To the Graduate Council:

I am submitting herewith a thesis written by Amy Ridler Shook entitled "A Morphometric Analysis of the Hominoid Iliac Crest." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Anthropology.

Andrew Kramer

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and recommend its acceptance:

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and Dean of the Graduate School

A Morphometric Analysis of the Hominid Iliac Crest

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Presented for the
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Degree
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Amy Ridler Shook

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DEDICATION

This thesis is dedicated to the memory of Mrs. Alice Ridler Struse and to my parents Mr. and Mrs. Henry Aden Shook for their boundless love and support in the face of my relentless independence. Thanks!

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ABSTRACT

Variations in hominoid pelvic morphology reflect modifications in the evolution of ape and human locomotion. Numerous studies have addressed the evolutionary significance of changes in the ilium from pongid to hominid. Of considerable interest has been the orientation and degree of lateral flare in the ilia and its role in bipedalism.

The iliac crest forms a distinctive S-shaped curve in modern humans reflecting biomechanical demands of bipedalism. The degree of curvature is greatly reduced in apes while early fossil hominids display a condition that is neither identical to apes nor to humans. Traditional morphometric analyses of evolutionary trends in iliac shape have had limited success because they have not succeeded in quantifying the entire form. In contrast, this thesis discusses the use of the convex hull as a methodology that more completely accounts for variation in the form of the hominoid iliac crest. In applying this methodology, this study has quantified the shape differences in the iliac crest between living pongids and hominids and applied these differences to fossil hominids in the attempt to identify evolutionary trends in development.

Photographic and video captured images of the superior aspect of the iliac crest are digitized for samples of 45 *Pan*, 12 *Gorilla*, casts of 4 fossil hominids (Sts 14, A.L. 288-1, KNM-WT 15000,and Kebara 2) and 43 modern humans. An additional image of the fossil KNM-ER 3228 was obtained through the generosity of Dr. Alan Walker of Johns Hopkins University. The images are first smoothed by Elliptical Fourier Analysis and then undergo shape analysis by constructing a convex hull (CH). Vertices of the CH are determined using a polygonal edge approximation and the resulting concavities reflect the magnitude and number of curvatures in the iliac crest. The vertices of the CH are then used to determine shape differences by three statistical applications; MANOVA, Posterior probability, and Tukey's Studentized Range Test.

Results indicate that differences in the shape of the iliac crest can be repeatedly quantified. Further significant differences exist between the iliac crest of hominids and pongids. Fossil hominids exhibit varying degrees of shape differences when compared to living groups. Evolutionary trends of development in the iliac crest can be hypothesized from the results.

Bipedalism of early hominids, as suggested by bony anatomy, indicates a form of locomotion similar to, but somewhat different from, modern humans. The CH is used here to quantify the shape differences among hominoid iliac crests in order to test the hypothesis that australopithecines represented an intermediate morphology through which later hominids evolved.

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CHAPTER 1

INTRODUCTION

Bipedal locomotion is regarded by many as the evolutionary hallmark of hominids. Human bipedalism is well defined, but the evolutionary pathway leading to this type of locomotion is unclear. Over time, numerous skeletal changes occurred that have been influenced by factors other than bipedalism such as parturition, encephalization, and body weight support. The discussion of the evolution of pelvic formation relies on data from a small number of fossils. To date, only two genera are known to have evolved habitual bipedalism, *Australopithecus* and *Homo*.

Biomechanical analysis has sought to determine the similarities and differences between these genera. Studies have addressed the multiplicity of factors in the development of bipedalism and the changes in structure and form of the pelvis. Early studies relied on measurement and observation resulting in univariate analyses but these studies could not synthesize the complex combination of features found in bipedalism. Multivariate studies have increased the available information and have maximized the ability to determine functional capabilities of often fragmentary fossil hominids and their relationship to the modern human pelvis.

This study focuses on the ilium, and in particular the development of the iliac crest and its relation to overall pelvic form. While certain observations have been made on the crest, quantification of the sigmoid or S-curve has not previously been undertaken. Through new morphometric techniques evolutionary changes in the iliac curve can be quantified to yield new information. The importance of this study lies in its contribution to our understanding of the function of the iliac crest with respect to the biomechanical efficiency of hominid bipedalism.

PONGID AND HOMINID: ILIAC FORM AND BIPEDALISM

Certain anatomical modifications have occurred in the pelvis from the quadrupedal tree dweller to the bipedal ground dweller. In order to address these modifications, a review of the anatomical and functional aspects of bipedal locomotion is necessary. The following discussion will address the differences between ape and human iliac morphology and the implications for locomotion.

Upright Posture

Upright posture is required for habitual bipedalism which places the center of gravity over two feet, a small supporting space (Figure 1). In humans, the center of gravity lies on a vector anterior to the second vertebra bisecting the mastoid process and temporalis muscle, anterior to the shoulder joints

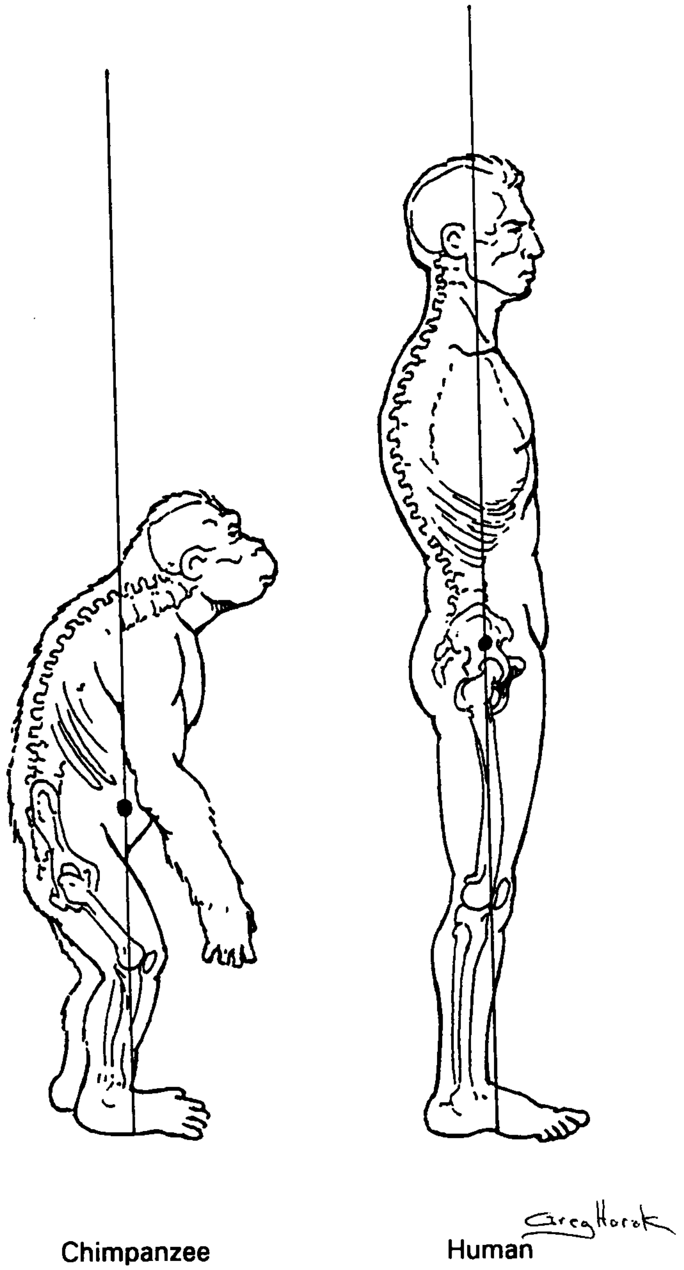

Figure 1. Chimpanzee and human bipedal posture. Vertical line denotes the center of gravity. The chimpanzee's center of gravity lies far forward of the pelvic girdle causing it to bend its knees for stability. The human center of gravity lies on top of the pelvis, creating stability on two feet. Adapted from Zilhman and Brunkner (1979) Hominid bipedalism: Then and now. Yrbk. Phys. Anthropol. 22:132-162.

running behind the hip joints and slightly in front of the knee and ankle joints (Aiello and Dean, 1990). When a chimpanzee walks bipedally, its center of gravity lies halfway between the pectoral and pelvic girdles close to the ventral wall. There is continuous activity in the hamstrings, quadriceps femoris and the gluteal muscles because the knee is constantly bent. Such activity is anatomically inefficient and can only be continued for a short time. In contrast, human locomotion is very efficient and requires low energy expenditures (Okada et al., 1976; Inman et al., 1981).

Bipedal Locomotion

The mechanics of bipedal locomotion are well documented and have been divided into a cycle. A complete walking cycle is from one heel strike to another by the same foot. The stance phase comprises 60%, while the swing phase the remaining 40% (Napier, 1967). Saunders et al. (1953) divide the components of bipedalism into three factors: center of gravity, gait, and energy expenditure.

In bipedalism, an upward and downward displacement of the body or the displacement of the center of gravity in the vertical plane occurs. A correlated displacement also occurs laterally in the horizontal plane which is visible as a sinusoidal curve. In the translation of the center of gravity, the human body conserves energy by creating a low amplitude, which is not fully developed until around seven years of age. An infant who is first learning to walk is very unstable. Children rely on abducted hips and arms to help support and balance the body by creating a larger base on which to stand. Swing and stance phases are very short and most of the limb muscles are continuously active creating an inefficient system (Suzuki, 1985). In contrast, adult humans use close to the "theoretical optimum" when walking and are more energy efficient than an adult quadruped such as a dog at the same speed (Alexander, 1980).

Analysis of human gait reveals six determinants: three of which flatten the arc of the center of gravity, two the pathway of the center of gravity, and one corrects the lateral displacement of the hip (Saunders et al., 1953). First, pelvic rotation occurs at the hip joint during stance phase both internally and externally; second, the pelvis tilts downward in relation to the horizontal plane on the side opposite the weight bearing leg; third, the knee flexes in the stance phase in a double knee lock to aid in flattening the arc. The fourth and fifth determine smooth arc progressions through certain actions of the foot and knee to create a fluid motion instead of a jerking one. The sixth determinant is lateral displacement of the hip which is held to a minimum by the tibiofemoral angle and hip abduction. Such control is an important factor in bipedal locomotion, and as Robinson et al. (1972) point out, control of lateral balance is the direct result of the re-orientation of the iliac blades.

According to Leutenegger (1974) the key to understanding human locomotion is to recognize that successful bipedalism relies on minimizing the distance between the sacroiliac and hip joints. Certain modifications have occurred in the bipedal pelvis particularly in the ilium to hold this distance to a minimum.

Iliac Morphology

In general, the human pelvis (Figure 2) is shorter, broader, and "three dimensional" while the ape's is long, narrow, and "two dimensional" (Leutenegger, 1974). Variations in these forms create differences in function. Differences in shape are dependent upon weight bearing through the hip from "forces produced by the pull of the principle muscle blocks attached to the pelvic girdle" in particular, those forces acting on the ilia (Ashton, 1981:79).

The ape and human ilium both have three surfaces and three crests but not all have the same orientation. The gluteal surface, iliac fossa, auricular surface and iliac crest have a common orientation across species. The acetabular margin is anterior in humans but lateral in apes while the sacral margin is posterior in humans and medial in apes. The human ilium is triangular in shape, wider than it is high, which successfully brings the sacroiliac joint closer to the hip joint.

The human ilium is orientated with a convex gluteal surface and a concave iliac fossa which creates an S-shaped curve at the crest (Figure 3). The S-shaped curve is formed anteriorly by the iliac tuberosity, which is long and directed posteriorly. It is the attachment site of the sacroiliac ligaments. The upper bend is the spina limitans which marks the transition between the iliac fossa and the iliac tuberosity. The anterior curve is marked by the iliac tubercle a bony buttress on the dorsal iliac surface, which lies at the proximal end of the iliac pillar.

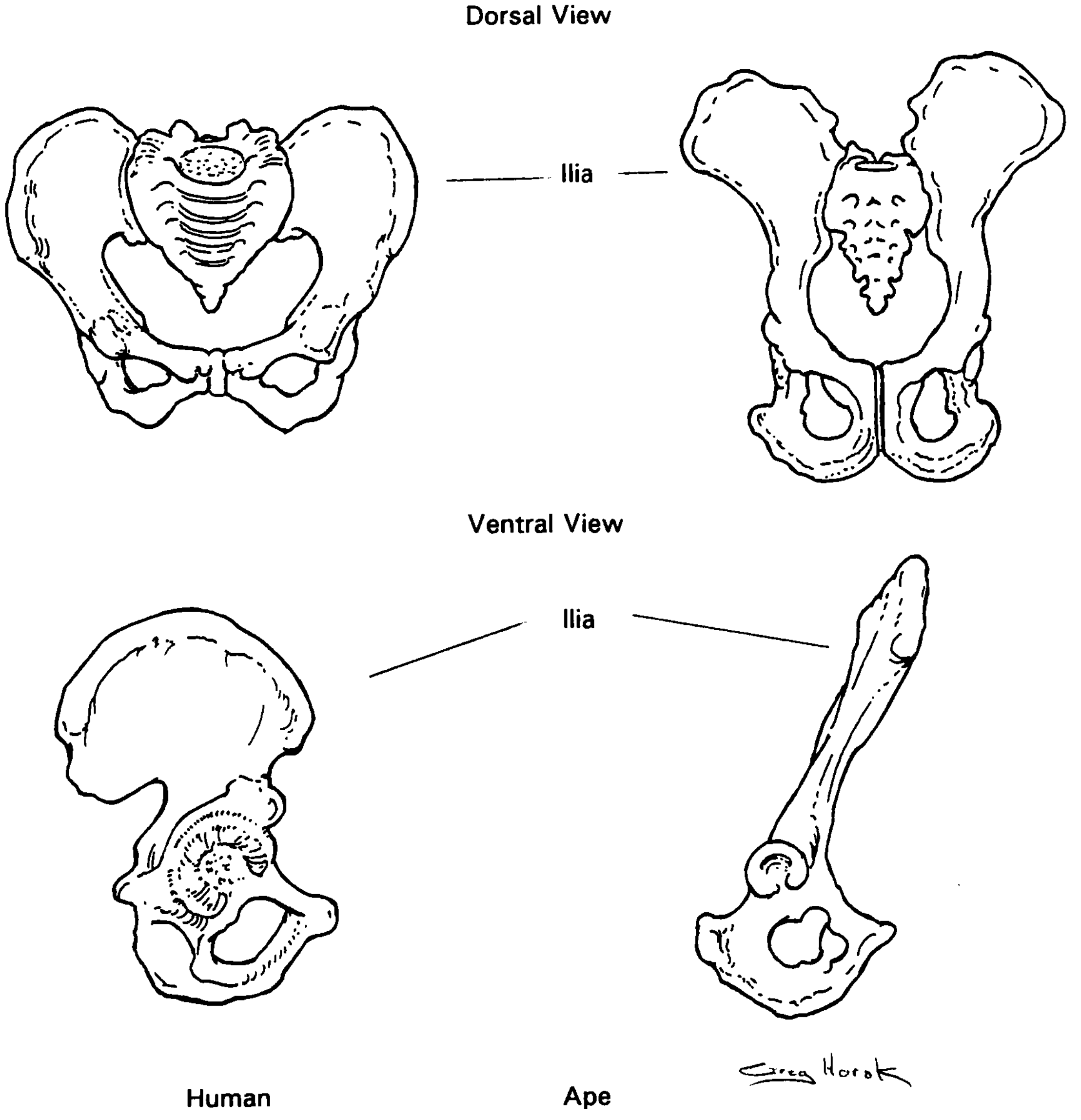

Figure 2. The ventral and dorsal views of the pelvis of a human (left) and an ape (right). The human pelvis is shorter and broader while the ape's is longer and more narrow.

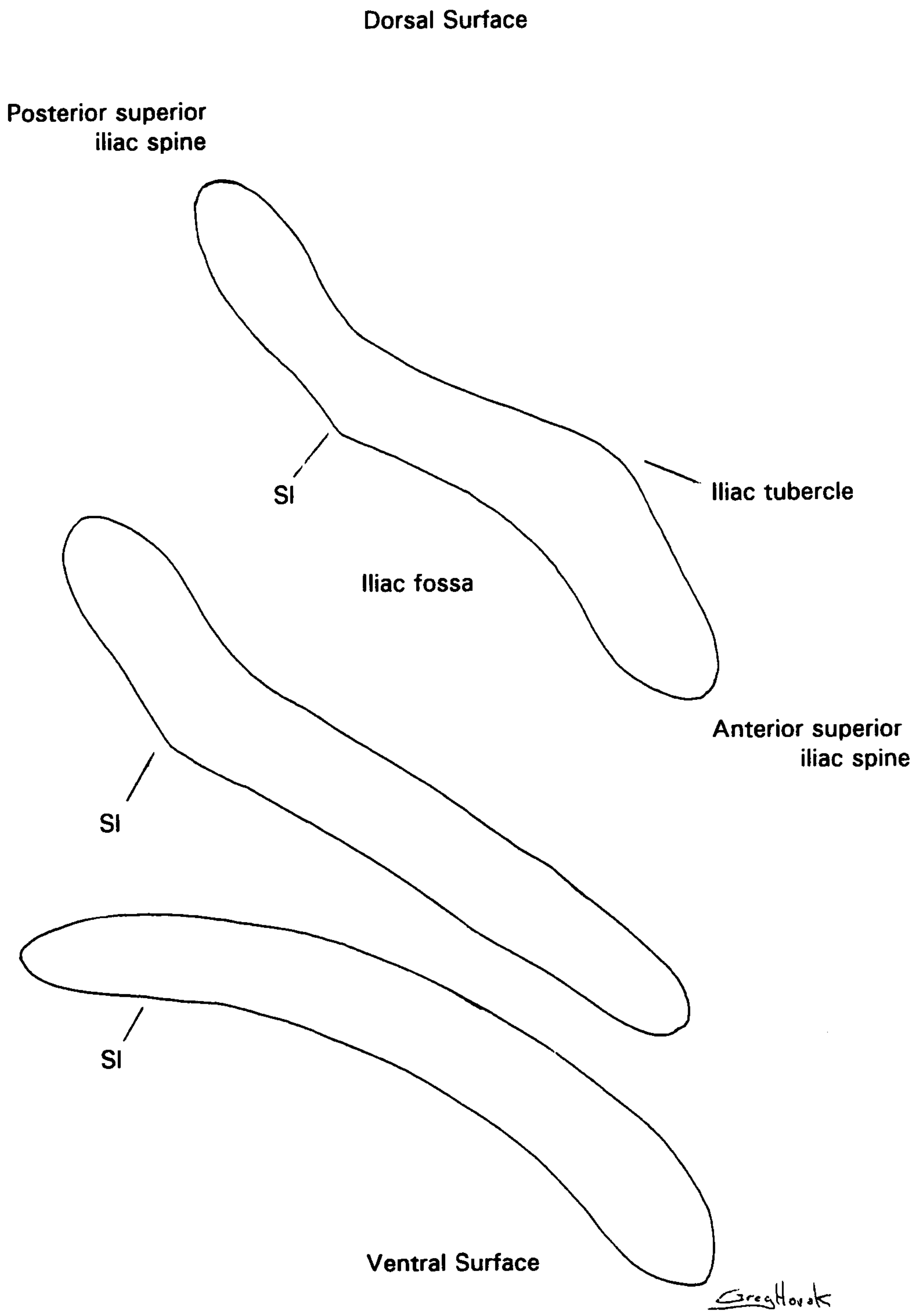

Figure 3. The superior view of the left iliac crest from a human (top), chimpanzee (middle) and gorilla (bottom). The ventral surface is facing downward. The human exhibits a double S-shape curve while the apes exhibit only a single curve. SI denotes spina limitans.

In general, the ape ilia are narrow and lie in almost the same plane as the back. Gorillas vary slightly from chimpanzees, having a wider anterior portion and a medialward curve. Muscular associations are the same between gorillas and chimpanzees (Robinson et al., 1972). The ape iliac crest lacks the S-shape and projects laterally from the midplane. The iliac tuberosity is greatly reduced and the iliac fossa and gluteal plane are in different orientation in order to support the quadrupedal trunk.

The S-shaped curve is the result of muscular demands placed on the crest during bipedal locomotion. Reynolds (1931) noted that the lateral expansion of the iliac crest places the abdominals in a position relative to the trunk in order to control lateral balance. According to Zuckerman et al. (1973) the primate pelvis is constructed along an overall mammalian pattern and the pelvis is affected by five main groups of muscles: the caudal extension of the erector spinae and abdominals which both insert on the iliac crest; the flexors which originate on the ventral surface of the ilium, the abductors which originate on the dorsal surface; and the hip stabilizers which originate at the acetabulum. While these muscular functions are important, the key differences among the hominoids lie in the functions of the gluteals.

Numerous researchers have noted the differences in form and function of the hominoid gluteals (Saunders et al.,1953; Mednick, 1955; Chopra, 1962; Napier, 1967; Zilhman, 1969; Robinson et al, 1972; Stern, 1972; Zuckerman et al., 1973; Sigmon, 1975; Zilhman and Brunker, 1979; Ashton et al.,1981;

Lovejoy, 1988). An alteration of muscle group function occurs in the gluteals from quadrupeds to bipeds. The following comparison of ape and human musculature will serve to illustrate these differences.

The gluteus maximus has a minor function in the ape pelvic musculature. The muscle is divided into two parts, the superior portion or the gluteus maximus proprius and the ischiofemoralis, the larger lower portion. The two act primarily as abductors and lateral rotators. The human gl. maximus is a single portion and is the largest muscle in the entire human body. It arises from the dorsal portion of the iliac crest, sacrum and coccyx and inserts into the iliotibial tract. During normal walking, gl. maximus helps to extend the thigh, a relatively minor activity. When the upper body is active especially during running, the gl. maximus is very active and helps stabilize the trunk and to keep the upper body from falling forward (Marzke et al., 1988). This stabilization is facilitated by the re-orientation of the iliac blades (Lovejoy, 1988).

In African apes, the lesser gluteals are the largest muscles and perform a much greater role. They function as extensors and are the main propulsive muscles. As noted above, humans have little need for extension in bipedalism. Instead they rely on the lesser gluteals for abduction which aids the unsupported leg during the walking cycle. The gl. medius and gl. minimus originate on the dorsal aspect of the human ilium and attach to the greater trochanter of the femur. The mediolaterally orientated ilia place the muscles in the proper position for abduction.

Numerous factors contribute to variation in pelvic morphology such as parturition, encephalization and weight support, as well as locomotion. The focus of this study relates only to the mechanical variations caused by bipedalism. Fossil hominids are not separated from one another by their bipedal mode of locomotion but rather the degree to which it was practiced. Most agree that early hominids practiced some type of bipedalism. The affect of their form of locomotion should be reflected in the pelvic structure. Modern bipeds and quadrupeds have distinct iliac morphology, directly related to their locomotion. Distinctions among fossil hominids are not as easily understood. The following section reviews major research concerning the function of the ilia in bipedal locomotion for various fossil hominids.

CHAPTER 2

LITERATURE REVIEW

> Man and man alone, is able to spring in any direction from a bipedal position, and, moreover, he alights from such a spring with a certainty of balance which enables him to repeat it in the same or different direction. (Reynolds, 1931:310).

Edward Reynolds' early study of the evolution of erect posture set the standard to which fossil hominids would be compared concerning bipedality. While his premise is not directly testable, by studying fossil morphology, many have attempted to expand Reynolds' conclusions on human's exclusive bipedal abilities. Differing camps exist concerning hominid bipedalism. The first suggests that early hominids had a form of bipedalism like modern humans (Dart, 1949b, 1957; Sigmon, 1971; Robinson et al., 1972; McHenry, 1975; Preuschoft, 1978; Berge, 1984; Rose, 1984; Hager, 1991). A second suggests that while bipedal, the type of bipedalism practiced was more ape-like (Mednick, 1955; Chopra, 1962; Napier, 1964, 1967; Zilhman and Hunter, 1972; Stern, 1972; Day, 1973; Oxnard, 1973, 1975; Zuckerman et al., 1973; Ashton et al., 1981; Stern and Susman, 1983). A third theory states that australopithecines had a hyper-developed hip morphology, that was even more efficient than modern humans (Lovejoy, 1973; Lovejoy et al.,1973; Lovejoy, 1975).

These studies fall into one of three methodological categories. The first is pure observation of the presence or absence of characteristics. Second, is univariate and bivariate quantifications. Third is multivariate analyses (Oxnard, 1973). Multivariate techniques were not widely applied until the 1970's. None, to date, have quantified the S-shape curve of the human ilium and compared it to fossil hominids which is the goal of this study. Approaches have utilized chimpanzee and other African apes as models of the hominoid common ancestor and precursor to australopithecines to conclude that early fossils are either more like humans, more like chimpanzees or completely unique. This section will review previous studies on hominid fossil pelvic morphology (Table 1).

The first australopithecine postcranial evidence was discovered in 1938 by Broom, a distal femur, TM 1513 (Broom and Schepers, 1946). During the 1940's, the first pelvic evidence was added, Sts 14, MLD 7 & 8, and SK 50 (Dart, 1949a, 1957; Broom and Robinson, 1950). Vrba's 1970 discovery of SK 3155 resulted in the first well preserved robust australopithecine pelvic evidence helping to substantiate efficient bipedalism for robust forms (Brain et al., 1974; McHenry, 1975). The discovery of A.L. 288-1 ("Lucy") has provided by far the best evidence of australopithecine pelvic anatomy available at this time (Johanson and Taieb, 1976). Of these specimens, A.L. 288-1 and Sts 14 are in the best condition and most often referred to in discussions on the origin of bipedalism.

TABLE 1. FOSSIL DISCOVERIES

SPECIMEN	SKELETAL ELEMENT	DISCOVERY	TAXON	LOCATION
TM 1513	Femur	1938	*Australopithecus africanus*	Sterkfontein, South Africa
Sts 14	Pelvis	1947	*A. africanus*	Sterkfontein, South Africa
MLD 7 MLD 8	Right ilium Ischium	1948	*A. africanus*	Makapansgat, South Africa
SK 50	Right ilium	1949	*Australopithecus robustus*	Swartkrans, South Africa
SK 3155	Right pelvis	1970	*A. robustus*	Swartkrans, South Africa
AL 288-1	Partial skeleton	1974	*Australopithecus afarensis*	Hadar, Ethiopia
OH 28	Femur & pelvis	1970	*Homo erectus*	Olduvai Gorge, Tanzania
Arago 44	Pelvis	1976	*H. erectus*	Arago, France
KNM-ER 3228	Pelvis	1976	*H. erectus*	East Turkana, Kenya
KNM-WT 15000	Partial skeleton	1984	*H. erectus*	West Turkana, Kenya
Kebara 2	Pelvis	1986	*Homo sapiens neanderthalensis*	Mt. Carmel, Israel

The majority of investigations which followed discovery addressed the efficiency of the type of bipedalism practiced and whether it mimicked human form. Information drawn from related fields such as anatomy and prosthetic research, was utilized to determine levels of effective bipedalism (Inman, 1947; Saunders et al., 1953; Elftman, 1954). For example, Elftman (1954) noted that the key to the function of the bipedal hip is the control of lateral stability. In fully modern humans, the development of the iliac tubercle and pillar indicates a mechanism for such control. These landmarks are related to the origin of the lesser gluteals which abduct the hip and medially rotate the thigh during bipedalism. The earliest fossil descriptions noted these affinities.

In his discussions of the "*Australopithecus prometheus*"[1] pelvis (MLD 7 and 8), Dart (1949a,b, 1957) concluded that the australopithecine ilia were similar to humans with a short and wide blade, a bent blade with a double concavity, anterior superior and inferior iliac spines and an iliac crest with two curves unlike the chimpanzee's which is short and straight (Dart, 1949b, 1957). He further noted that the hip region was designed to rotate the trunk upon a fixed thigh.

In his 1950 publication, Washburn states that "The origin of primates was primarily a locomotor adaptation" meaning that evolution was propelled by locomotor adaptations (1950:68). In hominoids, evolution was directed by the

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[1] "*Australopithecus prometheus*" is Dart's nomen MLD 7 & 8 (Makapansgat Limeworks Deposit) in 1948. This taxon was subsequently subsumed under *Australopithecus africanus*.

development of the gluteus maximus as an extensor. He states that the differences between apes and humans lie in the pelvis and foot and noted that the human ilium is short and broad and that it differs in certain details such as iliac crest shape. In his opinion, this would in turn affect function as "it is not the extent of the motion which is different but the ability to finish with a real drive" (Washburn, 1950:71). His results indicate that the ilium is acted upon mainly by the gluteus maximus and in the "man-ape" (*Australopithecus*) it is impossible to reconstruct the muscle as anything but an extensor.

> I think that we have every reason to believe that this [efficiency for plains dwelling] was fully achieved by the South African man-apes... it [the pelvis] is so human in form that some have argued that it must belong to an early hominid which became mixed in man-ape deposits.P.71

From observations of split-line patterns of bone thickness, Mednick (1955) offered an evolutionary sequence of pelvic structural development: a widening, bending back and shortening of the ilium; structural development of the iliac tubercle; shortening of the ischium and modification of the ischial tuberosity. Noting a single curve in the iliac crest and lack of a strong iliac tubercle and bony pillar, she concluded that australopithecines might represent a stage of bipedalism that either ceased to exist or developed into later humans (Mednick, 1955).

Chopra's 1962 study was a re-examination of Le Gros Clark's work (1955a, 1955b, as cited in Chopra, 1962) in which he expressed

> the belief that, while bipedal, the Australopithecines had not developed the erect posture to the degree of perfection found in modern man.P.94

Using Sts 14, MLD 7, humans and apes, he measured the angle between the iliac and ischial planes. His conclusions concurred with Mednick (1955) that the degree of backward rotation of the ilium was sufficient for erect posture but that the torsion of the plane suggested the musculature was "monkey-like as it was human in its disposition" (Chopra, 1962:101). Osteologically, the muscles were in a hominid orientation but their function was more monkey-like.

Napier (1964) was one of the first to investigate the difference between "*Paranthropus*" and *Australopithecus*. His conclusions indicated that the gracile form (*Australopithecus*) was more human-like,

> the robust type lacked the ability to transfer its body weight from foot to foot during walking...The gait of robust form suggested by these studies is probably best described as waddling.P.696

Neither form had all the characteristic of the human ilia, but Napier attributes the lack of an iliac tubercle and pillar in Sts 14 to its diminutive stature and light body weight. In a later study, Napier (1967) concludes that the form of bipedalism practiced in humans cannot be seen in the fossil record until at least 1 Ma (million years ago) .

In 1970 a new femoral shaft and pelvic fragment (OH 28) were found at Olduvai Gorge, Tanzania, by Mary Leakey. Day (1971) described the incomplete and slightly distorted ilia as: projected laterally, having a robust iliac pillar, prominent muscular attachments, an S-shaped iliac crest set wide to the acetabular plane, a distinct anterior inferior iliac spine, and a visible separation for the attachments of the gluteal muscles. Functionally, this pelvic fragment represented a hominid with a combination of features previously unknown, but indicative of a habitual upright biped. The muscle attachments indicated a well developed striding gait, weight which was successfully transferred through the pelvis from the trunk, and a center of gravity behind the line of pelvic rotation. He concludes that OH 28 closely resembles *Homo erectus*.

During the 1970s, functional analyses of living primates were performed to obtain quantitative data to better understand the evolution of hominid bipedalism. Based on myology and myography, Stern (1972) suggested that in humans the abductor function of the anterior portion of the gluteus maximus is key to pelvic development. Observations were made on dissections of 84 non-human primates and 40 human cadavers. Only in humans does the gluteus maximus have a strong attachment to the ilium and only in humans is the anterior portion much thicker. Stern's functional analysis is as follows: when weight falls on one leg from a height as during running, the trunk is flexed over the femur. It is the anterior portion of the gluteus maximus which keeps the trunk from falling forward. He concluded that this kind of specialization is more advanced on the Makapansgat ilium than in Sts 14 (Stern, 1972).

Oxnard (1973) applied multivariate techniques to handle large morphometric data sets or data which were too difficult to extrapolate by the human eye. He first superimposed Sts 14 on extant primate forms, to look at the unknown. Using canonical analysis he showed that factors relating to muscle functions of Sts 14 resembled apes while joint surfaces resembled humans. Second, he suggested use of median axis transforms to resolve the problems of overall pattern recognition. Transforms represent the shape in a simplified form which is easier to manipulate than the shape itself.

In a following study, Oxnard (1975) utilized multivariate analysis to help provide background on how primate genera separated according to function and structure. He metrically defined osteological features associated with muscles and joints of australopithecine and extant primate postcrania. Using canonical and general distance analyses he concluded that the human hip was unique. The twist in the iliac blade brought the lesser glutei into a different alignment than in either the fossils or other primates (Oxnard, 1975).

Zuckerman et al. (1973) analyzed 430 extant primates and the australopithecine Sts 14 using a character analysis for weight transfer and muscle pull in the pelvis. The characters were then submitted to univariate, bivariate, (analysis of variance and regression) and multivariate (Mahalanobis and canonical variance) techniques. Four osteometric points and two dimensions related directly to the iliac crest, though none quantified the S-curve. Conclusions state that australopithecines had an overall complex of features which occupied a unique position, distinct from man and all non-human primates, though more similar to humans (Zuckerman, et al., 1973).

With the discovery of SK 3155, attention returned to the morphology of the robust australopithecines (Brain, 1973; Brain et al, 1974). McHenry (1975) found that SK 3155 had the ability to extend and abduct the hip as do modern humans. His conclusions were drawn from calculations of the theoretical force of body weight on both muscle masses. The efficiency of the lesser gluteals is attributed to the lateral flare of the ilia which places the muscles in a position to stabilize the hip in a one-legged stance. Contrary to Napier (1964), he concluded that australopithecines, both robust and gracile were adapted for lateral balance control similar to that of *Homo* (McHenry, 1975).

Lovejoy performed a biomechanical analysis of the australopithecine gait to determine "the degree to which the locomotor adaptations of the *Australopithecus* are like those of modern man" (Lovejoy, 1973:147). He divided bipedal stride into three components; trunk progression, trunk support, and limb progression. Of these, trunk support was the most distinctive. Using Sts 14 and MLD 7, he concluded that "this extinct biped might have been superior to modern man" (Lovejoy, 1973:151). The capacity of the lesser gluteals to internally rotate the pelvis over the thigh, was sufficient in australopithecines because the laterally flaring ilia placed the attachments laterally as well.

In a review study, Lovejoy (1975) illustrated that differences in characters of the australopithecine ilia, ie. greater iliac flare, more protuberant anterior superior iliac spine, and a more anterior iliac pillar function efficiently for gait which fall within human ranges (Lovejoy, 1975). He challenges the notion that human bipedalism is regarded as a "locomotor pinnacle" (Lovejoy, 1975:323). He states that this is only the consequence of the ability to perform three elements of bipedalism and the adaptations necessary are present in both *H. sapiens* and *Australopithecus*.

Steudel (1978), using similar statistical methods to Zuckerman et al. (1973) and Oxnard (1975) tested a different set of variables to address pelvic structure and locomotion in early hominids. Eight measurements were taken on the pelves of 568 primates and compared to the fossils OH 28, Sts 14, and SK 3155. First a univariate analysis was performed to determine which variables varied significantly enough to produce discrimination. Then a canonical analysis was applied to allow for discrimination between species. A Pythagorean distance was also calculated between the centroid of each group and equivalent to Mahalanobis D^2 statistic.

The results disagreed with those of Zuckerman et al. (1973) and Oxnard (1975) who both concluded that the australopithecine gait occupies a unique position between apes and humans. Rather, Steudel states that the differences between the anterior portion of the iliac blade do not affect bipedalism and only represent morphological variations (Steudel, 1978).

Preuschoft (1978) suggested that a combination of biomechanical and statistical methodologies should be utilized to determine functional differences among fossil hominids concerning bipedalism. He points to methodological errors by Lovejoy et al. (1973) and Robinson et al. (1972), the latter particularly for drawing conclusions concerning the pelvis without providing evidence. His criticisms indicate caution when applying new methodology. Biomechanical methods should address those traits which are biomechanically adaptive to behavior, while statistical approaches should be mechanically meaningful from a functional point of view.

Zuckerman et al. (1973) attempted to determine if it was possible to quantify morphological features related to biomechanics. Ashton et al. (1981) intended to clarify and expand on that earlier study. They utilized 422 extant primates, as well as 5 different reconstructions of Sts 14 and Skhul IV. The character analysis was expanded from 17 to 25. Five osteometric points were defined on the iliac crest, though again none quantified the shape of the S-curve.

Ashton et al. (1981) utilized both univariate (analysis of variance and t-test) and multivariate (Mahalanobis general distance and cluster analysis) methods. The results placed Skhul IV within modern human variation. Two dimensions placed australopithecines in a unique rather than an intermediate position. These were the disposition of the sacro-iliac and hip joint, and the orientation of the iliac blade. They concluded that Sts 14 "may have been facultatively bipedal" (Ashton et al., 1981:94).

Sigmon (1982) conducted a study of locomotor morphology based on the incomplete innominate of Arago 44 to determine its placement in human evolution. A visual inspection of character traits indicated a prominent acetabulo-cristal buttress or iliac pillar, a well developed anterior iliac spine and a more forward and medialward deflection of the anterior portion of the blade. She did make a visual inspection and comparison of the S-curve stating that

> The sigmoid curvature of the iliac crests reflects this pattern in that the most anterior part of the curvature is located more forward and the medial deflection is more marked than is found in modern *Homo sapiens*.P.432

This would indicate a different pattern than that found in *Homo erectus* and *Homo sapiens*.

Metrical analysis confirmed these observations. Measurements of iliac height, thickness, and iliac crest length were taken. Arago 44 fell within modern human variation. In conclusion, she proposed a five stage progression of pelvic morphology: "*Paranthropus*" and "*Homo (Australopithecus) africanus*"; early *Homo erectus* represented by SK 3155; *Homo erectus* represented by OH 28 and Arago 44; *Homo sapiens neanderthalensis*; and modern *Homo sapiens.*

Stern and Susman (1983) addressed two questions concerning locomotion in *Australopithecus afarensis* by analyzing the postcranial remains. First, does the anatomy indicate other forms of locomotion than bipedalism and second, was the form of bipedalism practiced different from that of modern humans? The iliac data focused on AL 288-1. They observed the orientation of the iliac blade by "looking directly downward onto the surface of the iliac crest" (Stern and Susman, 1983:292). Observation revealed that the blade faced more posteriorly than laterally, indicating a more ape-like functional complex. The small iliac pillar was attributed to weakly functioning abductors.

> The lesser gluteal muscles effected stabilization of the pelvis on the femoral head by virtue of their ability to act as medial rotators on a flexed thigh rather than as abductors on an extended thigh.P.292

Rose (1984) examined the specimen KNM-ER 3228 discovered in Koobi Fora in 1976 (Leakey, 1976). Observations indicated a more laterally angulated ilium, an anteroposteriorly elongated iliac crest, a well developed iliac tubercle, and a marked sigmoid curve. A strong acetabulo-cristal buttress indicated a well developed mechanism for pelvic tilt. Based on comparative measurements, he suggested similarities to both OH 28 and Arago 44. Four of the 13 measurements were collected on the ilia including, anterior superior to posterior superior iliac spine length maximum and minimum iliac width and iliac height. All but the crest length of Arago 44 fell within the human range. Overall, he indicated that *Homo erectus* as represented by OH 28, Arago 44 and KNM-ER 3228 was "similar to *Homo sapiens* based on similar pelvic morphology" however, "There is a clear difference between these specimens and australopithecine material" (Rose, 1984:376).

A systematic study of the position of hominids was undertaken by Berge (1984) using 367 catarrhine, 44 modern humans, five australopithecines (AL 288, MLD 7, SK 50, SK 3155, Sts 14), and one *Homo erectus* (OH 28). A factor analysis of the functional components of the innominate was done. Of the 11 total, 7 measurements were taken on the ilia, two on the iliac crest.

Results showed that gracile's specializations were the same as those in *Homo erectus* and *Homo sapiens* while the robust specimens were spatially differentiated. Results indicate that morphological differences exist and are common between gracile and robust specimens. In the ilium, the blade is orientated laterally as is the iliac pillar, and the iliac spine is beaked and thickened. Functionally, the australopithecines are as bipedal as *Homo sapiens* but the type of bipedalism practiced is different. Berge concludes that the australopithecines had only a limited ability to bear weight and balance at the hip and that the gracile specimens are less advanced than the robusts in this function .

Brown et al.'s, (1985) announcement of an immature male *Homo erectus* has greatly increased the understanding of early hominid pelvic morphology. They noted that the specimen, KNM-WT 15000 is similar to OH 28, and KNM-ER 3228 but lacked the strongly developed iliac pillar. The species did maintain a substantial lateral iliac flare which, along with a long femoral neck, enhanced the biomechanical function of the abductors relative to modern humans.

In 1986, the first virtually complete Neandertal pelvis was found in Kebara Cave, on Mt. Carmel, Israel (Bar-Yosef et al., 1986). This specimen (Kebara 2) does not differ greatly from modern *Homo sapiens*, but features of the ilium do (Rak and Arensburg, 1987). The iliac pillar and iliac tubercle are very robust, the anterior superior iliac spine projects anteriorly, and the position of the ilia is different. In modern humans, the anterior portion of the ilium ascends in a straight line while in the Kebara specimen, it flares out over the body. The authors attribute the differences between Kebara 2 and modern humans to factors of locomotion and posture, not obstetrics and body weight as suggested by Trinkaus (1984) and Rosenberg (1986).

Marzke et al. (1988) corroborated the findings of Stern (1972) and Stern et al. (1980). They stated that the size and attachments of the cranial portion of the gluteus maximus are related to the requirements of trunk control during activities involving "major shifts in the center of gravity" (Marzke et. al., 1988:527). They utilized the electromyographs of the gluteus maximus in 6 adults to investigate the actions of normal walking, throwing, clubbing, digging, lifting and gathering from below the waist line. Three individuals showed minimal action during walking. All showed moderate to large action when the trunk moved over fixed legs. Conclusions indicate that early hominids such as AL 288-1, had the potential for these activities based on proportions of the attachments of gluteus maximus on the ilium.

Rak (1991) investigated the role of the pelvic anatomy in bipedal gait in AL 288-1. He noted that the pelvis is extremely wide bilaterally, not anteroposteriorly as in modern humans. Such dimensions would be biomechanically inefficient if it were not for the extreme lateral flare of the ilia. The lateral flare created a long lever arm for the abductors which stabilizes the hip when weight is born on one leg during stride. He indicates that the abductors were already functioning before the development of the lateral flare. In conclusion, Rak states that

> Lucy's pelvis does not represent simply an intermediate stage between a chimpanzee-like hominoid and *Homo sapiens*, nor is it essentially a modern pelvis. Although clearly bipedal and highly terrestrial, Lucy evidently achieved this mode of locomotion through a solution all her own. p.289

Such conclusions suggest that AL 288-1 may not be related to later modern humans.

To summarize, the amount of research dedicated to the origins of bipedal locomotion is extensive. Results and conclusions are drawn from simple observations to extensive calculations aided by complex statistics. The function of the gluteal muscles and their effect on the pelvis are key to the development of modern human bipedalism as pelvic form dictates successful bipedalism. One of three conclusions is usually drawn concerning the origins of bipedalism; early hominids walked bipedally like humans, bipedally like chimpanzees, or in a unique way not utilized by extant primates. Most recently, the debate has centered on the degree to which early hominids walked like modern humans.

CHAPTER 3

METHODOLOGY

A BRIEF HISTORY OF MORPHOMETRIC TECHNIQUES

Morphometry is the study of biological shapes utilizing mathematical methods and has been applied to both skeletal and soft tissue samples. Traditional methodologies are dependent upon presumably homologous landmarks in order to quantify form, however non-landmark based techniques exist as well. The following will be a brief review of the development of morphometric techniques and their relevance to the current study.

Discrete Forms

Some of the earliest quantifications of skeletal change evolved from comparative anatomy studies by Karl Pearson and the Biometric Laboratory of University College in London in the early part of this century. He defined bony landmarks on cranial material and calculated linear, curvilinear and angular measurements. Ratios were then combined to yield simple measures of shape (Moore, 1985). This method had two major deficiencies according to Moore (1985). First the method did not describe shape change but measured differences in shape. Second, an assumption was made that points maintained ontogenetic and phylogenetic stability.

D'Arcy Thompson took a different approach. In his 1917 publication, *On Growth and Form*, Thompson discussed co-ordinate transformation grids and the analysis of related forms. A grid is fit over one form to produce Cartesian co-ordinate points. The grid is then distorted to fit the second form so that the axes pass through equivalent points. The principle behind this method is similar to a cartographer "who transfers data to one projection or another and whose object is to secure...a complete correspondence" (Thompson, 1969:272). One of his most recognized studies using coordinate transforms compared modern human, chimpanzee and baboon skulls. While setting the stage for later developments, this method too was limited because it did little more than give a pictorial map (Moore, 1985).

The first quantified transform grids were obtained with the aid of computers in the 1960s. Sneath (1967) adapted a method from geology called "trend-surface analysis" which analyzes trends in geological contour maps[2]. The benefit of this analysis is that it determines the major trends in shape and expresses them as coefficients of the best fitting power or goodness of fit. He analyzed cranial material from modern *Homo sapiens, "Pithecanthropus erectus,"* *Australopithecus africanus* and *Pan troglodytes* to determine taxonomic divergences. His results were reported as the trend coefficient which is calculated by taking the square root of the mean of the squared coefficients of the goodness of fit. Variation unaccounted for is called the residual; large

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[2] This method is more thoroughly described in Miller (1956).

residuals may represent local morphogenetic difference in a biological framework.

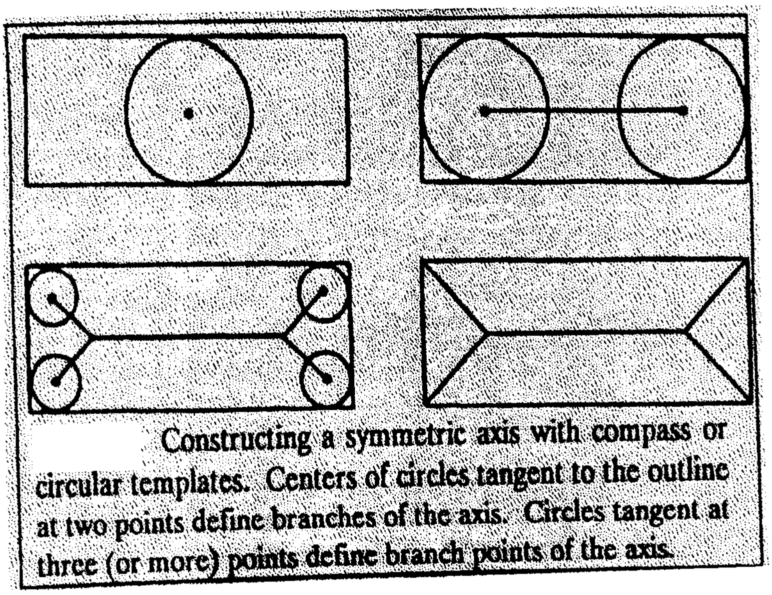
Blackith and Reyment (1971) and Reyment, Blackith and Campbell (1984) addressed the problem of morphometrics using a classical multivariate mathematical model. Their analyses depended upon distance calculations of homologous landmarks. They warn against two extremes, including:

> a tendency to accept all latent roots which are statistically significant as being of biological importance; at the other extreme, arbitrary rules are applied, irrespective of the sample size and the significance of the latent root. (Reyment et al., 1984:41)

With the introduction of biorthogonal grids, Bookstein (1992) and Bookstein et al. (1985) return to the Thompsonian approach. This method differs slightly in that it addresses shape change by representing shape transform between single forms and not simply shape differences. Biorthogonal grids have two axes which pass through each point at 90° angles to each other both before and after the transform. The curves tangent to these two axes can be joined to correspond to the change itself. In this way one can archive the form (Bookstein et al., 1985). The change is measured as dilatations which are ratios of the lengths of the grid segments.

Continuous Forms

While landmark based methodologies yield valuable information they are limited to discrete forms with identifiable homologous landmarks. Non-landmark or continuous form analysis began in the 1960s and is the focus of this research. Working in the area of speech and visual perception, Blum (1967) developed the median axis method to address shape in continuous closed forms. A median axes (Figure 4) can be described as "geometric transformations of an outline that identify a branching set of points that constitute the middle of a form" (Straney, 1990:179). Each branch point is



Constructing a symmetric axis with compass or circular templates. Centers of circles tangent to the outline at two points define branches of the axis. Circles tangent at three (or more) points define branch points of the axis.

Figure 4. Construction of a median axis. Source: Straney DO (1990) Median axis methods in morphometrics. In: FJ Rohlf and FL Bookstein (eds.): Proceedings of the Michigan Morphometrics Workshop. Ann Arbor: The University of Michigan Museum of Zoology, pp.179-200.

related to three or more outline points. Unlike Thompson's approach, Blum's approach "suggests that the co-ordinate system be built on the curve and space explored from the curve" (1967:378). Oxnard (1973) utilized median axis transformation and multivariate analysis to compare casts of chimpanzees, modern humans including pygmy, and the fossil hominid ilium Sts 14 and found patterns easily and quickly understood. He noted that the study of evolutionary morphology is difficult because there is a relation between shape and function, in that "biological shapes exist within the limits of biological function" (Oxnard, 1973:19). In his conclusions, Oxnard stated that the ultimate goal in morphometric analysis would be to

> depart entirely from the necessity to define reference points upon curved bones for the purpose of measurements, then even more information about form and pattern might stand uncovered (1973:169).

Bookstein (1979) suggests that the branch points in the median axes could be treated as landmarks by applying an algorithm to produce what he calls a line skeleton. The line skeleton is a symmetric axis which produces an estimate of the original outline through the branching points. He tested an ontogenetic series of human mandibles and found a significant stability of homologous branch points. Such homology is necessary to conclude relationships between forms (Straney, 1990).

Fourier analysis is another methodology useful in analyzing continuous forms. J.B.J. Fourier (1768-1830) originally developed this method for use in physics and engineering but it has been utilized in various fields (Lestrel, 1974). In this methodology, outlines are first defined in terms of equiangular polar coordinates from a center point (Moore, 1985). The sine and cosine of the coordinates are used to produce the amplitude coefficients of the shape or the harmonics. If the coefficients are all zero then the shape is a circle, otherwise, the harmonics describe the variations in outlines. The method has been very accurate in analyzing complex irregular forms, however, it can have biological limitations. Lestrel (1982) showed that differences in lower harmonics can be related to differences in morphologies while higher harmonics account for differences in fine detail.

An alternative method for describing continuous forms is the convex hull (CH). A CH can be used as a preliminary shape descriptor by artificially constructing landmarks on forms which otherwise do not have them. The concavities in the shape are then easily determined by taking the difference between the CH and the original form. Green (1981) more intuitively describes the CH:

> if we envisage the data points as pins in a board: a large elastic band is looped around the pins and released. The band will come to rest forming a polygon: the pins it touches are the extremes (Green, 1981: 3).

Once the landmarks (pins) have been constructed, a variety of morphometric analyses can be applied to determine the morphological significance. Holcomb and Konigsberg (in prep) have utilized this method in their analysis of sex differences on the human fetal sciatic notch. They conclude that although there is significant fetal sexual dimorphism in the sciatic notch, the notch is not a reliable sex indicator in fetal specimens.

In summary, the development of morphometric techniques has mainly focused on the analyses of ontogenetic and morphological data. Both landmark forms and continuous forms can be addressed. This analysis applies convex hulls to the iliac crests of various hominoids to determine if similarity in shape exists among them. In a bone with few homologous landmarks this method could prove very effective. Some caution is necessary when one considers stresses which may affect the bone after maturity. Stresses such as malnutrition, use and dis-use, and re-modeling have been shown to occur in long bone and in the skull (Schmidt, 1984; Angel, 1982). Possible mechanical effects post-maturity warrant caution unless future studies reveal that the pelvis is unaffected.

MATERIALS AND METHODS

Images of the superior view of the iliac crest from 104 hominoids were used in this study (Tables 2 and 3), including: 45 *Pan troglodytes*, 12 *Gorilla gorilla*, and casts of 4 fossil hominids A.L. 288-1 (*Australopithecus afarensis*), Sts 14 (*A. africanus*), KNM-WT 15000 (*Homo erectus*) and Kebara 2 (*H. sapiens neanderthalensis*). These images were collected at the Cleveland Museum of Natural History and were photographed using a 35mm camera with a scale of 3cm. An additional image of the original fossil KNM-ER 3228 (early *Homo*) was obtained through the generosity of Dr. Alan Walker of Johns Hopkins University. Images of a sample of modern humans from the Frank H. McClung Museum of the University of Tennessee were obtained through video capture using IBM Audio Visual Connection (AVC) for the PS/2 (see Appendix A for images of sample). Fink (1987:70) described this process in detail and noted the advantages of consistency, speed and a reduced chance for error: "error limits are within those one gets when measuring specimens by hand."

TABLE 2. COMPARATIVE SAMPLE

TAXON	MALE	FEMALE	COLLECTION
Pan troglodytes	27	18	CMNH[1]
Gorilla gorilla	6	6	CMNH
Homo sapiens	21	21	McClung[2]

[1] *Pan* and *Gorilla* data collected by photography.

[2] Modern human data collected by video capture.

TABLE 3. FOSSIL SAMPLE[1]

SPECIMEN	TAXON	COLLECTION
A.L.288-1	*A.afarensis*	CMNH[2]
Sts 14	*A.africanus*	CMNH
KNM-WT 15000	*H.erectus*	CMNH
KNM-ER 3228	early *Homo*	NMK[3]
Kebara 2	*H. sapiens neanderthalensis*	CMNH

[1] All fossil data collected by photography.

[2] CMNH - Cleveland Museum of Natural History.

[3] NMK - National Museum of Kenya. Photographed by M.Rose, supplied by A. Walker.

The ape and fossil hominid photographs were hand-scanned using a Logitech Scanman model 256 at 200 DPI and recorded by Logitech Fototouch version 2.1. The x,y coordinates of the outlines were collected through digitization using Sigma Scan/Image version 1.0 by Jandel Scientific. Outlines of all images were digitized to actual scale. Images were rotated when necessary and orientated with the ventral edge down and medial edge to the right. Left ilia were reflected around the y-axis into right views. Outlines were smoothed using an elliptical fourier program (EFA), written by Rohlf (1990 Michigan Morphometrics Workshop).

A convex hull (CH) program written by Dr. Lyle W. Konigsberg is applied to the outlines using polygonal edge approximation after Batchelor (1980). The CH records concavities when vertices are not adjacent on the edge of the figure. These are called Bookstein's shape coordinates and for the iliac crest, six points were recorded (Figure 5). The outline is rotated and scaled so that point D is set to (0,0) and point A to (1,0). For each specimen, two concavities were isolated and recorded as vertices X1,Y1-X4,Y4 (Figure 5). Data was then submitted to multivariate statistical analysis in SAS.

A one way multiple analysis of variance (MANOVA) was run on the vertices of the CH for all 104 cases. This analysis tests for significant differences but does not indicate where or between which species the differences exist. Post-hoc tests were run to determine at which vertices differentiation exist between the comparative samples and the fossils.

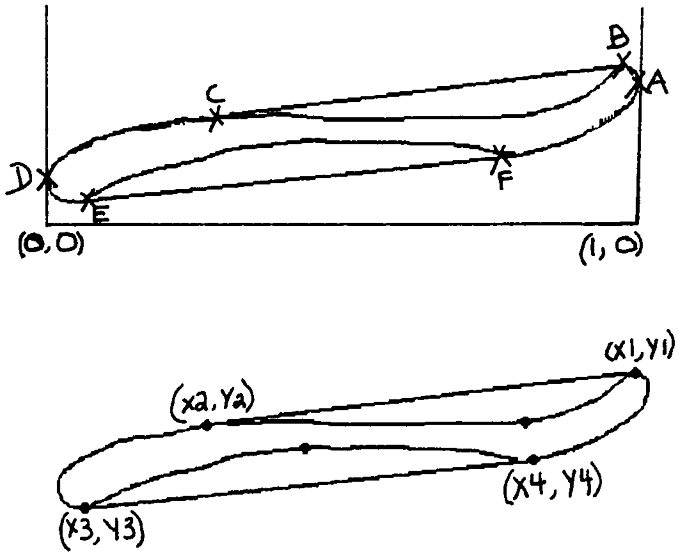


Figure 5. The CH created of the outline of KNM-WT 15000. The top figure illustrates points A-F of the CH. The bottom figure shows the four vertices isolated from the two greatest concavities.

A Tukey's studentized range test produced multiple comparison T-tests to determine whether mean differences exist between species. The vertices were plotted separately to graphically represent any clustering in the data. Finally, posterior probabilities of group membership were calculated for the fossils. This statistic tests the probability that an individual fossil could fall within either the human or ape clusters.

CHAPTER 4

RESULTS

Bivariate scatter plots of the raw data graphically illustrate clustering at each vertex (Figure 6). Each point represents a vertex constructed by the CH (see Appendix B for raw data). Plots X2,Y2 and X3,Y3 showed the strongest clustering between the non-fossil groups. In both plots, the fossils were distributed as follows: A.L. 288-1 fell within the ape cluster closest to *Pan*; KNM-WT 15000 and Sts 14 fell within the ape cluster as well but closer to *Gorilla*; Kebara 2 and KNM-ER 3228 both fell within the human cluster.

The statistical analyses reflected the results visually indicated by the scatter plots. The MANOVA (multiple analysis of variance) yielded both univariate and multivariate scores (Table D). The univariate scores were significantly different at the .05 level for all X and Y dimensions. Dimension X1 showed the least significance at P=.0243. The multivariate scores indicated significant differences at the .05 level between all vertices (the four points created by the CH) computed in the convex hull. MANOVA cannot discern between which groups differences existed. Group differences were obtained through two post-hoc analyses that tested for species effect.

The first analysis, Tukey's studentized range test, computed multiple T-tests for mean population differences (Table E). Table D only shows differences

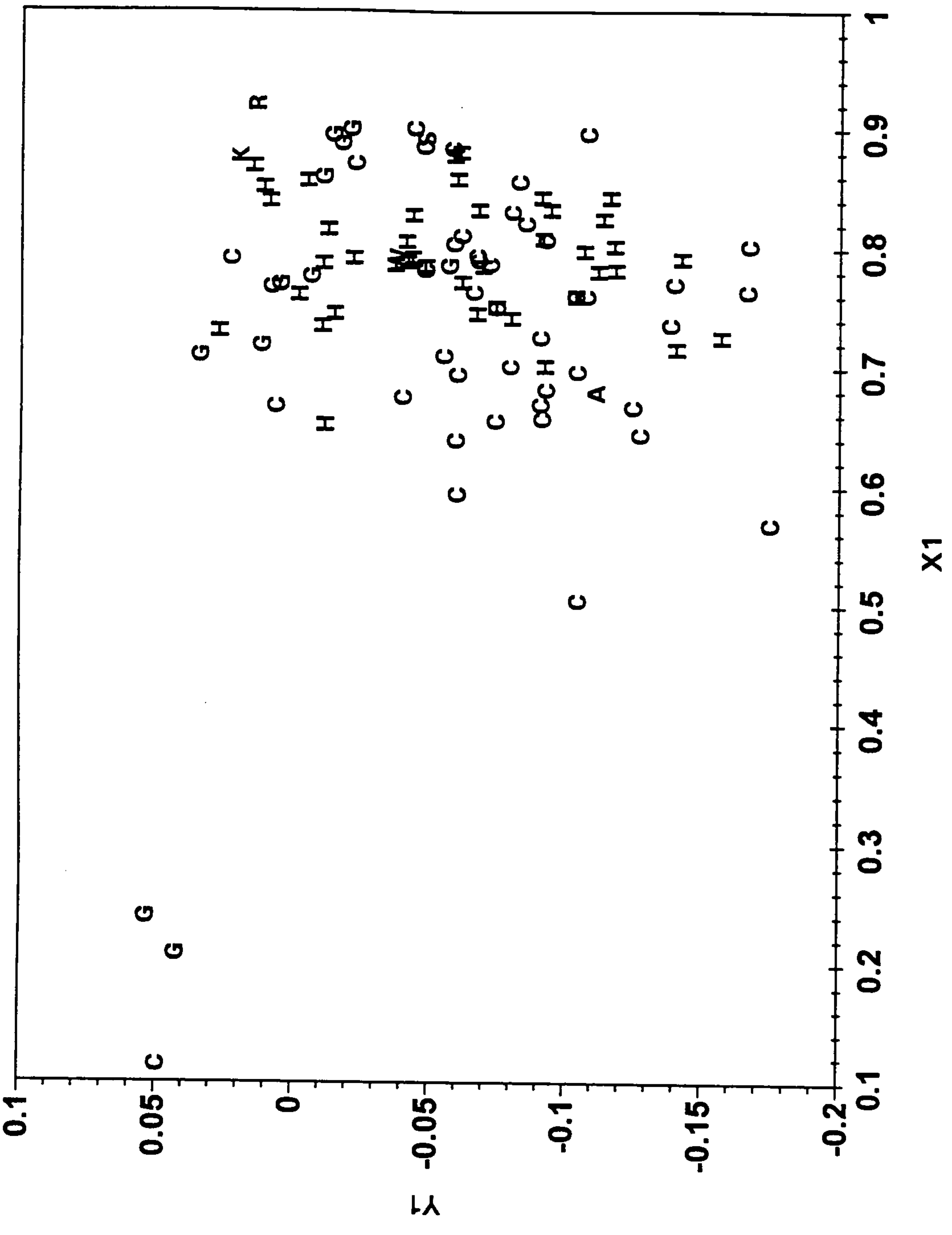


Figure 6. Bivariate scatter plots of the raw data. Each plot represents one vertex constructed from the CH. Plots X2,Y2 and X3,Y3 show the greatest separation between species. C = chimpanzee, G = Gorilla, H = human, A = AL.288-1, S = Sts14, K = Kebara, W = KNM-WT 15000, R = KNM-ER 3228.

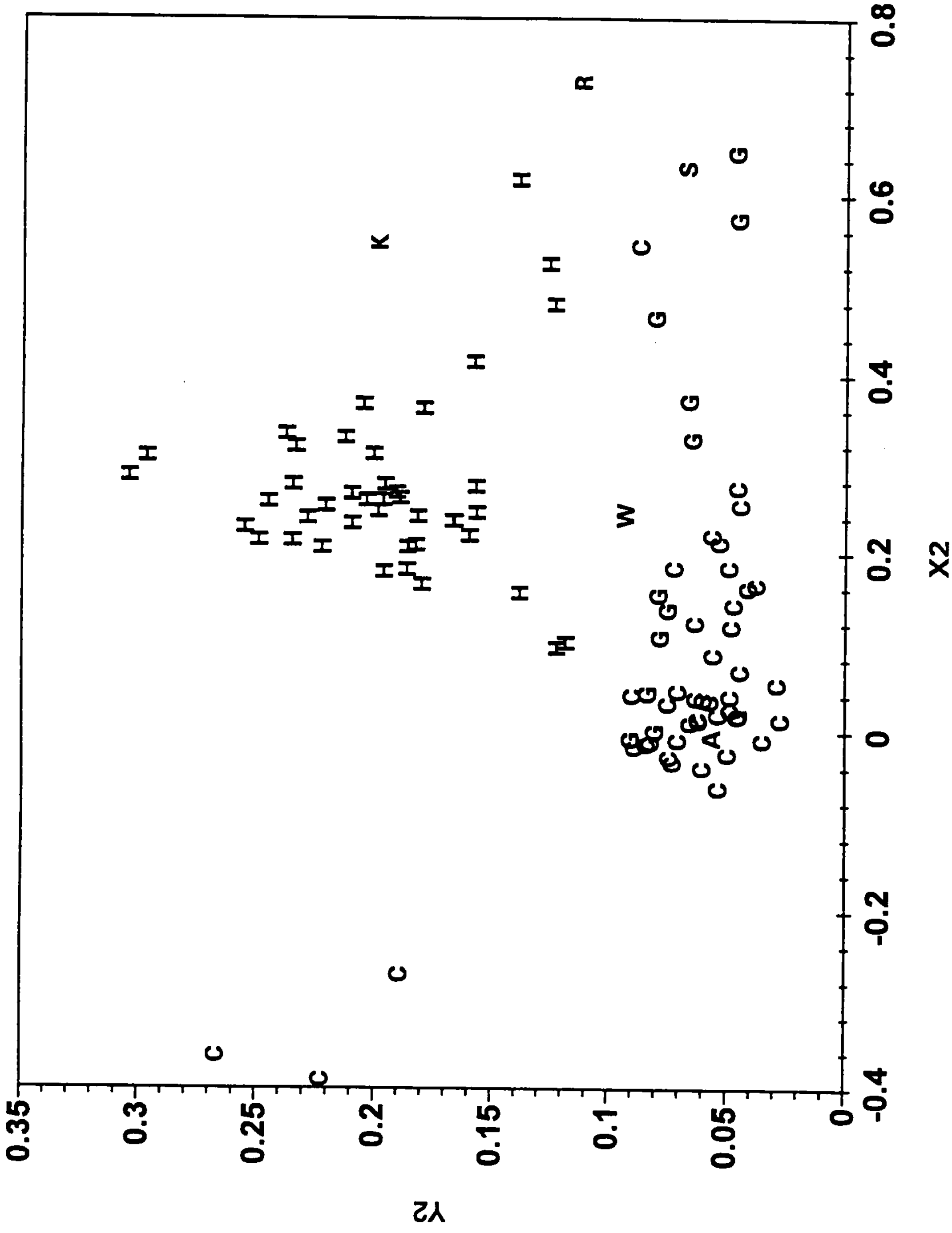


Figure 6. (continued)

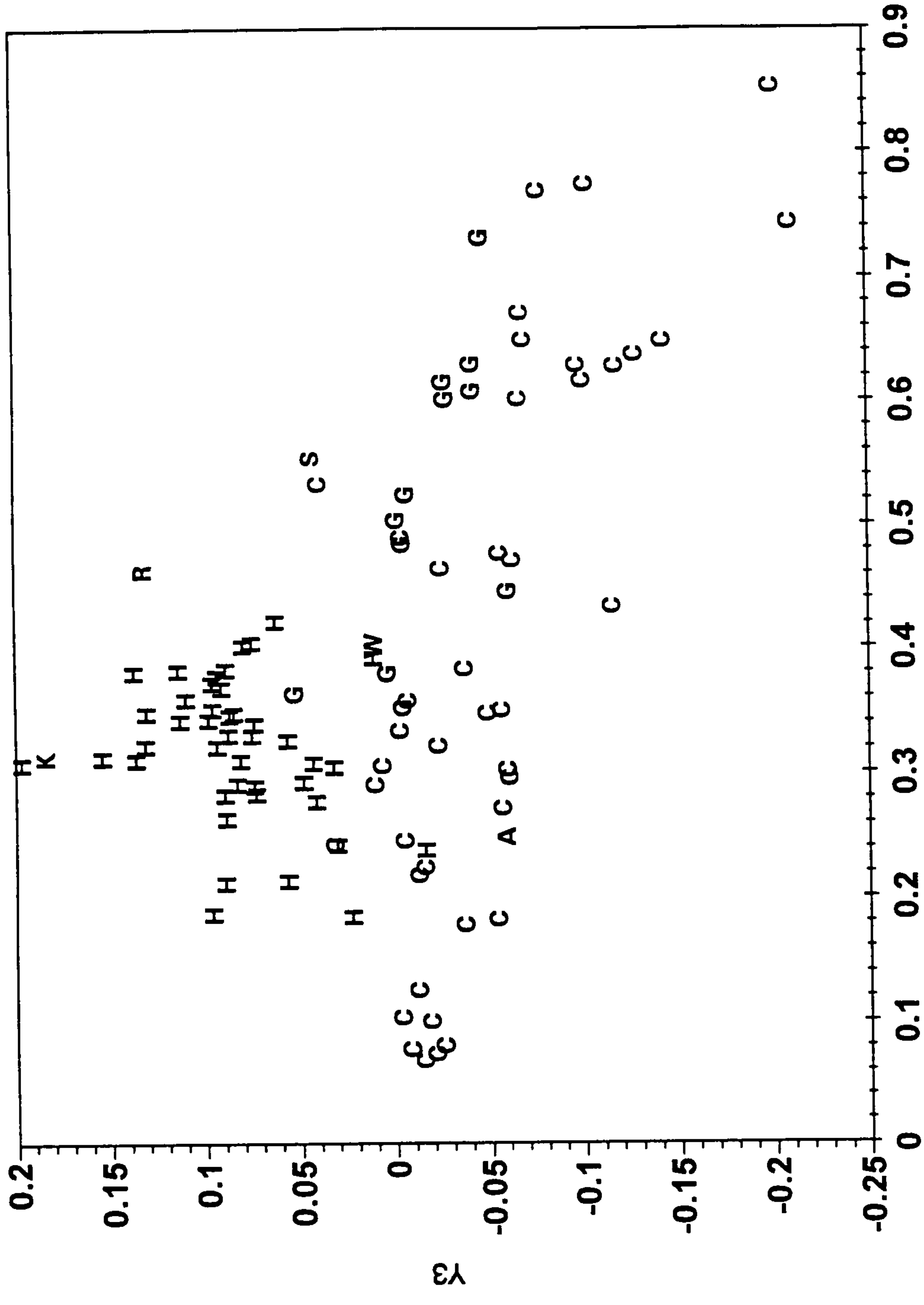


Figure 6. (continued)

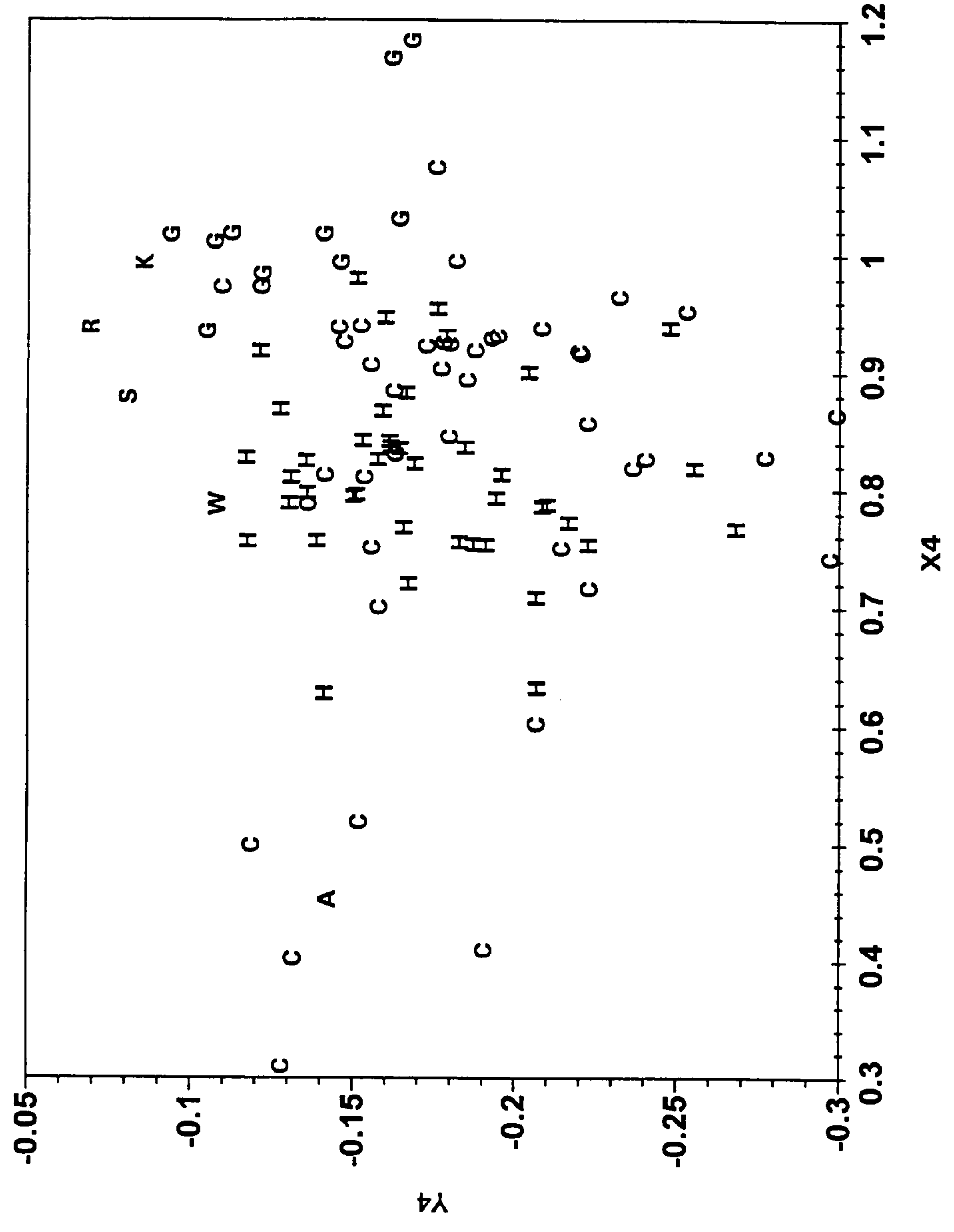


Figure 6. (continued)

TABLE 4. MANOVA.Significant differences indicated for all verticies.

UNIVARIATE SCORES		
Coordinates	**F value**	**Pr>F**
X1	3.27	0.0234
Y1	9.41	0.0001
X2	21.17	0.0001
Y2	7.42	0.0001
X3	5.27	0.0002
Y3	56.0	0.0001
X4	7.32	0.0002
Y4	10.12	0.0001
MULTIVARIATE SCORES		
Wilks Lambda	14.37	0.0001
Pilia's Trace	9.21	0.0001
Hotelling-Lawley	22.23	0.0001

significant at the .05 level with critical values for the range at 3.695. Results indicate that more significant between group variation exists within the Y-dimension than the X-dimension. No significant differences existed in the X1 dimension. Since this test only indicates mean population differences, a second post-hoc test was necessary to indicate species differences for the fossil hominids (Appendix C gives means and SD for each vertex).

The second post-hoc test, the posterior probability for group membership was calculated from a discriminant analysis (Table 6). The analysis was run

FIGURE 5. TUKEY'S STUDENTIZED RANGE TEST

SPECIES COMPARISON		LOWER CI	MEANS DIFFERENCE	UPPER CI
Y1	G - H	0.023538	0.063136	0.102733
	G - C	0.038269	0.077572	0.116875
Y2	H - F	0.025808	0.07929	0.132772
	H - C	0.100695	0.124949	0.149204
	H - G	0.088605	0.125609	0.162614
Y3	H - G	0.05846	0.10026	0.14206
	H - C	0.10452	0.13192	0.15932
	F - G	0.01141	0.07939	0.14737
	F - C	0.05085	0.11105	0.17125
Y4	F - H	0.026082	0.076204	0.126325
	F - C	0.035657	0.085601	0.015544
	H - G	-0.074147	-0.039468	-0.004789
	G - C	0.014444	0.048865	0.083286
X1	NO	SIGNIFICANT	SPECIES	DIFFERENCES
X2	F - C	0.17079	0.3585	0.5462
	H - C	0.14292	0.22835	0.31378
	G - C	0.06358	0.19295	0.32231
X3	G -H	0.06387	0.2003	0.33674
X4	F - G	-0.39082	-0.2028	-0.01478
	G - C	0.07453	0.18929	0.30406
	G - H	0.08311	0.19873	0.31435

TABLE 6. POSTERIOR PROBABILITY OF MEMBERSHIP

FOSSIL	MEMBERSHIP	PROBABILITY	
		APE	MODERN HUMAN
A.L. 288-1	Ape	0.9998	0.0002
Sts 14	Human	0.0024	0.9976
KNM-WT 15000	Ape	0.9045	0.0955
KNM-ER 3228	Human	0.0000	1.0000
Kebara 2	Human	0.0000	1.0000

twice. The first run set the parameters for the comparative samples. Apes were pooled to form one group while humans formed another. In the second run, the individual fossils were applied as unknowns. Results indicated the following for the fossil hominids: Kebara 2 and KNM-ER 3228 had a probability of 1 as being human; Sts 14 was also classified as a modern human but the probability was not as strong at .9976; A.L. 288-1 and KNM-WT 15000 were both classified as apes. Results for Sts 14 and KNM-WT 15000 were unexpected. Possible interpretations will be presented in the next section.

All the results indicate that significant differences exist among the iliac crests of fossil hominids. The shape of the iliac crest is successfully and repeatedly quantified in two-dimensions, a major innovation provided by this research compared to earlier studies. The relevance of the iliac crest shape, particularly with reference to the evolution of bipedalism and pelvic morphology as a whole will be addressed in the following section. Results indicate that digital analysis in association with multivariate statistics can be a valuable methodology in paleoanthropological investigations.

CHAPTER 5

DISCUSSION AND CONCLUSION

This study has demonstrated a relationship between the form of the hominoid iliac crest and the evolution of hominid bipedalism. The methodology presented here is a preliminary investigation of the use of the convex hull in a paleoanthropological context as a shape descriptor for forms which lack sufficient homologous landmarks for traditional multivariate analysis. Shape change in the iliac crest has received little attention in investigations of evolutionary trends in bipedalism. This study has successfully quantified this shape change through the use of the convex hull and multivariate statistics. Results illustrate the primary effects of two key muscle blocks in the evolution of the iliac crest and bipedalism; the abductors (gl. medius and gl. medius) and the obliques.

In modern humans the iliac crest forms a distinctive S-shaped curve. The upper bend (posterior portion) is marked by the spina limitans (Sl) and is present in all hominoids in this study. The lower bend (anterior portion) is marked by the iliac tubercle which lies at the proximal end of the iliac pillar or acetabulo-cristal buttress on the dorsal aspect. The presence of this feature is variable in the current sample and will be discussed later.

The iliac pillar strengthens the anterior portion of the iliac blade against the pull of the abductors (gl. medius and gl. minimus) during human bipedalism. The abductors stabilize the support leg during the swing phase. As the swing leg moves forward, the hip tilts toward the support leg through action of the abductors which shifts the center of gravity to maintain balance and upright posture.

On the ventral aspect opposite the iliac pillar is the iliac fossa. In humans this surface is concave, contrary to the condition found in apes. Chimpanzees have a flat ventral portion while in gorillas the entire ventral surface of the crest is concave, an artifact of this ape's almost exclusive quadrupedal posture. No delineation between the anterior and posterior portions of the crest exists. In modern humans, the shape of the iliac fossa places the internal and external obliques in a position that helps balance the trunk during bipedalism. Waterman (1929) noted this condition in her early publication on the evolution of the primate pelvis. She concluded that in humans the bone growth back from the SI is the result of both the abdominals and the abductors acting to maintain the center of gravity.

Results of this study suggest that the shape of the iliac crest in fossil hominids is comparable to those of living hominoids and that the evolutionary development of the hominid S-curve can be plausibly reconstructed. Of the four points illustrated by the bivariate plots generated from the CH, the second and third vertices showed the strongest separation between apes and humans. In humans these points correlate to the lower bend of the S-curve with vertex two representing the relative position of the iliac tubercle. Results from the multivariate analyses indicate the function of the abductors and the obliques. These muscle groups are critical to modern human bipedalism and membership classification of the fossil hominids presumably reflects their ability to walk bipedally.

A.L. 288-1 lacks a distinctive lower curve in the crest, a more ape-like morphology, indicating a locomotor pattern that is not identical to modern humans. The multivariate results classify A.L. 288-1 within the ape range for the degree of curvature in the iliac crest. The question remains as to whether or not this shape indicates a type of locomotion that is significantly different from that of modern humans.

Numerous researchers have debated the ability of the fossil hominid known as "Lucy" to walk bipedally. Morphologically, *A. afarensis* displays a number of primitive features associated with arboreal behavior, such as: a wide peroneal groove on the fibulae, a hamstring moment arm which exhibits a greater range than humans, reduced development in the sacroiliac ligament, a cranially directed glenoid fossa, a greater than average range for abduction at the hip, laterally directed iliac blades, small acetabulae, a humero-femoral index of 85, and long/curved proximal pedal phalanges (Stern and Sussman 1983; Sussman et al., 1984; McHenry, 1986).

Within the *A. afarensis* pelvis, a certain combination of features has been interpreted as a functional necessity for bipedalism. Rak (1991) explains that the widely flared ilia compensated for a narrow pelvic inlet,

> the combination of a narrow inlet and a laterally positioned iliac crest yields a more extreme lateral flare than would a wide inlet with a similarly positioned crest. p.286

This platypelloid shape would allow the center of gravity to fall low within the pelvis. Long femoral necks maintain the necessary distance between the hip joints and along with the extreme lateral flare, position the abductors to stabilize the hip during the swing phase. He concludes that the condition found in modern humans is probably derived:

> The narrow pelvis and the short femoral neck of the modern female may thus be viewed as secondarily derived traits and seem to have little in common with the primitive, narrow pelvis and the short-necked femurs found in the quadrupedal chimpanzee. (Rak, 1991:289)

Lovejoy (1973, 1988) and Lovejoy et al. (1973) has maintained the position that *A. afarensis* was fully bipedal and possibly hyper-efficient in its ability to abduct because less force would be necessary to stabilize the hip. In his opinion, the most important element of bipedal gait is stride and for the australopithecine he states the following:

> the ability of the australopithecine to stride depends simply and directly upon whether on not their joints and muscles were sufficiently adapted to perform the three basic elements of bipedal walking I have defined [trunk progression, trunk support, limb progression]. It is my opinion that not only are these capabilities clearly in evidence, but that there are, in fact, significant indications that this extinct biped might have been superior to modern man. (1973:151)

Others such as Stern and Susman (1983), Susman et al. (1984), and Berge (1984) maintain that *A. afarensis* practiced a mode of bipedal locomotion that was significantly different from modern humans. The conclusion is drawn from their belief that the evidence of gluteal, and in the case of Berge, the abdominal musculature is limited in its adaptation for habitual bipedalism.

Results from the current study seem to support these conclusions regarding A.L. 288-1. The lack of a well defined lower bend in the curve of the iliac crest indicates gluteal musculature which is not sufficiently developed to maintain lateral balance during bipedal gait. The diminutive size of "Lucy" on the open savannah would almost necessitate a dependence upon trees for, at the least, protection from predators. As Susman et al. (1984) assert:

> it is inconceivable to us that if the larger male *A. afarensis* were off foraging during the day, leaving the diminutive females with their offspring to fend for themselves, that the latter would have survived without recourse to the trees. Indeed, no living primate does so. p.151

However, I caution against concluding that bipedal behavior was absent. Allowing for a certain amount of arboreal behavior, *A. afarensis* when bipedal, was certainly more efficient than a chimpanzee in the same posture but probably not as efficient as a modern human.

Given the position of the other fossil hominids in the multivariate analysis, Sts 14's membership as a human is puzzling. It is important to note, however, that this classification may reflect distortion in the reconstruction.

Day (1973) concluded that the reconstruction may not accurately represent the specimen and that anatomical errors are present,

> I was considerably disturbed by the extent of its restoration and by the way in which it had been reconstructed...while it is true that this specimen shows many important anatomical features, very few measurements can be taken safely upon the fossil. pp. 30-31

However, he concluded that no indisputable evidence for quadrupedalism exists in the hominid fossil record.

The lateral support system for the genus *Australopithecus* was addressed by McHenry and Temerin (1979). They concluded that overall abductor force relative to body weight was similar between australopithecines and humans but the overall amount of force was less for the fossil hominid given its lower body weight. Similar results were found for hip extension and conclusions suggest that even though morphological differences exist between australopithecines and modern humans, abduction and extension were sufficient for bipedalism and did not allow for the muscular requirements of quadrupedal climbing.

McHenry (1986) compared the postcrania of *A. afarensis* and *A. africanus* and noted that dimensions between the two taxa were similar but unique to Hominoidea. He further noted that mosaic evolution is present. While significant cranial and dental differences existed between the two species, postcranially, the two were identical. Results from the current study disagree but McHenry's (1986) conclusion that, "resolution of the branching pattern within Hominidae must rely on the cranial and dental references"(p.187) cannot be disregarded until disputes over the reconstruction of Sts 14 can be resolved.

Association of KNM-WT 15000 with apes illustrates the retention of primitive features in this hominid. It represents a very early stage of *Homo erectus* which lived approximately 1.6 Ma. According to the dental and epiphysial age, this individual was 12 ± 1 years of age at his death (Brown et al., 1985). Unfused epiphyses indicate that the potential for further growth was quite large. The major pelvic elements were un-fused, a situation that occurs in white human males between 13-15 years (Smith, 1993). Smith suggests that this indicates an accelerated developmental pattern:

> members of *Homo erectus* may have attained much more of their adult size by early adolescence than modern humans typically do. (Smith, 1993:218)

At death, KNM-WT 15000 was 160 cm (5'3") and had he lived to adulthood, Ruff and Walker (1993) estimate his stature would have been between 177 to 193 cm (5'10" to 6'4").

In general, KNM-WT 15000 displays a mosaic of features. In the pelvis, many primitive hominid (ie. australopithecine-like) features are exhibited such as a marked degree of iliac flare, extremely long femoral necks, a narrow interacetabular distance, and a more gracile iliac tubercle. The specimen is best compared to OH 28, a *Homo erectus* from Olduvai which is geologically younger at 1Ma (Day, 1971). It is also similar to KNM-ER 3228 an early *Homo* from Koobi Fora which is dated to 1.95Ma (Rose, 1984). This study demonstrates that "the Boy" possessed a relatively uncurved iliac crest which Walker and Leakey (1993) attribute to the less developed iliac tubercle. In their opinion, this condition may reflect the immature age of the specimen,

> Had the Narikotome juvenile lived to maturity, it would have developed much stronger muscle scars and buttresses. These were only incipiently developed at the time of death. p.139

Given the mosaic of primitive and more advanced features found in this hominid and the lack of a strong iliac tubercle, one could conclude that KNM-WT 15000 had not developed a modern human mode of locomotion. However, given the overall similarity of shape to other *Homo erectus* specimens and modern humans the evidence is strong enough to conclude that the Narikotome Boy exhibits a morphology that in adulthood would most likely have resembled modern humans. It is important to note that developmental sequences for pelvic morphology are little addressed beyond epiphysial fusion rates. Muscular development and its impact on bone are questions that need to be addressed before conclusions on mature morphology are made. Another important factor to note is the extensive reconstruction present in casts of this specimen which may affect interpretations concerning its morphological characteristics.

In contrast, results from this study indicate that, KNM-ER 3228 had obtained the abdominal and pelvic musculature of a fully modern human. The taxonomic classification of KNM-ER 3228 has been problematic. In general, the fossil is referred to as an early *Homo* and has been attributed to both *Homo habilis* (Susman and Stern, 1982) and *Homo erectus* (Steudel, 1978). KNM-ER

3228 exhibits a unique suite of characters found in other material in the Plio-Pleistocene. Many of the characters identified on KNM-ER 3228 are present in Arago 44 (*H. erectus* or "archaic" *H. sapiens*) and the Broken Hill ("archaic" *H. sapiens*) os coxae E. 719 as well as OH 28 (*H. erectus*).

The first pelvic material discovered to exhibit this character suite was OH 28. In Brain et al. (1974), Robinson cautioned against accepting the assignment of OH 28 to *Homo erectus*,

> I believe it unwise in the extreme to accept the Bed IV innominate as normal unless other specimens are found that confirm its features. p.61

Since the discovery of OH 28, numerous other fossil have been found which exhibit the same character traits and today Olduvai Hominid 28 is commonly accepted as a *Homo erectus*.

Functionally, OH 28 represents a complex capable of modern bipedalism. Steudel (1978) states that

> All indications are that *H. erectus* was an efficient, erect walking form. The OH 28 pelvis itself is consistent with what one would expect of an erect biped. p.591

A number of common features exist between OH 28 and the later material Arago 44 and E. 719. These features are also present in KNM-ER 3228 such as: a strongly developed iliac pillar and tubercle, a deep fossa at the attachment point for the gluteus medius, a posteriorly and superiorly shallow iliac fossa, a small area for the sacro-iliac articulation, a large acetabulum, and a forward projecting anterior superior iliac spine (Day 1982, 1984; Rose, 1984; Stringer, 1986). The presence of these traits, particularly the robust iliac pillar in Arago 44 and E. 719 suggest a long stasis for this feature (Stringer, 1986).

Features present in the postcrania of *Homo habilis* have exhibited morphologies which support a significant amount of arboreal behavior. Susman and Stern (1982) noted that in OH 7, a habiline hand, the distal phalanges are robust and curved with rugose muscle markings indicating powerful grasping like that found in apes. Morphologies in the foot (OH 8) and tibia and fibula (OH 35) however, show a stronger resemblance to the condition found in modern humans which indicates a "bipedal striding gait" (p. 932). They conclude that,

> certain features of the limbs of *Homo habilis*... suggest a significant component of climbing behavior was present in the locomotor behavior of small Plio-Pleistocene hominids well beyond the point at which they became habitual bipeds. p.933

Susman et al.'s (1984) discussion of australopithecines concludes with their belief that at the time of *Homo erectus* sufficient adaptations were present for full-time terrestriality but that they:

> do not, however, feel that at the *afarensis* (or even *Homo habilis*) grade hominids were of sufficient size or cultural capacity for full-time terrestrial life. p.152

Whether features present in other aspects of KNM-ER 3228's postcrania were reminiscent of quadrupedal arboreal behavior will never be known. What can be said and is supported by this analysis is that the pelvic condition was most similar to *Homo sapiens* and did not resemble quadrupedal behavior. Further, in the evolutionary development of the iliac crest and the S-curve, KNM-ER 3228 had reached the condition found in modern *Homo sapiens.*

The Neandertal Kebara 2 ilium very closely resembles that of modern *Homo sapiens* but also exhibits some morphological differences including: forward projecting anterior superior and inferior iliac spines, the ilia extend in a fan-like manner unlike in modern humans in which they ascend vertically from the iliac body, the iliac pillar is extremely robust as is the iliac tubercle, and the iliac pillar lies close to the anterior margin of the blade (Rak and Arensberg, 1987). Rak and Arensberg attribute these differences to locomotor rather than obstetrical requirements as suggested by Rosenberg (1986), a conclusion not supported by this research.

Results here indicate that in the development of the iliac crest, Kebara 2 falls within the modern human range. The extreme robusticity of the iliac pillar and its positioning anteriorly on the iliac blade may represent stasis of this feature that Stringer (1986) suggests begins with KNM-ER 3228 1.8 million years earlier. It should be noted that Kebara 2 has been sexed as a male. The robusticity of the iliac pillar may simply represent overall robusticity for male Neandertals. Other features seem to indicate sexual dimorphism particularly an elongated pubic ramus and large subpubic angle (Rak and Arensberg, 1987). Rak has interpreted these features by stating that:

> the Kebara specimen and other Neandertal specimens contemporary with it have little bearing on the evolutionary history of modern humans. p.331

The overall shape of the iliac crest does not differ significantly from that of modern humans and no apparent break in this pattern exists from *Homo erectus* onward. If any locomotor differences are represented in other aspects of the ilia in Kebara 2 these differences do not extend to the function of the abductors.

CHAPTER 6

SUMMARY

The shape of the iliac crest of extant and extinct hominoids has been investigated in this study. Results indicate that the typical S-shape curvature in the crest appeared very early in the evolutionary history of bipedalism. By *Homo habilis/*early *Homo erectus* a fully bipedally adapted iliac crest was present indicating a modern configuration for the lesser gluteal muscles and abdominals. The pelvis of AL. 288-1 retained an ape-like morphology in its iliac crest, most likely a retention resulting from behavioral adaptations of continued tree use. While increases in hominid brain size through time certainly affected the evolution of the pelvis, this increase had little affect on the shape of the iliac crest. Encephalization mostly affects the true pelvis (Berge et al., 1984).

This study has revealed some limitations of previous interpretations of fossil hominid pelvic material, and offers some suggestions for future investigations. First, observations and investigations of immature ape and human ilia are necessary to more thoroughly test the hypothesis that KNM-WT 15000 exhibits a juvenile condition and therefore should not be considered necessarily ape-like. Second, the large amount of reconstruction on the pelvis of KNM-WT 15000 must be accounted foe in any interpretations about its age and morphology. Third, caution is necessary when drawing conclusions concerning Sts 14 because of its state of preservation. In support of this study's conclusions, well preserved pelvic features of Sts 14 suggest a more derived condition. Fourth and finally, information concerning stresses on the ilia during adulthood should be investigated.

The methodology presented in this study opens new doors for paleoanthropological investigations concerning shape and form. While traditional measurements are a necessity, shape investigations have been an area limited to visual inspection. The CH along with multivariate analyses successfully quantifies continuous forms and gives new insight to evolutionary shape change in the iliac crest.

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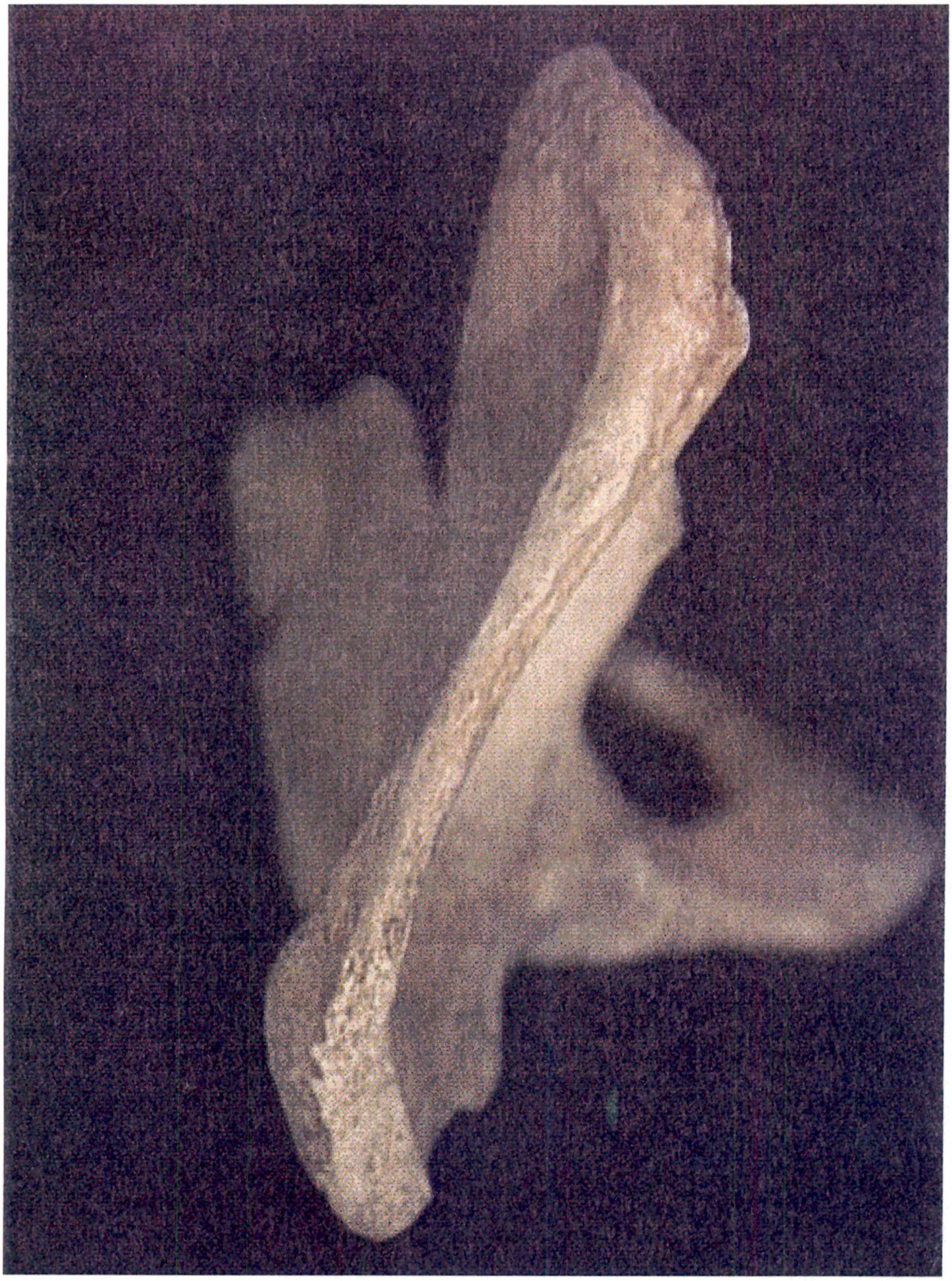
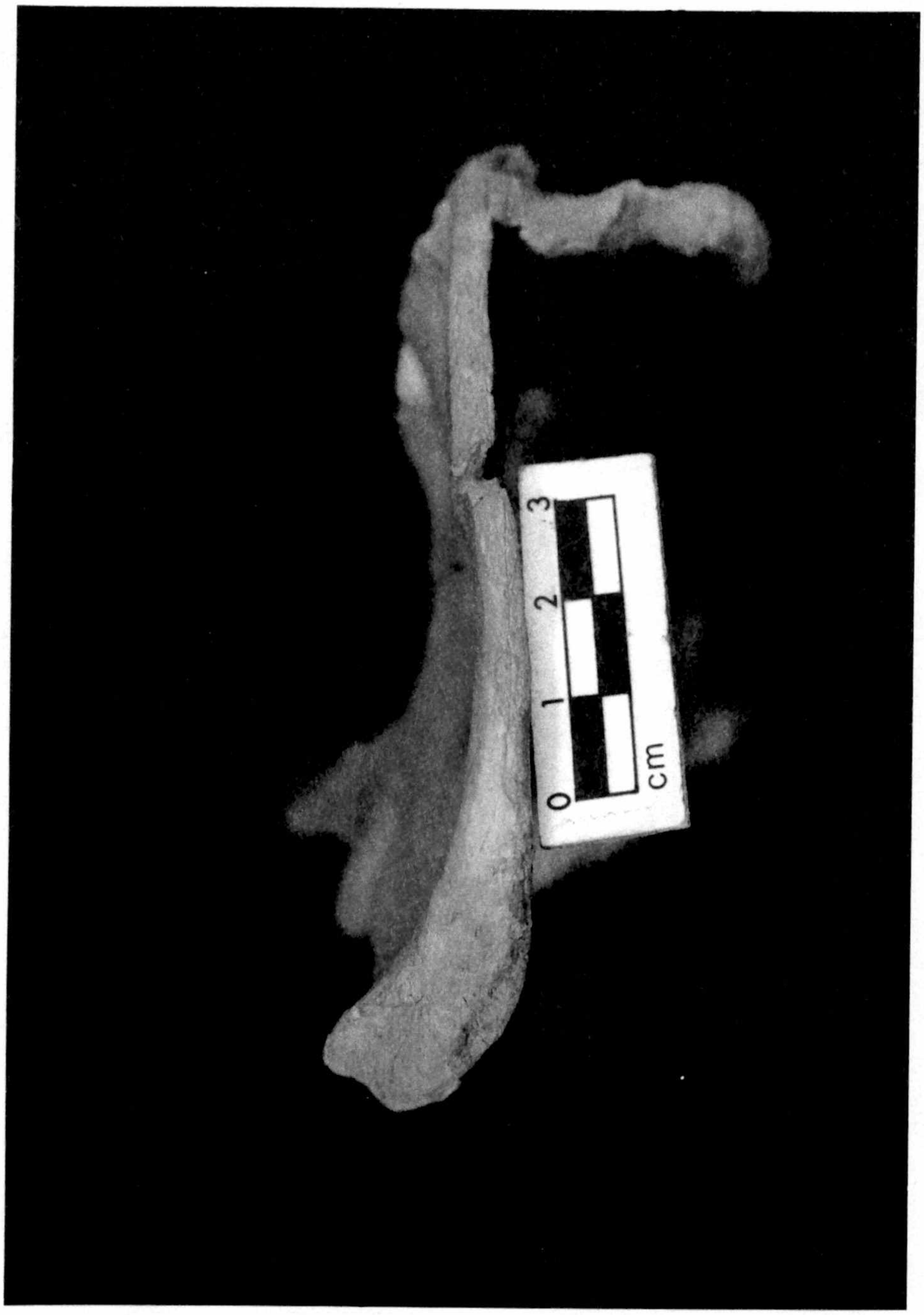
APPENDICES

APPENDIX A



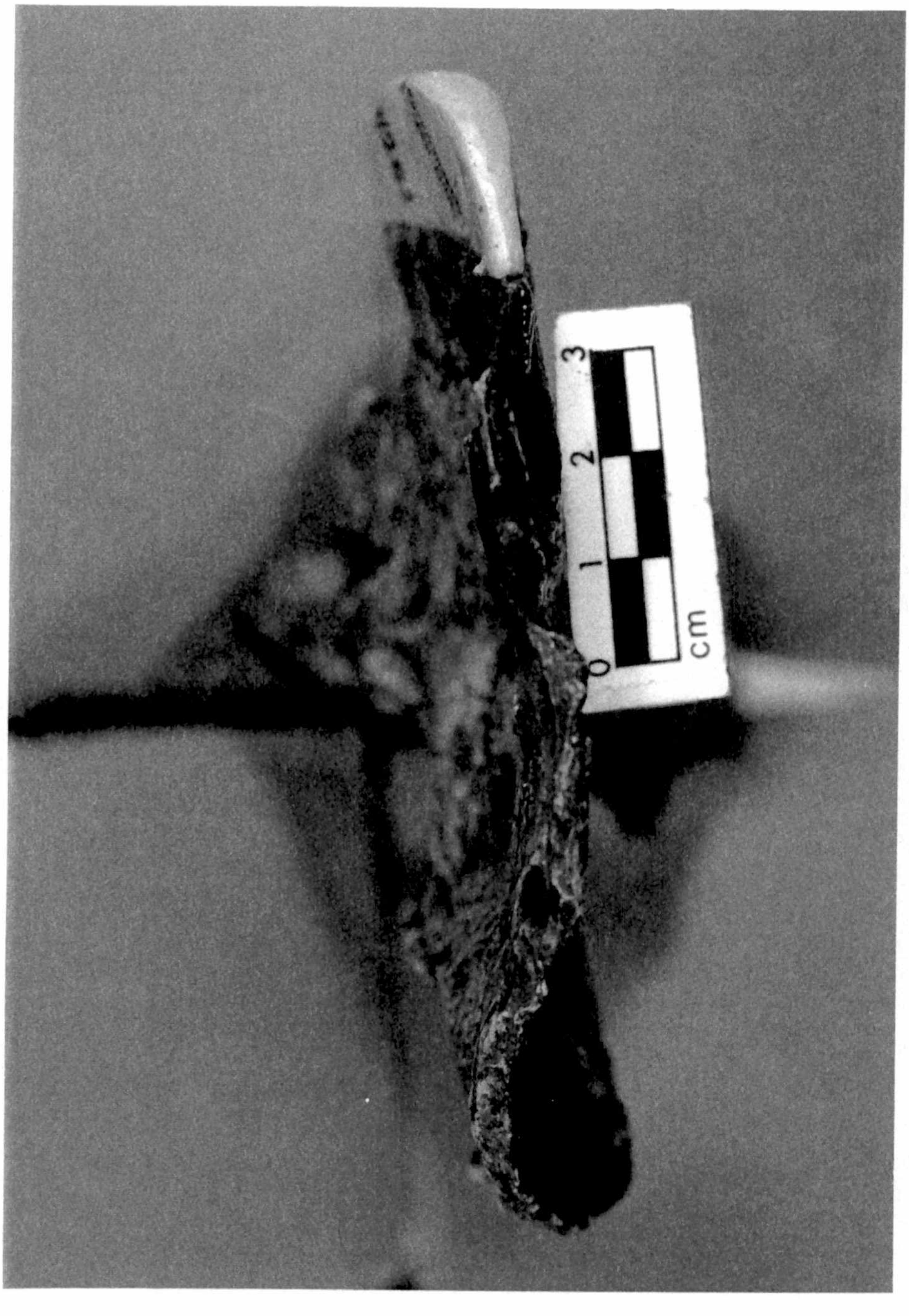
A-1. Iliac crest of modern human.

A-2. Iliac crest of KNM-ER 3228.



A-3. Iliac crest of AL 288-1.

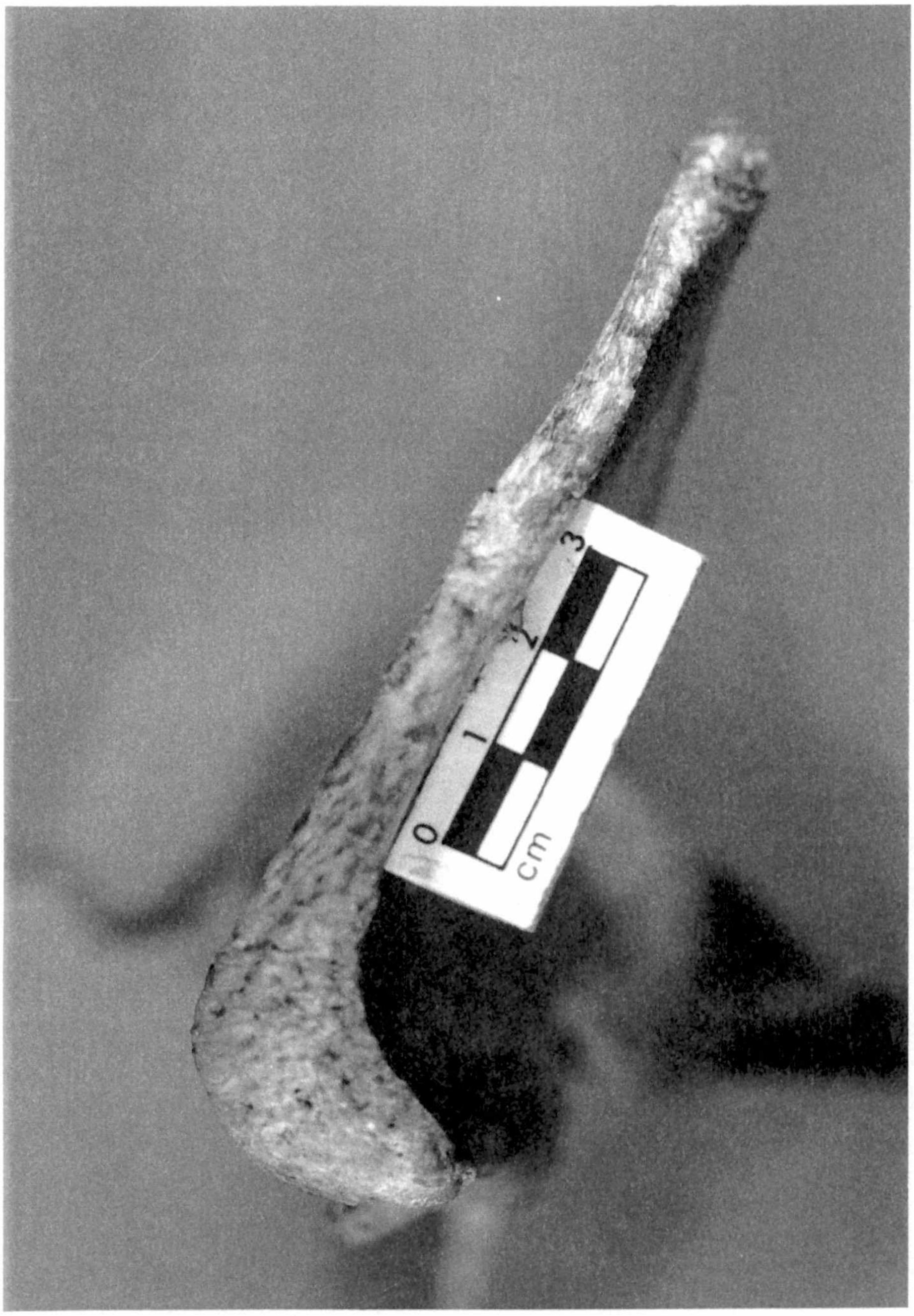
A-4. Iliac crest of Kebara 2.



A-5. Iliac crest of Sts 14

A-6. Iliac crest of KNM-WT 15000.

A-7. Iliac crest of a gorilla.



A-8. Iliac crest of a chimpanzee.

APPENDIX B

APPENDIX B
RAW DATA[1]

Sample	Ref	X1	Y1	X2	Y2	X3	Y3	X4	Y4
1056	C	0.568712	-0.17545	0.066861	0.043779	0.07379	-0.02172	0.409636	-0.19084
1426	C	0.785699	-0.07244	0.163900	0.037108	0.463853	-0.02582	0.925651	-0.17821
1433	C	0.791357	0.022321	0.543565	0.086656	0.532639	0.038715	1.074283	-0.1761
1434	C	0.763775	-0.16708	-0.01219	0.081505	0.742836	-0.21064	0.864734	-0.29951
1706	C	0.806278	-0.09319	0.160221	0.040453	0.321164	-0.02374	0.928909	-0.19327
1707	C	0.696045	-0.10489	0.040351	0.089376	0.432885	-0.11606	0.518962	-0.15221
1708	C	0.114775	0.048654	-0.38994	0.221759	0.636833	-0.12869	0.826374	-0.24097
1713	C	0.656698	-0.09181	-0.27066	0.188659	0.302496	-0.06028	0.856956	-0.22309
1719	C	0.708931	-0.05568	0.085259	0.055125	0.217572	-0.01337	0.70056	-0.15829
171	C	0.668588	-0.09131	0.121031	0.062697	0.295975	-0.06115	0.716209	-0.22336
1722	C	0.802901	-0.05934	-0.03413	0.072190	0.332906	-0.00372	0.812677	-0.14175
1726	C	0.788932	-0.06823	-0.06250	0.052837	0.615623	-0.10125	0.930781	-0.19501
1735	C	0.759002	-0.10828	0.037544	0.062471	0.852501	-0.2018	0.952285	-0.25362
1738	C	0.884776	-0.04841	0.014222	0.061476	0.670429	-0.06862	0.924201	-0.18028
1744	C	0.801962	-0.16758	0.024366	0.047976	0.271669	-0.05734	0.602574	-0.20713
1748	C	0.681094	-0.09331	0.044779	0.070078	0.224322	-0.01662	0.964252	-0.23277
749	C	0.900713	-0.04485	0.011959	0.061104	0.768338	-0.07836	0.938634	-0.14583
1758	C	0.830097	-0.08067	0.030929	0.074252	0.347000	-0.04971	0.915397	-0.22107
1759	C	0.792911	-0.06779	0.253498	0.043823	0.475950	-0.05652	0.917808	-0.22031
1761	C	0.749475	-0.0749	0.009568	0.064762	0.077653	-0.00852	0.78804	-0.13640
1766	C	0.674499	-0.04058	0.116894	0.047417	0.24575	-0.00591	0.994806	-0.18215
1768	C	0.666403	-0.12534	0.035868	0.059234	0.068273	-0.0153	0.750337	-0.21491
1769	C	0.700441	-0.07994	-0.00908	0.070096	0.349654	-0.05719	0.845784	-0.17990
1770	C	0.724760	-0.09127	0.017192	0.044983	0.125158	-0.01251	0.499442	-0.11902

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[1] C = chimpanzee, G = gorilla, H = human

Sample	Ref	X1	Y1	X2	Y2	X3	Y3	X4	Y4
1775	C	0.638752	-0.05993	-0.01749	0.088258	0.628159	-0.09829	0.922571	-0.17303
1797	C	0.809827	-0.06203	0.018998	0.05304	0.648492	-0.07003	0.939572	-0.15272
1799	C	0.708931	-0.05568	0.085259	0.055125	0.217572	-0.01337	0.70056	-0.15829
1843	C	0.762194	-0.06656	0.220106	0.055632	0.290336	0.009607	0.903481	-0.17765
1846	C	0.208896	0.041946	0.000598	0.079685	0.730864	-0.04765	1.011253	-0.10762
1882	C	0.643601	-0.12790	-0.00928	0.034259	0.080754	-0.02620	0.310020	-0.12842
1992	C	0.503925	-0.10535	-0.36327	0.266065	0.182184	-0.05459	0.741772	-0.29765
239	C	0.667303	0.005939	0.183101	0.071637	0.242445	0.030925	1.035527	-0.11916
2746	C	0.820596	-0.08573	0.033909	0.056566	0.382482	-0.03779	0.894047	-0.18553
2747	C	0.769631	-0.14042	-0.01391	0.083369	0.17761	-0.03712	0.828128	-0.27755
2771	C	0.693412	-0.06057	0.013588	0.026559	0.773764	-0.10408	0.926079	-0.14756
2823	C	0.654839	-0.07457	-0.02776	0.07373	0.103212	-0.00388	0.750928	-0.15614
3551	C	0.896406	-0.10856	0.211474	0.052487	0.357225	-0.00800	0.918840	-0.18801
3552	C	0.735749	-0.13909	0.052643	0.028170	0.100200	-0.01917	0.402776	-0.13195
444	C	0.802901	-0.05934	-0.03413	0.072190	0.332906	-0.00372	0.812677	-0.14175
458	C	0.781001	-0.04889	0.273643	0.045018	0.305336	0.005732	0.884531	-0.16304
459	C	0.883245	-0.05874	0.18349	0.048442	0.600589	-0.06712	0.906829	-0.15593
540	C	0.870947	-0.02309	-0.02443	0.049076	0.488936	-0.00489	0.972862	-0.11000
543	C	0.593368	-0.06053	0.141487	0.046538	0.627165	-0.11848	0.937369	-0.20887
628	C	0.855857	-0.08327	0.039370	0.047896	0.470644	-0.06324	0.810879	-0.15386
630	C	0.758915	-0.10423	-0.03967	0.059615	0.647776	-0.14348	0.81835	-0.23712
KEBARA	K	0.877445	0.019406	0.546853	0.198238	0.312066	0.183036	0.993607	-0.08601
AL288-1	A	0.678992	-0.11177	-0.00578	0.055647	0.248427	-0.05929	0.453679	-0.14246
STS14	S	0.892227	-0.04888	0.631405	0.066718	0.553342	0.042593	0.879436	-0.08103
WT15000	W	0.789415	-0.03868	0.243692	0.092493	0.401656	0.009660	0.788139	-0.10829
ER3228	R	0.92087	0.013243	0.590446	0.163331	0.462250	0.131381	0.938527	.069522
1020	G	0.239669	0.053156	0.135417	0.074145	0.600390	-0.02850	0.993898	-0.14641
1057	G	0.769841	0.004365	-0.00814	0.090045	0.628997	-0.04240	1.03105	-0.16465
1430	G	0.900369	-0.02146	0.018102	0.044526	0.606796	-0.04262	1.018001	-0.14120
1431	G	0.895210	-0.01475	0.573129	0.045001	0.502687	-0.00234	0.984331	-0.12219

Sample	Ref	X1	Y1	X2	Y2	X3	Y3	X4	Y4
1704	G	0.718690	0.011268	0.371230	0.065724	0.614429	-0.02763	1.182051	-0.16838
1709	G	0.776127	-0.00691	0.327634	0.064225	0.351181	-0.00537	0.93495	-0.10522
1710	G	0.888116	-0.01809	0.104763	0.077521	0.483695	-0.00527	0.972956	-0.12189
1764	G	0.710151	0.033641	0.464477	0.079817	0.362519	0.051912	1.16718	-0.16240
1765	G	0.859929	-0.01119	0.64747	0.04591	0.523606	-0.00741	1.018219	-0.11279
1782	G	0.784589	-0.05744	0.042397	0.082808	0.445081	-0.06065	0.830765	-0.16342
1846	G	0.208896	0.041946	0.000598	0.079685	0.730864	-0.04765	1.011253	-0.10762
1849	G	0.767510	0.007552	0.152220	0.078183	0.378691	0.002942	1.017101	-0.09422
16BY115	H	0.843108	-0.09176	0.309251	0.296110	0.312565	0.153146	0.938217	-0.24855
16BY430	H	0.857187	-0.00565	0.363489	0.178696	0.404044	0.073827	0.918934	-0.12180
16BY453	H	0.787483	-0.01137	0.320546	0.233193	0.381928	0.112671	0.756847	-0.11797
18AN44	H	0.827856	-0.04451	0.246268	0.156107	0.421349	0.061254	0.868088	-0.15959
1JE153	H	0.852179	0.010218	0.240355	0.227982	0.376996	0.092437	0.955187	-0.17661
1JE22	H	0.761339	-0.00249	0.275539	0.156352	0.325542	0.055155	0.811685	-0.13141
1JE48	H	0.880758	-0.06160	0.258556	0.244685	0.341525	0.111775	0.795225	-0.15070
38MG13	H	0.784449	-0.07001	0.182074	0.185644	0.213569	0.055339	0.72087	-0.16759
38MG38	H	0.842768	-0.11698	0.215507	0.248577	0.350380	0.094725	0.772752	-0.21735
38MG41	H	0.785761	-0.03791	0.207138	0.185132	0.338615	0.072670	0.789661	-0.13078
38MG42	H	0.825060	-0.11451	0.234048	0.209116	0.282721	0.088370	0.786318	-0.20920
40MR131	H	0.805555	-0.04200	0.334515	0.237156	0.347512	0.129631	0.796825	-0.15159
40MR187	H	0.759522	-0.10433	0.155569	0.137698	0.242456	0.029350	0.753537	-0.19158
40MR193	H	0.808123	-0.09216	0.247949	0.197877	0.330014	0.086428	0.756052	-0.18334
40MR200	H	0.802143	-0.11863	0.262260	0.188633	0.391451	0.009795	0.819074	-0.25613
40MR262	H	0.788336	-0.04267	0.368104	0.204337	0.342304	0.096803	0.843096	-0.15351
40MR357	H	0.781299	-0.11907	0.268639	0.190207	0.307845	0.041724	0.787766	-0.21064
40MR89	H	0.745581	-0.01569	0.209853	0.181799	0.277311	0.040331	0.842434	-0.16177
40MR93	H	0.780607	-0.11266	0.259862	0.202906	0.291275	0.081810	0.793366	-0.19475
40MR94	H	0.652390	-0.01207	0.206559	0.221923	0.211778	0.088425	0.823007	-0.16955
4MR187A	H	0.701267	-0.09293	0.099951	0.117572	0.184502	0.021701	0.628536	-0.14151
5AN1	H	0.858055	-0.06057	0.236907	0.166064	0.309829	0.080074	0.836289	-0.16491

Sample	Ref	X1	Y1	X2	Y2	X3	Y3	X4	Y4
5AN24	H	0.784797	-0.04885	0.164936	0.179237	0.283433	0.071832	0.757324	-0.13937
5AN4	H	0.771130	-0.06242	0.214839	0.234413	0.263546	0.087706	0.768857	-0.16618
5AN9	H	0.816259	-0.01318	0.479958	0.122774	0.367748	0.090076	0.828038	-0.11745
6BN105	H	0.840313	0.008167	0.524716	0.125005	0.382359	0.087686	0.825602	-0.13592
7HA20	H	0.725898	-0.15767	0.236857	0.165513	0.186830	0.095099	0.767454	-0.26883
7HA24	H	0.791903	-0.02270	0.230014	0.254401	0.358632	0.108666	0.947667	-0.16042
7HA46	H	0.716255	-0.14115	0.094047	0.121359	0.238198	-0.01735	0.633167	-0.20744
7HA56	H	0.832693	-0.09507	0.260247	0.195740	0.320868	0.092455	0.837161	-0.18507
7HA63	H	0.750647	-0.07491	0.253838	0.220373	0.345300	0.085947	0.709078	-0.20727
7HA73	H	0.791835	-0.04424	0.277886	0.234243	0.321618	0.130311	0.798297	-0.13634
7HA77	H	0.791763	-0.14308	0.241791	0.181111	0.304646	0.030932	0.753679	-0.22332
7HA84	H	0.741196	-0.08067	0.311738	0.199888	0.347049	0.083453	0.754498	-0.18766
8HA105	H	0.735218	-0.01108	0.179706	0.195477	0.289371	0.072678	0.883598	-0.16700
8HA151	H	0.731017	0.026561	0.287168	0.303732	0.307530	0.195776	0.981031	-0.15184
8HA20	H	0.797712	-0.10751	0.220433	0.159242	0.292614	0.046839	0.813550	-0.19655
8HA42	H	0.877869	-0.05956	0.415815	0.157203	0.401497	0.078511	0.837829	-0.16209
9BN12	H	0.832094	-0.06836	0.330400	0.212161	0.310485	0.135332	0.931989	-0.17924
9BN34	H	0.855890	-0.06570	0.267046	0.209289	0.371568	0.094839	0.826546	-0.15824
9BN81	H	0.869518	0.014134	0.617313	0.138281	0.380185	0.136323	0.869851	-0.12797
9BN96	H	0.745011	-0.06780	0.277587	0.194955	0.329493	0.073832	0.900454	-0.20497

APPENDIX C

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      MANOVA USING 8 COORDINATES AS DEPENDANT VARS: SIMPLE FACTORIAL
                           WITH SPECIES EFFECT
                       INCLUDES 8 UNIVARIATE TABLES

                     General Linear Models Procedure

Level of         -------------Y1-------------    -------------Y2-------------
SPECIES    N      Mean           SD               Mean           SD

C         45  -0.07573178     0.04793811       0.06962607     0.04563723
F          5  -0.03333640     0.05332263       0.11528540     0.06249908
G         12   0.00184058     0.03068431       0.06896583     0.01592520
H         42  -0.06129519     0.04724850       0.19457531     0.04338060

Level of         -------------Y3-------------    -------------Y4-------------
SPECIES    N      Mean           SD               Mean           SD

C         45  -0.04957649     0.05402000      -0.18306333     0.04697325
F          5   0.06147620     0.09655205      -0.09746280     0.02882803
G         12  -0.01791500     0.03031286      -0.13419817     0.02670094
H         42   0.08234238     0.03923263      -0.17366648     0.03701444

Level of         -------------X1-------------    -------------X2-------------
SPECIES    N      Mean           SD               Mean           SD

C         45   0.71953600     0.15061768       0.04282727     0.15182269
F          5   0.83178980     0.09850777       0.40132360     0.27407251
G         12   0.70992475     0.23625173       0.23577450     0.23280685
H         42   0.79356771     0.05134539       0.27117319     0.10020426

Level of         -------------X3-------------    -------------X4-------------
SPECIES    N      Mean           SD               Mean           SD

C         45   0.39630933     0.22309310       0.82418540     0.17224516
F          5   0.39554820     0.12041516       0.81067760     0.21359561
G         12   0.51907800     0.12051356       1.01347958     0.09285208
H         42   0.31877336     0.05791167       0.81474848     0.07729936
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VITA

Amy Ridler Shook was born on December 17, 1967 and raised in Virginia Beach, Virginia. She attended Norfolk Academy for twelve years and graduated in June of 1986. In August of that same year she enrolled at Dickinson College in Carlisle, Pa. While attending Dickinson College, she pursued a degree in Anthropology and graduated in 1990 with a Bachelor of Arts degree in Anthropology. In the fall of 1990, she entered The University of Tennessee, Knoxville where completed her Master of Arts degree in December of 1994. In June of 1994, she entered The George Washington University in Washington DC where she is pursuing a degree in Museum Education.