* appears, the acetabulum has become more human-like (Schultz 1969b; McHenry, 1975; Aiello and Dean, 1990). Further, the femoral neck in *A. afarensis* is relatively longer than in humans, but the bicondylar angle in the distal femur is higher than in apes (Stern and Susman, 1983). The femoral neck of *A. afarensis* is like humans in that it has thicker cortical bone at the superior aspect relative to the inferior aspect (Ohman, 1997). The condyles of the distal femur are anterior-posteriorly shorter in *A. afarensis* than in humans. The knee of *A. afarensis* exhibits ape-like features that suggest a more chimpanzee-like range of motion at the knee (Tardieu, 1981; Senut and Tardieu, 1985, Aiello and Dean, 1990). The distal tibia in *A. afarensis* exhibits size and shape dimorphism, in that the articular surface for the talus is flatter and more human-like in larger *A. afarensis* specimens, but is slightly angled and more ape-like in smaller specimens (Stern and Susman, 1983).

One issue worth noting is that there is a great deal of debate regarding limb proportions in *A. afarensis*. Do the relatively shorter legs of *A. afarensis* represent an ape-like proportion indicative of inefficient bipedal locomotion, or are the shorter legs expected ontogenetically for a hominin the same size of *A. afarensis* (Jungers, 1982; Jungers and Stern, 1983; Lewin, 1983; Wolpoff, 1983a, 1983b; Franciscus and Holliday, 1992; Holliday and Franciscus, 2009).

One hominin lineage that shows some divergence from modern humans is the recently discovered *Homo floresiensis* (Brown et al., 2004; Morwood et al., 2005; Jungers et al., 2009a, 2009b; Argue et al. 2006; Falk et al., 2007; Larson et al., 2007; Tocheri et al., 2007; Lyras et al., 2008). In considering the anatomy of the foot, the pattern of metatarsal robusticity is identical to modern humans (Jungers et al., 2009a, 2009b). Further, the presence of dorsal sulci at the heads of the metatarsals indicates human-like dorsiflexion at the metatarsophalangeal joints (Jungers et al., 2009a, 2009b). However, the foot is long relative to the length of the lower limb bones, falling outside of the range of modern humans but within the range of *Pan paniscus* (Jungers et al., 2009a). The hallux is shorter than in humans but within the range of *Pan* (Jungers et al., 2009a). The navicular is similar to apes, and Jungers et al. (2009a) report that it is unlikely that a medial longitudinal arch was present. This implies that weight transferred through the foot very differently than in modern humans, with weight bearing on the plantar portion of the navicular at toe off. This combination of apelike plesiomorphic traits and unique derived traits lead Jungers et al. (2009a) to conclude that *H. floresiensis* may descend from a hominin group that left Africa prior to (or at the same time as) *H. erectus*.

CHAPTER 4: MATERIALS AND METHODS

Methods

Research Objectives and Functional Basis

This study quantifies joint surface morphology of the proximal metatarsals in *Homo* (shod and unshod), *Gorilla*, *Pan*, *Hylobates*, and fossil hominins using three-dimensional morphometrics. The following hypotheses are investigated, with a discussion of the functional basis for these hypotheses.

H_1: Metatarsals 2 and 3 will exhibit expanded articular surfaces in humans, relative to apes, at the middle and plantar regions of the surface.

Functional explanation: Functional evidence for weight distribution in the foot in humans during bipedal locomotion, and apes in both bipedal and quadrupedal locomotion, demonstrates that stress and/or compression forces in the foot are more focused on the longitudinal arch in humans as weight transfers to the forefoot and hallux for toe-off, but force is focused on the bases of the medial cuneiform, cuboid, and proximal plantar aspect of MT 5 in apes as weight transfers across the calcaneus and from the medial midfoot to the lateral aspect of the foot (Leardini et al., 2007; D'Août et al., 2004; Vereeke at al., 2003; Chen et al., 2001; Jacob, 2001; Gefen et al., 2000; Giacomozzi, 2000; Kidd, 1999; Stokes et al., 1999; Sharkey and Hamel, 1998; Kidder et al., 1996; Sarmiento, 1994; Scott and Winter, 1993; Aiello and Dean, 1990; Lewis, 1989; Susman, 1983; Lewis, 1972; MacConnaill, 1950, 1966, 1969; Day and Napier, 1964; Elftman and Manter, 1935a; Weidenreich, 1923). In humans, the tarsometatarsal joint surfaces at MT 2 and MT 3 are load bearing as part of a stable longitudinal arch, whereas in apes there is no longitudinal arch. The bases of MT 2, MT 3, and MT 4 (especially MT 3) are subject to more stress relative to the other MT bases at the initial forefoot contact and early push off stages of locomotion (Chen et al., 2001; Gefen et al., 2000; Regan et al., 1999; Archibald et al., 1972; Manter, 1946). In humans, it is qualitatively observed that the proximal articular surfaces of MT 2 and MT 3 are expanded, especially in the middle region of MT 3, and at both the middle and plantar regions of MT 2 in humans relative to apes. The expanded surfaces promote the stability of the bony longitudinal arch in humans, which is supported by studies that report an increase in joint surface area increases joint stability (Hamrick, 1996a; Hamrick, 1996b; Godfrey et al., 1995; Godfrey et al., 1991; Swartz, 1989; Jungers, 1988; Ruff, 1988; Sarmiento, 1988; Stormont et al., 1985; Currey, 1984; Wainwright et al., 1982; Yalden, 1972).

H_2: Metatarsal 4 will have greater convex curvature of the articular surface in apes, relative to humans.

Functional explanation: The MT 4 surface is part of the relatively immobile longitudinal arch in humans, but in apes it is part of the “mid-tarsal” (mid-foot) break dynamic that occurs when weight transfers across the lateral portion of the ape foot (Vereeke et al., 2003, D’Août et al., 2002; DeSilva, 2010; Aiello and Dean, 1990; Lewis, 1989; Conroy and Rose, 1983; Bojsen-Moller, 1979; MacConnaill, 1950, 1966; Elftman and Manter, 1935a; Weidenreich, 1923). The MT 4 surface is notably convex relative to the human MT 4 surface, and DeSilva (2010) assessed maximum curvature and found that humans were notably flatter than apes. This observation will be further tested with multiple landmarks using three-dimensional morphometrics. The functional significance of the convex surface in apes is related to the flexibility of the tarso-metatarsal joints of MT 4 and MT 5 to the cuboid. The cuboid bears weight directly on its plantar aspect during locomotion in apes, because apes lack the longitudinal arch present in humans. In apes, as weight is transferred to the cuboid and along MT 5, flexion occurs at the calcaneocuboid joint and the tarso-metatarsal joints of MT 4 and 5. A highly convex MT 4 proximal articular surface facilitates this movement, as increased joint curvature has been shown to increase range of motion (Hamrick, 1996a; Hamrick, 1996b; Godfrey et al., 1995; Swartz, 1989; Jungers, 1988; Ruff, 1988; Sarmiento, 1988; Stormont et al., 1985; Currey, 1984; Wainwright et al., 1982; Godfrey et al., 1981; Yalden, 1972).

H_3: Metatarsal 5 will exhibit greater medio-lateral concavity and elongation in apes, relative to humans.

Functional explanation: Susman (1983) described the ape proximal articular surface of MT 5 as "elongated" in the medio-lateral direction. Qualitative observation also reveals a tendency for the surface to be more concave in African apes. These observations will be tested quantitatively. This morphology, like that of the proximal MT 4 surface, is closely connected to the mid-tarsal break present in apes (Vereeke et al., 2003; D'Août et al., 2002; DeSilva, 2010). It is important to note that the tarsometatarsal articulation of MT 5 at the cuboid occurs at an oblique angle due to the presence of the transverse arch. The observed concavity and elongation of the proximal MT 5 surface occurs with the medial aspect of the articular surface elevated relative to the lateral aspect. This concavity and orientation of the surface promote tarso-metatarsal dorsi-flexion during locomotion, evidenced by studies indicating increased curvature of joint surfaces suggesting increased range of motion (Vereeke et al., 2003; D'Août et al., 2002; Hamrick, 1996a; Hamrick, 1996b; Godfrey et al., 1995; Aiello and Dean, 1990; Lewis, 1989; Swartz, 1989; Jungers, 1988; Ruff, 1988; Sarmiento, 1988; Stormont et al., 1985; Currey, 1984; Conroy and Rose, 1983; Susman, 1983; Wainwright et al., 1982; Godfrey et al., 1981; Bojsen-Moller, 1979; Yalden, 1972; MacConnaill, 1966; MacConnaill, 1950).

H_4: Articular surface morphology for MT 1-5 will exhibit no significant differences between habitually shod and unshod humans.

Functional explanation: Acceptance of this hypothesis would be informative to studies of shod and unshod human foot morphology, which have until now usually focused on either gait or the gross external structure of the foot, without comparative osteological research (Charteris et al., 1981, 1982; Day and Wickens, 1980; Hilton, 1997; Kadambande et al., 2006; Rao and Joseph, 1992; Shulman, 1945; Sim-Fook and Hodgson, 1958; Stern and Susman, 1983; Thompson and Zipfel, 2005; Tuttle et al., 1991;

White, 1980; White and Suwa, 1987). To date, studies have shown that habitually unshod individuals have a more pronounced longitudinal arch, with fewer incidences of pathology. A recent study by Zipfel and Berger (2007) demonstrated that pathologies occurring in the metatarsals of shod and unshod individuals occur in the same locations (usually the metatarsal heads or bases) but in higher frequencies in habitual shod individuals. The metatarsals associated with pathology correspond to the most robust of the human metatarsals (Archibald et al, 1972).

Since non-pathological specimens will be selected for this study, it is likely that shod individuals will have "normal" arches and tarsometatarsal joints, and that they will be indistinguishable from unshod individuals. Non-pathological observations of differing shod/unshod foot function relate to increased tarso-phalangeal ranges of medio-lateral motion and greater fore-foot flexibility in unshod individuals (Kadambande et al., 2006; Thompson and Zipfel, 2005; Hilton, 1997; Rao and Joseph, 1992; Tuttle et al., 1991; Stern and Susman, 1983; Charteris et al., 1981, 1982; Day and Wickens, 1980; White, 1980; White and Suwa, 1987; Sim-Fook and Hodgson, 1958; Shulman, 1945;). It is likely, though untested before this study, that these observations do not affect the tarso-metatarsal joint surface morphologies.

H_5: Articular surface morphology for MT 5 in *A. afarensis* (A.L. 333-13 and A.L. 333-78) will exhibit greater affinities to the human MT 5 articular surface.

Functional explanation: Acceptance of this hypothesis would imply two things, 1) that *A. afarensis* has a stable tarso-metatarsal joint complex, lacking the dorsiflexion present in apes, and 2) that *A. afarensis* has developed lateral foot stability consistent with the lack of a midtarsal break and the development of a longitudinal arch (Vereeke et al., 2003, Berillion, 2003; D'Août et al., 2002; Stern, 2000; Latimer and Lovejoy, 1990a; Latimer and Lovejoy, 1990b; Latimer and Lovejoy, 1989; Susman, 1989; Latimer et al., 1987; Susman et al., 1984; Stern and Susman, 1983; Latimer et al., 1982). It is possible that this specimen will exhibit intermediate human/ape morphology. One cannot interpret the way articular surface morphology influences overall foot function without considering the foot as a complex structure. Intermediate morphology might indicate greater joint surface stability than in apes, but a tarso-metatarsal joint complex that has not evolved into a modern human form.

H_6: The *H. habilis* (OH 8) MT 2-5 articular surfaces will exhibit greater morphological affinity with human MT 2-5 surfaces.

Functional explanation: This likelihood is supported by a similar study to that presented here (Proctor et al, 2008). This study showed that the MT 1 proximal articular surface of *H. habilis* is indistinguishable from that of modern humans. This increases the likelihood that *H. habilis* had a fully developed longitudinal arch, with inflexible MT 4 and 5 articular surfaces, and more expanded MT 2 and 3 surfaces that support a load-bearing arch. Several researchers have argued for or against the presence of a longitudinal arch in *H. habilis* (OH 8), and finding that the OH 8 MT 5 surface is indistinguishable from the modern human MT 5 would be consistent with the observation that the OH 8 robusticity pattern fits the second most common modern human pattern (1>5>4>2>3), implying a similar pattern of weight distribution in the foot during locomotion (Proctor et al., 2008; Berillon, 2003; Kidd et al., 1996; Susman, 1983; Susman and Stern, 1982; Lewis, 1980; Oxnard and Lisowski, 1980; Leakey and Wood, 1974, Archibald et al., 1972; Day and Napier, 1964).

H_7: Fossil specimens in this study will show an MT 1 articular surface that is more human-like than ape-like in morphology.

The specimens STX 5017 and A. L. 333-54 were shown to more closely resemble apes in a previous study (Proctor et al., 2008). However, this current study includes additional landmarks that might reveal more information about the shape of the articular surface. The specimen STW 562 has been described as intermediate to humans and apes (Deloison, 2003). Although the surface is relatively deeply concave compared to modern humans, the surface is constricted in the central region as it is in humans (Latimer and

Lovejoy, 1990a; Deloison, 2003). The proximal articular surface of STW 573 (Little Foot) was described as ape-like by Clarke and Tobias, but as human-like by Harcourt-Smith (Clarke and Tobias, 1995; Harcourt-Smith, 2002).

In addition to these hypotheses, for each metatarsal the following hypotheses are tested:

H_8: There is no difference in size interspecifically.

H_9: There are no sex differences in size intraspecifically.

H_{10}: Differences in morphology interspecifically are unrelated to size.

H_{11}: Differences in morphology intraspecifically are unrelated to size.

H_{12}: There is no difference in articular surface shape between sexes intraspecifically

Materials

Five metatarsals were examined in this study (MT 1, MT 2, MT 3, MT 4, and MT 5). Where possible, only the left foot was sampled and an equal number of males and females from each species group were selected. For extant material, only complete metatarsals were examined if possible. Specimens were selected to be free of pathology. Adult specimens were chosen, based on collection records if possible or assessed based on full epiphyseal fusion of the metatarsals. See Figure 4.1 for a reference photo.

Sample

The collection sample for this study includes habitually shod and unshod groups of *Homo sapiens*. In addition, the following extant ape species were sampled: *Pan troglodytes*; *Gorilla gorilla*; *Hylobates lar* (see Table 4.1). Specimens from several fossil hominins were sampled, including *Australopithecus afarensis*, *Australopithecus africanus*, *Paranthropus robustus*, and several other specimens not yet assigned a genus or species.

Figure 4.1 Human proximal metatarsals A) MT 5; B) MT 4; C) MT 3; D) MT 2; E) MT 1

<u>*Homo sapiens*</u>

The habitually shod *Homo* sample was collected from the Hamann-Todd Collection at the Cleveland Museum of Natural History and the human osteology collection in the Department of Anthropology at the University of Iowa. The specimens were primarily medical school dissection cadavers and have varying degrees of documentation. The majority of the specimens have data indicating sex and age.

The unshod sample was collected at the National Museum, Bloemfontein, and the South African Museum in Cape Town, South Africa. All specimens are from pre-pastoral populations from several different South African localities. Some specimens have dates, most in the range of 2,000 to 5,000 bp, but many do not have dates due to the collection methods in obtaining them (Sealy, 2006). The South African sample presumably represents habitually unshod people, as they are pre-pastoral with behavior of late stone age people (Hausman, 1982; Roberts, 1989; Sealy and Pfeiffer, 2000; Stock and Pfeiffer, 2001).

<u>*Pan troglodytes*</u>

The *Pan* sample was collected at the Cleveland Museum of Natural History from the Hamann-Todd Collection. These are wild shot specimens; although most are documented as originating in Cameroon, some do not specify their African collection site.

Gorilla gorilla

Gorilla specimens were collected from the Cleveland Museum of natural History's Hamann-Todd Collection. These are wild shot specimens. Many of these specimens are documented to have been collected in Cameroon, but many have no specific collection location.

Hylobates lar

Hylobates specimens were collected in the Museum of Comparative Zoology at Harvard University. These are wild shot specimens collected by Sherwood Washburn during the Asiatic Primate Expedition.

Table 4.1 Samples of extant species

	MT 1	MT 2	MT 3	MT 4	MT 5
Homo (shod)	34	34	30	32	33
Homo (unshod)	31	33	35	33	42
Pan troglodytes	30	30	30	30	30
Gorilla gorilla	30	31	30	30	30
Hylobates lar	30	29	30	30	30

Fossil Specimens

The following fossil specimens were examined. Refer to Tables 4.2 and 4.3.

Australopithecus afarensis

A total of three specimen casts were examined at the Cleveland Museum of Natural History. They are accurate first-generation reference casts. All of the original specimens were collected in Hadar, Ethiopia (Latimer et al., 1982). The specimens studied include A.L. 333-54 (MT 1), A. L. 333-78 (MT 5), and A. L. 333-13 (MT 5). All of these specimens come from a left foot.

Australopithecus africanus

The "Little Foot" Stw 573 foot bones were examined, including the MT 1 and MT 2 elements from this specimen (Clarke, 1998; Clarke and Tobias, 1995). These specimens are reported to belong to Sterkfontein member 2, indicating they date at greater than 3 mya. Clarke and Tobias suggest these fossils belong to an early *A. africanus* or possibly another early australopith (Clarke and Tobias, 1995).

Homo habilis

The metatarsals belonging to OH 8 were included in this study. This specimen is traditionally assigned to *Homo habilis* and is dated at 1.8 to 1.9 mya (Day and Napier, 1964; Leakey et al., 1964, 1965; Susman and Stern, 1982, Wood, 1992). However, recent researchers have suggested that this foot belongs to the genus *Paranthropus* (Gebo and Schwartz, 2006; see also Wood and Constantino, 2007, and Susman, 2008, for an alternative view).

Paranthropus robustus

The SKX 5017 left MT 1 was examined. It is from member 1 lower bank, Swartkrans. This member has exclusively produced *Paranthropus* specimens, and this specimen has been assigned to this genus (Susman and Brain, 1988; Susman et al., 1989; Susman et al., 2001, Zipfel and Kidd, 2006).

Other Specimens

A number of metatarsal specimens in this study have not been given a definite genus and/or species. Their approximate affiliation is determined by their provenience. The right MT 1 specimen SK 1813 was examined. It was recovered from the faunal collection at the Transvaal Museum, Pretoria and could be from members 1 or 2 (Susman and de Ruiter, 2004). Its description makes it a likely candidate for the genus *Paranthropus* (Susman and de Ruiter, 2004; Zipfel and Kidd, 2006). The left MT 2 specimen SKX 247 from member 2 at Swartkrans could be either *Paranthropus* or *Homo* cf. *erectus*; Susman et al. describe the specimen as consistent with modern humans (Susman et al., 1989). This specimen was initially described as an MT 3, but Susman et al. later state that the specimen is actually a MT 2 (Susman et al., 2001). The MT 1 specimens Stw 562 and Stw 595 were examined. They are both from Sterkfontein member 4, and were described but not assigned a genus or species (Deloison, 2003).

The specimen Stw 595c, a right MT 2, from Sterkfontein member 4 was examined. This specimen was provided courtesy of Ron Clarke, and has not been described in any publication. A left MT 2, Stw 89 was examined (Deloison, 2003). This specimen is from Sterkfontein member 5. Another left MT 2 was examined, Stw 377. This specimen could be from either member 4 or 5. The following MT 3s were examined, recovered from Sterkfontein member 4: Stw 435, Stw 387, Stw 477, Stw 388 and Stw 496. All of these except Stw 238 were described by Deloison (2003). The MT 4 specimens Stw 485 and Stw 628 were examined. Both were recovered from Sterkfontein member 4. However, Stw 628 has not yet been described and was provided courtesy of Ron Clarke. Finally, the Stw 114/115 MT 5 was examined. It has been described previously, and belongs to member 4 or member 5 (Deloison 2003, Zipfel et al., 2009). It should be noted that Sterkfontein member 4 may bear specimens belonging to the genera *Australopithecus*, *Paranthropus*, or *Homo* cf. *habilis*. Member 5 is later and may bear *Paranthropus* or *Homo* cf. *erectus*. Specimens that may be from either of these members could possibly belong to any of these genera.

Data Collection

All specimens were first digitized using a Next Engine laser scanner (nextengine.com). This laser scanner is becoming a common tool in anthropological research (Tocheri et al., 2007). The scanner provides accuracy to 0.127 millimeters with 400 landmarks per square inch. A laser scanner is used instead of a microscribe for two reasons. The first reason is that the sizes of the articular surfaces examined are small, making use of a microscribe for recording landmarks difficult. Second, a laser scanner allows collection of far more landmarks over an entire joint surface, from which a smaller sample can be extracted for analysis. This allows greater flexibility and accuracy in landmark choice.

Laser scans of each specimen were exported to PLY files for use with the program Landmark. Landmark is a piece of data manipulation software produced in a joint effort by the Institute of Data Analysis and Visualization at the University of California, Davis, and NYCEP (the New York Consortium in Evolutionary Primatology). The software was used to apply landmarks to the imported PLY files of the specimens. Landmarks are applied on enlarged images, using an interface that allows close application of individual landmarks, and in this case curves with landmarks applied along those curves at equal intervals. In this way the landmarks applied take a smaller sample of the surface data in each laser scan. Once the landmarks were applied, the locations of the landmarks for each specimen were exported as a set of 3D landmarks to create an input data file to be analyzed with the data processing software *morphologika* © (O'Higgins and Jones, 1998; 2006). This program was used to conduct a principal components analysis and to construct wire frames for comparing morphology as it is reflected on different principal component axes. Additional analyses were conducted using NCSS, as described below.

Landmarks

Specific landmarks vary between the metatarsals due to morphological differences between the proximal articular surfaces of the metatarsals. Landmarks on the periphery of the surfaces in this study are defined by their location at the articular surface borders, where subchondral bone and cortical bone meet. In many cases these articular surfaces do not have points of reference that lend themselves to analysis with Type 1 or Type 2 landmarks, as defined by Bookstein (1991) and discussed by Zelditch et al. (2004). Most of the landmarks in this study are Type 2 or 3, with some Type 1 landmarks on MT 2, MT 3, and MT 4 where the proximal surface intersects with intermetatarsal facets. A Type 1 landmark is a landmark defined by the location from which two or more structures meet, if they meet at a precise location. An example of a Type 1 landmark is the craniometric point bregma, where the coronal suture and the sagittal suture meet. A Type 2 landmark is a point defined as the end point of a structure, such as the tip of a process or tooth, or an extreme point of curvature on a small structure. A Type 3 landmark is defined as an extreme point of curvature on a structure in reference to another point. For example, the furthest point on the metatarsal head from the proximal articular surface.

Landmark locations were chosen to maximize the information gathered about the overall outline shape of the articular surfaces, and multiple landmarks over the articular surface itself are chosen to capture curvature (concavity, convexity, "flatness") and overall shape, relative to the boundaries of the surface. The landmarks are discussed below.

Metatarsal 1 Landmarks

Landmarks for three-dimensional analysis of the proximal articular surface of MT 1 on the periphery of the surface are defined as follows: most dorsal point of the surface; most plantar point of the surface; most lateral point of the dorsal aspect; most lateral point of the plantar aspect; most medial point of the lateral invagination; most medial point of the dorsal aspect; most medial point of the plantar aspect, most lateral point of the medial invagination. Several landmarks are also taken between these extreme points. In addition, nine landmarks within the articular surface will be selected. There are three landmarks spaced evenly between each medial and lateral landmark at the dorsal, plantar, and invaginated aspects. This landmark scheme is similar to that used by Proctor et al. (2008), and is being revisited here to include original fossil specimens, most of which were not part of that previous study, and to include habitually unshod individuals. See Figure 4.2 and Table 4.4.

Metatarsal 2 Landmarks

Landmarks for three-dimensional analysis of the proximal articular surface of MT 2 on the periphery of the surface are defined as follows: the points at which the proximal surface intersects with the dorsal and plantar margins of articular surface for the lateral and medial cuneiforms; the most plantar point of the surface, and several intermittent places between these defined landmarks on the periphery of the surface. Three landmarks are spaced evenly between each of the medial and lateral surface points. These landmarks are chosen to reveal the overall shape of the articular surface, which is very important to the hypotheses tested, and to capture joint surface shape. See Figure 4.3 and Table 4.5.

Metatarsal 3 Landmarks

The MT 3 proximal articular surface is morphologically very similar to the MT 2 surface, and the same landmark scheme will be used but adjusted to account for the different intermetatarsal facets. See Figure 4.4 and Table 4.6.

Metatarsal 4 Landmarks

Landmarks for three-dimensional analysis of the proximal articular surface of MT 4 on the periphery of the surface are defined as follows: most medial point at the dorsal aspect, most medial point at the plantar aspect; most lateral point at the dorsal aspect; most medial point at the plantar aspect. In addition, five landmarks are placed on the articular surface edge between the most medial and lateral aspects at the dorsal, plantar, medial, and lateral sides of the surface. Five additional landmarks are placed on the articular surface, spaced evenly between landmarks on the dorsal and plantar surface edges. These landmarks are selected to most importantly reveal articular surface curvature (or lack thereof). See Figure 4.5 and Table 4.7.

Metatarsal 5 Landmarks

Landmarks for three-dimensional analysis of the proximal articular surface of MT 5 on the periphery of the surface are defined as follows: proximal surface at the intersection with the dorsal and plantar margins of the intermetatarsal facet for MT 4;

most lateral point of the surface. In addition, three landmarks are evenly spaced between these landmarks on the surface edge at the dorsal, plantar, and medial aspects. Finally, between the spaced dorsal and plantar landmarks on the surface edge, three additional landmarks are placed to show curvature and/or flatness. See Figure 4.6 and Table 4.8.

Table 4.2 Fossil Specimens Examined in this Study

	Taxon	**Element**	**Location**	**Observation**
A. L. 333-54	*A. afarensis*	MT 1	Hadar, Ethiopia	cast
A. L. 333-78	*A. afarensis*	MT 5	Hadar, Ethiopia	cast
A. L. 333-13	*A. afarensis*	MT 5	Hadar, Ethiopia	cast
Stw 573a	*A.* cf *africanus*	MT 1	Sterkfontein member 4	original
Stw 573d	*A.* cf *africanus*	MT 2	Sterkfontein member 4	original
SKX 5017	*P. robustus*	MT 1	Swartkrans member 1 lower bank	original
SK 1813	*Paranthropus* or *Homo*	MT 1 (R)	Swartkrans member 1 or member 2	original
SKX 247	*Paranthropus* or *Homo*	MT 2	Swartkrans member 2	original
Stw 562	*Paranthropus?* *A. africanus?*	MT 1 (R)	Sterkfontein member 4	original
Stw 595	*Paranthropus?*	MT 1 (R)	Sterkfontein member 4	original
Stw 595c	*Paranthropus?*	MT 2 (R)	Sterkfontein member 4	original
Stw 89	*Homo?*	MT 2	Sterkfontein member 4	original
Stw 377	Unassigned	MT 2	Sterkfontein member 4	original
Stw 387	Unassigned	MT 3	Sterkfontein member 4 or member 5	original

Table 4.2 continued

	Taxon	**Element**	**Location**	**Observation**
Stw 435	Unassigned	MT 3 (R)	Sterkfontein member 4	original
Stw 477	Unassigned	MT 3	Sterkfontein member 4	original
Stw 388	Unassigned	MT 3 (R)	Sterkfontein member 4	original
Stw 496	Unassigned	MT 3	Sterkfontein member 4	original
Stw 485	Unassigned	MT 4	Sterkfontein member 4	original
Stw 628	Unassigned	MT 4	Sterkfontein member 4	original
Stw 114/115	Unassigned	MT 5 (R)	Sterkfontein member 4 or 5	original
OH 8	*Homo habilis?*	MT 1	Olduvai Gorge, FLK NN level 3	original
OH 8	*Homo habilis?*	MT 2	Olduvai Gorge, FLK NN level 3	original
OH 8	*Homo habilis?*	MT 3	Olduvai Gorge, FLK NN level 3	original
OH 8	*Homo habilis?*	MT 4	Olduvai Gorge, FLK NN level 3	original
OH 8	*Homo habilis?*	MT 5	Olduvai Gorge, FLK NN level 3	original

Table 4.3 Materials and Collection Locations

Specimen	Location	N
Homo (shod)	U. Iowa, Cleveland Museum of Natural History	30-34
Homo (unshod)	South African Museum, Cape Town; National Museum, Bloemfontein	31-42
Gorilla	Cleveland Museum of Natural History	30-31
Pan	Cleveland Museum of Natural History & Field Museum of Natural History	30
Hylobates	Museum of Comp. Zoology, Harvard University	29-30
OH 8	Tanzania (scans provided by Jerry DeSilva)	1 (MT 1-MT 5)
SKX 5017	Transvaal Museum	1 (MT 1)
SK 1813	Transvaal Museum	1 (MT 1)
SKX 247	Transvaal Museum	1 (MT 3)
Stw 89	University of Witwatersrand	1 (MT 2)
Stw 377	University of Witwatersrand	1 (MT 2)
Stw 387	University of Witwatersrand	1 (MT 3)
Stw 388	University of Witwatersrand	1 (MT 3)
Stw 435	University of Witwatersrand	1 (MT 3)
Stw 477	University of Witwatersrand	1 (MT 3)
Stw 485	University of Witwatersrand	1 (MT 4)
Stw 496	University of Witwatersrand	1 (MT 3)
Stw 562	University of Witwatersrand	1 (MT 1)
Stw 573a, d	University of Witwatersrand	2 (MT 1, MT 2)
Stw 595, c	University of Witwatersrand	2 (MT 1, MT 2)
Stw 628	University of Witwatersrand	1 (MT 4)
Stw 114/115	University of Witwatersrand	1 (MT 5)

Table 4.3 continued

Specimen	**Location**	**N**
A.L. 333-54	Ethiopian National Museum (casts provided by the Cleveland Museum of Natural History)	1 (MT 1)
A.L. 333-13	Ethiopian National Museum (casts provided by the Cleveland Museum of Natural History)	1 (MT 5)
A.L. 333-78	Ethiopian National Museum (casts provided by the Cleveland Museum of Natural History)	1 (MT 5)

Data Analysis

Using *morphologika*, a Generalized Procrustes Analysis was conducted on the landmark data (Gower, 1975; Goodall, 1991). Generalized Procrustes Analysis places the coordinate landmarks of all cases on the same Cartesian grid in relationship to one another, and scales the landmarks by mathematically placing them as close to one another as possible without changing the overall relationship of the landmarks within a case. The program calculates a centroid landmark, and the Euclidean distance between the centroid and each landmark coordinate for the points in each case. Centroid size for each case is then calculated by summing the square of the distances between the centroid and the landmarks, and then taking the square root of these summed distances. This operation eliminates negative coordinate numbers. The original landmark coordinates are then divided by the calculated centroid size. The new landmark data for the cases are then superimposed using the centroid locations as a reference, and homologous landmarks between cases are fitted for maximum congruence. The result is a set of cases within Kendal's shape space that can be compared on the same coordinate grid while controlling for size (Harcourt-Smith, 2002; Kendal, 1984; O'Higgins and Jones, 1998).

Morphologika was also used to implement a principal components analysis (PCA) and to generate three-dimensional wire frame renditions of the articular surface morphology as reflected by associated principal components scores. These renditions are used to demonstrate the morphology that corresponds to principal component values and to compare differences in morphology at these values.

Since principal components analysis does not determine statistically significant differences between groups, an ANOVA was conducted on the principle components scores for each species group to determine whether differences in group means occur in the sample (Zelditch et al., 2004). In addition, a Tukey-Kramer (post hoc) Test was used to determine differences between specific group means. In many cases groups overlap to varying degrees on principle component axes, and this allows interpretation of which groups are statistically different independent of how they appear to group.

To test for relationships between size and shape, a regression analysis and/or ANCOVA was conducted between groups with different sizes and different principle components scores. The ANCOVA analysis included species group names as a variable to observe to what degree R^2 values increased compared to regression analysis using size and shape alone. Since each species group in this study have differing modes of locomotion, species groups can serve as a proxy for locomotion type. Importantly, each group with a different mode of locomotion also happens to be different in body size. This comparison can show whether belonging to a specific group alone is more important than size.

To evaluate observation error, each metatarsal for one case of *Gorilla gorilla* was scanned and processed five additional times. Repeated measures above four additional measurements do not yield a significant amount of additional error observation (Arnqvist and Mårtensson, 1998). The repeated measurements for this study were compared to the *Gorilla gorilla* sample group to compare variance as reflected in partial warp scores from a principal components analysis. When repeated measures cluster closely on principle component plots, this is an indication of a high degree of repeatability in the sampling method (Lockwood et al., 2002; Proctor et al., 2008; Maddux and Franciscus, 2009).

Figure 4.2 MT 1 landmarks

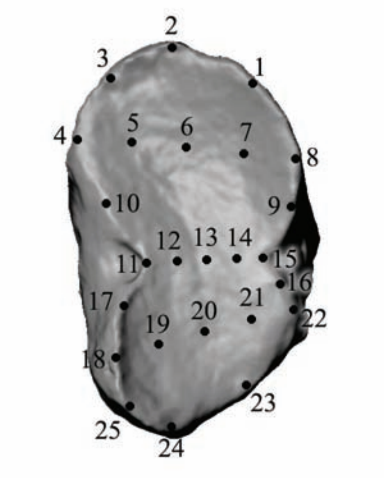


Figure 4.3 MT 2 Landmarks

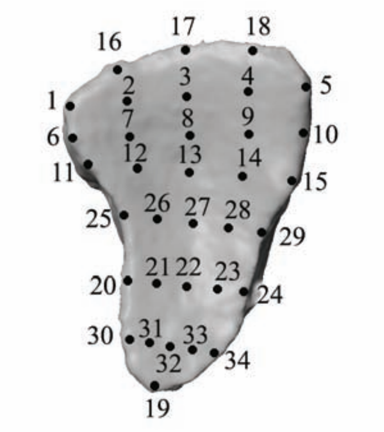


Figure 4.4 MT 3 Landmarks

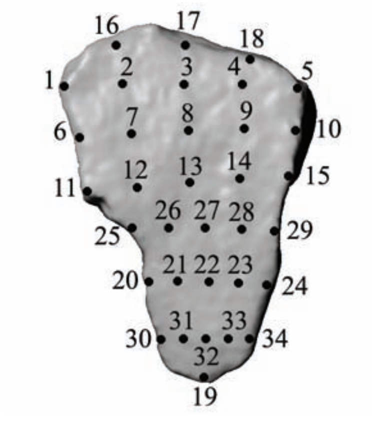


Figure 4.5 MT 4 Landmarks

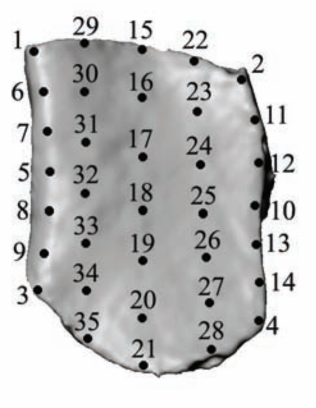


Figure 4.6 MT 5 Landmarks

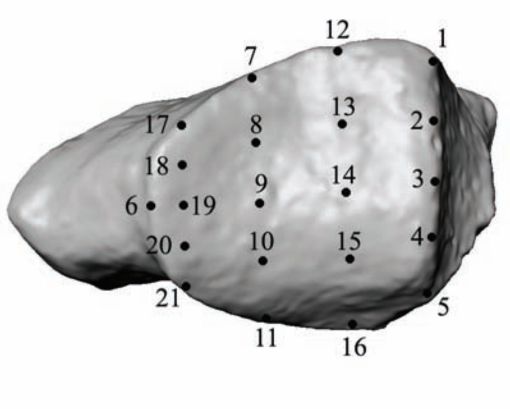


Table 4.4 Description of landmarks on the proximal MT 1 articular surface

Number	Landmark description
1	Midpoint between 2 and 8
2	Most dorsal point of the surface
3	Midpoint between 2 and 4
4	Most lateral point of the dorsal aspect
5	Midpoint between 4 and 6
6	Midpoint between 4 and 8
7	Midpoint between 6 and 8
8	Most medial point of the dorsal aspect
9	Midpoint between 8 and 15
10	Midpoint between 4 and 11
11	The narrowest point of the mid-lateral indentation
12	Midpoint between 11 and 13
13	Midpoint between 11 and 15
14	Midpoint between 13 and 15
15	The narrowest point of the mid-medial indentation
16	Midpoint between 15 and 22
17	Midpoint between 11 and 18
18	Most lateral point of the plantar aspect
19	Midpoint between 18 and 20
20	Midpoint between 18 and 22
21	Midpoint between 20 and 22
22	Most lateral point of the plantar aspect
23	Midpoint between 22 and 24
24	Most plantar point of the surface
25	Midpoint between 18 and 24

Table 4.5 Description of landmarks on the proximal MT 2 articular surface

Number	Landmark description
1	Articular surface intersection with dorsal margin of dorsal facet for lateral cuneiform
2	Midpoint between 1 and 3
3	Midpoint between 1 and 5
4	Midpoint between 3 and 5
5	Articular surface intersection with dorsal margin of facet for medial cuneiform
6	Midpoint of surface edge between 1 and 11
7	Midpoint between 6 and 8
8	Midpoint between 6 and 10
9	Midpoint between 8 and 10
10	Midpoint of surface edge between 5 and 15
11	Articular surface intersection with plantar margin of dorsal facet for lateral cuneiform
12	Midpoint between 11 and 13
13	Midpoint between 11 and 15
14	Midpoint between 13 and 15
15	Articular surface intersection with plantar margin of facet for medial cuneiform
16	Midpoint of surface edge between 1 and 17
17	Midpoint of surface edge between 5 and 17
18	Midpoint of surface edge between 5 and 15
19	Most plantar point of the articular surface
20	Midpoint of surface edge between 11 and 19
21	Midpoint between 20 and 22

Table 4.5 continued

22	Midpoint between 20 and 24
23	Midpoint between 22 and 24
24	Midpoint of surface edge between 15 and 19
25	Midpoint of surface edge between 11 and 20
26	Midpoint between 25 and 27
27	Midpoint between 25 and 29
28	Midpoint between 27 and 29
29	Midpoint of surface edge between 15 and 24
30	Midpoint of surface edge between 19 and 20
31	Midpoint between 30 and 32
32	Midpoint between 30 and 34
33	Midpoint between 32 and 34
34	Midpoint of surface edge between 19 and 24

Table 4.6 MT 3 Landmarks

Number	Landmark description
1	Articular surface intersection with dorsal margin of dorsal facet for MT 4
2	Midpoint between 1 and 3
3	Midpoint between 1 and 5
4	Midpoint between 3 and 5
5	Articular surface intersection with dorsal margin of facet for MT 2
6	Midpoint of surface edge between 1 and 11
7	Midpoint between 6 and 8
8	Midpoint between 6 and 10
9	Midpoint between 8 and 10
10	Midpoint of surface edge between 5 and 15
11	Articular surface intersection with plantar margin of dorsal facet for MT 4
12	Midpoint between 11 and 13
13	Midpoint between 11 and 15
14	Midpoint between 13 and 15
15	Articular surface intersection with plantar margin of facet for MT 2
16	Midpoint of surface edge between 1 and 17
17	Midpoint of surface edge between 5 and 17
18	Midpoint of surface edge between 5 and 15
19	Most plantar point of the articular surface
20	Midpoint of surface edge between 11 and 19
21	Midpoint between 20 and 22

Table 4.6 continued

22	Midpoint between 20 and 24
23	Midpoint between 22 and 24
24	Midpoint of surface edge between 15 and 19
25	Midpoint of surface edge between 11 and 20
26	Midpoint between 25 and 27
27	Midpoint between 25 and 29
28	Midpoint between 27 and 29
29	Midpoint of surface edge between 15 and 24
30	Midpoint of surface edge between 19 and 20
31	Midpoint between 30 and 32
32	Midpoint between 30 and 34
33	Midpoint between 32 and 34
34	Midpoint of surface edge between 19 and 24

Table 4.7 MT 4 Landmarks

Number	Landmark description
1	Most lateral point of the dorsal aspect
2	Most medial point of the dorsal aspect
3	Most lateral point of the plantar aspect
4	Most medial point of the plantar aspect
5	Midpoint between 1 and 3
6	A point 1/3 between 1 and 5
7	A point 2/3 between 1 and 5
8	A point 1/3 between 5 and 3
9	A point 2/3 between 5 and 3
10	Midpoint between 2 and 4
11	A point 1/3 between 2 and 10
12	A point 2/3 between 2 and 10
13	A point 1/3 between 10 and 4
14	A point 2/3 between 10 and 4
15	Midpoint between 1 and 2
16	A point 1/3 between 15 and 18
17	A point 2/3 between 15 and 18
18	Midpoint between 15 and 21
19	A point 1/3 between 18 and 21
20	A point 2/3 between 18 and 21
21	Midpoint between 3 and 4
22	Midpoint between 2 and 15
23	A point 1/3 between 22 and 25
24	A point 2/3 between 22 and 25
25	Midpoint between 22 and 28

Table 4.7 continued

26	A point 1/3 between 25 and 28
27	A point 2/3 between 25 and 28
28	Midpoint between 4 and 21
29	Midpoint between 1 and 15
30	A point 1/3 between 29 and 32
31	A point 2/3 between 29 and 32
32	Midpoint between 29 and 35
33	A point 1/3 between 32 and 35
34	A point 2/3 between 32 and 35
35	Midpoint between 3 and 21

Table 4.8 MT 5 Landmarks

Number	Landmark description
1	Articular surface intersection with dorsal margin of facet for MT 4
2	Midpoint between 1 and 3
3	Midpoint between 1 and 5
4	Midpoint between 3 and 5
5	Articular surface intersection with plantar margin of facet for MT 4
6	Most medial point of the articular surface
7	Midpoint between 17 and 1
8	Midpoint between 7 and 9
9	Midpoint between 7 and 11
10	Midpoint between 9 and 11
11	Midpoint between 6 and 5
12	Midpoint between 7 and 1
13	Midpoint between 12 and 14
14	Midpoint between 12 and 16
15	Midpoint between 14 and 16
16	Midpoint between 11 and 5
17	Midpoint between 6 and 7
18	Midpoint between 17 and 19
19	Midpoint between 17 and 21
20	Midpoint between 19 and 21
21	Midpoint between 6 and 11

CHAPTER 5: ASSESSMENT OF OBSERVATION ERROR

Methodology for Assessing Observation Error

In order to assess the degree to which observation error might influence the interpretation of the principle components analysis in this study, one *Gorilla* specimen was scanned with the Next Engine laser scanner five separate times for each metatarsal. Landmarks were applied to each separate laser scan according to the methods discussed previously for each metatarsal. Further, the landmarks were applied on separate days. The specimen used for the repeated measures in these analyses for assessing observation error was not included in the analyses reported in the following chapters to test for differences in articular surface shape of the proximal metatarsals. The landmarks for each repeated measure were combined with the other *Gorilla* specimens and subjected to a principle components analysis. The relative proximity of the repeated measures to one another in scatter plots is used to assess the repeatability of the methodology. This methodology has been successful employed previously in peer-reviewed journal articles, and is one accepted method for assessing repeatability in these kinds of studies (Lockwood et al., 2002; Proctor et al., 2008; Maddux and Franciscus, 2009). The primary goal of this assessment is to determine whether within a species group a particular specimen can reliably be sampled. The scatter plots presented below for each metatarsal show the same axes used in the morphological analyses reported in subsequent chapters.

Repeated Measures for Metatarsal 1

The following scatter plots in Figures 5.1, 5.2, and 5.3 show the placement of the repeated measure with the *Gorilla* sample (n = 30). The results are comparable to those in the study by Proctor et al. (2008) for assessing observation error of the landmarks for the MT 1 proximal articular surface. The repeated measures group closely on the PC 1, PC 2, PC 3, and PC 4 axes. Refer to Table 5.1 for the percentage of variation explained by each PC axis.

Table 5.1 Percentage of variation explained by each MT 1 PC axis

PC 1	PC 2	PC 3	PC 4
31%	14%	13%	8%

Figure 5.1 Scatter plot of MT 1 observation error for PC 1 and PC 2

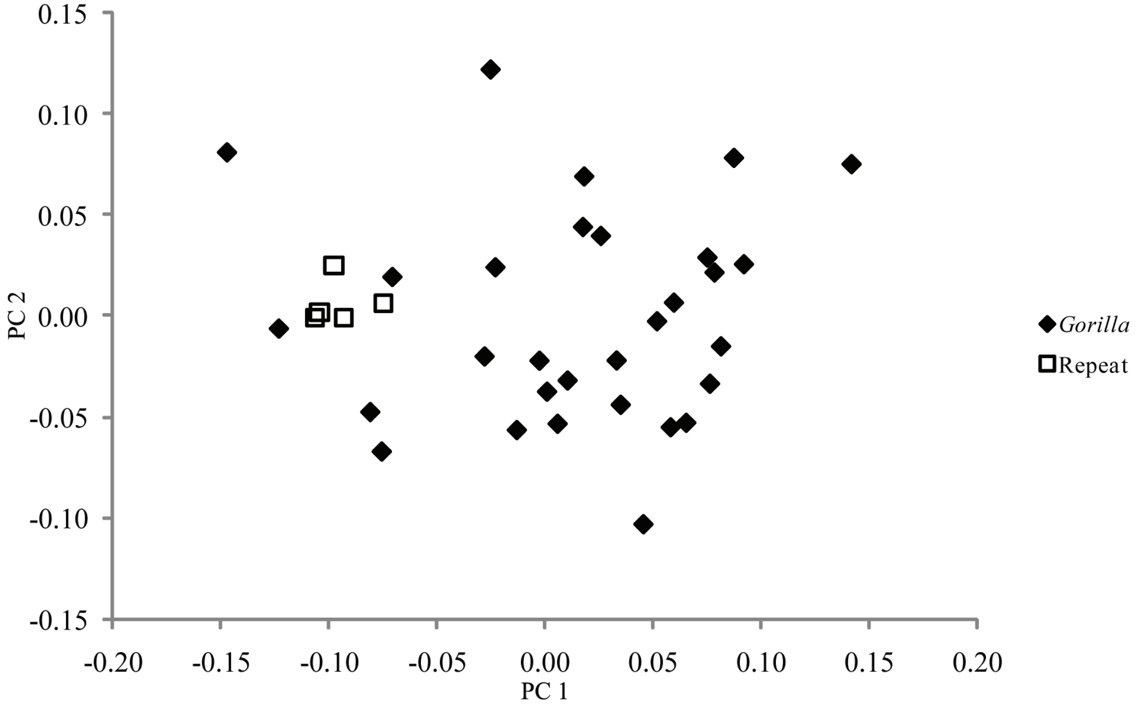


Figure 5.2 Scatter plot of MT 1 observation error for PC 1 and PC 3

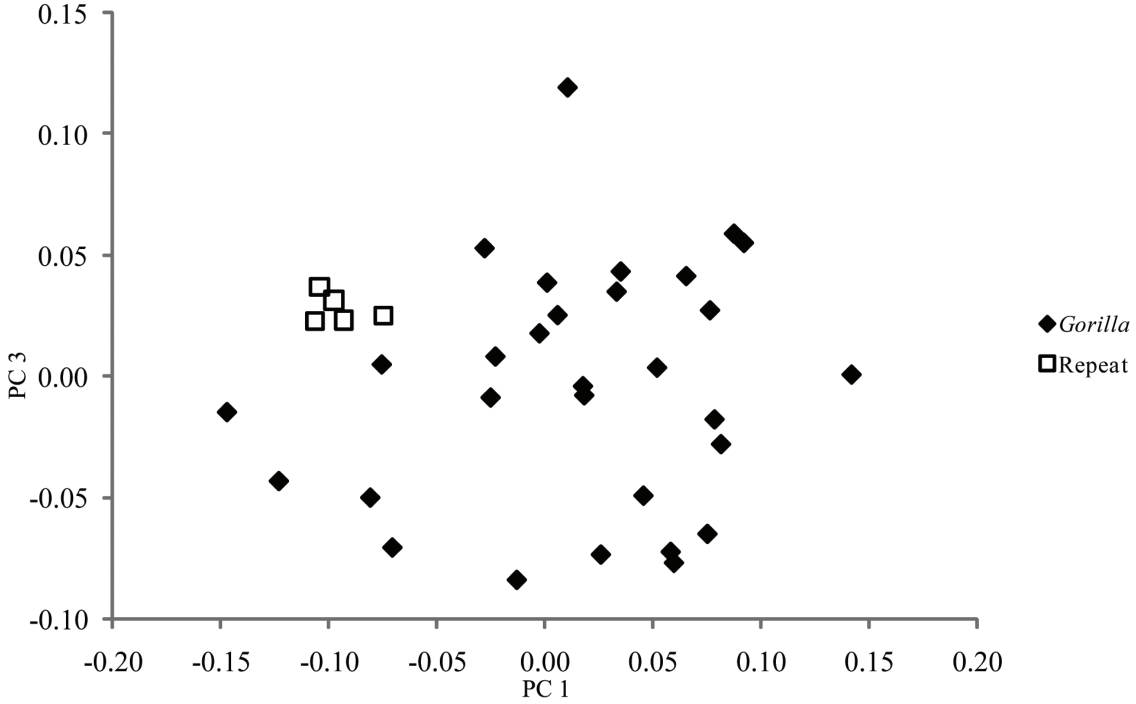
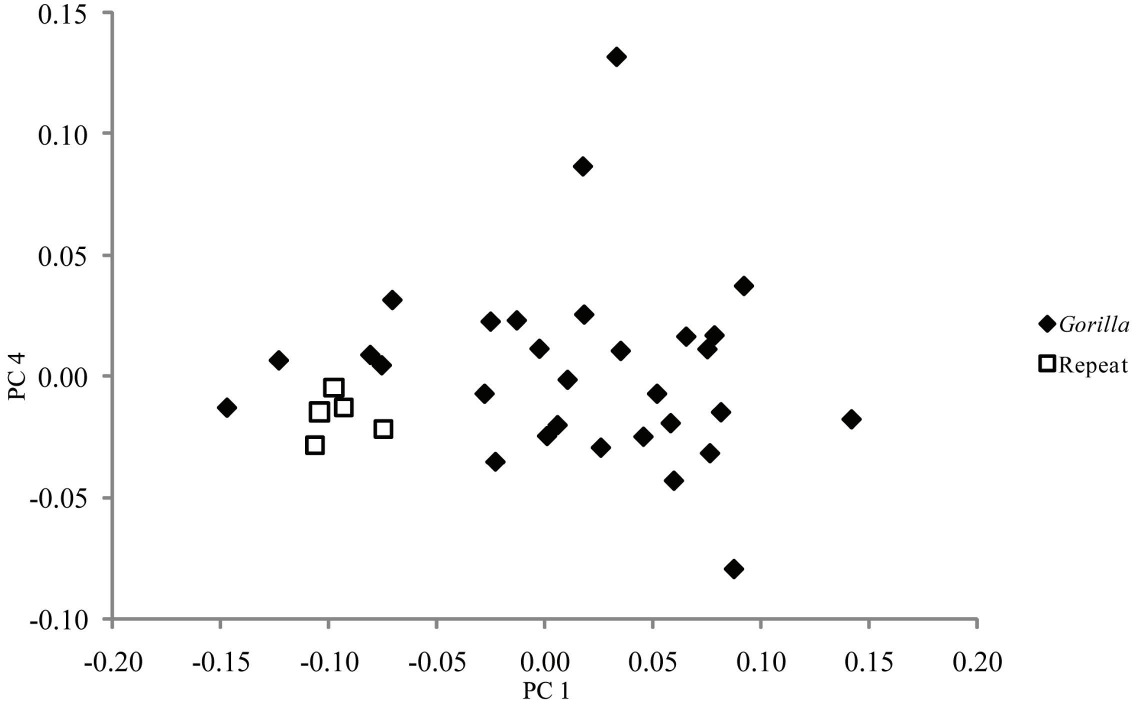


Figure 5.3 Scatter plot of MT 1 observation error for PC 1 and PC 4



Repeated Measures for Metatarsal 2

The scatter plots displayed in Figures 5.4, 5.5, and 5.6 show the placement of the repeated measure sample compared to the *Gorilla* sample (n = 30). The repeated measures group very closely on the PC 1, PC 2, PC 3, and PC 4 axes. This indicates a high degree of repeatability of the measures. See Table 5.2 for the variation explained by each axis.

Table 5.2 Percentage of variation explained by each MT 2 PC axis

PC 1	PC 2	PC 3	PC 4
21%	15%	15%	11%

Figure 5.4 Scatter plot of MT 2 observation error for PC 1 and PC 2

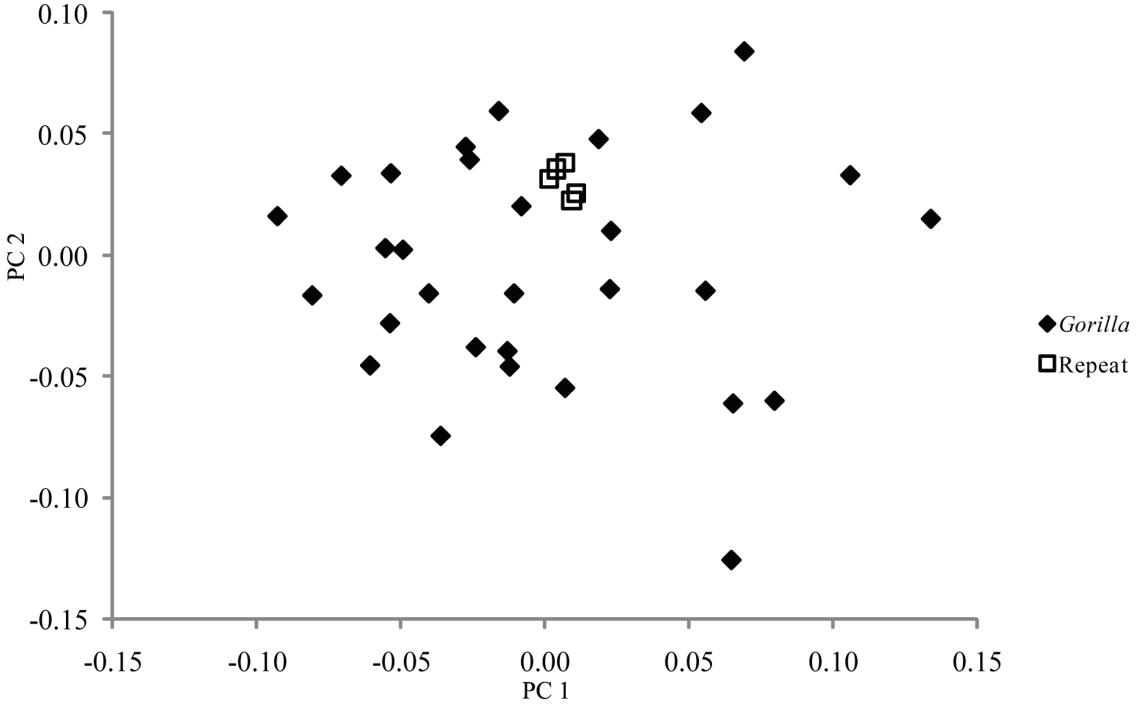


Figure 5.5 Scatter plot of MT 2 observation error for PC 1 and PC 3

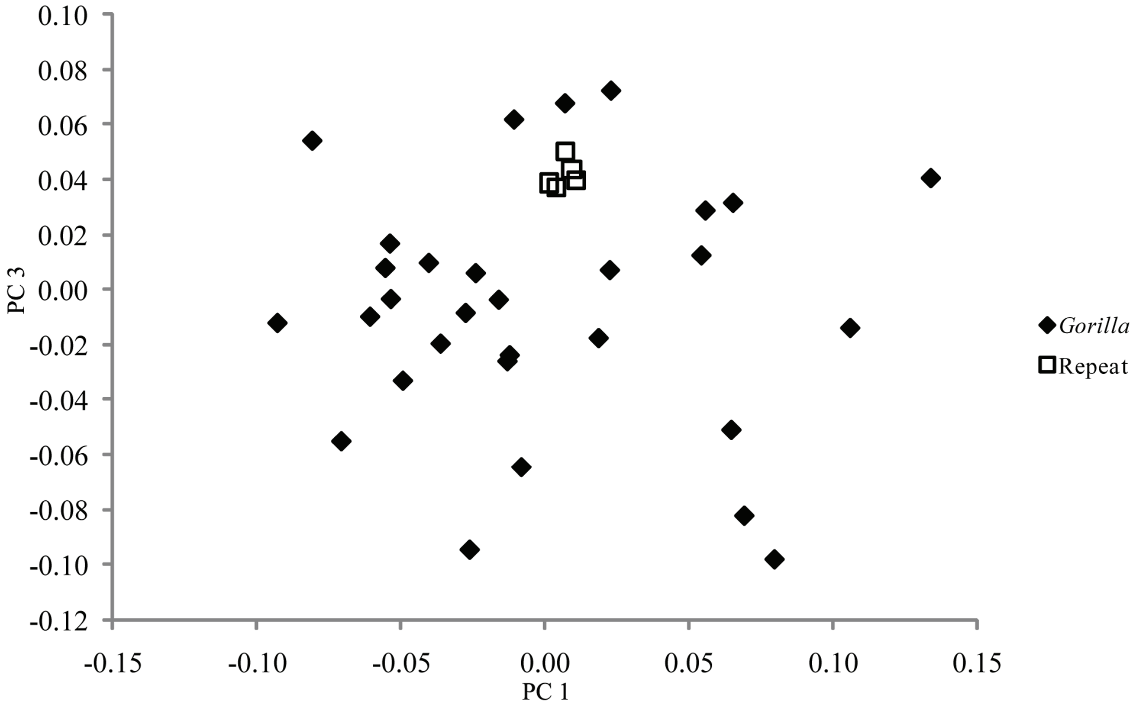
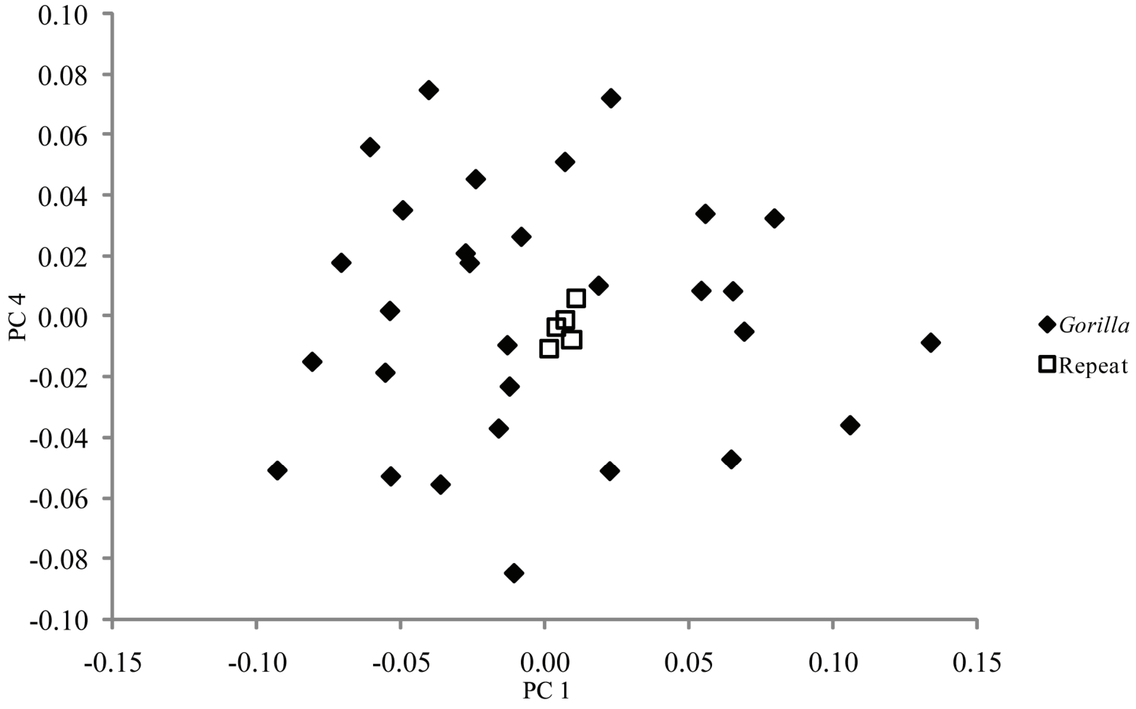


Figure 5.6 Scatter plot of MT 2 observation error for PC 1 and PC 4



Repeated Measures for Metatarsal 3

The scatter plots for MT 4 shown in Figures 5.7 and 5.8 compare the instances of repeated measures to the *Gorilla* sample (n = 30). The repeated measures group closely on the PC 1, PC 2, and PC 3 axes. There is a high degree of repeatability for the placement of landmarks on the MT 3 proximal articular surface. Refer to Table 5.3 for the variation explained by each axis.

Table 5.3 Percentage of variation explained by each MT 3 PC axis

PC 1	PC 2	PC 3
24%	21%	15%

Figure 5.7 Scatter plot of MT 3 observation error for PC 1 and PC 2

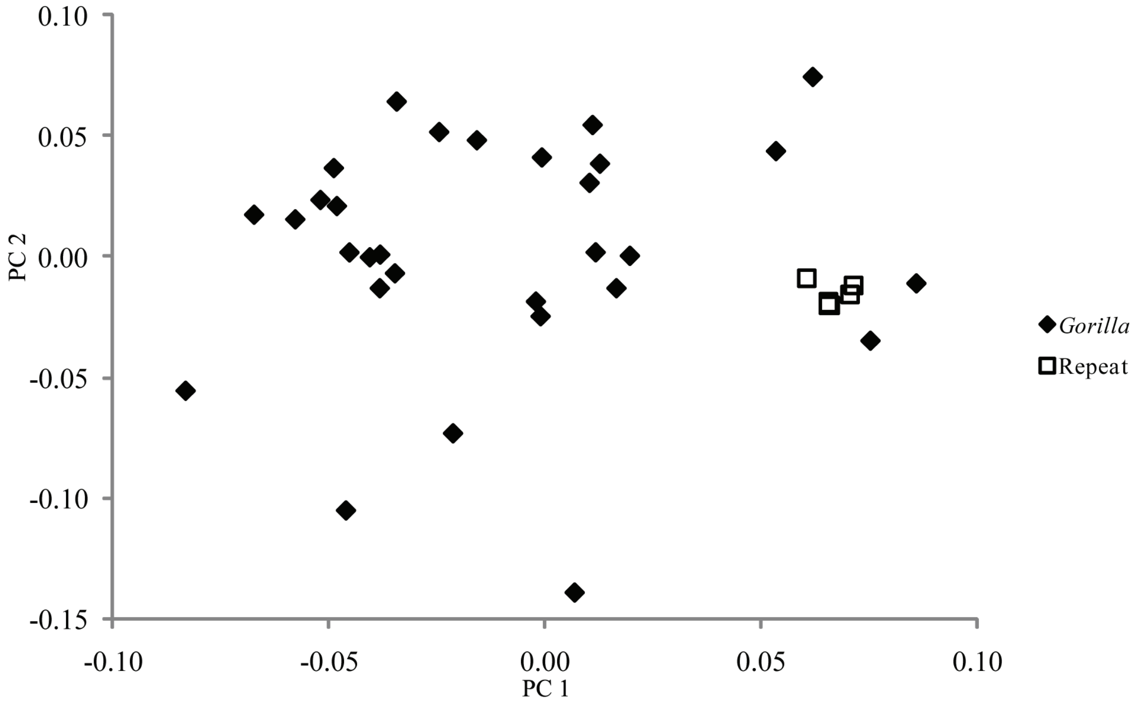
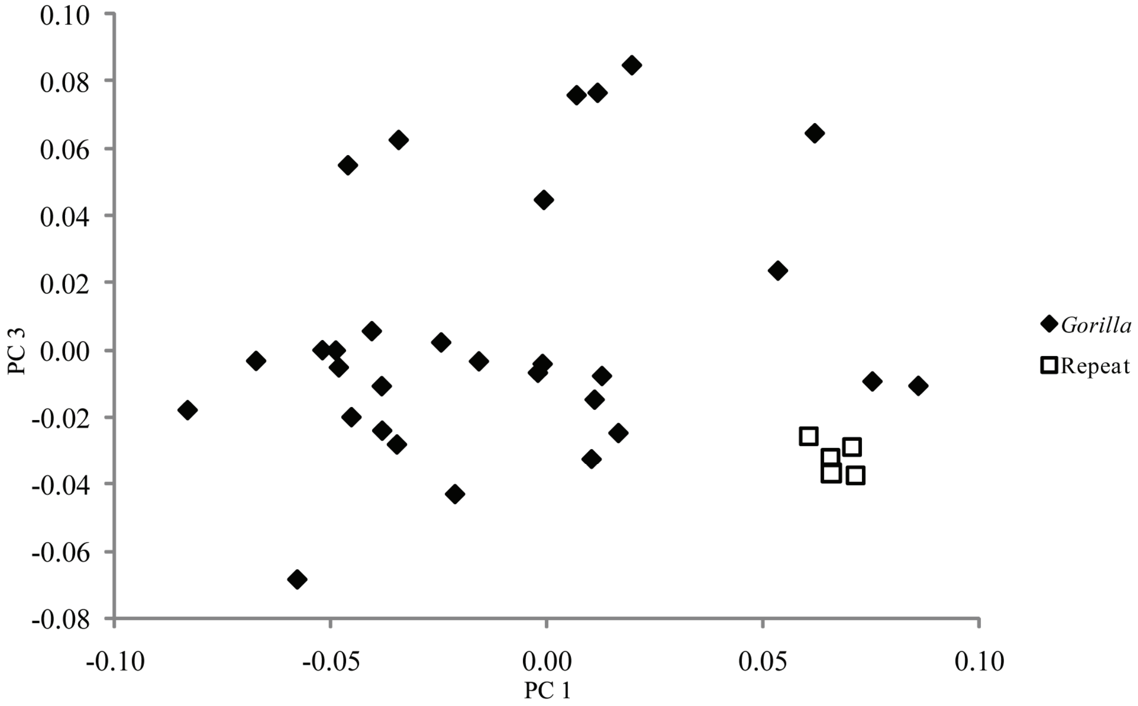


Figure 5.8 Scatter plot of MT 3 observation error for PC 1 and PC 3



Repeated Measures for Metatarsal 4

Scatter plots for MT 4 are presented in Figures 5.9 and 5.10 to compare the repeated measures to the *Gorilla* sample (n = 30). A high degree of repeatability for the placement of landmarks on the MT 4 proximal articular surface is indicated by how closely the repeated measure group on the PC 1, PC 2, and PC 3 axes. See Table 5.4 for the variation explained by each axis.

Table 5.4 Percentage of variation explained by each MT 3 PC axis

PC 1	PC 2	PC 3
33%	17%	12%

Figure 5.9 Scatter plot of MT 4 observation error for PC 1 and PC 2

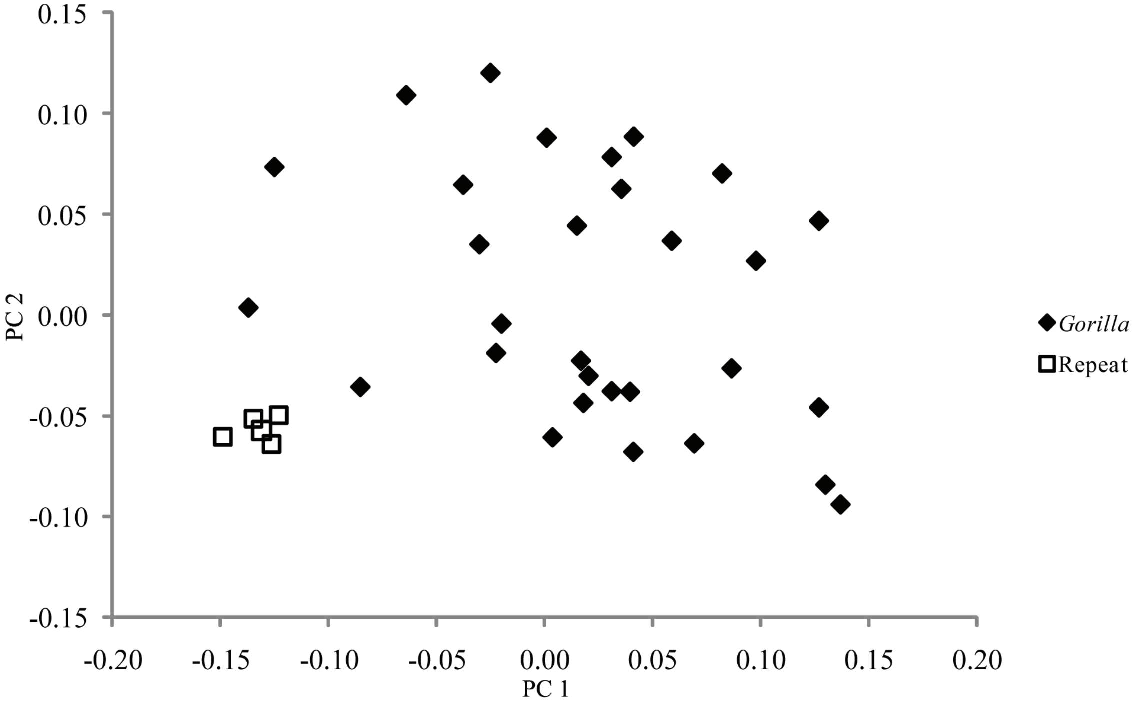
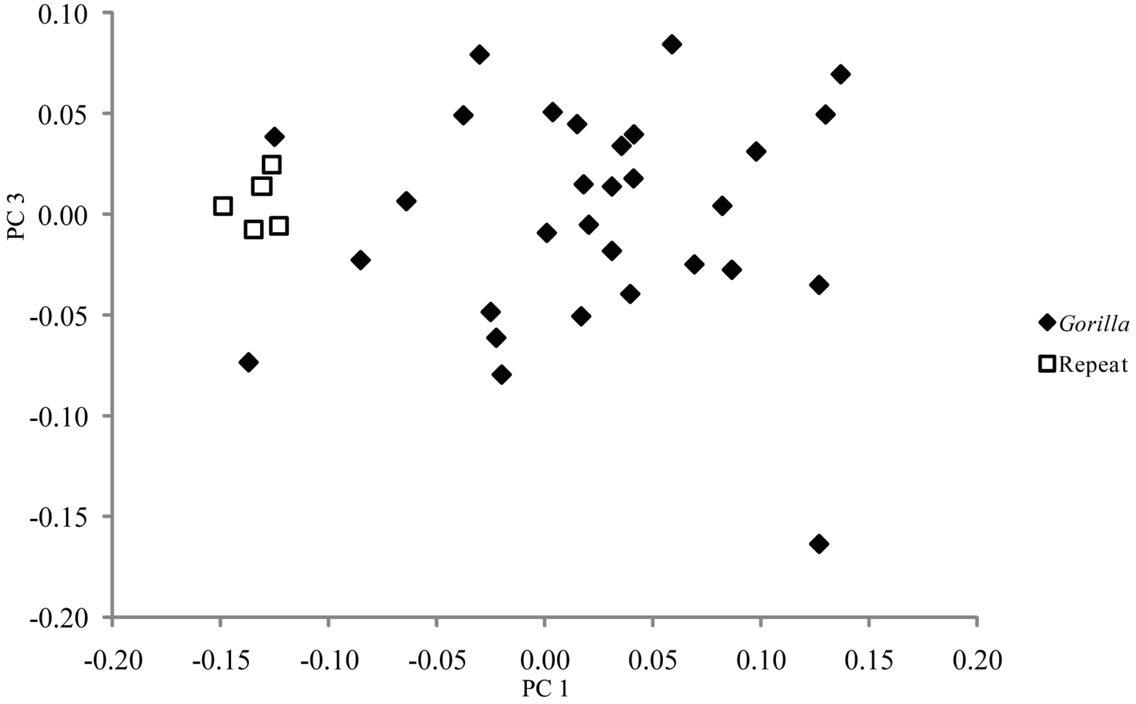


Figure 5.10 Scatter plot of MT 4 observation error for PC 1 and PC 3



Repeated Measures for Metatarsal 5

The scatter plots in Figures 5.11 and 5.12 present the grouping of the instances of the repeated measure compared to the *Gorilla* sample (n = 30). The repeated measures group closely on each axis; this indicates a high degree of methodological repeatability. Refer to Table 5.5 for the percentage of variation explained by each PC axis.

Table 5.5 Percentage of variation explained by each MT 5 PC axis

PC 1	PC 2	PC 3
38%	17%	13%

Figure 5.11 Scatter plot of MT 5 observation error for PC 1 and PC 2

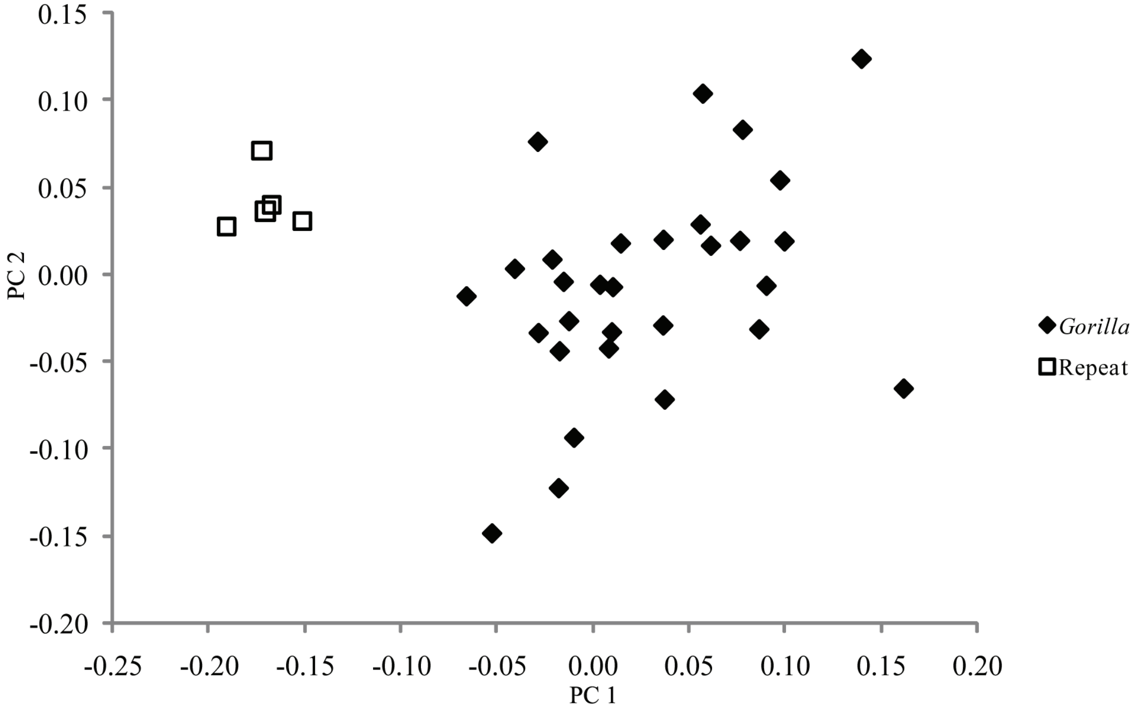
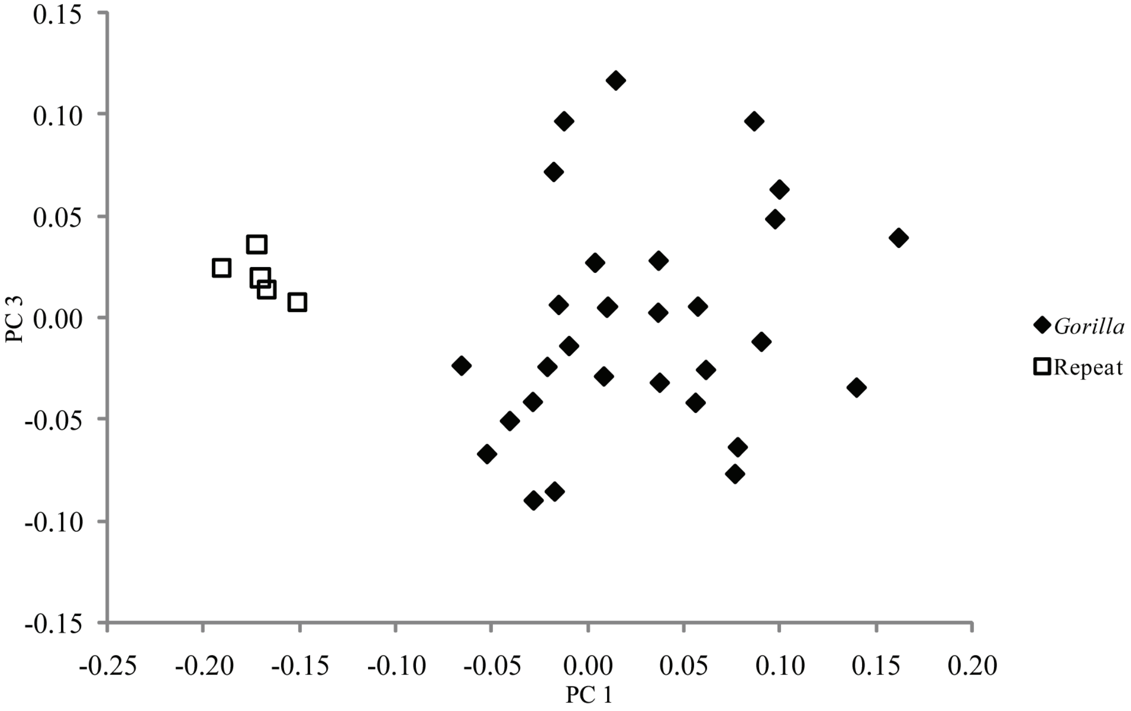


Figure 5.12 Scatter plot of MT 5 observation error for PC 1 and PC 3



CHAPTER 6: ANALYSIS OF METATARSAL 1

Interspecific MT 1 Shape Variation

A principal components analysis (PCA) was conducted to determine the most important trends in articular surface shape and whether species and shape can be differentiated to support or refute the hypotheses discussed in chapter 3. A previous study revealed significant differences in MT 1 proximal articular surface morphology between humans and apes (Proctor et al., 2008). The PCA resulted in the first four principal components representing a total of 71% of the variation observed in the sample (Table 6.1). The individual proportions for the principal components of PC 5 and higher were below 5% and are not morphologically revealing. Refer to Figures 6.1 and 6.2 for an example of each species and for photos of the fossils. Discussion of the PCA results follows.

Table 6.1 Proportion of PC Variance for MT 1

Proportion of Variance for MT 1			
PC 1	PC 2	PC 3	PC 4
33%	20%	10%	8%

Table 6.2 Extant Specimens in the MT 1 Analysis

Group	Number
Gorilla	30
Pan	30
Hylobates	30
Homo	34
unshod *Homo*	31

Figure 6.1 Extant groups photos for MT 1: A) recent *Homo*; B) unshod *Homo*; C) *Gorilla*; D) *Pan*; E) *Hylobates*.

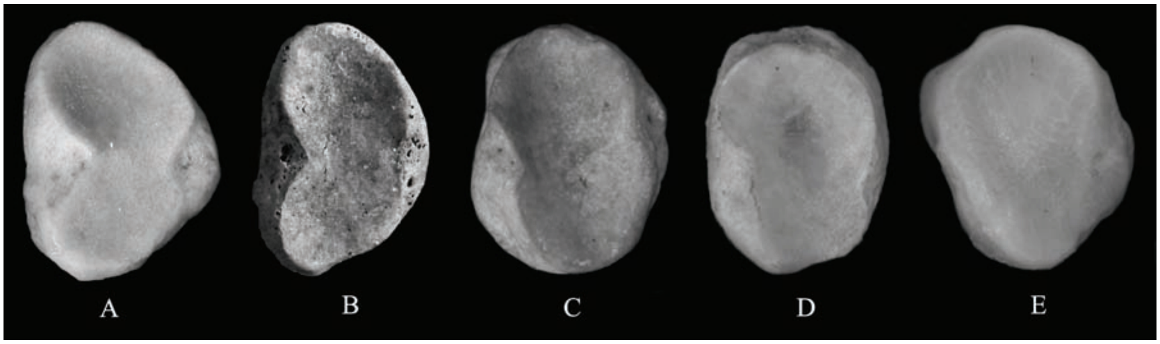


Figure 6.2 Fossils studied in the MT 1 analysis: A) A. L. 333-54; B) Stw 573 "Little Foot"; C) Stw 562 (reversed, this is a right); D) OH 8-H; E) SKX 5017. These specimens are not to scale.

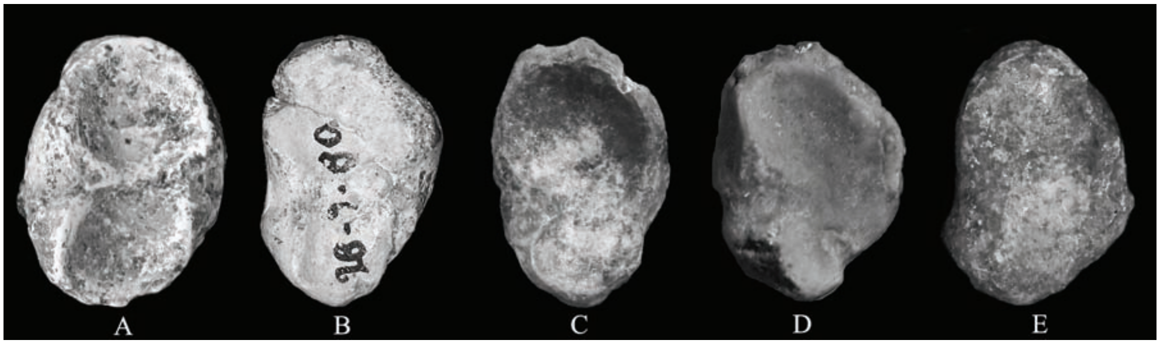


Table 6.3 Tukey-Kramer Multiple-Comparison Test for PC 1

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.11	*Pan*, *Hylobates*, *Homo*, unshod *Homo*
Pan	30	-0.07	*Gorilla*, *Homo*, unshod *Homo*
Hylobates	30	-0.06	*Gorilla*, *Homo*, unshod *Homo*
Homo	34	0.10	*Gorilla*, *Pan*, *Hylobates*
unshod *Homo*	31	0.11	*Gorilla*, *Pan*, *Hylobates*

MT 1 Principal Component 1

An ANOVA was conducted to test for differences in the means of PC 1 scores between groups, revealing a statistically significant result with a *p* value far below 0.001. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. The Tukey-Kramer post-hoc test was conducted with the ANOVA to determine which specific groups were statistically different, and the results are reported Table 6.3.

Both groups of humans are statistically different than all ape groups at the PC 1 axis. Apes and humans do not overlap. *Gorilla* is different from *Pan* and *Hylobates*, but *Hylobates* and *Pan* are not different at the PC 1 axis. However, all apes overlap one another at this axis, with *Hylobates* and *Pan* occupying an area closer to the 0.00 point and *Gorilla* tending toward the extreme negative area of the axis. Humans occupy the positive area of the axis exclusively, with no differentiation between recent *Homo* and unshod *Homo*. See Tables 6.4 and 6.5.

Table 6.4 Principal Component 1 Ranges

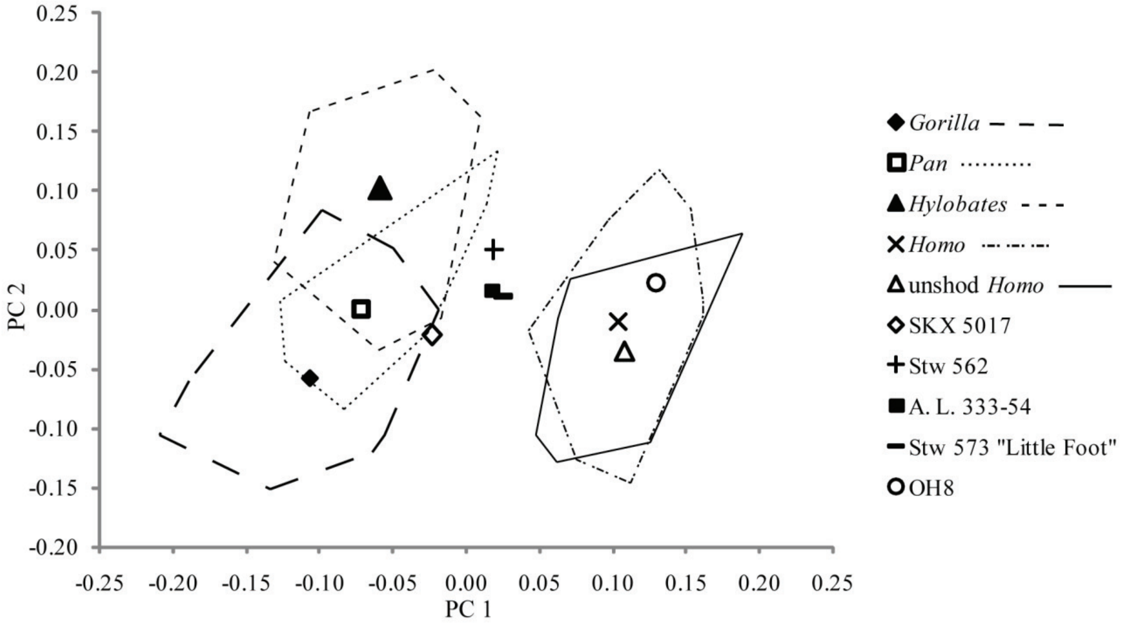
Group	Minimum	Maximum	Range
Gorilla	-0.21	-0.02	0.19
Pan	-0.13	0.02	0.15
Hylobates	-0.13	0.01	0.14
Homo	0.04	0.16	0.12
unshod *Homo*	0.05	0.19	0.14

The scatter plot presented in Figure 6.3 illustrates the areas of PC 1 and 2 occupied by the species groups and fossil specimens. The x-axis is PC 1 and the y axis is PC 2. The plotted symbol for each species group represents the group mean, with a line drawn to demonstrate the range occupied by the individual cases. Of the fossil specimens, only OH 8 overlaps humans at PC 1. The specimens Stw 562 and A. L. 333-54 are identical at this axis, and just overlap with *Pan* at its most extreme range. The "Little Foot" specimen Stw 573 occupies an area just outside of the range of *Pan* and well outside the range of *Homo*, placing it in an area intermediate to humans and apes but bearing some greater resemblance to apes. The specimen SKX 5017 groups with all ape groups and does not overlap humans.

Table 6.5 Fossil PC 1 Values

Specimen	PC 1
SKX 5017	-0.02
Stw 562	0.02
A. L. 333-54	0.02
Stw 573 "Little Foot"	0.03
OH 8	0.13

Figure 6.3 Plot of PC 1 and PC 2 group averages and fossil specimens for MT 1



Figures 6.4 and 6.5 show the morphology of the proximal articular surface at the extreme ranges of PC 1. It must be noted that by default all other PC scores are set to 0.00. The implication of this is that the morphology of PC 1 depicted is not entirely in isolation, and a combination of morphology from other PC axes is necessary to fully appreciate species-level morphology. However, this representation provides broad trends.

Figure 6.4 depicts the morphology at the -0.19 point of the PC 1 axis. This area is occupied by *Gorilla*, and as it gradually morphs toward the area occupied by humans as depicted by Figure 6.5 of morphology at the 0.16 axis point the surface becomes dramatically flatter. Within apes, the morphology changes from being a particularly deep surface at the negative aspect to having reduced oblique curvature toward the 0.00 axis. *Gorilla* is statistically different from *Pan* and *Hylobates,* but *Pan* and *Hylobates* are not statistically different from one another.

Figure 6.4 PC 1 (-0.19) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground). The dorsal aspect is at the top.

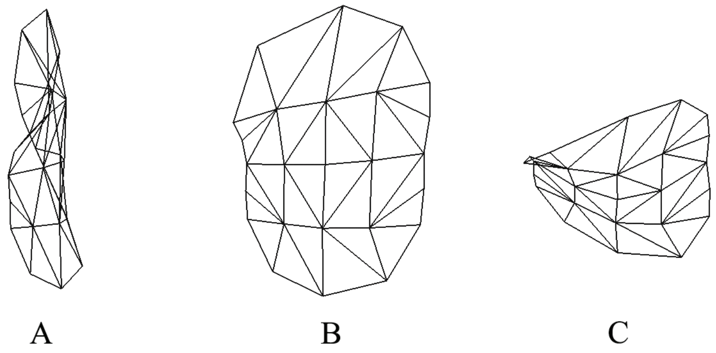
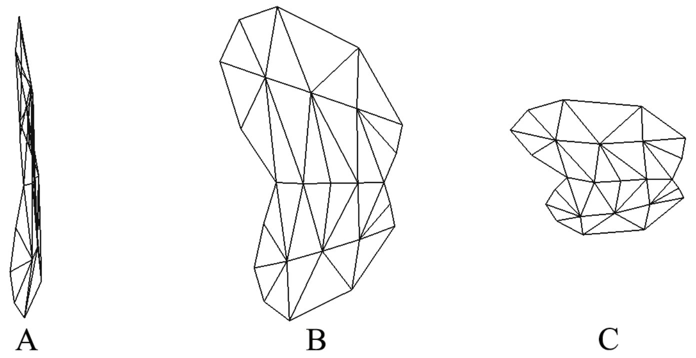


Figure 6.5 PC 1 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground). The dorsal aspect is at the top.



MT 1 Principal Component 2

The ANOVA to test for differences in the means of PC 2 scores between groups revealed a statistically significant result with a *p* value below 0.000. In addition, the following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test. All passed at the 0.05 significance level. A Tukey-Kramer post-hoc test was used with the ANOVA to determine which specific groups were statistically different, and the results are reported in Table 6.6.

Table 6.6 Tukey-Kramer Multiple-Comparison Test for PC 2

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.06	*Pan*, *Hylobates*, *Homo*
Pan	30	-0.03	*Gorilla*, *Hylobates*
Hylobates	30	0.10	*Gorilla*, *Homo*, unshod *Homo*, *Pan*
Homo	34	-0.01	*Gorilla*, *Hylobates*
unshod *Homo*	31	-0.04	*Hylobates*

All groups overlap on the PC 2 axis (Tables 6.7 and 6.8). Statistically significant PC 2 score differences occur between *Hylobates* and all other groups, *Pan* and *Gorilla*, *Homo* and *Gorilla* and *Hylobates*, and between unshod *Homo* and *Hylobates*. Since there is so much overlap at the PC 2 axis, it is more appropriate to interpret PC 2 morphology as it relates to humans and apes separately. The PC 2 axis influences shape somewhat differently depending on the location on the PC 1 axis, and since humans and apes share no overlap at the PC 1 axis it is important to interpret them in their own contexts.

Table 6.7 Principal Component 2 Ranges for MT 1

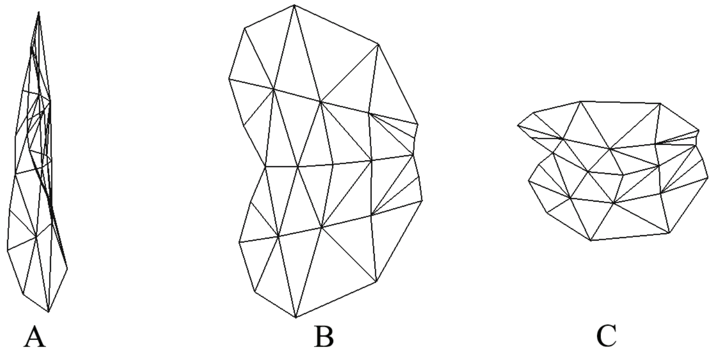
Group	Minimum	Maximum	Range
Gorilla	-0.15	0.08	0.23
Pan	-0.08	0.13	0.21
Hylobates	-0.03	0.21	0.24
Homo	-0.15	0.12	0.27
unshod *Homo*	-0.13	0.07	0.20

Table 6.8 Fossil PC 2 Values

Specimen	PC 2
SKX 5017	-0.02
Stw 562	0.05
A. L. 333-54	0.02
Stw 573 “Little Foot”	0.01
OH 8	0.02

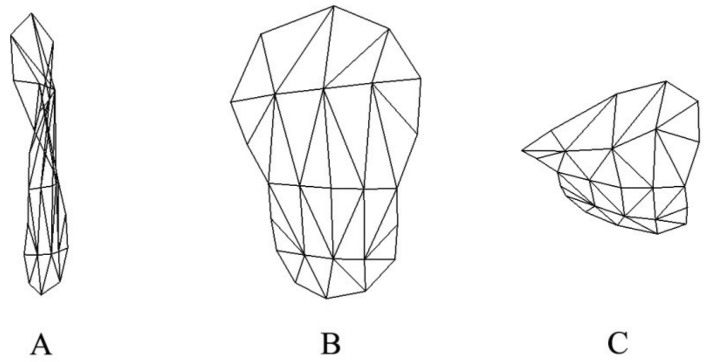
The overall morphological trend of the PC 2 axis is a narrower articular surface at the dorsal aspect on the positive portion of the PC 2 axis, and a wider plantar aspect relative to the dorsal breadth on the negative PC 2 axis (Figures 6.6 and 6.7). For humans, the combined effects of surface flatness on PC 1 restrict interpretation of the morphological change on the PC 2 axis to relate entirely to relative dorsal and plantar surface breath. The OH 8 *Homo habilis* specimen overlaps humans at the PC 2 axis, and is indistinguishable from the human morphology (Figure 6.3).

Figure 6.6 PC 2 (-0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



The ape groups all overlap, with *Gorilla* occupying more of the negative PC 2 axis and generally having a relatively wider plantar breadth and inferior curvature of the articular surface in the plantar portion. As the shape moves on the PC 2 axis and interacts with PC 1, the more positive extreme of PC 2 is occupied by *Hylobates* and demonstrates a narrower plantar aspect to the surface, with exaggerated curvature in the dorso-lateral and medio-plantar aspects of the surface. The dorsal and plantar surfaces exhibit a kind of torsion as the dorsal curvature is elevated at the medio-dorsal side of the surface and the latero-plantar portion. All fossil specimens overlap the ranges of all groups.

Figure 6.7 PC 2 (0.18) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 1 Principal Component 3

The ANOVA to test for differences in the means of PC 3 scores between groups revealed a statistically significant result with a *p* value far below 0.000. In addition, the following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test. All passed at the 0.05 significance level, except for the equal variance test. This is explained by three specimens of *Hylobates* and one specimen of *Pan* having a low PC 3 score that falls outside of one standard deviation for these respective groups.

A Tukey-Kramer post-hoc test was used with the ANOVA to determine which specific groups were statistically different, and the results are reported in Table 6.11.

Table 6.9 Tukey-Kramer Multiple-Comparison Test for PC 3

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.04	*Pan*, *Hylobates*, unshod *Homo*
Pan	30	-0.03	*Homo, Gorilla*
Hylobates	30	-0.02	*Gorilla*, *Homo*
Homo	34	0.02	*Pan*, *Hylobates,* unshod *Homo*
unshod *Homo*	31	-0.02	*Homo, Gorilla*

Table 6.10 Principal Component 3 Ranges

Group	Minimum	Maximum	Range
Gorilla	-0.06	0.16	0.22
Pan	-0.13	0.04	0.17
Hylobates	-0.13	0.05	0.18
Homo	-0.10	0.16	0.26
unshod *Homo*	-0.09	0.07	0.16

There are two groupings at this axis, with overlap among them all (see Table 6.12). *Gorilla* and *Homo* are not different at this axis, but are different from all other groups. *Pan*, *Hylobates*, and unshod *Homo* are not different at this axis, but are different from *Gorilla* and *Homo*. This axis only accounts for 10% of the variation between groups, and is similar to PC 2 in that it must be interpreted with the influence of PC 1. The lower axis of PC 3 demonstrates morphology of a wider dorsal surface with the dorso-medial aspect elevated or more proximal. The higher PC 3 values represent morphology of a relatively narrower surface. See Figures 6.8, 6.9, and 6.10.

The OH 8 specimen groups with *Homo*, unshod *Homo*, and *Gorilla*. The specimens Stw 562 and Stw 573 have the same PC 3 values and group with all groups except *Pan*. The *A. afarensis* specimen A. L. 333-54 groups only with *Homo* and *Gorilla*. The *P. robustus* specimen SKX 5017 overlaps all groups.

Table 6.11 Fossil PC 3 Values

Specimen	PC 3
SKX 5017	-0.02
Stw 562	0.05
A. L. 333-54	0.12
Stw 573 "Little Foot"	0.05
OH 8	0.07

Figure 6.8 Plot of PC 1 and PC 3 group averages and fossil specimens for MT 1

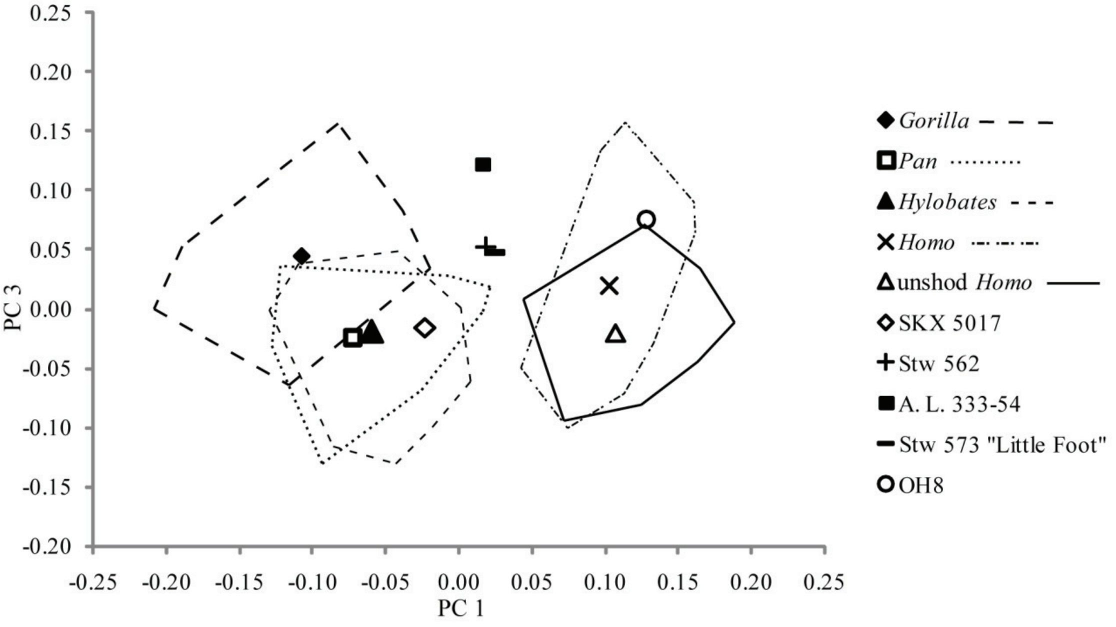


Figure 6.9 PC 3 (-0.11) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

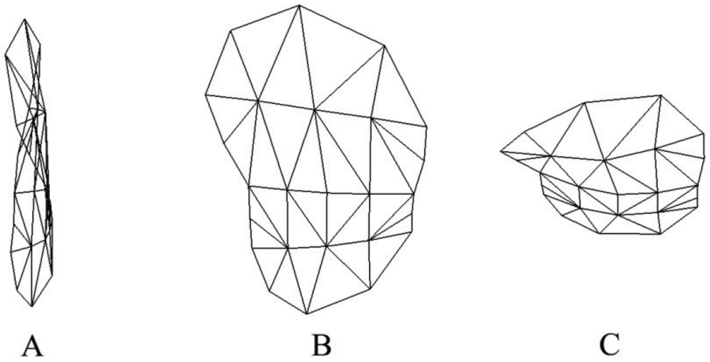
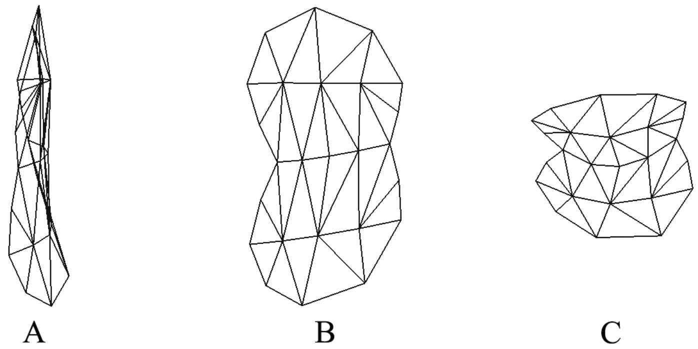


Figure 6.10 PC 3 (0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 1 Principal Component 4

As with PC 1 through PC 3, an ANOVA was conducted to test for differences in the means of PC 4 scores. The test revealed a statistically significant result with a *p* value below 0.000. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test. These tests passed at the 0.05 significance level. A Tukey-Kramer post-hoc test was used with the ANOVA to determine which specific groups were statistically different (Table 6.14).

Table 6.12 Tukey-Kramer Multiple-Comparison Test for PC 4

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.02	*Hylobates*
Pan	30	-0.04	*Homo,* unshod *Homo*, *Hylobates*
Hylobates	30	0.05	*Gorilla*, *Homo*, unshod *Homo*, *Pan*
Homo	34	0.01	*Pan*, *Hylobates*
unshod *Homo*	31	0.05	*Pan, Hylobates*

At the PC 4 axis *Pan* and *Hylobates* are different than all other groups, while *Homo* and unshod *Homo* are both different from *Pan* and *Hylobates* only. *Gorilla* is only different from *Hylobates*. See Figure 6.11. The axis provides little meaningful shape information that has not been reflected to some degree in the other PC axes. The medio-plantar portion of the surface at the positive portion of the axis is slightly narrowed, and the dorsal area wider. At the positive portion of the axis, the lateral side of the articular surface is slightly raised. Refer to Figures 6.12 and 6.13. All fossils overlap all groups (Table 6.15).

Table 6.13 Principal Component 4 Ranges

Group	Minimum	Maximum	Range
Gorilla	-0.09	0.05	0.14
Pan	-0.11	0.06	0.17
Hylobates	-0.04	0.16	0.20
Homo	-0.08	0.11	0.19
unshod *Homo*	-0.09	0.06	0.15

Table 6.14 Fossil PC 4 Values

Specimen	PC 4
SKX 5017	-0.02
Stw 562	0.03
A. L. 333-54	-0.04
Stw 573 “Little Foot”	0.02
OH 8	-0.01

Figure 6.11 Plot of PC 1 and PC 4 group averages and fossil specimens

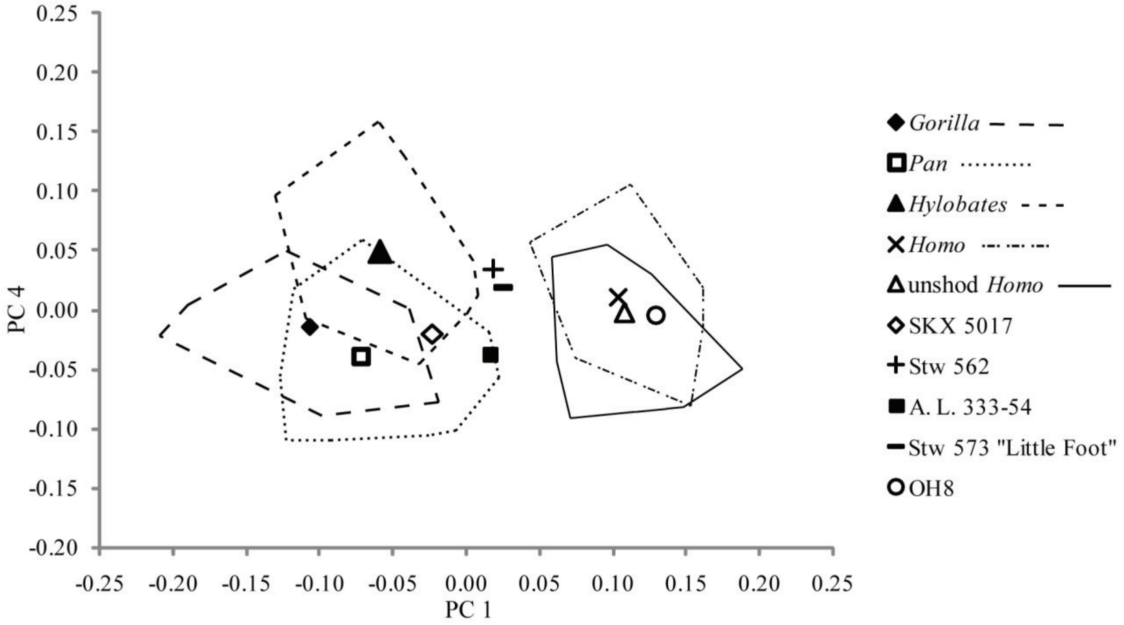


Figure 6.12 PC 4 (-0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

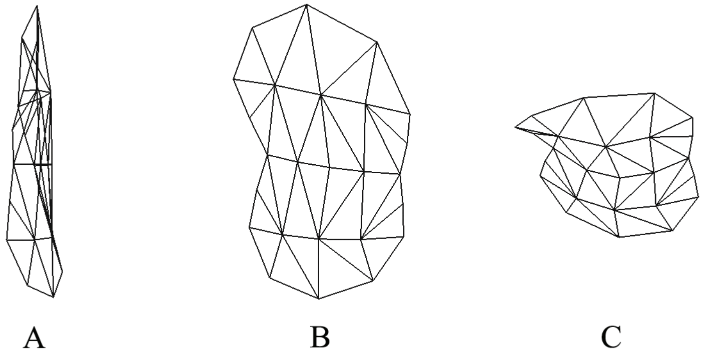
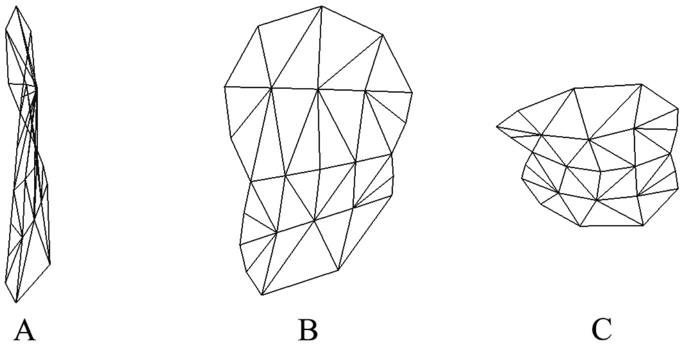


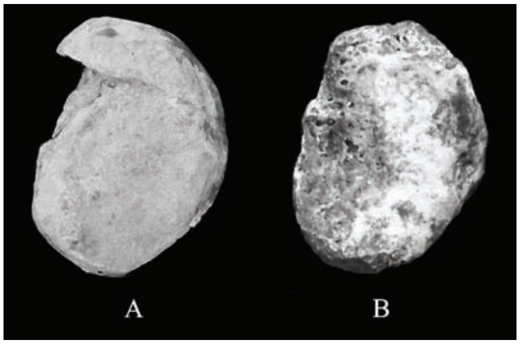
Figure 6.13 PC 4 (0.14) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



Fossils with Absent Data for MT 1

Two additional MT 1 fossils were examined, both with missing data due to taphonomic damage to the articular surfaces. The specimen SK 1813 is a nearly complete MT 1, but is missing a broken portion of the dorso-lateral part of the metatarsal base, including part of the proximal articular surface (Susman and de Ruiter, 2004). A principal components analysis was conducted by removing 5 landmarks from the analysis to account for the missing data. The specimen Stw 595 is a complete MT 1 except for the proximal articular surface, which has not been preserved on a substantial part of the surface leaving an area in the central portion of the surface intact. This specimen does not lend itself to a meaningful quantitative analysis for this study, but it is examined qualitatively in light of the results already described. See Figure 6.14.

Figure 6.14 MT 1 fossils with missing data: A) SK 1813; B) Stw 595. These specimens are both rights, but are reversed to appear as lefts for easy reference to other specimens.



Analysis of SK 1813

The principal components analysis that includes SK 1813 yielded similar results to the complete study discussed above. The missing data excluded the dorso-lateral portion of the articular surface from the analysis, thus it does not account for medio-lateral breadth of the dorsal part of the surface and it does not account for all dorsal surface curvature. The morphology represented on the PC axes is identical to the full analysis if missing data is accounted for, but the shape variation is divided differently on the PC axes such that the combined morphology represented by PC 1 and PC 2 separates humans and apes, rather than just the PC 1 axis as described above. The combined effects of the PC 1 and PC 2 axes reflect a flat and narrow surface in the area occupied by *Homo*, while the area occupied by the apes reflects a wider surface with greater curvature. The characteristic oblique curvature of the apes is visible in the medio-plantar area even though the corresponding curvature in the dorso-lateral area of the surface is missing from the analysis. Only the PC 1 and PC 2 axes are discussed here; the remaining axes do not reveal anything more about the surface morphology than has already been discussed.

Table 6.15 Proportion of PC Variance for MT 1 including SK 1813

Proportion of Variance for MT 1	
PC 1	PC 2
26%	24%

Note that the combined PC 1 and PC 2 axes in the previous analyses accounted for 53% of observable variation. The combined value for this analysis is 50% (Table 6.17). Tables 6.18 and 6.19 show the PC values. All of the fossils overlap all groups at the PC 1 axis, except OH 8 that does not overlap *Hylobates* and Stw 562 is just outside the range of unshod *Homo*. At the PC 2 axis SK 1813 does not overlap *Homo*, unshod *Homo*, or *Hylobates*. At this axis SKX 5017 does not overlap *Homo* and unshod *Homo*. All fossils are outside the range of *Gorilla* except SKX 5017 and SK 1813. In addition, OH 8 is also outside the range of *Pan*.

Table 6.16 Principal Component 1 Ranges

	PC 1		PC 2	
Group	Minimum	Maximum	Minimum	Maximum
Gorilla	-0.09	0.13	-0.21	-0.02
Pan	-0.04	0.13	-0.14	0.09
Hylobates	-0.03	0.22	-0.05	0.10
Homo	-0.20	0.08	0.00	0.16
unshod *Homo*	-0.17	0.00	-0.02	0.17

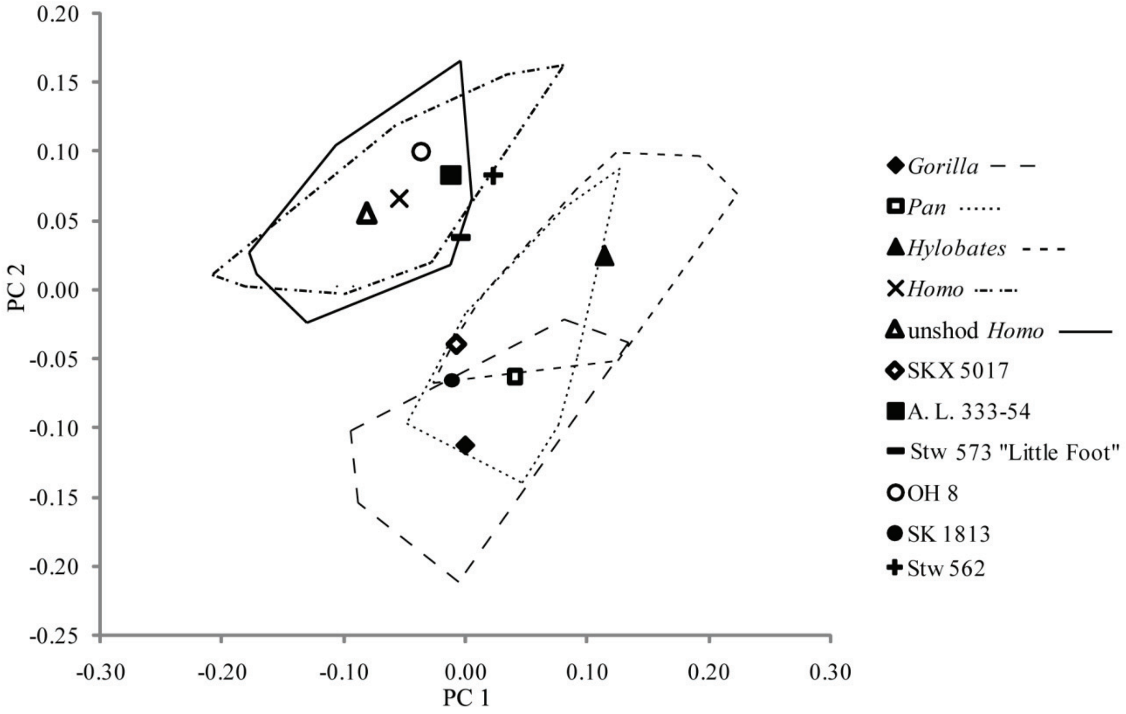
Table 6.17 Fossil PC 1 and PC 2 Values

Specimen	PC 1	PC 2
SKX 5017	-0.01	-0.04
Stw 562	0.02	0.09
A. L. 333-54	-0.01	0.08
Stw 573 “Little Foot”	0.00	0.04
OH 8	-0.04	0.10
SK 1813	-0.01	-0.07

The specimens A. L. 333-54 and Stw 573 group with *Homo* in this analysis, whereas in the previous analysis they did not group so closely. Since this analysis is missing data from the dorsal aspect of the MT 1 proximal surface, it suggests that one of the contributing factors of difference between these specimens and *Homo* is the degree of curvature, particularly at the dorsal aspect of the surface. Even with this missing data, the combined effect of PC 1 and PC 2 create a complete separation of humans and apes (Figure 6.15). This might imply that curvature in the planar aspect of the surface, and overall surface curvature and relative width is most import in distinguishing humans and apes from a functional perspective. One key finding in this analysis is that SK 1813 and SKX 5017 group closely with the apes. SKX 5017 from the previous analysis and from Proctor et al. also grouped with apes (Proctor et al., 2008).

The combined effects of PC 1 and PC 2 in this analysis are like the combined effects of these PC axes in the previous analysis. *Gorilla* has a much wider surface with greater surface curvature in the plantar aspect of the surface, and this morphology transitions along the plot until in *Hylobates* the plantar aspect of the surface is narrower and the dorsal aspect of the surface is highly curved with torsion relative to the plantar aspect. The specimens SKX 5017 and SK 1813 are located close together on the PC 1 and PC 2 axis. Although SK 1813 has not been attributed to a genus or species, Susman and de Ruiter describe it as being very similar to SKX 5017 and Stw 562 in a morphometric analysis using linear measurements of the metatarsal. This analysis of the MT proximal surface shows a clear division between SKX 5017, SK 1813, and apes compared to A. L. 333-54, OH 8, Stw 562, and humans. It is possible that Sk 1813 belongs to the genus *Paranthropus* and Stw 562 is *Australopithecus africanus*. This would suggest that *Paranthropus*, at least on the MT 1 proximal surface, is showing primitive traits that are not present in early *Homo* or the gracile australopiths.

Figure 6.15 Plot of the PC 1 and PC 2 axis including SK 1813



<u>Qualitative Analysis of Stw 595</u>

Deloison (2003) described Stw 595 as very similar to Stw 562. The proximal articular surface is too damaged to determine definitively whether its overall shape and curvature resembles Stw 562. However, when viewing Stw 595 at the medial aspect, what remains of the surface can be seen to have a definite concavity at the central area. This makes the plantar aspect of the surface project proximally. These fossils are also similar in that they have relatively round shafts, the heads are wider than the base, and they are less robust than SKX 5017. The specimen Stw 595 has not yet appeared in a published quantitative analysis, and a morphometric analysis using standard linear measurements would reveal its similarity or dissimilarity to other fossils more clearly.

Interspecific Size and Shape Relationships

Differences in size between groups were tested with an ANOVA and the Tukey-Kramer (post hoc) multiple-comparison test to look for differences between specific groups (Table 6.20). The ANOVA indicated a statistically significant difference in means with a p value well below 0.00. H_8 is falsified. The multiple-comparison test results are reported below, and they indicate significant differences between most groups. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test. These tests passed at the 0.05 significance level, except for the test for equal variance. A Shapiro-Wilk distribution test for normality was conducted. Normality could not be rejected for all species groups except *Gorilla*.

Table 6.18 Tukey-Kramer Multiple-Comparison Test for Centroid Size

Group	Specimens	Mean	Different From Groups
Gorilla	30	43.6	*Pan*, *Hylobates*, unshod *Homo*
Pan	30	35	*Homo,* unshod *Homo, Gorilla, Hylobates*
Hylobates	30	18.2	*Homo,* unshod *Homo, Gorilla, Hylobates*
Homo	34	46.1	*Pan*, *Hylobates,* unshod *Homo*
unshod *Homo*	31	37.9	*Homo,* unshod *Homo, Gorilla, Hylobates*

It is important to note that in terms of centroid size, there is no significant difference between *Gorilla* and recent *Homo*. Otherwise, all groups differ significantly in size. *Hylobates* has the narrowest range, and *Gorilla* has the widest, corresponding respectively to the species with the least sexual dimorphism and the species with the most (Table 6.21).

Table 6.19 Centroid Size Ranges

Group	Minimum	Maximum	Range
Gorilla	33.5	52.8	19.3
Pan	31.46	38.37	6.91
Hylobates	17.02	20.38	3.36
Homo	36.19	53.51	17.32
unshod *Homo*	32.13	45.71	13.58

Table 6.20 Fossil Centroid Sizes

Specimen	Centroid
SKX 5017	32.52
Stw 562	34.79
A. L. 333-54	36.09
Stw 573 “Little Foot”	31.37
OH 8	33.85

Regression analysis and an ANCOVA were conducted to determine whether there is a relationship between size and shape at the intraspecific level. The regression analysis resulted in a significant relationship between centroid size and each PC axis. Refer to Table 6.23.

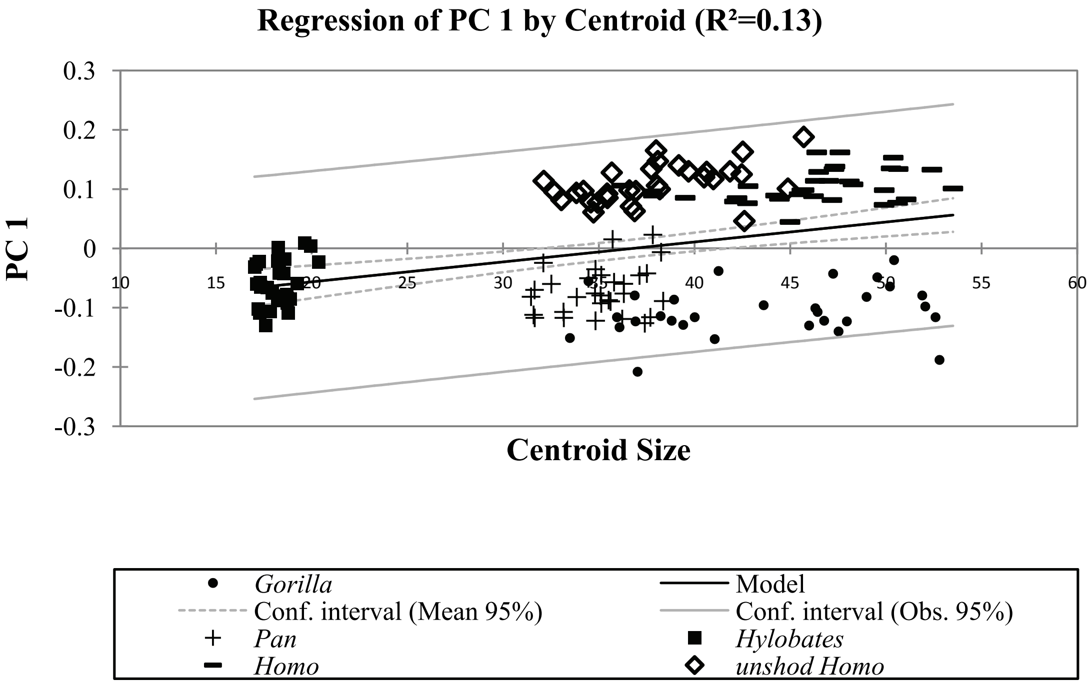
Table 6.21 Regression and ANCOVA results

	PC 1	PC 2	PC 3	PC 4
R^2 with PC and Size	0.13	0.27	0.10	0.14
R^2 with PC, Size, and Species	0.88	0.54	0.26	0.38

Although all of the regression results indicated significant relationships between size and shape, the R^2 values were relatively low when considering only centroid size and the PC scores as shape variables (Table 6.23). The ANCOVA test included the species as a qualitative variable, and in those results the R^2 value went up considerably, especially for PC 1 which is the most important variable for differentiating humans and apes in the PC analyses. Species is a better predictor for shape than size alone.

One factor that strongly influences these results is that *Hylobates* is very small compared to the other groups. This creates a statistical relationship between size and shape that is not useful or a very good predictive model. For example, *Hylobates* and *Pan* are not different in terms of PC 1 scores, but are very different in terms of size. Also note that recent humans and *Gorilla* are not different in size but are very different in shape at PC 1. Even though there are differences in size between recent and unshod *Homo* compared to *Pan*, there is much overlap. Therefore, size and shape seem to be less important than species as a variable. Species actually acts as a proxy for locomotion, since *Hylobates* and *Pan* are both more arboreal than other groups, *Gorilla* is more terrestrial, and both *Homo* groups are terrestrial and habitually bipedal. There does seem to be a trend among apes to have different morphology as size changes, but since *Pan* and *Hylobates* have similar shapes it seems that size is only a factor in that more arboreal primates tend to have smaller body sizes. Size does not seem to act on shape as strongly as locomotion acts on shape. See Figure 6.16.

Figure 6.16 MT 1 interspecific size regression for PC 1



The PC 2 axis is most informative when considering apes and humans separately. Figure 6.17 shows the regression analysis results for centroid size and PC 2. The R^2 value increases considerable when species is used as a variable, again suggesting that species, or locomotion, is more important than size in determining shape. The ape groups are all significantly different at this axis, but *Gorilla* and *Pan* show considerable overlap. The regression plot shows that all groups overlap considerable except for *Hylobates*, which has a different surface morphology at this axis. The usefulness of these results is limited in predicting shape based on size, because *Hylobates* is very different in size. Likewise, *Gorilla* is not significantly different at this axis from unshod *Homo*, but the centroid size between these two groups is significantly different.

Figure 6.17 MT 1 interspecific size regression for PC 2

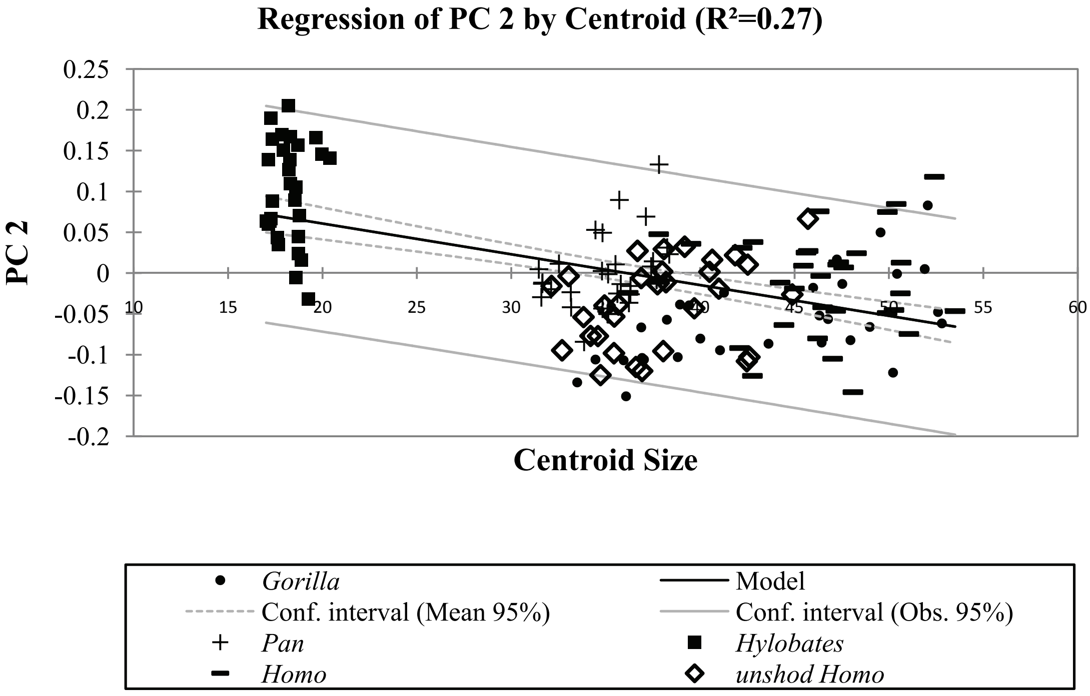
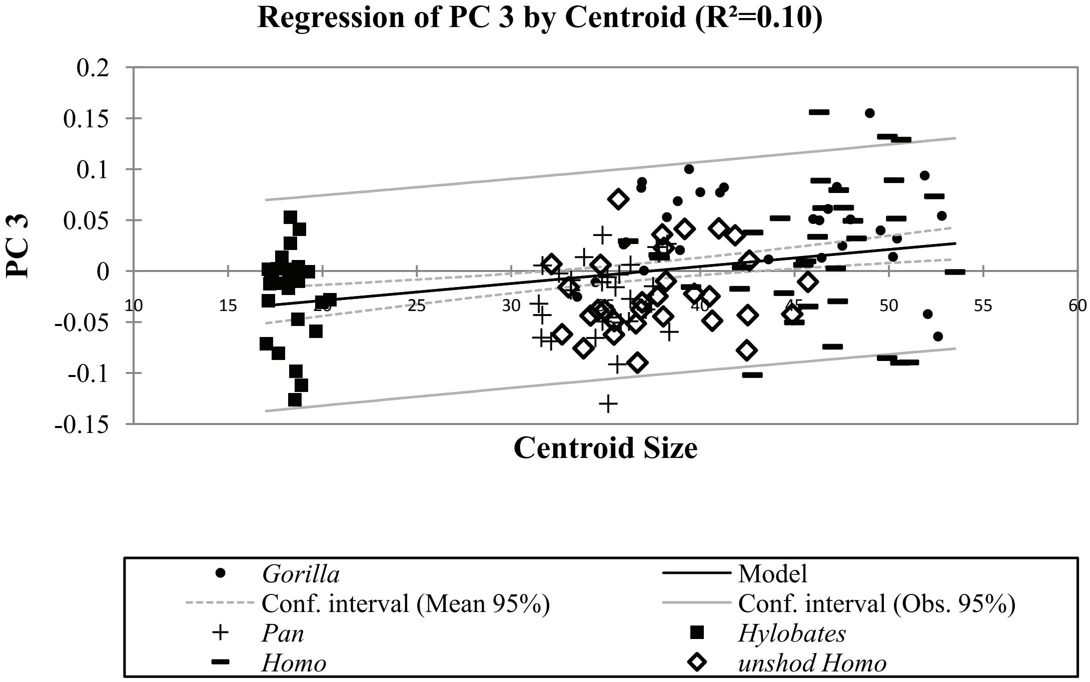
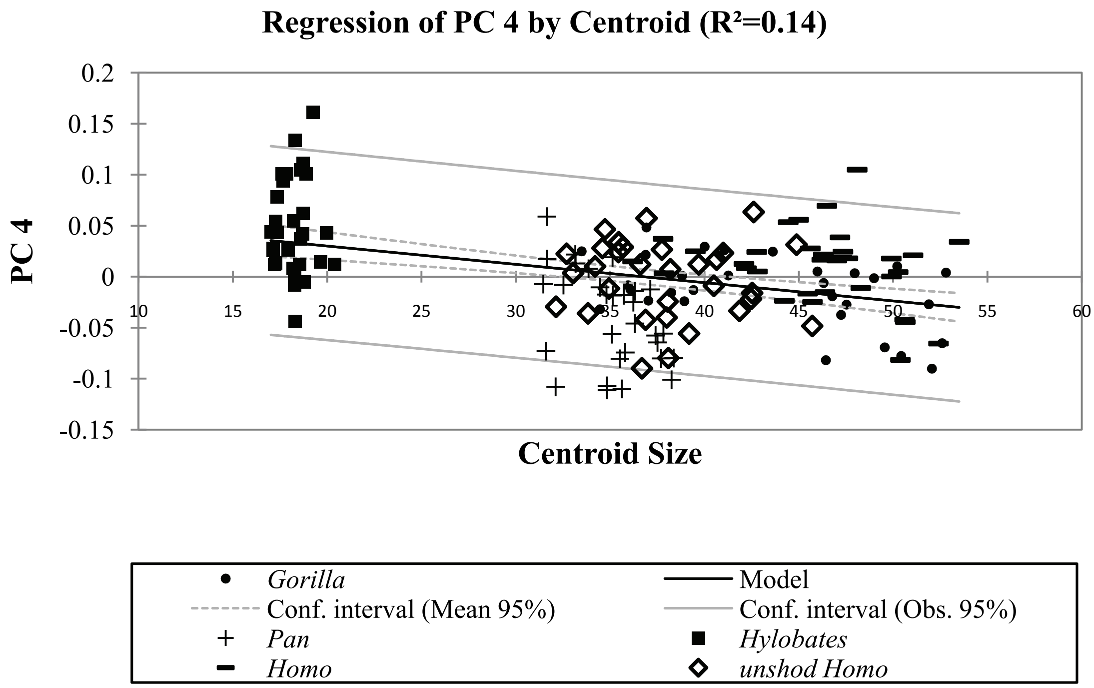


Figure 6.18 MT 1 interspecific size regression for PC 3



The PC 3 axis reflects a similar morphology as PC 2, but there is little to distinguish humans from apes at this axis. This axis may be more informative in terms of size related to shape, because *Gorilla* and recent *Homo* are similar in size and are not significantly different in shape on the PC 3 axis, while *Pan*, *Hylobates*, and unshod *Homo* are not different at this axis. The morphology of PC 3 is related to width of the dorsal aspect of the MT 1 proximal surface relative to the plantar width. This regression analysis (Figure 6.18) suggests that with increased body sixe there is a small effect of widening at the dorsal aspect of the surface.

Figure 6.19 MT 1 interspecific size regression for PC 4



The PC 4 axis is the least informative about shape, but does show a slight elevation of the articular surface at the medio-dorsal aspect, that is exaggerated at the positive portion of the axis that is occupied by *Hylobates*. *Hylobates* and *Pan* are not significantly different at this axis even though *Hylobates* has a range that encroaches further to the positive portion of the axis. See Figure 6.19). *Gorilla* is not different from *Pan* at this axis, and each *Homo* group is not different than *Gorilla*. *Hylobates* has the most extreme dorsal curvature of the apes from previous PC axes, and is consistent here. When including species names as a qualitative variable in an ANCOVA, the R^2 value goes up considerably. Due to the high degree of overlap of all groups at this axis with the only clear group separating slightly from the rest being *Hylobates*, it appears that the high degree of arboreality demonstrated by *Hylobates* is the most important variable in predicting shape for PC 4. The PC 4 axis reflects a subtle shape difference that is not unique to this axis because PC 2 demonstrates this shape difference more clearly.

To sum up the results relating size to shape, the regression analyses are not particularly revealing unless species is included as a variable. Any suggestion of effect due purely to size must be considered conservatively, because the only clear effect of size and shape is related to the considerable size difference between *Hylobates* and all other groups. The hypothesis (H_{10}) that observed differences in morphology between species are unrelated to size is not disproven; however, it is revealed that locomotion is more influential to morphology than size.

Intraspecific MT 1 Shape, Size, and Sex Variation

Although examining interspecific size and shape is not very informative for MT 1, examination of size and shape at the intraspecific level reveals trends within a species that are not reflected between species. To test the hypothesis that there are differences in size and shape between males and females of each species, t-tests assuming unequal variances were conducted for each variable. This form of test was used because it is more conservative, and because sample sizes for each sex were relatively low. If a difference in centroid size between sexes was indicated, and a difference in PC scores was indicated, regression analysis was conducted to determine whether size and shape are related.

Gorilla

Gorilla Size and Sex

There is a statistically significant difference in the centroid size between male and female gorillas, with a *p* value below 0.00 (Table 6.24). Males are significantly larger than females. The hypothesis (H_9) that there are no sex differences in size intraspecifically is rejected for *Gorilla*.

Table 6.22 *Gorilla* centroid size T-test comparing the sexes

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	37.75	48.78
Variance	5.45	7.42
Observations	14.00	16.00
df	28.00	
t Stat	-11.94	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.05	

Gorilla Shape and Size

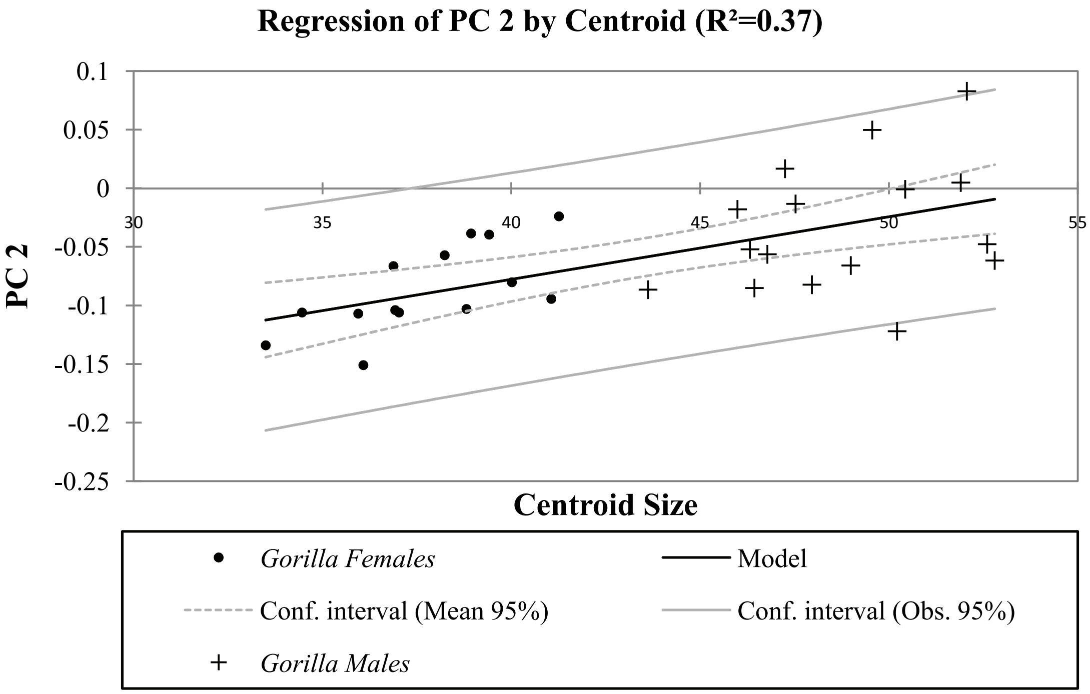
There is a statistically significant difference in shape between male and female gorillas at the PC 2 and PC 4 axes (Tables 6.25 and 6.26). Shape on the PC 2 axis is particularly informative about the differences of surface shape within ape groups. Regression analysis was done to look for relationships between these PC scores and size. There was a significant relationship between size and PC 2 shape with a *p* value below

0.000 and an R^2 of 0.37 (Figure 6.20). This analysis reveals that *Gorilla* females have predictably lower PC 2 scores than males. Females have a smaller range for PC 2 and tend to have a wider MT 1 articular surface in the dorsal aspect with greater oblique curvature than males.

Table 6.23 *Gorilla* PC 2 T-test comparing the sexes

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	-0.09	-0.03
Variance	0.00	0.00
Observations	14.00	16.00
Hypothesized Mean Difference	0.00	
df	27.00	
t Stat	-3.13	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.05	

Figure 6.20 Regression of PC 2 by centroid size for *Gorilla* males and females



The regression analysis for PC 4 and size was significant with a *p* value of 0.007 and an R^2 of 0.23 (Figure 6.21). *Gorilla* females tend to have slightly higher PC 4 scores, reflecting higher surface elevation in the medio-dorsal aspect, which is a factor that in apes contributes to the oblique curvature morphology.

The hypothesis (H_{11}) that differences in shape intraspecifically are unrelated to size is rejected for *Gorilla*. The most important finding is that smaller female gorillas have a larger plantar portion to the MT 1 proximal articular surface, amounting to a slightly exaggerated saddle joint morphology compared to other apes when combined with the placement on the PC 1 axis. The other apes on the PC 2 axis demonstrate somewhat more emphasis on curvature in the dorsal part of the surface.

Figure 6.21 Regression of PC 4 by centroid size for *Gorilla* males and females

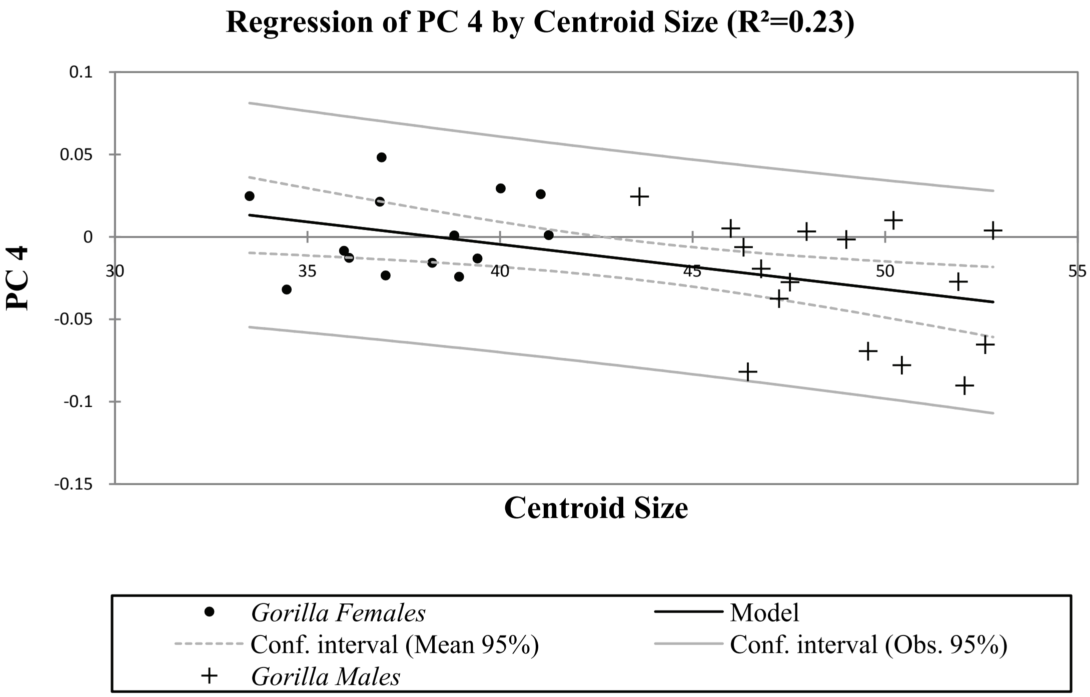


Table 6.24 *Gorilla* PC 4 T-test comparing the sexes

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	0.00	-0.03
Variance	0.00	0.00
Observations	14.00	16.00
df	26.00	
t Stat	2.65	
P(T<=t) one-tail	0.01	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.01	
t Critical two-tail	2.06	

Pan

Pan Size and Sex

There is a statistically significant difference in centroid size between males and females, with a $p < 0.00$ (Table 6.27). Males are significantly larger than females.

Table 6.25 *Pan* centroid size T-test comparing the sexes

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	34.45	36.42
Variance	4.75	1.32
Observations	21.00	9.00
df	26.00	
t Stat	-3.24	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.06	

Pan Shape and Size

The t-tests to find differences between males and females for shape as reflected on the PC axes resulted in no significant differences for all PC scores.

Hylobates

Hylobates Size and Sex

The t-test for determining whether there is a significant difference in centroid size between males and females resulted in no significant difference.

<u>*Hylobates* Shape and Size</u>

The t-tests to find differences between males and females for shape as reflected on the PC axes resulted in no significant differences for all PC scores.

Shod *Homo*

<u>Size and Sex</u>

The t-test to compare male and female centroid size resulted in a significant difference with $p < 0.000$ (Table 6.28). Recent human males are larger than females.

Table 6.26 *Homo* centroid size T-test comparing sexes

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	43.31	48.19
Variance	15.00	8.37
Observations	15.00	15.00
df	26.00	
t Stat	-3.91	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.06	

<u>*Homo* Shape and Size</u>

The t-tests for determining differences in shape between males and females yielded statistically significant results for PC 1 and PC 4 (Tables 6.29 and 6.30). The *p* value for PC 1 is 0.04 and the PC 4 *p* value is below 0.00. However, regression analysis was performed to test for a predictable relationship between size and shape on the PC 1 and PC 4 axes, and both analyses yielded insignificant results. The PC 1 *p* value was 0.07 and PC 4 had a *p* value of 0.09. Size cannot explain the difference between males and females. The differences in means are slight, and it is possible that a larger sample size would yield different results. There are not any documented differences in locomotion between males and females of recent *Homo* to explain the shape differences.

Table 6.27 *Homo* PC 1 T-test comparing sexes

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	0.10	0.11
Variance	0.00	0.00
Observations	15.00	15.00
df	27.00	
t Stat	-1.84	
P(T<=t) one-tail	0.04	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.08	
t Critical two-tail	2.05	

Table 6.28 *Homo* PC 4 T-test comparing sexes

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	0.03	-0.01
Variance	0.00	0.00
Observations	15.00	15.00
df	24.00	
t Stat	3.34	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.06	

Unshod *Homo*

Very little data is present to document which of the unshod *Homo* specimens are male and female. Therefore no examination of differences between males and females from this group was possible.

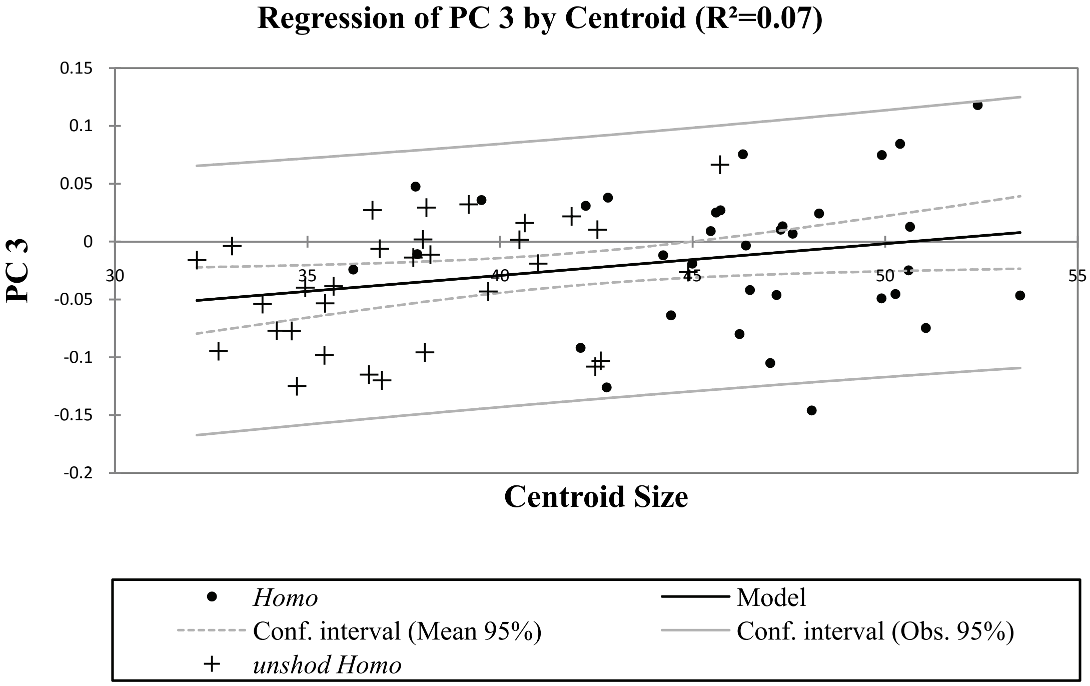
Recent and Unshod *Homo* Differences

As discussed in the PCA and ANOVA analyses, there is a significant difference in centroid size and PC 3 between recent *Homo* and unshod *Homo*. Since sex data is missing from the unshod sample, only size and shape as a whole for each group was compared.

Homo Comparative Shape

Regression analysis for centroid size and PC 3 was done to determine whether size is related to the PC 3 shape difference between recent *Homo* and unshod *Homo*. The analysis yielded a significant relationship with a $p = 0.03$ and an R^2 of 0.07, an extremely low amount of variation explained by size (Figure 6.22). Recent *Homo* has a higher PC 3 score on average than unshod *Homo*, which is slightly related to size. The morphology associated with a higher PC 3 score is a wider dorsal aspect to the surface relative to the plantar medio-lateral breadth.

Figure 6.22 Regression of PC 3 by centroid size for shod and unshod *Homo*



Discussion

The results of the MT 1 shape analysis corroborate Proctor et al. (2008), but some subtle differences emerge. The position of SKX 5017 on the PC axes shows affiliation with apes, and A. L. 333-54, although still grouping with apes, does not group with *Gorilla* or *Hylobates* and is closer to the area occupied by *Homo* compared to the previous study (Proctor et al., 2008). This can be explained due to the addition of landmarks that capture the additional morphology of this surface at the dorsal and plantar aspects. The specimen A. L. 333-54, while being deeply curved, lacks oblique curvature in the dorso-lateral area. This area was not captured by the landmarks in the previous study. In the main analysis that includes all landmarks, there is a clear morphological split between humans and apes. The fossil specimens show three "shape trends." The first is that OH 8 is indistinguishable from humans. Therefore, the hypothesis (H_6) that the proximal MT surfaces of OH 8 will resemble humans cannot be falsified.

The second shape trend is that SKX 5017 and SK 1813 (from the second analysis) show affiliation to the apes. All remaining fossil specimens for MT 1 are intermediate between humans and apes in shape. Therefore, the hypothesis (H_7) that the fossil specimens new to this kind of analysis (excluding A. L. 333-54 and SKX 5017) will more closely resemble humans is falsified.

The ape morphology reflected in the combination of the PC 1 and PC 2 axes is of a saddle joint, with oblique curvature in the medio-plantar and latero-dorsal areas. The surface is very curved in the dorsal and plantar aspects, and the overall surface is wider at the medio-lateral aspect relative to the dorso-plantar dimension. Within apes, the morphology changes from being a particularly deep surface at the negative aspect to having reduced oblique curvature toward the 0.00 axis of PC 1. *Gorilla* is statistically different from *Pan* and *Hylobates,* but *Pan* and *Hylobates* are not statistically different from one another. This corresponds to their broad locomotor differences, since *Gorilla* tends to be more terrestrial. *Gorilla* also tends to have greater curvature at the medio-plantar aspect of the articular surface, which is accompanied by a tendency for extra bone deposition just inferior to this curvature. This can be interpreted as a region that in *Gorillas* is subject to greater compressive forces and may relate to either their greater body size, greater terrestriality, or both. However, it is particularly interesting that *Pan* and *Hylobates* are not statistically different at the PC 1 axis regardless of the fact that *Pan* has a much larger body size and *Hylobates* is much more arboreal.

In contrast, the surface as represented on the PC 1 axis changes into a much flatter morphology at the positive area of the axis, where it ceases to represent a saddle joint.

The surface loses the oblique curvature characteristic of the apes, and the surface is constricted at the central area. In addition, the plantar aspect is narrower than the dorsal aspect and the surface as a whole is relatively narrower medio-laterally.

The morphology represented by STX 5017 is particularly ape-like compared to the other fossil specimens. This specimen has been attributed to the genus and species *Paranthropus robustus* and has been described as being similar in morphology to OH 8 (Susman and Brain, 1988). However, in comparing it to OH 8 it is important to note that the distal half of OH 8 is missing, and that in later analyses by Susman and DeRuiter SKX 5017 demonstrates apelike traits of the metatarsal head (Susman and DeRuiter, 2003). The proximal articular surface of SKX 5017 is not particularly deep, but it is ape-like in that it is relatively wide, lacks the human constriction to the central region, and demonstrates overall surface curvature that is deeper in the central area as opposed to the typical human condition of surface elevation in the central area. In addition, SKX 5017 demonstrates oblique ape-like surface curvature that is particularly expressed at the medio-plantar aspect. In this region it especially resembles *Gorilla*, as *Gorilla* tends to have additional curvature at the medio-plantar aspect relative to *Pan*.

The specimens A. L. 333-54, Stw 562 and Stw 573 group very tightly on the PC 1 axis. Of these, A. L. 333-54 has been attributed to the genus and species *Australopithecus afarensis*, Stw 573 has tentatively been assigned to *Australopithecus africanus*, and Stw 562 has not been assigned to a genus (Clarke and Tobias, 1995; Latimer et al. 1982; Latimer and Lovejoy, 1990; Deloison, 2003). Since Stw 562 comes from Sterkfontein member 4, it is possible that it is *Paranthropus* or early *Homo*. Of these three specimens, A.L. 333.54 and Stw 562 have deep articular surfaces and resemble each other somewhat more than either does Stw 573 that has a more shallow surface. All of these specimens have the characteristic human constriction of the central region and the plantar breadth is narrower than the dorsal breadth, making them similar to humans. The morphology of all of these specimens at the PC 1 axis is intermediate between humans and apes.

The *Homo habilis* specimen OH 8 groups well within the human PC 1 grouping. The articular surface is flat, and is constricted in the middle region. In shape it is indistinguishable from the human proximal surface. Since OH 8 also exhibits a medial facet for articulation with MT 2, it is highly probable that OH 8 represents a completely immobile human-like tarsometatarsal joint.

The PC 2 axis is most useful for distinguishing differences in articular surface shape between the ape groups, with a separation between *Gorilla* and the more arboreal groups. *Gorilla* occupies a more negative position on the PC 2 axis, while *Hylobates* is at the higher end of the axis and *Pan* is intermediate. The area occupies by *Hylobates* and *Pan* shows a tendency toward greater surface curvature, particularly in the dorso-medial area, and narrowing of the plantar portion of the articular surface. The surface of *Gorilla* is more uniformly wide and deep in the central area.

The results for the separate principle components analysis with specimen SK 1813 closely resembles the main analysis that includes all landmarks. In the full analysis SKX 5017 groups with apes, OH 8 groups with humans, and the remaining fossil specimens are intermediate between humans and apes. In the analysis for SK 1813 landmarks are missing in the dorso-lateral area of the articular surface. This results in all of the fossils more closely grouping with humans, except for SKX 5017 and SK 1813. The specimen SK 1813 has been described as being very similar to SKX 5017 (Susman and de Ruiter, 2004). This analysis corroborates those findings, further showing that the articular surfaces of these specimens are very similar. It is therefore likely that SK 1813 belongs to the genus *Paranthropus*. The combination of these analyses, if considering both the full analysis including all landmarks and the analysis with missing landmarks, shows a morphological split between the humans, apes, and fossil specimens.

This observation brings to question the idea that the genus *Paranthropus* is adapted to bipedalism in the same way and at the same time as *Homo habilis*, which has been proposed previously (Susman and Brain, 1988). If some of the unattributed fossils belong to *A. africanus* or *Homo habilis*, we may be observing a difference in morphology reflecting a lasting dependence on some form of arboreal behavior by *Paranthropus* even after the evolutionary line leading to modern humans is adapting to more efficient terrestrial bipedalism.

There is a significant relationship between size and shape for each of the four principle components discussed in these results. Therefore, the hypothesis (H_{10}) that differences in shape interspecificaly are unrelated to size is falsified. However, for all of the PC axes, and most especially for PC 1 and PC 2, the R2 value increases dramatically when species group names are included as a variable. This is particularly important when interpreting the effects of size on shape for the PC 1 and PC 2 axis, since these axes are the most revealing in terms of shape differences interspecificaly and interspecificaly. There is a significant difference in size between all groups except for *Gorilla* and shod *Homo*. Coupled with the extreme contrast in size between all other groups compared to *Hylobates*, care must be taken when interpreting the effects of size on shape. These groups happen to have differing body sizes while they also have varying modes of locomotion. If species group is considered a proxy for locomotion, it puts the results into a better context. When considering size alone for PC 1, size only accounts for 13% of the variance. When species groups are added the combined variation explained rises to 88%. Similarly, size alone accounts for 27% of the variation on the PC 2 axis. This axis is most important for showing differences between ape groups. The ape groups have a wide range of size across species, and including the species name as a proxy for locomotor differences raises the percentage of variation explained to 54%. These results show that size, shape, and locomotion are all important factors in interpreting shape differences between the groups.

The hypotheses (H_9) that there is no difference in size between sexes intraspecifically, (H_{12}) that there are no shape differences intraspecifically, and (H_{11}) that differences in shape between sexes intraspecifically are unrelated to size are all falsified for *Gorilla*. *Gorilla* males and females are significantly different in size and shape on the PC 2 and PC 4 axes. There is a significant relationship between size and shape at these axes. Of these results the most significant is their difference at the PC 2 axis. In a regression analysis size accounts for 37% of the variance at the PC 2 axis. Males tend to have a higher value on this axis compared to females. Overall this is a marginal difference in the larger context of all ape groups. However, it does show a slight tendency for males to have greater curvature in the dorso-medial area of the articular surface.

There are fewer differences between males and females within the groups *Pan* and *Hylobates*. There is a significant difference in size between *Pan* males and females, thus H_9 (that there are no size differences between sexes) cannot be rejected. However, there were no shape differences between males and females, thus H_{11} (differences in shape are unrelated to size) and H_{12} (that there is no differences in shape between sexes) cannot be falsified. Within *Hylobates*, there are no differences between males and females in terms of size and shape. Thus, H_9, $H_{11}$and H_{12} cannot be rejected.

Within the shod *Homo* group, there is a significant difference in size between males and females, and a significant difference in shape on the PC 1 and PC 4 axes. However, regression analysis revealed insignificant results when testing for a relationship between size and shape. Therefore, H_9 and H_{12} cannot be rejected, but H_9 cannot be rejected. The PC 4 axis is not very revealing in terms of shape, but the PC 1 axis is most important in distinguishing between humans and apes. Females have a mean PC 1 score that is only slightly lower than males (0.10 versus 0.11). It is likely that this result would not be significant with a larger sample size. The other possibility is that there is a slight difference in morphology due to differing locomotor habits. However, locomotor habits between human males and females have only been found to show a significant difference in an unshod population (Hilton, 1997).

It is revealing that the two *Homo* samples are not different at the PC 1 axis, which is the axis that best distinguishes human and ape morphology. There is an ongoing argument that apelike features of fossil hominins have little behavioral or functional significance, and that these characteristics are essentially vestigial or represent morphology that is not fully adapted to habitual and efficient bipedalism (Stern, 2000). There is an undercurrent in this debate that is seldom articulated clearly. This is the idea that habitually unshod individuals would have some sort of apelike appearance, and that since early hominins were unshod this can account for some similarities between apes and fossil hominins.

As discussed previously, unshod populations have greater flexibility of the forefoot and phalanges, but greater stability of the longitudinal arch. It is the longitudinal arch that is of particular importance when considering proximal metatarsal joint surface morphology. Rather than see a divergent unshod morphology, we find a wider range of morphology in the shod sample. The hypothesis (H_4) that habitually shod and unshod populations have no difference in morphology is rejected only for the PC 3 axis. However, the observable morphology suggests that the differences in morphology between shod and unshod samples are unrelated to apelike morphology. The positive area PC 3 axis is related to having a wider dorsal area of the surface, and shod *Homo* had a higher average PC 3 score compared to unshod *Homo*. The regression analysis for size and shape at PC 3 was significant, but size only explains 7% of the variation. It is probably that these results show population differences or a small difference only related to size. It must be kept in mind that the PC 3 axis is only responsible for 10% of the total variation in the MT 1 analysis.

CHAPTER 7: ANALYSIS OF METATARSAL 2

Interspecific MT 2 Shape Variation

Articular surface shape was examined using a principal components analysis to determine whether MT 2 proximal articular surface shape shows differences between species. The first four principal components represent 65% of the variation observed in the sample. The individual proportions for the principal components of PC 5 and higher were below 6% and are not morphologically revealing. See Table 7.1 for the proportions of variation represented by PC 1 though PC 4. Refer to Figures 7.1 and 7.2 for an example of each species and for photos of the fossils. Discussion of the PCA results follows.

Table 7.1 Proportion of PC Variance for MT 2

Proportion of Variance for MT 2			
PC 1	PC 2	PC 3	PC 4
31%	17%	11%	6%

Table 7.2 Extant Specimens in the MT 2 Analysis

Group	Number
Gorilla	31
Pan	30
Hylobates	29
Homo	34
unshod *Homo*	33

Figure 7.1 Extant groups in this study include the following: A) recent *Homo*; B) unshod *Homo*; C) *Gorilla*; D) *Pan*; E) *Hylobates*.

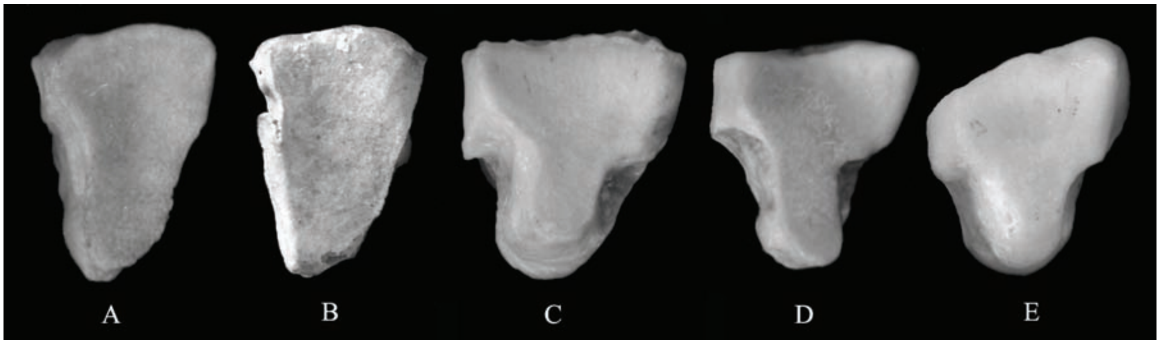
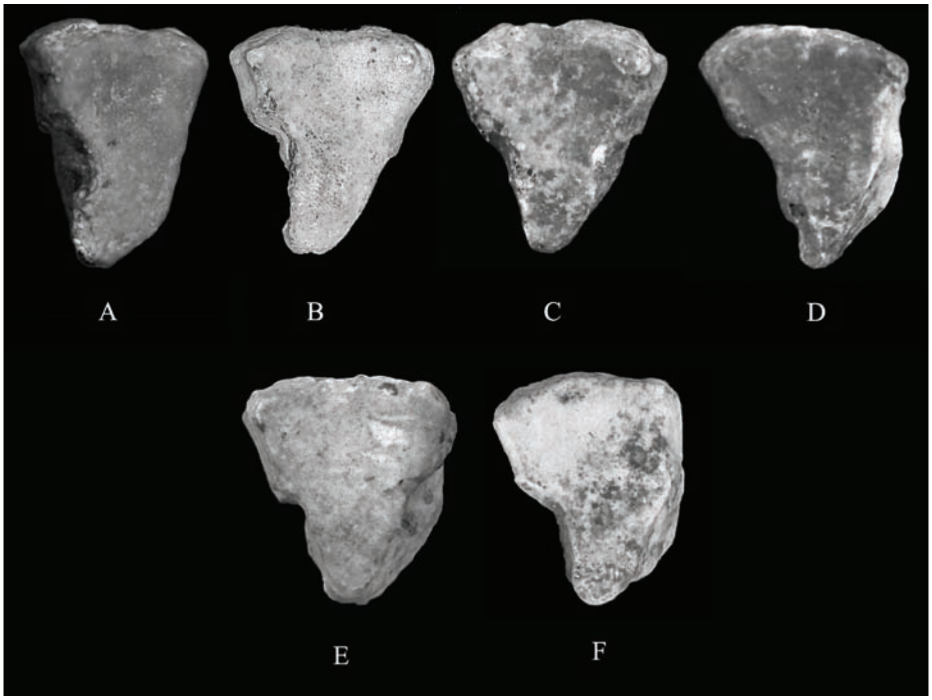


Figure 7.2 Fossils studied include: A) OH 8; B) Stw 573 "Little Foot"; C) Stw 377; D) Stw 595c (reversed, this is a right); E) Stw 89; F) SKX 247. These specimens are not to scale.



MT 2 Principal Component 1

There is separation of human and ape specimens on the PC 1 axis; an ANOVA was conducted to test for differences in the means of PC 1 scores between groups; there was a statistically significant result with a *p* value below 0.00. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported in Table 7.3.

Table 7.3 Tukey-Kramer Multiple-Comparison Test for PC 1

Group	Specimens	Mean	Different From Groups
Gorilla	31	-0.04	*Hylobates*, *Pan*, *Homo*, unshod *Homo*
Pan	30	-0.07	*Gorilla*, *Homo*, unshod *Homo*
Hylobates	29	-0.07	*Gorilla*, *Homo*, unshod *Homo*
Homo	34	0.08	*Hylobates*, *Pan*, *Gorilla*
unshod *Homo*	33	0.08	*Hylobates*, *Pan*, *Gorilla*

Table 7.4 Principal Component 1 Ranges for MT 2

Group	Minimum	Maximum	Range
Gorilla	-0.14	0.03	0.17
Pan	-0.16	0.00	0.16
Hylobates	-0.12	-0.04	0.08
Homo	0.02	0.15	0.13
unshod *Homo*	0.01	0.17	0.16

Table 7.5 Fossil PC 1 Values for MT 2

Specimen	PC 1
Stw 573 “Little Foot”	0.06
SKX 247	0.00
Stw 377	0.04
Stw 89	-0.01
Stw 595c	0.01
OH 8	0.10

The Tukey-Kramer post hoc test revealed that *Gorilla* is statistically different from all other groups at the PC 1 axis. *Pan* and *Hylobates* are not different from one another, but are different from all other groups. *Homo* and unshod *Homo* are different from all ape groups but not from one another.

Humans and apes are clearly differentiated on the PC 1 axis, with some overlap between *Gorilla* and both *Homo* groups (Figure 7.3; Table 7.4). All ape groups overlap one another, with *Hylobates* falling completely within the range of *Pan* and *Gorilla*. *Gorilla* has a range that projects into the positive range of PC 1, and projects further to the negative range. *Homo* and unshod *Homo* overlap completely, with unshod *Homo* having a slightly wider range.

The morphology on the PC 1 axis at the negative portion occupied by the ape groups is a relatively wide and concave dorsal surface and a narrow and flat plantar surface (Figure 7.4). The plantar and dorsal surface face in different directions, with the dorsal surface twisted toward the lateral side and the plantar surface toward the medial side. The morphology on the positive side of the axis occupied by both *Homo* groups is a narrower dorsal aspect of the surface and a relatively wider plantar portion, so that the dorsal and plantar aspects of the surface are much closer in width (Figure 7.5). The effect is an overall narrower surface with plantar expansion of the articular surface. The overall surface is slightly concave, with the dorsal and plantar aspects begin continuous instead of twisted in opposing directions as occurs in the apes.

The fossil specimens OH 8, Stw 377 and Stw 573 group with humans and do not overlap any ape groups on the PC 1 axis. The specimen Stw 595c falls in a narrow area of overlap between *Gorilla* and unshod *Homo*, but overlaps no other groups at this axis. The specimens SKX 247 and Stw 89 do not overlap the human groups or *Hylobates*, but overlap both *Pan* and *Gorilla*.

Figure 7.3 Plot of PC 1 and PC 2 group averages and fossil specimens for MT 2

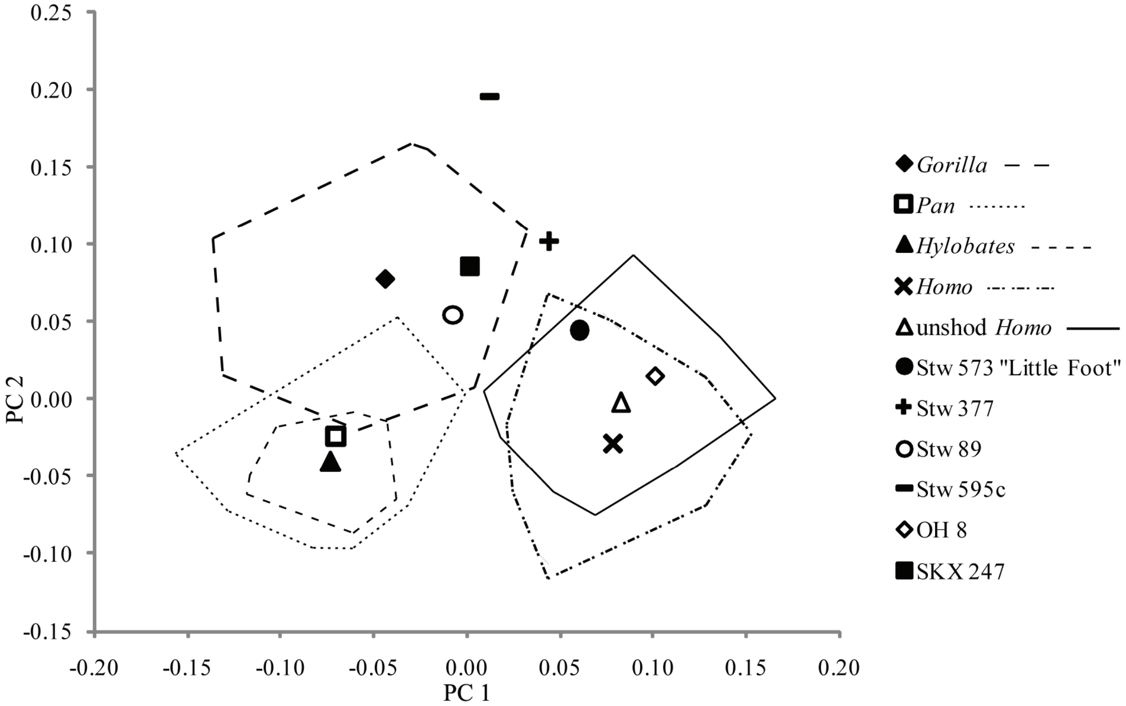


Figure 7.4 PC 1 (-0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

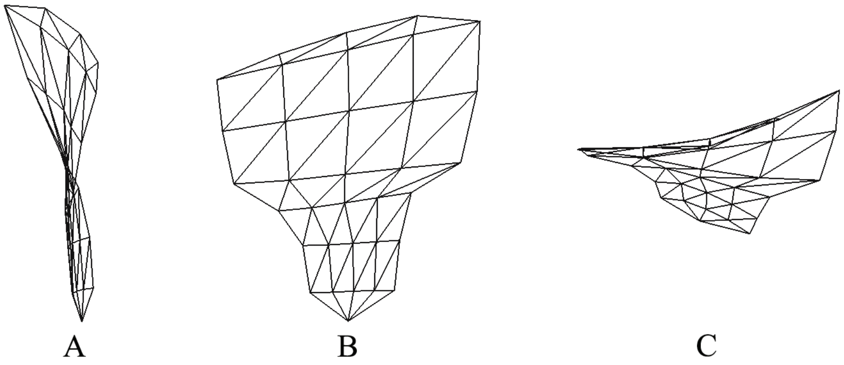
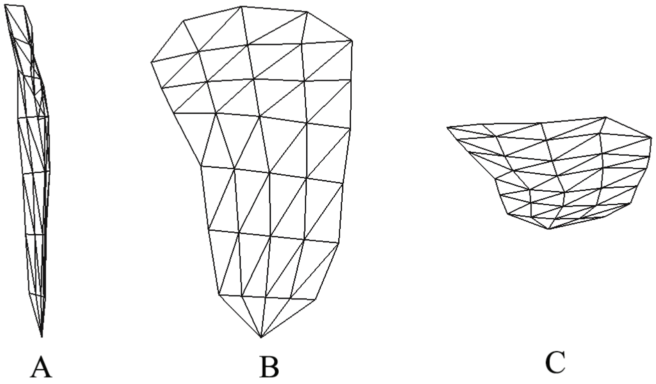


Figure 7.5 PC 1 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 2 Principal Component 2

An ANOVA was conducted to test for differences in the means of PC 2 scores between groups; there was a statistically significant result with a *p* value below 0.00. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level, except the Levene equal variance test. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. Refer to Table 7.6.

Table 7.6 Tukey-Kramer Multiple-Comparison Test for PC 2

Group	Specimens	Mean	Different From Groups
Gorilla	31	0.07	*Hylobates*, *Homo*, *Pan*, unshod *Homo*
Pan	30	-0.02	*Gorilla*
Hylobates	29	-0.04	unshod *Homo*, *Gorilla*
Homo	34	-0.03	unshod *Homo*, *Gorilla*
unshod *Homo*	33	-0.02	*Hylobates*, *Homo*, *Gorilla*

Table 7.7 Principal Component 2 Ranges for MT 2

Group	Minimum	Maximum	Range
Gorilla	-0.02	0.17	0.19
Pan	-0.10	0.05	0.15
Hylobates	-0.08	-0.01	0.07
Homo	-0.12	0.07	0.19
unshod *Homo*	-0.07	0.09	0.16

Gorilla is different from all other groups on the PC 2 axis, while *Pan* is only different from *Gorilla*. *Hylobates* and *Homo* are different from *Gorilla* and unshod *Homo*, but no other groups. Unshod *Homo* is different from all groups except *Pan*. The morphology at this axis should be interpreted with the acknowledgement that other axes also influence shape, and that human and ape groups have different influences from PC 1. The surface is flatter at the negative aspect of this axis, and is more curved, particularly at the dorsal portion of the surface, toward the positive side of the axis (Figure 7.6). At the positive aspect of the axis the surface is expanded and curved proximally on the medial middle area (Figure 7.7). In addition, the plantar aspect of the surface curves medially before reaching a plantar apex.

Gorilla is very different from the other apes at the PC 2 axis, with a surface that is expanded in the middle and medial portion of the dorsal surface. Although the means of the PC 2 axis are statistically different between *Homo* and unshod *Homo*, their ranges are not as different as between *Gorilla* and the other ape groups. *Homo* has a range that tends toward the negative PC 2 axis and unshod *Homo* trends more toward the positive axis. Part of the difference at the PC 2 axis is a larger facet for articulation with the medial cuneiform at the positive PC 2 axis. It is unclear if this is related to being more terrestrial and unshod, since it is a trait shared by *Gorilla*, or whether the difference between human groups is related to differences in populations with no functional significance.

The fossil specimen Stw 595c does not overlap any other groups and is located at an extreme positive location on the PC 2 axis. The specimens OH 8, Stw 573 and Stw 89 overlap both human groups, *Gorilla*, and *Pan*. SKX 247 overlaps *Gorilla* and unshod *Homo*; Stw 377 only overlaps *Gorilla*.

Table 7.8 Fossil PC 2 Values for MT 2

Specimen	PC 2
Stw 573 “Little Foot”	0.04
SKX 247	0.09
Stw 377	0.10
Stw 89	0.05
Stw 595c	0.20
OH 8	0.02

Figure 7.6 PC 2 (-0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

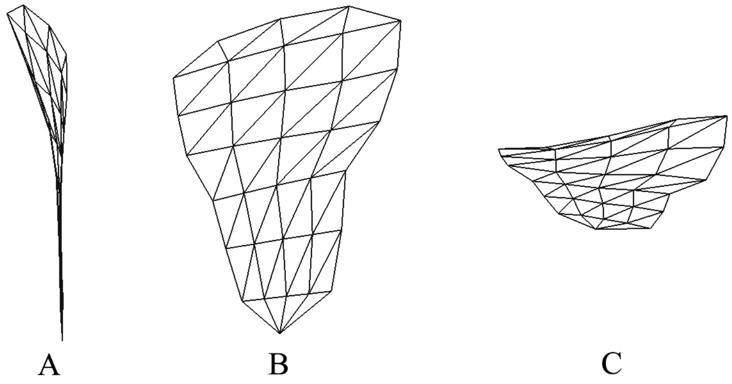
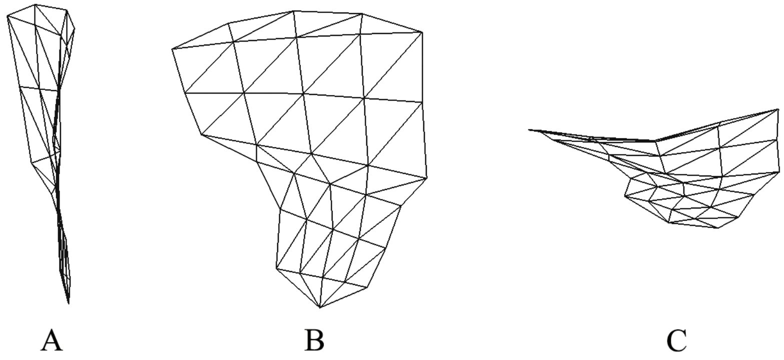


Figure 7.7 PC 2 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 2 Principal Component 3

An ANOVA was conducted to test for differences in the means of PC 3 scores between groups, with a statistically significant result and a *p* value below 0.00. In addition, the following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. Refer to Table 7.9.

On the PC 3 axis, *Gorilla* is only statistically different from *Hylobates*. *Pan* is different from *Homo* and *Hylobates*. *Hylobates* is different from all groups except *Homo*, and *Homo* is different from unshod *Homo* and *Pan*. Unshod *Homo* is different from *Hylobates* and *Homo*. Most fossil specimens overlap all groups except for Stw 89, which overlaps all groups other than *Homo*, and Stw 377 that overlaps all groups except *Pan* (Figure 7.10).

The differences in morphology on the PC 3 axis are subtle at each extreme on the axis (Figures 7.8 and 7.9). The positive extreme of the PC 3 axis represents an overall narrower surface in both the dorsal and plantar aspects, with the plantar aspect curving medially before reaching a plantar apex (Figure 7.9). In addition, the dorsal aspect is expanded dorsally. As with other axes after PC 1, it is more relevant to interpret these results as they pertain to apes and humans separately. *Pan* and *Gorilla* are not different from one another but both are different from *Hylobates*; *Pan* and *Gorilla* tend to have slightly narrower surfaces on this axis. Similarly, unshod *Homo* tends to have a narrower surface expanded in the dorsal direction compared to *Homo*.

Table 7.9 Tukey-Kramer Multiple-Comparison Test for PC 3

Group	Specimens	Mean	Different From Groups
Gorilla	31	0.06	*Hylobates*
Pan	30	0.02	*Hylobates*, *Homo*
Hylobates	29	-0.03	*Gorilla*, *Pan*, unshod *Homo*
Homo	34	-0.02	*Pan*, unshod *Homo*
unshod *Homo*	33	0.02	*Hylobates*, *Homo*

Table 7.10 Principal Component 3 Ranges for MT 2

Group	Minimum	Maximum	Range
Gorilla	-0.07	0.10	0.17
Pan	-0.04	0.11	0.15
Hylobates	-0.09	0.07	0.16
Homo	-0.09	0.04	0.13
unshod *Homo*	-0.08	0.15	0.23

Table 7.11 Fossil PC 3 Values for MT 2

Specimen	PC 3
Stw 573 "Little Foot"	0.00
SKX 247	0.01
Stw 377	-0.07
Stw 89	0.06
Stw 595c	-0.04
OH 8	-0.03

Figure 7.8 PC 3 (-0.08) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

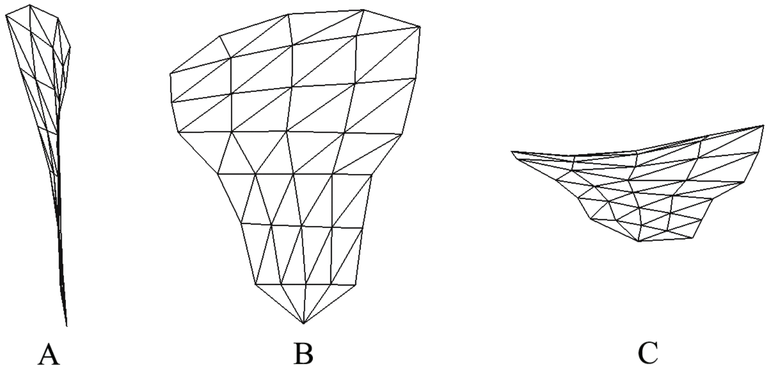


Figure 7.9 PC 3 (0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

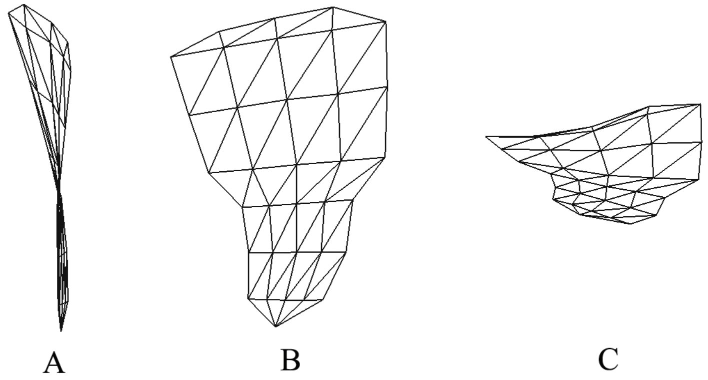
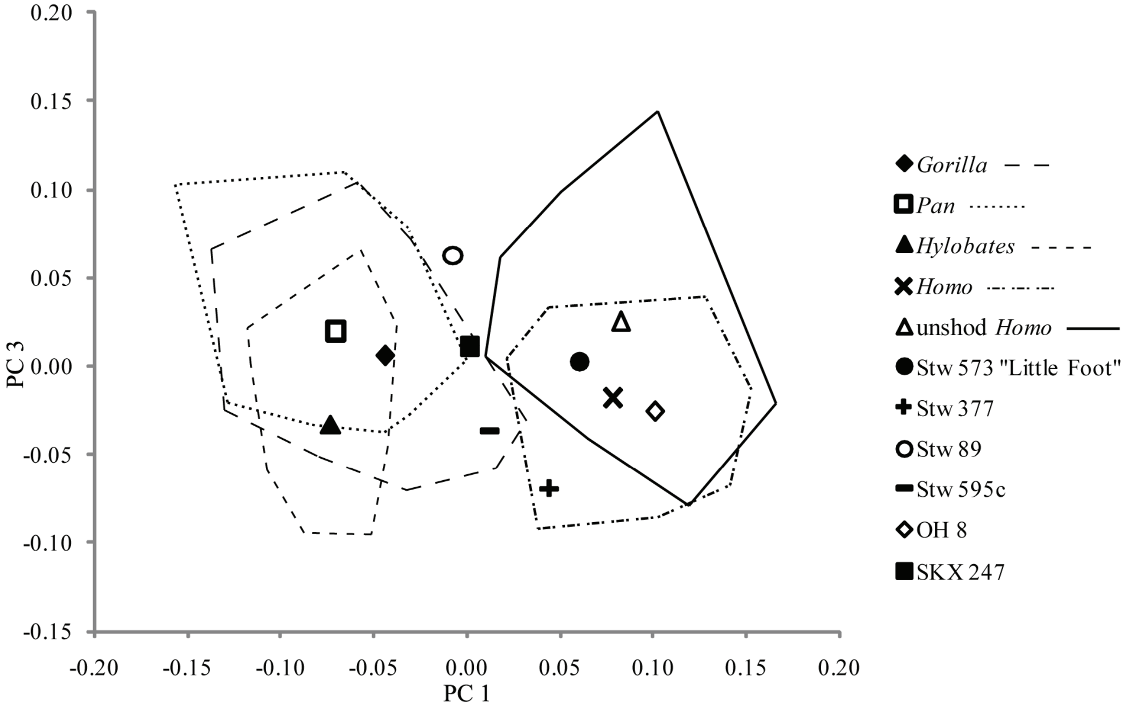


Figure 7.10 Plot of PC 1 and PC 3 group averages and fossil specimens for MT 2



MT 2 Principal Component 4

To test for differences in the means of PC 4 scores between groups, an ANOVA was conducted and resulted in a statistically significant *p* value below 0.00. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. A Tukey-Kramer post-hoc test was conducted with the ANOVA to test for statistically significant differences in means between specific groups. See Table 7.12.

There are two main groupings at this axis (Figure 7.13). *Gorilla*, *Pan*, and *Homo* are not different from each other but are different from unshod *Homo* and *Hylobates*. Unshod *Homo* and *Hylobates* are not different from one another. The fossil specimens OH 8, Stw 377, and Stw 573 overlap all groups on the PC 4 axis. The specimens Stw 89 and SKX 247 overlap only *Pan*, and Stw 595c does not overlap any groups on the PC 4 axis (Tables 7.13 and 7.14).

The PC 4 axis shows morphology at the negative aspect that has a narrower plantar surface that is curved medially and has greater dorsal curvature in the medio-lateral plane (Figure 7.11). The positive PC 4 axis shows morphology of a wider plantar surface; the dorsal surface is expanded at the dorsal articular surface edge (Figure 7.12).

Table 7.12 Tukey-Kramer Multiple-Comparison Test for PC 4

Group	Specimens	Mean	Different From Groups
Gorilla	31	-0.02	unshod *Homo*, *Hylobates*
Pan	30	-0.02	unshod *Homo*, *Hylobates*
Hylobates	29	0.02	*Pan*, *Gorilla*, *Homo*
Homo	34	-0.06	unshod *Homo*, *Hylobates*
unshod *Homo*	33	0.02	*Pan*, *Gorilla*, *Homo*

Table 7.13 Principal Component 4 Ranges for MT 2

Group	Minimum	Maximum	Range
Gorilla	-0.07	0.04	0.11
Pan	-0.08	0.04	0.12
Hylobates	-0.03	0.09	0.12
Homo	-0.09	0.06	0.15
unshod *Homo*	-0.03	0.05	0.08

Table 7.14 Fossil PC 4 Values for MT 2

Specimen	PC 4
Stw 573 “Little Foot”	0.03
SKX 247	0.08
Stw 377	0.02
Stw 89	0.08
Stw 595c	0.10
OH 8	-0.03

Figure 7.11 PC 4 (-0.08) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

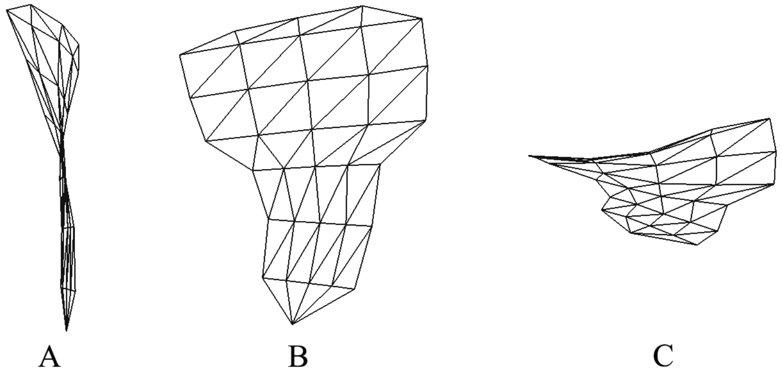


Figure 7.12 PC 4 (0.08) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

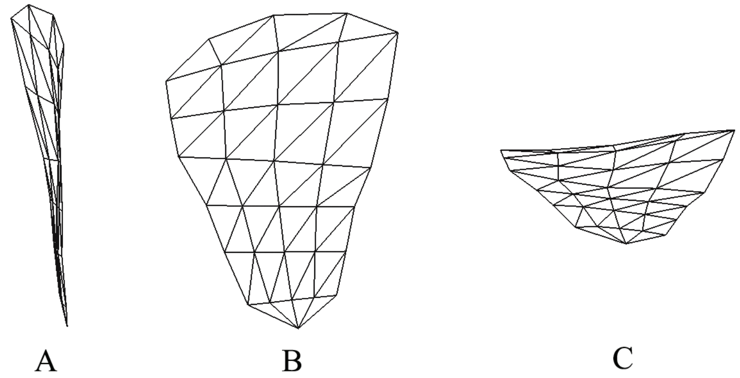
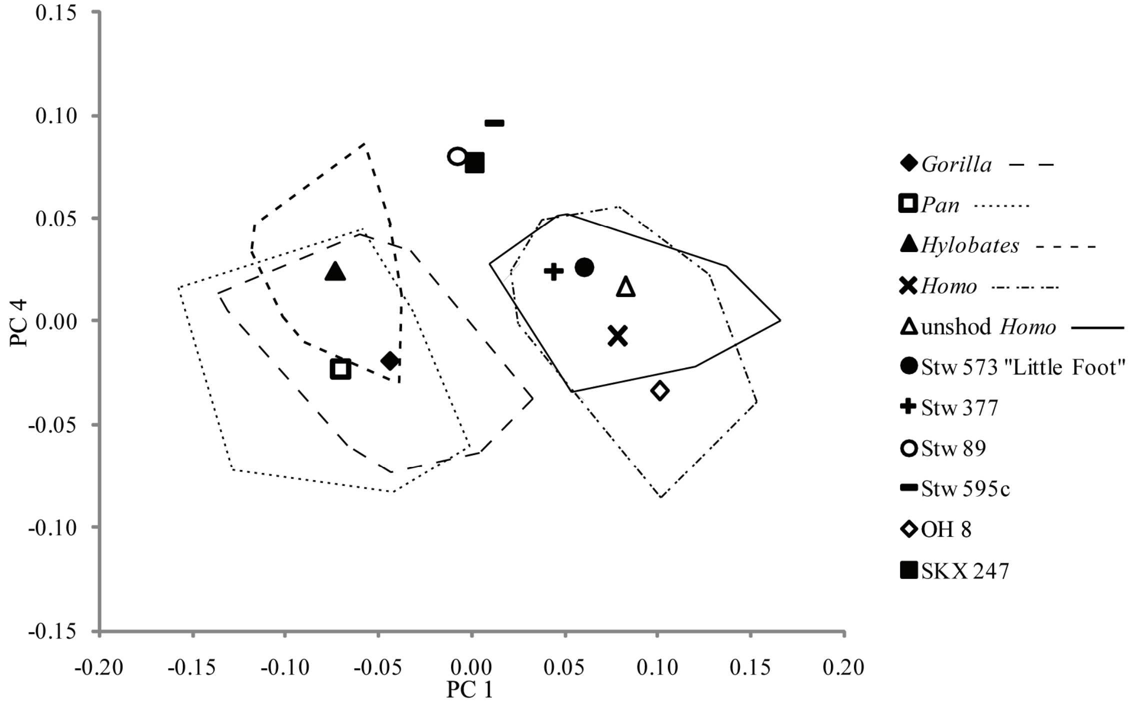


Figure 7.13 Plot of PC 1 and PC 4 group averages and fossil specimens



Interspecific Size and Shape Relationships for MT 2

An ANOVA was used to test for differences in centroid size between groups, and the Tukey-Kramer (post hoc) multiple-comparison test was used to look for differences between specific groups. There is a statistically significant difference in mean centroid sizes with a *p* value below 0.00. H_8 is falsified. The multiple-comparison test results are reported below. Tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test. These tests passed at the 0.05 significance level, except for the test for equal variance. A Shapiro-Wilk distribution test for normality was conducted. Normality could not be rejected for all species groups except *Gorilla*.

There is no significant difference between *Gorilla* and shod *Homo* in centroid size (Table 7.15). In addition, there is no difference in centroid size between *Pan* and unshod *Homo*. *Hylobates* is significantly different from all groups and has the narrowest range; *Homo* has the widest range, followed by unshod *Homo* and *Pan* (Table 7.16).

Table 7.15 Tukey-Kramer Multiple-Comparison Test for Centroid Size of MT 2

Group	Specimens	Mean	Different From Groups
Gorilla	31	39.66	*Hylobates*, *Pan*, unshod *Homo*
Pan	30	31.55	*Hylobates*, *Homo*, *Gorilla*
Hylobates	29	13.88	*Pan*, *Gorilla*, *Homo*, unshod *Homo*
Homo	34	38.67	*Hylobates*, *Pan*, unshod *Homo*
unshod *Homo*	33	32.62	*Hylobates*, *Homo*, *Gorilla*

Table 7.16 Centroid Size Ranges for MT 2

Group	Minimum	Maximum	Range
Gorilla	31.55	45.34	13.79
Pan	27.60	35.12	7.52
Hylobates	12.61	15.66	3.05
Homo	32.56	48.31	15.75
unshod *Homo*	28.01	38.06	10.05

Table 7.17 Fossil Centroid Sizes for MT 2

Specimen	Centroid
Stw 573 “Little Foot”	29.69
SKX 247	30.88
Stw 377	27.46
Stw 89	23.21
Stw 595c	23.13
OH 8	26.92

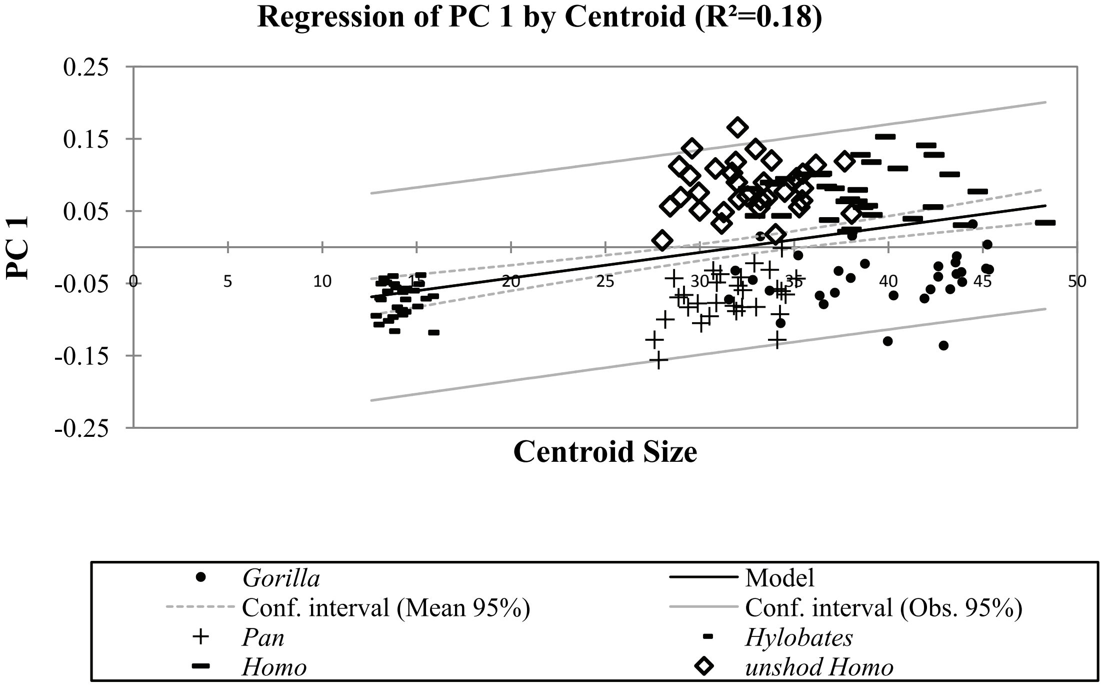
Regression analysis and an ANCOVA were conducted to determine whether there is a relationship between size and shape at the interspecific level. The regression analysis resulted in a significant relationship between centroid size and each PC axis. Refer to Table 7.18.

Table 7.18 Regression and ANCOVA results for MT 2

	PC 1	PC 2	PC 3	PC 4
R^2 with PC and Size	0.18	0.18	0.06	0.16
R^2 with PC, Size, and Species	0.83	0.57	0.23	0.32

Significant relationships exist between size and shape. However, the R^2 values were relatively low when considering only centroid size and shape variables. The R^2 values go up when species groups are used as a qualitative variable. The large disparity in size between *Hylobates* and the other species groups influences the results of these regression analyses. Excluding *Hylobates* from the regression analysis does not always eliminate a significant result, but in this case removing *Hylobates* from the comparison of PC 1 and centroid size did result in an insignificant relationship between size and shape.

Figure 7.14 MT 2 regression for interspecific comparison of PC 1 by centroid size

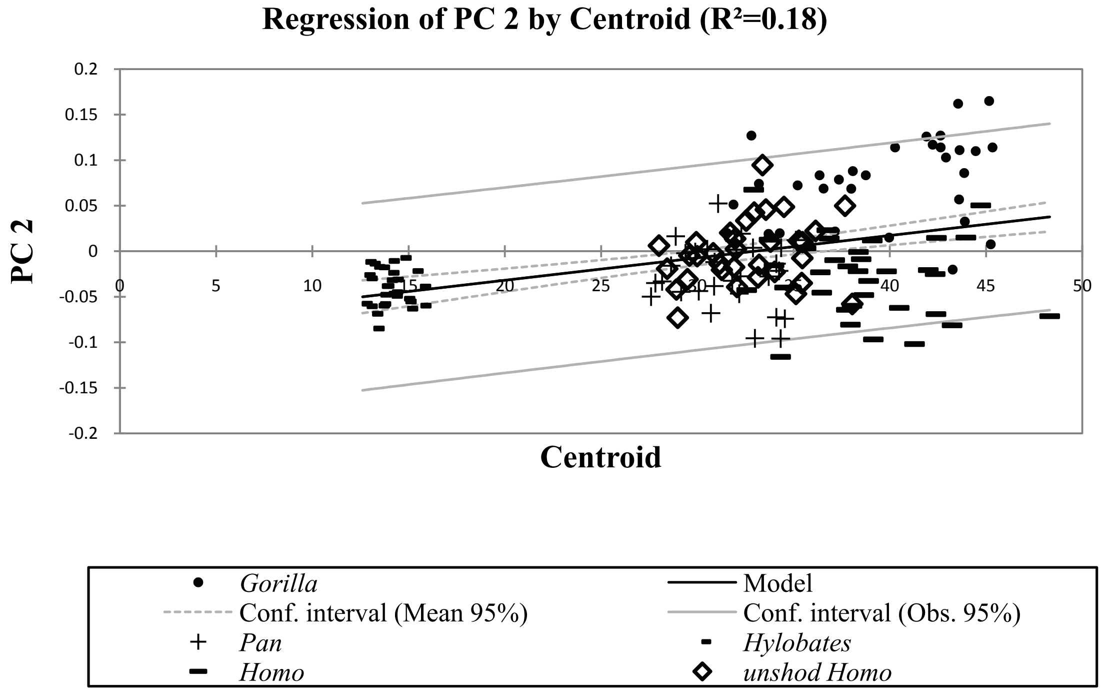


In considering size and shape for PC 1 and centroid size, the regression line divides species by PC 1 score, but aside from the fact that *Hylobates* has a much smaller body size, size does not seem to predict shape very well when considering the African apes and humans (Figure 7.14). As with the analysis of MT 1, PC 1 is most influenced by species as a proxy for locomotion.

In the regression analysis for PC 2 and centroid size, size does not appear to show a consistent relationship with PC 2 across humans and apes (Figure 7.15). *Gorilla* does have a higher PC 2 score and is larger in size compared to *Pan* and *Hylobates*, but unshod *Homo* is smaller than recent *Homo* and has higher PC 2 scores.

The R^2 for the regression analysis of PC 3 and centroid size is small (Figure 7.16). Unshod *Homo* and *Pan* are not significantly different in size and shape on the PC 3 axis. *Homo* and *Gorilla* are also not different in size and PC 3 shape. However, *Hylobates* is different from the other apes at this axis, and this is what is responsible for the relationship of size to PC 3 shape.

Figure 7.15 MT 2 regression for interspecific comparison of PC 2 by centroid size



Hylobates tends to have a higher PC 4 score than other groups (Figure 7.17). All other groups do not differ widely in range of PC 4, and overlap considerably. The greatest effect of size appears to be between *Hylobates* and all other groups, except *Hylobates* is not significantly different from unshod *Homo* at the PC 4 axis. *Gorilla*, *Pan*, and *Homo* are not different from another on the PC 4 axis, and even though unshod *Homo* is not different in size from *Pan* there seems to be an effect of smaller centroid size tends to have a higher PC 4 score.

Figure 7.16 MT 2 regression for interspecific comparison of PC 3 by centroid size

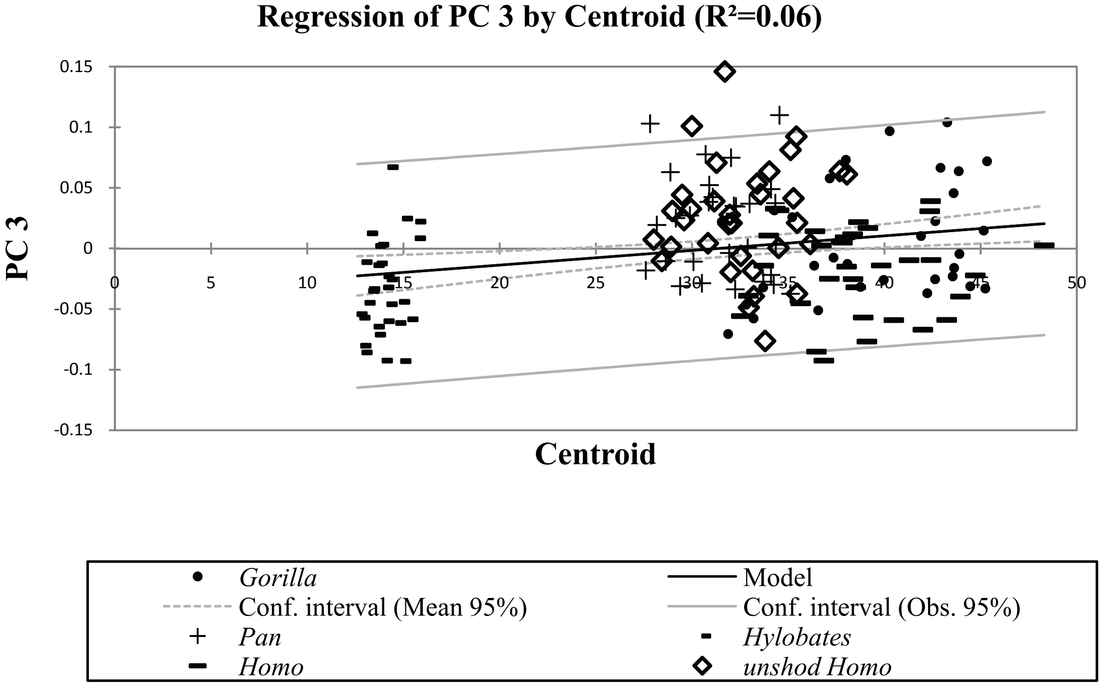
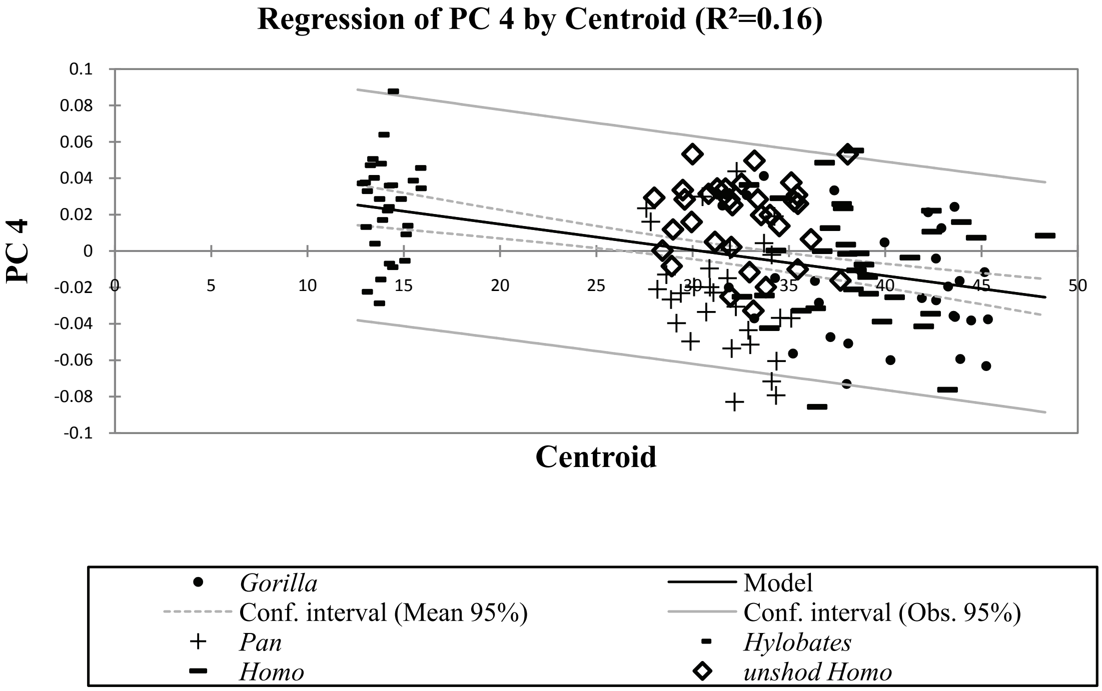


Figure 7.17 MT 2 regression for interspecific comparison of PC 4 by centroid size



Intraspecific MT 2 Shape, Size, and Sex Variation

T-tests assuming unequal variances were conducted between sexes within each sample group for each variable to test the hypothesis that there are differences in size and shape between males and females of each species. Regression analysis was conducted to determine whether size and shape are related if a difference in centroid size between sexes was indicated, and a difference in PC scores was indicated.

Gorilla

<u>*Gorilla* Size and Sex</u>

The t-test to determine whether there is a significant difference in mean centroid size yielded a significant result, with a *p* value of 0.00 (Table 7.19). Males are larger than females.

Gorilla Shape and Size

All t-tests to assess differences in shape between males and females as represented on PC axes1, 2, 3, and 4 yielded insignificant results. There is no difference in proximal MT 2 articular surface shape between males and females.

Table 7.19 T-test for comparison of centroid size between sexes in *Gorilla*

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	37.41	41.52
Variance	16.04	15.71
Observations	14.00	17.00
df	28.00	
t Stat	-2.86	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.01	
t Critical two-tail	2.05	

Pan

Pan Size and Sex

The t-test to assess whether *Pan* males and females have a significantly different centroid size yielded a significant result, with a $p = 0.00$ (Table 7.20). *Pan* males have significantly larger proximal MT 2 articular surfaces than *Pan* females.

Pan Shape and Size

All t-tests to assess differences in articular surface shape for PC axes 1, 2, 3, and 4 yielded insignificant results. There are no morphological differences in proximal PC 2 articular surface shape between *Pan* males and females.

Table 7.20 T-test for comparison of centroid size between sexes in *Pan*

t-Test: Two-Sample Assuming Unequal Variances		
	females	*males*
Mean	30.90	33.09
Variance	4.65	2.44
Observations	21.00	9.00
df	21.00	
t Stat	-3.12	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.72	
P(T<=t) two-tail	0.01	
t Critical two-tail	2.08	

Hylobates

Hylobates Size and Sex

The t-test to assess whether there is a significant difference between *Hylobates* males and females yielded an insignificant result. There is no difference in MT 2 proximal articular surface size between males and females.

Hylobates Shape and Size

The t-tests to determine whether males and females have different proximal MT 2 surface morphology yielded insignificant results for PC 1, PC 3, and PC 4, but yielded a significant difference between males and females for PC 2 with a $p = 0.02$ (Table 7.21). Even though there is no difference between males and females in terms of size, a regression analysis of PC 2 and centroid size was done to see if size and shape were related for PC 2. The regression analysis yielded insignificant results. The significant difference in shape as reflected on the PC 2 axis cannot be explained by size. It is possible that a larger sample size would yield insignificant results.

Table 7.21 T-test for comparison of PC 2 between sexes in *Hylobates*

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	-0.03	-0.05
Variance	0.00	0.00
Observations	17.00	12.00
df	27.00	
t Stat	2.08	
P(T<=t) one-tail	0.02	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.05	
t Critical two-tail	2.05	

Shod *Homo*

Size and Sex

The t-test to assess whether there is a difference in mean centroid size between *Homo* males and females yielded a significant result, with $p = 0.01$ (Table 7.22). Males have significantly larger proximal MT 2 articular surfaces than females.

Homo Shape and Size

T-tests yielded an insignificant result when comparing the means of PCs 1, 3, and 4, but there is a significant difference between males and females for PC 2 (Table 7.23). Males have a lower PC 2 score than females. A regression analysis was done to test whether there is a relationship between centroid size and PC 2 within *Homo*, and it yielded an insignificant result. Size does not explain the difference in articular surface shape between males and females on the PC 2 axis.

Table 7.22 T-test for comparison of centroid size between sexes in *Homo*

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	36.86	40.01
Variance	6.29	15.91
Observations	15.00	15.00
df	24.00	
t Stat	-2.59	
P(T<=t) one-tail	0.01	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.02	
t Critical two-tail	2.06	

Table 7.23 T-test for comparison of PC 2 between sexes in *Homo*

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	-0.01	-0.05
Variance	0.00	0.00
Observations	15.00	15.00
Hypothesized Mean Difference	0.00	
df	26.00	
t Stat	2.45	
P(T<=t) one-tail	0.01	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.02	
t Critical two-tail	2.06	

Unshod *Homo*

Sex data for most unshod specimens was unavailable, making it impossible to determine differences between sexes in regard to size and shape.

Recent and Unshod *Homo* Differences

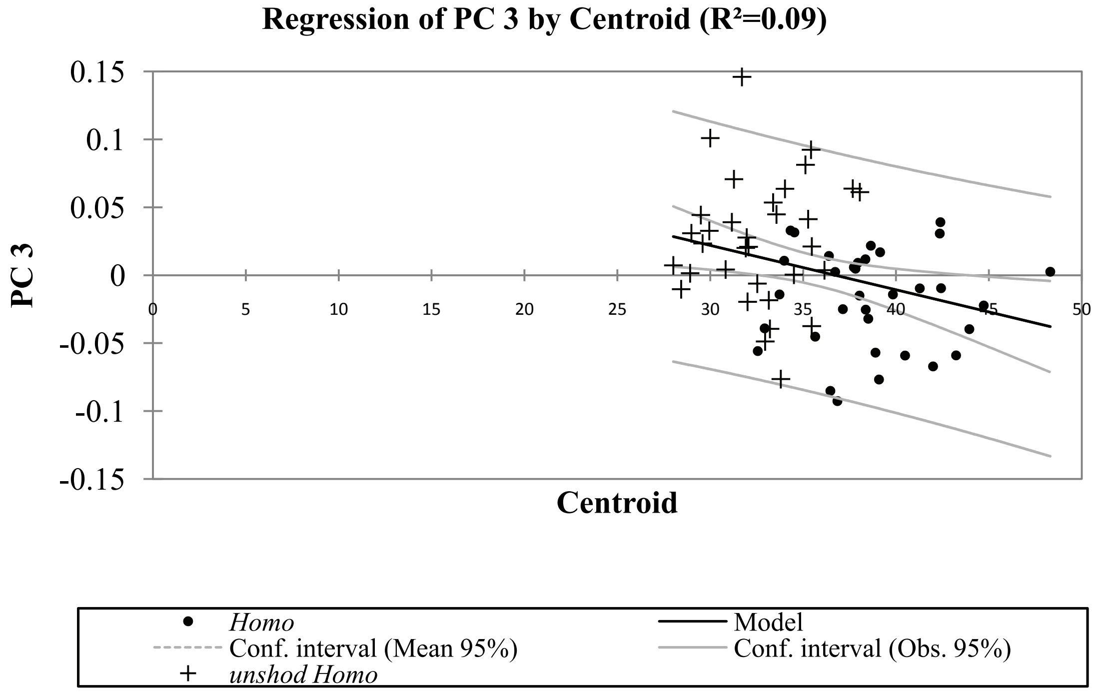
As discussed previously in the PCA and ANOVA analysis of PC scores, *Homo* and unshod *Homo* are significantly different in terms of centroid size and shape on the PC 2, 3, and 4 axes. They are not different on the PC 1 axis, which is the most important axis for distinguishing between human and ape morphology.

Homo Comparative Size and Shape

Regression analysis was done to test whether there is a relationship between size and shape within the *Homo* groups. The analysis yielded insignificant results for PC 2, but significant results for PC 3 and PC 4. Therefore, differences in morphology between recent and unshod *Homo* on the PC 2 axis cannot be explained by size. The difference could be insignificant functionally. Recent *Homo* has a PC 3 range that extends further on the negative area of the axis, which is associated a plantar area which extend in the plantar direction without deviating as much in the medial direction, and has a slightly narrower area at the dorsal surface where it meets the lateral facet for the medial cuneiform.

Regression of PC 3 by centroid size was significant with $p = 0.01$ and an R^2 of 0.09 (Figure 7.18). Similarly, regression of PC 4 by centroid size was significant with $p = 0.01$ and an R^2 of 0.09 (Figure 7.19).

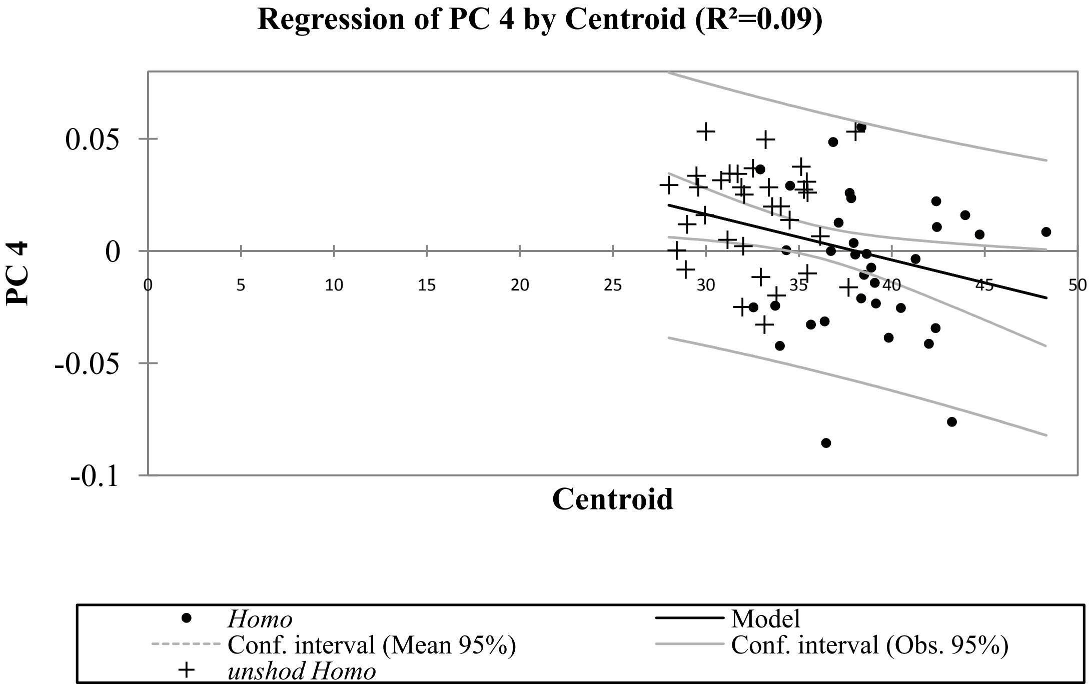
Figure 7.18 MT 2 regression of PC 3 by centroid size (shod and unshod *Homo*)



Specimens with a smaller centroid size tend to have higher PC 3 scores, which is associated with having a narrower plantar region relative to dorsal width of the proximal

MT 2 articular surface with the dorsal area slightly narrower and expanded in a dorsal direction. Smaller specimens similarly tend to occur at the more positive area of the PC 4 axis, with the lower PC 4 are having a slightly narrower and medially curved plantar area. The higher PC 4 specimens tend to have a proximal MT 2 shape that is more triangular without a sharp narrowing in the middle area before the plantar aspect of the surface.

Figure 7.19 MT 2 regression of PC 4 by centroid size (shod and unshod *Homo*)



Discussion

The hypothesis (H_1) that the human MT 2 proximal surface is expanded in the plantar region cannot be falsified. This shape is primarily represented on the PC 1 axis, showing that humans have a relatively narrower surface with an expanded plantar area. Interestingly, there is some overlap between humans and *Gorilla* at this axis, suggesting that the shape on the positive side of the axis may be related to relative terrestriality. The fossil specimens OH 8, Stw 573 (Little Foot), and Stw 377 are indistinguishable from humans in articular surface shape on the PC 1 axis. Therefore, H_6 cannot be falsified as OH 8 is indistinguishable from humans. The fossil specimen Stw 595c overlaps humans and *Gorilla*, but other groups on the PC 1 axis, while SKX 247 and Stw 89 overlap the African apes on PC 1 but no other groups. The only complete fossil specimen is Stw 89; the others are missing their distal ends. On the PC 1 axis Stw 89 overlaps *Gorilla* and *Pan*, and is close to SKX 247. There is a pronounced dorsal sulcus on the distal end of Stw 89, indicating a human-like hyperextension of the proximal phalange during locomotion. The shaft is slightly curved, and the head may exhibit some small amount of medial torsion. However, the dorsal area of the surface is wide and plantar aspect of the proximal articular surface is relatively narrow, and lacks the characteristic human expansion. This combination of traits represents a mosaic of traits, many of which clearly indicate adaptations to bipedalism and terrestriality, but the proximal surface is not consistent with human morphology. This could indicate that the longitudinal arch belonging to the specimens that do not overlap humans would not have been developed as fully as in humans, or it might indicate that if an arch was present the joint structure and component to the arch was less stable.

There are statistically significant differences in articular surface size between groups, with three groupings. *Gorilla* and *Homo* are not different in size, while *Pan* and unshod *Homo* are not different in size. Regression analyses resulted in significant relationships between size and PC 1, PC 2, PC 3, and PC 4. Therefore, the hypothesis (H_{10}) that differences in shape are unrelated to size cannot be falsified. Including species group names in the analysis increased the percentage of variation explained in the regression considerably. For PC 1, the variation explained rises from 18% to 83%. For PC 2, the variation explained rises from 18% to 57%. Although size does influence shape, belonging to one group or another is a better predictor of shape.

There is a significant difference in size between *Gorilla* males and females. The hypothesis H_9 (that there are no size differences between sexes) was falsified. However, there were no significant differences in shape between males and females. Thus, H_{12} (that there is no differences in shape between sexes) could not be falsified. Analysis of males and females within *Pan* yielded identical results; thus H_9 could be falsified but H_{12} could not be falsified. There is no difference in size between males and females within *Hylobates*, and H_9 could not be falsified. However, H_{12} was falsified due to a significant difference in articular surface shape between males and females. Within the *Homo* group, there is a significant difference in size between males and females, so that H_9 was falsified. In addition, there was a significant difference between males and females on the PC 2 axis, so that H_{12} was falsified. However, regression analysis yielded insignificant results, and H_{11} could not be falsified.

As noted previously, there is a significant difference in size between unshod *Homo* and *Homo*. In addition, there is a significant different between these groups for PC 2, PC 3, and PC 4. Of these, a significant relationship exists between size and shape for PC 3 and PC 4, both of which have R2 values of .09. Therefore, the variation explained by size is low, with size unable to explain any of the variation for PC 2. The interpretation of shape for these axes indicates that unshod *Homo* may have a slightly narrower plantar aspect to the articular surface, which tends to curve medially toward the plantar apex.

CHAPTER 8: ANALYSIS OF METATARSAL 3

Interspecific MT 3 Shape Variation

Articular surface shape was examined using a principal components analysis to determine whether MT 3 proximal articular surface shape shows differences between species. The first three principal components represent 52% of the variation observed in the sample. Principal component 4 accounted for 11% of the variation, but did not reveal anything new about morphology not represented in PCs 1-3; no groups were statistically different from one another at the PC 4 axis. The individual proportions for the principal components of PC 5 and higher were below 8% and are not morphologically revealing. See Table 8.1 for the proportions of variation represented by PC 1, PC 2, and PC 3. Refer to Figures 8.1 and 8.2 for an example of each species and for photos of the fossils. Discussion of the PCA results follows.

Table 8.1 Proportion of PC Variance for MT 3

Proportion of Variance for MT 3		
PC 1	PC 2	PC 3
24%	16%	12%

Table 8.2 Extant Specimens in the MT 3 Analysis

Group	Number
Gorilla	30
Pan	30
Hylobates	30
Homo	30
unshod *Homo*	35

Figure 8.1 Extant groups for MT 3 photos: A) recent *Homo*; B) unshod *Homo*; C) *Gorilla*; D) *Pan*; E) *Hylobates*.

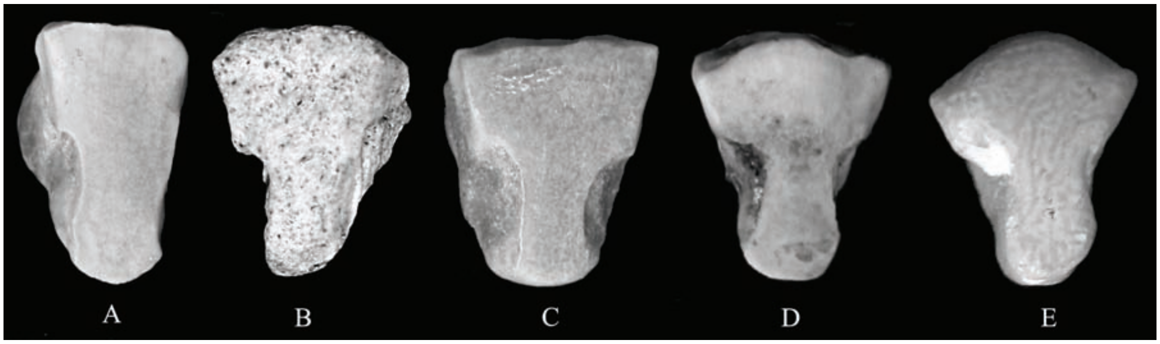
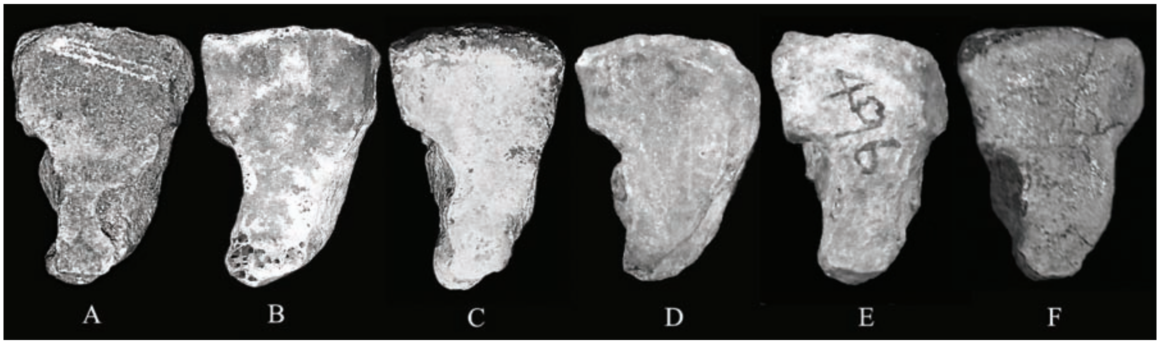


Figure 8.2 MT 3 fossil photos: A) Stw 387; B) Stw 388 (this is a right, reversed); C) Stw 435 (this is a right, reversed); D) Stw 477; E) Stw 496; F) OH 8. These specimens are not to scale.



MT 3 Principal Component 1

There are clear groupings with overlap of human and ape specimens on the PC 1 axis (Figure 8.3); an ANOVA was conducted to test for differences in the means of PC 1 scores between groups; there was a statistically significant result with a *p* value below 0.00. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported in Table 8.3.

Table 8.3 Tukey-Kramer Multiple-Comparison Test for PC 1

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.06	unshod *Homo*, *Homo*, *Hylobates*
Pan	30	0.05	unshod *Homo*, *Homo*, *Hylobates*
Hylobates	30	0.02	unshod *Homo*, *Homo*, *Gorilla*, *Pan*
Homo	30	-0.05	*Hylobates*, *Gorilla*, *Pan*
unshod *Homo*	35	-0.07	*Hylobates*, *Gorilla*, *Pan*

Table 8.4 Principal Component 1 Ranges for MT 3

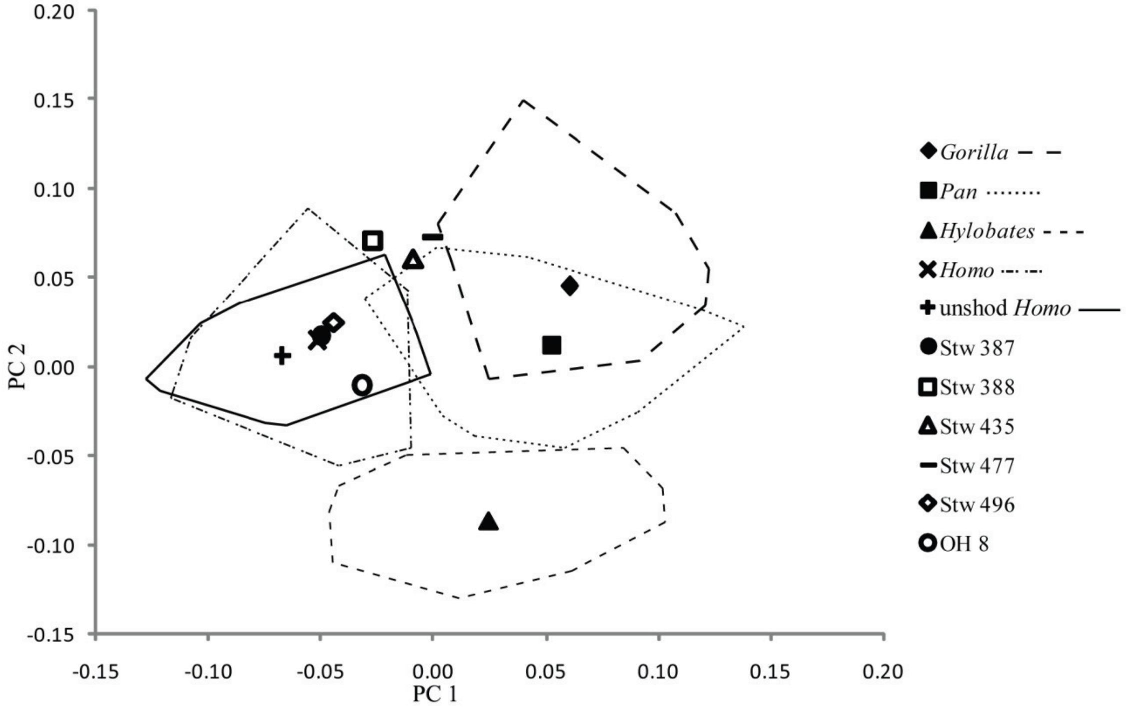
Group	Minimum	Maximum	Range
Gorilla	0.00	0.12	0.12
Pan	-0.03	0.14	0.17
Hylobates	-0.05	0.10	0.15
Homo	-0.12	-0.01	0.11
unshod *Homo*	-0.13	0.00	0.13

Table 8.5 Fossil PC 1 Values for MT 3

Specimen	PC 1
Stw 387	-0.05
Stw 388	-0.03
Stw 435	-0.01
Stw 477	0.00
Stw 496	-0.04
OH 8	-0.03

Both human groups are statistically different from all ape groups. *Pan* and *Gorilla* are not significantly different from one another, but *Hylobates* is different from the other apes and humans. The PC 1 plot shows that *Hylobates* overlaps both human and African apes, with slightly more overlap with the apes. *Pan* overlaps humans to a lesser degree, and the range of *Gorilla* just barely connects with the extreme higher range of unshod *Homo*.

Figure 8.3 Plot of PC 1 and PC 2 group averages and fossil specimens



The negative portion of the PC 1 axis, primarily occupied by humans, reflects a relatively narrow, flat articular surface (Figure 8.4). The dorsal and plantar aspects of the surface are of similar width, creating a rectangular surface shape. The positive area of PC 1 is occupied especially by the African apes, and reflects a surface that is markedly wide at the dorsal area and extremely narrow in the plantar aspect (Figure 8.5). In addition, the shape for the African apes slightly convex, especially at the dorsal aspect.

Figure 8.4 PC 1 (-0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

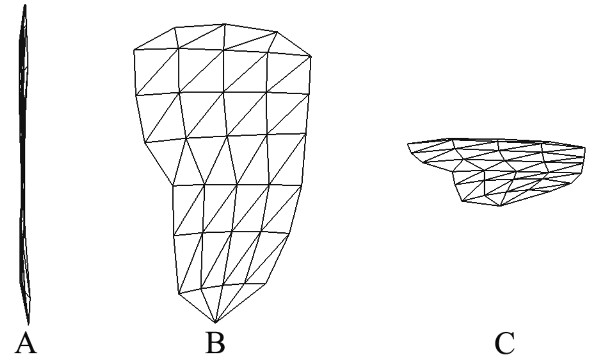
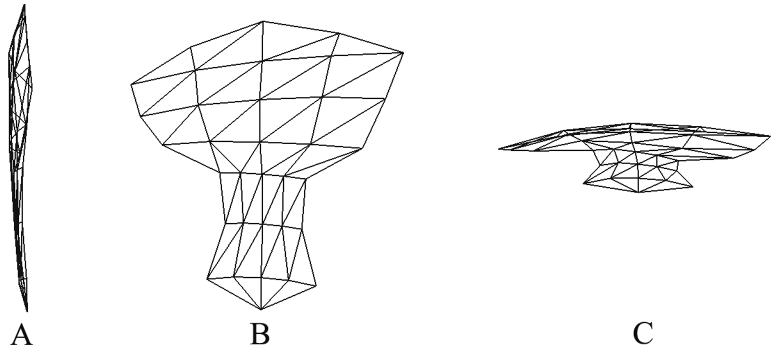


Figure 8.5 PC 1 (0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



Recent *Homo* and unshod *Homo* are indistinguishable at the PC 1 axis. There appears to be combined effects between PC 1, PC 2, and size that will be discussed in the next section. Over all, there is a visual trend for the smaller bodied and more arboreal ape groups to have lower average PC 1 scores combined with lower PC 2 scores.

All of the fossil specimens group with humans, though Stw 477 lies exactly where *Gorilla* and unshod *Homo* overlap. In addition, all fossil specimens overlap *Hylobates* in the same area it overlaps *Homo*. Only Stw 477 overlaps *Gorilla*, but all specimens other than Stw 387 and Stw 386 overlap *Pan*. Of the specimens that overlap, OH 8 and Stw 388 just overlap the extreme negative range of *Pan*.

MT 3 Principal Component 2

An ANOVA was conducted to test for differences in the means of PC 2 scores between groups, with a statistically significant result and a *p* value below 0.00. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All failed at the 0.05 significance level, except for the test for equal variance. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported in Table 8.6.

Table 8.6 Tukey-Kramer Multiple-Comparison Test for PC 2

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.05	unshod *Homo*, *Homo*, *Pan, Hylobates*
Pan	30	0.01	*Hylobates*, *Gorilla*
Hylobates	30	-0.09	unshod *Homo*, *Homo*, *Gorilla*, *Pan*
Homo	34	0.00	*Hylobates*, *Gorilla*
unshod *Homo*	35	0.01	*Hylobates*, *Gorilla*

The results show that there three groupings on the PC 2 axis. *Gorilla* is different from all other groups and has a higher average PC 2 score. Both human groups and *Pan* group together and are not statistically different from one another. *Hylobates* is different from all groups and has a lower average PC 2 score. See Figure 8.3.

Table 8.7 Principal Component 2 Ranges for MT 3

Group	Minimum	Maximum	Range
Gorilla	-0.01	0.15	0.16
Pan	-0.05	0.07	0.12
Hylobates	-0.13	-0.04	0.09
Homo	-0.06	0.09	0.15
unshod *Homo*	-0.03	0.06	0.09

Table 8.8 Fossil PC 2 Values for MT 3

Specimen	PC 2
Stw 387	0.02
Stw 388	0.07
Stw 435	0.06
Stw 477	0.07
Stw 496	0.03
OH 8	-0.01

The extreme negative portion of the PC 2 axis, occupied by *Hylobates*, reflects a round dorsal surface and relatively narrower plantar portion of the surface. The most striking difference is that the surface is highly convex. At the extreme positive area occupied by *Gorilla*, the dorsal surface is more rectangular in shape, with a wider plantar aspect that is expanded at the lateral aspect. In addition, the surface is slightly convex.

None of the fossil specimens overlap *Hylobates* at the PC 2 axis (Tables 8.7 and 8.8). All fossils overlap *Gorilla* and *Pan*, with OH 8 just overlapping at the most extreme lower point of the range of *Gorilla*. Stw 388 and Stw 477 just overlap the upper extreme of *Pan*. All fossil specimens overlap *Homo*, with Stw 388 and Stw 477 falling just outside the upper range of unshod *Homo*. The combined effects of PC 1 and PC 2 on the fossil specimens make all of the specimens overall appear to share much more in common with humans than apes. The specimens OH 8, Stw 387, and Stw 496 particularly share affinity with both human groups.

Figure 8.6 PC 2 (-0.11) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

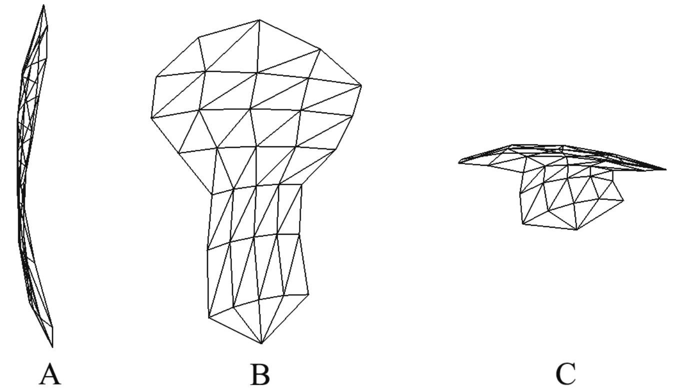
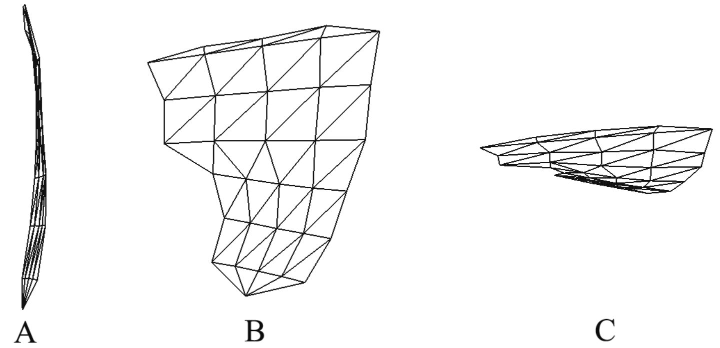


Figure 8.7 PC 1 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 3 Principal Component 3

An ANOVA revealed a statistically significant result with a *p* value below 0.00 when comparing PC 3 scores between groups in this analysis. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All failed at the 0.05 significance level, except for the test for equal variance. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported in Table 8.9.

All groups overlap considerably at the PC 3 axis (Figure 8.7). There is not a dichotomy between apes and humans at this axis as there is in several other MT surface analyses. *Gorilla* is only different from *Hylobates* and *Pan*. *Pan* is different from Recent *Homo* and *Gorilla* (Table 8.9). *Hylobates* is different from *Gorilla*, while recent *Homo* is only different from *Pan*. Unshod *Homo* is not different from any other group.

The PC 3 axis for the analysis of MT 3 largely reflects analytical noise (Figures 8.8 and 8.9). There is a low tendency at the positive are of the axis for the surface to be slightly convex. At the extreme negative area of the PC 3 axis the dorsal surface is relatively larger to a small degree, with the plantar area slightly shorter in the dorso-plantar aspect.

Table 8.9 Tukey-Kramer Multiple-Comparison Test for PC 3

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.02	*Hylobates*, *Pan*
Pan	30	0.02	*Gorilla*, *Homo*
Hylobates	30	0.01	*Gorilla*
Homo	30	-0.02	*Pan*
unshod *Homo*	35	0.06	None

Table 8.10 Principal Component 3 Ranges for MT 3

Group	Minimum	Maximum	Range
Gorilla	-0.10	0.07	0.17
Pan	-0.04	0.10	0.14
Hylobates	-0.06	0.12	0.18
Homo	-0.22	0.09	0.32
unshod *Homo*	-0.16	0.06	0.22

Table 8.11 Fossil PC 3 Values for MT 3

Specimen	PC 1
Stw 387	-0.03
Stw 388	-0.04
Stw 435	0.09
Stw 477	0.06
Stw 496	0.03
OH 8	0.01

Figure 8.8 Plot of PC 1 and PC 3 group averages and fossil specimens for MT 3

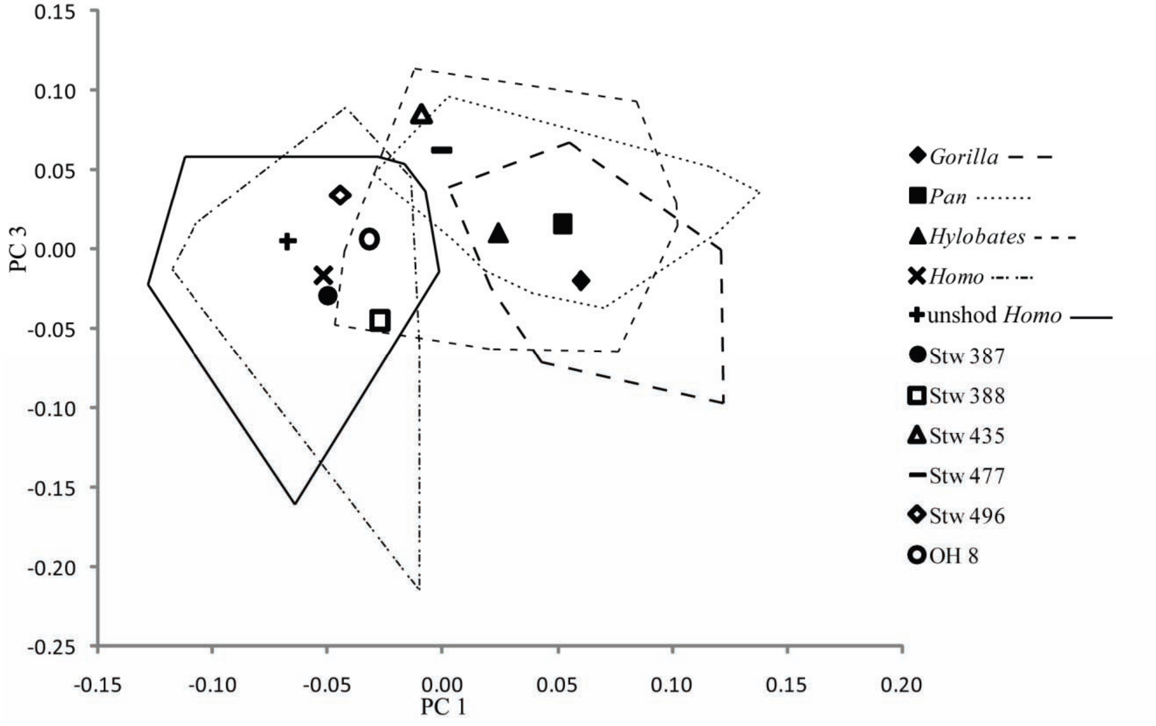


Figure 8.9 PC 3 (-0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)

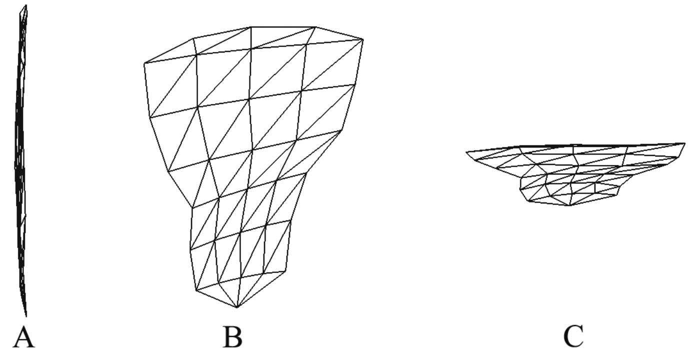
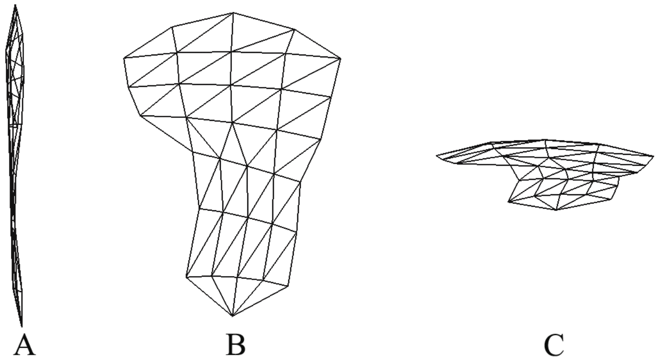


Figure 8.10 PC 3 (0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

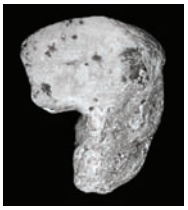


Fossils with Absent Data for MT 3

Stw 238

The fossil specimen Stw 238 is a proximal right MT 3. The dorsal surface is intact, but the plantar aspect is absent except for the lateral edge (Figure 8.10). The dorsal surface is flat. Its overall appearance is very similar to the other South African MT 3 specimens, and even though most of the plantar portion in missing, it can be discerned that the lateral surface edge does not curve toward the medial aspect to create a narrow surface as is the case with apes. Its appearance is consistent with the other fossil specimens, and has more in common with *Homo* than the apes.

Figure 8.11 Stw 238, right side flipped to appear as a left



Interspecific Size and Shape Relationships

An ANOVA was conducted to test for differences in centroid sized between groups. The result was significant, with a $p < 0.00$. H_8 is falsified. In addition, tests for skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test were conducted. All passed at the 0.05 level except for the test of equal variance. A Tukey-Kramer post-hoc test was conducted to find differences in centroid size between specific groups. See Table 8.12.

Table 8.12 Tukey-Kramer Multiple-Comparison Test for Centroid Size of MT 3

Group	Specimens	Mean	Different From Groups
Gorilla	30	39.75	*Hylobates, Pan,* unshod *Homo*
Pan	30	31.62	*Hylobates, Homo, Gorilla*
Hylobates	30	12.80	*Pan,* unshod *Homo, Homo, Gorilla*
Homo	30	38.30	*Hylobates, Pan,* unshod *Homo*
unshod *Homo*	35	33.45	*Hylobates, Homo, Gorilla*

Table 8.13 Centroid Size Ranges for MT 3

Group	Minimum	Maximum	Range
Gorilla	31.44	48.67	17.23
Pan	27.78	35.31	7.53
Hylobates	11.55	14.47	2.92
Homo	30.79	46.16	15.37
unshod *Homo*	27.75	41.10	13.35

There are three distinct size groupings. *Hylobates* is the smallest group and is significantly smaller that all other groups. Unshod *Homo* and *Pan* are not different in size from one another but both are different in size from all other groups. Similarly, recent *Homo* and *Gorilla* are not different in size but both are different from all other groups.

Table 8.14 Fossil Centroid Sizes for MT 3

Specimen	Centroid
Stw 387	30.35
Stw 388	33.42
Stw 435	33.56
Stw 477	29.46
Stw 496	31.11
OH 8	29.46

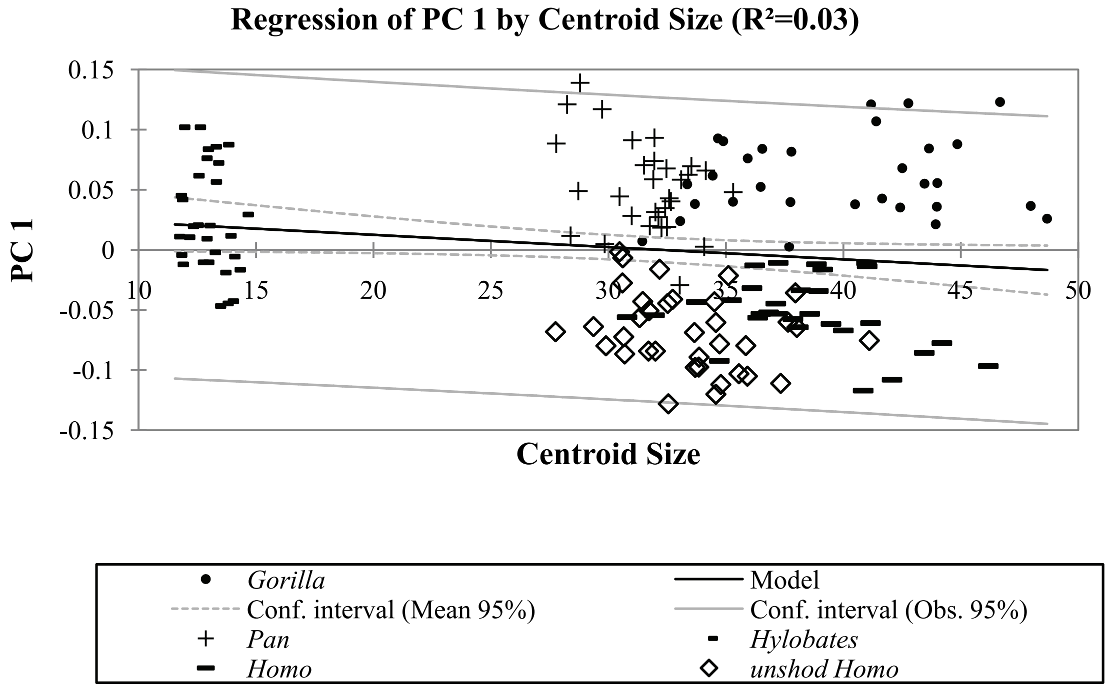
Regression analysis and an ANCOVA were conducted to determine whether there is a relationship between size and shape at the intraspecific level (Table 8.15). The regression analysis resulted in a significant relationship between centroid size and each PC axis.

Table 8.15 Regression and ANCOVA results

	PC 1	PC 2	PC 3
R^2 with PC and Size	0.03	0.65	0.06
R^2 with PC, Size, and Species	0.71	0.73	0.13

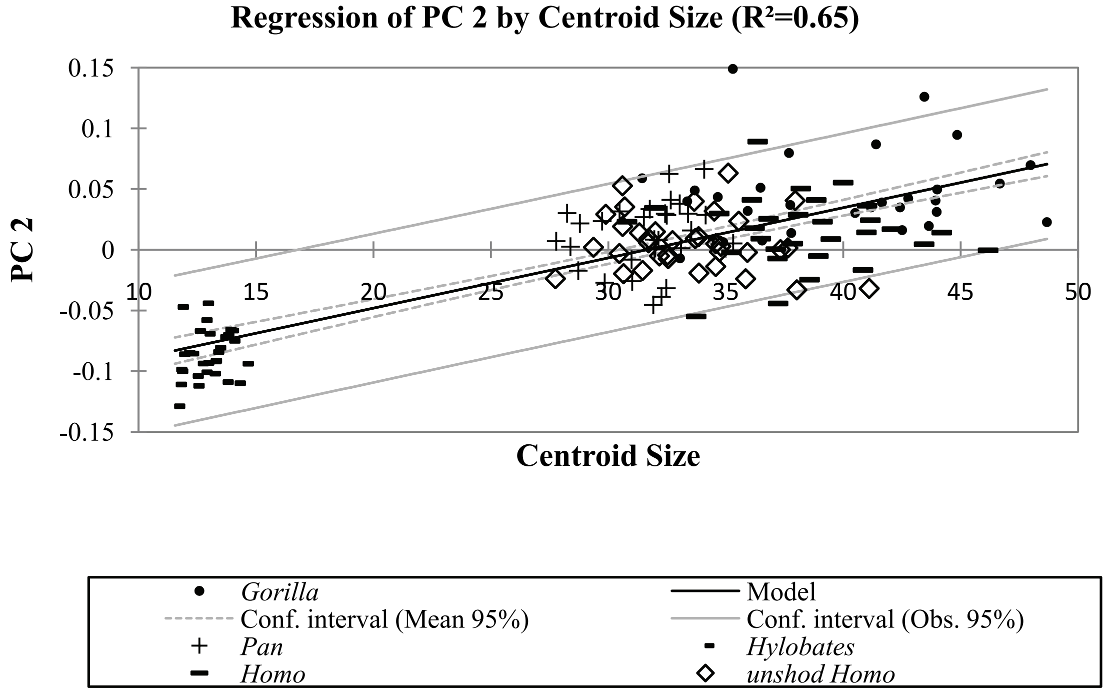
The PC 1 score is the most important for illustrating the differences between human and ape proximal MT 3 shape. When considering PC 1 scores and centroid size alone, there is a borderline significant relationship, with $p = 0.048$ (Figure 8.11). However, when considering species group in an ANCOVA, the R^2 increases dramatically. The human groups are not very different in articular surface size compared to the African apes, but the increase in the percentage of variation explained when combining size with species indicates that species, or locomotion, is the biggest determinate of articular surface shape.

Figure 8.12 Regression for interspecific PC 1 and size relationships for MT 3



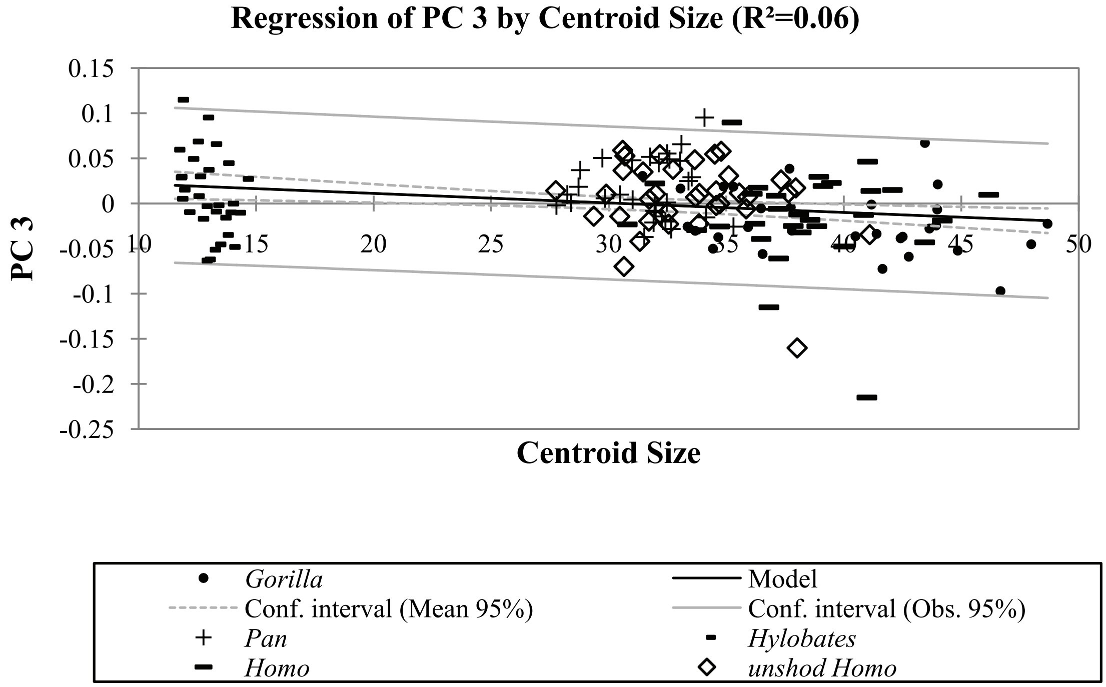
There is a very strong relationship between size and shape on the PC 2 axis, with a p value below 0.00 (Figure 8.12). The R^2 increases when species is used as a variable, but not so dramatically as with PC 1. *Hylobates* is the most different at the PC 2 axis and is the smallest. The larger groups have a tendency to have a less convex, flatter, or even slightly concave surface whereas *Hylobates* has a markedly convex surface. While *Hylobates* overlaps humans more than the other ape groups on the PC 1 axis, the morphology of *Hylobates* is unique from all groups when combined with PC 2. The question remains as to whether the unique morphology exhibited in *Hylobates* is more of a factor of size or whether it is locomotion, and additional arboreal primate samples will need to be included in later analyses to isolate this. Recent work has showed that the midtarsal break actually involves a great deal of mobility at the MT 4 and MT 5 tarsometatarsal joints in apes and is evidenced by greater MT 4 proximal articular surface convexity (DeSilva, 2010). Greater convexity of the proximal metatarsal articular surface is suggestive of greater flexion, and since *Hylobates* is markedly convex at the MT 3 proximal surface one can produce the hypothesis that this greater flexibility of the midtarsal area extends further medially to the MT 3 tarsometatarsal joint in *Hylobates*.

Figure 8.13 Regression for interspecific PC 2 and size relationships for MT 3



The *p* value for the regression analysis of PC 3 as explained by centroid size was less than 0.00 (Figure 8.13). However, the R^2 value is low. Even though the morphology of PC 3 does not distinguish as clearly between species groups, there is a slight tendency for smaller sized specimens to have a higher PC 3 score.

Figure 8.14 Regression for interspecific PC 3 and size relationships for MT 3



Intraspecific MT 1 Shape, Size, and Sex Variation

The following section discusses the results of analysis to determine whether there are size and/or sex related influences on shape within groups.

Gorilla

Gorilla Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with a *p* value of 0.23. There is no difference in proximal articular MT 3 surface size between males and females.

Gorilla Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.45, for the PC 2 t-test it was 0.12, and for the PC 3 t-test it was 0.35. There are no articular surface shape differences between males and females.

Pan

Pan Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with a *p* value of 0.25. There is no difference in proximal articular MT 3 surface size between males and females.

Pan Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.47, for the PC 2 t-test it was 0.22, and for the PC 3 t-test it was 0.35. There are no articular surface shape differences between males and females.

Hylobates

Hylobates Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with a *p* value of 0.20. There is no difference in proximal articular MT 3 surface size between males and females.

Hylobates Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.37, for the PC 2 t-test it was 0.07, and for the PC 3 t-test it was 0.29. There are no articular surface shape differences between males and females.

Shod *Homo*

Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with a *p* value of 0.09. There is no difference in proximal articular MT 3 surface size between males and females.

Homo Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.18, for the PC 2 t-test it was 0.25, and for the PC 3 t-test it was 0.24. There are no articular surface shape differences between males and females.

Unshod *Homo*

Recent and unshod *Homo* Differences

As indicated by the ANOVA reported above, there is a significant difference in MT 3 articular surface size between recent *Homo* and unshod *Homo*.

Homo Comparative Shape

The ANOVA results reported previously for PC 1, PC 2, and PC 3 revealed that there are no shape differences between recent *Homo* and unshod *Homo*.

Discussion

The combined effects of PC 1 and PC 2 produces three distinct groups, with some overlap that is especially pronounced on the PC 2 axis between the African apes and human groups. The results of this analysis are very similar to the analysis of MT 2. On the PC 1 axis, humans have a relatively narrow articular surface that is expanded in the plantar area compared to the apes. Therefore, H_1 (that the human MT 3 will have an expanded articular surface) cannot be falsified. However, this analysis differs from the analysis of MT 2 in that *Pan* overlaps human groups on the PC 1 axis, whereas *Gorilla* did for MT 2. *Hylobates* also overlaps with humans, but the *Hylobates* shape is highly influenced by PC 2. The *Gorilla* shape is also influenced by PC 2 on the opposite axis. The combined effects for *Gorilla* indicate a surface shape that is wide in the dorsal area, narrow in the plantar area, but relatively flat with some indication of concavity. *Pan* is in an intermediate position on the PC 2 axis. The extreme shape of *Hylobates* on PC 2 indicates a surface that is narrow in the plantar aspect and rounded in the dorsal aspect. Most importantly, the surface of *Hylobates* is markedly convex.

A recent study by DeSilva (2010) found that the midtarsal break observed in non-human primates is not only the result of movement at the calcaneocuboid joint but also at the tarsometatarsal joints for MT 4 and MT 5 with the distal cuboid. A consequence of this motion is that the proximal MT 4 and MT 5 surfaces are markedly convex to allow the joint to dorsiflex. The presence of extreme convexity on the proximal MT 3 articular surface suggests that in *Hylobates* the lateral flexibility of the foot may extend further medially that it does in apes. This hypothesis should be tested in a later study.

All of the fossil specimens fall in the range of humans on the PC 1 axis, but Stw 435 and Stw 477 overlap apes to a greater degree. The specimen OH 8 overlaps humans and is grouped most strongly with humans; thus, H_6 cannot be falsified.

Very similarly to the analysis of MT 2, in terms of centroid size *Gorilla* and *Homo* are not different. Likewise, *Pan* and unshod *Homo* are not different in size, but

Hylobates is different from all other groups. Regression analysis yielded a significant result with a relationship between size and each PC axis. The hypothesis (H_{10}) that differences in shape between species are not related to size is falsified. However, the portion of variance due to size alone is very closely related to the way the groups are clustered on the PC 1 and PC 2 axes. The portion of variance explained by size for PC 1 is only 3%. Although there is a division between humans and African apes on the PC 1 axis, even those pairing that do differ in size do not do so dramatically. *Hylobates* is the smallest group and overlaps the center area of the range of groupings on the PC 1 axis. This is in direct contrast to the relationship between size and shape on the PC 2 axis, where size explains 65% of the variation. This is most important for interpreting shape differences between ape groups, as there is a clear gradation of shape change on the PC 2 axis from larger bodied *Gorilla* through intermediate *Pan* and finally to smaller *Hylobates* that has an extreme location on the negative PC 2 axis.

An interesting finding for the MT 3 proximal articular surface is that there are no intraspecific differences in size between males and females for any of the groups, thus H_9 is not falsified. This is surprising, particularly for *Gorilla* which is known to have considerable sexual dimorphism. It is possible that the overall dimensions MT 3 are different between the sexes, with males have a longer more robust metatarsal, for instance, but at least in terms of articular surface size there is no difference. A hypotheses can be put forth to explain this by the idea that the MT 3 proximal surface is under less stress during locomotion for all groups. In apes much of the stress is on the lateral foot, and in humans weight quickly transitions to the medial side of the foot. This leaves the MT 3 surface the area with the least burden during locomotion. In apes, MT 2 is in opposition to the hallux, and even though the base of the metatarsal is not subject to the same kind of compressive forces as the human foot in this region during locomotion, apes do subject this area to stress through grasping and locomotion in trees. It is therefore not surprising that MT 2 would show differences in size between males and females in dimorphic groups.

Although unshod *Homo* and shod *Homo* are different in terms of articular surface size, no significant differences in PC scores occurred. Therefore, the hypothesis (H_4) that there are no significant differences in surface shape between shod and unshod humans cannot be falsified for MT 3.

CHAPTER 9: ANALYSIS OF METATARSAL 4

Interspecific MT 4 Shape Variation

A principal components analysis was conducted to assess whether MT 4 proximal articular surface shape shows differences between species. A total of 65% of the variation in this analysis accounts for PCs 1, 2, and 3. Principal component 4 and beyond were not revealing in terms of shape differences. Although PC 3 does not show differences between any of the groups in this analysis, it does show a trend of shape reflected by all species, and is thus found meaningful enough to be described here. Refer Table 9.1 for the proportions of variation represented by PC 1 though PC 3. See Figures 9.1 and 9.2 for an example of each species and for photos of the fossils. The PCA results are discussed below.

Table 9.1 Proportion of PC Variance for MT 4

Proportion of Variance for MT 4		
PC 1	PC 2	PC 3
30%	23%	12%

Table 9.2 Extant Specimens in the MT 4 Analysis

Group	Number
Gorilla	30
Pan	30
Hylobates	30
Homo	32
unshod *Homo*	33

Figure 9.1 MT 4 extant groups photos: A) recent *Homo*; B) unshod *Homo*; C) *Gorilla*; D) *Pan*; E) *Hylobates*.

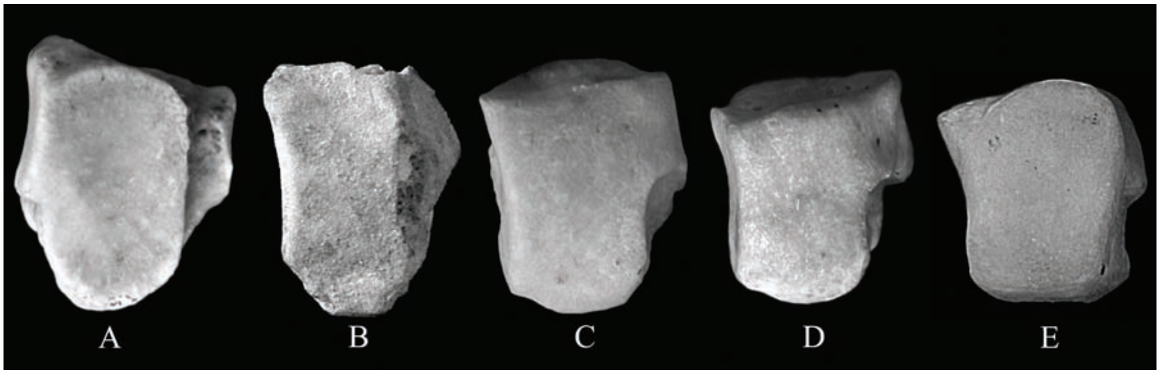
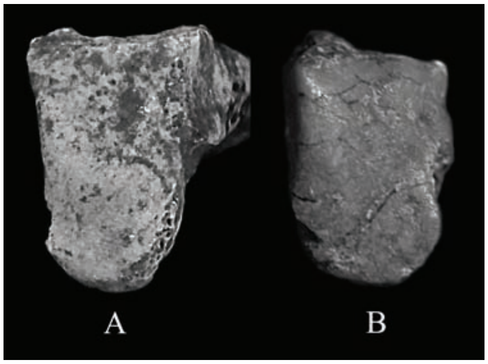


Figure 9.2 MT 4 fossil photos; A) Stw 628, a right flipped to appear as a left; B) OH 8



MT 4 Principal Component 1

The PC 1 axis shows three groupings; an ANOVA was conducted to test for differences in the means of PC 1 scores between groups. This analysis yielded a statistically significant result with $p < 0.0001$. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. A Tukey-Kramer post-hoc test was conducted with the ANOVA to test for statistically significant differences in means between specific groups. Refer to Table 9.3.

Table 9.3 Tukey-Kramer Multiple-Comparison Test for PC 1

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.10	*Hylobates*, unshod *Homo*, *Homo*
Pan	30	-0.11	*Hylobates*, unshod *Homo*, *Homo*
Hylobates	30	-0.01	*Pan*, *Gorilla*, unshod *Homo*, *Homo*
Homo	32	0.11	*Pan*, *Gorilla*, *Hylobates*
unshod *Homo*	33	0.09	*Pan*, *Gorilla*, *Hylobates*

The groupings on the PC 1 axis agree with the post-hoc test for differences between group means (Figure 9.3). The African apes are not different from one another, and the *Homo* groups are similarly undifferentiated. Between the humans and African ape groups lie *Hylobates*, which is statistically different from all other groups.

Table 9.4 Principal Component 1 Ranges for MT 4

Group	Minimum	Maximum	Range
Gorilla	-0.17	-0.03	0.14
Pan	-0.21	-0.01	0.21
Hylobates	-0.07	0.06	0.12
Homo	0.03	0.18	0.15
unshod *Homo*	-0.01	0.15	0.16

Table 9.5 Fossil PC 1 Value for MT 4

Specimen	PC 1
Stw 628	0.00
OH 8	0.08

The overall shape trend on the PC 1 axis is as follows. At the negative aspect of the axis, occupied primarily by *Pan* and *Gorilla*, shows a highly convex articular surface Figure 9.4). In addition, the articular surface is expanded at the dorso-medial aspect with surface curvature extended to this area as well. On the positive extreme of the PC 1 axis, occupied by the human groups, the surface flattens out considerably (Figure 9.4). There is some small amount of convexity. The overall surface shape is more rectangular, with parallel medial and lateral surface edges. *Hylobates* occupies a space in between the other groups on the PC 1 axis. The fossil specimen OH 8 overlaps both human groups on PC 1, and does not overlap any ape groups. In contrast, Stw 628 only overlaps unshod *Homo* and *Hylobates*.

Figure 9.3 Plot of PC 1 and PC 2 group averages and fossil specimens for MT 4

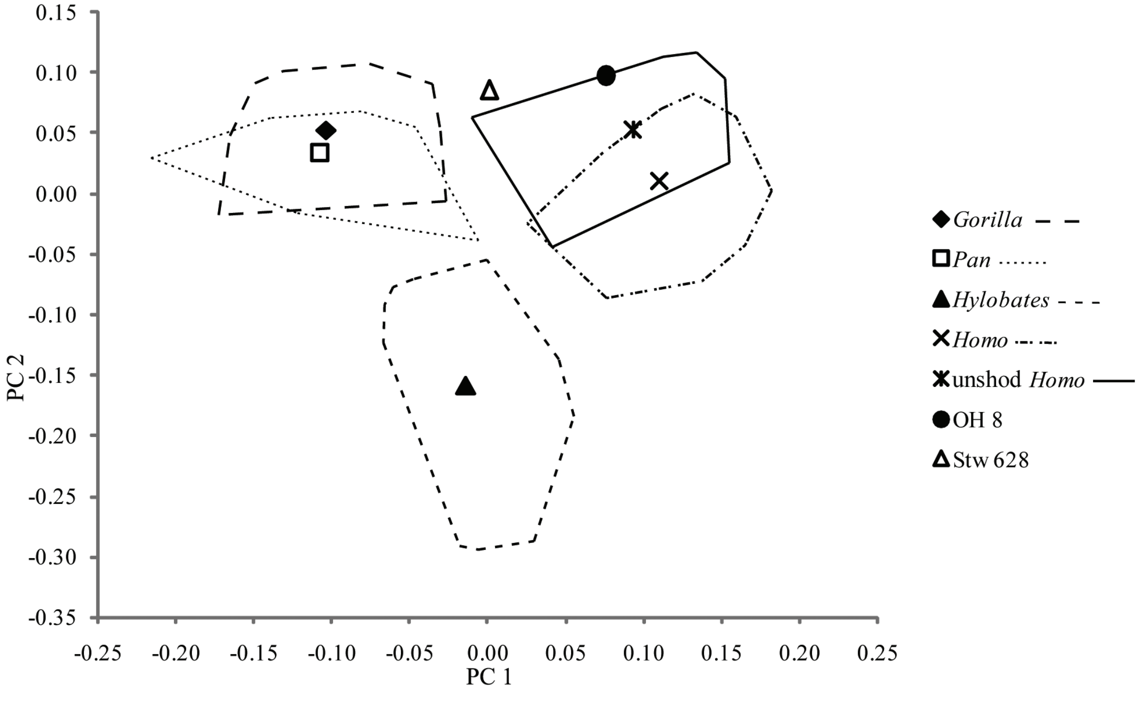


Figure 9.4 PC 1 (-0.14) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

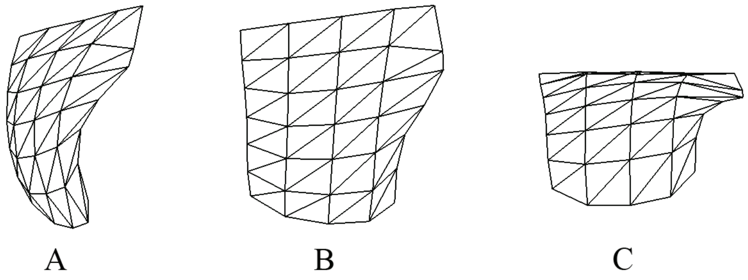
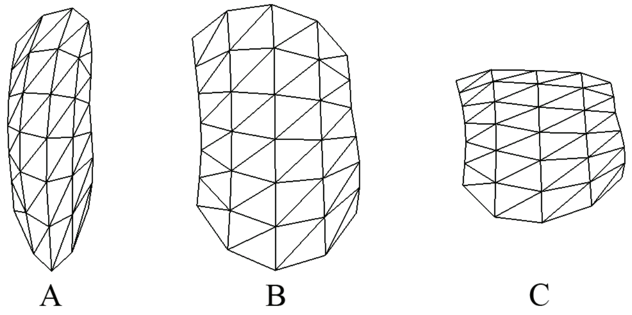


Figure 9.5 PC 1 (0.12) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



MT 4 Principal Component 2

To test for differences in the means of PC 2 scores between groups, an ANOVA was used that yielded a statistically significant result with a $p < 0.0001$. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All failed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported Table 9.6.

Table 9.6 Tukey-Kramer Multiple-Comparison Test for PC 2

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.05	*Hylobates*, *Homo*
Pan	30	0.03	*Hylobates*
Hylobates	30	-0.16	*Homo*, *Pan*, *Gorilla*, unshod *Homo*
Homo	32	0.01	*Hylobates*, *Gorilla*, unshod *Homo*
unshod *Homo*	33	0.05	*Hylobates*, *Homo*

Table 9.7 Principal Component 2 Ranges for MT 4

Group	Minimum	Maximum	Range
Gorilla	-0.02	0.11	0.13
Pan	-0.04	0.07	0.12
Hylobates	-0.29	-0.05	0.24
Homo	-0.09	0.08	0.17
unshod *Homo*	-0.04	0.12	0.16

Table 9.8 Fossil PC 2 Values for MT 4

Specimen	PC 4
Stw 628	0.09
OH 8	0.10

On the PC 2 axis, *Gorilla* is statistically different from *Homo* and *Hylobates*. *Pan* is only different from *Hylobates*, and *Hylobates* is different from all groups. *Homo* is different from all groups except *Pan*, and unshod *Homo* is different from *Hylobates* and *Homo*.

Figure 9.6 PC 2 (-0.18) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

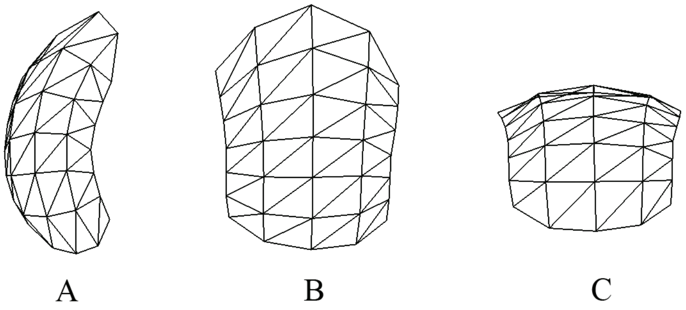
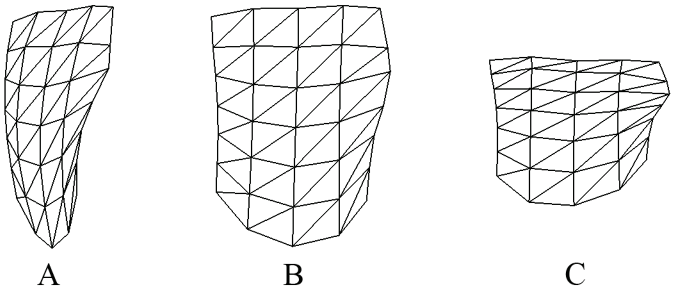


Figure 9.7 PC 2 (0.07) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



As with all interpretations of shape as reflected on PC axes it is important to note that in interpreting shape, the other axis is by default set to 0.00. In describing PC 2 shape, the strong influences of PC 1 on the African ape and human groupings should be kept in mind. The mean PC 2 score for *Hylobates* is close to 0.00; thus, the PC 2 morphology is especially revealing of the shape difference between *Hylobates* and all other groups. *Hylobates* occupies an extreme negative area of PC 2. This area shows most extreme convexity that extends further to the dorsal area than in other apes, and is somewhat reminiscent of the dorsal expansion on the human distal MT 1 articular surface (Figure 9.6). Three specimens of *Hylobates* are at the most extreme point of PC 2, and those specimens showed an even greater dorsal extension of the surface than that reflected in the wireframe of shape at the -0.18 point of the PC 2 axis. When viewing the -0.18 wireframe from the proximal aspect, the surface is rounded at the dorsal area. The lateral and medial sides of the surface extend further to curve around the lateral and medial sides of the metatarsal. The dorso-medial aspect of the surface is not extended.

All other groups occupy an area of the axis much closer to 0.00, or higher, with some differences in means as noted above. The shape shown on the positive area of the PC 2 axis has much reduced convexity, with some extension of the surface at the dorso-medial area (Figure 9.7). The fossils OH 8 and Stw 628 overlap unshod *Homo* and *Gorilla*, but no other groups on the PC 2 axis.

MT 4 Principal Component 3

An ANOVA revealed a statistically insignificant result with $p = 0.27$ when comparing PC 3 scores between groups in this analysis. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA (Table 9.9).

Table 9.9 Tukey-Kramer Multiple-Comparison Test for PC 4

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.01	None
Pan	30	-0.01	None
Hylobates	30	0.00	None
Homo	32	0.01	None
unshod *Homo*	33	-0.01	None

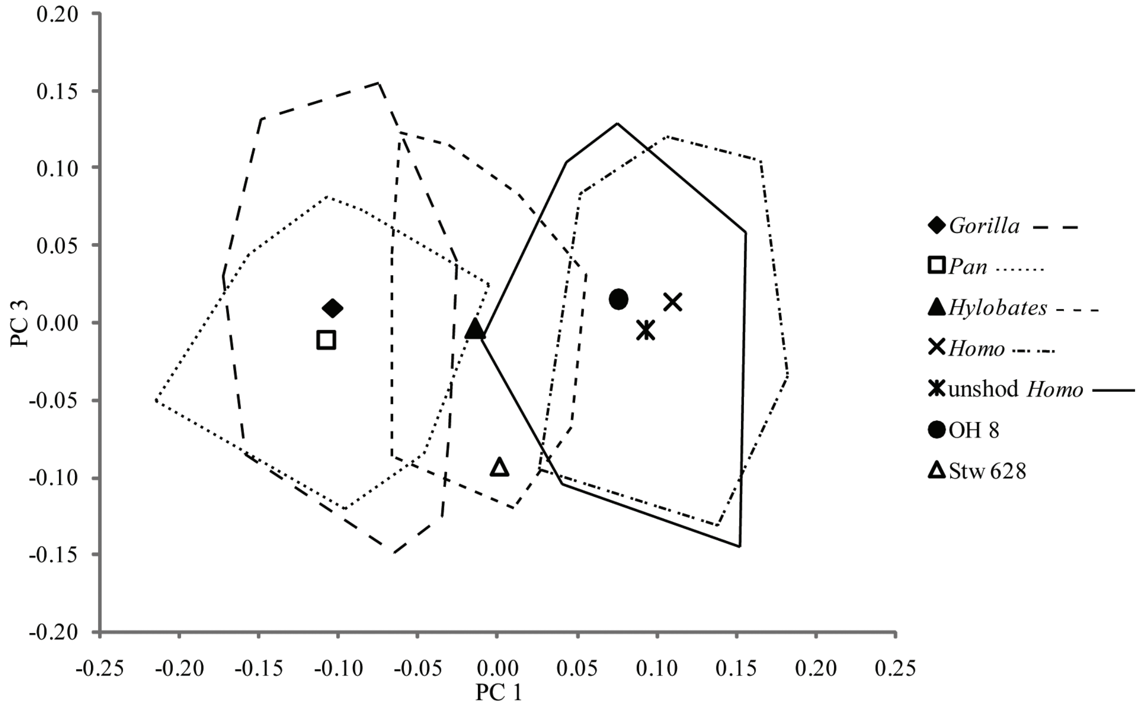
Table 9.10 Principal Component 3 Ranges for MT 4

Group	Minimum	Maximum	Range
Gorilla	-0.15	0.15	0.30
Pan	-0.12	0.08	0.20
Hylobates	-0.12	0.13	0.24
Homo	-0.13	0.12	0.25
unshod *Homo*	-0.14	0.13	0.27

Table 9.11 Fossil PC 3 Values for MT 4

Specimen	PC 3
Stw 628	-0.09
OH 8	0.02

Figure 9.8 Plot of PC 1 and PC 3 group averages and fossil specimens for MT 4



All groups overlap considerably on the PC 3 axis, and there are no differences between group means (Figure 9.8). The shape trend on the PC 3 axis reflects a relatively narrow surface at the negative area of the axis, and a wider surface at the positive area of the axis (Figures 9.9 and 9.10). No group means are different at this axis. The variation in surface width is common trait between groups. The fossil specimens overlap all groups at the PC 3 axis.

Figure 9.9 PC 3 (-0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

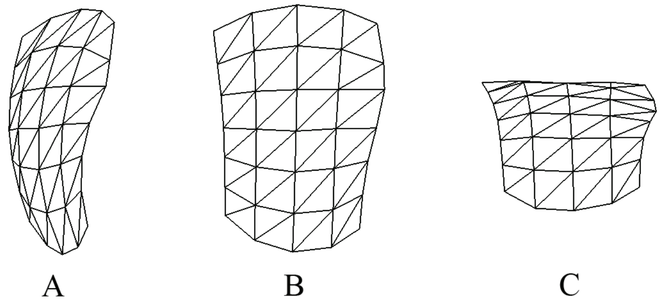
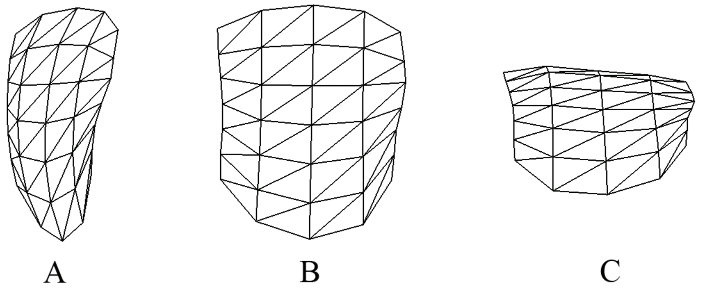


Figure 9.10 PC 3 (0.10) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).



Fossil with Absent Data for MT 4

Stw 485

The fossil specimen Stw 485 is a proximal left MT 4 (Figure 9.11). A significant portion of the medio-plantar surface is absent, but the portion present indicates that the surface is relatively flat. Further, it lacks extension of the dorso-medial area that occurs in apes. It has the general appearance of a human-like MT 4 joint surface and closely resembles Stw 628. An attempt was made to analyze this specimen with the other samples by eliminating missing landmarks and estimating the location of the landmarks on the medial surface edge. However, the analysis did not yield meaningful results. For this reason the analysis of this specimen is qualitative.

Figure 9.11 Photo of Stw 485

Interspecific Size and Shape Relationships

An ANOVA was conducted to test for differences in centroid sized between groups. The result was significant, with $p < 0.0001$. H_8 is falsified. In addition, tests for skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test were conducted. All passed at the 0.05 level except for the test of equal variance. A Tukey-Kramer post-hoc test was conducted to find differences in centroid size between specific groups. See able 9.12.

In terms of articular surface size, *Gorilla*, *Homo*, and *Hylobates* are different from each other and all other groups. *Pan* and unshod *Homo* are not different from each other, but each is different from all other groups.

Table 9.12 Tukey-Kramer Multiple-Comparison Test for Centroid Size of MT 4

Group	Specimens	Mean	Different From Groups
Gorilla	30	39.79	*Hylobates*, unshod *Homo*, *Pan*, *Homo*
Pan	30	30.57	*Hylobates*, *Homo*, *Gorilla*
Hylobates	30	12.80	unshod *Homo*, *Pan*, *Homo*, *Gorilla*
Homo	32	33.87	*Hylobates*, unshod *Homo*, *Pan*, *Gorilla*
unshod *Homo*	33	30.07	*Hylobates*, *Homo*, *Gorilla*

Table 9.13 Centroid Size Ranges for MT 4

Group	Minimum	Maximum	Range
Gorilla	31.95	47.61	15.67
Pan	26.95	34.02	7.07
Hylobates	11.36	15.00	3.65
Homo	28.19	39.15	10.96
unshod *Homo*	24.97	36.05	11.08

Table 9.14 Fossil Centroid Sizes for MT 4

Specimen	Centroid
Stw 628	26.89
OH 8	28.46

A regression analysis was conducted to determine whether there is a relationship between size and shape at the intraspecific level for PC 1 (Table 9.15). The test yielded an insignificant result with $p = 0.29$. There is no relationship between size and shape on the PC 1 axis. Regression analysis and an ANCOVA were conducted to determine whether there is a relationship between size and shape at the intraspecific level for PC 2

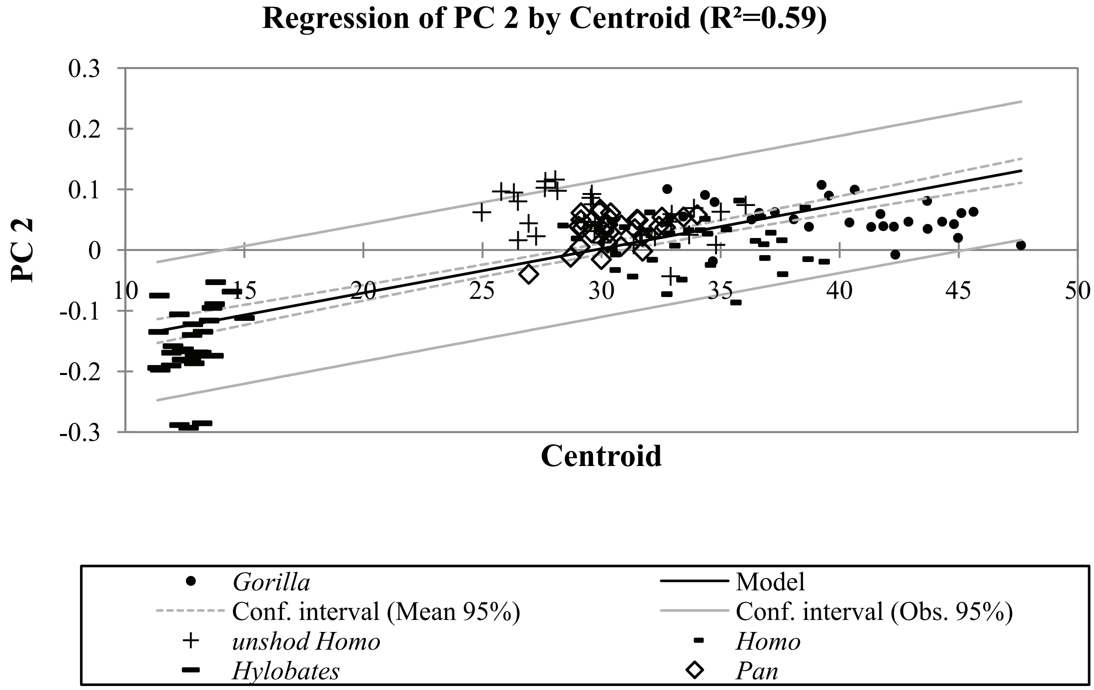
(Table 9.15). The regression analysis resulted in a significant relationship between centroid size and each PC 2, with $p < 0.001$ (Figure 9.12). The ANCOVA included species group names as a variable, and was significant with $p < 0.001$. The R^2 value for the linear regression was 0.59, and went up to 0.81 when species was included in ANCOVA analysis. A regression analysis was not conducted to compare centroid size with PC 3 because no groups are significantly different on the PC 3 axis.

Table 9.15 Regression and ANCOVA results

	PC 1*	PC 2
R^2 with PC and Size	0.007	0.59
R^2 with PC, Size, and Species	-	0.81

**Regression of centroid size and PC 1 yielded an insignificant result.*

Figure 9.12 Regression for interspecific comparison of PC 2 by centroid size



By including species in the regression analysis of centroid size and PC 2, the amount of variation explained increases by 22%. The biggest difference at the PC 2 axis and in centroid size is between *Hylobates* and all other groups. Recent analysis of the so-called midtarsal break present in apes reflects movement at the proximal MT 4 and MT 5 joint surfaces in addition to movement at the proximal cuboid joint (DeSilva, 2010). The extreme curvature present in *Hylobates*, combined with articular joint surface excursion to the dorsal aspect suggests that the range of motion at this joint in *Hylobates* is greater than in African apes. Whether that mobility is related to smaller body size or greater arboreality is undeterminable in this analysis without including similarly sized primates that are more terrestrial.

Intraspecific MT 4 Shape, Size, and Sex Variation

The following section discusses the results of analyses to determine whether there are size and/or sex related influences on shape within groups.

Gorilla

Gorilla Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with p = 0.26. There is no difference in proximal articular MT 4 surface size between males and females.

Gorilla Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The p value for the PC 1 t-test was 0.07, for the PC 2 t-test it was 0.17, and for the PC 3 t-test it was 0.26. There are no articular surface shape differences between males and females.

Pan

Pan Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with $p = 0.06$ (Table 9.16). There is no difference in proximal articular MT 4 surface size between males and females.

Table 9.16 T-test to compare PC 1 between sexes in *Pan*

t-Test: Two-Sample Assuming Unequal Variances		
	Females	*Males*
Mean	-0.12	-0.08
Variance	0.00	0.00
Observations	21.00	9.00
df	21.00	
t Stat	-2.24	
P(T<=t) one-tail	0.02	
t Critical one-tail	1.72	
P(T<=t) two-tail	0.04	
t Critical two-tail	2.08	

Pan Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. The tests revealed an insignificant result for PC 2 ($p = 0.15$) and PC 3 ($p = 0.14$). The p value for the PC 1 t-test was significant with $p = 0.02$. Since there is not a significant difference in articular surface size between males and females, size cannot explain this difference between males and females. It is possible that larger sample sizes would yield an insignificant result, particularly because there is a fairly large difference between the number of males and females compared.

Hylobates

Hylobates Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated an insignificant relationship with p = 0.40. There is no difference in proximal articular MT 4 surface size between males and females.

Table 9.17 T-test to compare PC 3 between sexes in *Hylobates*

t-Test: Two-Sample Assuming Unequal Variances

	Females	*males*
Mean	-0.03	0.03
Variance	0.00	0.00
Observations	17.00	13.00
df	27.00	
t Stat	-3.07	
P(T<=t) one-tail	0.00	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.00	
t Critical two-tail	2.05	

Hylobates Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. Tests for PC 1 and PC 2 revealed an insignificant result. The p value for the PC 1 t-test was 0.47, for the PC 2 t-test it was

0.29. There is a significant difference between males and females for PC 3, with p = 0.002 (Table 9.17). Males have a higher average score, which is associated with a relatively narrower articular surface. Since there is no difference in size between males and females, size cannot account for this difference.

Shod *Homo*

Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males and females. The result indicated a significant relationship with p = 0.02 (Table 9.18). There is a significant difference between males and females in proximal articular MT 4 surface size.

Table 9.18 T-test to compare centroid size between sexes in *Homo*

t-Test: Two-Sample Assuming Unequal Variances

	Females	*Males*
Mean	32.77	35.10
Variance	6.10	9.30
Observations	14.00	15.00
df	26.00	
t Stat	-2.27	
P(T<=t) one-tail	0.02	
t Critical one-tail	1.71	
P(T<=t) two-tail	0.03	
t Critical two-tail	2.06	

<u>*Homo* Shape and Size</u>

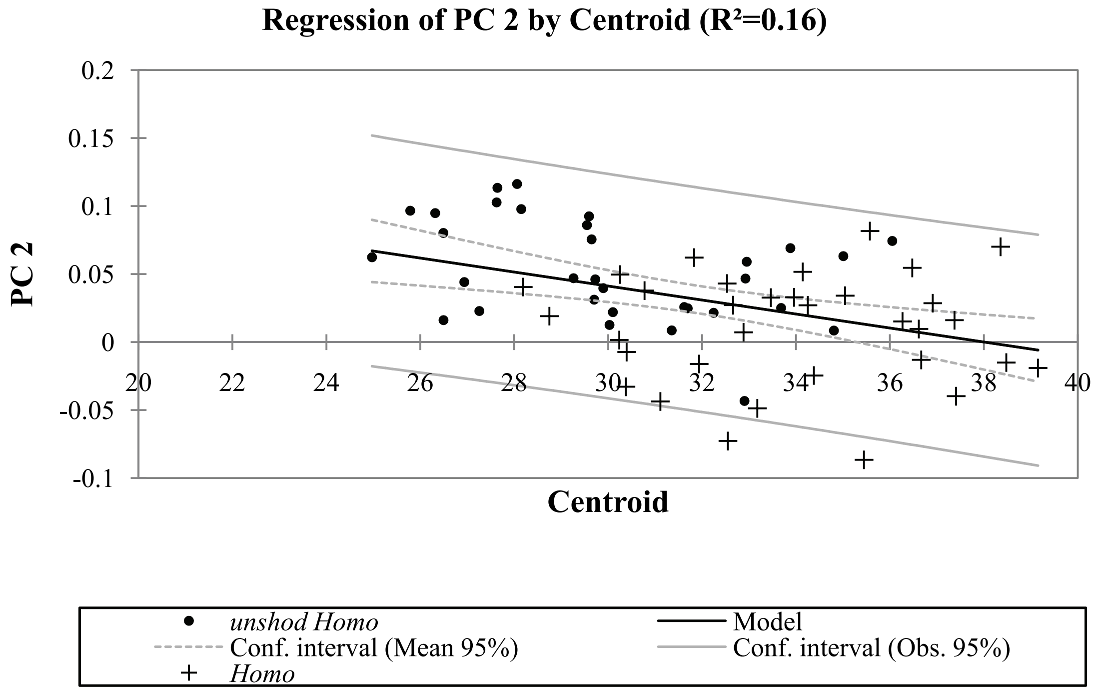
T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.35, for the PC 2 t-test it was 0.46, and for the PC 3 t-test it was 0.42. There are no articular surface shape differences between males and females.

Unshod *Homo*

<u>Recent and Unshod *Homo* Differences</u>

As indicated by the ANOVA reported above, there is a significant difference in MT 4 articular surface size between recent *Homo* and unshod *Homo*.

Figure 9.13 Regression for PC 2 by centroid size (shod and unshod *Homo*)



Homo Comparative Shape

The ANOVA results reported previously for PC 1, PC 2, and PC 3 revealed that *Homo* and unshod *Homo* are significantly different at the PC 2 axis. A regression analysis to look for a relationship between centroid size and PC 2 yielded a significant result with $p = 0.001$ and an R^2 of 0.16 (Figure 9.13). Shod *Homo* is larger than unshod *Homo*, and has a tendency to have a lower PC 2 score. The lower PC 2 score indicates a slightly more convex articular surface in shod *Homo*. Size accounts for 16% of the variation. To what degree population differences or differences due to shod or unshod habits account for the rest of the variation is indeterminable in this analysis. One hypothetical model is that habitually unshod feet develop a flatter articular surface during growth and development for greater stability of the joint.

Discussion

As with many of these analyses, the combination of PC 1 and PC 2 is most revealing in terms of shape differences between groups. In this case it is even truer because there were no differences between groups on the PC 3 axis. This axis essentially reflects variable surface width that exists in all groups. However, the differences reflected on the PC 1 and PC 2 axis are revealing and reflect function of the joint very closely.

When plotting a combination of PC 1 and PC 2, there are three groupings that do not overlap. African apes are not different from one another on the PC 1 axis and group together. Both human groups are not different from one another and group together on the positive side of PC 1 and PC 2. *Hylobates* occupies an area between these groupings on PC 1, but is located in an extreme negative area of PC 2. As predicted in the hypothesis (H_4), apes have a highly convex articular surface. Therefore, H_4 cannot be falsified. This finding corroborates DeSilva’s (2010) findings when he quantified maximum curvature relative to dorso-plantar surface height. However, one additional finding here is that *Hylobates* has an extreme degree of surface curvature.

The African ape proximal MT 4 articular surface is highly convex, with extension of the surface in the dorso-medial aspect. *Hylobates* usually lacks this extension, but has a highly convex surface that extends further to the dorsal aspect of the metatarsal. This suggests that *Hylobates* has a greater degree of flexion at this joint relative to the African apes, which dovetails into the observation that the MT 3 surface of *Hylobates* is likewise highly convex relative to other groups. The presence of the dorso-medial extension of the surface in African apes may be a consequence of a higher transverse arch in the foot compared to *Hylobates*. A higher arch changes the angle at which the bones articulate, raising the intermetatarsal facet for MT 3. This observation has been made by this author qualitatively, but it is a hypothesis that should be tested in a later study.

All groups are different from one another in articular surface size except for *Pan* and unshod *Homo*. A regression analysis yielded an insignificant result when looking for a relationship between size and PC 2. However, a significant result was obtained with PC 3. Size explains 59% of the variation. This is not a surprising result since *Hylobates* is so different from all other groups on the PC 2 axis and is also much smaller than all other groups.

An unexpected result was obtained when testing for differences in size between sexes within each group. All ape groups showed an insignificant result when testing for differences in mean centroid size for MT 4. Therefore, the hypothesis (H_9) that there is no difference in size between sexes cannot be rejected for the ape groups. This is an interesting finding, especially when considering that a similar result was obtained for MT 3. The high degree of flexion at this joint that occurs with apes may relieve the need to have a larger articular surface for load bearing. However, there is a significant difference between human males and females in terms of centroid size. The hypothesis (H_9) that there is no difference in size between sexes is rejected for humans. This joint is relatively inflexible in humans, bearing a load during locomotion without a midfoot break.

The hypothesis (H_{12}) that there are no differences in articular surface shape between sexes intraspecifically cannot be falsified for *Gorilla*. There are no differences in shape between males and females. This hypothesis cannot be falsified for *Pan*, since there is a difference between males and females at the PC 1 axis. However, males and females are not different in terms of size so size cannot explain this shape difference. Females have a lower PC 2 score than males, indicating a surface that extends further to the dorsal aspect. Since this seems to indicate greater flexion at this joint in *Hylobates*, it's possible that even though the surface itself is not larger in males, the overall larger body size of males compared to females influences the surface morphology due to different arboreal behavior. H_{12} cannot be falsified for *Hylobates*; there is a significant difference in PC 3 scores between males and females. Males tend to have a slightly narrower surface relative to females. Since the sexes are similar in size, it cannot explain this shape difference.

The hypothesis (H_4) that there are no significant differences in articular surface shape between shod and unshod humans is falsified. There is a significant difference between these groups at the PC 2 axis. Shod humans have a marginally greater degree of curvature. Regression analysis shows that size accounts for 16% of the variation. This can be interpreted in a couple of ways. The remaining explanation for the shape difference could simply be a population difference that has no functional significance. Another possibility is that the articular surface in the unshod group responds developmentally to produce a flatter articular surface. One way to approach this question in a later study would be to measure ground reaction forces in the lateral midfoot during locomotion, to compare how force differs in unshod humans and shod humans while wearing shoes during locomotion.

CHAPTER 10: ANALYSIS OF METATARSAL 5

Interspecific MT 5 Shape Variation

Proximal articular surface shape was analyzed with a principal components analysis. The combined variation explained by PCs 1-3 is 57% (Table 10.1). Principal component 4 and higher did not reveal meaningful shape variation shape. The table below reports proportions of variation represented by PC 1, PC 2, and PC 3. Refer to Figures 10.1 and 10.2 for an example of each species and for photos of the fossils. The PCA results are discussed below.

Table 10.1 Proportion of PC Variance for MT 5

Proportion of Variance for MT 5		
PC 1	PC 2	PC 3
26%	19%	12%

Table 10.2 Extant Specimens in the MT 5 Analysis

Group	Number
Gorilla	30
Pan	30
Hylobates	30
Homo	33
unshod *Homo*	42

Figure 10.1 MT 5 extant groups photos: A) *Gorilla*; B) *Pan*; C) *Hylobates*; D) *Homo*; E) unshod *Homo*.

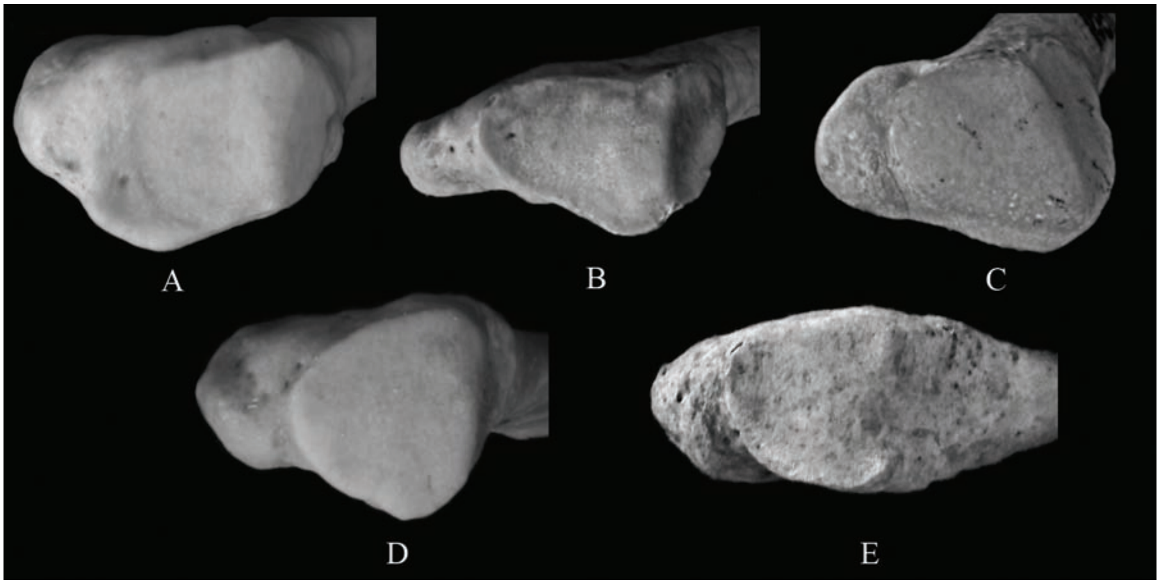
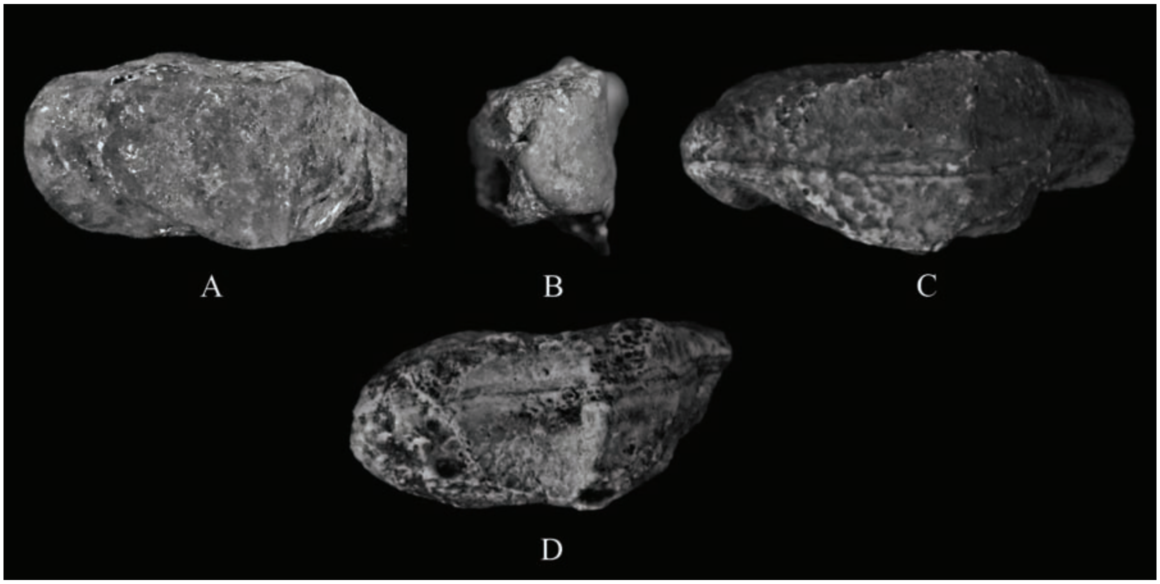


Figure 10.2 MT 5 fossil photos; A) Stw 114/115 (Right, flipped to appear as a left); B) OH 8; C) AL 333-78; D) AL 333-13



MT 5 Principal Component 1

The PC 1 axis shows considerable overlap between all groups, which is different from the analysis of metatarsals 1-4 in that the PC 1 axis is often the axis that shows the greatest differences between humans and apes (Figure 10.3). An ANOVA was conducted to test for differences in the means of PC 1 scores between groups. This analysis yielded a statistically significant result with $p < 0.0001$. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. A Tukey-Kramer post-hoc test was conducted with the ANOVA to test for statistically significant differences in means between specific groups. See Table 10.3.

Even though all groups overlap, there are differences in the mean PC 1 scores among many groups. *Gorilla* is different from all groups. *Pan* is different from all groups except *Hylobates*, while *Hylobates* is only different from *Gorilla*. *Homo* and unshod *Homo* are both only different from the African apes, *Pan* and *Gorilla*, but not *Hylobates*.

Table 10.3 Tukey-Kramer Multiple-Comparison Test for PC 1

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.06	*Homo*, unshod *Homo*, *Hylobates*, *Pan*
Pan	30	0.06	*Homo*, unshod *Homo*, *Gorilla*
Hylobates	30	0.03	*Gorilla*
Homo	33	0.00	*Gorilla*, *Pan*
unshod *Homo*	42	-0.01	*Gorilla*, *Pan*

Table 10.4 Principal Component 1 Ranges for MT 5

Group	Minimum	Maximum	Range
Gorilla	-0.18	0.06	0.24
Pan	-0.03	0.16	0.19
Hylobates	-0.13	0.14	0.27
Homo	-0.10	0.14	0.24
unshod *Homo*	-0.12	0.17	0.29

Table 10.5 Fossil PC 1 Value for MT 5

Specimen	PC 1
Stw 114/115	0.02
OH 8	-0.22
AL 333-78	-0.10
AL 333-13	0.00

The articular surface shape on the negative PC 1 axis is medio-laterally more narrow and expanded in the dorso-plantar aspect (Figure 10.4). Further, the surface is convex both in the dorso-plantar plane and the medio-lateral plane. At the positive area of the PC 1 axis the articular surface is medio-laterally expanded and wide relative to its dorso-plantar height (Figure 10.5). The surface is convex in the dorso-plantar plane but concave in the medio-lateral plane. The *Pan* grouping is closer to the extreme positive range of PC 1, while the range of *Homo* and *Hylobates* extends more negatively on the PC 1 axis. *Gorilla* is grouped more towards the negative area of the PC 1 axis. The unshod *Homo* group spans a considerable range, similar to *Homo* but extending further positively and negatively. Of the fossil specimens, AL 333-13, AL 333-78, and Stw 114/115 overlap both human groups. The specimen AL 333-78 also overlaps all ape groups except *Pan*, while AL 333-78 and Stw 114/115 overlap all ape groups. The specimen OH 8 does not overlap any other groups, which is attributed to the fact that it has an articular surface which is medio-laterally narrow to an extreme degree relative to the other specimens of all groups.

Figure 10.3 Plot of PC 1 and PC 2 group averages and fossil specimens for MT 5

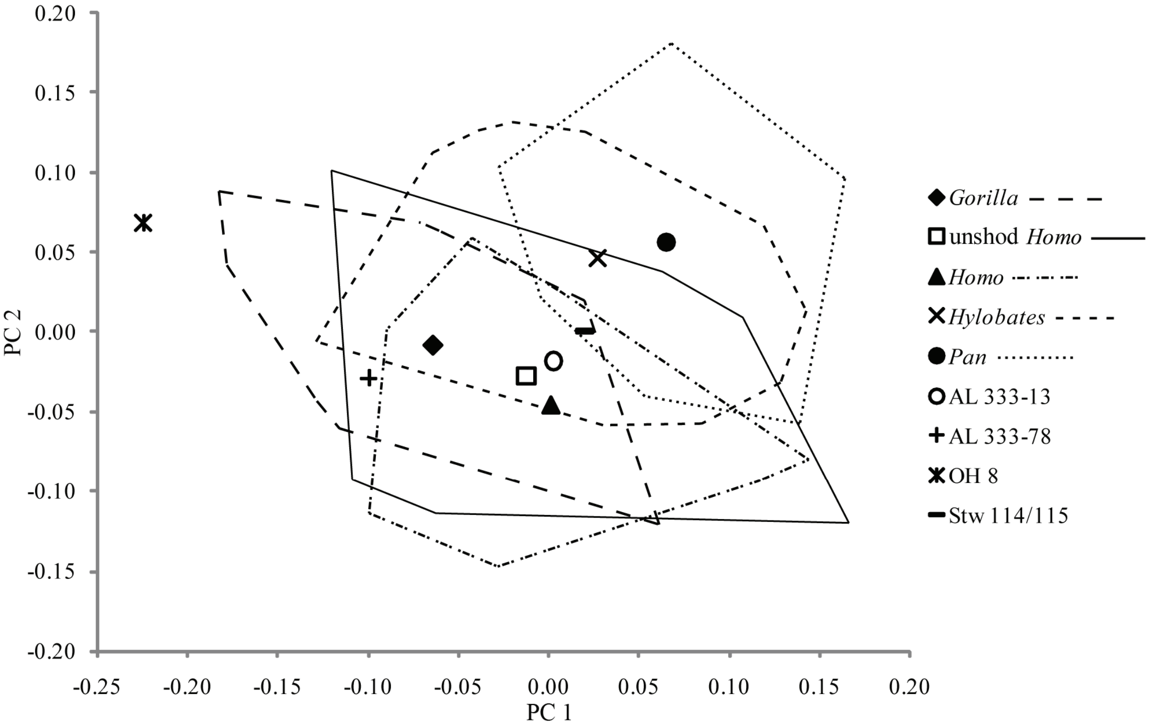


Figure 10.4 PC 1 (-0.19) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground).

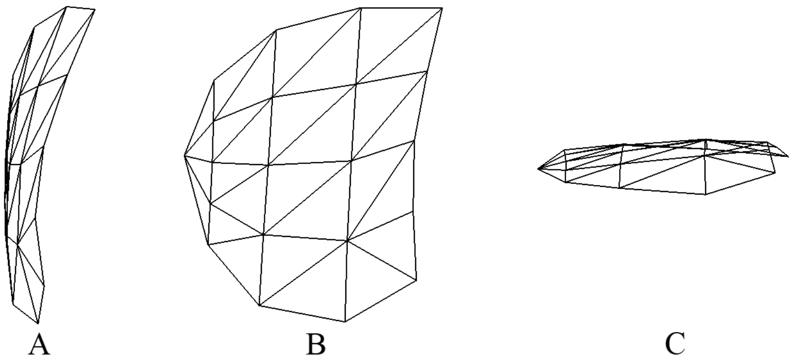
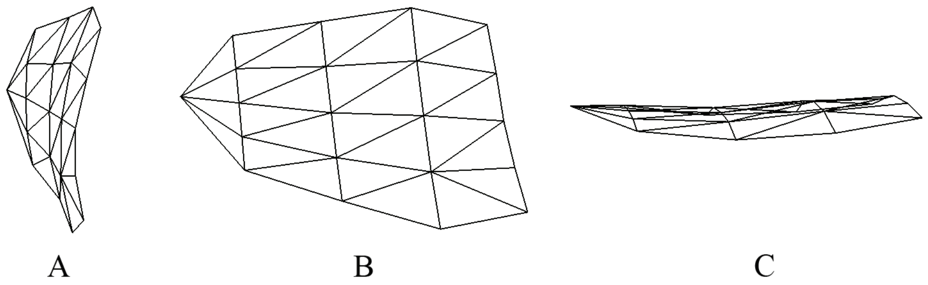


Figure 10.5 PC 1 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)



MT 5 Principal Component 2

An ANOVA was conducted to test for differences in the means of PC 2 scores between groups. The analysis yielded a statistically significant result with a $p < 0.0001$. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All passed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. The results are reported in Table 10.6).

Table 10.6 Tukey-Kramer Multiple-Comparison Test for PC 2

Group	Specimens	Mean	Different From Groups
Gorilla	30	0.00	*Homo*, *Hylobates*, *Pan*
Pan	30	0.06	*Homo*, unshod *Homo*, *Gorilla*
Hylobates	30	0.05	*Homo*, unshod *Homo*, *Gorilla*
Homo	33	-0.05	*Gorilla*, *Hylobates*, *Pan*
unshod *Homo*	42	-0.03	*Hylobates*, *Pan*

There are two main groupings on the PC 2 axis and all groups overlap one another Figure 10.3). Nonetheless, the PC 2 axis does a better job of distinguishing between more terrestrial groups versus more arboreal groups compared to the PC 1 axis. One grouping consists of *Pan* and *Hylobates*, both of which are statistically different from all other groups but not one another. The second grouping consists of *Gorilla* and both human groups, but even though shod *Homo* groups more with *Gorilla*, their mean PC 2 scores are significantly different.

Table 10.7 Principal Component 2 Ranges for MT 5

Group	Minimum	Maximum	Range
Gorilla	-0.12	0.09	0.21
Pan	-0.06	0.18	0.24
Hylobates	-0.06	0.13	0.19
Homo	-0.15	0.06	0.21
unshod *Homo*	-0.12	0.10	0.22

Table 10.8 Fossil PC 2 Values for MT 5

Specimen	PC 2
Stw 114/115	0.00
OH 8	0.07
AL 333-78	-0.03
AL 333-13	-0.02

The shape represented on the PC 2 axis is that of an articular surface that is flatter at the negative area with the medial surface edge sloped obliquely with the dorsal portion extending more medially (Figure 10.6). At the positive area of the PC 2 axis the surface is highly convex at the positive area of the axis (Figure 10.7). In addition, at the positive side of the axis the surface is obliquely sloped with the plantar portion extending more medially. The ranges of *Pan* and *Hylobates* extend further toward the positive axis of PC 2, while *Gorilla* and both groups of *Homo* tend toward the negative aspect of the PC 2 axis. The specimens AL 333-13, AL 333-78, and Stw 114/115 overlap all groups, but they occupy a location more central to the human groups and *Gorilla*. The specimen OH 8 overlaps all groups except shod *Homo*.

Figure 10.6 PC 2 (-0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)

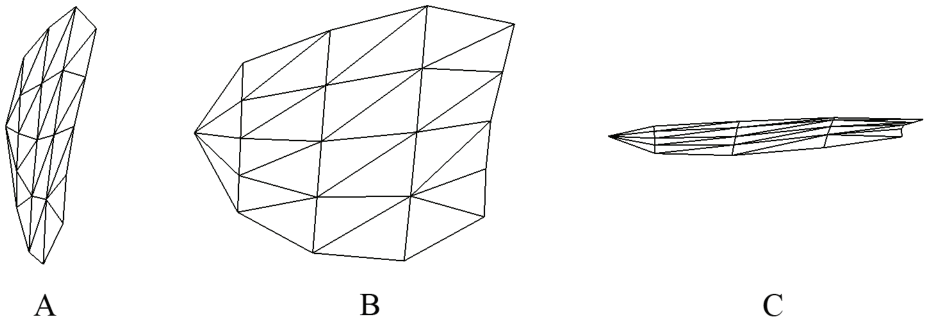
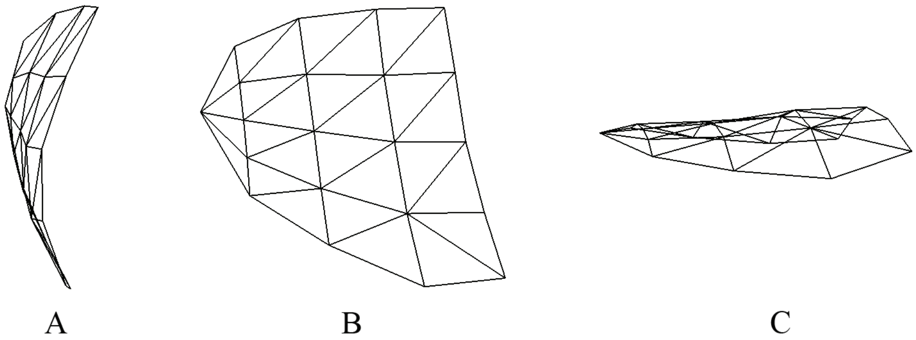


Figure 10.7 PC 2 (0.16) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)



MT 5 Principal Component 3

An ANOVA to test for differences between PC 3 score group means yielded a statistically significant result with $p < 0.0001$. The following tests for assumptions of data normality were conducted: skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and the Levene equal variance test. All but the skewness test failed at the 0.05 significance level. To test for statistically significant differences in means between specific groups, the Tukey-Kramer post-hoc test was conducted with the ANOVA. See Table 10.9.

In terms of group mean differences, there are two groupings (Figure 10.8). *Hylobates* is different from all other groups, and there is no difference in mean PC 3 scores between *Pan*, *Gorilla*, and both human groups. *Pan* has a much smaller range than any other group on the PC 3 axis, and *Gorilla* is similarly different from the other groups (Table 10.10). All groups overlap on this axis, and all fossils overlap all groups, except OH 8, which does not overlap *Pan*.

Table 10.9 Tukey-Kramer Multiple-Comparison Test for PC 3

Group	Specimens	Mean	Different From Groups
Gorilla	30	-0.02	*Hylobates*
Pan	30	-0.01	*Hylobates*
Hylobates	30	0.05	*Gorilla*, *Pan*, *Homo*, unshod *Homo*
Homo	33	-0.01	*Hylobates*
unshod *Homo*	42	-0.05	*Hylobates*

Shape at the negative portion of the PC 3 axis shows a lightly convex surface in the dorso-plantar plane and it is slightly concave in the medio-lateral plane (Figure 10.9).

The surface is expanded in the medio-plantar area. The shape at the positive area of the PC 3 axis is expanded in the dorsal area of the articular surface and is much more convex in the dorso-plantar plane (particularly at the dorsal aspect) and slightly convex in the medio-lateral plane (Figure 10.10).

Table 10.10 Principal Component 3 Ranges for MT 5

Group	Minimum	Maximum	Range
Gorilla	-0.09	0.06	0.15
Pan	-0.06	0.03	0.09
Hylobates	-0.15	0.13	0.28
Homo	-0.12	0.12	0.24
unshod *Homo*	-0.10	0.10	0.20

Table 10.11 Fossil PC 3 Values for MT 5

Specimen	PC 3
Stw 114/115	-0.03
OH 8	0.04
AL 333-78	-0.02
AL 333-13	0.02

Figure 10.8 Plot of PC 1 and PC 3 group averages and fossil specimens for MT 5

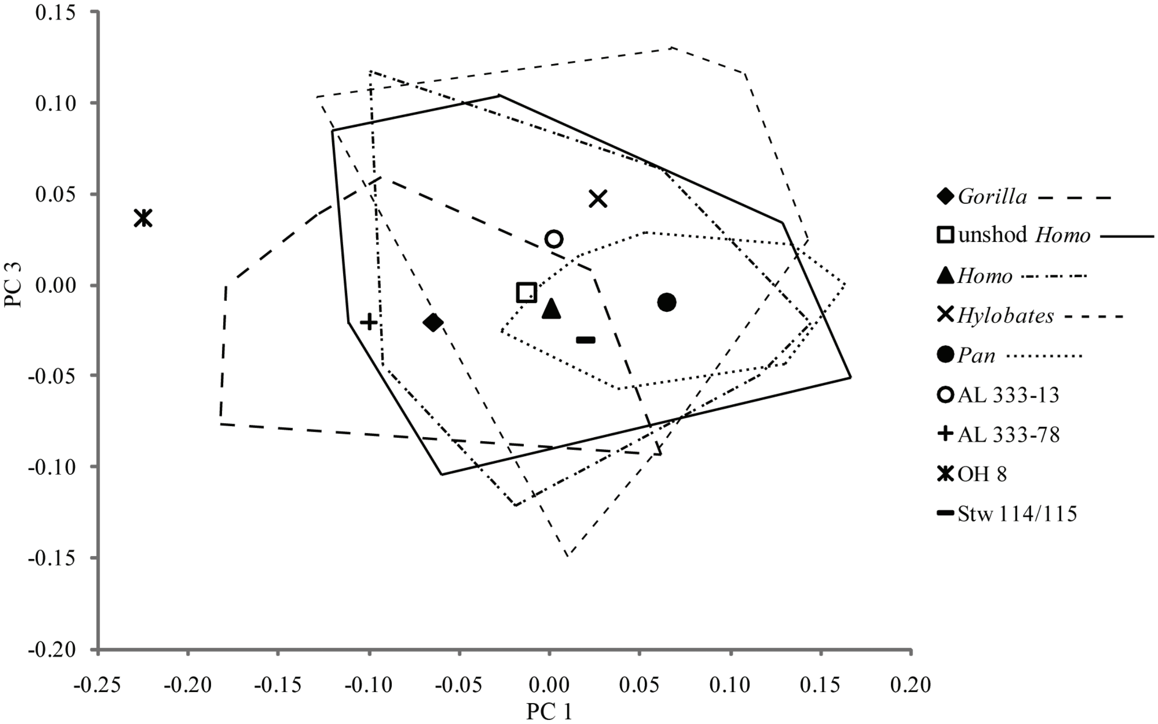


Figure 10.9 PC 3 (-0.13) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)

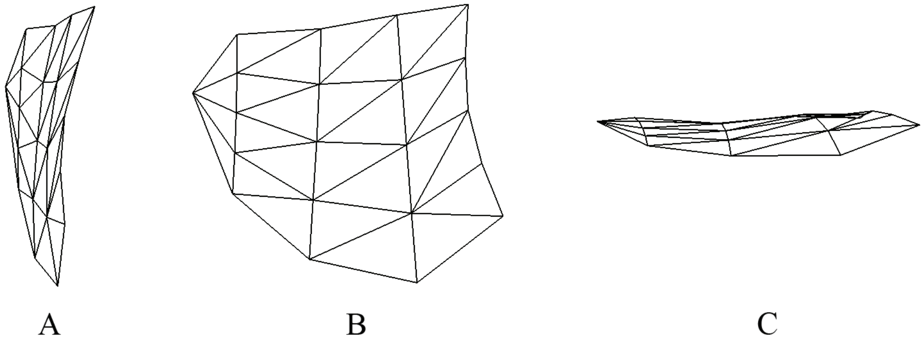
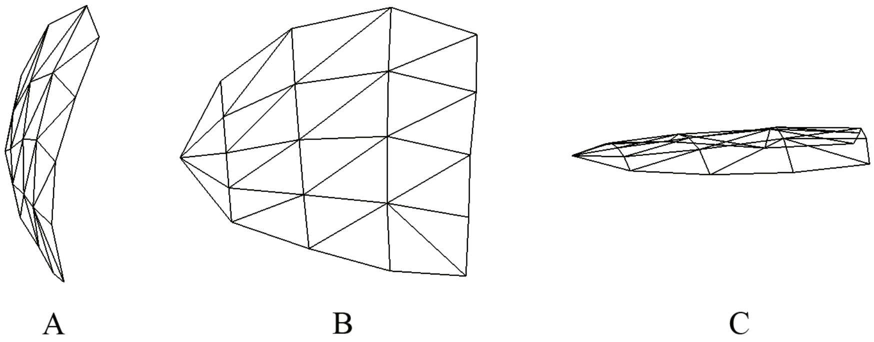


Figure 10.10 PC 3 (0.11) A) medial view; B) proximal view; C) proximal view, tilted in the plantar direction (foreground)



Interspecific Size and Shape Relationships

An ANOVA was conducted to test for differences in centroid sized between groups. The result was significant, with $p < 0.0001$. H_8 is falsified. Tests for skewness normality of residuals, kurtosis normality of residuals, omnibus normality of residuals, and a Levene equal variance test were conducted. The skewness and kurtosis tests passed at the 0.05 level, but the normality and equal variance tests failed. A Tukey-Kramer post-hoc test was conducted to find differences in centroid size between specific groups. The results are presented in Table 10.12.

Table 10.12 Tukey-Kramer Multiple-Comparison Test for Centroid Size of MT 5

Group	Specimens	Mean	Different From Groups
Gorilla	30	28.29	*Homo*, unshod *Homo*, *Pan*, *Hylobates*
Pan	30	21.30	*Hylobates*, *Homo*, *Gorilla*
Hylobates	30	8.35	*Homo*, unshod *Homo*, *Pan*, *Gorilla*
Homo	33	26.03	*Hylobates*, unshod *Homo*, *Pan*, *Gorilla*
unshod *Homo*	42	22.50	*Hylobates*, *Homo*, *Gorilla*

All groups have significant differences in mean articular surface size as reflected in centroid size, except for unshod *Homo* and *Pan*. The sizes can be ranked with *Gorilla* the largest, followed by shod *Homo*, then *Pan* and unshod *Homo*. *Hylobates* is the smallest.

Table 10.13 Centroid Size Ranges for MT 5

Group	Minimum	Maximum	Range
Gorilla	21.18	34.69	13.51
Pan	17.19	23.99	6.8
Hylobates	7.04	10.27	3.23
Homo	17.31	30.85	13.54
unshod *Homo*	15.75	29.57	13.82

Table 10.14 Fossil Centroid Sizes for MT 5

Specimen	Centroid
Stw 114/115	20.42
OH 8	13.60
AL 333-78	20.02
AL 333-13	21.73

A regression analysis and ANCOVA were conducted to determine whether there is a relationship between size and shape at the intraspecific level for PC 1. The regression analysis yielded a significant result with $p = 0.007$. The ANCOVA included species groups as a variable, and the test was significant with $p < 0001$. There is a relationship between size and shape on the PC 1 axis (Table 10.15). The R^2 value for the linear regression of PC 1 and size was 0.04, and went up to 0.35 when species was included in ANCOVA analysis (Figure 10.11). Regression analysis and an ANCOVA were conducted to determine whether there is a relationship between size and shape at the intraspecific level for PC 2. The regression analysis resulted in a significant relationship between centroid size and PC 2, with $p < 0.0001$ (Figure 10.12). The ANCOVA included species group names as a variable, and was significant with $p < 0.0001$. The R^2 value for the linear regression with PC 2 and size was 0.17, and went up to 0.40 when species was included in the ANCOVA analysis. Finally, regression analysis and an ANCOVA were also conducted to determine whether there is a relationship between size and shape at the intraspecific level for PC 3. The regression analysis resulted in a significant relationship between centroid size and PC 3, with $p < 0.0001$ (Figure 10.13). The ANCOVA included species group names as a variable, and was significant with $p < 0.0001$. The R^2 value for the linear regression with PC 2 and size was 0.19, and went up to 0.21 when species was included in the ANCOVA analysis.

The biggest gains in explaining differences in shape and size while including species group names occurred in PC 1 and PC 2. The amount of variation explained in the regression of PC 1 and size is very small, which is not surprising since the range of shape variation on this axis is large with considerable overlap between groups. The PC 2 axis is the most interesting in terms of shape and function, with the more terrestrial groups have negative scores and the arboreal groups having more positive scores. The terrestrial groups are also the larger groups. The PC 3 axis is less informative about shape differences, although *Hylobates* does have a tendency to be further toward the positive aspect of the PC 3 axis, with greater articular surface curvature at the dorsal area of the surface. It is not surprising that including group names as a variable in the PC 3 and size regression does not increase the percentage of variation explained by very much, since the only significant difference in PC 3 group means at this axis are between *Hylobates* and every other group. The other groups encompass a fairly wide size range.

Table 10.15 Regression and ANCOVA results

	PC 1	PC 2	PC 3
R^2 with PC and Size	0.04	0.17	0.19
R^2 with PC, Size, and Species	0.35	0.40	0.21

Figure 10.11 MT 5 regression for interspecific PC 1 and centroid size relationships

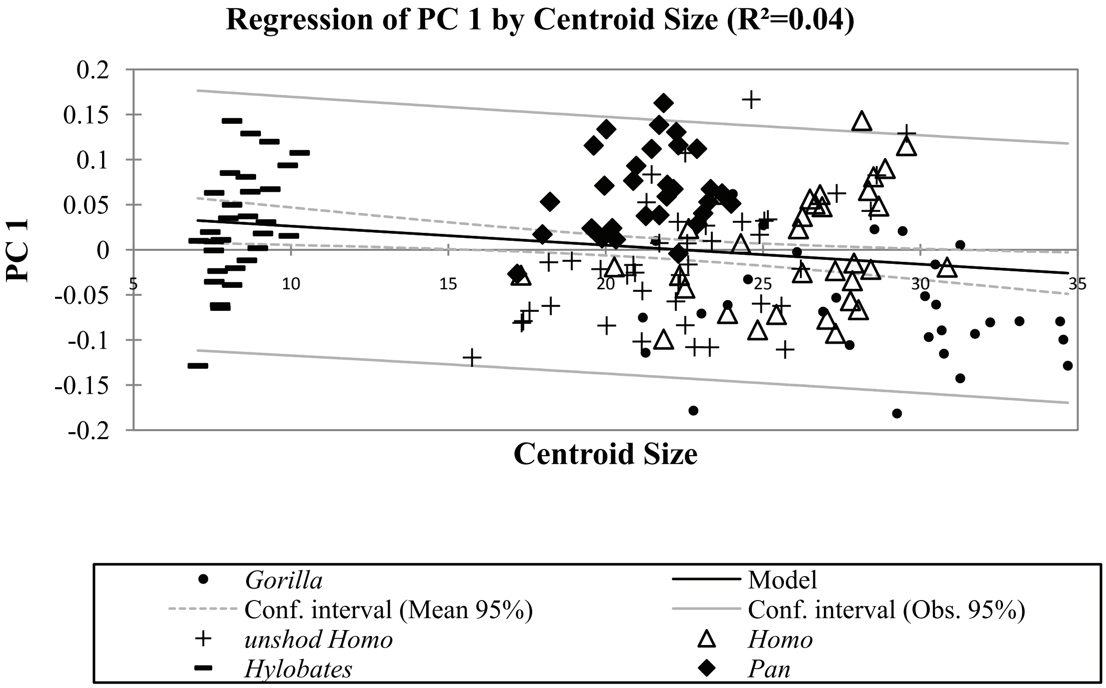


Figure 10.12 MT 5 regression for interspecific PC 2 and centroid size relationships

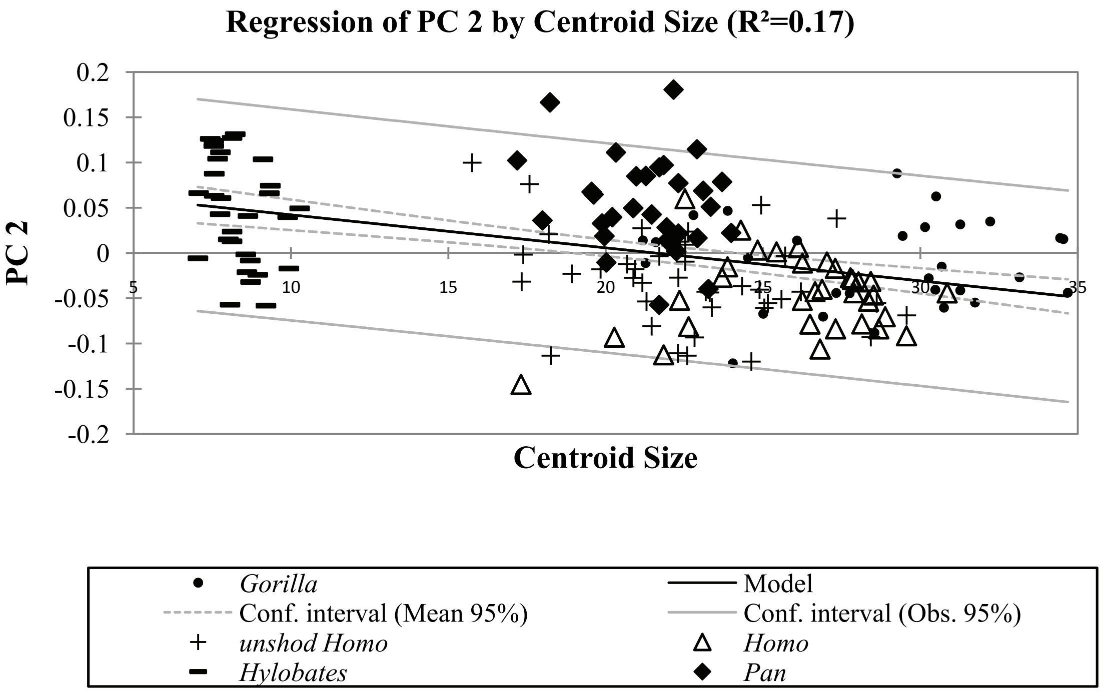
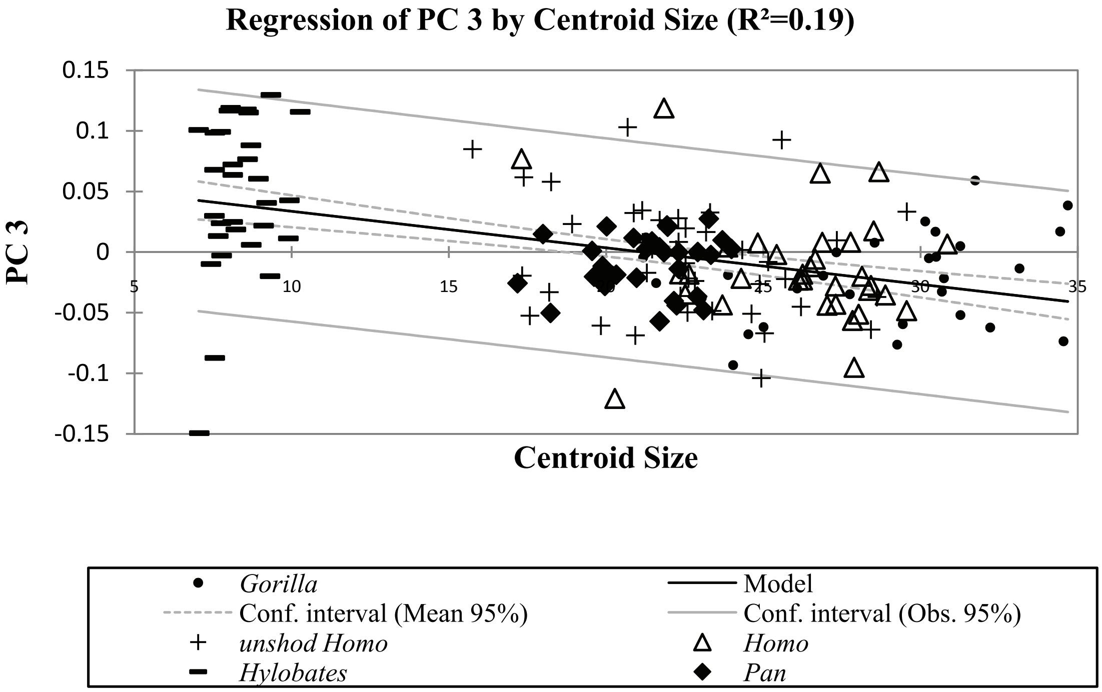


Figure 10.13 MT 5 regression for interspecific PC 3 and centroid size relationships



Intraspecific MT 5 Shape, Size, and Sex Variation

The following section discusses the results of analyses to determine whether there are size and/or sex related influences on shape within groups.

Gorilla

Gorilla Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males (n = 16) and females (n = 14). The result indicated an insignificant relationship with *p* = 0.29. There is no difference in proximal articular MT 5 surface size between males and females.

Gorilla Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.23, for the PC 2 t-test it was 0.19, and for the PC 3 t-test it was 0.47. There are no articular surface shape differences between males and females.

Pan

Pan Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males (n = 9) and females (n = 21). The result indicated an insignificant relationship with *p* = 0.46. There is no difference in proximal articular MT 5 surface size between males and females.

Pan Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. The tests revealed an insignificant result for PC 1 (p = 0.18), PC 2 (*p* = 0.40), and PC 3 (*p* = 0.10). There are no differences between males and females in terms of articular surface shape.

Hylobates

Hylobates Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males (n = 14) and females (n = 16). The result indicated an insignificant relationship with $p = 0.38$. There is no difference in proximal articular MT 5 surface size between males and females.

Hylobates Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. Tests for PC 1 ($p = 0.18$), PC 2 ($p = 0.40$), and PC 3 ($p = 0.25$) revealed insignificant results.

Table 10.16 MT 5 t-test for comparing centroid size between sexes in *Homo*

t-Test: Two-Sample Assuming Unequal Variances

	F	*M*
Mean	25.30197	27.41265
Variance	6.557942	4.114836
Observations	14	15
df	25	
t Stat	-2.44	
P(T<=t) one-tail	0.01	
t Critical one-tail	1.70	
P(T<=t) two-tail	0.02	
t Critical two-tail	2.06	

Shod *Homo*

Size and Sex

A t-test assuming unequal variance was conducted to compare centroid size between males (n = 15) and females (n = 14). The result indicated a significant relationship with *p* = 0.01 (Table 10.16). There is a significant difference between males and females in proximal articular MT 5 surface size. Refer to Table 10.16.

Homo Shape and Size

T-tests were conducted for PC 1, PC 2, and PC 3 to compare mean principal component scores between males and females. All tests revealed an insignificant result. The *p* value for the PC 1 t-test was 0.33, for the PC 2 t-test it was 0.34, and for the PC 3 t-test it was 0.12. There are no articular surface shape differences between males and females.

Unshod *Homo*

Recent and Unshod *Homo* Differences

As indicated by the ANOVA reported above, there is a significant difference in MT 5 articular surface size between recent *Homo* and unshod *Homo*.

Homo Comparative Shape

The ANOVA results reported previously for PC 1, PC 2, and PC 3 revealed that *Homo* and unshod *Homo* are not significantly different at any of the PC axes.

Discussion

One of the interesting findings for the MT 5 proximal articular surface is that the difference in shape between humans and apes is not as dramatic as one might expect, especially in light of the dramatic differences in the other metatarsals and in the fact that there is a functional difference between humans and apes in the lateral foot. Nonetheless, there are important differences in shape and trends that can be described that separate not just humans from apes, but the more arboreal *Pan* and *Hylobates* compared to *Gorilla*.

The most important shape differences are reflected on the PC 1 and PC 2 axes. It is most useful to interpret the effects of these axes combined. All groups overlap each other on these axes. The main shape trends observable on the PC 1 axis include a medio-laterally narrow surface with greater dorso-plantar convex curvature at the negative portion of PC 1 axis. On the positive side of the PC 1 axis, the surface is elongated in the medio-lateral plane with medio-lateral concave curvature and lessened dorso-plantar convex curvature. The shape trends on the PC 2 axis include a flat surface at the negative side of the axis and extreme dorso-plantar convex curvature at the positive side of the axis. On the PC 1 axis, *Gorilla* is different from all groups in terms of its mean PC score. *Pan* is different from all groups except *Hylobates*. Both human groups are different from the African apes, but not *Hylobates*. *Hylobates* is only different from *Gorilla*. On the PC 2 axis, *Gorilla* is different from shod *Homo*, *Pan*, and *Hylobates*. *Pan* and *Hylobates* are not different from one another but are different from all other groups. Both human groups are different from *Hylobates* and *Pan*, and shod *Homo* is further different from *Gorilla*.

Interpreting the combined effects of these axes, *Pan* and *Hylobates* occupy the positive areas of PC 1 and PC 2. On both axes these areas reflect a surface that has a high degree of convex curvature in the dorso-plantar plane. *Pan*'s extreme location on PC 2 also indicates that in *Pan* the surface tends to be medio-laterally extended to a greater degree. In contrast, both human groups and *Gorilla* occupied a similar are on these axes, with shod *Homo* having a smaller range on the PC 1 axis. Shod *Homo* has a much more conservative shape, with a tendency to have a flatter surface and it is approximately equal in dorso-plantar height relative to medio-lateral width. Unshod *Homo* also tends to have a flatter surface, but a much wider range of shape in terms of medio-lateral width relative to dorso-plantar height. The shape shown by *Gorilla* does not tend to be as medio-lateral elongated as the other apes, showing a tendency to be narrower but with greater dorso-plantar convex curvature and little medio-lateral curvature.

Therefore, the hypothesis (H_3) that apes will show medio-lateral concavity and elongation relative to humans is falsified when comparing humans to *Gorilla*, but not falsified in comparison to *Pan* and *Hylobates*. The added observation for *Pan* and *Hylobates* is that their surface shape combines medio-lateral concavity with dorso-plantar convexity.

Gorilla bears considerable similarity to the human groups, but also has a range that extends much further toward the extreme negative area of PC 1. Of the fossil specimens, OH 8 occupies an area on the extreme negative of PC 1, overlapping no other groups at this axis. This reflects the fact that the surface of OH 8 is very medio-laterally narrow and has a great deal of dorso-plantar curvature. Remembering that OH 8 shows great similarity to humans in its MT 4 articular surface shape, it seems unlikely that this morphology reflects a highly mobile proximal MT 5 joint. However, the possibility cannot be ruled out that there may be greater flexibility in this joint compared to modern humans. Based on these observations, the hypothesis (H_6) that OH 8 will show greater similarity to humans in articular surface shape is falsified for MT 5.

The interpretation of the other fossil specimens is unclear. The specimens primarily overlap both human groups and *Gorilla*, but with no particularly greater affinity to any of these groups. The specimen AL 333-78 overlaps humans and *Gorilla* on the PC 1 and PC 2 axes, but the combined placement of this specimen on these axes places it outside of the grouping of shod humans and within only unshod *Homo* and *Gorilla*. Still, this does not necessarily indicate greater affinity to *Gorilla* compared to unshod *Homo*. Overall, the results for MT 5 indicate that the most arboreal species are most differentiated in articular surface shape, but the more terrestrial groups are not. From a functional point of view, this suggests that observing the proximal MT 5 surface alone without reference to the other metatarsal proximal surfaces is less informative in being a predictor of function when looking at the hominin fossils.

In terms of articular surface size, all groups are different from one another except *Pan* and unshod *Homo*. The hypothesis H_8 (there is no difference in size interspecifically) is falsified. In addition, H_{10} (differences in surface shape interspecifically are unrelated to size) is falsified due to a significant result in regression analysis comparing size and shape for each PC axes in this study. The amount of variation explained by size for PC 1 is low at 4%. Size explains 17% of PC 2, which is not unexpected since *Pan* and *Hylobates* have more extreme ranges on this axis. However, the gains in terms of explaining the variation increase a great deal when including species group names in the analysis. The amount explained for PC 1 rises to 35% and for PC 2 rises to 40%. This indicates that size has less of an effect than simply which group a specimen belongs to. This can be interpreted as reflecting mode of locomotion.

In terms of articular surface size, there are no intraspecific differences in the ape groups. The hypothesis (H_9) that males and females have different mean sizes is falsified for the ape groups. However, it is not falsified for *Homo*. Males are significantly larger than females. One model for this explanation follows closely with that proposed for MT 4. Despite the high degree of sexual dimorphism in *Gorilla*, males and females are different in articular surface size. Since all of the apes have lateral midfoot flexibility, the load requirements on the joint surface may be reduced compared to in *Homo*. As a consequence, joint surface size is more closely related to overall body size. The hypothesis (H_{12}) that there are differences in articular surface shape between sexes is falsified for MT 5. There are no differences in shape at any axis for any apes or human groups.

CHAPTER 11: DISCUSSION AND CONCLUSIONS

Considerable discussion has been offered for each metatarsal analysis. These findings are presented again here. Additional discussion serves to interpret the results in a holistic fashion to assess the entire tarsometatarsal joint complex in relation to function. One important synthesis to draw from the results of these analyses is the interpretation of what degree and in what pattern the tarsometatarsal joints achieve a human-like shape in the fossil hominins.

MT 1 Results

The position of SKX 5017 on the PC axes shows affiliation with apes, and A. L. 333-54, although still grouping with apes, does not group with *Gorilla* or *Hylobates*. The specimen A. L. 333-54, while being deeply curved, lacks oblique curvature in the dorso-lateral area. In the main analysis that includes all landmarks, there is a clear morphological split between humans and apes. The fossil specimens show three “shape trends.” The first is that OH 8 is indistinguishable from humans. Therefore, the hypothesis (H_6) that the proximal MT surfaces of OH 8 will resemble humans cannot be falsified.

The second shape trend is that SKX 5017 and SK 1813 (from the second analysis) show affiliation to the apes. All remaining fossil specimens for MT 1 are intermediate between humans and apes in shape. Therefore, the hypothesis (H_7) that the fossil specimens new to this kind of analysis (excluding A. L. 333-54 and SKX 5017) will more closely resemble humans is falsified.

The ape morphology reflected in the combination of the PC 1 and PC 2 axes is of a saddle joint, with oblique curvature in the medio-plantar and latero-dorsal areas. The surface is highly curved in the dorsal and plantar aspects, and the overall surface is wider at the medio-lateral aspect relative to the dorso-plantar dimension. Within apes, the morphology changes from being a particularly deep surface at the negative aspect to having reduced oblique curvature toward the 0.00 axis of PC 1. *Gorilla* is statistically different from *Pan* and *Hylobates,* but *Pan* and *Hylobates* are not statistically different from one another. This corresponds to their broad locomotor differences, since *Gorilla* tends to be more terrestrial. *Gorilla* also tends to have greater curvature at the medio-plantar aspect of the articular surface, which is accompanied by a tendency for extra bone deposition just inferior to this curvature. This can be interpreted as a region that in *Gorillas* is subject to greater compressive forces and may relate to either their greater body size, greater terrestriality, or both. However, it is particularly interesting that *Pan* and *Hylobates* are not statistically different at the PC 1 axis regardless of the fact that *Pan* has a much larger body size and *Hylobates* is much more arboreal.

In contrast, the surface as represented on the PC 1 axis changes into a much flatter morphology at the positive area of the axis, where it ceases to represent a saddle joint. The surface loses the oblique curvature characteristic of the apes, and the surface is constricted at the central area. In addition, the plantar aspect is narrower than the dorsal aspect and the surface as a whole is relatively narrower medio-laterally.

The morphology represented by STX 5017 is particularly ape-like compared to the other fossil specimens. This specimen has been attributed to the genus and species *Paranthropus robustus* and has been described as being similar in morphology to OH 8 (Susman and Brain, 1988). However, in comparing it to OH 8 it is important to note that the distal half of OH 8 is missing, and that in later analyses by Susman and DeRuiter SKX 5017 demonstrates apelike traits of the metatarsal head (Susman and DeRuiter, 2003). The proximal articular surface of SKX 5017 is not particularly deep, but it is ape-like in that it is relatively wide, lacks the human constriction to the central region, and demonstrates overall surface curvature that is deeper in the central area as opposed to the typical human condition of surface elevation in the central area. In addition, SKX 5017 demonstrates oblique ape-like surface curvature that is particularly expressed at the medio-plantar aspect. In this region it especially resembles *Gorilla*, as *Gorilla* tends to have additional curvature at the medio-plantar aspect relative to *Pan*.

The specimens A. L. 333-54, Stw 562 and Stw 573 group very tightly on the PC 1 axis. Of these, A. L. 333-54 has been attributed to the genus and species *Australopithecus afarensis*, Stw 573 has tentatively been assigned to *Australopithecus africanus*, and Stw 562 has not been assigned to a genus (Clarke and Tobias, 1995; Latimer et al. 1982; Latimer and Lovejoy, 1990; Deloison, 2003). Since Stw 562 comes from Sterkfontein member 4, it is possible that it is *Paranthropus* or early *Homo*. Of these three specimens, A.L. 333.54 and Stw 562 have deep articular surfaces and resemble each other somewhat more than either does Stw 573 that has a more shallow surface. All of these specimens have the characteristic human constriction of the central region and the plantar breadth is narrower than the dorsal breadth, making them similar to humans. The morphology of all of these specimens at the PC 1 axis is intermediate between humans and apes.

The *Homo habilis* specimen OH 8 groups well within the human PC 1 grouping. The articular surface is flat, and is constricted in the middle region. In shape it is indistinguishable from the human proximal surface. Since OH 8 also exhibits a medial facet for articulation with MT 2, it is highly probable that OH 8 represents a completely immobile human-like tarsometatarsal joint.

The PC 2 axis is most useful for distinguishing differences in articular surface shape between the ape groups, with a separation between *Gorilla* and the more arboreal groups. *Gorilla* occupies a more negative position on the PC 2 axis, while *Hylobates* is at the higher end of the axis and *Pan* is intermediate. The area occupied by *Hylobates* and *Pan* shows a tendency toward greater surface curvature, particularly in the dorso-medial area, and narrowing of the plantar portion of the articular surface. The surface of *Gorilla* is more uniformly wide and deep in the central area.

The results for the separate principle components analysis with specimen SK 1813 closely resembles the main analysis that includes all landmarks. In the full analysis

SKX 5017 groups with apes, OH 8 groups with humans, and the remaining fossil specimens are intermediate between humans and apes. In the analysis for SK 1813 landmarks are missing in the dorso-lateral area of the articular surface. This results in all of the fossils more closely grouping with humans, except for SKX 5017 and SK 1813. The specimen SK 1813 has been described as being very similar to SKX 5017 (Susman and de Ruiter, 2004). This analysis corroborates those findings, further showing that the articular surfaces of these specimens are very similar. It is therefore likely that SK 1813 belongs to the genus *Paranthropus*. The combination of these analyses, if considering both the full analysis including all landmarks and the analysis with missing landmarks, shows a morphological split between the humans, apes, and fossil specimens.

This observation brings to question the idea that the genus *Paranthropus* is adapted to bipedalism in the same way and at the same time as *Homo habilis*, which has been proposed previously (Susman and Brain, 1988). If some of the unattributed fossils belong to *A. africanus* or *Homo habilis*, we may be observing a difference in morphology reflecting a lasting dependence on some form of arboreal behavior by *Paranthropus* even after the evolutionary line leading to modern humans is adapting to more efficient terrestrial bipedalism.

There is a significant relationship between size and shape for each of the four principle components discussed in these results. Therefore, the hypothesis (H_{10}) that differences in shape interspecificaly are unrelated to size is falsified. However, for all of the PC axes, and most especially for PC 1 and PC 2, the R2 value increases dramatically when species group names are included as a variable. This is particularly important when interpreting the effects of size on shape for the PC 1 and PC 2 axis, since these axes are the most revealing in terms of shape differences interspecificaly and interspecificaly. There is a significant difference in size between all groups except for *Gorilla* and shod *Homo*. Coupled with the extreme contrast in size between all other groups compared to *Hylobates*, care must be taken when interpreting the effects of size on shape. These groups happen to have differing body sizes while they also have varying modes of locomotion. If species group is considered a proxy for locomotion, it puts the results into a better context. When considering size alone for PC 1, size only accounts for 13% of the variance. When species groups are added the combined variation explained rises to 88%. Similarly, size alone accounts for 27% of the variation on the PC 2 axis. This axis is most important for showing differences between ape groups. The ape groups have a wide range of size across species, and including the species name as a proxy for locomotor differences raises the percentage of variation explained to 54%. These results show that size, shape, and locomotion are all important factors in interpreting shape differences between the groups.

The hypotheses (H_9) that there is no difference in size between sexes intraspecifically, (H_{12}) that there are no shape differences intraspecifically, and (H_{11}) that differences in shape between sexes intraspecifically are unrelated to size are all falsified for *Gorilla*. *Gorilla* males and females are significantly different in size and shape on the PC 2 and PC 4 axes. There is a significant relationship between size and shape at these axes. Of these results the most significant is their difference at the PC 2 axis. In a regression analysis size accounts for 37% of the variance at the PC 2 axis. Males tend to have a higher value on this axis compared to females. Overall this is a marginal difference in the larger context of all ape groups. However, it does show a slight tendency for males to have greater curvature in the dorso-medial area of the articular surface.

There are fewer differences between males and females within the groups *Pan* and *Hylobates*. There is a significant difference in size between *Pan* males and females, thus H_9 (that there are no size differences between sexes) cannot be rejected. However, there were no shape differences between males and females, thus H_{11} (differences in shape are unrelated to size) and H_{12} (that there is no differences in shape between sexes) cannot be falsified. Within *Hylobates*, there are no differences between males and females in terms of size and shape. Thus, H_9, $H_{11}$and H_{12} cannot be rejected.

Within the shod *Homo* group, there is a significant difference in size between males and females, and a significant difference in shape on the PC 1 and PC 4 axes. However, regression analysis revealed insignificant results when testing for a relationship between size and shape. Therefore, H_9 and H_{12} cannot be rejected, but H_9 cannot be rejected. The PC 4 axis is not very revealing in terms of shape, but the PC 1 axis is most important in distinguishing between humans and apes. Females have a mean PC 1 score that is only slightly lower than males (0.10 versus 0.11). It is likely that this result would not be significant with a larger sample size. The other possibility is that there is a slight difference in morphology due to differing locomotor habits. However, locomotor habits between human males and females have only been found to show a significant difference in an unshod population (Hilton, 1997).

It is revealing that the two *Homo* samples are not different at the PC 1 axis, which is the axis that best distinguishes human and ape morphology. There is an ongoing argument that apelike features of fossil hominins have little behavioral or functional significance, and that these characteristics are essentially vestigial or represent morphology that is not fully adapted to habitual and efficient bipedalism (Stern, 2000). There is an undercurrent in this debate that is seldom articulated clearly. This is the idea that habitually unshod individuals would have some sort of apelike appearance, and that since early hominins were unshod this can account for some similarities between apes and fossil hominins.

As discussed previously, unshod populations have greater flexibility of the forefoot and phalanges, but greater stability of the longitudinal arch. It is the longitudinal arch that is of particular importance when considering proximal metatarsal joint surface morphology. Rather than see a divergent unshod morphology, we find a wider range of morphology in the shod sample. The hypothesis (H_4) that habitually shod and unshod populations have no difference in morphology is rejected only for the PC 3 axis. However, the observable morphology suggests that the differences in morphology between shod and unshod samples are unrelated to apelike morphology. The positive area PC 3 axis is related to having a wider dorsal area of the surface, and shod *Homo* had a higher average PC 3 score compared to unshod *Homo*. The regression analysis for size and shape at PC 3 was significant, but size only explains 7% of the variation. It is probably that these results show population differences or a small difference only related to size. It must be kept in mind that the PC 3 axis is only responsible for 10% of the total variation in the MT 1 analysis.

MT 2 Results

The hypothesis (H_1) that the human MT 2 proximal surface is expanded in the plantar region cannot be falsified. This shape is primarily represented on the PC 1 axis, showing that humans have a relatively narrower surface with an expanded plantar area. Interestingly, there is some overlap between humans and *Gorilla* at this axis, suggesting that the shape on the positive side of the axis may be related to relative terrestriality. The fossil specimens OH 8, Stw 573 (Little Foot), and Stw 377 are indistinguishable from humans in articular surface shape on the PC 1 axis. Therefore, H_6 cannot be falsified as OH 8 is indistinguishable from humans. The fossil specimen Stw 595c overlaps humans and *Gorilla*, but other groups on the PC 1 axis, while SKX 247 and Stw 89 overlap the African apes on PC 1 but no other groups. The only complete fossil specimen is Stw 89; the others are missing their distal ends. On the PC 1 axis Stw 89 overlaps *Gorilla* and *Pan*, and is close to SKX 247. There is a pronounced dorsal sulcus on the distal end of Stw 89, indicating a human-like hyperextension of the proximal phalange during locomotion. The shaft is slightly curved, and the head may exhibit some small amount of medial torsion. However, the dorsal area of the surface is wide and plantar aspect of the proximal articular surface is relatively narrow, and lacks the characteristic human expansion. This combination of traits represents a mosaic of traits, many of which clearly indicate adaptations to bipedalism and terrestriality, but the proximal surface is not consistent with human morphology. This could indicate that the longitudinal arch belonging to the specimens that do not overlap humans would not have been developed as fully as in humans, or it might indicate that if an arch was present the joint structure and component to the arch was less stable.

There are statistically significant differences in articular surface size between groups, with three groupings. *Gorilla* and *Homo* are not different in size, while *Pan* and unshod *Homo* are not different in size. Regression analyses resulted in significant relationships between size and PC 1, PC 2, PC 3, and PC 4. Therefore, the hypothesis (H_{10}) that differences in shape are unrelated to size cannot be falsified. Including species group names in the analysis increased the percentage of variation explained in the regression considerably. For PC 1, the variation explained rises from 18% to 83%. For PC 2, the variation explained rises from 18% to 57%. Although size does influence shape, belonging to one group or another is a better predictor of shape.

There is a significant difference in size between *Gorilla* males and females. The hypothesis H_9 (that there are no size differences between sexes) was falsified. However, there were no significant differences in shape between males and females. Thus, H_{12} (that there are no differences in shape between sexes) could not be falsified. Analysis of males and females within *Pan* yielded identical results; thus H_9 could be falsified but H_{12} could not be falsified. There is no difference in size between males and females within *Hylobates*, and H_9 could not be falsified. However, H_{12} was falsified due to a significant difference in articular surface shape between males and females. Within the *Homo* group, there is a significant difference in size between males and females, so that H_9 was falsified. In addition, there was a significant difference between males and females on the PC 2 axis, so that H_{12} was falsified. However, regression analysis yielded insignificant results, and H_{11} could not be falsified.

As noted previously, there is a significant difference in size between unshod *Homo* and *Homo*. In addition, there is a significant different between these groups for PC 2, PC 3, and PC 4. Of these, a significant relationship exists between size and shape for

PC 3 and PC 4, both of which have R2 values of .09. Therefore, the variation explained by size is low, with size unable to explain any of the variation for PC 2. The interpretation of shape for these axes indicates that unshod *Homo* may have a slightly narrower plantar aspect to the articular surface, which tends to curve medially toward the plantar apex.

MT 3 Results

The combined effects of PC 1 and PC 2 produces three distinct groups, with some overlap that is especially pronounced on the PC 2 axis between the African apes and human groups. The results of this analysis are very similar to the analysis of MT 2. On the PC 1 axis, humans have a relatively narrow articular surface that is expanded in the plantar area compared to the apes. Therefore, H_1 (that the human MT 3 will have an expanded articular surface) cannot be falsified. However, this analysis differs from the analysis of MT 2 in that *Pan* overlaps human groups on the PC 1 axis, whereas *Gorilla* did for MT 2. *Hylobates* also overlaps with humans, but the *Hylobates* shape is highly influenced by PC 2. The *Gorilla* shape is also influenced by PC 2 on the opposite axis. The combined effects for *Gorilla* indicate a surface shape that is wide in the dorsal area, narrow in the plantar area, but relatively flat with some indication of concavity. *Pan* is in an intermediate position on the PC 2 axis. The extreme shape of *Hylobates* on PC 2 indicates a surface that is narrow in the plantar aspect and rounded in the dorsal aspect. Most importantly, the surface of *Hylobates* is markedly convex.

A recent study by DeSilva (2010) found that the midtarsal break observed in non-human primates is not only the result of movement at the calcaneocuboid joint but also at the tarsometatarsal joints for MT 4 and MT 5 with the distal cuboid. A consequence of this motion is that the proximal MT 4 and MT 5 surfaces are markedly convex to allow the joint to dorsiflex. The presence of extreme convexity on the proximal MT 3 articular surface suggests that in *Hylobates* the lateral flexibility of the foot may extend further medially that it does in apes. This hypothesis should be tested in a later study.

All of the fossil specimens fall in the range of humans on the PC 1 axis, but Stw 435 and Stw 477 overlap apes to a greater degree. The specimen OH 8 overlaps humans and is grouped most strongly with humans; thus, H_6 cannot be falsified.

Very similarly to the analysis of MT 2, in terms of centroid size *Gorilla* and *Homo* are not different. Likewise, *Pan* and unshod *Homo* are not different in size, but *Hylobates* is different from all other groups. Regression analysis yielded a significant result with a relationship between size and each PC axis. The hypothesis (H_{10}) that differences in shape between species are not related to size is falsified. However, the portion of variance due to size alone is very closely related to the way the groups are clustered on the PC 1 and PC 2 axes. The portion of variance explained by size for PC 1 is only 3%. Although there is a division between humans and African apes on the PC 1 axis, even those pairing that do differ in size do not do so dramatically. *Hylobates* is the smallest group and overlaps the center area of the range of groupings on the PC 1 axis. This is in direct contrast to the relationship between size and shape on the PC 2 axis, where size explains 65% of the variation. This is most important for interpreting shape differences between ape groups, as there is a clear gradation of shape change on the PC 2 axis from larger bodied *Gorilla* through intermediate *Pan* and finally to smaller *Hylobates* that has an extreme location on the negative PC 2 axis.

An interesting finding for the MT 3 proximal articular surface is that there are no intraspecific differences in size between males and females for any of the groups, thus H_9 is not falsified. This is surprising, particularly for *Gorilla* which is known to have considerable sexual dimorphism. It is possible that the overall dimensions MT 3 are different between the sexes, with males have a longer more robust metatarsal, for instance, but at least in terms of articular surface size there is no difference. A hypotheses can be put forth to explain this by the idea that the MT 3 proximal surface is under less stress during locomotion for all groups. In apes much of the stress is on the lateral foot, and in humans weight quickly transitions to the medial side of the foot. This leaves the

MT 3 surface the area with the least burden during locomotion. In apes, MT 2 is in opposition to the hallux, and even though the base of the metatarsal is not subject to the same kind of compressive forces as the human foot in this region during locomotion, apes do subject this area to stress through grasping and locomotion in trees. It is therefore not surprising that MT 2 would show differences in size between males and females in dimorphic groups.

Although unshod *Homo* and shod *Homo* are different in terms of articular surface size, no significant differences in PC scores occurred. Therefore, the hypothesis (H_4) that there are no significant differences in surface shape between shod and unshod humans cannot be falsified for MT 3.

MT 4 Results

As with many of these analyses, the combination of PC 1 and PC 2 is most revealing in terms of shape differences between groups. In this case it is even truer because there were no differences between groups on the PC 3 axis. This axis essentially reflects variable surface width that exists in all groups. However, the differences reflected on the PC 1 and PC 2 axis are revealing and reflect function of the joint very closely.

When plotting a combination of PC 1 and PC 2, there are three groupings that do not overlap. African apes are not different from one another on the PC 1 axis and group together. Both human groups are not different from one another and group together on the positive side of PC 1 and PC 2. *Hylobates* occupies an area between these groupings on PC 1, but is located in an extreme negative area of PC 2. As predicted in the hypothesis (H_4), apes have a highly convex articular surface. Therefore, H_4 cannot be falsified. This finding corroborates DeSilva's (2010) findings when he quantified maximum curvature relative to dorso-plantar surface height. However, one additional finding here is that *Hylobates* has an extreme degree of surface curvature.

The African ape proximal MT 4 articular surface is highly convex, with extension of the surface in the dorso-medial aspect. *Hylobates* usually lacks this extension, but has a highly convex surface that extends further to the dorsal aspect of the metatarsal. This suggests that *Hylobates* has a greater degree of flexion at this joint relative to the African apes, which dovetails into the observation that the MT 3 surface of *Hylobates* is likewise highly convex relative to other groups. The presence of the dorso-medial extension of the surface in African apes may be a consequence of a higher transverse arch in the foot compared to *Hylobates*. A higher arch changes the angle at which the bones articulate, raising the intermetatarsal facet for MT 3. This observation has been made by this author qualitatively, but it is a hypothesis that should be tested in a later study.

All groups are different from one another in articular surface size except for *Pan* and unshod *Homo*. A regression analysis yielded an insignificant result when looking for a relationship between size and PC 2. However, a significant result was obtained with PC 3. Size explains 59% of the variation. This is not a surprising result since *Hylobates* is so different from all other groups on the PC 2 axis and is also much smaller than all other groups.

An unexpected result was obtained when testing for differences in size between sexes within each group. All ape groups showed an insignificant result when testing for differences in mean centroid size for MT 4. Therefore, the hypothesis (H_9) that there is no difference in size between sexes cannot be rejected for the ape groups. This is an interesting finding, especially when considering that a similar result was obtained for MT 3. The high degree of flexion at this joint that occurs with apes may relieve the need to have a larger articular surface for load bearing. However, there is a significant difference between human males and females in terms of centroid size. The hypothesis (H_9) that there is no difference in size between sexes is rejected for humans. This joint is relatively inflexible in humans, bearing a load during locomotion without a midfoot break.

The hypothesis (H_{12}) that there are no differences in articular surface shape between sexes intraspecifically cannot be falsified for *Gorilla*. There are no differences in shape between males and females. This hypothesis cannot be falsified for *Pan*, since there is a difference between males and females at the PC 1 axis. However, males and females are not different in terms of size so size cannot explain this shape difference. Females have a lower PC 2 score than males, indicating a surface that extends further to the dorsal aspect. Since this seems to indicate greater flexion at this joint in *Hylobates*, it's possible that even though the surface itself is not larger in males, the overall larger body size of males compared to females influences the surface morphology due to different arboreal behavior. H_{12} cannot be falsified for *Hylobates*; there is a significant difference in PC 3 scores between males and females. Males tend to have a slightly narrower surface relative to females. Since the sexes are similar in size, it cannot explain this shape difference.

The hypothesis (H_4) that there are no significant differences in articular surface shape between shod and unshod humans is falsified. There is a significant difference between these groups at the PC 2 axis. Shod humans have a marginally greater degree of curvature. Regression analysis shows that size accounts for 16% of the variation. This can be interpreted in a couple of ways. The remaining explanation for the shape difference could simply be a population difference that has no functional significance. Another possibility is that the articular surface in the unshod group responds developmentally to produce a flatter articular surface. One way to approach this question in a later study would be to measure ground reaction forces in the lateral midfoot during locomotion, to compare how force differs in unshod humans and shod humans while wearing shoes during locomotion.

MT 5 Results

One of the interesting findings for the MT 5 proximal articular surface is that the difference in shape between humans and apes is not as dramatic as one might expect, especially in light of the dramatic differences in the other metatarsals and in the fact that there is a functional difference between humans and apes in the lateral foot. Nonetheless, there are important differences in shape and trends that can be described that separate not just humans from apes, but the more arboreal *Pan* and *Hylobates* compared to *Gorilla*.

The most important shape differences are reflected on the PC 1 and PC 2 axes. It is most useful to interpret the effects of these axes combined. All groups overlap each other on these axes. The main shape trends observable on the PC 1 axis include a medio-laterally narrow surface with greater dorso-plantar convex curvature at the negative portion of PC 1 axis. On the positive side of the PC 1 axis, the surface is elongated in the medio-lateral plane with medio-lateral concave curvature and lessened dorso-plantar convex curvature. The shape trends on the PC 2 axis include a flat surface at the negative side of the axis and extreme dorso-plantar convex curvature at the positive side of the axis. On the PC 1 axis, *Gorilla* is different from all groups in terms of its mean PC score. *Pan* is different from all groups except *Hylobates*. Both human groups are different from the African apes, but not *Hylobates*. *Hylobates* is only different from *Gorilla*. On the PC 2 axis, *Gorilla* is different from shod *Homo*, *Pan*, and *Hylobates*. *Pan* and *Hylobates* are not different from one another but are different from all other groups. Both human groups are different from *Hylobates* and *Pan*, and shod *Homo* is further different from *Gorilla*.

Interpreting the combined effects of these axes, *Pan* and *Hylobates* occupy the positive areas of PC 1 and PC 2. On both axes these areas reflect a surface that has a high degree of convex curvature in the dorso-plantar plane. *Pan*'s extreme location on PC 2 also indicates that in *Pan* the surface tends to be medio-laterally extended to a greater degree. In contrast, both human groups and *Gorilla* occupied a similar are on these axes, with shod *Homo* having a smaller range on the PC 1 axis. Shod *Homo* has a much more conservative shape, with a tendency to have a flatter surface and it is approximately equal in dorso-plantar height relative to medio-lateral width. Unshod *Homo* also tends to have a flatter surface, but a much wider range of shape in terms of medio-lateral width relative to dorso-plantar height. The shape shown by *Gorilla* does not tend to be as medio-lateral elongated as the other apes, showing a tendency to be narrower but with greater dorso-plantar convex curvature and little medio-lateral curvature.

Therefore, the hypothesis (H_3) that apes will show medio-lateral concavity and elongation relative to humans is falsified when comparing humans to *Gorilla*, but not falsified in comparison to *Pan* and *Hylobates*. The added observation for *Pan* and *Hylobates* is that their surface shape combines medio-lateral concavity with dorso-plantar convexity.

Gorilla bears considerable similarity to the human groups, but also has a range that extends much further toward the extreme negative area of PC 1. Of the fossil specimens, OH 8 occupies an area on the extreme negative of PC 1, overlapping no other groups at this axis. This reflects the fact that the surface of OH 8 is very medio-laterally narrow and has a great deal of dorso-plantar curvature. Remembering that OH 8 shows great similarity to humans in its MT 4 articular surface shape, it seems unlikely that this morphology reflects a highly mobile proximal MT 5 joint. However, the possibility cannot be ruled out that there may be greater flexibility in this joint compared to modern humans. Based on these observations, the hypothesis (H_6) that OH 8 will show greater similarity to humans in articular surface shape is falsified for MT 5.

The interpretation of the other fossil specimens is unclear. The specimens primarily overlap both human groups and *Gorilla*, but with no particularly greater affinity to any of these groups. The specimen AL 333-78 overlaps humans and *Gorilla* on the PC 1 and PC 2 axes, but the combined placement of this specimen on these axes places it outside of the grouping of shod humans and within only unshod *Homo* and *Gorilla*. Still, this does not necessarily indicate greater affinity to *Gorilla* compared to unshod *Homo*. Overall, the results for MT 5 indicate that the most arboreal species are most differentiated in articular surface shape, but the more terrestrial groups are not. From a functional point of view, this suggests that observing the proximal MT 5 surface alone without reference to the other metatarsal proximal surfaces is less informative in being a predictor of function when looking at the hominin fossils.

In terms of articular surface size, all groups are different from one another except *Pan* and unshod *Homo*. The hypothesis H_8 (there is no difference in size interspecifically) is falsified. In addition, H_{10} (differences in surface shape interspecifically are unrelated to size) is falsified due to a significant result in regression analysis comparing size and shape for each PC axes in this study. The amount of variation explained by size for PC 1 is low at 4%. Size explains 17% of PC 2, which is not unexpected since *Pan* and *Hylobates* have more extreme ranges on this axis. However, the gains in terms of explaining the variation increase a great deal when including species group names in the analysis. The amount explained for PC 1 rises to 35% and for PC 2 rises to 40%. This indicates that size has less of an effect than simply which group a specimen belongs to. This can be interpreted as reflecting mode of locomotion.

In terms of articular surface size, there are no intraspecific differences in the ape groups. The hypothesis (H_9) that males and females have different mean sizes is falsified for the ape groups. However, it is not falsified for *Homo*. Males are significantly larger than females. One model for this explanation follows closely with that proposed for MT 4. Despite the high degree of sexual dimorphism in *Gorilla*, males and females are different in articular surface size. Since all of the apes have lateral midfoot flexibility, the load requirements on the joint surface may be reduced compared to in *Homo*. As a consequence, joint surface size is more closely related to overall body size. The hypothesis (H_{12}) that there are differences in articular surface shape between sexes is falsified for MT 5. There are no differences in shape at any axis for any apes or human groups.

Other Findings

It has been suggested that the early hominin foot becomes more stable beginning with the lateral side of the foot, so that the medial side of the foot retains primitive features later in the evolution of a modern human foot (Kidd et al., 1998, 1999; Kidd and Oxnard, 2005; Zipfel et al., 2009; DeSilva, 2010). This explanation is offered due to the observation that many hominin specimens seem to retain ape-like traits of the first metatarsal, such as a deep articular surface with A. L. 333-54. This idea is congruent with the observation that more weight is on the lateral side of the foot during ape locomotion relative to human locomotion, where weight transfers to the medial side of the foot. Therefore, a model in which the lateral side of the foot develops stability first as hominins adapt to more efficient bipedal locomotion is logical.

However, even though this model may be useful in interpreting other skeletal adaptations of the foot, the results of this study do not clearly support or refute this model in regard to articular surface morphology. Intermediate morphology between humans and apes is observed in the fossil hominins in each metatarsal. Beginning with the first metatarsal, the morphology of humans and apes is very different due to the different joint functions between these groups. In the analysis of MT 1, OH 8 is the only fossil specimen that is clearly more human-like. The robust australopiths, as represented by SKX 5017 and potentially SK 1813 are ape-like. The remaining specimens are intermediate in shape. This suggests both that OH 8 (*Homo habilis?*) had already achieved a relatively modern medial foot. *Paranthropus* seems to retain an ape-like medial foot that may retain some opposability. The foot of the remaining specimens that may represent *A. africanus* show intermediate morphology, the function of which is up for debate. Even if these hominins did not retain a grasping foot, the medial foot would have lacked a modern longitudinal arch at the medial aspect.

The MT 2 and MT 3 articular surfaces also show a trend of intermediate morphology in the fossil specimens. Here again, OH 8 is human-like. In addition, Stw

573 (Little Foot) is human-like. These two examples are especially important because they represent one foot from the same specimen when comparing the results to MT 1. Little Foot is intermediate between apes and humans in MT 1 surface shape, but very human-like when looking at the shape of MT 2. The specimens SKX 247 and Stw 595c, both of which may belong to the genus *Paranthropus*, are very ape-like in the MT 2 analysis. However, the specimen Stw 377 shows intermediate morphology between humans and apes. In the analysis of MT 3 we still see intermediate morphology of many fossil specimens, but OH 8 is humanlike, as are Stw 387 and Stw 435.

Broadly in the medial foot, if we include MT 3 even though it is often considered to be part of the lateral pillar, there does seem to be a trend for the fossil specimens to appear ape-like, which is exaggerated even further for MT 1 and MT 2. The hominin specimens that are most intermediate are the ones that potentially belong to the genus and species *A. africanus*, while the most ape-like are *Paranthropus*.

Interpreting the results of the MT 4 analysis is somewhat hindered since there are only two fossil specimens included. However, OH 8 is again indistinguishable from humans, in this case unshod humans specifically. The other specimen, Stw 628, could be *Homo* or *Paranthropus*, and is in an intermediate position between humans and apes, but shows some greater similarity to the unshod human group. In the analysis of MT 5, there is a considerable difference between the more arboreal groups, *Pan* and *Hylobates*, compared to humans. However, *Gorilla* also bears a great deal of similarity to humans, even though *Gorilla* has a tendency to have a much more convex surface in the dorso-plantar plane. All fossil specimens in the MT 5 analysis except OH 8 cluster in an area of overlap between humans and *Gorilla*. In this case, it can be said that the fossil hominin specimens are adapted to terrestrial locomotion at least as well as humans and *Gorilla*, but they are not particularly different from *Gorilla*. The specimen OH 8 is somewhat unusual, which is mainly due to having an extremely narrow surface.

These results do not clearly support or refute a model of lateral to medial modern adaptation. However, a clear trend does emerge. The specimen OH 8, representing *H. habilis*, is human-like in all analyses except in the MT 5 analysis. In the MT 5 results this specimen has a very medio-laterally narrow surface that places it outside of the range of the human groups. It does overlap unshod *Homo* on the PC 2 axis. The specimens representing *A. afarensis* and potentially *A. africanus* are intermediate between humans and apes. However, this is not always true since Little Foot is identical to humans in MT 2 articular surface shape but is intermediate between humans and apes for MT 1. The specimens that may belong to the genus *Paranthropus* are ape-like in the analyses, and this suggests a functional adaptation unlike the other hominins.

Functional Interpretation for *Paranthropus*

One should draw functional interpretations of the fossil findings with caution. However, due to the placement of the fossil specimens in the PC analyses, there is compelling evidence to suggest a morphological split between gracile australopiths and early *Homo* on one hand and *Paranthropus robustus* on the other. Previous studies have suggested that *Paranthropus robustus* does not have a modern toe-off mechanism (Susman and Brain, 1988; Susman and de Ruiter, 2004). Both SKX 5017 and SK 1813 have a dorsal sulcus, indicating hyperextension of the proximal phalange during locomotion, which occurs in humans but not apes (Susman and Brain, 1988; Susman and de Ruiter, 2004). This observation, combined with the fact that these specimens exhibit torsion of the metatarsal head that is intermediate between humans and apes, led Susman and de Ruiter (2004) to conclude that the hallux is in a unique position during toe-off compared to humans. When the specimens SKX 5017 and SK 1813 are held in a human-like position so that the proximal articular surface is perpendicular to the substrate, metatarsal head torsion places the head in opposition to MT 2. As a consequence, these MT 1 specimens cannot be in a permanent adducted position to the same degree as modern humans. The MT base must be rotated relative to the base of modern humans.

The base of these specimens must be in an abducted and rotated position so that the MT 1 head is parallel to the ground to allow hyperextension of the proximal phalange. The observed shape of the proximal articular surface of SKX 5017 and SK 1813 corroborates Susman and de Ruiter's (2004) findings, and further suggests that *Paranthropus robustus* has a mobile tarsometatarsal joint that is capable of a degree of rotation and abduction. It is when the hallux is in the abducted position that hyperextension of the proximal phalange is possible.

Intraspecific Size and Joint Loading

An interesting result that occurs in these analyses is that joint surface size is not always different between males and females in African apes, despite overall sexual dimorphism that is especially pronounced in *Gorilla*. Earlier studies have predicted and shown that joint surface size increases at a predictable rate when compared to body size (Alexander, 1980; Hamrick, 1996). There were no differences in articular surface size between *Hylobates* males and females, which is not surprising since they are not sexually dimorphic. However, *Pan* and *Gorilla* males and females are only significantly different in articular surface size for MT 1 and MT 2, while in *Homo* there is a significant difference in surface size between males and females for all of the proximal metatarsal articular surfaces.

Hamrick (1996) found that articular surface size increases as body size increases, and that the larger the degree of curvature on a male joint (such as the proximal articular surfaces of MT 4 and MT 5) the greater the degree of mobility. However, he also found that degree of surface curvature is unrelated to size, and degree of curvature is most closely related to function. Therefore, the best interpretation of these results related to sex is as follows. The MT 1 and MT 2 proximal articular surfaces are more load-bearing than the lateral proximal metatarsals. They are not necessarily more load bearing during terrestrial locomotion, but these joints oppose each other for grasping and when engaging in arboreal locomotion. The joint size for MT 3, MT 4, and MT 5 in the African apes must increase in size at a different rate compared to a joint with greater load bearing, so that even though the surface size is related to body size in general, there must be a larger degree of overlap in surface size even when body sizes differ significantly. This must occur despite the fact that apes walk with most ground reaction forces on the lateral side of the foot, especially at the MT 4 and MT 5 areas (Vereeke et al., 2003). Since these joints are highly flexible in apes, the burden of weight load is reduced when flexion occurs, distributing the weight to the plantar portion of the lateral metatarsals and to the calcaneocuboid joint. This is unlike what occurs in humans with a longitudinal arch. This observation supports Hamrick's (1994) study of articular joint surfaces, and provides additional evidence of the relationship between joint size and load bearing.

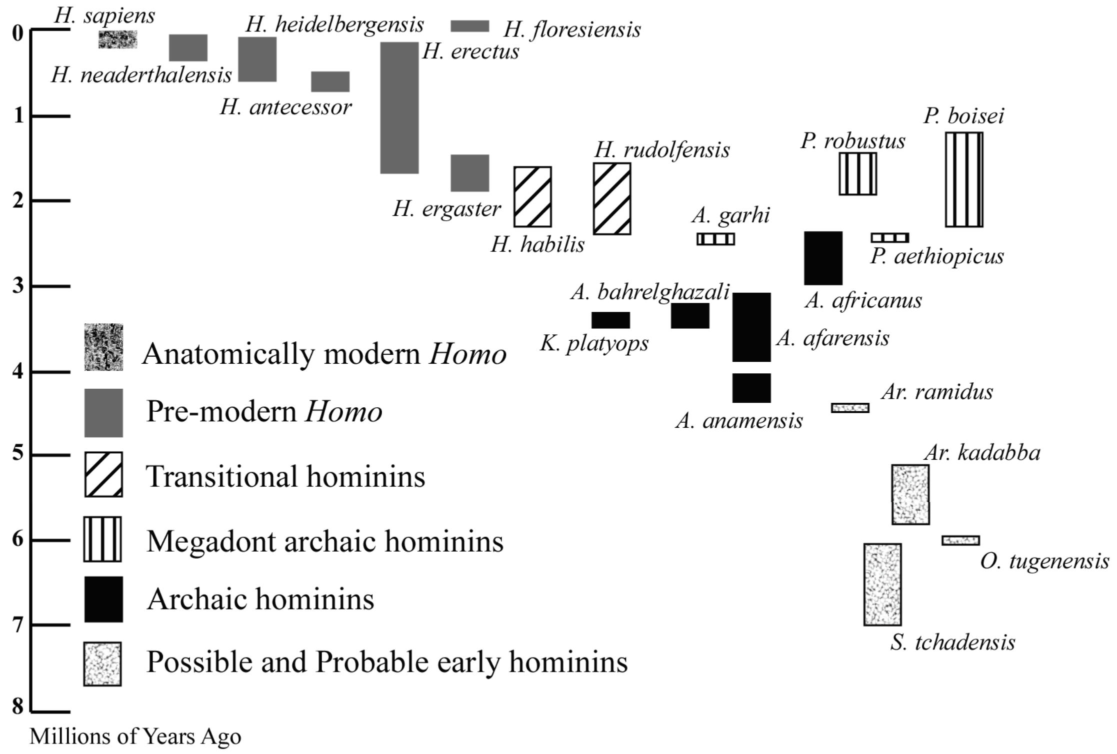
The shod human group shows significant differences between males and females in articular surface size at each metatarsal because the longitudinal arch increases their load during bipedal locomotion. This observation provides an explanation for why the shod human group is not different in articular surface size compared to *Gorilla* for MT 1, MT 2, and MT 3 despite the fact that *Gorilla* is larger in body size than *Homo*. The medial metatarsals experience considerable pressure forces as weight shifts medially for toe-off (Chen et al., 2001; Gefen et al., 2000; Giacomozzi et al., 2000; Scott and Winter, 1993; Manter, 1946).

Phylogenetic Bases

Current phylogenetic analysis shows four broad hominin groups (excluding modern humans) that of primary concern in this research, pre-modern *Homo*, transitional hominins, megadont archaic hominins, and archaic hominins (Strait and Grine, 2004; Kimbel et al., 2004; Wood and Langren, 2008). The hominin taxonomy in Figure 11.1 is useful for presenting a context foe the morphology patterns revealed in this study.

The articular surface analyses results presented here show archaic hominins (*A. afarensis* and *A. africanus*) to be transitional or intermediate in shape between humans and apes. Their range of variation overlaps humans and apes, especially when humans and apes themselves overlap in shape groupings. However, these gracile australopiths are more intermediate when there is a clearer division of shape between humans and apes. In contrast, *H. habilis*, as represented by OH 8, is indistinguishable from modern humans in most analyses. This suggests that in terms of function this region of anatomy is already becoming modern in the transitional hominins, or at least in *H. habilis*. The more ape-like medial foot of *P. robustus* shows a reversal of this anatomy. Since the megadont archaic hominins are likely to be descended from the archaic hominins (probably *A. afarensis* specifically) it is unlikely that the ape-like articular surface features of *P. robustus* have been inherited directly from an ape ancestor. This does not mean that all megadont hominins share this anatomy. There is currently a dearth of post-cranial evidence for the other megadont hominins.

Figure 11.1 Hominin Phylogeny adapted from Wood and Langren (2008).



Future Studies

The results of these analyses suggest several future areas of research. The relationship of joint size to body size needs to be further investigated, with particular emphasis on the rate at which joint surfaces increase in size relative to body size in joints with different load bearing and functional characteristics. Another area of future research is to investigate the dorsiflexion capability of *Hylobates*, and to test the prediction that lateral flexion of the foot extends further medially than in African apes, to the MT 3 proximal articular surface. Finally, further investigation of articular surface shape should be carried out on primates of different sizes and modes of locomotion. For instance, the question of how a more terrestrial lifestyle such as that exhibited by baboons influences the articular surface shape can be useful in interpreting fossil hominins. The baboon rear foot has a tendency to be digitigrade during locomotion, with less heel contact to the substrate. This could result in greater load bearing on the tarsometatarsal joints, and it could have implications for how joint surface shape reflects load bearing and function in a terrestrial foot that does not have a longitudinal arch.

APPENDIX A: FIRST METATARSAL FOSSIL PHOTOS

Figure A.1 A. L. 333-54 (left); A) lateral; B) medial; C) proximal; scale bar = 1 cm

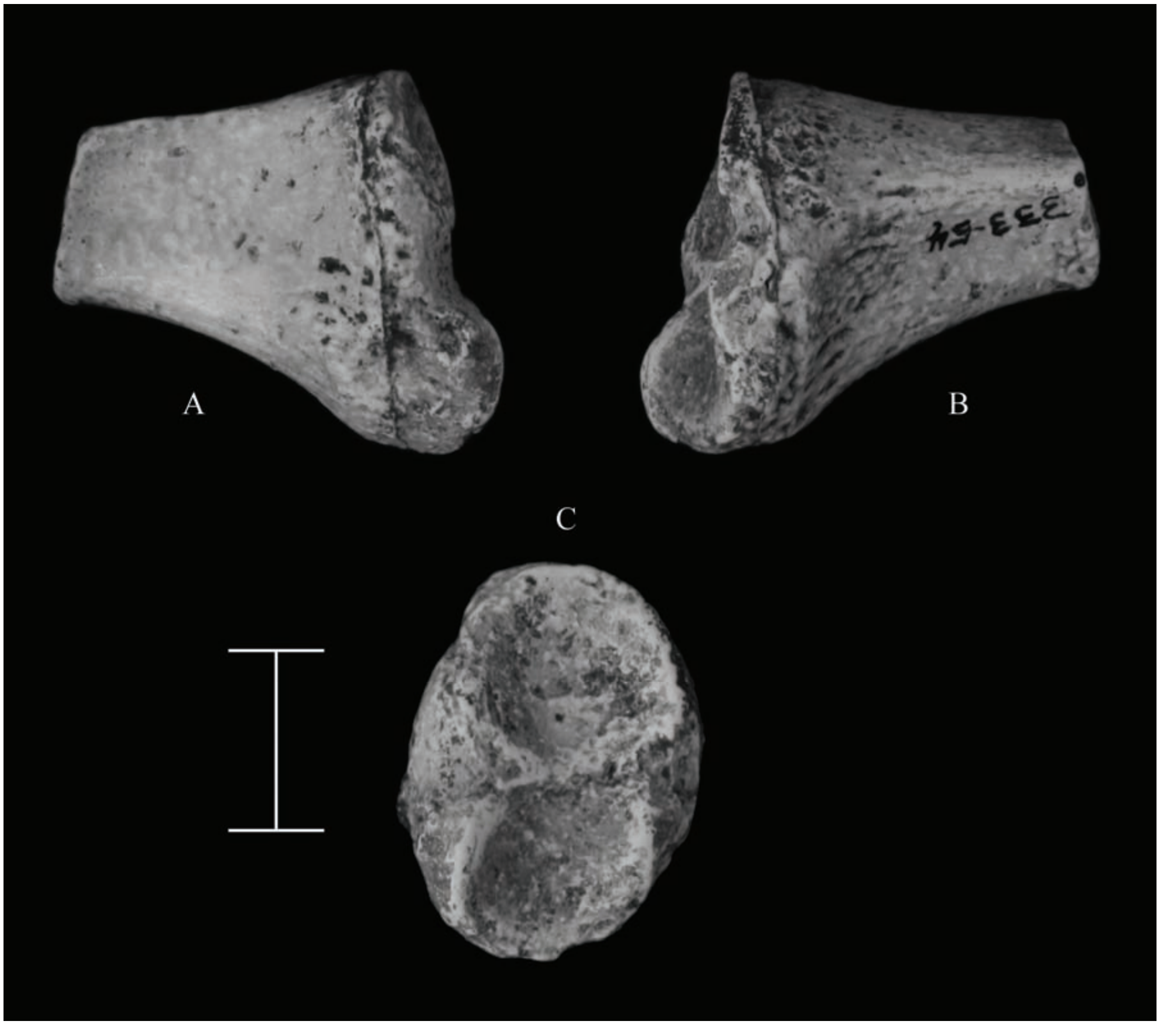


Figure A.2 SK 1813 (right); A) medial; B) proximal; scale bar = 1 cm

Figure A.3 A. L. 333-54 (left); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure A.4 Stw 562 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure A.5 Stw 573 “Little Foot” (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

Figure A.6 Stw 595 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

APPENDIX B: SECOND METATARSAL FOSSIL PHOTOS

Figure B.1 SKX 247 (left); A) lateral; B) medial; C) proximal; scale bar = 1 cm

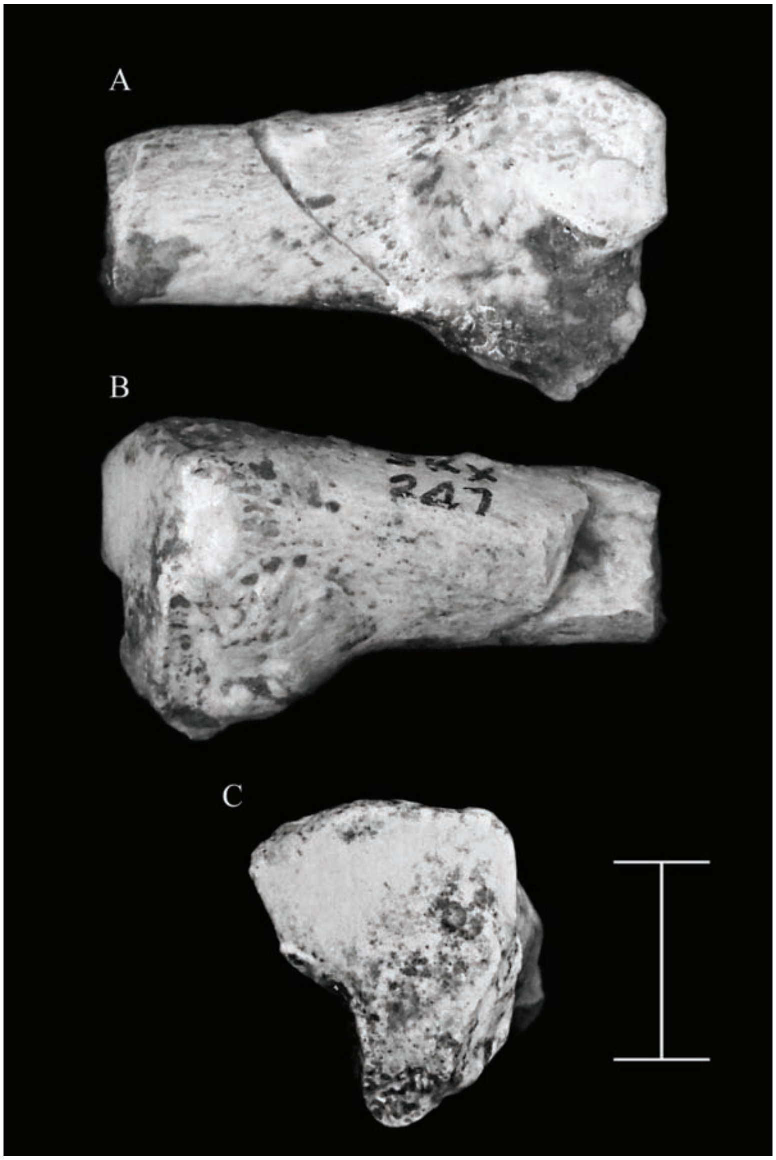


Figure B.2 Stw 89 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

Figure B.3 Stw 377 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

Figure B.4 Stw 573d (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

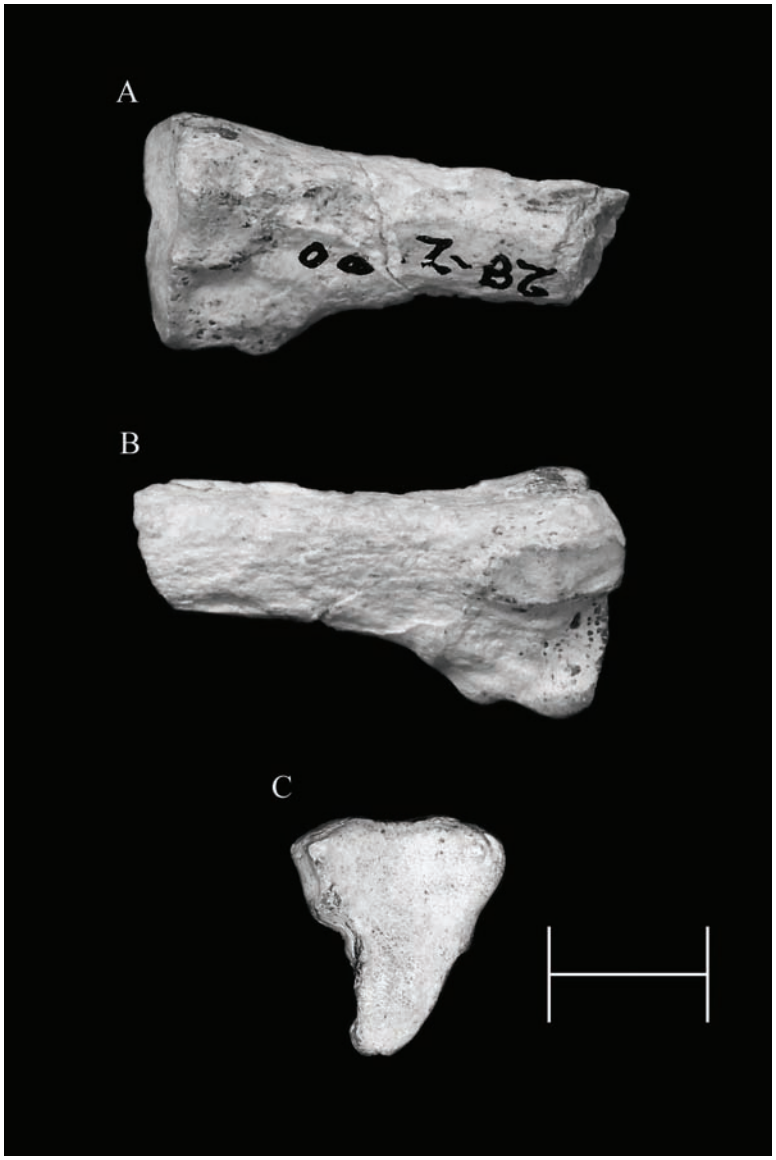
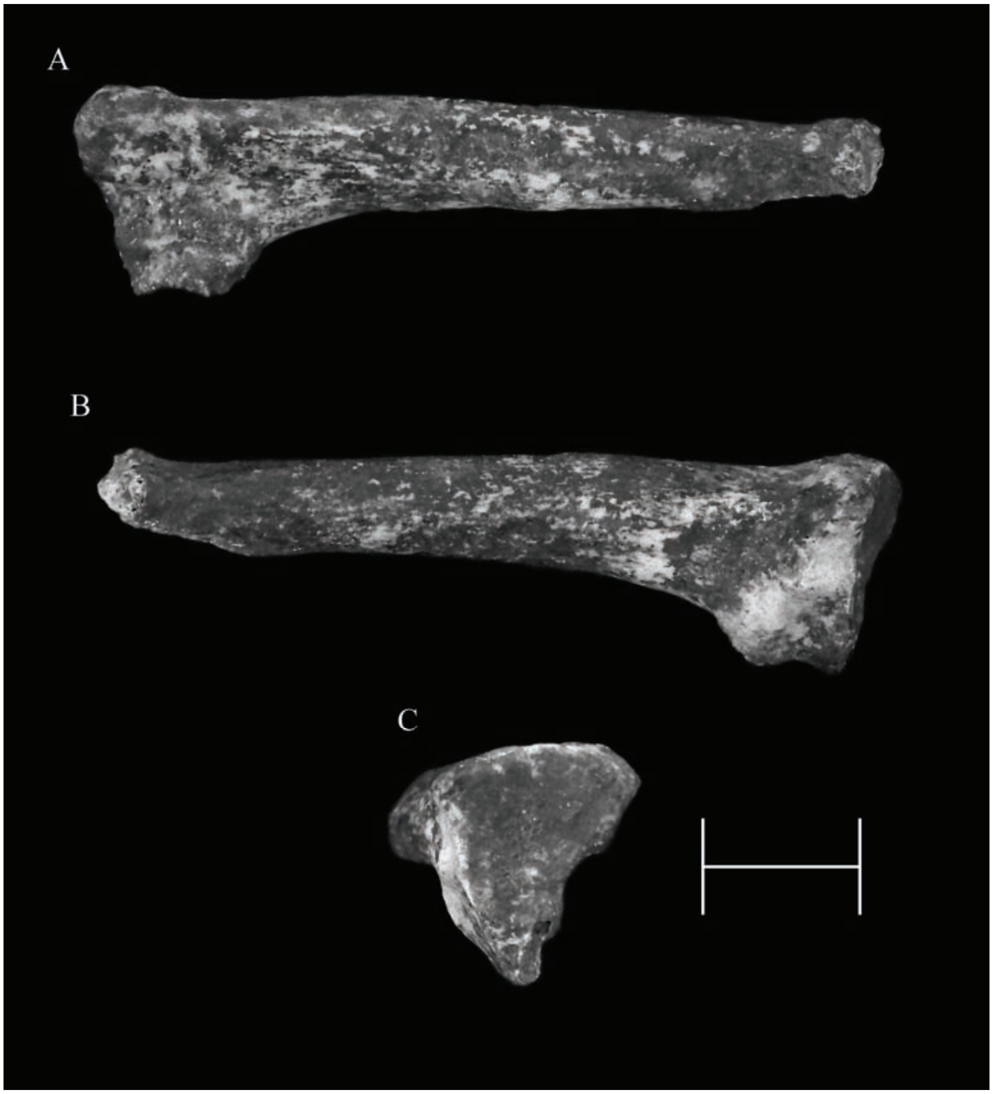


Figure B.5 Stw 595c (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm



APPENDIX C: THIRD METATARSAL FOSSIL PHOTOS

Figure C.1 Stw 387 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

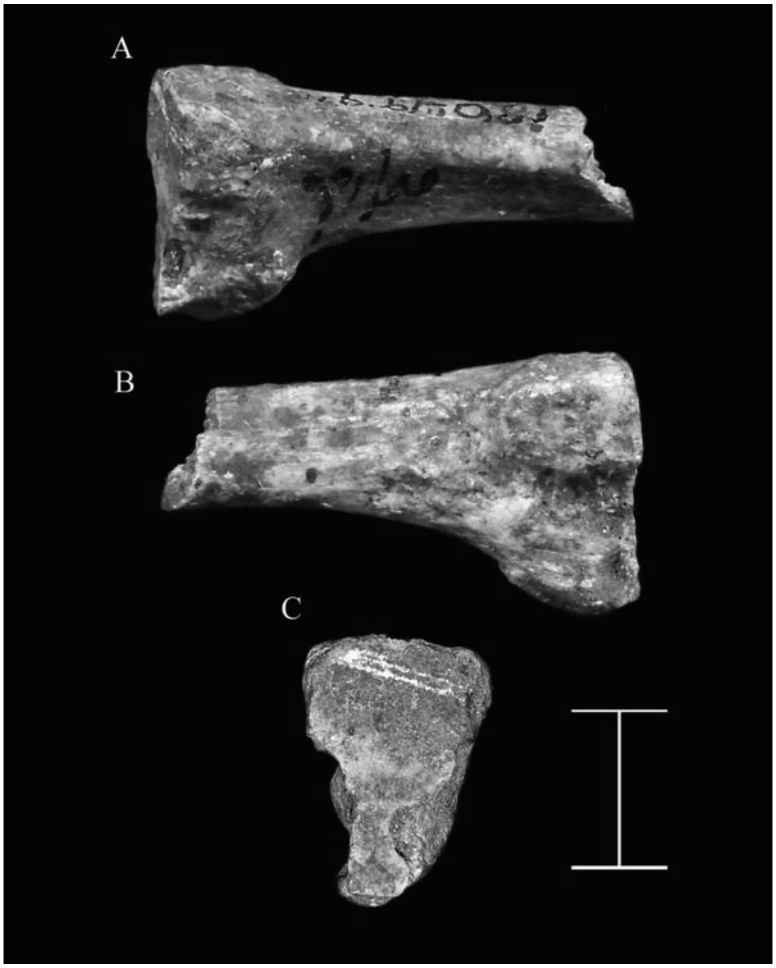


Figure C.2 Stw 388 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure C.3 Stw 435 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure C.4 Stw 477 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

Figure C.5 Stw 496 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

APPENDIX D: FOURTH METATARSAL FOSSIL PHOTOS

Figure D.1 Stw 485 (left); A) medial; B) lateral; C) proximal; scale bar = 1 cm

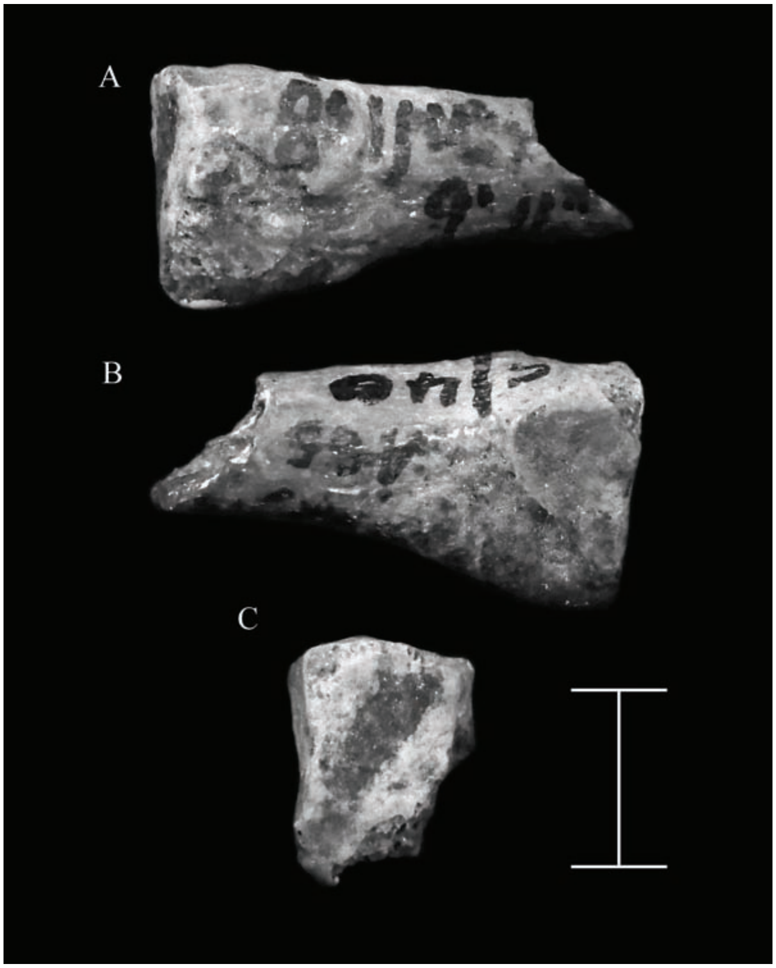


Figure D.2 Stw 628 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

APPENDIX E: FIFTH METATARSAL FOSSIL PHOTOS

Figure E.1 A. L. 333-13 (left); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure E.2 A. L. 333-13 (left); A) lateral; B) medial; C) proximal; scale bar = 1 cm

Figure E.3 Stw 114/115 (right); A) lateral; B) medial; C) proximal; scale bar = 1 cm

REFERENCES CITED

Abitbol, MM (1987) Evolution of the lumbosacral angle. Am J Phys Anth 72: 361-372.

Adams DC, Rohlf FJ and Slice DE (2004) Geometric Morphometrics: Ten Years of Progress Following the 'Revolution.' Ital J Zool 71: 5-16.

Ahern JCM (2005) Foramen Magnum Position Variation in *Pan troglodytes*, Plio-Pleistocene Hominins, and Recent *Homo sapiens*: Implications for Recognizing the Earliest Hominins. Am J Phys Anth 127: 267-276.

Aiello L and Dean C (1990) Human Evolutionary Anatomy. London: Elsevier.

Aiello LC and Collard M (2001) Our Newest Oldest Ancestor?. Nature 410: 526-527.

Ajmani ML, Ajmani K, Jain SP. 1984. Variations in the articular facets of the adult cuneiform bones. Anthropol Anz 42:121-126.

Alexander RM (1980) Forces in animal joints. Eng Med 9:93-97.

Archibald JD, Lovejoy CO and Heiple KG (1972) Implications of Relative Robusticity in the Olduvai Metatarsus. Am J Phys Anth 37: 93-96.

Ardrey R (1961) African Genesis. New York: Atheneum.

Argue D, Donlon D, Groves C, Wright R (2006) Homo floresiensis: microcephalic, pygmoid, Australopithecus or Homo? J Hum Evol 51:360–374.

Arnqvist G and Mårtensson T (1998) Measurement error in geometric morphometrics: empirical strategies to assess and reduce its impact on measures of shape. Acta Zool Sci Hung 44 (1-2): 73-96.

Ashton EH and Zuckerman S (1952) Age changes in the position of the occipital condyles in the chimpanzee and gorilla. Am J Phys Anth 10: 227-228.

Ashton EH and Zuckerman S (1956) Age changes in the position of the foramen magnum in hominoids. Proc Zool Soc Lon 126: 315-325.

Beauvilain A and Le Guellec Y (2004) Further details concerning fossils attributed to *Sahelanthropus tchadensis* (Toumaï). S Af J Sci 100: 142-144.

Bennett MB and Ker RF (1990) The mechanical properties of the human subcalcaneal fat pad in compression. J Anat 171: 131-138.

Berillon G (1999) Geometric pattern of the hominoid hallucial tarsometatarsal complex. Quantifying the degree of hallux abduction in early hominins. C R Acad Sci Paris *328:*627-633.

Berillon G. 2003. Assessing the Longitudinal Structure of the Early Hominin Foot: A Two-dimensional Architecture Analysis. Hum Evol 18: 113-122.

Broom R (1938) The Pleistocene anthropoid apes of South Africa. Nature 142: 377-379.

Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko, Wayhu Saptomo E, Awe Due R. (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 431:1055–1061.

Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blonel C, Bocherens H, Boisserie JR, De Bonis L, Coppens Y, Dejax J, Denys C, Duringer P, Eisenmann V, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Campomanes PP, Del Leon MP, Rage JC, Sapanet M, Schulster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazzo A and Zollikofer C (2002) A new hominin from the Upper Miocene of Chad, Central Africa. Nature 418 (11): 145-151.

Bojsen-Moller F (1979) Calcaneocuboid joint and stability of the longitudinal arch of the foot at high and low gear push off. J Anat *129:*165-76.

Bookstein, FL (1991) Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge University Press.

Carrier DR (1984) The Energetic Paradox of Human Running and Hominin Evolution. Cur Anth 25 (4):483-495.

Chaplin G, Jablonski NG, and Cable NT (1994) Physiology, thermoregulation and bipedalism. J Hum Evol 27: 497-510.

Charteris J, Wall JC and Nottrodt JW (1981) Functional reconstruction of gait from the Pliocene hominin footprints at Laetoli, northern Tanzania. Nature 290: 496-498.

Charteris J, Wall JC and Nottrodt JW (1982) Pliocene Hominin Gait: New Interpretations Based on Available Footprint Data From Laetoli. Am J Phys Anth 58: 133-144.

Chen W, Tang F, and Ju C (2001) Stress distribution of the foot during mid-stance to push-off in barefoot gait: a 3-D finite element analysis. Clin Biomech 16: 614-620.

Ciochon RL and Curruccini RS (1977) The coraco-acromial ligament and projection index in man and other anthropoid primates. J Anat 124: 627-632.

Clarke RJ (1998) First ever discovery of a well-preserved skull and associated skeleton of Australopithecus. S. Af. J. Sci. (94) 10: 460-463.

Clarke RJ, and Tobias PV (1995) Sterkfontein member 2 foot bones of the oldest South African hominin. Science *269:*521-4.

Conroy GC, and Rose MD (1983) The evolution of the primate foot from the earliest primates to the Miocene hominoids. Foot Ankle *3:*342-64.

Currey J (1984) The Mechanical Adaptations of Bone. Princeton: Princeton University Press

D'Aout K, Aerts P, De Clercq D, De Meester K, and Van Elsacker L (2002) Segment and joint angles of hind limb during bipedal and quadrupedal walking of the bonobo (Pan paniscus). Am J Phys Anthropol *119:*37-51.

D'Août K, Vereecke E, Schoonaert K, De Clercq D, Van Elsaker L and Aerts P (2004) Locomotion in bonobos (Pan paniscus): differences and similarities between bipedal and quadrupedal terrestrial walking, and a comparison with other locomotor modes. J Anat 204: 353-361.

Dart RA (1925) *Australopithecus africanus*: the ape-man of South Africa. Nature 115: 195-197.

Dart RA (1926) Taung and its significance. Nat Hist 26: 315-327.

Dart RA (1953) The Predatory Transition from Ape to Man. Int Anth Lang Rev 1:201-217.

Dart RA (1972) Adventures with the missing link. Ann Arbor: University Microfilms.

Darwin C (1871) The Descent of Man and Selection in Relation to Sex. New York : Penguin Classics (reprint 2004).

Day MH (1967) Olduvai Hominin 10: a Multivariate Analysis. Nature 215: 323-324.

Day MH (1973) Locomotor features of the lower limb in hominins. Symp Zool Soc Lond 33: 29-51.

Day MH (1977) Locomotor adaptation in man. Biol Hum Affairs. 42: 149-151.

Day MH (1980) Laetoli Pliocene hominin footprints and bipedalism. Nature 286: 385-387.

Day MH (1986) Bipedalism: Pressures, Origins and Modes. *In* Major topics in primate and human evolution. Wood B, Martin L and Andrews P, *eds*. Cambridge University Press: Cambridge.

Day MH and Napier JR (1964) Fossil Foot Bones. Nature 4923: 969-201.

Day MH and Napier JR (1966) A Hominin Toe Bone from Bed I, Olduvai Gorge, Tanzania. Nature 5052: 929-930.

Day MH and Wood BA (1968) Functional Affinities of the Olduvai Hominin 8 Talus. Man 3 (3): 440-455.

Day, MH, and Wickens, EH (1980) Laetoli Pliocene hominin footprints and bipedalism. Nature 286:386-387.

Dean MC and Wood BA (1981) Metrical analysis of the basicranium of extant hominoids and Australopithecus. Am J Phys Anth 54: 63-71.

Dean MC and Wood BA (1982) Basicranial anatomy of Plio-Pleistocene hominins from East and South Africa. Am J Phys Anth 59: 157-174.

Deloison Y (1985) Comparative Study of Calcanei of Primates and *Pan-Australopithecus-Homo* Relationship. In P Tobias (ed.): Hominin Evolution: Past, Present and Future. New York: A. R. Liss, pp. 143-147.

Deloison Y (2004) Fossil foot bones anatomy from South Africa between 2.4 and 3.5 MY old. Interpretation in relation to the kind of locomotion (trans). Biom Hum et Anthropol 21:189-230.

DeSilva, JM. 2010. Revisiting the “midtarsal break”. Am J Phys Anthropol (141)2:245-258.

Duncan AS, Kappelman J, and Shapiro LJ (1994) Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. Am J Phys Anthropol *93:*67-81.

Dykyj D, Ateshian GA, Trepal MJ, and MacDonald LR (2001) Articular geometry of the medial tarsometatarsal joint in the foot: comparison of metatarsus primus adductus and metatarsus primus rectus. J Foot Ankle Surg *40:*357-65.

Elftman H (1960) The Transverse Tarsal Joint and Its Control. Clin Orthop *16:*41-6.

Elftman H (1969) Dynamic structure of the human foot. Artif Limbs *13:*49-58.

Elftman H, and Manter J (1935a) Chimpanzee and Human Feet in Bipedal Walking. Am J Phys Anthropol *1:*69-79.

Elftman H, and Manter J (1935b) The Evolution of the Human Foot, with Especial Reference to the Joints. J Anat *70:*56-67.

Erdemir A, Hamel AJ, Fauth AR, Piazza SJ and Sharkey NA (2004) Dynamic Loading of the Plantar Aponeurosis in Walking. J Bone Joint Surg Am 86:546-552.

Etkin W (1954) Social Behavior and the Evolution of man’s Mental Faculties. Am Nat 88 (840): 129-142.

Evans FG and Krahl VE (1945) The torsion of the humerus: a phylogenetic study from fish to man. Am J Anat 76: 303-337.

Falk D, Hildebolt C, Smith K, Morwood MJ, Sutikna T, Jatmiko, Wayhu Saptomo E, Imhof H, Seidler H, Prior F (2007) Brain shape in human microcephalics and Homo floresiensis. Proc Natl Acad Sci 104, 2513–2518.

Franciscus RG and Holliday TW (1992) Hindlimb skeletal allometry in Plio-Pleistocene hominins with special reference to AL-288-1 (Lucy). Bull mém Soc anthropol Paris 4: 5-20.

Galik K, Senut B, Pickforn M, Gommery D, Treil J, Kuperavage AJ and Eckhardt RB (2004) External and Internal Morphology of the BAR 1002’00 *Orrorin tugenensis* Femur. Science 305: 1450-1453.

Gebo DL (1992) Plantigrady and foot adaptation in African apes: implications for hominin origins. Am J Phys Anthropol *89:*29-58.

Gebo DL, Schwartz GT. 2006. Foot bones from Omo: implications for hominid evolution.Am J Phys Anthropol 129:499–511.

Gefen A, Megido-Ravid M, Itzchak Y, and Arcan M (2000) Biomechanical Analysis of the Three-Dimensional Foot Structure During Gait: A basic Tool for Clinical Applications. J Biomech Eng (22) 6: 630-639.

Giacomozzi C, Macellari V, Leardini A, and Benedetti MG (2000) Integrated pressure-force-kinematics measuring system for the characterization of plantar foot loading during locomotion. Med & Bio Eng & Comp (38) 2: 156-163.

Godfrey L, Sutherland M, Boy D, and Gomberg N (1991) Scaling of limb joint surface areas in anthropoid primates and other mammals. J Zool 223: 603-625.

Godfrey L, Sutherland M, Paine R, Williams F, Boy D, and Vuillaume-Randriamanantena M (1995) Limb joint surface areas and their ratios in Malagasy lemurs and other mammals. Am J Phys Anthropol 97: 11-36.

Gommery D and Senut B (2006) The terminal thumb phalanx of *Orrorin tugenensis* (Upper Miocene of Kenya). Geobios 39: 372-384.

Goodall C (1991) Procrustes methods in the Statistical Analysis of Shape. J R Statist Soc B 53(2): 285-339.

Gower JC (1975) Generalized Procrustes Analysis. Psychometrika *40:*33-51.

Guy F, Lieberman DE, Pilbeam D, del León MP, Likius A, Mackaye HT, Vignaud P, Zollikofer C and Brunet M (2005) Morphological affinities of the *Sahelanthropus tchadensis* (Late Miocene hominin from Chad) cranium. P N A S 102 (52): 18836-18841.

Haile-Selassie Y (2001) Late Miocene hominins from the Middle Awash, Ethiopia. Nature 412: 178-181.

Haile-Selassie Y, Suwa G and White TD (2004) Late Miocene Teeth from Middle Awash, Ethiopia, and Early Hominin Dental Evolution. Science 303: 1503-1505.

Hamrick MW (1996a) Articular Size and Curvature as Determinants of Carpal Joint Mobility and Stability in Strepsirhine Primates. J Morphol 230: 113-127.

Hamrick MW (1996b) Functional morphology of the lemuriform wrist joints, and the relationship between wrist morphology and positional behavior in arboreal primates. Am J Phys Anthropol 100: 585-604.

Harcourt-Smith WEH (2002) Form and Function in the Hominoid Tarsal Skeleton, University College London.

Harcourt-Smith WEH and Aiello LC (2004) Fossils, feet and the evolution of human bipedal locomotion. J Anat 204: 403-416.

Hausman AJ, (1982) The biocultural evolution of Khoisan populations of Southern Africa, Am J Phys Anthropol 58 (4): 315–330.

Hay RL and Leakey MD (1982) The fossil footprints of Laetoli. Sci Amer 246: 50-57.

Hewes GW (1961) Food transport and the Evolution of Hominin Bipedalism. Am Anthro 63 (4): 687-710.

Hewes GW (1964) Hominin Bipedalism: Independent Evidence for the Food Carrying Theory. Science 146: 416-418.

Hicks JH (1953) The mechanics of the foot. I. The joints. J Anat *87:*345-57.

Hicks JH (1954) The mechanics of the foot. II. The plantar aponeurosis and the arch. J Anat *88:*25-30.

Hicks JH (1955) The foot as a support. Acta Anat (Basel) *25:*34-45.Hill K (1982) Hunting and Human Evolution. J Hum Evol 11: 521-544.

Hilton CE (1997) Comparative Locomotor Kinesiology in Two Contemporary Hominid Groups: Sedentary Americans and Mobile Venezuelan Foragers. PhD Dissertation. The University of New Mexico.

Holliday TW, Franciscus RG (2009) Body size and its consequences: Allometry and the lower limb length of Liang Bua 1 (*Homo floresiensis*). J Hum Evol 57(3):223-228.

Howells W (1959) Mankind in the Making. Doubleday: New York.

Hrdlicka A (1937) The gluteal ridge and gluteal tuberosities (3rd trochanters). Am J Phys Anthropol 23: 129-198.

Hunt KD (1994) The evolution of human Bipedality: ecology and functional morphology. J Hum Evol 26: 183-202.

Hunt KD (1996) The postural feeding hypothesis: an ecological model for the evolution of bipedalism. S Af J Sci 92 (2): 77-90.

Isidro A, Gonzalez-Casanova JC. 2002. A glimpse into the evolution of the hallucial tarso-metatarsal joint. Foot Ankle Surg 8:169-174.

Issac G (1978) The Food-sharing Behavior of Protohuman Hominins. Sci Am 238: 90-108.

Jablonski NG and Chaplin G (1993) Origin of habitual terrestrial bipedalism in the ancestor of the Homininae. J Hum Evol 24: 259-280.

Jacob HAC (2001) Forces acting in the forefoot during normal gait – an estimate. Clin Biomech 16: 783-792.

Johanson DC, Taieb M and Coppens Y (1982a) Pliocene Hominins From the Hadar Formation, Ethiopia (1973-1977): Stratigraphic, Chronologic, and Paleoenvironmental Contexts, With Notes on Hominin Morphology and Systematics. Am J Phys Anth 57: 373-402.

Johanson DC, Lovejoy CO, Kimbel WH, White TD, Ward SC, Bush ME, Latimer BM and Coppens Y (1982b) Morphology of the Pliocene partial hominin skeleton (AL 288-1) from the hadar formation, Ethiopia. Am J Phys Anth 57: 403-452.

Jolly CJ (1970) The seed-eaters: A new model of hominin differentiation based on a baboon analogy. Man (5) 1: 5-26.

Jones F (1944) Structure and Function as seen in the Foot. Baltimore: Williams & Wilkins.

Jungers WL (1982) Lucy's Limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. Nature 297: 676-678.

Jungers WL (1984) Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. Y Phys Anth 27: 73-97.

Jungers WL (1988) Relative joint size and hominid locomotor adaptations with implications for the evolution of hominid bipedalism. J Hum Evol 17: 247-265.

Jungers WL and Stern JT. (1983). Body proportions, skeletal allometry and locomotion in the Hadar hominds: a reply to Wolpoff. J Hum Evol. 12: 673-684.

Jungers WL, Harcourt-Smith WEH, Wunderlich RE, Tocheri MW, Larson SG, Sutikna T, Awe Due R, and Morwood MJ (2009a) The foot of Homo floresiensis. Nature 459:81-84.

Jungers WL, Larson SG, Harcourt-Smith W, Morwood MJ, Sutikna T, Due Awe R, Djubiantono T (2009) Descriptions of the lower limb skeleton of Homo floresiensis. J Hum Evol 57(5):538-554.

Kadambande S, Khurana A, Debnath U, Bansal M and Hariharan K (2006) Comparative anthropometric analysis of shod and unshod feet. The Foot16: 188-191.

Keith A (1928) The History of the Human Foot and its Bearing on Orthopaedic Practice. J Bone Joint Surg *11:*10-32.

Kendal DG (1984) Shape manifolds, procrustean metrics, and complex projective spaces. Bull London Math Soc *16:*81-121.

Kidd R. (1998) The past is the key to the present: thoughts on the origins of human foot structure, function and dysfunction as seen from the fossil record. Foot 8:75–84.

Kidd R (1999) Evolution of the rearfoot. A Model of Adaptation with Evidence from the Fossil Record. J Am Podiatr Med Assoc *89:*2-17.

Kidd R, Oxnard C. (2005) Little foot and big thoughts—a re-evaluation of the Stw573 foot from Sterkfontein, South Africa. HOMO J Comp Hum Biol 55:189–212.

Kidd RS, O'Higgins P and Oxnard CE (1996) The OH8 foot: a reappraisal of the functional morphology of the hindfoot utilizing a multivariate analysis. J Hum Evol 31: 269-291.

Kidder SM, Abuzzahab, FS Jr., Harris GF, Johnson JE (1996) A System for the Analysis of Foot and Ankle Kinematics During Gait. IEEE Trans Rehab Eng 4 (1): 25-32.

Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC (2006) Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. J Hum Evol 51: 134-152.

Knussman R (1967) Humerus, Ulna und Radius der Simiae. Bibliotheca Primatologica, Vol. 5 Basel: S. Karger.

Larson SG, Jungers WL, Morwood MJ, Sutikna T, Jatmiko, Wahyu Saptomo E, Awe Due A, Djubiantono T (2007) Homo floresiensis and the evolution of the hominin shoulder. J Hum Evol 53:718–731.

Latimer B (1991) Locomotor adaptations in Australopithecus afarensis: the issue of arboreality. In *Origine(s) de la Bipédie Chezles Hominidés* (eds Coppens Y, Senut B): 169-176. Paris: Editions du CNRS.

Latimer B, Lovejoy CO, Johanson D, and Coppens Y (1982) Hominin Tarsal, Metatarsal, and Phalangeal Bones Recovered From the Hadar Formation: 1974-1977 Collections. Am J Phys Anthropol *57:*701-719.

Latimer B, Ohman JC and Lovejoy CO (1987) Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. Am J Phys Anth 74: 155-175.

Latimer B, and Lovejoy CO (1989) The Calcaneus of *Australopithecus afarensis* and Its Implications for the Evolution of Bipedality. Am J Phys Anthropol *78:*369-86.

Latimer B, and Lovejoy CO (1990a) Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am J Phys Anthropol *82:*125-33.

Latimer B, and Lovejoy CO (1990b) Metatarsophalangeal joints of *Australopithecus afarensis*. Am J Phys Anthropol *83:*13-23.

Leakey MD (1971) Olduvai Gorge, Volume 3. Cambridge: Cambridge University Press.

Leakey MD (1981) Tracks and tools. Philos. Trans Roy Soc Lond B 292:96102.

Leakey L, Tobias P, Napier J. 1965. A new species of the genus Homo from Olduvai Gorge. Curr Anthr 6 (5):424-427.

Leakey L, Tobias P, Napier J. 1964. A new species of the genus Homo from Olduvai Gorge. Nature 202:7-9.

Leakey REF and Wood BA (1974) New Evidence of the Genus Homo from East Rudolf, Kenya II. Am J Phys Anth 39: 355-368.

Leakey MD and Hay RL (1979) Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. Nature **278**: 317 – 323.

Leakey MG, Feibel CS, McDougall I, Ward C and Walker A (1988) New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature 393: 62-66.

Leardini A, Benedetti MG, Berti L, Bettinelli D, Nativo R, and Giannini S (2007) rear-foot, mid-foot and fore-foot motion during the stance phase of gait. Gait & Posture 25: 453-462.

Le Gros Clark WE (1971) The Antecedents of Man. Edinburgh: Edinburgh University Press.

Le Minor J, and Winter M (2003) The intermetatarsal articular facet of the first metatarsal bone in humans: a derived trait unique within primates. Ann Anat *185:*359-365.

Lessertisseur J, and Jouffroy FK (1973) [Locomotory trends in primates expressed by the foot ratios. The adaptation to bipedalism (author's transl)]. Folia Primatol (Basel) *20:*125-60.

Leutenegger W (1977) A functional interpretation of the sacrum of *Australopithecus africanus*. S Af J Sci 73: 308-310.

Lewin R (1983) Do ape-size legs mean ape-like gait?. Science 221: 537-538.

Lewis OJ (1972) The evolution of the hallucial tarsometatarsal joint in the Anthropoidea. Am J Phys Anthropol *37:*13-33.

Lewis OJ (1980a) The joints of the evolving foot. Part II. The intrinsic joints. J Anat *130:*833-57.

Lewis OJ (1980b) The joints of the evolving foot. Part III. The fossil evidence. J Anat *131:*275-98.

Lewis OJ (1981) Functional Morphology of the Joints of the Evolving Foot. Symp zool Soc Lond *46:*169-188.

Lewis OJ (1989) Functional Morphology of the Evolving Hand and Foot. Oxford: Clarendon Press.

Lisowski FP, Albrecht GH and Oxnard CE (1974) The Form of the talus in Some Higher Primates: A Multivariate Study. Am J Phys Anth 41: 191-216.

Lisowski FP, Albrecht GH and Oxnard CE (1976) African Fossil Tali: Further Multivariate Morphometric Studies. Am J Phys Anth 45: 5-18.

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

Louchart A, Wesselman H, Blumenschine RJ, Hlusko LJ, Njau JK, Black MT, Asnake M, and White TD (2009) Taphonomic, Avian, and Small-Vertebrate Indicators of Ardipithecus ramidus Habitat. Science 326 (66):66e1-66e4.

Lovejoy CO (1981) The Origin of Man. Science 211: 341-350.

Lovejoy CO (1988) Evolution of human walking. Sci Am 259: 82-89.

Lovejoy CO (2009) Reexamining Human Origins in Light of Ardipithecus ramidus Science 326 (74) 74e1-74e8.

Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. 2009. Combining Prehension and Propulsion: The Foot of Ardipithicus ramidus. Science 326 (76): 72e1-72e8.

Lovejoy CO, Suwa G, Spurlock L, Asfaw B, and White TD (2009) The Pelvis and Femur of Ardipithecus ramidus: The Emergence of Upright Walking. Science 326 (71) 71e1-71e6.

Lovejoy CO, Simpson SW, White TD, Asfaw B, and Suwa G (2009) Careful Climbing in the Miocene: The Forelimbs of Ardipithecus ramidus and Humans Are Primitive. Science 326 (70) 70e1-70e8.

Lyras GS, Dermitzakis MD, Van Der Geer AAE, Van Der Geer SB, De Vos J (2009) The origin of Homo floresiensis and its relation to evolutionary processes under isolation. Anthropol Sci 117:33-43.

MacConaill M (1945) The Postural Mechanism of the Human Foot. Proc Royal Irish Acad *50B:*265-278.

MacConaill M (1950) The movements of bones and joints: The synovial fluid and its assistants. J Bone Jt Surg 32B: 244-252.

MacConaill M (1966) The geometry and algebra of articular kinematics. Biomed Eng 1: 205-212.

MacConaill M, and Basmajian J (1969) Muscles and Movements. Baltimore: Williams & Wilkins.

Maddox SD and Franciscus RG (2009) Allometric scaling of infraorbital surface topography in Homo. J Hum Evol 56:161-174.

Manter JT (1946) Distribution of compression forces in the joints of the human foot. Anat Rec (96) 3: 313-321.

Martin R, and Saller K (1959) Lehrbuch der Anthropologie, Vol. 2, 3rd edn. Struttgart: Gustav Fisher.

McHenry HM (1975) A new pelvic fragment from Swartkrans and the relationship between the robust and gracile australopithecines. Am J Phys Anth 43: 245-262.

McHenry HM, and Jones AL (2006) Hallucial convergence in early hominins. J Hum Evol *50:*534-9.

Merker B (1984) A Note on Hunting and Hominin Origins. Am Anthro 86 (1): 112-114.

Midlo C (1934) Form of Hand and Foot in Primates. Am J Phys Anthropol *14:*337-389.

Morton D (1922) Evolution of the Human Foot I. Am J Phys Anthropol *5:*305-336.

Morton D (1924) Evolution of the Human Foot II. Am J Phys Anthropol *6:*1-52.

Morton D (1926) Significant Characteristics of the Neanderthal Foot. Natural History *26:*310-314.

Morton D (1935) The Human Foot. New York: Columbia University Press.

Morwood MJ, Brown P, Jatmiko, Sutikna T, Wahyu Saptomo E, Westaway KE, Awe Due R, Roberts RG, Maeda T, Wasisto S, Djubiantono T (2005) Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. Nature 437:1012–1017.

Napier JR (1960) Studies of the hands of living primates. Proc Zool Soc Lon 134: 647-657.

Napier JR (1980) Hands. London: George Allen & Unwin.

Nawoczenski DA, Baumhauer JF, and Umberger BR (1999) Relationship between Clinical Measurements and Motion of the First Metatarsophalangeal Joint During Gait. J Bone Joint Surg Am *81:*370-6.

O'Higgins P, and Jones N (1998) Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. J Anat *193 (Pt 2):*251-72.

O'Higgins P and Jones N (2006) Tools for statistical shape analysis. Hull York Medical School. http://www.york.ac.uk/res/fme/resources/software.htm

Ohman JC, Krochta TJ, Lovejoy CO, Mensforth RP, and Latimer B (1997) Cortical Bone Distribution in the Femoral neck of Hominoids: Implications for the Locomotion of *Australopithecus afarensis*. Am J Phys Anth 104: 117-131.

Ohman JC, Lovejoy CO and White TD (2005) Questions about *Orrorin* Femur. Science 307: 845.

Olson TR, and Seidel MR (1983) The evolutionary basis of some clinical disorders of the human foot: a comparative survey of the living primates. Foot Ankle *3:*322-41.

Oxnard CE (1972) Some African Fossil Foot Bones: A Note on the Interpolation of Fossils into a Matrix of Extant Species. Am J Phys Anth 37: 3-12.

Oxnard CE and Lisowski FP (1980) Functional Articulation of Some Hominoid Foot Bones: Implications for the Olduvai (Hominin 8) Foot. Am J Phys Anth 52: 107-117.

Peicha G, Labovitz J, Siebert FJ, Grechenig W, Weiglein A, Preidler KW, Quehenberger F (2002) The anatomy of the joint as a risk factor for Lisfranc dislocation and fracture dislocation. J Bone Joint Surg 84B: 981-985.

Pickford M and Senut B (2001) The geological and faunal context of Late Miocene hominin remains from Lukeino, Kenya. C R Acad Sci Paris 332: 145-152.

Proctor DJ (2005) Morphometrics and multi-landmark depth analysis of the proximal hallucal metatarsal articular surface in hominoid. M.A., Florida Atlantic University, United States -- Florida.

Proctor DJ, Broadfield, D, and Proctor K (2008) Quantitative Three-Dimensional Shape Analysis of the Proximal Hallucial Metatarsal Articular Surface in *Homo*, *Pan*, *Gorilla*, and *Hylobates*. Am J Phys Anth 135:216-224.

Rao UB and Joseph B (1992) The influence of footwear on the prevalence of flat foot. J Bone Joint Surg 74-B: 525-527.

Ravey M (1978) Bipedalism: an early warning system for Miocene hominoids. Science 199: 372.

Regan MH, Case DT, and Brundige JC (1999) Articular Surface Defects in the Third Metatarsal and Third Cunieform: Nonosseous tarsal Coalition. Am J Phys Anth 109: 53-65.

Reimann R, and Marlovits S (1992) [Biomechanics of the joints of the large toe. Shape and movement of the first tarsometatarsal joint and of the medial cuneonavicular joint]. Acta Anat (Basel) *144:*30-5.

Rhoads JG and Trinkaus E (1977) Morphometrics of the Neaderthal Talus. Am J Phys Anth 46: 29-44.

Roberts N (1989) The Holocene—an environmental history, Basil Blackwell Inc., Oxford.

Rodman PS and McHenry HM (1980) Bioenergetics and the origin of Hominin Bipedalism. Am J Phys Anth 52: 103-106.

Rose MD (1991) The Process of Bipedalization in Hominins. *In* Origine(s) De la Bipédie Chez les Homininés. Coppens Y and Senut B, eds. Paris: CNRS.

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

Sarmiento EE (1988) Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. Int J Primatol 9:281-345.

Sarmiento E (1994) Terrestrial Traits in the Hands and Feet of Gorillas. American Museum Novitiates *3091:*1-56.

Sealy, J (2006) Diet, Mobility, and Settlement Pattern among Holocene Hunter-Gatherers in Southernmost Africa. Curr Anthrop (47) 4: 569-595.

Sealy J, Pfeifer S (2000) Diet, body size, and landscape use among Holocene people in the Southern Cape, South Africa, Curr Anthropol 41 (4):642–655.

Schultz A (1923) Fetal growth in man. Am J Phys Anthropol *6:*389-399.

Schultz A (1924) Growth studies on primates bearing upon man's evolution. Am J Phys Anthropol *7:*149-164.

Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. Hum Biol 2: 303-438.

Schultz AH (1950) The physical distinction of man. Proc Am Phil Soc 94: 428-449.

Schultz AH (1955) The position of the occipital condyles and of the face relative to the skull base in primates. Am J Phys Anth 11: 277-310.

Schultz AH (1961) Vertebral column and thorax. Primatologia 1: 1-66.

Schultz A (1963) The Relative Lengths of the Foot Skeleton and its Main Parts in Primates. Symp zool Soc Lond *10:*199-206.

Schultz AH (1969a) The Life of the Primates. London: Weidenfeld and Nicolson.

Schultz AH (1969b) Observations on the acetabulum of primates. Folias Primatol 11: 181-199.

Scott SH and Winter DA (1993) Biomechanical model of the human foot: Kinematics during the stance phase of walking. J Biomechanics 26 (9): 1091-1104.

Senut B (1981) Humeral outlines in some hominoid primates and in Plio-Pleistocene hominins. Am J Phys Anth 56: 275-283.

Senut B and Tardieu C (1985) Functional aspects of Plio-pliestocene Hominin limb bones: implications for taxonomy and phylogeny. *In* Ancestor: the Hard Evidence. Ed Delson E. New York: A Liss.

Senut B, Pickford M, Gommery D, Mein P, Cheboi K and Coppens Y (2001) First hominin from the Miocene (Lukeino Formation, Kenya). C R Acad Sci Paris 332: 137-144.

Sharkey NA and Hamel AJ (1998). A dynamic cadaver model of the stance phase of gait: performance characteristics and kinetic validation. Clin Biomech 13: 420-433.

Shereff MJ, Bejjani FJ, and Kummer FJ (1986) Kinematics of the first metatarsophalangeal joint. J Bone Joint Surg Am *68:*392-8.

Shipman P (1986) Scavenging or Hunting in Early Hominins: Theoretical Framework and Tests. Am Anth 88 (1): 27-43.

Shulman SB (1945) Survey in China and India of feet that have never worn shoes. J Nat As Chiro 39: 26-30.

Sim-Fook L, Hodgson AR. 1958. A Comparison of Foot Forms Among the Non-Shoe and Shoe-Wearing Chinese Population. J Bone Joint Surg 40: 1058-1062.

Sinclair ARE (1986) Migration and hominin bipedalism. Nature 324: 307-308.

Stanford CB (1998) To Catch a Colobus. *In* The Primate Anthology. Ciochon RL and Nisbett RA, *eds*. Prentice Hall: Upper Saddle River.

Stanford CB (2002) Brief communication: Arboreal bipedalism in Bwindi chimpanzees. Am J Phys Anth 119: 87-91.

Stanford CB (2006) Arboreal bipedalism in wild chimpanzees: Implications for the evolution of hominid posture and locomotion. Am J Phys Anth 129: 225-231.

Stern JT (2000) Climbing to the Top: A personal memoir of *Australopithecus afarensis*. Evol Anth 9 (3): 113-133.

Stern JT and Susman RL (1981) Electromyography of the gluteal muscles in *Hylobates*, *Pongo*, *Pan*: application for the evolution of hominin bipedality. Am J Phys Anth 55: 153-166.

Stern JT and Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anth. 60: 279-317.

Steudel-Numbers K (2003) The energetic cost of locomotion: humans and primates compared to generalized endotherms. J Hum Evol 44: 255-262.

Stock J, Pfeiffer S (2001) Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the Southern African Later Stone Age and the Andaman Islands. Am J Phys Anthropol 115:337–348.

Stokes IAF, Hutton WC, and Stott JRR (1979) Forces acting on the metatarsals during normal walking. J Anat (129) 3: 579-590.

Stormont T, An K, Morrey B, and Chao E (1985) Elbow joint contact study: Comparison of techniques. J Biomech 18:329-336.

Strait DS and Grine FE (2004) Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. J Hum Evol 47: 399-452.

Susman RL (1983) Evolution of the Human Foot: evidence from Plio-Pleistocene Hominins. Foot Ankle *3:*365-76.

Susman RL (1989) New hominin fossils from the Swartkrans formation (1979-1986 excavations): postcranial specimens. Am J Phys Anthropol *79:*451-74.

Susman RL (2008) Brief Communication: Evidence Bearing on the status of Homo habilis at Olduvai Gorge. Am J Phys Anthropol *137:*356-361.

Susman RL, Stern J. (1982) Functional Morphology of Homo habilis. Science 217:931-934.

Susman RL, Stern JT, Jr., and Jungers WL (1984) Arboreality and bipedality in the Hadar hominins. Folia Primatol (Basel) *43:*113-56.

Susman RL, Brain TM (1988) New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. Am J Phys Anthropol *77:*7-15.

Susman RL and Stern J (1991) Locomotor behavior of early hominids: epistemology and fossil evidence. In *Origine(s) de la Bipédie Chezles Hominidés* (eds Coppens Y, Senut B): 121-131. Paris: Editions du CNRS.

Susman RL, deRuiter DJ, Brain CK. 2001. Recently identified postcranial remains of Paranthropus and early Homo from Swartkrans Cave, South Africa. J Hum Evol 41:607-629.

Susman RL and de Ruiter DJ (2004) New hominin first metatarsal (SK 1813) from Swartkrans. J Hum Evol 47: 171-181.

Suwa G, Asfaw B, Kono RT, Kubo D, Lovejoy CO, and White TD (2009) The Ardipithecus ramidus Skull and Its Implications for Hominid Origins. Science 326 (68):68e1-68e7.

Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO, and White TD (2009) Paleobiological Implications of the Ardipithecus ramidus Dentition. Science 326 (69) 94-99.

Swartz SM (1989) The functional morphology of weight-bearing: Limb joint surface area allometry in anthropoid primates. J Zool 218: 441-460.

Szalay F, and Dagosto M (1988) Evolution of Hallucial grasping in the primates. J Hum Evol *17:*1-33.

Tardieu C (1981) Morpho-functional analysis of the articular surfaces of the knee-joint in primates. In Primate Evolutionary Biology. *Eds* Chiarelli AB and Corruccini RS. Berlin: Springer Verlag.

Taylor CR, Schmidt-Nielson K and Raab JL (1970) Scaling of energetic costs of running to body size in mammals. Am J Physiol 219: 1104-1107.

Thompson A (1889) The influence of posture on the form of the articular surfaces of the tibia and astragalas in the different races of man and the higher apes. J Anat 23: 616-639.

Thompson ALT and Zipfel B (2005) The unshod child into womanhood-forefoot morphology in two populations. The Foot 15: 22-28.

Thordarson DB, Schmotzer, H, Chon, J, Peters, J (1995) Dynamic Support of the Human Longitudinal Arch: A Biomechanical Evaluation. Clin Orthop 316: 165-172.

Tocheri MW, Orr CM, Larson SG, Sutikna T, Jatmiko, Saptomo EW, Due RA, Djubiantono T, Morwood MJ and Jungers WL (2007) The primitive wrist of Homo floresiensis and its implications for hominin evolution.Science (317)5845: 1743-5.

Trinkaus E (1983) Functional aspects of Neandertal pedal remains. Foot Ankle *3:*377-90.

Trinkaus E (2005) Anatomical evidence for the antiquity of human footwear use. J Arch Sci 32: 1515-1526.

Tuttle RH (1981) Evolution of hominin bipedalism and prehensile capabilities. Phil Trans Soc Lond B 292: 89-94.

Tuttle RH and Basmajian JV (1974) Electromyography of brachial muscles in *Pan* g*orilla*, and hominoid evolution. Am J Phys Anth 41: 71-90.

Tuttle RH, Webb DM and Baksh M (1991) Laetoli Toes and Australopithecus afarensis. 6(3): 193-200.

Vereecke E, D'Aoûte KD, Clercq DD, Elsaker LV, and Aerts P (2003) Dynamic Plantar pressure Distribution During Terrestrial Locomotion of Bonobos (*Pan paniscus*). Am J Phys Anthropol 120: 373-383.

Vignaud P, Duringer P, Mackaye MT, Likius A, Blondel C, Boisserie JR, de Bonis L, Eisenmann V, Etienne ME, Geraads D, Guy F, Lehmann T, Lihoreau F, Lopez-Martinez N, Mourer-Chauviré C, Otero O, Rage JC, Schuster M, Viriot L, Zazzo A and Brunet M (2002) Geology and palaeontology of the Upper Miocene Toros-Menalla hominin locality, Chad. Nature 418 (11): 152-155.

Wainwright SA, Biggs W, Currey J, and Gosline J (1982) Mechanical Design in Organisms. Princeton: Princeton University Press.

Walmsley T (1933) The vertical axes of the femur and their relations. A contribution to the study of the erect posture. J Anat 67: 284-300.

Ward CV (2002) Interpreting the posture and locomotion of Australopithecus afarensis: where do we stand? Am J Phys Anthropol 119 (S35): 185-215.

Ward C, Leakey M and Walker A (1999) The new hominin species *Australopithecus anamensis*. Evol Anthro 7 (6): 197-205.

Ward C, Leakey M and Walker A (2001) Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J Hum Evol 41: 255-368.

Washburn SL (1960) Tools and Human Evolution. Sci Amer 203 (3) 63-75.

Washburn SL (1967) Behavior and the origin of Man. Proc R Ant 1967: 21-27.

Washburn SL and Lancaster CS (1968) The Evolution of Hunting. *In* Man the Hunter, Lee RB and DeVore I, *eds*. Aldine Publishing Company: Chicago.

Weidenreich F (1923) Evolution of the Human Foot. Am J Phys Anthropol *5:*1-10.

Weidenreich F (1940) The External Tubercle of the Human Tuber Calcanei. Am J Phys Anthropol *23:*473-487.

Wheeler PE (1984) The Evolution of Bipedality and Loss of Functional Body Hair in Hominins. J Hum Evol 13: 91-98.

Wheeler PE (1985) The Loss of Functional Body Hair in Man: the Influence of Thermal Environment, Body Form, and Bipedality. J Hum Evol 14: 23-28.

Wheeler PE (1991) The thermoregulatory advantages of hominin bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. J Hum Evol 21: 107-115.

Wheeler PE (1994) The foraging times of bipedal and quadrapedal hominins in open equatorial environments (a reply to Chaplin, Jablonski, & Cable, 1994). J Hum Evol. 27: 511-517.

White, TD (1980) Evolutionary implications of Pliocene hominin footprints. Science 208:176-176.

White TD and Suwa G (1987) Hominin Footprints at Laetoli: Facts and Interpretations. Am J Phys Anth 72:485-514.

White TD and Johanson DC (1989) The Hominin Composition of Afar Locality 333: Some Preliminary Observations. *In* Homininae. Milan: Editoriale Jaca Book. 97-101.

White TD, Suwa G and Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominin from Aramis, Ethiopia. Nature 371: 306-312.

White TD, Suwa G and Asfaw B (1995) Corrigendum *Australopithecus ramidus*, a new species of early hominin from Aramis, Ethiopia. Nature 371: 306-312.

White TD, Ambrose SH, Suwa G, Su DF, DeGusta D, Bernor RL, Boisserie JR, Brunet M, Delson E, Frost S, Garcia N, Giaourtsakis IX, Haile-Selassie Y, Howell FC, Lehmann T, Likius A, Pehlevan C, Saegusa H, Semprebon G, Teaford M, and Vrba E (2009) Macrovertebrate Paleontology and the Pliocene Habitat of Ardipithecus ramidus. Science 326 (67):87-93.

White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, and WoldeGabriel G (2009) Ardipithecus ramidus and the Paleobiology of Early Hominids. Science 326 (64): 75-86.

Wiley DF, Amenta N, Alcantara DA, Ghosh D, Kil YJ, Delson E, Harcourt-Smith W, Rohlf FJ, St. John K, Hamann B. 2005. Evolutionary Morphing. Proceedings of IEEE Visualization.

Wilkinson JL (1954) The Terminal Phalanx of the Great Toe. J Anat *88:*537-541.

WoldeGabriel G, Ambrose SH, Barboni D, Bonnefille R, Bremond L, Currie B, DeGusta D, Hart WK, Murray AM, Renne PR, Jolly-Saad MC, Stewart KM, and White TD (2009) The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of Ardipithecus ramidus. Science 326 (65):65e1-65e5.

Wolpoff MH (1983a) Lucy's Little Legs. J Hum Evol 12: 443-453.

Wolpoff MH (1983b) Lucy's lower limbs: long enough for Lucy to be fully bipedal? Nature 304: 59-61.

Wolpoff MH (1999) Paleoanthropology 2nd Ed. New York: McGraw-Hill.

Wolpoff MH, Senut B, Pickford M and Hawks J (2002) *Sahelanthropus* or *'Sahelpithecus'*? Nature 419 (10): 581-582.

Wood BA (1974) Olduvai Bed I Post-cranial Fossils: A Reassessment. J Hum Evol 3: 373-378.

Wood BA. 1992. Origin and evolution of the genus Homo. Nature 355:783–790.

Wood B and Constantino P (2007) Paranthropus boisei: Fifty years of Evidence and Analysis. Am J Phys Anthropol Yr bk Phys Anthro 50:106-137.

Wood B and Lonergan N (2008) The hominin fossil record: taxa, grades and clades. J Anat 212: 354-376.

Wrangham RW (1980) Bipedal Locomotion as a Feeding Adaptation in Gelada Baboons, and its Implications for Hominin Evolution. J Hum Evol 9: 329-331.

Yalden DW (1972) The form and function of the carpal bones in some arboreally adapted mammals. Acta Anat 82:383-406.

Zelditch, ML; Swiderski, DL; Sheets, DH; Fink, WL (2004) Geometric Morphometrics for Biologists: A Primer. New York: Elsevier.

Zipfel B and Kidd R (2006) Hominin first metatarsals (SKX 5017 and SK 1813) from Swartkrans: A morphometrics analysis. HOMO J Comp Hum Biol 57:117-131.

Zipfel B and Berger LR (2007) Shod versus unshod: The emergence of forefoot pathology in modern humans? The Foot 17: 205-213.

Zipfel B, DeSilva JM and Kidd RL (2009) Earliest complete fifth hominin metatarsal – Implications for the evolution of the lateral column of the foot. Am J Phys Anth 140: 532-545.

Zollikofer CPE, de León MSP, Lieberman DE, Guy F, Pilbeam D, Likius A, Mackaye HT, Vignaud P and Brunet M (2005) Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434 (7): 755-759.