FUNCTIONAL ALLOMETRY OF THE POSTCRANIAL SKELETON IN AFRICAN HOMINOIDS:

AN ANALYSIS OF LOCOMOTOR AND BODY SIZE CONSTRAINTS ON SKELETAL MORPHOLOGY IN EXTANT AND EXTINCT TAXA.

VOLUME I

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Abstract

This study focuses upon broader aspects of allometry in the postcranial skeleton of extant and extinct African hominoids. Three specific areas of relevance were examined. A mutually complementary analysis of patterns of relative scaling of the epiphyses and diaphyses in extant and extinct taxa was proceeded by an investigation of patterns of morphological shape variability in selected upper and lower limb epiphyses using Generalised Procrustes Analysis of 3D landmark configurations. A final section examines patterns of morphological integration in the pelvis and lower limb of extant and extinct hominids with specific focus on the influences of body size and body shape and its concomitant effects upon femoral diaphyseal morphology. Six hypotheses were formulated and formally tested in this study.

The extant African apes are confirmed as displaying a relative epiphyseal and diaphyseal “profile” that comprises relatively larger upper limb dimensions and relatively smaller lower limb dimensions relative to the morphological “profile” of recent humans. Recent humans possess significantly larger lower limb dimensions than *Pan* and *Gorilla* relative to geometric size. Application of this methodology to the *Australopithecus afarensis* partial skeleton, AL 288-1 (“Lucy”) reveals this diminutive female possessed a relative epiphyseal profile that is distinctly “hominid”, rather than “hominoid”. Significant differences exist in the geometric configurations of the distal humerus, proximal ulna and proximal femur of extant and extinct hominoids. With respect to distal humeral and proximal ulnar geometry, the African apes can be reliably distinguished from recent and fossil hominids (including *Australopithecus*). Morphological differences in the external geometry of the articular surface of the proximal ulna of the African apes and extant and extinct hominids are more profound, and possibly reflect adaptations to locomotor behaviour in *Pan* and *Gorilla*. Significant differences in proximal ulna articular geometry of Eurasian Neandertals with contemporary and later hominids were confirmed.

Overwhelming evidence emerges to support the hypothesis that the hominid pelvis is a highly integrated, morphological unit whose form is covariant to a significant degree with observed variability in body size and body shape. The *Australopithecus* and Neandertal pelvis display unique patterns of bivariate and multivariate scaling, probably reflecting “adaptive” and “passive” allometric distinctions. The scaling of the lever arm and load arm of the hip joint display a consistent pattern of sexual dimorphism in the African apes that remained apparently unaffected by obstetrical constraints in *Homo* females. The hypothesis that observed distinctions in anterior pelvic proportions would have significant concomitant influences on femoral diaphyseal morphology is only partially supported by the results of this study. Furthermore, the results of this study suggest that theoretical assumptions of relative hip joint scaling in *Australopithecus* and later hominids (including *H. erectus* and *H. neanderthalensis*) and inferred locomotor distinctions based upon them should be revised. Geometric analysis of the proximal femur of extant and extinct African hominoids yields results which are both consistent with, and contradict, prior observations using simple linear metrics.

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Chapter 1. Introduction.

"If this work is not both pleasant and profitable to the reader, the author most freely and openly declares that the fault must be in his performance, and it cannot be any deficiency in the subject."

Daniel Defoe (1660-1731). A Tour through England and Wales. Volume I.

1.1 Allometry

1.1.1 Allometry: A method or a process?

"Allometry is defined as the study of proportion changes correlated with variation in size of either the total organism or the part[s] under consideration...the size differences may arise in ontogeny, phylogeny or the static comparison of related forms differing in size; the term is not confined to any on form of mathematical expression, such as the power function" (Gould, 1966:629). Indeed, size is such a crucial influence in organismal biology (e.g., Calder, 1984; Schmidt-Nielsen, 1984; Peters, 1985) that some workers have lamented "the tyranny of size" (Oxnard & De Winter, 2001; see also Jungers *et al.*, 1995) in comparative morphometrics. Nevertheless, Gould's definition (Gould, 1966) recognises many crucial facets that underscore the importance (and pitfalls) inherent in the application of the allometric approach in comparative biology. At a most basic level, allometry is a *methodological* approach to understanding interrelationships between the size of the constituent parts of an organism and the whole (Huxley, 1924; 1932; Huxley & Teissier, 1936; Gould, 1966, 1971; Shea, 1985; Jungers, 1984, 1985*a,b*). However, allometric approaches have the potential to yield powerful insights into our understanding of "...those aspects of form which are not correlated with size and hence non-allometric" (Gould, 1966:604).

Studies of growth (ontogenetic allometry) require detailed data taken on organisms (or individuals) over a fixed time and are both laborious and expensive (see Cock, 1966; Shea, 1981, 1985). In contrast, static (adult) allometric analyses are relatively inexpensive and can considerably increase 'effective' sample sizes in statistical comparisons. The latter consideration is of paramount importance in some allometric comparisons (intra-specific allometry), but less so in others (inter-specific allometry). This is because variance and covariance of the dependent and independent variables determine the coefficients (slope, intercept and correlation coefficient) and confidence intervals traditionally reported in allometric comparisons (Sokal & Rohlf, 1995; Zar, 1996; see Smith, 1996).

Gould (Gould, 1966) attempted to resolve the confusion in allometric terminology by adopting Rörhs' (Rörhs, 1961) definitions that consider the nature of the data and the hypotheses of the model. As such, static allometric comparisons can be applied to samples at the inter-specific (between species in a genus), intra-specific (individuals or geographic varieties within a species) or evolutionary levels. Comparative studies of differences in relative proportions between evolutionary lineages can be undertaken at both levels (see Laird, 1965, 1966*a*,*b*; Laird *et al.*, 1968; Barton & Laird, 1969; Cheverud, 1982), but due to logistical constraints and availability of existing comparative data they are mainly static in focus (see Gould, 1966).

Functional Allometry of the Locomotor Skeleton.

The "classic" allometry formula proposed by Huxley (1924) is a power function of the form:

$$Y = bXk$$

Which can be re-written in linear (logarithmic) form as:

$$\mathrm{Log}\ Y = \log b + k*\log X$$

Where Y is the dependent variable and X is the independent variable (usually body mass in comparative applications), and *b* and *k* are constants. D'Arcy Thompson (Thompson, 1942) championed the view that logarithmic transformation of the data in static allometric applications is unnecessary because the relationship between the dependent and independent variables will be generally linear (i.e., non-curved) prior to calculating the equation. Moreover, as Thompson observed (Thompson, 1942), the power function is unnecessarily laborious and, with the exception of ontogenetic comparisons, this method has been largely abandoned in allometric comparisons in favour of regression models. Gould (Gould, 1966:595) championed the use of regression models in allometric analyses primarily because any deviation of the y-axis from zero indicates allometry. More crucial, however, was the retreat in comparative biology from the theoretical premise that the constants of the power equation were equivalent to general "laws" (see Reeve & Huxley, 1945; Jungers, 1984, 1985).

Allometry is thus an invaluable, but not infallible, "descriptive tool of gross morphology" (Giles, 1956). The ongoing (and as yet unresolved) debate surrounding the issue of whether to use Model I or Model II regression formulae (Teissier, 1948; Kermack & Haldane, 1950; Jolicoeur, 1963, 1975; Ricker, 1973; Kuhry & Marcus, 1977; Wolpoff, 1985; Aiello, 1992; Smith, 1993) in allometric analyses perhaps best illustrates the warning that "the presentation of allometric exponents and constants is not equivalent to an explanation" (Jungers, 1984:78). Except in cases where the correlation coefficient approximates 0.9 or above, Least-Squares, Major Axis and Reduced Major Axis regression models (and their residuals) cannot be considered to be equivalent (Rayner, 1985; Aiello, 1992). Nevertheless, the continued reification of regression exponents in explanations of "structural scaling" phenomena (e.g., McMahon, 1973, 1975*a*,*b*; Alexander *et al.*, 1979*a*; Jungers, 1984, 1985, 1988, 1990; Christiansen, 1999) and "evolutionary changes in size and shape " (White & Gould, 1965; Gould, 1966, 1971, 1975) remain common.

Indeed, one such specific hypothesis is that relative proportions will remain constant with increasing size. This is referred to as *Isometry*, and residual variation around the slope (relative to body weight the slope of y/x will be 0.333 [Alexander, 1981; Jungers, 1988, 1990]. White & Gould (White & Gould, 1965) have proposed that positive or negative allometric deviations in the relative parts (quantified by residual variance on the dependent [y] axis) might reflect evolutionary or "structural scaling" modifications to organismal morphology with increasing body size (see also Gould, 1971). This is perfectly illustrated by the example of theoretical approaches to structural scaling in mammalian long bones (see below). Nevertheless, as Gould (Gould, 1971:129) has cautioned "...geometric similarity is a problem, not an expectation".

Growth is a multiplicative process (Huxley, 1924, 1932; Laird, 1965, 1966*a*,*b*; Laird *et al.*, 1968; Barton & Laird, 1969; Tanner, 1989; Healy & Tanner, 1981), and differences in adult vertebrate skeletal morphology (e.g., limb proportions, craniofacial morphology) are probably synonymous reflections of differences in relative morphogenetic processes (see Schultz, 1926*a*,*c*, 1973; Shea, 1985, 1988, 1989, 1993). Nevertheless, statements relating to the nature and timing of the appearance of observed morphological differences during ontogeny cannot be resolved from static allometric comparisons (Cheverud, 1982; Shea, 1981, 1985, 1988, 1989, 1993). Only embryological and comparative ontogenetic studies yield insights in to problems of evolutionary morphological divergence (e.g., White & Gould, 1965; Gould, 1977; Alberch *et al.*, 1979; Shea, 1989, 1993), In this "evolutionary ontogenetic" context, allometry is both a *method* and a *process*, nevertheless, we must proceed from the assumption that "evolutionary *k* is generally not equal to ontogenetic *k*" (Cock, 1966:184). The constants are not phylogenetic correspondences.

The multivariate extension of the allometry equation proposed by Jolicoeur (Jolicoeur, 1963; Jolicoeur & Mosimann, 1960), involves decomposition of the variance-covariance matrix of a series of metrical variables using Principal Components Analysis. While this approach has been subjected to extensive criticism in its two dimensional form (Major Axis Regression; see Ricker, 1973; Rayner, 1985; Aiello, 1992), the application of Principal Components Analysis to ontogenetic and static allometry problems has been extensively pursued during the past 40 years (Mosimann and Jolicoeur, 1960; Guttman & Guttman, 1963, 1965; Gould, 1965; Alberch *et al.*, 1979; Shea, 1981, 1984, 1985; Shea and Bailey, 1996). Jolicoeur (Jolicoeur, 1963; see also Mosimann & Jolicoeur, 1960) has asserted that the first Principal Component of a variance-covariance matrix represents an axis of generalised 'size', if the component loadings of individual variables uniformly high and positive. Given that the second Principal Component lies orthogonal to, and is thus independent of, the first Principal Component (Blackith and Reyment, 1970; Reyment, 1994; Flury, 1988), PC2 has often been cited as a 'shape' component (Alberch *et al.*, 1979; Shea, 1981, 1985). Recent developments, such as Common Principal Components (CPC) analysis allow statistical comparison of a series of group specific principal components (Flury, 1988; Arioldi & Flury, 1988; Klingenberg, 1996; Steppan, 1997*a,b*; Arnold & Phillips, 1999; Phillips & Arnold, 1999) of n>2 covariance matrices, with great promise for allometry (see especially Klingenberg, 1996).

1.1.2 Structural scaling hypotheses in Mammalian functional morphology

Theories of Geometric and Elastic similarity make explicit predictions about the nature of scaling relationships in the limbs of mammals with respect to applied forces engendered by differential (i.e., allometric) size constraints. "Geometric" similarity (Galilei, 1638; McMahon, 1973, 1975*a,b*; Alexander, 1977, 1985*a,b*; Economos, 1983) proposes that as animal body size increases, resistance to failure (i.e., buckling) during loading in the limb bones decreases as a direct consequence of changing area/volume relationships. Briefly stated, the total load supported by a column liable to bending varies inversely with the second power of length under Euler's theorem (see also McMahon, 1973, 1975*a,b*).

As skeletal structures are scaled up, area/volume proportions decrease as the 2/3 (0.66) power of any change in linear dimensions (e.g., length). Given that resistance to stress acting at a particular section is directly related to cross-sectional area (or diameter), and that force must be meaningfully proportional to weight (or volume), then mechanical constraints would engender a limit to absolute body size increase with respect to safety factors during loading. Geometric similarity (or "similitude") is thus equivalent to Isometry. That is, the length and diameter of the limb bones in a large range of mammals regressed on body weight would be expected to yield bivariate scalar constants (slopes) of 0.333 (Alexander *et al*., 1979*a*).

McMahon (McMahon, 1973, 1975*a*,*b*) has proposed that the scaling of the length and diaphyseal proportions in artiodactyls, together with the principal force characteristics for the "bending" of the trunk in mammals, confirm Euler's theorem with respect to *elastic* buckling. Under the "elastic similarity" hypothesis (McMahon, 1973, 1975*a*,*b*) or the "Galileo-Rashevsky" principle (Economos, 1983), the length of a long bone is proportional to the 0.75 power of the diaphyseal diameter, indicating that resistance to bending and torsional stresses in the diaphysis is *proportionally increased* relative to length with increasing body mass (McMahon, 1973, 1975*a*,*b*; see also Selker & Carter, 1989). Relationships between the two variables, and with body mass are thus allometric, not isometric, indicating a change shape with increasing body size in order to withstand stresses during loading.

Alexander and his colleagues (Alexander, 1977, 1985; Alexander *et al*., 1979*a*) computed linear regression solutions for limb bone lengths and diaphyseal midshaft diameter against body mass within the *Mammalia* in an explicit test of the "geometric" and "elastic" similarity hypotheses (Alexander *et al*., 1979*a*; see also Alexander, 1985*a*,*b*). While they (Alexander *et al*., 1979*a*), determined that extant primates did not deviate noticeably from the "mouse to elephant" solution with respect to midshaft diaphyseal proportions, relative humeral and femoral lengths were considerably greater in primates than in fissipeds or bovids (Alexander, 1985; Alexander *et al.*, 1979*a*). Relative length of the tibia and metatarsals in primates are discernibly less elongate relative to the proximal segment of the lower limb (Alexander *et al.*, 1979*a*).

With mean scaling functions [slopes] of 0.35 and 0.36 for length and diameter respectively (All elements), Alexander and his colleagues (Alexander *et al.*, 1979*a*; Table 3; Alexander, 1985*a*,*b*) concluded that their data suggests scaling relationships of length and diameter in mammalian long bones that are more in accordance with predictions based on "geometric similarity" (i.e. Isometry = 0.333), than "elastic similarity" ($L = 0.25*W$ & $D = 0.38*W$ [McMahon, 1973, 1975*a*,*b*]). Alexander (Alexander, 1985*b*) does concede that the elastic similarity hypothesis may explain structural adaptations to mechanical stresses in the drunk during gravitational loading. Nevertheless, Alexander (Alexander, 1985*b*) has cautioned morphologist's that, "It seems unprofitable in any case to persist in looking for similarity principles. There is no reason to expect evolution to seek similarity as such...Until we have a theory of scaling that explains body proportions in some such terms, our theories will be unsatisfactory" (Alexander, 1985*b*:37).

This first part of this cautionary lament has been reinforced by the results of a comprehensive allometric analysis of relative limb proportions in mammals by Christiansen (Christiansen, 1999). His study (Christiansen, 1999) revealed the existence of differential scaling relationships within the *Mammalia*. Slopes were consistently steeper in smaller mammals relative to large mammals, suggesting adherence to a "geometric", rather than an "elastic", scaling phenomena in smaller mammalian species (Christiansen, 1999). Interestingly, these differences are apparently more pronounced in the distal limb segments (Christiansen, 1999). Unfortunately, Christiansen (Christiansen, 1999) provided no quantitative data on body mass for the species included in his analysis, which precluded the statistical analysis of both relevant parameters independent to an appropriate physiological and functional baseline (e.g., Alexander, 1977, 1985*b*; Alexander *et al.*, 1979; Jungers, 1984, 1985; Ruff, 2002, 2003).

Observed variability in locomotor repertoire and in the relative limb proportions of extant hominoids (Mollison, 1911; Schultz, 1926*a,b*, 1930, 1937; Ashton *et al.*, 1975; Oxnard, 1975, 1983; Stern & Oxnard, 1973; Jouffroy & Lessertisseur, 1979; Preuschoft, 1979; Preuschoft *et al.*, 1998; Jungers, 1984, 1985; Demes & Günther, 1989; Günther *et al.*, 1992), dictate that standardised theoretical scaling coefficients cannot strictly apply (see Jungers, 1988*a*; Ruff, 2002). While there is evidence that diaphyseal proportions (e.g., diameters, circumferences, cross-sectional areas) are positively allometric with body mass (Steudel, 1981*a,b*, 1985; Hartwig-Scherer, 1993, 1994; Ruff, 2003) in anthropoid primates, long bone lengths display negative allometry with body mass and body length (Steudel, 1982*a,b*, 1985; Jungers, 1984, 1985; Konigsberg *et al.*, 1998; Hens *et al.*, 1998, 2000).

Extant *Homo* differs from *Pan* and *Gorilla* in the relative proportions of the upper and lower limb, particularly the proximal segments (Mollison, 1911; Schultz, 1926*a,b*, 1930, 1937; Ashton *et al.*, 1975; Oxnard, 1975, 1983; Stern & Oxnard, 1973; Jungers, 1984, 1985). However, no such differences exist in the distal segment proportions of the lower limb (tibio/femoral) in the African apes. This contrasts with the obvious differences in brachial indices (Mollison, 1911; Schultz, 1926*a*,*b*, 1930, 1937; Ashton *et al.*, 1975; Oxnard, 1975, 1983; Jungers, 1984, 1985). Nevertheless, do significant scaling differences exist in the relative proportions of the locomotor skeleton (epiphyseal joints, diaphyseal area parameters) in the extant African apes (*Pan*, *Gorilla* & *Homo*), and can these be profitably related to mechanical demands consistent with both locomotor and relative size (body size and body shape) constraints?

1.2 Perspectives on the evolution of the hominid locomotor system

1.2.1 Introduction

This contribution considers several aspects of functional morphological variability in the extant hominoids. The specific aims of this study were two-fold. Firstly, to establish the underlying nature and basis of morphological variability in the hominoid skeleton with particular reference to locomotor adaptations (e.g., *Homo* V's *Pan* & *Gorilla*), and the influence of absolute and relative body size on skeletal proportions and morphological form (*Homo*). A second, but related aspect of the anlyses sought to utilise the extant data as a morphological framework for interpreting ambulatory and non-ambulatory locomotor behavioural distinctions in extinct fossil hominids, particularly *Australopithecus* and "archaic" *Homo*. Taken together, the overall "goal" of this study was to yield further insights in to proposed "patterns" of morphological evolution in the locomotor skeleton of extinct hominids.

Functional Allometry of the Locomotor Skeleton.

This analysis focuses upon the functional implications of observed differences in the relative scaling of the epiphyses and diaphyses of the upper and lower limb of the extant African hominoids (*Gorilla*, *Pan* and *Homo*), and compare patterns of geometric variability in the elbow joint and proximal femur of extant hominids will be determined using 3D scaling methods that isolate overall size effects. Patterns of geometric shape variability are expected to yield crucial information relating to locomotor *habitus* (Ohman *et al.*, 1997; Lovejoy *et al.*, 2002), and hypothesised behavioural diversity in extinct hominids, particularly *Australopithecus* and the Eurasian Neandertals.

The consequential effects of observed variation in body size and body shape upon the morphology of the pelvis and lower limb in recent *Homo* and Plio-Pleistocene fossil hominids will be assessed in a final section of this analysis. The aim of these analyses was to explicitly test a series of hypotheses relating to morphological integration in the hominid pelvis and its functional consequences. It is envisaged that this approach will shed light on aspects of morphological evolution in the pelvis of extinct fossil hominids, particularly *Australopithecus* and *Homo neanderthalensis*, and provide insights in to proposed distinctions in locomotor function. Prior to the presentation of the specific hypotheses to be addressed in this analysis, a discussion of the evolution of the locomotor system of extinct fossil hominid and behavioural interpretations of these morphological transformations will be presented.

particularly in the upper limb. While there is a sound basis for inferring different epigenetic profiles for the developmental history of the epiphyses and diaphysis of any specific long bone (e.g., Ruff, 1990; Ruff *et al.*, 1991; Ruff *et al.*, 1993; Lieberman *et al.*, 2001), there exist profound underlying similarities in their broad generative histories (e.g., Kimura, 2002).

Jungers (1988*a*, 1990) presented evidence relating to the adaptive nature of observed distinctions in relative joint size in the upper and lower limbs (hereafter referred to as "distributive profiles") of extant and extinct hominoids. Recent humans contrast with all extant hominoid taxa by virtue of their uniformly large lower limb epiphyses, an obvious adaptation to bipedal progression in our species. In contrast, the extant hominoids, particularly *Pan* and *Gorilla*, were characterised by uniformly large upper limb epiphyses, most notably the components of the elbow complex and the distal radius. The latter almost certainly has a functional role in dissipating forces in the radio-carpal joint during ground contact of the flexed hand in pronograde terrestrial knuckle walking (Jenkins & Fleagle, 1975).

In contradistinction to the distributive profile observed in recent humans, Jungers (Jungers 1988*a*, 1991) observed that the diminutive *Australopithecus afarensis* female, AL 288-1 ("Lucy") had relatively smaller lower limb epiphyses, especially the relative size of the femoral head. Ruff (Ruff, 1998) has proposed that the relative size of the femoral head of the AL 288-1 partial skeleton is not relatively smaller than would be typical of a human of similar body size. However, Ruff (Ruff, 1998) argues that confounding relationships in the pelvo-femoral complex of

1.2.2 Relative proportions of the epiphyses and diaphyses

Following theoretical expectations (Pauwels, 1980; Paul, 1967, 1976; Frankel & Burstein, 1970; Nordin & Frankel, 1989*a,b*; Alexander, 1980; Ruff, 1988, 2002, 2003), a strict allometric relationship is to be expected between increasing body mass and the surface area (or some linear proxy) of a weight-bearing articular surface. Locomotor classifications of previous workers (e.g., Napier & Napier, 1965; Napier & Walker, 1967*a,b*; Ashton & Oxnard, 1964; Stern & Oxnard, 1973), support the existence of *a priori* distinctions in the postcranial skeleton of recent *Homo* and the extant African apes, and that these should meaningfully reflect observed differences in limb use during locomotion. Ruff (Ruff, 2002, 2003) has demonstrated that significant scaling differences exist in the relative proportions of forelimb and hindlimb epiphyseal dimensions of extant hominoids (*Hylobates*, *Pongo*, *Pan* & *Gorilla*) relative to diaphyseal shaft strength. The Asian hominoids (*Hylobates* & *Pongo*) display relatively greater proximal humeral and femoral epiphyseal area relative to *Pan* and *Gorilla* when expressed as a proportion of relative shaft strength (Ruff, 2002). It is likely that these scaling differences are a reflection of increased compressive/tensile stresses in the forelimb and hindlimb of the Asian hominoids relative to the African apes. However, this may merely be a function of phyletic inertia.

In the case of extinct hominids, such distinctions may primarily reflect fundamental differences in gait and posture (as proposed by some worker's for *Australopithecus*), or they may simply reflect different habitual loading intensities engendered by elevated or diminished activity levels or discreet behaviours, *Australopithecus afarensis* would have mediated a *relatively larger* femoral head than is typical in a human of her body size if this species was a facultative biped.

Obvious differences exist in the loading patterns of the upper limb within the extant African hominoids that can be directly related to observed differences in locomotor habitus within and between species (e.g., Ashton & Oxnard, 1964; Ashton *et al.*, 1975; Oxnard, 1975, 1983; Senut, 1981*a,b,c*; Senut & Tardieu, 1985; Taylor, 1995, 1997). Whereas *Pan* and *Gorilla* routinely subject their upper limb and pectoral girdle to tensile (during climbing) and compressive (during terrestrial progression) forces, recent and fossil members of the genus *Homo* do not directly employ their upper limbs during locomotion. However, as outlined earlier, there is growing concern among researchers that traditional feedback models characterising the loading history of a skeletal element and its observed morphology may be too simplistic (e.g., Ohman & Lovejoy, 2001; Ohman *et al.*, 2000; Lovejoy *et al.*, 1999, 2002; Currey, 2002). Nevertheless, observed differences in the pattern of force transmission during locomotion should leave an indelible impression upon the components of the locomotor system (i.e., muscles and bone), particularly in environmentally labile constituents (e.g., diaphyseal cortical bone [Ruff *et al.*, 1993, 1994; Trinkaus *et al.*, 1994; Ohman *et al.*, 1997; Lieberman *et al.*, 2001]), but also in epiphyseal morphology (e.g., Rose, 1983, 1988; Harrison, 1989; Schmitt, 2003).

The mechanical expectations engendered by such radical differences in forelimb use in terms of relative joint "size" and diaphyseal "robusticity" have been outlined in an earlier section of this chapter. Predicted differences in epiphyseal shape in the upper limb between taxa, even those engaging in such distinct postural repertoires, are generally more difficult to elucidate. Several crucial aspects of the developmental history of diarthroidal joints renders them particularly suitable to form-function investigation's (e.g., Murray, 1926; Fell & Robison, 1929; Fell & Canti, 1934; Warren, 1934; Haines, 1947; Ruff *et al.*, 1991; Ruff *et al.*, 1993; Lieberman *et al.*, 2001). Significant morphological shape differences are hypothesised to exist in both the distal humerus and proximal ulnar epiphyses of the extant African hominids. *Pan* and *Gorilla* are predicted to share underlying morphological similarities in their epiphyseal geometry due to shared locomotor patterns. Indeed, if this expectation is supported then it will further embellish the functional valence of epiphyseal shape differences between *Pan*, *Gorilla* and the *Hominini*, as the former are no longer considered to be an inclusive natural group.

There has been considerable debate concerning the inferred role of the upper limb in the locomotor repertoire of *Australopithecus afarensis* (i.e., Stern, 2000; Stern & Susman, 1983; Susman *et al.*, 1984, 1985), and clear distinctions in the articular morphology of the distal humerus and proximal ulna of specimens allocated to *Australopithecus* have been cited (Senut, 1981*a,b,c*; Senut & Tardieu, 1985; McHenry & Corruccini, 1978; Aiello *et al.*, 1999). Several recent studies have identified subtle deviations from recent humans in the distal humeral and proximal ulnar articular morphology of Eurasian Neandertals (e.g., Churchill *et al.*, 1996; Pearson *et al.*, 1998; Yokely & Churchill, 2002; but see Groves, 1998), which possibly reflects increased stability of the elbow joint during flexion and extension. This morphological configuration has been viewed as a reflection of differential, behaviourally induced, loading regimes in the elbow joint in Neandertals and some earlier hominids relative to more recent humans. Furthermore, Yokely and Churchill (Yokely & Churchill,

2002) have proposed that the biological-behavioural feedback mechanism (e.g., Schmitt *et al.*, 2003) that promoted the distinctive morphology of the Neandertal elbow joint complex is consistent with the inferred phylogenetic status of Neandertals relative to *Homo sapiens*.

1.2.3 Functional morphological integration in the hominid lower limb

The hypothesised prevalence of 'ecogeographical patterning', such as Bergmann's and Allen's "rules" (Bergmann, 1847; Allen, 1877) in recent and fossil hominid's (Roberts, 1953, 1978; Roberts & Bainbridge, 1963; Ruff, 1991, 1994; Holliday, 1995, 1997*a*,*b*) makes specific predictions concerning the nature of geographical cline distributions in hominid gross physiognomy. Increases in body laterality (i.e., M-L pelvic breadth) will be expected to have important consequential effects on the scaling relationships of mechanical lever and load arms, and the "principal determinants of pelvic shape" (e.g., dimensions of the ilium, ischium and pubis). More importantly, under the "cylindrical model" (Ruff, 1991, 1993), increasing lateral pelvic breadth leads to an increase in body mass regardless of any subsequent increase in stature.

It has been proposed that observed differences in the functional morphology of the *Homo erectus* pelvis and proximal femur can be explained by an absolute elongation of the mechanical load arm for body mass (biacetabular diameter) in this species with respect to recent human population's (Ruff, 1995). Ruff (Ruff, 1995, 1998) has argued that the elongated femoral neck of early Pleistocene fossil hominids manifests a significant mechanical advantage relative to the condition seen in

Pliocene hominids (AL 288-1, *A. afarensis*; Sts 14, *A. africanus*). Biomechanical femoral neck length in *Australopithecus* is significantly shorter relative both to femoral length and the inter-acetabular distance of the anterior pelvis (Robinson, 1972; Lovejoy *et al.*, 1973; Lovejoy, 1988; McHenry & Corruccini, 1976; Jungers, 1991). Lengthening the proportions of the lever arm at the hip joint increases the mechanical advantage of the abductor muscles in addition to moderating the joint reaction force at the hip joint (Frankel & Burstein, 1970; Pauwels, 1980; Nordin & Frankel, 1989*b*). Thus, the proportions of the lever arm in *Australopithecus* are considered to be poorer mediatiors of hip joint reaction force than in *Homo erectus* (Ruff, 1995, 1998).

Ruff (Ruff, 1995) has further proposed that a functional relationship exists between the length of the pelvic load arm, degree of iliac flare and the development of the iliac ‘pillar’. All are hypothesised to be products of an absolutely large M-L (Bicristal) pelvic diameter. More crucially, the bending forces imposed upon the proximal femur occur predominantly in the M-L plane of the sub-trochanteric diaphysis. Thus, the functional anatomy of isolated proximal femora can yield crucial insights in to the nature of force transmission and morphological adaptation to bending stresses in various hominid taxa (e.g., Ruff *et al.*, 1993, 1994; Ruff & Trinkaus, 1999*a*,*b*; Trinkaus 2000*b*), and increasing the sample size provides additional evidence in support of the mechanical model (Ruff, 1995, 1998).

The anatomy of the Kebara 2 pelvis has confirmed the presence of certain morphological anomalies in Eurasian Neandertals (McCown & Keith, 1939; Trinkaus, 1983*a*, 1984*a*, 1988; Tompkins & Trinkaus, 1987; Rak, 1990*b*, 1991; Rak &

Arensburg, 1987). That Neandertals possessed absolutely and relatively long, antero-posteriorly narrow "tapered" superior pubic ramus and a large interacetabular distance relative to recent humans has long been observed. Bicristal and biacetabular diameter in the Kebara 2 Neandertal pelvis are considerably larger than is typical in recent humans, however recent evidence suggests that this may be the norm rather than the exception for earlier *Homo* (Walker & Ruff, 1993; Rosenberg 2001; Arsuaga *et al.*, 1999). In contrast to Trinkaus (Trinkaus, 1983), Walker (Walker, 1993) considers the Neandertals to possess an absolutely larger biomechanical femoral neck length than recent humans, thus moderating the mechanical disadvantages engendered by an absolutely larger inter-acetabular distance. There may be significant non-locomotor selection pressures on the allometric relationship of these variables.

In a comprehensive recent analysis of differences in traditional measures of postcranial robusticity recent and Middle-Upper Pleistocene *Homo*, Pearson (Pearson, 1997) established that patterns of robusticity throughout the postcranial skeleton are far from uniform, although some general distinctions emerge. Samples characterised by extreme levels of diaphyseal robusticity in the lower limb do not display, as a rule, extreme levels of diaphyseal robusticity in the upper limb (Pearson, 1997: Tables 5.7 & 5.8), although correlation's between the various "robusticity indices" calculated by Pearson (Pearson, 1997; table 5.2) were generally good. Proximate Anatomical elements (e.g., humerus and radius, radius and ulna, femur and tibia) yielded correlation coefficients that were stronger than with elements that were more anatomically distant (Pearson, 1997).

Neandertals, Upper Palaeolithic Europeans and high latitude recent human populations possess more "robust" lower limb elements (femur & tibia), than the Upper Pleistocene *Homo sapiens* sample from Skhul-Qafzeh. This supports the contentions of Ruff and his colleagues (Ruff *et al.*, 1993) that relative body size (among other factors) has a crucial impact on levels diaphyseal robusticity in the lower limb. In contrast, Eurasian Neandertals display only moderate levels of diaphyseal robusticity in the upper limb relative to both recent and Upper Pleistocene fossil hominids, particularly in their distal segments (Hartwig-Scherer, 1994; Pearson, 1997). The latter finding is extremely surprising as Neandertals display extreme abbreviation of their distal limb segments (or brachial indices) relative to their Eurasian Upper Pleistocene successors and many recent human populations (Holliday, 1995, 1997*a,b*, 2000).

Trinkaus and his long-term research have proposed that different *patterns* of loading leave diagnostic 'signatures' in hominid limb bones (Trinkaus, 1997; Trinkaus *et al.*, 1991; Trinkaus *et al.*, 1994; Trinkaus *et al.*, 1998*a,b*, 1999; Trinkaus & Ruff, 1999*a,b*; Trinkaus & Churchill, 1999; see also Ruff *et al.*, 1993). Generalised patterns of robusticity, such as external dimensions of a diaphysis or cortical area determined from its cross-section, primarily reflect magnitudes and frequencies of loading (i.e., intensity). Differences in cross-sectional shape reflects structural resistance to bending moments, which can be taken to be synonymous with long-term differences in, or genetic responses to, specific loading regimes (e.g., Ruff *et al.*, 1993; 1994, Trinkaus, 1997; Trinkaus *et al.*, 1998*a,b*; 1999). Both reflect "activity patterns" at some basic level (Pearson, 1997, 2000), but differences in shape are more informative in discerning subtle and more mechanically demanding behavioural changes, especially during childhood and adolescence (Ruff *et al.*, 1994).

Pearson (Pearson, 1997) also investigated differences in external diaphyseal shape and articular robusticity in recent and fossil *Homo*. Correlation coefficients for the matrix of long bone diaphyseal shape indices were generally low, even among neighbouring elements (e.g., femur and tibia, humerus, radius and ulna). The strongest correlation coefficient was returned for the platycnemic and midshaft indices of the tibia, a not surprising result given the topographical approximation of the nutrient foramen and the location of the midshaft (Pearson, 1997; table 5.10). A surprisingly low correlation exists between the pilasteric (midshaft) and platymeric (subtrochanteric) indices of the femoral diaphysis in Pearson's pooled sample (Pearson, 1997), although this is significant at the $p<0.001$ level of probability. It is possible that this low correlation might be a result of pooling such diverse geographical samples, which is consistent with the highly significant effects that group identity had in his 2-way ANOVA (Pearson, 1997; Table 5.11). These findings underscore the need for a comprehensive analysis of purported functional relationships between anterior pelvic morphology and femoral diaphyseal morphology (e.g., Ruff, 1995) in recent and fossil *Homo*.

Chapter 2. Hypotheses to be tested

2.1 Introduction

Interspecific and intraspecific allometry manifests structural interrelationships established during pre-natal and post-natal ontogeny. Relative scaling differences between closely related organisms might be profitably equated with functional adaptation, particularly in the locomotor system. Morphological "adaptations" are defined by explication to observed differences in postural and locomotor behaviours in extant taxa (e.g., Oxnard, 1975, 1983; Zuckerman *et al.*, 1973; Schmidt, 2003). Nevertheless, mechanical constraints are not the sole mediators of skeletal morphology in terrestrial vertebrates. Phylogenetic (i.e. morphogenetic) constraints upon morphological integration are crucial dictates of structural covariance in complex anatomical units, such as the diarthroidal joints and the pectoral and pelvic girdles of the mammalian skeleton. Thus, phylogentic constraints not only manifest ancestral adaptive morphological histories (e.g., Alberch *et al.*, 1979; Shea, 1984, 1988, 1989), they also dictate limits to morphological potential in vertebral structural design (e.g., Lockwood & Fleagle, 2000). The external geometry of the organism and its constituent parts, or "body size and body shape", would be expected to have significant structural consequences for three-dimensional skeletal structures, such as the mammalian pelvic girdle. Therefore, analyses of allometric scaling relationships within the pelvic girdle of recent hominids can potentially yield crucial insights in to hypotheses concerning functional (i.e. mechanical) equivalence in extinct hominids that differ notably in absolute body size and in their relative skeletal proportions (e.g., *Australopithecus afarensis* and *Homo erectus* [Ruff, 1993, 1995, 1998]).

Three specific research foci have been identified. The first considers the functional implications of differences in the relative scaling of long bone epiphyses and diaphyses, a second constitutes an exploratory investigation in to patterns of geometric variation in selected upper and lower limb epiphyses, and a final section of focuses upon patterns of morphological integration in the pelvic girdle and lower limb in bipedal hominids. The following hypotheses will be tested in this thesis.

*Ho*1: The extant African apes are expected to display proportionally larger upper limb epiphyses and diaphyses and proportionally smaller lower limb epiphyses and diaphyses than *Homo.*

*Ho*2: No significant differences exist in the relative size of the lower or upper limb epiphyses *within* recent humans, whereas differences in the relative size of the diaphyses will be more apparent. These differences are expected to be manifest to a greater degree in upper limb, rather than lower limb.

*Ho*3: If *Australopithecus afarensis* (AL 288-1) was habitually adapted to terrestrial bipedal locomotion, then this species should display an epiphyseal "distributional profile" that more closely approximates that of *Homo* rather than *Pan* or *Gorilla.*

*Ho*4: The principal dimensions of the *Ossa Coxae* (ilium, ischium, pubis and sacrum) will be significantly correlated with changes in M-L pelvic breadth in recent *Homo.*

*Ho*5: Following Ruff (Ruff, 1995, 1998) a significant functional relationship is proposed to exist between the load arm/lever arm proportions of the hip joint and femoral diaphyseal shape (Area/ML & Area/AP indices) in recent humans.

*Ho*6: The observed differences in femoral midshaft and subtrochanteric proportions in *Australopithecus* and archaic *Homo* (including Neandertals) are primary consequences of proposed distinctions in anterior pelvic proportions and increased hip joint reaction force related to increased body size.

Chapter 3. Materials & Methods

3.1 Sampling Methodology

The most important factor determining sampling methodology was the need to effectively sample the entire range of body size and body shape variation within *Homo sapiens*. In order to achieve a representative sampling of body size and body shape variation in extant *Homo*, samples from different geographic regions of the Old and New World were subjected to metrical and landmark survey. With respect to the extant African apes, it was decided to concentrate on the broad specific divisions within the *Hominoidia* (*Pan paniscus*, *Pan troglodytes* and *Gorilla*). Western Lowland gorilla (*Gorilla g. gorilla*) and *Pan. t. troglodytes* subspecies, both from West-Central Africa, were included in this analysis.

A further requirement was that the specimens within the chosen samples should be relatively well preserved, possessing a fairly complete pelvis and/or the majority of the long bone elements that were necessary for the effective completion of the study. In the end, the samples included within this study are far from ideal, and further sampling of *Homo*, *Pan* and *Gorilla*, together with *Pongo*, will greatly enhance the project. However, due to financial and time constraints an extended period of sampling was simply not feasible. Nevertheless, the final sample inventory fulfils the primary expectations of the experimental design employed in this analysis.

3.1.1 Metrical Variables

In order to test the hypotheses outlined in Chapter 2, a series of simple linear dimensions of the *Ossa Coxae*, and the epiphyses, diaphyseal circumferences and M-L and A-P proportions of the long bone elements were collected on individual skeletons using Mitutoyo™ digital calipers and a Paleo-tech Concepts™ osteometric fieldboard and flexible measuring tape. The majority of these variables are listed in the "Osteometrie" section of the most recent edition of R. Martin's standard text (Bräuer, 1988; Knußmann, 1988) and were measured according to standard protocol. A complete inventory of the linear measurements included in this analysis is detailed in Appendix I with accompanying diagrams. Sample means for these variables are given in Appendix III. Tests for intra-observer replication error for the linear variables are reported in the appropriate section below. The archaeological samples included in this analysis were sexed using standardised comparative assessment of morphological variation of the inferior pubic ramus and the sciatic notch (e.g., Phenice, 1969; Bass, 1986; White, 1991, 1998; Day & Pitcher-Wilmott, 1975).

3.1.2 Landmark Co-ordinates

A series of 3-dimensional landmark co-ordinates were collated in order to 'capture' difference in epiphyseal geometry of the distal humerus, proximal ulna and proximal femur in all suitably preserved recent and fossil specimens. Graphical illustration of the derivation of the landmark coordinates used in this analysis and their resulting "wireframe" renderings are given in Appendix II.

3.2 Materials

3.2.1 Extant Samples

Recent Human "Macro-Sample" (*n*= 162; M= 115/F=45)

The recent human "Macro-Sample" is a composite sample that represents almost the entire range of "body size" variation within recent *Homo*. The aim of assembling the "Macro-Sample" was to construct a 'constrained' test of size-dependent allometry. The sample is composed chiefly of two Museum collections; The Rudolf-Virchow Sammlung (*n*=61) and the collections of the Natural History Museum, UK (*n*=32). Additional material was derived from the collections of the Maxwell Museum of Anthropology (*n*=14), the Museé de L'Homme (*n*=7) and the National Museum of Natural History (*n*=6). To this "core" of 120 specimens was added the entire African Pygmy (*n*=17) and Southeast Asian Negrito (*n*=25) samples, which are detailed below, were added.

The geographical constitution of the "Macro-Sample" is listed in Table 1. When the African Pygmy and Southeast Asian Negrito samples are excluded, the maximum subset samples are the Caucasus Tartars (*n*=15), the OMI Historic sample (*n*=14) and the Native British Columbian's (*n*=12). These four samples constitute 10.49%, 15.43%, 9.26%, 8.6% and 7.41% of the effective sample size, respectively. Approximately 49% of the remaining individuals derive from geographic localities that constitute less than 3.5% of the total sample constitution. Considerable care was taken to ensure that subset samples with extreme physiques (e.g., Inuit, Nilotics, Australian Aborigines) were excluded from the "Macro-Sample". This effectively constrains variation in "body shape" within the sample. However, some variation in body shape will be inherent in the remaining samples. It is likely that this will be size-dependent.

Preservation in this sample is generally excellent and 138 specimens possess associated pelvic material of which 129 preserve their diagnostic pubic morphology. A majority of the specimens in the Virchow Collection had sexes assigned to them, whereas the remaining collections rarely did (the exception being the specimens from the Smithsonian Institute). Close inspection of the specimens in the Virchow Collection corroborated pre-assigned gender in nearly all cases (the exceptions being those to which no gender had been assigned). For the remaining samples, the morphology of the pubic symphysis or the greater sciatic notch was employed in gender attribution.

African Pygmies (*n*=17; M=10/F=7)

The African Pygmy sample included in this study is a composite collection of individuals derived from the osteological collections of several Institutions. These are the Institute of Anthropologie, Université de Genéve (*n*=5), the National Museum of Natural History ([Smithsonian Institute] *n*=5) and the Institut Royale de Sciences Naturelle de Belgique (*n*=6). A single female skeleton was measured at the Natural History Museum, UK. This sample was assembled over a period of some 18 months during various fieldwork visits (April 2000-December 2001). Information on the geographical provenience and ethnic affiliations of this sample were not available, although it is likely that the collection samples Efe, Mbuti and Akka Pygmy groups.

Southeast Asian Negritos (*n*=25; M=19/F=6)

The Southeast Asian Negrito sample is another composite sample derived from the collections of several Institutions including the Museé de L'Homme (*n*=19), the Rudolf Virchow Sammlung (*n*=5). All specimens are derived from localities in the Philippine Islands. This material was measured at the Humboldt Universitat, Berlin and the Museé de L'Homme, Paris in February 2000 and July 2001.

South African Bantu (*n*=60; M=30/F=30)

The Bantu sample included in this analysis is derived from the Raymond Dart Collection and is housed in the Dept. of Anatomical Sciences, University of the Witwatersrand. This collection was measured in July 2000. The sample consists of roughly equal numbers of Xhosa (*n*=28) and Zulu (*n*=24) tribal groups, with small additional individuals of Soto, Ndeb, Kala and Venda tribal status. Statistical comparison of the four long bones (Humerus, Radius, Femur & Tibia) of the Xhosa and Zulu samples using *t*'-tests assuming unequal sample variances (Sokal & Rohlf, 1995) indicated that differences between the sub-samples were not statistically significant (*p=0.05*), and these were pooled accordingly. The recent human specimens in the R.A. Dart collection are the remains of individuals who voluntarily bequeathed their cadavers to the University of the Witwatersrand Medical School. All individuals in the Dart Collection lived in the District of Johannesburg. The records of the Dart

Collection accurately record age-at-death and sex status, in addition to the tribal affiliation of the individuals.

Medieval Hungarians ([Magyars] *n*= 50; M=26/F=24)

The specimens are the remains of individuals recovered from the burial site of Tizafured-Nagykenderfoldek, Northeastern Hungay, which has been securely dated to the late 10th Century AD (Fóthi, 1996, 2000; Fóthi & Fóthi, 1996). These individuals represent the earliest phases of the Slavic migration and settlement of Central-Eastern Europe (Magyarsk), from which a majority of present-day indigenous Hungarians (Magyars) are derived (Fóthi, 1996, 2000; Fóthi & Fóthi, 1996). The material is housed in the Dept. of Anthropology, The Hungarian Natural History Museum, Budapest, and was measured in October 2000. The skeletal material is in a generally excellent state of preservation and 47 individuals (94%) of the sample have associated pelvic material with which reliable sex-assessments could be reached. With regards to sexing of the specimens, some 47 individuals (80%) preserved the pubic region, which was preferred over the sciatic notch in gender assessment. Those few individuals lacking associated pelvic material were allocated sex by Discriminant Function Analysis using the lengths, circumferences and epiphyseal dimensions of the upper limb elements (Humerus, Radius & Ulna) of individuals whose gender could be reliably determined by diagnostic pelvic criteria.

Saint Mary's Church ([Coventry] *n*=38/M=25/F=13)

The skeletal remains from St. Mary's Church, Coventry, date from the Late 18th Century to the Mid 19th Century and was recovered during controlled exhumation as part of a rescue project by researchers and volunteers from the Coventry Archaeological Field Unit and the University of Leicester. A small sub-section of the material is currently housed in the School of Archaeological Studies and the School of Pre-Clinical Sciences, University of Leicester under the direction of Dr. Jennifer Wakely. The deliberate burials represent the remains of an urban populace in an early Industrial context. A majority of the individuals in the Cemetery engaged in some form of industrial labour or commercial activity. Many of the specimens were found in lead-lined coffins with associated coffin plates inscribing the name of the individual and their approximate age-at-death. Unfortunately, the remaining specimens have now been reburied. As with the archaeological material from Hungary, sex-assessments were primarily based upon the morphology of the pubic ramus, however the morphology of the sciatic notch was consulted where necessary. This material was studied at the University of Leicester in December 2000 and January 2001.

Caucasus Tartars (M=15)

The small sample of male Tartars was used exclusively in the analysis of relative epiphyseal and diaphyseal proportions. These individuals are housed in the Rudolf-Virchow Sammlung, Humboldt Universitat, Berlin. All individuals were collected from the Caucasus region of Russia, including a single individual from Armenia. These individuals were measured in late February, 2000.

Australian Aborigines (*n*=30; M=21/F=29)

The Australian Aboriginal osteological sample is derived from a number of Institutions, most notably the collections of the Natural History Museum, UK (*n*=12) and the National Museum of Natural History ([Smithsonian Institute] *n*=13). Three skeletons from the American Museum of Natural History and a single individual in excellent condition from the RISNB, Bruxelles, were studied. This material was measured over a period of one year (April 2000-April 2001). With the exception of a few outstanding specimens, the sample included here represents the entire series of Aboriginal Australian postcranial specimens in Western Institutions. The geographic provenience of some of the specimens, particularly those from the NMNH, is known. Unfortunately, specimens are derived from locations that are geographically dispersed from the Northern Territories to Tasmania. There is absolutely no basis for inferring that this collection of individuals represents a 'sample' in anything other than a statistical sense, and even then there may be considerable problems in amalgamating such individuals (see Macho & Freedman, 1987).

In their analyses, Macho and Freedman (Macho & Freedman, 1987) employed univariate and multivariate statistical approaches to assess levels of significance of anthropometric data taken on several Aboriginal tribes by A.A. Abbie. They (Macho & Freedman, 1987) rejected the null-hypothesis of homogeneity between the Australian aborigines included in their analysis. However, an analysis of the mean data used in their analysis (Macho & Freedman, 1987), with data augmented from the literature (Gallagher, *unpublished study*), found that Australian Aborigines tend to 'cluster' together and away from other geographical recent human samples. The extreme 'linear' physique of Australian Aborigines is uniform throughout the continent and differentiates them from neighbouring Asiatic and Indo-European populations (Abbie, 1975; Eveleth & Tanner, 1976, 1990). The individuals included in this analysis all share these underlying similarities in body size and body shape and it was felt that the sample could be amalgamated on these grounds.

Southwest Amerindians (*n*=46; M=27/F=19)

The Southwest Amerindian skeletal sample included in this analysis is composed of two distinct Native American collections housed in the Maxwell Museum of Anthropology, University of New Mexico. The Southwest Amerindian sample was measured in April 2001. The largest sub-sample (*n*=30) derives from the pre-Pueblo deposits of the Late Prehistoric Pottery Mound site in the Rio Grande valley, North-Central New Mexico. The remaining sample consists of pre-Historic (i.e., pre-1840) burials of no discernible tribal affiliation from localities around Albuquerque and Santa Fe. There were no laws in New Mexico prohibiting the internment of individuals on private property, so Native American status cannot be assumed in the Historic individuals of the OMI collection in the Maxwell Museum. This is much less of a problem for the Prehistoric specimens, which predate the European expansions in the Western United States by a considerable time-span (Komar, *pers. comm*).

The preservation of the Southwest Amerindian sample is fairly good. Some 42 individuals (91.3%) possess associated pelvic material, but only 26 individuals (56.5%) preserve the morphology of the pubic region. As a result, far more of these individuals had to be sexed using the sciatic notch. The four remaining individuals were assigned gender on the basis of their posterior-probabilities in a DFA of the upper limb bone lengths and epiphyseal and diaphyseal parameters (see above). This method can accurately distinguish between the sexes.

Libben Amerindians (*n*=40; M=19/F=21)

The Late Prehistoric Woodland sample from Libben, Ohio (Lovejoy *et al.*, 1977) is housed in the Dept. of Anthropology, Kent State University. This material was studied in April 2001. A series of linear measurements collected by Katherine Russell and Brian Grafton were to be intended to be included the appendix to an edited volume on the skeletal biology of the Libben site (Lovejoy *et al.*, n.d.). This volume has not yet appeared in print. A copy of the data collected by Russell and Grafton was made available from Dr. Owen Lovejoy and were supplemented by additional required metrics. In all cases the pelvic measurements were re-measured to ensure consistency in the measurement protocol.

The preservation of this material is fairly good, and there is no post-mortem distortion and erosion of the specimens. Associated pelvic material was available for 33 individuals (82.5%) of which only 18 individuals preserved the inferior pubic ramus to facilitate sex assessment. Russell and Grafton (Russell & Grafton, n.d.) determined the gender of individual specimens using several techniques of varying degrees of accuracy in each case (Grafton, *pers. comm.*). Their seemed no *apriori* basis to question their judgement.

Pan paniscus **(*n*=18; M=11/F=7)**

Specimens of *Pan paniscus* are housed in the Museé Royale L'Afrique Centrale, Tervuren. The material was measured in February 2001. The effective sample sizes are far from desirable, however this collection is the single, largest sample of bonobos outside the Democratic Republic of Congo. Many of the specimens were obtained from the wild during the Belgian administration of Central Africa, whereas others are from the Zoological Park at Antwerp (Van Neer, *pers. comm.*).

Pan troglodytes **(*n*=44; M=19/F=25)**

The chimpanzee sample included in this study (*Pan t. troglodytes*) is permanently housed in the Powell-Cotton Museum, Birchington, UK. The sample was studied in August 2001. The collection was assembled under the direction of Major H. Powell-Cotton in the early 20th Century and consists of wild-killed animals from the Cameroons. This material was collected exclusively for Major Powell-Cotton by his agents in Western Africa, Mssrs. M. H. Merfield and W. Zenker, and comprise both individuals which died of natural causes and because of hunting by local human tribes (M. Harman, *pers. comm.*). The specimens were sexed in the wild prior to decomposition and additional notes with each specimen record several important personal details including external pathologies, colour of the hair and the extended length (crown-heel) of the individuals. The material is in excellent condition.

Gorilla gorilla (*n*=50; M=25/F=25)

The gorilla sample (*Gorilla g. gorilla*) was measured at the Powell-Cotton Museum in September 2001. M.H. Merfield collected wild-killed individuals from the territories of the Cameroons during the 1920's and 1930's. The material is in excellent condition.

3.2.2 Palaeontological Samples

Australopithecus anamensis/Australopithecus afarensis

A cast of the Kanapoi (KNM-KP 271) distal humerus (Patterson & Howells, 1967) was made available for study at the Natural History Museum by Prof. M.H. Day and Prof. C.B. Stringer. The original specimens are housed in the National Museums of Kenya, Nairobi (Leakey *et al.*, 1995). Casts of the Hadar specimens of *Australopithecus afarensis* (Johanson *et al.*, 1982; Lovejoy *et al.*, 1982*a*,*b*,*c*) were studied at the University of the Witwatersrand and the Cleveland Museum of Natural History. These data were re-checked using the casts at the Museé de L'Homme. The original specimens are housed in the Paleoanthropology Laboratory, National Museum of Ethiopia. I am particularly indebted to Dr. Jim Ohman for making available his cast of the reconstruction of the A.L. 288-1 pelvis by C. O. Lovejoy

(Lovejoy, 1988; Tague & Lovejoy, 1986, 1998). A cast of this reconstruction is on permanent loan in Dr. Ohman's laboratory.

Australopithecus africanus/Australopithecus robustus

The fragmentary and distorted elements comprising the partial female skeleton (Sts 14) of *Australopithecus africanus* from Sterkfontein (Broom, Robinson, & Schepers, 1950; Robinson, 1972) and the Sts 34 and TM1513 right and left distal femora from Sterkforntein were studied at the Flagship Memorial Trust (formerly the Transvaal Museum) in Pretoria. The intensive and ongoing exploration of the Sterkfontein deposits by researchers at the University of the Witwatersrand has yielded a substantial postcranial sample of *Australopithecus africanus*, much of which is currently awaiting publication (see Berger & Tobias, 1996; McHenry & Berger, 1998*a*,*b*; Häusler and Berger, 2001). The most promising of these new specimens is the partial male pelvis and upper limb skeleton (Stw 431), which may be of the order of c3-2.8 Myrs. old (McHenry & Berger, 1998*a*; Häusler, 2001; Berger *et al.*, 2002). This specimen comprises partial right clavicle, together with a right distal humerus and diaphysis with associated partial radius and ulna (McHenry & Berger, 1998*a*,*b*; Häusler, 2001). Neither of these two partial skeletons comprises sufficient elements of the upper and lower limbs to be included in this study as an individual (see, e.g., Chapter 4). Two proximal femoral specimens from Sterkfontein (Sts 99 & Sts 25) have been described by Häusler (Häusler, 2001), and the two proximal right femora attributed to *Paranthropus* (*Australopithecus*) *robustus* from Swartkrans (SK 82, SK 97) have been described in detail by Robinson (Robinson, 1972).

Koobi Fora specimens (*Australopithecus boisei/Homo sp.*)

Casts of the postcranial specimens from Koobi Fora were made available for study at the Natural History Museum, UK, by Prof. M.H. Day and Prof. C.B. Stringer. The original specimens are housed in the National Museums of Kenya, Nairobi. Several of the specimens can be confidently allocated to either *Australopithecus boisei* or *Homo habilis*, although several can only be assigned at the genus level alone (McHenry, 1994). The two most complete specimens are KNM-ER 1472 & ER 1481a are demonstrably *Homo*. Measurements and landmark inventories of these casts were re-checked with available specimens at the Museé de L'Homme Paris. Individual specimens are listed in Appendix 5. References for the original descriptions for these specimens can be found in Day (Day, 1986*b*).

Homo erectus

Casts of the femora from Trinil (Day & Molleson, 1973) and Zhoukoudian (Weidenreich, 1941), were made available at the Natural History Museum, UK, by Prof. M.H. Day and Prof. C.B. Stringer. The originals of these specimens are housed in the Senckenberg Institute, or were irretrievably lost. Casts of the Zhoukoudian femora can be obtained at the American Museum of Natural History. A cast of the subadult *Homo erectus* skeleton, KNM-WT 15000 was measured at Liverpool John Moores University and these data were re-checked against the available casts at the Museé de L'Homme, Paris and against the published metrics in Walker and Leakey (Walker and Leakey, 1993). The original specimen is housed in the National Museums of Kenya.

Homo heidelbergensis

The original specimens of the partial skeleton from Kabwe (Smith-Woodward, 1921; Pycraft *et al.*, 1928) and the proximal femur from Berg Aukas (Grine *et al.*, 1995) were measured at the Natural History Museum (UK) and the Dept. of Anatomical Sciences, University of the Witwatersrand (RSA), respectively. Casts of the available specimens from Tautavel ([Arago] de Lumley and de Lumley, 1982) were studied at the Natural History Museum and the Museé de L'Homme, Paris.

Homo neanderthalensis

The original specimens from the Feldhofer Grotto (Rheineisches Landesmuseum), Krapina (Croatian Natural History Museum), Fond-de-Foret, Spy D'Orneau (RISNB), Amud and Kebara (Sackler Faculty of Medicine, University of Tel-Aviv) were studied at their respective repositories. Unfortunately, none of the original Neandertal specimens from Institutions in France were available for study, so casts of La Chapelle-aux-Saints, La Ferrassie 1 & 2 and La Quina H5 were studied at the Museé de L'Homme, the Insitut de Paleontologie Humaine and the Dept. of Anthropology, University of New Mexico. Raw measurements of the Regourdou partial skeleton were taken from the comparative description of this individual (Vandermeersch & Trinkaus, 1995). Available casts of the Shanidar Neandertal individuals, studied at the National Museum of Natural History (Smithsonian Institute) and Museé de L'Homme, Paris were used for the landmark survey and for specific measurements designed for this study. The measurements in Trinkaus

(Trinkaus, 1983*a*) were used as the primary reference source for the Shanidar Neandertals.

Homo sapiens (Upper Pleistocene)

Early Upper Palaeolithic (*n*=25; *M*=15; *F*=4; *U*=6)

Upper Palaeolithic technologies appear in Eurasia during late Oxygen Isotope Stage 3 ([35-32 Kyrs BP] Straus, 1983; 1990; Mellars, 1988, 1990; Stringer & Gamble, 1993; d'Errico *et al.*, 1998; Klein, 1999; Foley & Lahr, 1997, 1998; Churchill & Smith, 2000*b*) and continue throughout OIS 2 (30-13 Kyrs) to the terminal phase of the last glaciation (Stringer & Gamble, 1993). The origins of the first recognised lithic tradition of the Upper Palaeolithic in Eurasia, the Aurignacian, cannot be confidently assigned to any particular hominid 'morph' (Gambier, 1989; Churchill & Smith, 2000*b*), although the continuity and geographic prevalence of this industry is clearly associated with *Homo sapiens*. Nevertheless, the early Aurignacian deposits at Vindjia (G1), which have been recently dated to 29.5-27 Kyrs (Smith *et al.*, 1999; Wild *et al.*, 2000; Paunovic *et al.*, 2001), are associated with Neandertals (Wolpoff *et al.*, 1981; Smith, 1984; Smith *et al.*, 1989; Ahern & Smith, 2002).

The oldest postcranial specimens of *Homo sapiens* from Eurasia are associated with Aurignacian and Gravettian Industries and are dated to between 32-24.5 Kyrs (Churchill & Smith, 2000*b*). The earliest specimens in Central Eurasia include the single partial humerus from Vogelherdhöle ([Vogelherdhöle III] Churchill & Smith, 2000*a*) and the upper and lower limb fragments from Mladec (Lautsch), which have been described in detail by Smith and his associates (Smith, 1984; Churchill & Smith, 2000*a,b*). These specimens are housed in the Dept. of Anthropology; Universitat Tüebingen and the Naturhistorisches Museum, Wien, respectively.

The partial skeletons from Sungir ([Sungir 1] Khrisanfova, 1984; Boulygina & Khrisanfova, 2000) and the Gower Peninsula ([Paviland 1] Green *et al.*, 2001), together with the Willendorf femur ([Willendorf 1] Teschler-Nicola & Trinkaus, 2001) and associated skeletons from Dolni Vestonice and Pavlov (Svoboda, 1988; Alt *et al.*, 1997; Trinkaus & Jelinek, 1997; Sladek *et al.*, 2000) are associated with Gravettian industries. Raw measurements of the now destroyed hominid sample from Predmosti, Moravia, were derived from Matiegka's (Matiegka, 1938) original study.

With the exception of the Predmosti, Sungir and Willendorf specimens, data for which were collated from the published literature, and the cast of the Vogelherdhöle III humerus, the original specimens were made available for study. These are housed at various Institutions, including the University Museum, University of Oxford (Paviland 1), the Archaeologiký Ústav, Akademie ved Ceské Republicky, Brno & Dolní Vestonice (Dolni Vestonice & Pavlov). Several of the Italian Early Upper Palaeolithic specimens were studied, including Barma Grande II and the Grotte des Enfants hominins. Barma Grande II is housed in the Museo Civico, Finale Liguria, and the Grotte des Enfants (Grotte Grimaldi) are permanently housed in the Musée d'Anthropologie Préhistorique, Monaco.

Late Upper Palaeolithic (*n*=27; M=14/F=7;U=6)

Sufficiently preserved remains of Late Upper Palaeolithic (c22-10 Kyrs) *Homo sapiens* are not more numerous than those from the Early Upper Palaeolithic when one ignores the substantial series of isolated specimens from the Arene Candide site. However, in order to maximise the sample sizes for the Generalised Procrustes Analysis (GPA) of upper and lower limb epiphyseal geometry in recent and fossil humans, the Arene Candide isolated specimens were digitised using a Microscribe 3DX digitiser (see below). A complete inventory of these specimens appears in Appendix IV.

Two LUP partial skeletons from the Ohalo and Nahal-Ein-Gev in the Levant ([Ohalo II]; Hershkovitz *et al.*, 1995; [Nahal-Ein-Gev 1] Arensburg, 1977; Arensburg & Bar-Yosef, 1973) were studied at the Sackler Faculty of Medicine, University of Tel-Aviv, Israel. All remaining samples were from Western, Central and Southern Europe. The three partial skeletons from Neussing and Oberkassel (Neuessing II, Oberkassel 1 & 2) were made available for study at the Staatssammlung für Anthropologie und Paläoanatomie, München. The partial skeletons of Terminal Pleistocene/Early Holocene age from Gough's Cave and Veyrier were studied at The Natural History Museum, London and the Institut of Anthropology, University of Genéve.

The Italian Upper Palaeolithic sample is by far the largest, and comprises the male and female skeletons from the Veneri Cave (Parabita 1 & 2), the four individuals from San Teodoro and a similar number from Barma Grande, and the multiple

Terminal Pleistocene specimens from Arene Candide. The original specimens from Parabita are housed in the Dept. of Archaeology, University of Pisa and Paglicci is housed in the Dept. of Archaeology, University of Sienna. The San Teodoro specimens are housed in the Italian Institute Prehistoria and Protohistoria, Firenze (San Teodoro 3,4 & 5) and the Museo Geologico Gemmellaro, University of Palermo (San Teodoro 1). Arene Candide II is permanently curated in the Museo Civico, Finale Liguria, whereas the remaining specimens are housed in the Museo Archaeoligia, Genova Pegli. The Barma Grande specimens (Barma Grande 1,3,5 & unnumbered) were made available for study at the Museo Preistoria, Balzi Rossi.

Homo sapiens **(Holocene)**

Holocene (*n*=22; *M*=10/F=2/*U*=10)

Several Early and Middle Holocene specimens from the Levant and Africa were included in this study. These comprise the Natufian specimens from Ain Mahalla, Hayonim and Nahal-Oren in the Levant. All these specimens are permanently housed at the Sackler Faculty of Medicine, University of Tel-Aviv, Israel. The African specimens are derived from various localities in Eastern and Southern Africa including Lothagam [4b], Makalia [1], Lochinvar, Chencherere [II] and Gamble's Cave. The Lothagam 4*b* cranium and partial skeleton is housed in the National Museum of Natural History (Smithsonian Institute), Washington DC, whereas remaining specimens are all permanently stored in the The Natural History Museum, London. The Cape Flats (Cape Flats 1) sub-fossil partial skeleton was studied at the Flagship Memorial Trust (formerly the Transvaal Museum) in Pretoria.

3.3 Methods

3.3.1 Data Collection

A series of linear variables were collected upon all paired and non-pared elements of the listed long bones of the hominoid postcranial skeleton (see Appendix I). A full inventory of the sample descriptive statistics for males and females is given in Appendix III. All measurements were taken according to the latest edition of the Lerbuch der Anthropologie (Knuβmann, 1988; Bräuer, 1988). However some additional measurements were collated, and these are discussed in Appendix I. Linear measurements were restricted to the epiphyses and midshaft diaphyses of the major long bones and preferably duplicated pelvic components. This was not possible for many archaeological specimens. Individuals were selected primarily by the preservation of pelvic remains and only specimens with 80% + of the requisite long bones. Few of the archaeological samples comprise individuals with complete skeletons and therefore sample sizes are far from ideal. In contrast, the African ape samples are exceptionally well preserved and individuals with complete skeletal inventories are the rule rather than the exception.

Three-dimensional landmark co-ordinates from the distal humeral, proximal ulna, and proximal femoral epiphyses were collected using a Microscribe 3D-X portable registrator (see Fig. 1), which is accurate to the nearest 0.05 mm. As the aims of this analysis were to compare epiphyseal geometry in the recent and fossil hominids and the extant African apes with a view to eliciting potential functional information, a fairly large series of landmarks were defined. These broadly define the three-dimensional external geometry of a particular epiphysis. All specimens (extant and extinct) were stabilised prior to digitisation using a portable clamp and stand, which was stationed within the digitising sphere of the Microscribe 3DX. (see Fig. 1)

According to Bookstein (Bookstein, 1991), landmark data sets typically comprise three distinct classes of landmark, whose definitions are given in table 2. All of the landmarks collated for this analysis are of Type II or Type III class. That is to say, they define external morphological boundaries and while they must correspond between specimens, few are homologous in a biological or developmental sense. As such, digitisation error is expected to be greater in Type II and Type III landmarks than in Type I landmark data sets (Bookstein, 1991; Dryden & Mardia, 1998; O'Higgins, 2000*b*). All of the landmarks defined here can be replicated on an identical or different specimen (see Appendix II), and several have been utilised by previous researchers (e.g., Bacon, 2000). Nonetheless, an experimental investigation in to the degree of error in repeated re-survey of a single specimen and multiple specimens is presented in a later section of this chapter.

Series of landmark co-ordinates contain crucial information relating to intrinsic form, in addition to the nature of form differences between reference and comparator specimens (Bookstein, 1991). Explicitly, landmark configurations contain information relating to the geometry of data, mathematics of deformation (see below) and the explanations of biology (Bookstein, 1991: 61). Bookstein (Bookstein, 1991: 61; see also Dryden & Mardia, 1998; O'Higgins, 2000*b*), regards landmarks as a concept in the canon of evolutionary morphology: "Landmarks are the points at which one's explanations of biological processes are grounded...[and]...landmark-based morphometrics is the embodiment within biometrics of the functional form of biological explanation" (Bookstein, 1991:61). The form of skeletal tissue, particularly epiphyseal and diaphyseal morphologies, are taken to reflect functional demands imposed during growth and development (e.g., Russell, 1916; Thompson, 1917, 1942; Huxley, 1932; Gans, 1967). Statistical comparison of landmark configurations of the weight bearing epiphyses in extant and extinct fossil hominids is a crucial comparative extension of previous studies and the hypotheses outline in Chapter 2.

18 landmarks were defined on the distal humeral epiphysis (see Appendix II). These landmarks contain important spatial information concerning the size and shape of the trochlea and capitulum, the location and proportions of the olcecranon fossa and the projection and depth of the medial epicondyle. All previous investigations using non-parametric and multivariate statistical procedures (McHenry & Corruccini, 1975; Senut, 1981*a*,*b*,*c*; Senut & Tardieu, 1985; Jungers, 1988; Lague & Jungers, 1996) have confirmed the existence of numerous features that distinguish *Pan* and *Gorilla* from *Homo*, but also *Australopithecus* from *Homo*. Wolpoff's contention (Wolpoff, 1999), that Senut's comparative anatomical studies (Senut, 1981*a*,*b*,*c*; Senut & Tardieu, 1985), have over-emphasised the affinities of the KNM-KP 271 (*Australopithecus anamensis*; Leakey *et al.*, 1994, 1998) humerus from Kanapoi (Patterson & Howells, 1968) has been confirmed by Bacon (Bacon, 2000) in her recent two-dimensional analysis using geometric morphometric procedures. Bacon (Bacon, 2000) was able to morphologically distinguish the distal humeral morphology of the extant African apes from that of recent *Homo*, and also *Australopithecus* specimens from *Homo*. Bacon considers the KNM-KP 271 distal humerus to be morphologically "...closer to other australopithecines than to many modern groups"

(Bacon, 2000: 485). Yokley and Churchill, (Yokley & Churchill, 2002) have proposed that Eurasian Neandertals and can be distinguished from other specimens, including recent humans, by derived "characters" relating to the expansion of the olecranon fossa and a decrease in the thickness of the medial and lateral 'pillars'.

14 landmarks were defined on the proximal articular region of the ulna in the extant and extinct samples (Appendix II). As with the distal humerus, recent and fossil hominids differ perceptibly from *Pan* and *Gorilla* in their epiphyseal articular morphology, but also from each other (Aiello *et al.*, 1999). Aiello and her associates (Aiello *et al.*, 1999) could effectively distinguish the African apes from a large, geographically disparate sample of recent *Homo*, but could also discriminate *Australopithecus* from early *Homo* and later hominids. Churchill and his colleagues (Churchill *et al.*, 1996; Holliday *et al.*, 1993; Pearson, 1997; Pearson *et al.*, 1998) have proposed that "archaic" humans, including the Neandertal's and early *Homo sapiens* from Southern Africa contrast with recent humans by virtue of their "relatively high and long olecranon processes, distally placed *m. brachialis* tuberosities, medio-lateral (ML) wide proximal shafts, relatively short coronoid processes and AP narrow proximal shafts" (Churchill *et al.*, 1996: 226). While this view has been challenged (Groves, 1998; Pearson *et al.*, 1998), there remains convincing evidence for morphological differences in the ulna and radius of Middle-Upper Pleistocene fossil hominids (Boule, 1911-1913; McCown and Keith, 1938; Endo & Kimura, 1970; Trinkaus, 1983; Trinkaus & Churchill, 1988; Tobias, 1971; Churchill, 1994, 1996; Pearson & Grine, 1996, 1997).

13 landmark co-ordinates were defined on the proximal femur (see Appendix II). The original intention was to capture the proportions of the femoral head and neck, the greater trochanter and the proximal femoral diaphysis. Unfortunately, the margin of error involved in the proximal femoral diaphysis was considered to be too great, and these additional landmarks, together with those from the lesser trochanter, were dropped from the analysis. The remaining co-ordinates sample spatial geometric variability in the proportions of the femoral head, neck and greater trochanter alone. Only complete specimens could be used in the resulting analyses, and it is unfortunate that several important specimens such as KNM-ER 1481a and KNM-ER 1472, both attributed to early *Homo* (Wood, 1992*a*,*b*, 1996; McHenry, 1991, 1994*b*; McHenry & Corruccini, 1978), could not be included in the study.

Previous investigations by workers such as Day and his associates (Day, 1971, 1973, 1976, 1979, 1986*a*,*b*; Kennedy, 1973, 1983*a*,*b*, 1984, 1992) and McHenry and Corruccini (McHenry & Corruccini 1976*a*,*b*, 1978), have identified morphological distinctions between the proximal femora of *Australopithecus* and early *Homo*, and early *Homo* (i.e., *H. erectus*) from later *Homo*, including Neandertals. Some workers consider these features to be correlated in a functionally meaningful manner and that they reflect different levels of locomotor competency or pattern (e.g., Day, 1979; 1982; Stern & Susman, 1983; Susman *et al.*, 1984, 1985; Ruff, 1995). In contrast, Lovejoy and his colleagues (Lovejoy, 1975, 1979, 1982; Lovejoy, Heiple & Burstein, 1973; Lovejoy *et al.*, 2002; Latimer *et al.*, 1987; Ohman *et al.*, 1997) have proposed that all hominids, perhaps *Ardipithecus ramidus* (White *et al.*, 1994; 1995; de Heinzelin *et al.*, 2001; Hailie-Selassie 2001), were obligate bipeds. Given that testing these two hypotheses involves morphological comparison and functional inference based upon the principle of correspondence (Thompson, 1917, 1942; Woodger, 1945; Bookstein, 1991, 1996*a,b*; Bookstein *et al.*, 1985), Geometric Morphometrics is a powerful analytical approach to morphological comparisons of samples and individual specimens.

3.3.2 Analytical Methodology

3.3.2.1 Relative proportions of the long bone epiphyses and diaphyses

In the first instance, non-parametric sex-specific sample comparisons of the size-standardised linear variables from the epiphyseal and diaphyseal parameters were performed using the Kruskal-Wallis procedure with paired-sample Mann-Whitney *U'* tests in post-hoc comparisons (Sokal & Rohlf, 1995). The Geometric Mean (*GM*ALL) of the total matrix, and the respective GM's of the upper and lower limb parameters (*GM*UL & *GM*LL) were calculated and employed as the denominator to create a series of dimensionless indices for each respective variable. The Geometric Mean is calculated from log-transformed variables according to the equation given in Sokal & Rohlf (Sokal and Rohlf, 1995).

$$GM = \sqrt{Y1*Y2*Y3*\ldots Yn}$$

The geometric mean is the square root of the multiplied product of *n* raw (i.e., non- transformed) variables.

Pairwise sample comparisons of the size-standardised long bone and epiphyseal and diaphyseal proportions were undertaken using a non-parametric Kruskal-Wallis n-sample test. Following this, pairwise statistical differences were assessed using a non-parametric Mann-Whitney *U* test. All analyses were performed in SPSS V10 (SPSS Inc. 2000). Least Squares regression (Model I) and Reduced Major Axis (Model II) regression models were computed and sample significance tests of the slope and intercepts were assessed using the procedures outlined in standard statistical texts (Sokal & Rohlf, 1995; Zar, 1996). Slope and elevation tests for the RMA solutions were those developed by Tsutakawa and Hewitt (Tsutakawa & Hewett, 1977) and Clarke (Clarke 1980). All these procedures were performed using a Visual Basic programme RMAGO written by Mr. Mike Dainton.

Differences in the relative proportions of the limbs and lateral body breadth, and the relative size of the epiphyses and diaphyses of recent and fossil hominids have been discussed in a previous chapter (Chapter 1). In this analysis, the geometric mean of the total series of epiphyseal breadths and diaphyseal circumferences were calculated, as in the analysis of extant hominids. In order to incorporate the partial female *Australopithecus afarensis* skeleton, all of the diaphyseal and two epiphyseal variables [PHB & DTP] were excluded from the calculation of *GM*ALL. In the first instance, *GM*ALL was used as the independent variable (denominator) to calculate relative body proportional and epiphyseal indices in suitably preserved fossil samples.

In a further analysis, a "constrained" test of allometry was defined using the *GM*ALL of the recent human "macro-sample" as the independent variable upon which Model I (LSR) regression solutions were computed. The recent human "macro-sample" (see above) is unique in that it samples the entire range of body size variability while restricting extreme variance in body proportions. Thus in all cases, correlation coefficients and the regression slopes of the epiphyseal variables on *GM*ALL are expected to be high. Allometric scaling deviations in fossil hominid specimens, particularly *A. afarensis*, were determined by calculating the standardised residuals of the fossil specimens from their predicted estimates based upon the recent human scaling solution. To directly assess deviations of the Plio-Pleistocene fossil specimens from the extant African apes, a series of "combined" sample LSR solutions of the epiphyseal dimensions on *GM*ALL for the African apes were computed. Standardised deviations of the fossil specimens based on their predicted values derived from these equations were computed. The LSR models and their respective 95% confidence intervals were computed using SPSS V10 (SPSS Inc. 1999). The standardised residual of a single specimen (extant or extinct) from a Model I or Model II linear solution is calculated as follows:

$$Y = \beta * X +/- \alpha \text{ followed by } Y\mathit{observed} - Y\mathit{predicted}/\mathrm{SEE}$$

Where X is the independent variable and the SEE = Standard Error of the Estimate

Principal Components Analysis (PCA) was performed on each sample covariance matrix of the raw variables and the resulting Eigenvalues and Eigenvectors were extracted. Principal Components Analysis is a data reduction technique that resolves a correlation or covariance matrix of diagonal components to a smaller series of Euclidean vectors, or factors (Blackith & Reyment, 1970; Flury, 1988; Tabachnick & Fidell, 1991; Bookstein, 1991, 1996*a*). In PCA, the first Component has the largest

Eigenvalue, with the second PC usually being orthogonal to, and independent of, the first PC (Blackith & Reyment, 1970; Flury, 1988; Tabachnick & Fidell, 1991).

Multivariate analysis of the fossil specimens utilised both Principal Components Analysis (PCA) and Canonical Variates Analysis (CVA). Both analyses were performed in SPSS V10 (SPSS Inc., 2000), using the sample sex-specific mean parameters of the extant African hominid samples. In contrast to previous analyses, however, the raw data for all specimens was log-transformed and standardised by the geometric mean (as in the visual comparisons of the epiphyseal variables), thus computing Darroch and Mosimann's "log-size and log-shape" variables (Darroch & Mosimann, 1985; see also Mosimann, 1970; Mosimann & James, 1979; Bookstein, 1991). PCA was then computed on the covariance matrix of these variables (including log-size) in SPSS. The resulting component scores for all specimens for the entire series of eigenvalues were then entered in to a Canonical Variates Analysis.

Canonical Variates Analysis (CVA) differs from Principal Components Analysis in several important respects (Blackith & Reyment, 1970; Tabachnick & Fidell, 1991; Pearson *et al.*, 1998). Canonical Variates Analysis is simply an extension of the two-group Discriminant Function Analysis applied to *n* predefined classificatory groups (Blackith & Reyment, 1970; Tabachnick & Fidell, 1991). Crucially, CVA is not a classificatory technique (Blackith & Reyment, 1970; Tabachnick & Fidell, 1991), although classification statistics for known and unknown cases can be produced by the analysis. Rather, CVA is a multivariate approach which "identifies" group differences via the reduction of within-group variance-covariance matrices to a series of latent vectors, of which the first CV is typically the greatest

(Blackith & Reyment, 1970; Tabachnick & Fidell, 1991). Furthermore, CVA differs from PCA in that successive vectors are not constrained to be orthogonal and can be correlated with the first (Blackith & Reyment, 1970; Tabachnick & Fidell, 1991).

As Blackith and Reyment (Blackith & Reyment, 1970) have remarked, unlike in PCA, there is no biological justification for reification of the first latent root as a size vector, even though "size" may be the important contributory factor in centroid segregation. Nor is there sound justification for exclusion of Canonical Axes from which the latent vector is a minimal contributor to the total "explained" variance (see also Corruccini, 1978; Oxnard, 1978). Oxnard (Oxnard, 1976, 1983) has routinely used the high-dimensional plotting method of Andrews (Andrews, 1972), to graphically depict group differences throughout the total number of possible latent vectors.

Lord Zuckerman and his colleagues (Zuckerman *et al.*, 1973; Ashton & Oxnard, 1964; Ashton *et al.*, 1977, 1981; Oxnard, 1976, 1983) have extensively applied Canonical Variates Analysis to the locomotor morphology of extant and extinct Primates (see also Day & Wood, 1968; Wood, 1973; Lisowski *et al.*, 1973, 1974; McHenry & Corruccini, 1975, 1976*a*,*b*, 1978). They (Zuckerman *et al.*, 1973; Ashton *et al.*, 1981; Oxnard, 1976, 1983) have argued that the pelvic anatomy of *Australopithecus* is unique, and cannot be accommodated in a known *n*-dimensional space of comparative primates of known locomotor affinities (see also, McHenry, 1991). Similarly, Wood (Wood, 1991) has demonstrated that CVA can be a crucial analytical technique for determining whether two unknown cases (i.e., fossil crania) approximate one another in a manner that is discernible in known biological groups.

Wood (Wood, 1991, 1992) used CVA to test the hypothesis that proposed sexual dimorphism in *Homo habilis* based upon morphological variation in KNM-ER 1470 and KNM-ER 1813 is of a similar degree to that seen in *Pan* and *Gorilla* (see also Blackith & Reyment, 1970). Thus CVA was deemed a suitable post-hoc investigative technique of dispersion in known and unknown taxonomic groups of different locomotor affinities.

3.3.2.2 Functional modelling of the hominid hip and lower limb

Several linear measurements of the pelvis are considered here to be the "Principal Determinants of Pelvic Form". These variables are listed in Table 3 and are illustrated graphically in Appendix 1. They comprise the overall proportions of the ilium, sacrum, ischium and pubis, as well as maximum dimensions of the medio-lateral and antero-posterior axes of the hominid pelvic girdle. There is good reason to accept that many of the variables will be highly correlated, particularly with the overall linear axes of the pelvic girdle. Thus, where relative scaling differences do occur, they are of possible functional significance (e.g., the proportions of the ilium and pubic ramus in *Australopithecus* and *Homo neanderthalensis*). More importantly, however, this analysis examines whether or not such proportional differences are primary consequences of increasing body mass in extant and extinct hominids.

The aims of this analysis was to investigate hypotheses relating to the consequential effects of increasing absolute and relative body size, and patterns of covariance in important parameters of functional significance at the entire hip joint (e.g., pelvis and femoral diaphyseal parameters). Medio-lateral (M-L) and antero-posterior (A-P) dimensions of the femoral midshaft and sub-trochanteric diaphysis were used to calculate estimated cross-sectional area, which was modelled as an ellipse according to the following formula:

$$\textbf{Elliptical Area} = (\pi/4) \times \textbf{M-L} \times \textbf{A-P}$$

Midshaft and sub-trochanteric M-L and A-P diameters were standardised to elliptical cross-sectional area as indices with elliptical area as the numerator. While these variables are, by necessity, highly correlated, significant differences in fossil hominid diaphyseal proportions are readily apparent (e.g., Day, 1971; Kennedy, 1983*a,b*, 1984; Trinkaus, 1983*a,b*; Lovejoy & Trinkaus, 1980; Trinkaus *et al.*, 1991, 1994; Trinkaus & Ruff, 1999*a,b*; Ruff, 1988, 1989, 1995, 2000, 2002, 2003; Ruff *et al.*, 1993, 1994; Ruff *et al.*, 1999). Ruff (Ruff, 1995, 1998; see also Ruff *et al.*, 1999) has argued that while consistent morphological differences exist in comparisons between species within the genus *Homo* (e.g., *Homo erectus*, *Homo neanderthalensis* versus *Homo sapiens*), these differences do not faithfully reflect postural and progressional repertoire distinctions (Trinkaus & Ruff, 1999*a,b*). Morphological differences in the locomotor skeleton of *Australopithecus* and *Homo* are considered by some workers to be of functional significance, reflecting varfying degrees of locomotor adaptation in Plio-Pleistocene fossil hominids (Day, 1973, 1976, 1979; Ruff, 1995, 1998; Ruff *et al.*, 1999).

The development of a 2D static model for the human hip joint was proposed as early as 1935 by Friedrich Pauwels (see Pauwels, 1980; see also Marquet, 1985), and is reproduced and modified here as Figure 2. In this model, the parameters of primary importance are the applied force (pressure) occurring at the femoral head, and the relationship between the load arm for the vector of body mass acting at the hip joint (interacetabular distance or some correlated subdivision [see Ruff, 1995]) and the lever arm of the abductor muscles (biomechanical femoral neck length). Frankel and Burstein (1970:24-26) have demonstrated that the abductor force (*P*, in their annotation) can be easily calculated from these parameters once a ratio of the load arm/lever arm has been calculated and body mass has been readjusted to account for the missing mass of the lower limb during single leg stance.

Frankel and Burstein (Frankel and Burstein, 1970), give a value for the mass of a single lower limb as one-sixth of body weight (or mass X by the gravitational constant), with the remaining weight (five-sixths of body weight) being employed in the calculation of both *P* and for the magnitude of force acting on the femoral head, *F* (Frankel and Burstein, 1970). In their study of frozen cadavers, Dempster and Gaughran (Dempster and Gaughran, 1967) demonstrated that the overall distribution of mass in the lower limb approximates 34% of the total body mass (see Demes and Günther, 1989). While Frankel and Burstein's (Frankel and Burstein, 1970) approximation that the mass of a single leg is one-sixth, or 16.67%, of body mass, their failure to discount the corresponding mass of the opposite leg from the remaining mass of the body leads to an excessive value of weight acting on the hip joint. Dempster and Gaughran's (Dempster and Gaughran, 1967) approximation of 66% for mass of the body discounting the lower limbs (or *Wb* [Ruff, 1995]) was derived from estimated body weight (estimated mass X gravitational constant), for all suitably preserved individual skeletons collected as part of this study.

The load and lever arms of the hip and the degree of 'relative pressure' (Lovejoy, Heiple and Burstein, 1973) acting on the hip joint in bipedal hominids can be related simply. Changes in the proportions of the load arm, *Dw,* and the lever arm of the abductor muscles, *Dm* (following Ruff, 1995) will alter the joint reaction force passing through the hip joint in the following fashion. Increasing *Dw* relative to *Dm* will lead to an increase in the joint reaction force acting at the acetabulum in the hominid hip. Alternatively, decreasing this proportional ratio will lead to a decrease in the reaction force at the hip joint. Discrepancies in the force vectors characterising of the weight of the trunk and the ground reaction force (equivalent to body weight) during single stance must be balanced by the contractile force exerted by the abductor muscles in order to maintain static equilibrium (e.g., Frankel & Burstein, 1970; Pauwels, 1980; Marquet, 1985; Ruff, 1995). Thus, according to Ruff's model (Ruff, 1995, 1998) the relationships between body weight (*W*) and its load arm (*Dw*) are equivalent to the product of the lever arm (*Dm*) and abductor force (*M*). The missing parameter (*M*), is simply calculated as:

$$W + Dw = Dm + M$$

Thus, *M* is merely the product of *W* + *Dw* divided by *Dm*, where *W* is weight derived from body mass multiplied by the gravitational constant, *Dm* is biomechanical femoral neck length (Lovejoy and Heiple, 1970), and *Dw* is bi-acetabular diameter corrected according to the method explained in Ruff (1995) and detailed with figure 2. Thus, Ruff's *M* (Ruff, 1995) differs from that of Frankel (Frankel and Burstein, 1970; Nordin and Frankel, 1989*b*) in that the value of *W* is not adjusted to calculate the weight actually acting at the hip joint (*Wb* in Ruff, 1995). Following this, the joint reaction force at the hip, J, is derived simply as $J = W + M$ (Ruff, 1995).

Least Squares Regression & Reduced Major Axis regression models were used to investigate those hypotheses relating to patterns of morphological integration in the hominid pelvis outlined in Chapter 2. As before, post-hoc regression analyses of the RMA and LSR slopes and intercepts were performed using RMAGO. Differences in parameters derived from the static functional model equations for the various sample groups were compared using non-parametric Kruskal-Wallis multiple sample comparisons and paired Mann-Whitney U tests for sex-specific samples, in addition to bivariate regression comparisons using RMAGO.

Following these comparisons, the analysis focuses upon specific anatomical features, such as the relationships between important theoretical parameters of pelvic functional morphology with absolute and relative approximations of femoral head size, relative body size and the femoral cross-sectional diaphyseal parameters. With respect to the femoral head, absolute antero-posterior breadth was included as a dependent parameter with no correction for body mass and also as an index of "relative pressure" (Lovejoy, Heiple & Burstein, 1973). Lovejoy, Heiple and Burstein (Lovejoy, Heiple & Burstein, 1973) define the index of relative pressure of the femoral head in *Australopithecus africanus* (Sts 14) and recent humans (Libben Amerindians) as femoral head area (FHD squared) divided by estimated body mass (in grams) using appropriate prediction equations (e.g., Ruff *et al.*, 1997). Body mass was estimated using the geometric prediction equations of Ruff (Ruff, 1991, 1993, 1994; Ruff & Walker, 1993; Ruff *et al.*, 1997; see also Holliday, 1995). On a linear scale, increasing relative pressure indices signify a relative decrease in the size of the femoral head proportional to body mass.

Relative body size is defined following Ruff (Ruff, 1991, 1993, 1994; Ruff & Walker, 1993), as an index of lateral body breadth (Bi-iliac diameter), relative to absolute body height (e.g., Stature). In a large geographical samples, ecogeographical variability in body shape and limb proportions (e.g., Holliday, 1995, 1997a,b; Holliday & Trinkaus, 1991; Holliday & Ruff, 1997) must be controlled when estimating stature from the long bones of the skeleton (see also Pearson, 1899; Hens *et al.*, 2000; Ruff *et al.*, 1997 & Supplemental Information). In this study, available prediction equations for the long bones of the postcranial skeleton were restricted to the femur and the humerus, and are presented in table 4.

Femoral equations derived from a recent study of Portuguese cadavers (De Mendonça, 2000), were used to estimate stature for the European skeletons (e.g., Medieval Hungarians, Caucasus Tartars). Stature estimates for the African Bantu and Australian Aboriginal skeletons were derived from the published equations of Trotter & Gleser (Trotter & Gleser, 1952, 1958), and the stature of individuals in the two Native American samples (Southwest & Libben Amerindians), were derived from the published estimates of Genoves (Genoves, 1967). As the African Pygmies and Southeast Asian Negritos fall generally outside the range of known variation in body size in those recent human samples for which prediction equations are known, estimates were derived from the "femur/stature" ratio developed by Feldesman and his associates (Feldesman, Kleckner & Lundy, 1990; Feldesman & Fountain, 1996). While this "generalised" method has been criticised by Ruff and his colleagues (e.g., Ruff, 1994; Ruff & Walker, 1993; Holliday & Ruff, 1997), for its failure to account for known variability in "ecogeographical patterning", by Ruff's own admission (Ruff, 1993; Fig. 1), these two diminutive groups are likely to have fundamentally different body proportions than Nilotics and other Sub-Saharan African peoples (see also Hiernaux, 1985). As such, the stature estimates for these groups are purely "approximations" of overall linear size.

Calculated cross-sectional area and standardised medio-lateral (M-L) and antero-posterior (A-P) diameters of the femoral midshaft and sub-trochanteric diaphyses were considered independently. In both cases, initial regression analyses and post-hoc significance tests of the slope and elevations for the sample-specific solutions (RMA & LSR) were computed using RMAGO with a variety of independent variables. In the first instance sample-specific variability in M-L and A-P diaphyseal proportions were assessed by regressing M-L and A-P standardised diameters upon cross-sectional area, and also on each other. Further analyses, which were duplicated for both sectional locations of the femoral diaphysis, intended to assess the dependence of the diaphyseal parameters upon important functional dimensions of the pelvis, specifically the body weight load arm (*Dw*), abductor force lever arm (*Dm*), and the index of these parameters (*Dw*/*Dm*).

With respect to the fossil samples, a mutually compatible analytical approach was preferred. The functional model parameters were calculated as in the extant hominid specimens using the method outline in Ruff (Ruff, 1995; see above). Body Mass and Stature were estimated for sufficiently preserved individuals (e.g., AL 288-1; AT-1, Kebara II and the European EUP and LUP *Homo sapiens*) using "appropriate" prediction equations from various sources, including Ruff, Trinkaus and Holliday (Ruff, Trinkaus & Holliday, 1997). As the Kebara Neandertal has only a fragmentary associated proximal femur, *Dm* was determined using the Neandertal average of the biomechanical length of the femoral neck (see Chapter 7). The cross-sectional areas of the femoral midshaft and sub-trochanteric diaphyses were calculated using the equation for an ellipse, and the M-L and A-P shaft diameters were standardised as for the recent human samples.

Visual comparisons of the relevant functional model parameters in the extinct fossil hominid specimens are comprehensively discussed. In order to establish the significance of observed differences in fossil hominid diaphyseal proportions, LSR models of the recent human "macro-sample" were calculated in a "constrained" allometric hypothesis (see above). Initially, a three-stage approach was utilised which focussed purely upon variability in hominid femoral morphology. Femoral midshaft and sub-trochanteric diaphyseal proportions (M-L & A-P) were regressed on the relevant estimated cross-sectional area and on each other. In the following stages, the diaphyseal parameters were regressed upon the biomechanical length of the femoral neck (*Dm*), and upon femoral head diameter. In all cases, standardised residuals of the individual fossil specimens from the recent human "macro-sample" LSR functions were calculated and deviations were discussed accordingly.

Further analysis sought to examine relationships of the femoral diaphyseal proportions with an absolute measure of body size (i.e., Bi-cristal Diameter), and also examined scaling relationships of parameters of specific functional importance. These included the body weight lever arm and abductor force load arm proportions, but also the "principal determinants of pelvic form" in suitably preserved fossil hominid pelves. The "principal determinants of pelvic form are listed in table 4. The specific aim of this section of the analysis was to examine potential differences in structural scaling which may reflect underlying allometric differences in absolute and relative body size, and also to explicitly test certain assumptions relating to proposed locomotor differences in Plio-Pleistocene hominids.

Principal Components Analysis was performed on the covariance matrix of the six raw "principal determinants of pelvic shape" for the sex-specific sample means of the recent and fossil hominid groups. Special cases, such as the AL 288-1, AT-1 and the Kebara II pelvis were entered independently. Classification based upon morphological differences was not the desired objective of this analysis, rather, differences in pelvic proportions between the samples and the elucidation of underlying allometric constraints was the objective. As such, PCA was preferred to Canonical Variates Analysis (Blackith & Reyment, 1970; Flury, 1988; Bookstein, 1991, 1996*a*; Reyment, 1996; Groves, 1998; see also Pearson *et al.*, 1998).

3.3.2.3 Geometric Morphometrics (Generalised Procrustes Analysis)

The "new" or "geometric" morphometrics (Kendall, 1984, 1989; Bookstein, 1982, 1984, 1991, 1996*a*,*b*; Rohlf, 1990, 1996, 2000; Rohlf & Bookstein, 1990; Rohlf & Slice, 1990; Goodall, 1991; Slice, 1993, 1996; Mardia & Dryden, 1989; Mardia & Walder, 1994; Dryden & Mardia, 1998; Marcus *et al.*, 1996; Small, 1996; O'Higgins, 2000*b*), constitutes a novel approach to morphological *shape* comparisons in functional morphology and palaeontology. Unlike "traditional" statistical methods in biometry that rely upon spatially 'unrelated' linear dimensions (e.g., ANOVA, Linear Regression, PCA, CVA; see Sokal & Rohlf, 1995; Zar, 1996; Blackith & Reyment, 1970; Reyment, 1996; Reyment *et al.*, 1984), morphometric approaches utilise predefined spatial co-ordinates in k=2/3 dimensions to explicitly 'capture' geometric (Bookstein, 1982, 1991, 1996*a*,*b*; Small, 1996; Dryden & Mardia, 1998; see above).

Dryden and Mardia (Dryden & Mardia, 1998: pp 1,23), define size, shape and size and shape as the following;

> A ***size measure*** $g\ (aX)$ is any positive real valued function of the configuration matrix such that:
>
> $$g\ (aX) = ag\ (X)$$
>
> ***Shape*** is all the geometrical information that remains when location, scale and rotational effects are filtered out from an object
>
> ***Size- and-Shape*** is all the geometrical information that remains when location and rotational effects are filtered out from an object

The natural measure of "size" in Procrustes Geometry is Centroid Size (Bookstein, 1991, 1996*a*; Mardia & Dryden, 1989; Rohlf & Slice, 1990; Goodall, 1991; Small, 1996; Dryden & Mardia, 1998; O'Higgins, 2000*b*). Centroid Size is the square root of the summed-squared Euclidean distances of the individual landmarks from the centroid of the form (Bookstein, 1991; Small, 1996; Dryden & Mardia, 1998; O'Higgins, 2000*b*). Goodall and Mardia (Goodall & Mardia, 1992; see also Dryden & Mardia, 1998:58; O'Higgins, 2000*b*), provide a summary flow chart for the principal 'hierarchies' of the various spaces encountered in statistical shape analysis. This is presented here as figure 3. Translation of the various configurations is followed by removal of scalar (size) and rotational (location and orientation) effects (Kendall 1984, 1989; Small, 1996; Dryden & Mardia, 1998). Once the effects of geometric size and rotation are removed, the individual specimen configurations can be projected in to Kendall's "shape-space" (Bookstein, 1986, 1991; Marcus *et al.*, 1996; O'Higgins, 2000*a,b*; O'Higgins & Dryden, 1992; O'Higgins & Jones, 1998*a,b*).

Kendall's "shape space" for triangles is represented a sphere in three-dimensions (Bookstein, 1991; Small, 1996; Mardia & Dryden, 1992; Small, 1996; Dryden & Mardia, 1998; O'Higgins, 2000*a*), and a curved segmental manifold in two-dimensions. In Kendall's shape space (Fig. 4), equilateral triangles are sited at the northern 'pole' of the global distribution and isosceles triangles are distributed across the longitudinal intersections from the 'pole' towards the equator. Collinear forms are distributed across the equator. Kendall's "shape space" is curvilinear and non-Euclidean (Bookstein, 1991; Small, 1996; Mardia & Dryden, 1992; Small, 1996; Dryden & Mardia, 1998; O'Higgins, 2000*a,b*). Kendall (Kendall 1986, 1989) and Bookstein (Bookstein, 1986, 1991) both concur that Bookstein 'shape co-ordinates' (see Bookstein, 1991) occupy a linear tangent space that lies orthogonal to Kendall's shape space. This "tangent space" is Euclidean, and facilitates the approximation of the both the mean form, and a statistical comparison of shape differences between specimens.

Projection of the individual shapes around their consensus to a Euclidean tangent space leads to the derivation of a series of tangent space co-ordinates around the mean shape. The linear tangent space projection is conceptually equivalent to a geographer translating coincident localities on the globe to a scaled map where 'distances' in shape space are preserved (e.g., Bookstein, 1991, 1996*a*,*b*; Goodall, 1991; Small, 1996; Dryden & Mardia, 1998; O'Higgins, 2000*a*,*b*). The variance-covariance matrix of the tangent space co-ordinates can be used compute Multivariate statistical approaches (e.g., PCA, CVA).

Thin-plate splines (Bookstein, 1991; Yaroch, 1996; Dryden & Mardia, 1998; O'Higgins & Jones, 1998), is an objective mathematical approach to the Cartesian Co-ordinates used by D'Arcy Wentworth Thompson in his celebrated treatise on the functional and phylogenetic predicates of morphological form (Thompson, 1917, 1942; see also Medawar, 1945). Sneath (Sneath, 1967) used cubic spline deformation grids to illustrate the principal morphological differences in a series of extant and extinct hominid species, including *Australopithecus africanus*, *Homo erectus*, *Homo neanderthalensis* and *Homo sapiens*. However, subsequent workers (e.g., Bookstein, 1989, 1991; Small, 1996; Dryden & Mardia, 1998), have remarked that while Sneath's quadratic transformation algorithm captures the "principle" shape differences between specimens, these are accentuated.

Bookstein's approach (Bookstein, 1991; see also Bookstein, 1996*a*; Dryden & Mardia, 1998) is based on the theoretical deformation of a thin sheet of steel ("the spline" [Yaroch, 1996]), characterising principal and minor axes of morphological transformation between two specimens (see Bookstein, 1991: 316-357). This procedure is referred to as "warping" (Bookstein, 1991; Dryden & Mardia, 1998). The transformation function between two superimposed landmark configurations (i.e., specimens) constitutes the "bending-energy matrix" (Bookstein, 1990*a*,*b*, 1991; Rohlf & Bookstein, 1990; Dryden & Mardia, 1998). An example of this method as applied to two different fossil hominid crania is shown in figure 5.

Generalised Procrustes Superimposition and full-tangent space projection from Kendall's "shape-space" were performed using the programme *Morphologika* (O'Higgins & Jones, 1998*a*), which was obtained from Prof. P. O'Higgins and University College London. As with other available statistical programmes on the Stony Brook University Morphometrics pages (e.g., GRF-ND), *Morphologika* calculates the consensus least-squares configuration, projects the dispersion around the consensus configuration to co-ordinates in Kendall's "shape-space" and derives linear tangent space co-ordinates as a covariance matrix. While current releases of *Morphologika* do not include an option for calculating resistant-fit consensus iteration, the programme does have the option to perform a partial projection of the Kendall co-ordinates in to tangent space, perhaps minimising shape distortions (e.g., Goodall, 1991; Small, 1996).

Morphologika differs from these individual programmes in performing a PCA on the covariance matrix of tangent space co-ordinates and utilises Bookstein's technique of "thin-plate" splines to compare the nature of morphological shape differences across component axes (i.e., negative-positive) and between individual specimens. The resulting images can be captured for importation in to other platforms, including movie producers (e.g., Niewhoener, 2001, 2002). The only severe drawback with *Morphologika* is that specimens with missing landmarks (e.g., fossils) cannot be included in the analysis. As such, fossil sample sizes are not especially large. The resulting PC scores from the analyses of the configurations of the distal humeral, proximal ulnar and proximal femoral landmark series were entered in to a CVA in SPSS (SPSS Inc., V10).

The underlying nature of morphological change on the principal component axes of the tangent space co-ordinates was explored using thin-plate spline transformations in 3 dimensions in *Morphologika* (O'Higgins & Jones, 1998*a*). The primary data for these morphological transformations comprises a series of 2D "meshes" which link pairs of landmarks to form an overall appraisal of the geometric configurations of the distal humeral, proximal ulnar and proximal femoral epiphyses. Paired-sample differences in Procrustes Chord means and statistical significance levels were assessed using a non-parametric permutation test supplied and written by Prof. Paul O'Higgins.

3.4 Assessment of Measurement Error

3.4.1 Measurement Error of the Linear Variables

Approximation of measurement error in the linear variables follows and expands upon the methodology used by O.M. Pearson (Pearson, 1997) in his exploration of the postcranial evidence for the origins of 'anatomically-modern' humans. Pearson (Pearson, 1997) compared all measurements used in his study (n=124), which were taken on 20 skeletons housed in the Dept. of Anatomical

Sciences, SUNY (Stony Brook), the American Museum of Natural History and the National Museum of Natural History (Smithsonian Institute). Pearson (Pearson, 1997) determined levels of error in individual measurements using the mean percentage prediction error favoured by Smith (Smith 1984, 1996) in his analysis of linear regression models. This is calculated using the following equation:

$$100*(\text{Survey } 1 - \text{Survey } 2)/(\text{Survey } 2)).$$

In addition to this primarily descriptive metric, this study used paired t-tests on a large series of linear measurements (n=96) taken on 20 specimens housed in the Rudolf-Virchow Sammlung, Humboldt Universitat, Berlin. All measurements were collected using a pair of 200mm Mitutoyo™ Digital Calipers and a Paleotech Concepts™ Osteometric Fieldboard and flexible nylon tape measure. As the selected skeletons were extremely well preserved, measurements were taken on all available bi-lateral elements. The first survey of this material was undertaken in late Februrary, 2000 and the same series of skeletons was completed in late October.

The results of the paired Student's *t* tests and the associated mean percentage prediction errors are shown in table 5. For the upper limb variables (n=49), the linear dimensions of the midshaft diaphysis were generally statistically significant ($p=<0.01$) in the two series of measurements. Interestingly, midshaft diaphyseal circumferences of the humerus and radius were not significantly different, although comparisons of the midshaft circumference of the clavicle did reach statistical significance. Mean approximates of the height of the glenoid fossa and the maximum breadth of the scapula in the two samples were found to be significantly different (*p*=<*0.001*), and the medio-lateral breadth of the olecranon fossa also differed significantly in the two groups (i.e., surveys).

With respect to the epiphyseal dimensions of the upper limb, the medio-lateral breadth of the distal radial epiphysis and the majority of the linear dimensions taken on the articular region of the ulna were found to be significantly different using pairwise Student's *t* tests (*p*=<*0.05*). Surprisingly, the dorso-ventral diameter of the proximal ulnar epiphysis and the 'true' height of the coronoid process did not differ in the two-sample comparisons. For the upper limb variable subset, there is general agreement between the results of the paired Student's *t* tests and the magnitude of the mean percentage prediction errors (MPPE's). MPPE values range from 0.35% to 10.5% in the upper limb variable subset (see table 5), however, a substantial majority of the individual MPPE's (39/49 [79.6%]), were below 5%.

The lower limb variable subset (*n*=47) is slightly smaller than the upper limb series. The medio-lateral breadths of the acetabulum and the ilium, together with the antero-posterior diameter of the *processus tranversaris* of the sacrum were found to differ significantly in the two series of measurements (*p*=<*0.05*). The distance from the outer margin of the centroid of the proximal aspect of the ischial tuberosity to the centre of the acetabulum also differed significantly (*p*=<*0.001*). This variable was dropped from the study. As with the upper limb, both innominates were measured where preserved. With the sole exception of the medio-lateral and antero-posterior diameter of the sub-trochanteric diameter, all remaining femoral diaphyseal dimensions (including the femoral midshaft) differed significantly between the two samples (*p*=<*0.01*). The supero-inferior height and the antero-posterior breadth of the femoral neck, together with the biomechanical length were also found to differ significantly between the two samples (see table 5). Surprisingly, both the maximum and physiological lengths of the tibia in the two series differed statistically (*p*=<*0.05*), however, only a single diaphyseal dimension (midshaft A-P diameter), was found to differ in the pairwise comparisons of the two series of measurements.

As with the upper limb series, there is general agreement between the results of the pairwise Student's *t* tests and the calculated MPPE's. Nevertheless, there are some important exceptions. For example, average percentage deviations of the diaphyseal midshaft circumference of the femur and the maximum and physiological lengths of the tibia in the two samples are less than 1.5%. In a substantial majority of cases (e.g., 35/45 [74.5%]), individual MPPE's are less than 5% (table 5).

The results of this study both agree, and contrast, with results obtained by Pearson (Pearson, 1997). In cases where variables in the two studies overlap, results are generally similar. The finding that smaller linear measures tend to yield higher systematic error approximations than larger metrics is substantiated by results from several upper limb measurements (clavicle, proximal ulna). Nevertheless, the higher systematic error of the linear dimensions of the diaphyseal midshaft of both the upper limb and lower limb elements requires further deliberation. While a component of this difference must reflect intra-observer measurement error, there are other quite interesting considerations. Pearson (Pearson, 1997) only measured a single side of any individual specimen, usually the right. In the majority of cases in this study, both left and right dimensions were included in the comparisons in this study. Differential approximations of diaphyseal dimensions in the upper and lower limb might reflect changing patterns of bi-lateral asymmetry within the samples. This hypothesis will not be tested here. With few exceptions, the variables used in this analysis were not significantly different in the measurement survey.

3.4.2 Approximation of digitisation error of epiphyseal geometry

Approximation of error in the 3D landmark co-ordinates for the distal humeral, proximal ulnae and proximal femoral epiphyses consisted of repeated survey of single elements from a comparative African ape and a recent human skeletal series housed in the Osteology Laboratory, University of Liverpool, under the direction of Dr. Gabrielle Macho. Each specimen was digitised six times over a period of two days. The 'reference' sample in the Generalised Procrustes Analysis comprised the Pan paniscus sample for the Distal Humerus and Proximal Ulna landmark series and the Magyar and Coventry samples for the Proximal Femur landmark series.

In the analysis of the distal humeral landmark configurations, a right distal humerus of *Pan troglodytes* was digitised independently in a total of six iterations (see above). PCA of the tangent space co-ordinates was performed using *Morphologika* (O'Higgins & Jones, 1998), and a recent European reference sample (n=47) was used to calculate the Procrustes consensus configuration. Not surprisingly (see Fig. 6), the recent human sample differs notably in its position on PC1 from the repeated iterations of the single African ape configuration. With respect to the *Pan troglodytes* distal humeral specimen, variation on PC1 is relatively constrained relative to variation on PC2. A thin-plate spline rendering of the morphological transformations of the "centroid" of the distribution of the repeated series (Reference) and the "centroid" specimen of the *Pan troglodytes* sample on PC1/PC2 is shown in figure 7. There appear to be quite significant morphological differences between the specimens, but it is unlikely that the tight clustering of the repeated samples is due to digitisation error.

With respect to the geometry of the proximal ulna, once again the right specimen from the *Pan troglodytes* individual was used (Fig. 8). A total of 37 *Pan troglodytes* specimens were used to fit the GPA consensus and full-tangent space projection in *Morphologika*. As before, the *Pan troglodytes* proximal ulna from the 'repeated' series is well differentiated from its contemporaries on PC1. Variance in the repeated surveys (i.e., individual "specimens") of *Pan troglodytes* is relatively constrained on both PC1 and PC2. As with the Distal Humerus, although significant morphological variation is observed between the "centroid" iteration of the repeated series and the target *Pan troglodytes* specimen, it is highly unlikely that this reflects measurement error (Fig. 9).

With respect to the proximal femur, a recent human specimen was used. As before, this was digitised six times over a period of two days. A comparative sample of 36 recent European femora (Magyars & Coventry) was used to derive the consensus configuration in the least-squares orthogonal fitting procedure (see above). In contrast to the previous error assessments, there is no distinct separation of the recent human proximal femoral iterations (HACB 1) from the recent Europeans (see Fig., 10), and variance in the iterated specimen is confined to PC2 alone. Thin-plate spline "warping" of the two extreme 'specimens' on PC2 (Fig., 11) reveals no notable morphological distinctions.

Chapter 4. Relative scaling of the long bone epiphyses and diaphyses

4.1 Introduction

This chapter presents results of investigations into the relative scaling of linear dimensions of the epiphyses and diaphyses of the upper and lower limb in extant African hominoids (*Gorilla*, *Pan* & *Homo*), and their functional implications. Patterns of variation in living taxa are used as a framework to interpret the functional anatomy of extinct Plio-Pleistocene hominids. Particular attention is directed to the morphology of the female *Australopithecus afarensis* partial skeleton, AL 288-1 ("Lucy"), and inferences for posture and locomotion in Pliocene early hominids. This chapter also addresses patterns of relative scaling of the epiphyses and diaphyses of later Pleistocene groups (e.g., *Homo neanderthalensis* and Upper Pleistocene *Homo sapiens*), in order to test current propositions of habitual activity differences among these hominids.

A comparative scaling method based upon the geometric mean is outlined for partial skeletons that lack associated or suitably preserved pelvic material from which reliable and independent body mass estimates can be derived. There currently exist no species-specific reference equations for body mass determination in individual skeletons of the extant African apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla*), although this might be possible for *Pan paniscus* (Wendelin, *pers. comm.*). The "All Hominoid" equations developed by McHenry (1988, 1992*a*,*b*) ignores probable variation in the scaling of epiphyseal and diaphyseal dimensions within the African apes, much of which remains unexplored (but see Jungers, 1988*a*, 1990, 2003).

Assessments of the reliability of this method will be determined statistically by comparison of the geometric means (*GM*ALL, *GM*UL, *GM*LL) with mean body mass estimates derived from equations published in Ruff *et al.* (Ruff *et al.*, 1997), and reference sources (Smith & Jungers, 1997).

4.2 Validation of the Geometric Mean as a "body size" proxy

The product-moment correlation matrices for the geometric mean series of Total, Upper, and Lower limb dimensions (*GM*ALL, *GM*UL & *GM*LL, respectively) with estimated body mass for the sample means are shown in tables 6-8. Several correlation matrices were calculated. In all cases, correlation coefficients for the geometric means of the epiphyseal and diaphyseal variables and body mass are highly significant ($p=<0.001$). A slightly better 'fit' is obtained for the 'All Hominoid' sample (including the African apes), for *GM*ALL and *GM*UL (see table 6). Only the coefficient for *GM*LL on estimated body mass is improved by excluding the African apes (table 7). Thus, for the samples included in this study, the geometric means are valid alternative descriptors of hominid body size. However, only *GM*ALL will be retained in further analyses.

Profiles of the group specific geometric means clearly parallel expected patterns in body mass both within *Homo*, and between *Homo* and the African apes (see Fig. 12). Males are represented first in the histogram. Statistical significance of the gender-specific sample medians was assessed using appropriate non-parametric statistical comparisons. Clear differences exist between the male and female means within the recent human samples and in the African apes, with the exception of *Pan* *paniscus*, which is consistent with observed sexual dimorphism in body mass (e.g., Eveleth & Tanner, 1976, 1990; Smith & Jungers, 1997). Levels of male-female differences in geometric size are accentuated in *Gorilla*, the most sexually dimorphic extant hominid taxon. Within *Homo*, putative sexual dimorphism in epiphyseal and diaphyseal geometric size is quite marked and generally exceeds that seen in *Pan troglodytes*.

4.3 Univariate comparisons of the epiphyses and diaphyses

Results of the sex-specific Kruskal-Wallis non-parametric group comparisons of the "size-adjusted" epiphyseal and diaphyseal variables are detailed in table 9. Kruskal-Wallis non-parametric comparisons were highly significant across all sex-specific comparisons ($p=<0.001$; see table 9). The results of the post-hoc Mann-Whitney *U* two-sample comparisons are given in tables 10-27. Descriptive statistics for the raw sample data from which these indices are derived is given in Appendix III, which is stored on the accompanying CD disk. In the following histograms, male sub-sample means are always illustrated first.

Pairwise comparisons of the transverse diameter of the proximal humerus [PHB] using the Mann-Whitney *U* test reveals that with few exceptions, *Pan paniscus* possess relatively larger proximal humeral epiphyses than recent humans do. Statistical comparisons with *Pan troglodytes* (males only) were also significant ($p=0.05$). These differences are graphically illustrated using mean, rather than median, sample values in figure 13. Mann-Whitney *U* test comparisons of *Pan troglodytes* and *Gorilla gorilla* with the recent human samples reveals a mixed pattern of differences. Male *Pan troglodytes* and *Gorilla gorilla* samples do not possess relatively larger proximal humeral epiphyses than African Pygmies or Southeast Asian Negritos, but their female counterparts display significantly larger and smaller PHB values, respectively (see Fig. 13).

Significant sexual dimorphism in the relative size of the proximal humeral epiphysis in *Pan troglodytes* and *Gorilla gorilla* are evident in the pairwise comparisons with recent human groups. With the exception of the African Bantu (Dart Collection) and Australian Aboriginal samples, male indices of relative PHB in *Pan troglodytes* and *Gorilla gorilla* are not significantly different from the Southwest or Libben Amerindians, or from Medieval Hungarians (*Pan troglodytes* alone). Results of the female non-parametric comparisons were significant in all cases with the exception of the female Hungarian and Southwest Amerindian samples. South African Bantu and Australian Aborigines possess notably smaller relative proximal humeral epiphyses than remaining recent human and African ape samples (see Fig. 13). With the exception of male and female pairwise comparisons with the African Pygmies and female Bantu with the Libben Amerindians, the remaining comparisons were statistically significant ($p=<0.001$).

A more consistent pattern of results emerges from the Mann-Whitney U pairwise comparisons of relative humeral biepicondylar breadth [BIEPIC] in the recent human samples and the African apes. Comparisons of the African apes (*P. pansicus, P. troglodytes and G. gorilla*) with the recent human samples were statistically significant in all cases. The African apes possess uniformly larger relative BIEPIC indices than recent humans (see Fig. 14). Interestingly, comparisons of the

BIEPIC index within the African apes reveals significant differences between both *Pan* species (males and females) with *Gorilla.* The magnitude of the differences is notably greater in *Pan troglodytes* versus *Gorilla* ($p=<0.001$), and is less so in *Pan paniscus*, particularly in males. Variability within *Homo sapiens* in the relative size of the distal humeral epiphysis is constrained. Nevertheless, significant differences were detected in pairwise comparisons of male Southeast Asian Negritos with Libben Amerindians ($p=<0.05$), and in the South African Bantu males with Southwest and Libben Amerindians ($p=<0.05$ and $p=<0.01$, respectively). Female Australian Aborigines possess significantly smaller relative distal humeral epiphyses than Libben Amerindian females ($p=<0.05$).

Similarly, results of the pairwise comparisons of the relative size of the midshaft circumference of the humerus [HMC] for the African apes samples with recent humans are statistically significant ($p=<0.05$). Mean differences across the samples for relative HMC indices are shown in figure 15. African apes possess significantly larger relative humeral midshaft circumferences than do recent humans. Significant differences exist in relative humeral midshaft circumference in *Pan* and *Gorilla.* The gorilla sample displays significantly larger HMC values than *Pan troglodytes* ($p=<0.001$; both sexes) and *Pan paniscus* ($p=<0.05$ and $p=<0.01$; males and females, respectively).

Considerable variability exists in the relative size of the humeral midshaft within recent humans, but significant differences were restricted to pairwise comparisons of male samples alone. The most consistent differences are to be found in comparisons of the Southeast Asian Negrito and the Australian Aboriginal samples.

Both possess relatively larger median relative humeral midshaft circumference indices than other human samples, particularly the Southwest ($p=<0.01$; both comparisons) and Libben Amerindians ($p=<0.01$; Southeast Asian Negritos).

With respect to the relative size of the radial head [RHD], Mann-Whitney pairwise comparisons of the male and female African Pygmy samples with *Gorilla gorilla* and *Pan paniscus*, respectively, were not significantly different. In all remaining cases, African apes possess relatively larger proximal radial epiphyses (see Fig. 16). Comparisons of *Pan* (*P. paniscus*, *P. troglodytes*) with *Gorilla* reveal that gorilla's possess significantly smaller proximal radial epiphyses ($p=<0.05$). Although the relative RHD indices of male and female *Pan troglodytes* samples are greater than the corresponding values in *Pan paniscus*, these do not reach statistical significance. With the sole exception of female comparisons with the Southeast Asian Negritos, African Pygmies display relatively larger proximal radial epiphyses than remaining human samples. Australian Aboriginal males have relatively larger RHD indices than the Medieval Hungarian males ($p=<0.001$).

Pairwise comparisons of *Pan paniscus* and *Pan troglodytes* (both sexes) with recent humans for the relative circumference of the radial midshaft [RMC] were statistically significant in all cases. RMC indices for *Gorilla* did not differ significantly from the African Pygmies, Southeast Asian Negritos or the Australian Aborigines (both sexes), and the Medieval Hungarians (males alone). Not surprisingly, significant differences exist in the relative size of the radial midshaft in *Gorilla* and *Pan* ($p=0.001$). Interestingly, the radial midshaft in *Pan troglodytes* is relatively larger than in *Pan paniscus* (Fig. 17), but the observed differences reach statistical significance in females alone (*p=<0.01*). This replicates the pattern observed for the relative size of the radial head, but is of a greater magnitude. The Southeast Asian Negritos, African Pygmies and Australian Aborigines possess the largest mean RMC indices, and are notably different from the relatively smaller diaphyseal circumferences of the Amerindian radii. Median RMC indices are significantly different from all remaining human samples, including the Southwest Amerindians (*p=<0.001*). Radial midshaft proportions of the Southwest Amerindian males are significantly lower than other samples.

Results of the pairwise Mann-Whitney *U* test comparisons for the transverse diameter of the distal radial epiphysis [DRB] are given in tables 10-27. The African apes all possess distal radial epiphyses that are relatively larger than in recent humans (Fig. 18). All pairwise comparisons were highly significant (*p=<0.01*). Significant differences exist in the relative size of the distal radial epiphysis within the African apes, including *Pan*. The size of the articular surface of the distal radius is relatively greater in *Pan paniscus* compared with *Pan troglodytes*, and both subspecies of *Pan* display relatively larger distal radii than *Gorilla*. Median DRB indices for the South African Bantu males are significantly smaller than in the African Pygmies (*p=<0.01*) and Southeast Asian Negritos (*p=<0.01*). Significant differences (*p=<0.01*) were detected in comparisons of male Southeast Asian Negritos and Medieval Hungarians (Magyars). With regards to the females, the South African Bantu possess significantly smaller DRB indices than Australian Aborigines. Female Australians have the largest relative distal radial epiphyses of any recent human sample included in this study.

A contrasting pattern of results was generated by pairwise comparisons of the relative size of the articular surface of the proximal ulna [PUB] in recent *Homo* and the African apes with respect to sex. Within samples of males, *Pan paniscus* and *Pan troglodytes* returned results that were significant in all cases, whereas male *Gorilla* median values differed significantly only from Libben Amerindian males (see Fig. 19). In all cases, the relative size of the proximal ulna is greater in *Pan* than in recent humans ($p=<0.01$), whereas the proximal ulnar epiphyseal proportions of *Gorilla* fall within the range of variation in recent humans.

With respect to the females, there exists a general tendency for the median index of *Pan paniscus* to be significantly greater than in recent humans with the exception of the African Pygmies and Southeast Asian Negritos. These latter samples have the greatest mean relative PUB dimensions of all recent humans (see Fig., 19) In contradistinction, *Pan troglodytes* females possess median PUB indices that cannot be statistically distinguished from Medieval Hungarian and Libben Amerindian females. In both cases, the relative size of the proximal ulnar epiphysis in *Pan troglodytes* is proportionally greater than in recent humans. Female gorillas possess relatively smaller PUB values than the Southeast Asian Negrito ($p=<0.05$) and South African Bantu ($p=<0.05$).

Variation in the relative size of the proximal ulnar epiphysis within the African apes follows a consistent pattern independent of sex. *Pan paniscus* possess relatively larger PUB indices than *Pan troglodytes*, which in turn possess relatively larger proximal ulnar articular surfaces than do gorillas of corresponding sex. Thus, within the African apes, there exists a general trend in which the relative size of the proximal ulnar epiphysis is inversely (i.e., negatively) covariant with increasing body size (Fig. 19). However, patterns of variability within *Pan* indicate that the situation is more complex. Notable distinctions in PUB proportions of *Pan paniscus* males and females do not correspond with differences in geometric "size". Similarly, differences in relative PUB proportions in male and female *Pan troglodytes* are relatively minor, despite clear differences in geometric size.

With the exception of the Libben Amerindians, a similar pattern of relative scaling of the proximal ulnar epiphysis exists in recent humans. Female indices are notably larger than in their male counterparts (Fig. 19). The relationship with increasing body size is more ambiguous. While it is true that Medieval Hungarians possess the smallest PUB indices, and the largest geometric means (at least in the males), clear differences in PUB indices of the Amerindian samples are apparently independent of relatively comparable geometric means.

Pairwise comparisons of the Medieval Hungarians with other samples yields significant differences with respect to the Southeast Asian Negritos ([both sexes] $p=<0.01$), South African Bantu ([both sexes] $p=<0.01$), and Libben Amerindian ([males only] $p=<0.001$) samples. In all cases, median (and mean) PUB indices for the Medieval Hungarians are lower. The relative size of the proximal ulnar epiphysis is significantly greater in the Libben sample than in their Southwest Amerindian counterparts ($p=<0.01$). Female Libben Amerindians possess significantly smaller relative PUB indices than female Negrito ($p=<0.001$) and South African ($p=<0.01$) samples.

In a substantial majority of cases, pairwise comparisons of the ulnar midshaft product [UMP] in African ape and recent human samples were significantly different (*p=<0.01*). With the exception of the South African Bantu, Medieval Hungarians and Libben Amerindians, the African apes display significantly larger relative ulnar midshaft products (A-P x M-L diameter). Once again, variability within African ape samples indicates a degree of dependency (i.e., allometry) of relative PUB with increasing geometric size (see Fig. 20). *Pan troglodytes* males and females possess greater relative ulnar midshaft products than do male and female *Pan paniscus*, while *Gorilla* male and female indices are considerably larger than those of *Pan*. This is confirmed by an extremely strong positive correlation of UMP on geometric size in the African apes ($r = 0.996$; $p=<0.001$; $n=6$).

Within recent *Homo*, the most striking anomaly is the relative size of the ulnar midshaft in the Medieval Hungarian males. The mean index for this sample exceeds that seen in male gorillas. Pairwise comparisons of relative ulnar midshaft indices of the Magyar males with remaining human samples were statistically significant (*p=<0.001*). Magyar females also possess extremely large ulnar midshaft product indices, significantly exceeding all other human samples except the African Pygmies and Libben Amerindians. There is a significant relationship between UMP indices and *GM*ALL in recent humans ($r = 0.668$; $p=<0.001$; $n=14$), although this is not of the same magnitude as in the African apes. This probably reflects the extreme "robusticity" of the Magyar and Libben ulnae (males and females), but is also related to the observation that African Pygmies possess relatively larger ulnar midshaft products than would be expected based upon their small geometric size.

Functional Allometry of the Locomotor Skeleton.

The relative size of the femoral midshaft circumference [FMC] is significantly lower in the African apes than in recent humans (Fig. 21), particularly in male gorillas that possess the lowest FMC index of the extant African hominids. Pairwise comparisons of the male gorillas with all other samples, including *Pan*, are highly significant in all cases ($p=<0.01$). The relative FMC index of female gorillas differs significantly from the African Pygmies, Southeast Asian Negritos and the South African Bantu ($p=<0.01$), only. Mean and median FMC indices of these samples are among the largest of the recent human female sub-samples included in this study (see Fig. 21), and the hypothesis that female gorillas possess *consistently smaller* relative FMC indices than recent humans cannot be sustained.

Similarly, *Pan troglodytes* females display relative FMC indices that are not significantly different from a majority of the recent human samples with the exception of those cited previously. *Pan paniscus* males differ significantly in their median FMC proportions from only the Southeast Asian Negritos, whereas *Pan troglodytes* males possess significantly smaller relative FMC indices than the Negritos, Medieval Hungarians and Australian Aborigines ($p=<0.01$). Comparison of these results and mean distributions detailed in figure 21 suggests that the hypothesis that *Pan paniscus* and *Pan troglodytes* (both sexes) would be expected to possess consistently smaller relative FMC indices must also be rejected.

The expectation that the African apes (*P. paniscus*, *P. troglodytes*, *G. gorilla*) will possess a smaller femoral head diameter [FHD] relative to overall geometric size is sustained (see Fig. 22). In all cases, results of the pairwise Mann-Whitney *U* tests for relative FHD in the African apes versus recent humans are highly significant (*p*=<*0.001*). A surprising finding is that significant differences exist in the relative size of the femoral head within the African apes, and that this is allometric, at least in males. *Pan paniscus* males possess larger median (and mean) FHD indices than *Pan troglodytes* and *Gorilla gorilla* (*p*=<*0.05* and *p*=<*0.001*, respectively), a finding that is replicated in the female comparisons with respect to *Pan troglodytes* alone (*p*=<*0.05*). *Pan troglodytes* males are characterised by femoral head dimensions that are relatively larger than *Gorilla* males (*p*=<*0.01*). Female comparisons were not significantly different. Variation within *Homo* in relative femoral head size is relatively minor, and no apparent relationship exists between increasing relative FHD indices and geometric size. Libben Amerindians possess larger proximal femoral epiphyses relative to geometric size than remaining human samples. In contrast, Australian Aboriginal males possess relatively smaller FHD indices than would be expected relative to geometric size. In many cases, pairwise comparisons of these samples with remaining samples yielded moderately significant coefficients (*p*=<*0.05* or *p*=<*0.01*).

Similarly, the relative size of the two components of the knee joint, the distal femur ([FBB] Fig. 23) and proximal tibia ([PTB] Fig. 24) are significantly larger in recent humans than in extant African hominids (*p*=<*0.001*). Relative size of the distal femoral and proximal tibial epiphyses is significantly larger in *Pan pansicus* than in *Pan troglodytes* (*p*=<*0.01*; both sexes) and *Gorilla gorilla* (*p*=<*0.001*; males only). Pairwise comparisons of the FBB and PTB indices of female *Pan troglodytes* and *Gorilla* samples are significantly different, indicating notably larger knee-joint components in the *Gorilla* sample relative to geometric size. A contrasting pattern emerges from the comparison of the male *Pan troglodytes* and *Gorilla* samples. The two samples differ in the relative size of the proximal tibial epiphysis alone (*p=<0.01*), and these dimensions are relatively larger in *Pan* than in *Gorilla*. Comparisons of the mean values suggest that these differences are relatively moderate.

Variability in the relative size of the knee-joint components within recent humans is more problematic. The differences are relatively minor (see Figs. 23 & 24), but in some cases are highly significant. As with the femoral head, there appears to be no consistent relationship between relative epiphyseal size variation and geometric size. African Pygmy and Southeast Asian Negrito females possess notably larger distal femoral, but not proximal tibial epiphyses than their male counterparts and many other samples of significantly greater geometric size (e.g., Bantu, Magyars). Native Americans display relatively large knee-joint components, particularly the Libben sample (males and females).

With the exception of male gorillas versus African Pygmies, Mann-Whitney *U* test comparisons of African ape and recent human samples with respect to the relative size of the distal tibial product [DTP = A-P x M-L diameters], are highly significant (*p=<0.01*). On the whole, recent humans are characterised by uniformly larger distal crural articular surfaces relative to geometric size than the extant African apes (Fig. 25). There exists a clear allometric relationship between the relative size of the distal tibial epiphysis and increasing geometric size in the African apes. *Pan troglodytes* (males and females) possess greater DTP indices than do *Pan paniscus* males and females, but these do not reach statistical significance. Pairwise comparisons of both sub-species of *Pan* with *Gorilla* (both sexes) reveal highly significant differences in the relative size of the distal tibia. *Gorilla gorilla* possesses significantly larger distal tibial epiphyses than *Pan*, a pattern that is accentuated in male gorillas relative to females. The correlation coefficient for the DTP on *GM*ALL in the African apes is highly significant ($r = 0.997; p=<0.001, n=6$).

A significant allometric relationship dominates the pattern of intra-group differences in the relative size of the distal crural articular area in recent humans. The correlation coefficient between DTP and *GM*ALL in the recent human samples is extremely high ($r = 0.915; p=<0.001; n=14$). While the biomechanical implications of this unexpected allometric relationship are relatively clear (see discussion), the existence of such a relationship is unexpected. That a positive allometric relationship exists is puzzling, especially given that no such size-dependent relationship characterises the relative size of the femoral head or epiphyseal dimensions of the knee-joint in *Homo*. Both the hip and the knee are directly subjected to compressive stress during stance and progression in bipedal hominids. African Pygmies (both sexes) and Southeast Asian Negritos (males only) possess significantly smaller distal tibial epiphyses relative to their overall geometric size ($p=<0.01$). Medieval Hungarians and the Native American samples possess distal crural articulations that are relatively larger than comparative humans of slightly reduced geometric size (e.g., Australian Aborigines, South African Bantu).

Non-parametric pairwise comparisons of tibial midshaft circumference [TMC] in the African apes with recent *Homo* (both sexes) yield universally significant results. The African apes display uniformly smaller tibial diaphyseal circumferences than recent humans when these are corrected for variance in geometric size (Fig. 26).

There is considerable allometric variation within the African apes. A highly significant negative correlation ($r = -0.899$; $p=<0.001$, $n=6$) was established between relative TMC and the geometric mean of the epiphyseal and diaphyseal parameters. Highly significant ($p=<0.01$) differences exist between median TMC indices of *Pan paniscus* and *Pan troglodytes* in the males alone. Female comparisons were not statistically significant. This reflects the fact that female *Pan troglodytes* possess relatively larger tibial diaphyses relative to geometric size than their male counterparts (see Fig. 26). *Gorilla* (males and females) possesses significantly smaller relative TMC indices than either *Pan paniscus* or *Pan troglodytes* ($p=<0.001$).

As with the relative area of the distal tibial epiphysis, a corresponding negative relationship exists between *GM*ALL and the mean TMC indices in recent humans, although this does not reach statistical significance at $\alpha = 0.05$ ($r = -0.443$; $p=<0.11$; $n=14$). Medieval Hungarians (both sexes) are characterised by relatively smaller tibial diaphyseal circumference indices than many other human samples, whereas African Pygmies and Southeast Asian Negritos possess TMC indices that are considerably greater than is typical. Australian Aboriginal females have extremely robust tibiae relative to most recent human comparators ($p=<0.01$).

4.4 Bivariate analyses of epiphyseal and diaphyseal scaling

Bivariate regression solutions and post-hoc significance tests for the RMA and LSR equations of the "raw" (i.e., non-standardised) epiphyseal and diaphyseal parameters on the geometric mean for all variables are detailed in tables 28-41. Only the results of the significance tests for the slopes and intercepts of the RMA solutions will be discussed in depth here for reasons outlined previously. Correlation coefficients for proximal humeral breadth [PHB] are positive and highly significant (*p=<0.001*). With the exception of *Gorilla gorilla* (with both Native American samples), slope differences in RMA solutions were not detected. Significant slope differences exist between the Amerindian samples and various recent human samples (table 28; Fig. 27). The slopes were significantly higher in the Amerindian samples in all pairwise comparisons. Significant intercept differences in RMA solutions are observed for both species of *Pan* (*P. paniscus* and *P. troglodytes*), and for *Gorilla* with a majority of the recent human samples. In all cases, intercept differences indicate significantly larger PHB dimensions in the African apes relative to recent *Homo*. Within extant *Homo*, significant differences were detected for the intercepts of Australian Aborigines with most samples, and for the Bantu with the European and Amerindians (table 28). These differences record elevated epiphyseal size in the Australian Aborigines relative to *GM*ALL in the recent human samples, and reduced PHB values relative to *GM*ALL in the Bantu relative to samples of equivalent "*GM* size".

Correlation coefficients for the bi-epicondylar breadth of the humerus [BIEPIC] and *GM*ALL are universally positive and highly significant (*p=<0.001*). Significant slope differences were detected for the African apes with the Bantu, Medieval Hungarian and Australian Aborigines (table 29; Fig. 28). The slope of the *Pan paniscus* (Bonobo) equation was significantly lower than in comparative human samples, whereas those for *Pan troglodytes* and *Gorilla gorilla* were considerably greater. Confidence intervals for the slopes of the African ape RMA solutions all encompass Isometry, as do the equations for the African Pygmy, Southeast Asian

Negrito and Native American samples. Significant intercept differences were found in comparisons of the African apes with all recent humans and between *Gorilla* and both subspecies of *Pan*. These results are consistent with previous observations that the African apes possess relatively larger distal humeral epiphyses than recent humans (Jungers, 1988*a*, 1990; Gallagher, *this study*), and this common pattern is accentuated in *Gorilla* relative to *Pan*. Within *Homo*, Australian Aborigines possess relatively smaller BIEPIC dimensions than most recent humans, and the African Bantu have relatively smaller dimensions than the Native American populations.

With the exception of the Southwest Amerindians, correlation coefficients for humerus midshaft circumference [HMC] and *GM*ALL are highly significant ($p=<0.001$) and positive. 95% Confidence Intervals for the RMA solutions for all samples encompass isometry, with the exception of the Medieval Hungarians. Significant differences in pairwise comparisons of the African ape and recent human equations were detected for the Magyars alone (*Pan* and *Gorilla*). RMA slopes are significantly higher in *Pan* and *Gorilla* relative to the Magyars. With respect to elevation differences, with the exception of *Pan troglodytes* versus the African Pygmies, African apes possess significantly greater intercepts than the entire recent human sample for HMC. This corresponds to uniformly larger relative HMC values in the African apes. Variation within recent humans indicates that Australian Aborigines possess relatively narrower humeral diaphyses than most recent humans. Significant intercept differences between the Negritos and the Bantu reflect absolute differences in values of *GM*ALL rather than relative differences in relative diaphyseal "size" (table 30; Fig. 29).

Sample correlations for the transverse diameter of the radial head [RHD] are significantly positive in all cases (*p=<0.001*). No RMA solution yields confidence intervals that include Isometry. Significant slope differences for the RMA equations were detected for *Gorilla gorilla* versus both species of *Pan*, and were significantly lower in *Gorilla* (Table 31; Fig. 30). Significant intercept differences exist for the African apes versus recent humans, indicating that African apes possess relatively larger radial head dimensions than is typical for *Homo* (Jungers, 1988*a*). Surprisingly, significant elevation differences exist between *Pan* and *Gorilla*, denoting significantly larger relative proximal radial epiphyses in *Pan*. African Pygmies possess a relatively larger radial head diameter than is typical of recent humans, particularly those of significantly greater geometric size (e.g., Bantu, Magyars, Amerindians).

Correlation coefficients for the RMA solutions of radial midshaft circumference [RMC] are high and positive (*p=<0.001*). Pairwise comparisons of the sample slope differences for the African ape and recent human equations are not uniform (table 32; Fig. 31). Gorillas have significantly lower slopes than Negritos and Australian Aborigines, but a significantly higher slope than Libben Amerindians. Slope differences with the Libben sample are accentuated in both species of *Pan* (*p=<0.001*), but significant differences between *Pan paniscus* and *Pan troglodytes* are due to several positive outliers in the latter. Significant slope differences exist between *Pan troglodytes* and *Gorilla gorilla.* Highly significant differences exist in the elevations of the RMA equations for both species of *Pan* relative to all recent human samples and also with *Gorilla* for *Pan troglodytes*. *Pan paniscus* has relatively larger radial midshaft circumference values than are typical for *Gorilla*, but these do not reach statistical significance. Considerable variability exists in the relative size of the radial midshaft in recent humans. Significantly lower values in both Amerindian samples versus contemporary humans were detected. Significantly larger relative differences in RMC values for the African Pygmies and Southeast Asian Negritos relative to the South African Bantu ($p=<0.05$ and $p=<0.001$, respectively) were also confirmed.

Correlation coefficients for regressions of distal radial breadth [DRB] are positive and highly significant (table 33; Fig. 32). Of the African apes, only *Pan troglodytes* exhibit's consistent slope differences in the pairwise comparisons with all recent humans except Libben Amerindians. Significant slope differences also exist between *Pan troglodytes* and *Pan paniscus*, and also with *Gorilla* ($p=<0.05$ and $p=<0.001$, respectively). Significant elevation differences were detected for the RMA solutions of *Pan* and *Gorilla* with recent humans. These results confirm previous observations (e.g., Jungers, 1988*a*, 1990; Gallagher, 2002), which found that the African apes possess relatively larger DRB values than recent *Homo*. This morphological contrast is accentuated in *Pan* relative to *Gorilla*.

With the exception of the African Pygmies, Medieval Hungarians and Southwest Amerindians, correlation coefficients for the proximal articular breadth of the ulna [PUB] with *GM*ALL are positive and highly significant (table 34; no figure). Significant slope differences were confirmed for *Pan troglodytes* versus the African Pygmies, Negritos and Australian Aborigines, and for *Gorilla* versus the Libben Amerindians. The "Quick test" for RMA intercept's (Tsutakawa & Hewett, 1977) detected significant differences in pairwise comparisons of *Pan* with most recent humans. Significant elevation differences were detected between the elevations for

Pan troglodytes with those of *Gorilla*. *Pan troglodytes* display a relatively larger proximal ulnar articular surface than *Gorilla*. These results contrast with previous observations (Jungers 1988*a*, 1990) and earlier findings in this study that detected a 'complex' of proportionally larger epiphyses in the elbow joint of the extant African apes.

Results of the regressions of the midshaft product of the ulna [UMP] are presented in table 35. Correlation coefficients are positive and highly significant, despite the existence of positive outlying clusters in the *Pan troglodytes* and *Gorilla* samples. Significantly higher RMA slopes for *Pan troglodytes* and *Gorilla* were detected in all pairwise comparisons with recent humans and also with *Pan paniscus*. Significant differences in RMA intercepts were found in all comparisons of *Pan paniscus* and *Pan troglodytes* with recent humans with the exception of the African Pygmies and Southeast Asian Negritos (*Pan troglodytes*). Relatively larger UMP values also characterise the comparisons of *Gorilla gorilla* with recent humans, but these differences reach statistical significance in a single case (Australian Aborigines). Both subspecies of *Pan* have relatively larger ulnar midshaft diaphyseal dimensions than *Gorilla* that are highly significant ($p=<0.001$). Within recent *Homo*, African Pygmies have relative UMP values that are significantly greater than is typical for other human samples, whereas Australian Aboriginal ulnae are characterised by reduced midshaft proportions relative to remaining human populations.

Few notable differences exist between *Homo* and the African apes with respect to femoral midshaft circumference [FMC]. Pearson correlation coefficients all exceed 0.7 and are highly significant (*p=<0.001*). Only *Gorilla* manifests a significant slope difference with some recent humans (Bantu, Magyars, Southwest Amerindians and both subspecies of *Pan*; see table 36), but this is apparently due to an extreme negative outlier. Both species of *Pan* (*P. paniscus* and *P. troglodytes*) possess relatively smaller FMC values than the Southeast Asian Negritos (*p=<0.05*).

Differences in the diameter of the femoral head (FHD) in the African apes and recent human samples are well defined. Correlation coefficients are universally strong, positive and highly significant (table 37; Fig. 34). None of the sample RMA solutions encompass Isometry within their 95% confidence intervals. With the exception of the African Pygmies, the *Gorilla* sample slope differs significantly from all recent human samples, and even *Pan troglodytes* (*p=<0.001*). African ape RMA elevations are significantly different from recent humans, reflecting the relatively smaller hip joint component in the African apes (e.g., Lovejoy, 1973, 1975, 1978, 1988; Lovejoy & Heiple, 1970; Lovejoy, Heiple & Burstein, 1973; Jungers 1988*a*, 1990).

Unexpected differences exist between *Pan* and *Gorilla*. Significant elevation differences were returned in comparisons of *Pan troglodytes* with *Gorilla*, indicating a slight proportional increase in the size of the femoral head relative to geometric size in *Pan*. There is considerable variation in the relative size of the femoral head within recent *Homo*, as noted previously. Australian Aborigines possess significantly smaller relative FHD values than all remaining samples, including the diminutive African Pygmy and Southeast Asian Negrito samples. This cannot be due to absolute differences in body size in these populations.

Highly significant correlations exist between the transverse diameter of the femoral condyles [FBB] and *GM*ALL for all samples (*p=<0.001*). *Gorilla gorilla* possesses significantly lower RMA slopes than the Amerindian samples and *Pan troglodytes*. A substantial majority of the population RMA slopes, excluding African Pygmies, Magyars and gorillas, include the coefficient for isometry within their 95% CI's. Significant elevation differences were detected in 99% of pairwise comparisons of the African apes with recent humans, once again reflecting the relatively larger femoral epiphyses in recent *Homo*. Highly significant RMA intercept differences were detected for the Australian Aborigines with most, but not all, recent humans. Australian Aborigines do not possess significantly larger distal femoral epiphyses than *Pan paniscus*.

Correlation coefficients for regressions of proximal tibial breadth [PTB] on *GM*ALL are highly significant and positive in all cases (table 39; Fig. 36). With the exception of the Bantu, Magyar, *Pan troglodytes* and *Gorilla* samples, 95% CI's for the RMA slopes incorporate isometry. Significant slope differences in the pairwise comparisons of gorillas with some, but not all, recent humans were revealed. Significant intercept differences for the RMA solutions of the African Apes and recent humans are consistent with previous findings for the distal femoral epiphysis. African Apes have proximal tibial epiphyses that are relatively smaller than in recent *Homo*. Australian Aborigines possess relatively smaller PTB values than the Amerindian, Bantu and Medieval Hungarian populations. Australians also possess relatively smaller proximal tibial epiphyses than African Pygmies and Southeast Asian Negritos, but these do not reach statistical significance.

Significant differences exist in the scaling of the epiphyseal area of the distal tibia in the African apes and recent humans. In recent humans the distal crural epiphysis is clearly enlarged relative to overall geometric size and contrasts with the morphology of the African hominoids. Correlation coefficients are positive and highly significant ($p=<0.001$). The RMA slope of the bonobo sample differs significantly from those calculated for the recent human samples ($p=<0.001$), whereas slope differences in *Pan troglodytes* and *Gorilla gorilla* reach extreme levels of significance ($p=<0.001$) with the Southwest Amerindians alone. Significant elevation differences were observed in the pairwise comparisons of recent *Homo* and the African apes ($p=<0.001$). The regression models clearly correspond with results obtained previously using the proportional indices.

With the exception of *Pan troglodytes*, remaining sample correlation coefficients of the tibial midshaft circumference [TMC] with the geometric mean exceed 0.7 (table 41; Fig. 38). All are statistically significant at $p=<0.001$ level of probability. To the exclusion of *Gorilla*, the RMA slopes yield 95% confidence intervals that include the coefficient for Isometry. Statistical slope differences were detected in all pairwise comparisons of *Gorilla* with remaining samples with the exception of the African Pygmies. Significant elevation differences were found in nearly all comparisons of the African ape solutions with those of recent *Homo*. This confirms previous observations that recent humans possess relatively larger tibial diaphyseal circumferences than the extant African hominoids. Relative scaling of TMC in *Pan* differs significantly from *Gorilla* and is closer to the condition seen in *Homo* (i.e., relatively larger). Variation of relative TMC in recent humans indicates that the Medieval Hungarians are characterised by significantly smaller tibial midshaft diaphyses than Australian Aborigines, Southwest and Libben Amerindians. These samples have the largest relative TMC indices in the recent humans included in this study.

4.5 Relative epiphyseal size in the Plio-Pleistocene fossil hominids

4.5.1 Univariate comparisons of relative epiphyseal size

Comparisons of the geometric means of the extant samples (including the diaphyseal dimensions) and the extant and fossil samples (epiphyses only), are presented for comparative purposes in figures 12 & 39. The Geometric means are notably smaller in extant samples in the second series, owing to the exclusion of the diaphyseal variables and two epiphyseal parameters [PHB & DTP]. Nonetheless, the *GM*'s in the two series are highly correlated ($r = 0.991$; $p=<0.001$). The *GM* profile of *Pan paniscus* differs slightly in the second series, with a small elevation in the level of sexual dimorphism in "geometric size". Nevertheless, it is doubtful that this would affect the comparisons to any considerable extent. The Upper Pleistocene *Homo GM*'s fall well within the range of variation in recent *Homo*, whereas that of AL 288-1 *(A. afarensis)* is considerably lower and is comparatively closer to *Pan paniscus* females.

The relative "profiles" of the distal humeral epiphysis [BIEPIC] in the extant samples is identical to the pattern observed previously; in all cases the African apes possess uniformly larger epiphyses than recent humans (Fig. 40). All of the fossil specimens, including *Australopithecus afarensis* (AL 288-1), conform to the extant hominid pattern with respect to the relative proportions of the distal humerus. The early Upper Pleistocene *Homo sapiens* female from Qafzeh (Qafzeh 9) displays a relatively smaller distal humeral epiphysis than is typical for recent humans.

With the exception of the single Neandertal male specimen (Feldhofer 1), the relative size of the radial head [RHD] in fossil hominids falls at the upper ranges of variation in recent humans (see Fig. 41). None approach the extreme proportions of the proximal radius seen in the extant African apes. Similarly, the relative size of the distal radial epiphysis [DRB] in fossil specimens generally fall within the range of variation seen in recent humans and contrast with the proportionally large distal radii of the extant African apes (see Fig. 42). Surprisingly, the female early Upper Pleistocene *Homo sapiens* individual from the Levant (Qafzeh 9) displays a relatively large distal radial epiphysis and approximates *Gorilla.* Considerable variability is present within extant and extinct fossil samples with regard to the relative size of the proximal ulna. No clear distinctions between recent humans, African apes or extinct fossil hominids in the relative size of the proximal ulna exist. This casts doubt on the functional valence of the relative size of the proximal ulna.

Not surprisingly, clear distinctions exist in the relative size of the femoral head in extant and extinct hominids compared with the African apes that is of obvious functional significance. All of the specimens/samples assigned to the genus *Homo* (*Homo neanderthalensis*, *Homo sapiens*) possess femoral head dimensions that are significantly larger relative to geometric size than the African apes and are proportionally equivalent to that seen in recent humans (see Fig. 44). Relative size of the femoral head in AL 288-1 (*Australopithecus afarensis*) is considerably smaller than in recent humans. However, the femoral head proportions of AL 288-1 is discernibly larger than the proportionally greatest FHD index in the extant African apes (AL 288-1 = 91.14; *Gorilla* female = 82.93), and is very close to the average FHD of African Bantu females (FHD = 95.46).

The epiphyseal proportions of the *Australopithecus afarensis* knee-joint [FBB & PTB] appear similarly "intermediate" between the African apes and *Homo* (see Figs. 45 & 46). An intermediate "classification" of the relative proportions of the distal femur and proximal tibia disguises the fact that in *Australopithecus afarensis* these dimensions are considerably greater than the largest average indices in the African apes (FBB: AL 129-1 = 168.1, *Gorilla* female = 153.91; PTB = AL 129-1 = 161.8, *Gorilla* female = 144.38). The lowest mean value for the relative size of the distal femur is that of the African Bantu females (FBB = 168.52), whereas the proportions of the proximal tibia in AL 288-1 exceed those of Qafzeh 9 and Feldhofer 1 (157.6 & 156.7, respectively).

4.5.2 Bivariate perspectives on relative epiphyseal size in fossil hominids

Highly significant slope differences (*p=<0.001*) exist between the recent human and African ape regression solutions with respect to the proportions of the distal humeral epiphysis [BIEPIC]. As the regression lines diverge with increasing "geometric size", significance tests for the elevations were not significant (see Fig. 47; table 42). Interestingly, the two regression lines converge as they approach the geometric size of AL 288-1 (*Australopithecus afarensis*), suggesting that this diminutive female may actually have possessed distal humeral epipihyseal proportions that are perhaps "isometric" (proportionally equivalent) for her geometric size based upon extant analogues.

Such a conclusion is supported by examination of the standardised residuals of AL 288-1 from the African ape (Fig. 48) and recent human (Fig. 49) models. Comparatively, AL 288-1 appears much more "ape-like" in her approximation to the African ape model for BIEPIC than do later Pleistocene *Homo*, whereas with respect to the recent human model AL 288-1 displays proportionally small distal humeral epiphyses relative to her geometric size (see also table 43). AL 288-1 is exceeded in her negative deviation from the recent human regression model by various Pleistocene fossil specimens.

Pairwise comparisons of the LSR slope and elevations for RHD in the African apes and recent humans were highly significant (*p=<0.001*; table 42). The relative size of the proximal radial epiphysis [RHD] in A.L. 288-1 is proportionally small compared to the African ape (Figs. 50, 51 & 52), but not recent human standards. With respect to recent humans, AL 288-1 displays a RHD value that is proportionally equivalent for her geometric size (Fig. 51). Surprisingly, the Feldhofer Neandertal has a relatively small radial head diameter relative to geometric size, which contrast with its relatively large distal radius.

Within the remaining fossil samples, the extreme levels of gender variation in the relative size of the radial head is revealed in the standard deviations of the Predmosti early Upper Palaeolithic specimens (see Fig. 51). The Predmosti male specimens (Predmosti 3, 9 and 14; Holliday, 1997*a*; Pearson, 1997) display relatively large proximal radii, whereas those of the female specimens, Predmosti 4 and 10 possess notably smaller proximal radii relative to their geometric size. Comparatively, these gender-based scaling differences in the Early Upper Palaeolithic amplify the contrasting proportions of the proximal radius in the male Neandertal specimen.

Significant slope and elevation differences exist between the African apes and the recent humans in the relative size of the distal radial epiphysis. Standard deviations of the predicted values of the fossil specimens (including AL 288-1) generally fall below two S.D. units of the African ape model, with the sole exception of the Early Upper Pleistocene female from Qafzeh (Qafzeh 9) and the later Upper Pleistocene male from Dolni Vestonice (DV 14), who possess comparatively large distal radii (see Figs. 54, 55, 56). Interestingly, the relative proportions of the distal radius of AL 288-1 are relatively small compared to standardised prediction from the recent human model, but this specimen is not unique.

With the exception of Predmosti 3, the relative size of the distal radial epiphysis of remaining Predmosti specimens are inordinately small, contrasting with their large proximal radial proportions, at least in the males (see Fig. 55). The distal radial proportions of the late Upper Pleistocene males from Grotte des Enfants 6, Gough's Cave 1 and Chencherere II are also relative small, falling below 1 S.D. of the recent human model. All remaining specimens, including the Feldhofer Neandertal, display relative radial proportions that fall within 1 S.D. of the predicted values derived from the recent human model (Fig. 55).

Significant differences in the LSR slope (*p=<0.01*) and elevation (*p=<0.05*) were detected in comparisons of the African ape and recent human "macro-sample" solutions for the relative size of the proximal ulnar epiphysis (not shown). As a general rule, the African apes apparently possess proportionally larger proximal ulnar epiphyses relative to geometric size than is typical in recent *Homo*. Nevertheless, there exists considerable overlap in the samples. This supports previous observations regarding the valence of the relative size of the proximal ulna as a discriminatory parameter of the extant African hominoids.

Standardised residuals of several fossil specimens from the African ape model are positive, indicating that the predicted PUB values for these individuals were underestimates of the actual observed values. AL 288-1, the Feldhofer Neandertal, Dolni Vestonice 13 and the two early Holocene African specimens (Makalia I and Chencherere II) all possess relatively larger proximal ulnar epiphyses than *Pan* and *Gorilla* individuals of equivalent geometric size (not shown). Standardised residuals from the recent human LSR model for the fossil specimens demonstrate that all specimens that deviate positively from the ape model also deviate positively from recent *Homo*. The PUB proportions of the Feldhofer Neandertal are notably greater relative to geometric size, whereas remaining fossil specimens displaying positive deviations all fall within 1 standard deviation. If scaled equivalently to a recent human of similar geometric size, AL 288-1 has relatively smaller proximal ulnar proportions, but these are not of the same magnitude as those of Skhul IV, Arene Candide II or Hayonim 29.

Not surprisingly, highly significant elevation differences exist between the recent humans and the African apes in the LSR of femoral head diameter [FHD] on geometric size (Fig. 56). The position of AL 288-1 is apparently intermediate between the Ape and human distributions, thus confirming previous observations (Jungers, 1988*a*, 1991; Ruff, 1988, 1998; see previous section). Standardised residuals and percentage prediction errors (tables 44-50) for the fossil hominid specimens show that in all cases, the African ape prediction equation yields estimates which are demonstrably lower than the observed FHD's (Fig. 58). The deviation of AL 288-1 from the African ape LSR model is 2 SD above zero, although this is considerably lower than those of more recent hominids.

The unique proportions of the femoral head of AL 288-1 are apparent in her standardised residual from the recent human LSR model (Fig. 57). AL 288-1 has a femoral head diameter that is nearly 2 SD's below zero, indicating that relative femoral head is not proportionally equivalent to recent humans and is considerably smaller. With some exceptions, many of the fossil specimens evince relatively larger proximal femoral epiphyses proportional to their *GM*. There is no apparent evidence of gender-bias in the variability of the relative size of the femoral head in geologically (i.e., EUP), or stratigraphically (e.g., Dolni Vestonice, Predmosti, Grotte des Enfants) contemporary, individuals. Although the relative size of the femoral head in the sole Neandertal specimen of sufficient preservation (Feldhofer 1) is relatively larger than expected, it does not exceed the range of variation in other specimens.

Post-hoc tests for the elevations of the African ape and recent human regression equations for relative FBB and PTB are highly significant ($p=<0.001$).

Highly significant slope differences were detected between the two models for relative FBB ($p=<0.001$). The proportionally larger distal femoral and proximal tibial epiphyses of recent humans relative to the extant African apes is confirmed for all fossil specimens, including AL 288-1 (see Figs. 59 & 62). Standardised residuals of estimates for FBB in the fossil hominids yielded by the African ape model are shown in figure 61. All deviations are positive and exceed 3 SD units. In contrast to the relative size of the femoral head, the deviation from the ape model of AL 288-1 is not observably different from the later Pleistocene *Homo neanderthalensis* and *Homo sapiens* individuals.

The standard deviations of the proximal tibial epiphysis proportional to geometric size in the fossil hominid sample are again positive relative to the African ape regression model, but are of a lower magnitude (Fig. 64). The deviation of the AL 288-1 *A. afarensis* female from the African ape condition is again equivocal. AL 288-1 approaches the Early Upper Pleistocene Skhul IV, the Feldhofer Neandertal and several other Late Upper Pleistocene *Homo sapiens* specimens in the relative size of her proximal tibial epiphysis. With respect to the recent human model, AL 288-1 apparently possesses distal femoral which are proportionally equivalent (i.e., isometric) for her geometric size. In contrast to the pattern observed in her proximal femoral epiphysis, the proportions of distal femur in this diminutive *Australopithecus afarensis* female are remarkably “hominid” (Fig. 60). In contradistinction, the standard deviation of the proximal tibial epiphysis in AL 288-1 is negative, indicating a proportionally smaller PTB than is predicted from the recent human model. However, this is only slightly lower (less than 0.5 SD) from the predicted value. Considered together, the proportions of the knee-joint epiphyses in recent humans are not quantitatively different from later Pleistocene *Homo*, which is in marked contrast to the relative size of the femoral head.

4.5.3 Multivariate perspectives on epiphyseal scaling in fossil hominids

An initial attempt to compute a Principal Components Analysis using Darroch and Mosimann's (Darroch & Mosimann, 1985) "log-shape" variables was unsuccessful. Both the Kaiser-Meyer-Olkin [KMO] and Bartlett's coefficient of sphericity indicated that the covariance matrix was unsuited to factor analysis. Normalisation of the indices to the original scale did not facilitate a better fit, whereas the covariance matrix of the raw variables proved to be better suited to PCA. Thus, non-standardised data (size and shape) was entered into PCA.

The KMO coefficient of sampling adequacy (0.862) and Bartlett's test (χ = 463.465; $p=<0.001$) indicated that the covariance matrix of the raw data was suitable for factor modelling. Seven non-rotated orthogonal vectors were extracted using Principal Component decomposition. A summary table of the eigenvalues, together with the respective contribution to the total explained variance is detailed in table 51. The first Principal Component accounted for approximately 79.75% of the total variance, with subsequent factors accounting for the residual of a total of 98.38% of the total variance. The remaining factors were retained for use in the subsequent Canonical Variates Analysis.

The re-scaled variable loadings on the first component are uniformly high and positive, suggesting that this is a "generalised size vector" (Shea, 1981, 1985). This view is confirmed by the correlation coefficient of the PC scores of the first component with "Geometric Size" (Spearman's *rho*; $r = 0.972$; $p=<0.001$). Of the subsequent component scores, only those for PC3 display moderate correlations with geometric size ($r = 0.329$; $p=<0.05$). The second factor accounts for 14.95% of the total variance and is bipolar. The distal humeral, proximal and distal radial epiphyses contribute heavily to the explained variance on this axis and are positive (see table 52). The proximal tibial epiphysis is also positively loaded on PC2, but to a lesser extent than the three upper limb variables. The proximal ulna and the proximal and distal femoral epiphyses are negatively loaded on PC2.

A bivariate scatterplot of the component scores of PC2 on PC1 for the extant and extinct hominids reveals that PC2 effectively distinguishes the African apes from the bipedal fossil hominids (Fig. 65). The position of AL 288-1 ("Lucy") is equivocal; she clearly falls with the recent humans by virtue of the low negative loadings of her distal humeral and proximal and distal radial epiphyses. However, the positive loading of the proximal tibial epiphysis on the second principal component compromises clear-cut locomotor distinctions. Parametric and non-parametric correlation matrices indicate that all four upper limb variables (BIEPIC, RHD, DRB & PUB) are negatively correlated with the lower limb variables, including the proximal tibia. Previous observations of the allometry coefficients of the lower limb epiphyses show that these display negative allometry in *Pan* and *Gorilla*, but this does not explain the positive loading of the proximal tibia on the second axis.

Succeeding PC's are dominated by high positive loadings of single variables. Axis 3, which accounts for slightly under 3% of the total variance is dominated by the positive loading of the proximal ulnar epiphysis. Component four apparently reflects positive variability in the distal radial epiphysis. None of these subsequent axes effectively distinguish recent and fossil hominids for the African apes (see Figs. 66 & 67).

Canonical Variates Analysis (CVA) yielded five functions accounting for 100% of the total variance. The first eigenvalue accounts for 87.9% of the total variance, while the second and third eigenvalues comprise 8.7% and 2.4% of the variance, respectively. Wilks' Lambda indicates that the first two components maximise group separation ($p=<0.001$). Not surprisingly, the effective separation of the African apes and the bipedal hominids on the second axis is due to the high coefficient of PC2 (see Fig. 68; table 54). Interestingly, PC7 yields the highest coefficient on Canonical Axis 2. The component loadings on PC7 are generally low, and the axis is dominated by the positive loading of the radial head diameter.

The morphological affinities of AL 288-1 clearly lie with the recent human samples, particularly the African Pygmies and Southeast Asian Negritos, which she approximates closely in geometric size. The discriminatory power of the second PC is confirmed, suggesting that the African apes are united by their shared state of relatively large upper limb epiphyses. AL 288-1 on the other hand, does not possess similar upper limb epiphyseal proportions. Classification of the samples indicates that the African apes can be effectively segregated from the recent humans with no error, whereas within recent humans there is considerable variability. AL 288-1 was entered as a special case, and was classified as a recent human.

Thus, with respect to the relative "profiles" of the upper and lower limb epiphyses the affinities of the fossil hominid samples (including *Australopithecus afarensis*) are with recent humans, not the African apes. In many respects this is not surprising, as there is little doubt that all species from *Homo ergaster* onwards are habitual terrestrial bipeds. However, the relative size of the lower limb epiphyses in *Australopithecus afarensis*, particularly the femoral head, has been the subject of intense debate (e.g., Jungers, 1988*a*, 1990, 1991 V's: Ruff, 1988, 1998; Lovejoy, 1973, 1975, 1988; Lovejoy *et al.*, 1973). The results of this study suggests that relative to "geometric size", the upper and lower limb epiphyseal "profile" of AL 288-1 ("Lucy") is distinctly "hominid" rather than "hominoid".

4.6 Summary

This chapter investigated univariate, bivariate and multivariate patterns of variability in the relative scaling of linear approximations of epiphyseal joint size and diaphyseal midshaft proportions in a large, geographically disparate sample of recent humans and the extant African apes (*Pan* and *Gorilla*). Specific hypotheses relating to structural scaling with a valid skeletal approximation of body size (*GM*ALL) and differential locomotor behaviour were explored.

Clear differences in the relative epiphyseal and diaphyseal proportions exist between recent humans and the African apes, and the first hypotheses outlined in Chapter 2 is confirmed. *Pan* and *Gorilla* generally display relatively larger upper limb joints and diaphyseal circumferences than recent humans when expressed as a proportion of geometric size (*GM*ALL). The relative size of the lower limb epiphyses and diaphyses of recent humans are, with few exceptions, proportionally greater than those of the African apes. The second hypothesis, which posits that inter-sample variance in the relative size of the epiphyses in the upper and lower limb in recent *Homo* would be constrained relative to levels of variance in diaphyseal proportions is not sustained. Recent humans display considerable variation in the relative size of *both* their upper and lower limb joints and diaphyseal circumferences. Interestingly, variation in the relative size of the epiphyses and diaphyses of the distal elements of the upper limb (radius and ulna) are significantly lower in *Gorilla* relative to the two species of *Pan.*

Convincing support emerges in support of the view that these reflect epigenetically mediated locomotor adaptations. The partial female *Australopithecus afarensis* skeleton (AL 288-1 ["Lucy"]) is demonstrated to possess a distinctly "hominid", rather than "hominoid", relative epiphyseal profile in her upper and lower limb. This finding is consistent with the expectations of the third hypothesis outlined previously. Relative size of the upper and lower limb epiphyses of Late Pleistocene *Homo* (Neandertals and *Homo sapiens*) are highly variable, even within contemporary hominid sub-sets (Eurasian EUP and LUP hominids). No apparent differences exist in the relative scaling of the lower limb epiphyses in Late Pleistocene fossil hominids compared with recent humans.

Chapter 5. Geometric Analysis of the Hominoid Upper Limb

5.1 Introduction

The following chapter presents the results of an exploratory Generalised Procrustes Analyses (GPA) of the landmark co-ordinates taken on the distal humerus and proximal ulna in a large series of recent humans, extant African apes, and suitably preserved fossil hominids sampling both *Australopithecus* and *Homo*. GPA of the landmark co-ordinates was performed using the integrated analysis package *Morphologika* (O'Higgins & Jones, 1998*a*). A Principal Component Analysis (PCA) was calculated on the variance-covariance matrix of tangent space co-ordinates (Kendall, 1984) after GPA orthogonal fitting. Determination of morphological similarity in the fossil specimens was assessed by the calculation of Mahalanobis' squared distance coefficients and by performing a Canonical Variates Analysis (CVA) on the resulting PC scores of individual specimens. Shape differences in sufficiently large extant samples (*Homo*, *Pan* & *Gorilla*) were determined using non-parametric pairwise permutation tests with a programme supplied by Professor Paul O' Higgins. Visual assessment of shape differences between samples and individual fossil specimens was facilitated by the technique of thin-plate splines (Bookstein, 1991; O'Higgins & Jones, 1998*a*).

5.2 Analysis of the distal humerus in extant and extinct hominoids

5.2.1 Permutation comparisons of the extant samples

Results of the pairwise permutation tests for differences in distal humeral shape are presented in table 55, which is located with the Appendices in Volume II of the thesis. In all comparisons, sex sub-samples were pooled to maximise effective sample size in the pairwise analyses. With few exceptions, pairwise comparisons of the sample consensus configurations using the permutation tests (1000 iterations) were all significantly different ($p=<0.001$). African Pygmies did not differ significantly in their consensus configurations from the Southeast Asian Negritos, the South African Bantu were not demonstrably different from the Australian Aborigines, who in turn did not differ notably in their consensus configuration from the Libben Amerindians. Not surprisingly, Southwest Amerindians do not differ significantly in their consensus configuration from the Libben Amerindians.

5.2.2 Generalised Procrustes Analyses

A two-dimensional graphical rendering of the distal humerus landmark configurations for the total sample (n=325) of 18 landmark co-ordinates after Procrustes rotation, translation, re-scaling and, where appropriate, reflection, is shown in figure 70. The warp utility in *morphologika* facilitates effective visual rendering of the nature of morphological change across individual component axes of interest (i.e., negative score to positive scores) and is a crucial tool in any exploratory shape analysis of the geometric configurations. Several axes of interest were determined, and the morphological components of these shape changes are described below.

Principal Components Analysis of the tangent space co-ordinates yielded 51 axes (18 x 3 –3*df*). Of these, only the first 10 components were retained for further investigation. The first PC accounted for only 15% of the total variance, with subsequent 9 axes accounting for a cumulative 62.4% of the variance (table 56). The correlation matrix for the total sample reveals that the first component alone is highly correlated with centroid size (table 57; r = 0.629; p=<*0.001*). Subdivision of the samples in to recent human and African ape subsets (tables 58 & 59) reveals that the correlation coefficient of the first PC scores with centroid size in recent humans is substantially lower than in the total sample and is negative (r = -0.267; n=185; p=<*0.001*). The correlation coefficient of PC1 and Centroid Size in the African apes is positive and highly significant (r = 0.604; n=101; p=<*0.001*).

A bivariate scatter plot of the first and second component axes is shown in figure 71. The African apes, especially *Gorilla* and to a lesser extent, *Pan*, can be distinguished from the majority of recent humans by their consistent positive scores on the first Principal Component. In contrast, the recent humans tend to have extreme negative to relatively low positive scores on PC1. The negative relationship between PC1 scores and Centroid Size is clearly evident in the recent human samples; only the African Pygmies and Southeast Asian Negritos have PC1 scores that are positive. There is, however, considerable variability in the Negrito PC1 scores. Visual inspection of the distribution of the individual specimens along the first axis suggests that variation in recent humans along PC 1 generally approximates that seen in the

African apes, whereas on the second axis recent (and fossil) hominids display considerably greater variability.

Exploration of the morphological shape changes in the Distal Humerus on the first PC axis from negative to positive (holding shape change on the Y-axis constant [zero]) are presented in figures 71 & 72. A more detailed depiction of the morphological transformations on PC1 and PC2 (using wireframe renderings, landmark numbers, and TPS "warps") is included as an AVI movie file on an accompanying CD-ROM. Briefly summarised; morphological changes along PC1 (negative-positive) record a gradual postero-superior displacement of the medial epicondyle, a change in the breadth and location of the olecranon fossa, and a decrease in the anterior projection of the capitulum. Changes in the morphology of the medial epicondyle and, to a lesser extent, the capitulum, are clearly visible in the sequence in *norma frontalis* from extreme negative to extreme positive (Figs. 71 & 72).

Greater appreciation of the total morphological change in distal humeral geometry along the first component axis is revealed when viewed in *norma verticalis* (Fig. 72). The transformation in the articular surface of the distal humerus of the African apes from the recent human condition involves a reduction in the overall proportions of the articular surface and an increase in the linear distance of landmarks of the anterior articular surface and those of the olecranon fossa. This reflects the decreasing M-L breadth of the olecranon fossa and increasing A-P depth of the articular surface of the African ape distal humerus relative to recent humans.

Morphological changes in distal humeral morphology along the second component axis are detailed in *norma frontalis* and *norma verticalis* (Figs. 71 & 73), once again holding the X-axis scores constant at zero. The extreme negative to positive variation in PC scores on this axis corresponds to a decrease in the height of the olecranon fossa, coupled with a marked increase in the sagittal and transverse planes of the distal humerus. Specifically, this involves an increase in projection of the medial epicondyle (posterior deflection) coupled with increasing medio-lateral breadth of the articular surface. A notable decrease in the antero-posterior breadth of the distal humerus is evident. There is no corresponding change in the supero-inferior height of the articular surface on the second component axis, but there is a notable increase in the projection of the capitulum (see Fig. 73).

To reiterate an earlier observation, recent humans display considerable variability in their PC2 scores, which directly corresponds with the morphological transformations outlined above. Certain sample distinctions can be made. For example, the African Bantu display low negative scores compared to the high positive scores of the two Native American samples (SW Amerindians and Libben Amerindians), with no clear differences in PC1 scores between the groups. Native American distal humeral geometry differs from the South African Bantu by virtue of increased anterior projection of the capitulum, a relatively greater projection of the medial epicondyle and increased medio-lateral breadth of the articular surface (particularly of the capitulum). Native American distal humerii also display an overall decrease in the relative antero-posterior plane of the distal humerus and a decrease in the height of the olecranon fossa.

Thin-plate spline transformations ([“TPS”) Bookstein, 1990, 1991; Yaroch, 1996; O’Higgins & Jones, 1998*a*) of the two extreme individuals on PC1 and PC2 is a useful graphical tool for displaying patterns of shape change between specimens. TPS “warping” of an African Bantu male (AD 3585; CS = 87.585) to a male *Gorilla* (M856; CS = 108.795) representing extreme variation on PC1 in *norma frontalis* and *norma lateralis* is shown in figure 74. The first two representations are of the unwarped Bantu specimen. Clear shape changes in the proportions of the olecranon fossa, the transverse plane of the articular surface and the morphology of the medial epicondyle are evident. In *norma verticalis*, these morphological changes, together with the decrease in the projection of the capitulum are more apparent.

With respect to the Y-axis, the extreme morphological changes in recent humans can be visualised using an Australian Aborigine as the extreme negative reference (RCS207342; CS = 91.218) and a SW Amerindian as the extreme positive target shape (BPM 60.198; CS = 84.248). The Native American specimen displays a marked increase in the anterior projection of capitulum, together with a slight decrease in the medio-lateral plane of the articular surface and increased projection of the medial epicondyle (Fig. 75). Interestingly, when viewed in *norma verticalis*, with the exception of the increased anterior projection of the capitulum, the principal differences between the two specimens appears to be a consequence of a *uniform shape change* along the entire medio-lateral axis of the distal humerus in the Amerindian specimen.

A bivariate scatterplot of the PC4 to PC1 is shown in figure 76. With the exception of one extreme female *Pan troglodytes* specimen (PCM 501), there is a strong positive correlation between the African apes specimens on these axes (*r* = 0.719; *p*=*<0.001*), and also between PC4 and Centroid Size (*r* = 0.665; *p*=*<0.001*). The *Gorilla* sample lies at the extreme range of this correlated distribution, whereas there is considerable overlap between *Pan paniscus* and *Pan troglodytes*. This suggests that factors other than a simple linear size change are operating on this fourth component in the African apes.

Shape changes on PC4 comprise an increase in the height and breadth of the olecranon fossa, which is shifted more medially with increasing positive scores on this axis and a committal M-L expansion of the articular surface, particularly of the capitulum. There is also evidence of a slight postero-superior 'deflection' and an increase in the medial projection of the medial epicondyle in the African apes on PC4. Using the exploration tool in *morphologika* (holding the X-axis constant), the morphological shape changes on PC4 are suggestive of a *uniform shape change* of overall medio-lateral expansion of the distal humerus with increasing positive scores on this axis (see Fig. 76). As a non-significant correlation exists between PC4 and PC2 in either the total or recent human matrices, this uniform morphological transformation on PC4 is considered to be inclusive to the African apes.

The PC scores of the specimens allocated to the genus *Australopithecus* (KNM-KP 271, AL 322-1, AL 288-1 & KNM ER 739) on PC1 range from low negative to low positive and on PC2 from high negative to low positive (see Fig. 71). All specimens can be distinguished from the African apes by virtue of their medio-laterally wider olecranon fossae, their anteriorly displaced and relatively moderately projecting medial epicondyle and in their anterior projection and degree of medio-lateral expansion of the capitulum. However, there is considerable variability in individual specimens (and species) included in this analysis. The component scores of AL 322-1 on PC2 are low negative contrast with other *Australopithecus* individuals who have moderate positive scores on PC2.

From a morphological perspective, variation within *Australopithecus* on PC1 and PC2 is superficially quite extreme. However, TPS transformation of AL 322-1 (reference) to AL 288-1 yields crucial insights in to relative shape variation in the distal humerus of a single species, *Australopithecus afarensis*, independent of differences in Centroid Size (AL 322-1, CS = 70.304; AL 288-1, CS = 65.284). Relative to AL 332-1, the geometry of the AL 288-1 distal humerus in *norma verticalis* displays medio-lateral and antero-posterior expansion that manifests an increase in the projection and orientation of the medial epicondyle (see Fig. 77), with a slight increase in the height of the olecranon fossa (Fig. 77; *norma frontalis*). Similarly, TPS transformation of AL 322-1 to the Early Pleistocene "robust" specimen, KNM-ER 739 reveals only moderate changes in the orientation and relative projection of the medial epicondyle (Fig. 78), despite the closer proximity of the East Turkana specimen to the African apes on the first axis.

"Morphing" the reference shape (AL 322-1) to the 4.1 Myr old *Australopithecus anamensis* specimen from Kanapoi (Leakey *et al*., 1995; Senut, 1981*a,b,c*; Bacon, 2000) reveals a similar pattern and degree of relative shape change (Fig. 79), albeit with some distinctions between specimens. The medio-lateral expansion of the entire distal humeral epiphysis and expansion and slight posterior reorientation of the medial epicondyle seen in AL 288-1 relative to the reference is mirrored in the transformation of AL 322-1 to KNM-KP 271. However, as noted in the initial description of the specimen (Patterson & Howells, 1967), and in successive discussions (e.g., McHenry, 1994*b*; McHenry & Corruccini, 1975, Senut, 1981*c*, Leakey *et al.*, 1995, 1998), KNM-KP 271 *does* display an anteriorly expanded capitulum relative to AL 322-1 (*contra* Wolpoff, 1999). This seemingly contrasts with the recent findings of Bacon (Bacon, 2000), who found no evidence of "*Homo*-like" affinities in the *A. anamensis* distal humerus (see also Wolpoff, 1999).

The morphological distinctions of the reputed "early *Homo*" distal humerus from East Turkana, KNM-ER 1504 (McHenry, 1994; McHenry & Corruccini, 1975, Senut, 1981*c*; Bacon, 2000) relative to *Australopithecus* were explored using TPS with two reference shapes, AL 322-1 and KNM-ER 739. Comparisons with AL 322-1 (Fig. 80) demonstrate the overall expansion of the KNM-ER 1504 distal humerus in the M-L plane, however there is no subsequent expansion and re-orientation of the medial epicondyle relative to the *A. afarensis* individual. The East Turkana specimen clearly displays both anterior and supero-inferior expansion of the capitulum relative to AL 322-1.

The anterior expansion of the capitulum in ER 1504 and a slight lateral expansion of the M-L plane of the olecranon fossa are fairly moderate morphological changes that distinguish KNM-ER 1504 from the geologically contemporary KNM-ER 739 (Fig. 81). The overall pattern of variation in the distal humeral geometry of Late Pliocene-Early Pleistocene fossil specimens testifies to the presence of subtle, rather than marked distinctions between specimens. None of the australopithecine specimens included in this study display morphological affinities with the African apes and none fall outside the broad ranges of variability in distal humeral geometry present in extant *Homo sapiens*. These results do not accord with the relatively clear-cut morphological distinctions between *Australopithecus* and *Homo* presented by Bacon (Bacon, 2000), in her recent analysis of 2D landmark co-ordinates. This apparent contradiction will be discussed in detail in a later chapter.

The Late Middle/Early Upper Pleistocene distal humerus from the Omo 1 *Homo sapiens* partial skeleton has been dated to approximately 120 Kyrs BP (Butzer *et al.*, 1969; Day & Stringer, 1982). This specimen is an extreme outlier from recent humans on PC2 (see Fig. 71), but not on PC1, where is score is low negative. In contrast, the PC scores of the *Homo heidelbergensis* (*H. rhodesiensis*) Middle Pleistocene distal humerus from Kabwe, Zambia, fall almost central to the recent human distribution on PC1 and PC2. Centroid Size values of the two specimens are virtually identical (Kabwe, CS = 96.552; Omo 1, CS = 95.682).

TPS transformations of the two specimens using the chronologically earlier Kabwe distal humerus as the reference reveals that the Omo humerus displays a uniform expansion along its antero-posterior axis with a subsequent decrease in the relative medio-lateral wall of the olecranon fossa (Fig. 82). The capitulum of the Omo humerus is proportionally larger than that of Kabwe, with a notable expansion of the anterior and inferior projection. The Omo distal humeral configuration can be accommodated within the range of variation seen in the Southwest Amerindian sample, which can be morphologically distinguished from other recent human samples (i.e., African Bantu, Late Medieval British, Australian Aborigines) by virtue of their A-P expanded distal humeral geometry.

In contrast to the Omo specimen, the Eurasian Neandertals (*Homo neandertalensis*) cluster together by virtue of their shared positive component scores on PC1 and PC2. With the exception of the African Pygmies and the ER 739 distal humerus, the Neandertals occupy the extreme upper ranges of variation in the hominid distribution on PC1. TPS transformation of the Kabwe distal humerus to the Neandertal type specimen (Feldhofer 1, CS = 100.274) reveals that the Neandertal specimen exhibits a slight medial expansion and posterior deflection of the medial epicondyle, but this is not especially pronounced (Fig. 83). Contrary to expectations, there is no notable medio-lateral expansion of the olecranon fossa of the Feldhofer Neandertal relative to the *Homo heidelbergensis* specimen.

Morphological variability in distal humeral geometry of the five Neandertal individuals of sufficient preservation (Feldhofer 1, Shanidar 1, Krapina 160, 161, 170) was explored using TPS with the Feldhofer Grotto specimen retained as the reference in all comparisons. Relative shape variability in the distal humerus of the Eurasian Neandertals is of a relatively low magnitude. The Krapina Kr170 distal humerus differs morphologically from the Feldhofer Grotto individual by virtue of its relatively shorter medio-lateral expansion of the olecranon fossa and slight supero-inferior increase in the height of the medial epicondyle (Fig. 84). These differences primarily reflect the position of the specimens on PC1 (see above). The medial epicondyle of Kr161 evinces a similar supero-inferior expansion of the medial epicondyle to that seen in the Kr170 specimen (Fig. 85), whereas there are no notable distinctions in the morphology of the Shanidar 1 and Feldhofer Neandertal (Fig. 86).

Morphological comparisons of the Eurasian Neandertals with their immediate geological predecessors are quite informative, with a relatively consistent pattern of shape contrasts emerging. "Morphing" the Kr160 Neandertal distal humerus from Krapina to the Early Upper Palaeolithic distal humerus from Dolni Vestonice (DV 14, CS = 96.355), illustrates the subtle antero-posterior displacement of landmark points of the articular and posterior face of the distal humerus. Relative to the Kr160 specimen (see Fig. 87), Dolni Vestonice 14 displays a slight increase in the anterior projection of the medial wall of the trochlea and a slight overall enlargement of the capitulum (A-P & S-I). There is also a slight increase in the antero-posterior depth of the medial epicondyle.

When viewed in *norma frontalis* (Fig. 87), there is a moderate displacement of landmarks denoting an expansion of the superior surface of the olecranon fossa and of the S-I height of the medial epicondyle in the EUP specimen. Comparisons with the Gravettian distal humeral specimen from Pavlov (Pavlov 1, CS = 102.39 [Fig. 88]) also reveal an increase in the projection and height of the capitulum, but no corresponding increase in projection of the medial wall of the trochlea. Similarly, while Pavlov 1 displays and increase in the S-I height of the medial epicondyle, there is no increase in antero-posterior depth.

Interestingly, while the morphological distinctions between both recent and fossil *Homo* and the African apes are relatively pronounced, particularly on the first principal component, questions arises as to the nature of morphological variability within the extant African ape genera, *Pan* and *Gorilla.* As observed earlier, in contradistinction to recent *Homo*, shape variability in the African apes on PC1 is apparently highly correlated with Centroid Size. Figure 89 details the morphological transformations of the extreme reference and target specimens on PC1 in a single sample, *Gorilla*.

Relative to the reference shape (M128, CS = 152.653), the target specimen (M136, CS = 110.249), displays a marked decrease in the medio-lateral breadth of the articular surface, coupled with an increase in the projection and posterior deflection of the medial epicondyle in *norma verticalis* (Fig. 89). When viewed in *norma frontalis*, the changes in the proportions and relative location of the medial epicondyle, and those of the olecranon fossa are clearly demonstrated. The increasing postero-superior deflection of the medial epicondyle, together with the increasing height and decreasing medio-lateral breadth of the olecranon fossa are evident in *Gorilla*.

Morphological change on the second principal component within *Gorilla* is equally distinctive. Relative to the reference specimen (M264, CS = 147.583) the extreme positive target shape on PC2 (M300, CS = 119.713), displays a notable increase in the anterior projection of the capitulum, decrease in M-L breadth of the olecranon fossa and a slight increase in the A-P depth and overall expansion of the medial epicondyle (Fig. 90). In *norma frontalis*, the increased anterior projection and M-L truncation of the olecranon fossa are particularly visible, as is the increase in the medial projection of the medial epicondyle. There exists considerable shape variability in distal humeral geometry within extant Western lowland gorillas (*Gorilla g. gorilla*).

5.2.3 Canonical Variates Analysis

Canonical Variates Analysis (CVA) of the PC scores for the first 10 Principal Components were computed in SPSS (Version 10). The recent human samples and the African apes were entered as groups (*n*=11), whereas the fossil individuals were entered as special cases regardless of whether sample size was sufficient to compute individual groups. Of the 10 Canonical Discriminant Functions that were extracted, the first six accounted for roughly 99% of the variance (table 60). Of these, the first Canonical Axis [CV1] accounted for 64% of the total variance, while successive axes (CV2, CV3, CV4) accounted for a cumulative variance of 96% (see table 60 for individual components).

The standardized Canonical Discriminant Coefficients (table 61), reveal that Canonical Axis 1 is dominated by positive loadings of PC1 and PC6, and high negative loading of PC4. Principal component scores from PC2, PC4, PC5 and PC7 load positively on CV2, whereas component scores from PC3 and PC5 are negatively loaded on the second Canonical Axis. A bivariate scatterplot of these two axes reveals that they effectively discriminate the recent and fossil hominids from the extant African apes with few exceptions (see Fig. 91). Of the African apes, only a single *Pan paniscus* individual was misclassified as hominid, with remaining misclassifications to *Pan troglodytes*. Overlap between *Pan troglodytes* and *Gorilla* resulted in slight levels of misclassification (*n*=4). Misclassifications among recent humans resulted in only two individuals being misclassified as African apes. The discriminatory power of CV1 is evident in the differences in the group centroids. The group centroids of the recent human samples score negatively on CV1, whereas the African ape centroids are positively located on Canonical Axis 1. This confirms previous observations from the Principal Components Analysis of tangent space co-ordinates of the GPA superimposition of the distal humeral landmark data. The extant African apes can be reliably distinguished from recent humans by virtue of a suite of morphological features in their distal humerii on PC1, but also on PC4. No such clear-cut distinctions are evident on CV2, CV3 or CV4 (Fig. 92).

Examination of the classifications of the ungrouped fossil hominid specimens reveals that assignments were affected in some cases by the scores of the fossil on PC2 and PC1. Not a single *Australopithecus* distal humeral specimen was assigned to the African apes. The Kanapoi distal humerus (KNM-KP 271) was classified as an Australian Aboriginal, whereas the two *A. afarensis* specimens (AL 288-1 & AL 322-1) were assigned to the Negrito and Bantu samples, respectively. Interestingly, the KNM-ER 739 specimen, which has been regarded as being morphologically and taxonomically distinct from contemporary *Homo* (e.g., ER1504), is assigned to the same group (African Pygmies), regardless of overall differences in size and subtle differences in the size and projection of the capitulum (table 62).

The morphological distinctions proposed to exist between the Kabwe and Neandertal distal humerii were not confirmed by assignment using Canonical Variates Analysis. Kabwe, Shanidar 1 and two of the Krapina distal humerii (Kr160 & Kr161) were assigned to the same group (Southeast Asian Negritos). Surprisingly, the Kr170 distal humerus was classified as *Gorilla*, reflecting the extreme positive score of this specimen on PC1. The Feldhofer Grotto specimen was classified as a Magyar and, not surprisingly given its extreme location on PC2, the Omo 1 Early Upper Pleistocene *Homo sapiens* specimen was classified as an Amerindian.

No significant morphological distinctions in articular morphology of the distal humerus of Eurasian Neandertals relative to their immediate geological successors (Early Upper Palaeolithic) were revealed in the classificatory statistics of the CVA (see table 62). A substantial majority (*n*=5, 71.4%) of the EUP specimens were assigned to the African Pygmies or Southeast Asian Negritos. Surprisingly, one Late Upper Pleistocene specimen (San Teodoro 1) was incorrectly classified as *Pan troglodytes*, despite the relatively moderate overlap of the PC1 component score of this individual with the lowest scoring *P. troglodytes* individuals on this axis. The remaining LUP specimens were generally classified as Native Americans or as Southeast Asian Negritos.

The degree of relative shape variation seen within the African Pygmy and Southeast Asian Negrito samples can comfortably accommodate the morphological variability observed in most fossil hominid groups (e.g., *Australopithecus*, Neandertals etc.). The range of variability in the geometry of the distal humerus in *Australopithecus* is relatively large, and exceeds in absolute terms that seen in most recent human samples. With few exceptions (e.g., KNM-ER 739) all specimens fall within the range of variation observed in recent humans on PC1 and PC2. Canonical Variates Analysis (CVA) confirms that the morphological affinities of the distal humerus of *Australopithecus* lie with recent humans rather than the extant African apes. Similarly, little support emerges for conferring "derived" morphometric status to the distal humeral morphology of Eurasian Neandertals relative to earlier and later hominid groups. While the Neandertal distal humerus does differ consistently in overall morphology and geometry from other "archaics" and recent *Homo*, these differences are relatively minor. Future analyses of morphometric shape variability in archaic and recent *Homo* that includes Neandertal distal humerii as an independent group might furnish meaningful discrimination between hypodigms.

5.3 Analysis of the proximal ulna in extant and extinct hominids

In the first analysis, 303 specimens were entered in to the GPA and Principal Components Analysis. The African apes could be clearly distinguished from the recent humans by the positive group centroids on PC1 and, to a lesser degree PC2. The African Bantu were isolated from remaining recent human samples by their extreme negative component scores on PC1 and by their positive scores on PC2.

Investigation of the relative shape differences of these did not reveal any consistent pattern that initially suggests a uniform error in the registration of the specimens. In fact, there appeared to be a "uniform shape change" between the specimens in this cluster and remaining recent humans, which relates to the degree of relative "shear" of the olecranon process relative to the coronoid process within recent *Homo*. However, exclusion of the entire Bantu sample and some remaining outliers from other groups (Negritos = 2, Australians = 2, Libben = 2), produced a radical change in the tangent space residuals and the basic pattern of shape change. Accordingly, the results of the second GPA model were retained in this analysis and the Bantu sample was excluded. This problem is under current investigation by the author.

5.3.1 Permutation comparisons of the extant samples

Permutation tests for pairwise sample shape differences are detailed in table 63. Nearly all comparisons are significant at the $\alpha = 0.05$ level of probability and many reach a higher level of statistical significance ($p=<0.01$, $p=<0.001$). There are few exceptions. African Pygmies do not differ significantly from the Southeast Asian Negritos and the Libben Amerindian proximal ulnae do not differ significantly in their Procrustes Chord and consensus configuration from the SW Amerindians and even *Pan pansicus*.

5.3.2 Generalised Procrustes Analyses

14 landmark co-ordinates in the 258 extant and extinct hominid specimens that spatially define size and shape of the articular morphology of the proximal ulna were entered in to a Generalised Procrustes Analysis. Two-dimensional graphical rendering of the 3D landmark consensus configuration "clusters" after rotation, translation, reflection and re-scaling to "Centroid Size" is shown in figure 94. Principal Components Analysis of the linear tangent space co-ordinates of the 14 landmark points in 3D space yielded 39 PC's ($14p \times 3k - 3df$), of which the first 10 components accounted for approximately 73% of the total variance (see table 64).

The first Principal Component (PC1) accounted for 25% of the total variance, with successive PC's (PC2, PC3, PC4) accounting for a cumulative variance of only 50%. The correlation coefficient for Centroid Size and PC1 in the total sample is moderate but highly significant (table 65; $r = 0.576$; $p=<0.001$). PC2 is also positively correlated with Centroid Size ($r = 0.462$, $p=<0.001$). Subdivision of the sample in to recent humans and the African apes yields a contrasting picture (tables 66 & 67). In the recent humans, the correlation coefficients of the PC scores with Centroid Size are negative and non-significant with the sole exception of PC5 ($r = 0.319$; $p=<0.01$). In the African apes, the correlation coefficient of centroid size with PC1 is also non-significant, whereas PC's 2, 3 & 7 are negatively and significantly correlated with Centroid Size ($p=<0.01$). PC4 and PC10 are positively correlated with Centroid Size in the African Apes ($p=<0.05$).

A clear distinction exists between the recent humans and the extant African apes in their component scores on PC1 (see Fig. 94). The scores of the African apes are negative, whereas recent human scores extend from low negative to low positive. Surprisingly, the *Gorilla* sample can be clearly distinguished from *Pan paniscus* and *Pan troglodytes* by virtue of their negative scores on the second component axis. AL 288-1 (*A. afarensis*) and KNM-BK 66 (*H. sp. indet.*) clearly cluster with the recent humans and lie some distance from the extant African apes on PC1. The Upper Pleistocene fossil samples (Neandertals, EUP, LUP, Early Holocene) display marked levels of variability in the PC1 and PC2 component scores and many lie close to the centre of the *Pan paniscus* cluster on PC1 and PC2. Only one fossil specimen (Dolni Vestonice 13, approaches *Gorilla* in its PC scores (see Fig. 94).

Exploration of the morphological shape changes in proximal ulna articular anatomy was undertaken using the available options and the wireframe rendering in *morphologika* (O'Higgins & Jones, 1998). For each axis, the shape changes were visualised in three perspectives; *norma lateralis* (facing the radial notch), *norma* *verticalis* and posterior to the olecranon process. As before, the principal morphological changes along PC1 and PC2 using wireframe renderings, landmark numbers and TPS deformations are included as AVI movie files on the accompanying CD-ROM. The morphological changes from decreasing negative to increasing positive component scores on PC1 in *norma lateralis, norma verticalis* and in posterior aspect are detailed in figure 95. There exists a clear tendency in recent humans towards dorso-ventral increase in the articular surface, an anterior displacement and increase in the relative proportions (especially the anterior component) of the radial notch and, a decrease in the relative height of the coronoid process.

When viewed from *norma verticalis* and posteriorly from the olecranon fossa, these shape changes are confirmed (Fig. 95). However, there is also a distinct increase in the relative breadth of the olecranon process relative to the coronoid in recent and fossil hominids relative to the extant African apes. The decrease in the height of the coronoid process and the subsequent reduction in the dorso-ventral dimensions of the *M. brachialis* insertion are shown to be due to a lateral displacement of the apex of the coronoid process. There is relatively no change in the degree of shear of the principal axis of the olecranon process relative to the coronoid.

Morphological transformations of the wireframe models on the second principal component (from negative-positive) in *norma lateralis*, *norma verticalis,* and in posterior view (Fig. 96), involve a reduction in the relative length and breadth of the articular surface of the ulna in recent humans. Much of the reduction in the breadth of the coronoid process actually involves a reduction in the anterior expansion and reorientation of the radial notch with increasing positive scores. The question as to precisely which morphological features distinguish *Gorilla* from *Pan* will be explored using thin-plate splines.

A TPS rendering of the extreme morphological variability on PC1 is shown by morphing the *Pan troglodytes* reference specimen (PCM 219; CS = 89.437) to the Australian Aborigine target shape (BMNH1893; CS = 60.194). The reduced height of the coronoid process relative to the olecranon and the increased proportions of the radial notch in the Australian are clearly apparent in *norma lateralis* and in posterior view (Fig. 97). Increase in the relative breadth of the olecranon process and the proportions of the *M. brachialis* insertion are also distinct in the Australian Aborigine relative to *Pan troglodytes.*

The nature of morphological variability on PC2 in the extant and extinct hominids is demonstrated using a Native Southwest American reference (BPM60.5; CS = 69.852) to an African Pygmy target (No. 5; CS = 69.095). There is a notable decrease in the height of the coronoid process relative to the olecranon process, with a decrease in the relative breadth of the coronoid and infero-medial displacement of the radial notch (Fig. 98). Morphological distinctions between *Gorilla* and *Pan troglodytes* were also assessed using TPS. Warping the *Gorilla* reference (M20; CS = 116.980) to an individual approximating the centroid of the *Pan troglodytes* distribution (PCM425; CS = 80.425) reveals that *Pan troglodytes* displays a decrease in the dorso-ventral breadth and the posterior proportions of the articular surface (i.e., the olecranon process) relative to *Gorilla* (see Fig. 99). There is also a notable reduction in the height of the coronoid process relative to the olecranon and in the relative breadth of the coronoid process in *Pan troglodytes*.

The pattern of morphological variability in proximal ulnar morphology in the Australian Aboriginal sample detected in the first analysis is apparent on PC3 (Fig. 100). In contrast to the first analysis, the Southwest Amerindian sample also displays marked variation in the orientation on the olecranon process relative to the coronoid process. As stated earlier, there appears to be little basis for inferring that the morphological changes on PC3 from negative to positive scores in the recent humans is due to registration error. Many fossil specimens, including two Neandertals and the majority of the Late Upper Palaeolithic specimens have negative PC scores on the third axis. Variation in this third component reflects the "relative shear" of the long axis of the olecranon process relative to the coronoid. Recent and fossil human specimens with negative scores display coincident long axes of the olecranon and coronoid, whereas those with positive scores display olecranon "shearing". Variation along the third Principal Component in recent humans also records a notable decrease in the height of the coronoid process relative to the position of the radial notch and *M. brachialis* tuberosity in recent and fossil *Homo*.

Morphological differences between the *Australopithecus afarensis* female specimen, AL 288-1 ("Lucy") and *Pan troglodytes* were assessed using TPS. In actuality, morphing AL 288-1 to *Pan troglodytes* samples the "morphological continuum" on the first Principal Component, with *P. troglodytes* being considerably far removed from the location of AL 288-1 than is *P. paniscus* (see Fig. 94). Only one *Pan troglodytes* specimen has a negative PC score on the second Principal

Component. Relative to AL 288-1, *Pan troglodytes* (Fig. 101) displays a significant increase in the height of the coronoid process and an associated increase in the depth and length of the *M. brachialis* insertion. There is also a notable decrease in the dorso-ventral axis of the articular surface and a decrease in the depth of the radial notch in the African ape specimen. In posterior view, AL 288-1 displays and demonstrable increase in the M-L breadth of the olecranon process relative to that seen in *Pan troglodytes*.

TPS "morphing" of AL 288-1 (CS = 51.475) to the KNM-BK 66 (CS = 60.23) Middle Pleistocene *Homo* ulna from Baringo-Kapthurin (Solan & Day, 1992) reveals few morphometric shape differences in the geometry of the proximal articular region. Renderings in *norma lateralis* and in posterior view (Fig. 102) suggest that the most obvious difference between the two specimens is the reduced medio-lateral breadth of the articular surface in the Baringo-Kapthurin specimen. There is also evidence of a slight reduction in the D-V axis of the proximal articular surface, with a committal posterior displacement of the radial notch. There is, however, no change in the proportions of the radial notch or in the relative size of the olecranon and coronoid processes.

Thin-plate spline transformations were used to directly assess the validity of the hypothesis concerning morphological change in the proximal ulna of Eurasian Neandertal's and African Early Upper Pleistocene *Homo sapiens* (Omo-Kibish 1). Relative to KNM-BK 66 (Fig. 103 [CS = 73.66]), Omo 1 displays a marked increase in the A-P breadth of the articular surface, increase in the relative size of the radial notch and an increase in the height of the coronoid process relative to the olecranon process. When viewed in *norma verticalis*, it becomes apparent that the articular margins of the Omo 1 ulna are medio-laterally wider than in the Baringo-Kapthurin (KNM BK 66) specimen.

Transformation of the reference (KNM-BK 66) to two of the Neandertal ulnae from the Shanidar Cave, Iraq (Shanidar 4 & 6), reveals a similar pattern of differences in the articular morphology as that of the Omo ulna. These differences are less pronounced in the two Neandertal ulnae. Relative to KNM-BK 66, the Neandertal ulnae display a notable increase in the height of the coronoid process relative to the olecranon process and a subsequent increase in the relative size of the radial notch in *norma lateralis* (Figs. 104 & 105). When the transformations are viewed in the posterior reference plane, the increased medio-lateral breadth of the Neandertal ulna is readily discernible, particularly in Shanidar 6. The increase in the height of the coronoid appears to be greater in Shanidar 4 (CS = 75.648) than in Shanidar 6 (CS = 66.091) relative to KNM-BK 66 in posterior view (Figs. 104 & 105). However, when the transformations are viewed in *norma verticalis* the increased height and breadth of the coronoid process together with the concomitant increase in the proportions of the radial notch is noticeably greater in Shanidar 6.

Quite considerable variability exists in the morphology of the proximal ulna in both Eurasian Neandertals and Early Upper Pleistocene *Homo sapiens* specimens (see Fig. 94). TPS "morphing" of Skhul IV (CS = 72.813) to Shanidar 5 (CS = 72.941), an extreme outlier of the Eurasian Neandertals reveals the extent of this variability. It should be remembered that Skhul IV is as removed from Omo 1 along the same morphological "trajectory" on PC1 and PC2 as is Shanidar 5 from the Neandertal "centroid". Relative to Skhul IV, Shanidar 5 displays an inferior displacement of the radial notch and a notable decrease in the A-P axis of the proximal articular surface (Fig. 106; *norma lateralis*). In posterior view, the profound decrease in the M-L plane of the articular surface in Shanidar 5 relative to Skhul IV is more noticeable (Fig. 105).

Shanidar 1 (CS = 79.225) displays a slight posterior displacement of the coronoid process with a subsequent reduction in the proportions of the radial notch relative to Skhul IV (Fig. 107). Shanidar 1 is further demonstrated to be proportionally narrower across the medio-lateral axis of the articular surface than Skhul IV when viewed in the posterior plane. Warping the spline in posterior view suggests a slight increase in the height of the coronoid process relative to the olecranon in the Neandertal specimen. However, this is not supported by the view in *norma lateralis* (see Fig. 107). It seems likely that coronoid height in Shanidar 1 is similar to Skhul IV, but it appears higher as a direct consequence of the posterior displacement of the radial notch and the overall decrease in the medio-lateral proportions of the proximal radius relative to the Levantine *Homo sapiens* specimen.

In contrast to the Eurasian Neandertals, the Early Upper Palaeolithic Europeans manifest considerable variation in their proximal ulnar morphology, even in conspecific individuals such as the Dolni Vestonice specimens. Using Shanidar 1 as the reference, TPS morphing to Dolni Vestonice 13 (CS = 81.449) and Dolni Vestonice 14 (CS = 81.802), reveals a strikingly different pattern of morphological differences. Relative to Shanidar 1, DV13 displays a distinct increase in the height of the coronoid process relative to the olecranon process and a contiguous increase in the relative proportions of the radial notch (see Fig. 108). There is also a notable decrease in the overall D-V proportions of the articular surface and an increase in the medio-lateral breadth of the anterior ulna in DV13 that is partly, but not entirely, a consequence of the increased anterior expansion and reorientation of the radial notch. In contradistinction, DV 14 (Fig. 109) displays no discernible increase in the height of the coronoid process or the radial notch and is medio-laterally narrower than the Shanidar 1 proximal ulna. It does, however, possess an articular surface that is dorso-ventrally narrower than Shanidar 1, which unites this specimen with DV13.

In retrospect, results of the GPA and PCA analyses suggest that the anatomy and three-dimensional geometry of the proximal ulna in recent humans and the extant African apes is consistently different. With respect to the fossil specimens, none of the pre-*Homo sapiens* specimens displays a morphological configuration that presupposes affinities with *Pan* or *Gorilla*. Levels of variation in the proximal ulna of Upper Pleistocene *Homo sapiens* samples is extreme, and far exceeds that seen in many recent human samples. While there are apparently few consistent morphological differences in proximal ulna geometry between recent humans and Eurasian Neandertals, definite distinctions between Neandertals and European EUP specimens exist. Nevertheless, Eurasian Neandertal ulna morphology is closer to early Holocene and recent humans than it is to European Upper Palaeolithic specimens.

5.3.3 Canonical Variates Analysis

Eight Canonical Discriminant Functions were extracted from the matrix of the first 10 Principal Component scores. The first Canonical Variate (CV) accounted for

60.6% of the total variance, while the second CV accounted for 24.4% of the total variance. Canonical Variate Axes 3-6 contributed the remaining cumulative variance of 99% (see table 68). Wilks' Lambda yielded Chi-square coefficients that were highly significant for the first 6 Canonical Variate components. A bivariate scatterplot of CV2 versus CV1 is shown in figure 110.

With few exceptions, CV1 effectively distinguishes between the African apes and the recent human samples. This finding is not surprising as PC1 makes an overwhelming contribution to the discrimination between samples. The morphological transformations from negative to positive scores on PC1 in the GPA analysis of the 14 landmark coordinates can effectively distinguish recent humans from *Pan* and *Gorilla*. Given this finding, the effective discrimination of *Pan* from *Gorilla* on the second CV is not unexpected. PC1 and PC2 are not independent (see above). The underlying morphological differences on PC2 (see above) from negative to positive scores can effectively distinguish *Pan* from *Gorilla* with no exceptions (see below).

Examination of the Standardised Discriminant Function Coefficients reveals that PC3 contributes positively to the discrimination of *Pan* and *Gorilla*, whereas PC10 negatively contributes to the explanatory "power" of CV2 (see table 69). Exploration of the morphological changes upon these axes reveals that they primarily reflect (negative-positive) axes of change in the relative proportions of the anterior (i.e., coronoid) and posterior (i.e., olecranon) processes in the M-L plane and, consequentially, the proportions and orientation of the radial notch. As explained previously, these fundamental proportional morphological differences to a greater and lesser extent separate *Pan* from *Gorilla* on PC2.

Interestingly, the third Canonical Variate effectively separates *Pan paniscus* from *Pan troglodytes* and *Gorilla gorilla* by virtue of their extreme negative scores on this axis (Fig. 111). Variable loadings on the third canonical axis are dominated by the positive contributions of PC4, PC5 and PC8 and negative loadings of PC6 (see table 69). The height and medio-lateral proportions of the coronoid process and the proportions and orientation of the radial notch are demonstrably different in *Pan troglodytes* relative to *Pan paniscus*. The latter more closely approximates extant and extinct hominids in its proximal ulnar morphology as shown previously in the TPS transformation of AL 288-1 to the two species of *Pan*.

The results of the classifications are extremely reliable. Only a single recent human was incorrectly classified as *Pan paniscus* and there was no misclassification of *Pan* and *Gorilla*. The misclassification rate of *Pan troglodytes* and *Pan paniscus* is also low (n=2), and both can be effectively distinguished from *Gorilla*. With respect to the fossils, the overwhelming majority are morphologically indistinguishable from recent humans, including the AL 288-1 and KNM-BK 66 specimens (table 70). A single Upper Pleistocene specimen, Arene Candide 12.2, was incorrectly classified as an African ape (*Pan troglodytes*). In general, the extreme levels of variability inherent in the proximal ulna geometry of the fossil *Homo sapiens* specimens does not translate to high misclassification error in the CVA.

5.4 Summary

Generalised Procrustes Analysis, thin-plate spline morphing procedures and post-hoc multivariate statistical assessment reveal that the epiphyseal geometry of the distal humerus and proximal ulna in recent humans can be reliably distinguished from *Pan* and *Gorilla*. Relative to the extant African apes, the distal humerus of recent humans displays a medially less-projecting and anteriorly oriented medial epicondyle, a medio-laterally wider olecranon fossa and a more anteriorly projecting capitulum. The proximal ulna of recent *Homo* contrasts with that of *Pan* and *Gorilla* by virtue of a D-V expanded articular surface, location and morphology of the radial notch and in the medio-lateral proportions of the coronoid process and the decreased height of the olecranon process. Morphological distinctions in the proximal ulnar geometry of *Pan* and *Gorilla* equivocally reflect size-dependent shape changes reflected in the M-L and D-V proportions of the articular surface and the proportions of the olecranon and coronoid processes.

While the articular geometry of the distal humerus and proximal ulna of specimens attributed to *Australopithecus* are demonstrated to be morphologically indistinguishable from recent and fossil *Homo*, several distinctions are apparent in the elbow-joint morphology of Eurasian Neandertals relative to earlier and more recent *Homo*. Relative to other fossil *Homo* specimens, the distal humerus of Neandertals manifests a uniform shape change in the morphology of the medial epicondyle, capitulum and medial wall of the trochlea. Previous observations of morphological distinctions in proximal ulna morphology of Eurasian Neandertals and Upper Pleistocene *Homo sapiens* are largely supported. Eurasian Neandertals display increased Dorso-Ventral and reduced Medio-Lateral proportions of the articular surface and a decreased height of the coronoid process relative to the olecranon. However, in contradistinction to the current consensus, the results of these analyses suggest that Neandertals *do not* display a morphologically "archaic" proximal ulna, and that considerable variability exists in the proximal ulna morphology of both Pleistocene and recent *Homo sapiens*.

Chapter 6. Geometric Analysis of the Hominoid Proximal Femur

6.1 Introduction

The results presented in this chapter relate to hypotheses concerning the anatomical geometry of the proximal femur in extant and extinct hominoids. In order to test hypotheses concerning the functional morphology of the lower limb in extant and extinct hominids, Generalised Procrustes Analysis (GPA) was performed on 13 landmarks that broadly define the spatial geometry of the proximal femoral epiphysis. These landmarks were taken on a large comparative sample comprising recent *Homo*, *Pan*, *Gorilla*, and extinct Plio-Pleistocene fossil specimens including *Australopithecus*, *Homo erectus*, *Homo rhodesiensis* and *Homo neanderthalensis*. The aims of this analysis were to rigorously assess functional geometric differences between the extant African hominids, and the nature of morphological differences in extant fossil taxa. Principal Components Analysis and Canonical Variates Analysis were utilised.

6.2 Proximal femoral geometry in extant and extinct African hominoids

6.2.1 Permutation comparisons of the extant samples

The African apes display GPA geometric configurations that differ significantly from the recent human samples included in this study (see table 71). Significant shape differences exist within the African apes. The consensus configuration of *Pan paniscus* is significantly different from that of *Pan troglodytes*, and *Gorilla* (*p=<0.001*). Interestingly, the differences in Procrustes chord are notably greater in the comparisons of *Pan paniscus* and *Pan troglodytes* than they are between the latter and *Gorilla*. Thus, proximal femoral geometry of *Pan troglodytes* approximates that more closely that of *Gorilla* than it does *Pan paniscus*.

The African Pygmies and the Southeast Asian Negritos differ significantly in their Procrustes geometry of the proximal femur relative to nearly all other recent human samples, but not from each other (see table 71). Surprisingly, the Southeast Asian Negrito proximal femoral consensus configuration does not differ statistically from the Australian Aborigine configuration. Generally, significant differences in proximal femoral geometry in the recent human samples do not follow a consistent pattern. While the Bantu differ from all remaining samples with the exception of the Australian Aborigines, the Aborigines do not differ from Libben Amerindians. Similarly, Southwest Amerindians do not differ in their Procrustes consensus configurations from the high-latitude Europeans (Magyars and Coventry), while the Libben Amerindians do. Pairwise comparisons of the Native American samples did not reach statistical significance.

6.2.2 Generalised Procrustes Analysis

A two-dimensional rendering of the 278 individual geometric configurations after rotation translation, rescaling and, where necessary, reflection using GPA orthogonal superimposition is shown as figure 112. A total of 36 Principal Components were extracted from the covariance matrix of the tangent space co-ordinates (Kendall, 1986, 1989; Bookstein, 1991; Goodall, 1991; Small, 1996), using

Morphologika (O'Higgins & Jones, 1998), of which the first 10 accounted for approximately 78% of the total variance (table 72). The component scores from these first 10 PC's were retained for use in a Canonical Variates Analysis (see Section 6.2.3).

The first Principal Component accounts for 33% of the total variance while the second to the fifth Principal Components summate a little over 61% of the total variance (table 72). A bivariate scatterplot of the first two Principal Components is shown in figure 113. With the exception of the *Pan paniscus* sample, which falls roughly intermediate, the remaining African apes can be convincingly distinguished from recent *Homo* by their positive scores on PC1. Recent humans and the extant African apes seem to approximate each other closely in their relative distributions on PC2. The position of the substantial majority of fossil specimens on PC1 is unequivocal; all fall within the range of variation seen in recent *Homo* and are generally quite distinct from *Pan troglodytes* and *Gorilla.*

Variability in *Australopithecus* is more problematic. The AL 288-1 (*A. afarensis*) and KNM-ER 1503 (*A. boisei*) proximal femora lie at the extremes of the range of positive scores in recent *Homo* on PC1. There is consistent overlap between these specimens (and recent humans) in proximal femoral geometry with *Pan paniscus*. In contradistinction, the position of the purported *Australopithecus afarensis* male (AL 333-3 [Lovejoy *et al.*, 1982*c*]) lies far removed from recent humans on PC1 with *Pan troglodytes* and *Gorilla* (see Fig. 113). AL 288-1 and KNM-ER 1503 are relatively proximate to the Lower Pleistocene adolescent *Homo erectus* femur (KNM-WT 15000), and also the Middle Pleistocene *Homo* *heidelbergensis* femur from Kabwe (E907). Surprisingly, many pre-recent (i.e., Upper Pleistocene) hominid femora are morphologically 'united' by their extreme negative component scores on PC2. This "cluster" also includes the Trinil 1 and Feldhofer Grotto femora. The Trinil femur is considered by Day to be an unequivocal *Homo sapiens* specimen (Day & Mollison, 1973; Day, 1976, 1984, 1986*a*,*b*). However, this specimen is far removed from the recent human centroid on the second Component Axis.

As in previous analyses, the nature of morphological shape variability on the first and second Principal Components of the tangent space co-ordinates was explored using the utility tool in *morphologika* (O'Higgins & Jones, 1998*a*). As before, the principal morphological transformations along PC1 and PC2 are graphically depicted using wireframe renderings, landmark numbers, and TPS deformation grids on an accompanying CD-ROM. Morphological variability along PC1 from extreme negative to extreme positive scores is illustrated in *norma verticalis* and in *norma lateralis* in figure 114. With decreasing distance to, and increasing distance from, zero on PC1 there is a manifest increase in both the depth and height of the greater trochanter relative to the femoral neck and femoral head and a perceptible decrease in the medio-lateral breadth of the entire proximal femur. When viewed in *norma lateralis* (Fig. 114) the superior surface of the greater trochanter becomes distinctly flattened, reflecting a notable decrease in the relative medio-lateral projection of this feature in *Pan troglodytes* and *Gorilla* compared to that seen in *Homo* and some *Pan paniscus* specimens.

Patterns of variability in proximal femoral geometry encompassed by PC2 are shown in *norma verticalis* and *norma lateralis* in figure 115. Principal morphological changes along this axis involve a demonstrable decrease in the length of the femoral neck and an increase in the antero-posterior axis of the proximal femur. The latter is evident in the changes in the relative proportions of the greater trochanter and the femoral head (*norma verticalis*). A definite increase in the supero-inferior height of the femoral head and medial projection of the greater trochanter above the trochanteric fossa are apparent on this axis. These features are presumably less well developed in some *Australopithecus* and "archaic" *Homo* individuals relative to recent humans. There are, however, some recent humans who approach the fossil specimens in their morphology.

Extreme variability on both the first and second principal components can be visualised using thin-plate splines (TPS). Patterns of morphological change on PC1 (Recent *Homo* V's: *Pan troglodytes* and *Gorilla*) can be convincingly demonstrated using an extreme reference ([Australian] OX60.4; CS = 97.678) to a *Gorilla* target (M128; CS = 80.465). In *norma verticalis* (Fig. 116) the changes in the height and depth of the greater trochanter in the target shape are pronounced, and this is further elaborated when the transformation is viewed in *norma lateralis*. Interestingly, the TPS "morphing" of the PC1 extremes reveals that the increase in the height of the greater trochanter is accompanied by a discernible increase in the supero-inferior depth of the femoral head in *Gorilla* relative to the M-L dimensions. This shape change should not be confused with an increase in the relative size of the femoral head in *Gorilla*, but confirms that the African ape femoral head is distinctly ovoid in cross-section in comparison to the spherical hominid femoral head. The TPS transformation suggests that this is due to the increase in the S-I axis of the femoral head.

Morphological transformations on the second Principal Component were visualised for the recent human sample using TPS with an extreme South African Bantu reference (AD199; CS = 95.181) and an Aboriginal Australian target (RCS204211; CS = 95.507). In *norma verticalis* (Fig., 117), a distinct decrease in the M-L breadth of the femoral neck and increase in the A-P dimensions of the femoral head are clearly visible. The distinct increase in the M-L expansion of the greater trochanter is also clearly evident. This latter shape change is more perceptible when the transformation is viewed in *norma lateralis*. The S-I proportions of the femoral head in the target specimen are also significantly enlarged relative to the reference specimen.

With respect to the African apes, specifically *Pan troglodytes* and *Gorilla*, a comparable pattern of morphological change emerges on PC2. TPS "morphing" of the *Pan troglodytes* reference (Z34; CS = 90.431) to the *Gorilla* target (M57; CS = 126.251) reveals a palpable increase in both the antero-posterior and medio-lateral proportions of the greater trochanter and femoral head and the significant decrease in the length of the femoral neck in the *Gorilla* target specimen (Fig., 118). The correspondence of these morphological shape changes on the second Principal Component indicates that an equivocal relative elongation of the femoral neck in bipedal hominids relative to the African apes cannot be sustained when the relevant interlandmark distances are rescaled to Centroid Size. While it is true that a relatively long femoral neck and a proportionally small femoral head distinguish many Plio-

Pleistocene fossil specimens from recent humans (see Fig. 113), a contiguous morphological "vector" can be identified in the African apes.

The remaining 5 PC's accumulate up to 78% of the total variance (table 72). Correlation matrices of the total sample, recent humans and the African apes reveal a uniform non-significant relationship between Centroid Size and PC1 throughout the comparisons (tables 73, 74 & 75). Indeed, in the total (extant and extinct) and recent human samples, only a single PC correlates significantly with Centroid Size ($p=<0.01$). In the total sample, PC4 is weakly and negatively correlated with Centroid Size (r = -0.233, $p=<0.01$), and in the recent human sample PC9 is similarly correlated with centroid size (r = -0.266, $p=<0.01$).

Exploration of the morphological changes along these axes from negative to positive PC scores reveals notable changes in the breadth and height of the greater trochanter. On PC4, decreasing distance to, and increasing distance from zero coincides with a supero-medial shift in the landmark defining the anterior expansion of the greater trochanteric plane (insertion of *M. piriformis*) and an increase in the breadth of the femoral neck and femoral head. In contrast, variation on PC9 records a positive expansion of the anterior and posterior components of the greater trochanteric plane with a subsequent increase in height and decrease in A-P breadth of the femoral neck as it approaches the junction with the femoral head. There is no distinguishable change in the relative proportions of the femoral head on PC9. These axes do not distinguish recent *Homo* from the African apes, nor do they effectively distinguish individual hominid samples or fossil specimens/samples.

Correlation coefficients for Centroid Size with the PC scores in the African ape sub-sample are notably better than in the recent *Homo*. PC's 6,8 and 9 all correlate positively with Centroid Size, whereas PC's 4,5 and 10 correlate moderately but negatively with Centroid Size. A bivariate scatterplot of PC4 and PC6 is shown in figure 119. Despite the highly significant correlation between the component scores on PC4 and PC6, there is little evidence of an inverse negative relationship in the African apes. While a majority of *Gorilla* specimens do posses positive scores on PC6 and negative scores on PC4 and *Pan troglodytes* displays negative scores on PC6 and positive scores on PC4, the individual distributions do not reflect this pattern. We must conclude that the correlation with Centroid Size on both these axes is coincidental.

The obvious difference in location of the smaller and larger *Australopithecus afarensis* proximal femora on the first two principal components suggests notable morphological distinctions. Using the AL 288-1 proximal femur as the reference, TPS morphing to the AL 333-3 specimen reveals that there are distinct morphological contrasts in the relative proportions of the greater trochanter, femoral neck and the femoral head. Surprisingly, the relatively large-scale comparative differences between these specimens using traditional linear measurements (e.g., Lovejoy *et al.*, 1982*b*; McHenry, 1988, 1992*a*) do not translate to observed disparities in Centroid Size between the two specimens (see table 78).

When the TPS transformation is viewed in *norma lateralis* (Fig. 120), the increased height and depth of the greater trochanter and the flattening of the superior surface are clearly evident in the AL 333-3 proximal femur. There are notable increases in the S-I proportions of the femoral head and femoral neck, but no consequential changes in the relative length of the femoral neck. When the transformation is viewed in *norma verticalis* (Fig. 120), the increased relative size of the A-P diameters of the greater trochanter and femoral neck in the AL 333-3 proximal femur relative to AL 288-1 are clearly visible.

Any attempt to interpret the differences in proximal femoral geometry in the two *Australopithecus afarensis* specimens as a consequence of allometric size differences are confounded by comparable morphological differences in the KNM-ER 1503 (*Australopithecus boisei*) proximal femur. Centroid Size in KNM-ER 1503 is substantially less than in AL 288-1 (see table 78), which again contrasts with comparisons using linear dimensions where KNM-ER 1503 is intermediate in "overall size" between AL 288-1 and AL 333-3. KNM-ER 1503 differs from AL 288-1 by virtue of its supero-inferiorly expanded greater trochanter and relatively more vertical superior surface, and also in its proportionally greater femoral neck and femoral head (see Fig. 121). The antero-posterior dimensions of the femoral neck and greater trochanter are also expanded in the Early Pleistocene Koobi Fora hominid relative to the morphological pattern of the Middle Pliocene Hadar specimen (*norma verticalis*).

Previous statistical assessments of morphological differences between *Australopithecus* and Early Pleistocene femora assigned to the genus *Homo* (e.g., McHenry & Corruccini, 1976*a*, 1978) could not be replicated in this analysis due to missing landmarks in the proximal femoral geometry of KNM-ER 1472 and KNM-ER 1481a. The nature of morphological differences in the proximal femur of early *Homo* and *Australopithecus* were determined using the adolescent KNM-WT 15000

Homo erectus right proximal femur as the reference. Using the KNM-WT 15000 specimen as the reference, the principal differences in proximal femoral geometry of the KNM-WT 15000 and the AL 333-3 specimen lies in the S-I expansion of the greater trochanter in the Hadar hominid (see Fig. 122). There is a subtle expansion in the supero-inferior height of the AL 333-3 articular surface when viewed in *norma lateralis*. Surprisingly, there is no evidence of a proportional medio-lateral expansion of the femoral neck in the *Homo erectus* proximal femur relative to the AL 333-3 *Australopithecus afarensis* specimen (Fig., 122). When viewed in *norma verticalis*, there is a palpable increase in the antero-posterior proportions of the femoral neck in AL 333-3, confirming Day's (Day, 1971, 1976, 1982, 1984) view that the femoral neck in *Homo erectus* is unusually "tapered" relative both to *Australopithecus* and recent *Homo*.

Morphological comparisons of the KNM-WT 15000 proximal femur with the problematic Trinil 1 femur (Day & Molleson, 1973; Day, 1971, 1976, 1984, 1986*a*,*b*), reveals a striking resemblance in overall proximal femoral geometry, despite the degree of difference on PC1 (see Fig. 123). Multivariate analyses by Day (Day, 1971, 1986*a*; Day & Molleson, 1973) have concluded that the femoral morphology of the Trinil 1 specimen is virtually indistinguishable from *Homo sapiens*, and is thus quite distinct from that of *Homo erectus* in a number of features (see also Kennedy, 1983*a*,*b*, 1984).

TPS transformation of the West Turkana reference to the Javan hominid indicates that the major differences between the specimens lie in the relative proportions of the greater trochanter, which is higher and deeper in KNM-WT 15000

(Fig. 123). There is also a suggestion of a slight decrease in the relative length of the femoral neck in the Trinil specimen compared to KNM-WT 15000. This morphological difference appears to be a direct consequence of the decreased height of the superior surface of the greater trochanter relative to the femoral neck. When the transformation is viewed in *norma lateralis*, there is a slight increase in the supero-inferior breadth of the femoral head in Trinil 1. Transformation of KNM-WT 15000 to the Middle Pleistocene E-970 femur from Kabwe evinces a pattern of morphological differences that is even less dramatic (Fig. 124). The Kabwe proximal femur is confirmed as displaying a relatively shorter femoral neck, but one that is is slightly expanded antero-posteriorly compared to the geometric configuration in KNM-WT 15000 (Kennedy, 1983*a*,*b*, 1985). There is also a subtle overall expansion (A-P and S-I) of the femoral head in the Kabwe hominid.

In contrast to the "archaic" *Homo* proximal femora included in this analysis, the Early Upper Pleistocene *Homo sapiens* specimen from the Levant (Skhul IV) falls approximately at the centre of the recent human distribution on PC1 and PC2 and is thus far removed from the *Homo erectus*, *Homo heidelbergensis* and *Homo neanderthalensis* femora (see Fig. 113). Comparisons of the proximal femoral geometry of Skhul IV were undertaken using two taxonomically distinct reference specimens; the Kabwe E907 proximal femur (*H. heidelbergensis*) and the Feldhofer Neandertal. Both TPS transformations reveal a consistent pattern of morphological differences viewed in *norma verticalis* and *norma lateralis*, although the differences are more extreme when the Kabwe femur is used as the reference specimen.

When viewed in *norma verticalis* (Figs. 125 & 126), the femoral neck of the Skhul IV hominid is remarkably shorter and antero-posteriorly broader than either of the two reference specimens, particularly Kabwe. The greater trochanter of the Early Upper Pleistocene *Homo sapiens* specimen is also distinctly expanded medio-laterally and antero-posteriorly, and a discernible increase in the antero-posterior proportions of the femoral head relative to the *Homo heidelbergensis* and *Homo neanderthalensis* femora is apparent. With respect to the geometry of the greater trochanter, differences between the two reference specimens and the target specimen can be demonstrated to involve a distinct medial expansion of the superior surface above the trochanteric fossa (Figs. 125 & 126; *norma lateralis*). These morphological differences are especially marked when the Skhul IV specimen is compared to the Kabwe proximal femur. The relative size of the femoral head and the proportions of the femoral neck are also notably increased in Skhul IV relative to the Neandertal and *Homo heidelbergensis* femora. Interestingly, differences in the proportions of the femoral neck in the Skhul IV specimen are appreciable when linear measurements are compared. The Skhul IV femoral neck is larger in its supero-inferior aspect than are other Middle-Upper Pleistocene "archaic" *Homo* specimens. However, relative differences in the size of the femoral head in the Skhul IV specimen could not be validated by comparisons of linear measurements.

Cursory examination of the ranges of variability in PC2 component scores in the extant African apes indicates that this is of an order with that seen in recent *Homo*. However, the African apes display considerably greater variability on PC1. In order to ascertain whether or not the comparative morphometric differences in proximal femoral geometry of the two *Australopithecus afarensis* specimens are unusually discordant, a more detailed comparative investigation using thin-plate splines is desirable. Therefore, morphological transformations across the ranges of variation in PC1 and PC2 component scores within all three extant samples (*Pan paniscus*, *Pan troglodytes* and *Gorilla gorilla*) were assessed.

Morphological changes along PC1 in *Pan paniscus* were assessed using the RG84031 (CS = 73.476) specimen as the reference and the RG27096 (CS = 73.261) specimen as the target. There is considerable morphological overlap between *Pan paniscus* and recent humans on both the first and second component axes (see Fig. 127). Principal morphological differences between the specimens lies in the relative height and depth of the greater trochanter, slight medio-lateral increase in the length of the femoral neck and an increase in the supero-inferior proportions of the femoral head with increasing positive scores on PC1. With respect to PC2, morphing the reference specimen (RG29035, CS = 75.731) to the target specimen (RG29063, CS = 77.185) reveals the medial expansion of the superior surface of the greater trochanter (above the trochanteric fossa) and a definite shortening of the femoral neck in the target specimen (Fig. 128). The proportions of the femoral neck and femoral head of the target specimen are uniformly increased in both the supero-inferior and antero-posterior direction.

In *Pan troglodytes*, TPS transformation of the reference specimen (PCM 254.3; CS = 80.737) to the target specimen (PCM724; CS = 90.329), yields a more marked level of morphological change (Fig. 129). In *norma verticalis*, the increased antero-posterior breadth of the femoral neck and the greater trochanter are clearly apparent. Additionally, the superior surface of the trochanter becomes vertically oriented and there is a distinct increase in the supero-inferior height of the femoral head in the target specimen. The most obvious difference in the proximal femoral geometry of the two specimens is the pronounced increase in the height and depth of the greater trochanter in the target, which is evident in *norma lateralis* (Fig., 130). Morphological transformation across PC2 in *Pan troglodytes* is equally marked. Relative to the reference specimen (Z34; CS = 90.431), the femoral neck of the target specimen (PCM454; CS = 79.797) is considerably reduced in its medio-lateral aspect and the superior surface of the greater trochanter displays significant medial expansion (see Fig. 130). More crucially, there is a palpable increase in the antero-posterior and supero-inferior proportions of the femoral neck and femoral head in the target.

Not surprisingly, given the overlap of *Pan troglodytes* and *Gorilla* specimens on PC1 and PC2 (see Fig. 113), a virtually identical pattern of morphological changes in the proximal femur occurs in extreme specimens of *Gorilla* using TPS morphing procedures (Figs. 131 & 132). Comparisons of the reference (M89; CS = 98.018) and target specimens (M879; CS = 128.582) indicates that a common African ape pattern of increasing height and depth of the greater trochanter, increased S-I breadth of the femoral head and antero-posterior breadth of the femoral neck with increasing distance from zero on PC1 is universal (Fig. 131). Similarly, changes in proximal femoral geometry in *Gorilla* on PC2 morphing the reference specimen (M798; CS = 106.8) to the target (M372; CS = 102.605) also support a shared commonality in *Pan troglodytes* and *Gorilla gorilla* (Figs. 130 & 132). Specimens displaying increasing positive scores on PC2 evidence a dramatic reduction in the medio-lateral length of the femoral neck with subsequent increases in its supero-inferior and antero-posterior proportions. The femoral head is relatively larger and the antero-posterior breadth of the greater trochanter is notably greater in the target specimen. There is also a distinct medial expansion and horizontal reorientation of the superior surface of the *trochanter major*.

The observed differences in proximal femoral geometry of the two *Australopithecus afarensis* specimens (AL 288-1 & AL 333-3) are neither *qualitatively* or *quantitatively* different from the patterns of morphological variation present in *Pan troglodytes* and *Gorilla*. The extreme position of the AL 333-3 hominid on the first Principal Component, and the nature of morphological distinctions from AL 288-1 strongly suggest that *Australopithecus afarensis* displayed a level of intra-specific morphological variability that is distinctly hominoid, rather than hominid. The functional implications, if any, of this shared morphological commonality with some, but not all, of the extant African ape taxa will be discussed in a later chapter of this thesis.

6.2.3 Canonical Variates Analysis

Canonical Variates Analysis of the PCA scores for individual specimens yielded 10 discriminant functions (table 76). Of these, the first six Canonical Variates (CV's) approximated 99% of the total variance. CV1 and CV2 accounted for 68.1 and 14.5 % of the variance, respectively. Canonical Variates 3 to were deemed to be highly significant using Wilks' Lambda ($p=<0.01$). A bivariate scatterplot of CV1 and CV2 is shown as figure 133.

As in previous analyses, recent humans and the extant African apes are distinguished by the differential loci of the centroids on the first Canonical Variate (see Fig. 133). In the analysis of the proximal femoral PC scores, the African apes are principally discriminated by their positive scores on CV1, whereas recent humans display generally negative CV1 scores. *Pan paniscus* specimens included here generally overlap with recent humans, and are quite distinct from *Pan troglodytes* and *Gorilla*. Not surprisingly, the component scores on PC1 load positively and highest on the first Canonical Variate, while PC4 is negatively loaded on CV1 (table 77). Morphological changes occurring across PC1 have been detailed using total sample and intra-specific African apes references in the preceding section of this chapter, but it is worth re-iterating those occurring on PC4.

Decreasing distance to, and increasing distance from, zero on PC4 denotes a supero-medial displacement of the landmarks defining the anterior expansion of the greater trochanteric plane and an increase in the antero-posterior proportions of the femoral neck and femoral head. In the African apes at least, the component scores on PC1 and PC4 are positively but moderately correlated (r = 0.405; $p=<0.001$), indicating an implicit allometric relationship between the different aspects of geometric distinctions on these two components which have been verified in recent humans. *Pan troglodytes* and *Gorilla gorilla* femora can be morphologically distinguished from recent humans by virtue of proportional differences in the greater trochanter, femoral neck and femoral head. The greater trochanter is higher and deeper, less broad, while the femoral neck is proportionally shorter and antero-posteriorly thicker. As a general rule, the femoral head is proportionally smaller in extant African hominoids in comparison to recent humans (e.g., Jungers, 1988*a*, 1990, 1991; *this study* [Ch. 4]).

With few exceptions, *Pan troglodytes* specimens can be distinguished from *Gorilla* by virtue of their positive discriminant scores of the second Canonical Variate axis (see Fig. 133). Standardised Canonical Discriminant Coefficients (see table 100) reveal that this separation is due to the positive loading of PC4, PC5, PC8 & PC10 and negative loadings of PC2 and PC7. Morphological variation across the four positive components (PC's 4,5,8,10) reveals a shared common pattern of increased relative proportions of the femoral head and greater trochanter and in the relative length of the femoral neck with decreasing distance to, and increasing distance from, zero. The component scores on any of these axes cannot discriminate between *Pan troglodytes* and *Gorilla*. Similarly, negative components do not easily yield a recognisable distinction between the African apes. The morphological changes along PC2 have been outlined in depth in an earlier section, and again involve changes in the relative length of the femoral neck and femoral head as we move along this axis.

A bivariate scatterplot of CV3 on CV2 is illustrated in figure 134. Interestingly, PC6 did not contribute to the discriminatory power of *Pan troglodytes* and *Gorilla* on CV2, yet it remains the sole Principal Component that effectively distinguishes *Pan troglodytes* from *Gorilla*. Exploration of the morphological change across PC6 indicate that the morphological differences between *Pan troglodytes* and *Gorilla* can be found in the relatively broader antero-posterior proportions of the greater trochanter and in the more horizontally orientated superior surface in *Gorilla*.

Furthermore, the antero-posterior proportions of the femoral head are slightly increased in *Gorilla* relative to *Pan troglodytes*.

With the exception of the AL 333-3 (*Australopithecus afarensis*) and the Hayonim 29 (*Homo sapiens*) proximal femora which are classified as *Pan troglodytes* and *Pan paniscus*, respectively, all remaining fossil specimens are assigned to recent *Homo* on the basis of the relative loci on PC1 and PC2 (table 78). Interestingly, with the exception of the two *A. afarensis* proximal femora (AL 288-1 and AL 333-3), the remaining Lower and Middle Pleistocene specimens are allocated to the Native American samples. AL 288-1 and the Feldhofer Neandertal are assigned to the African Bantu.

6.3 Summary

Morphological differences in proximal femoral geometry in the extant African hominoids and suitably preserved fossil hominids were explored using Generalised Procrustes Analysis, thin-plate splines and post-hoc multivariate analyses (PCA, CVA). The proximal femur of recent *Homo* can be distinguished from *Pan troglodytes* and *Gorilla* by virtue of a reduction in the height and increased A-P breadth of the greater trochanter, a more inclined superior surface of the greater trochanter, a relatively shorter M-L femoral neck, and a relatively larger and more spherical femoral head. Morphological comparisons of recent *Homo* and *Pan paniscus* reveal that these differences are less apparent. The proximal femur of Plio-Pleistocene specimens attributed to *Australopithecus*, "early" and "archaic" *Homo* contrast with a majority of recent humans by virtue of their M-L broader and A-P narrower proximal femora and relatively smaller articular proportions.

Previously observed distinctions in the proximal femur of *Australopithecus* and "early *Homo*" were not replicated using the Geometric Morphometrics approach. Relative to KNM-WT 15000, australopithecine femora do not manifest a pronounced reduction in relative femoral neck length or decreased relative femoral head size. Morphological differences between KNM-WT 15000 and Trinil 1 are relatively minor, and both specimens are removed from recent humans on PC2. The proximal femoral morphology of the reputed male *Australopithecus afarensis* specimen (AL 333-3), is morphologically indistinguishable from *Pan troglodytes* and *Gorilla.* TPS exploration of morphological differences within *Pan* and *Gorilla* reveals that the geometric distinctions between AL 288-1 and AL 333-3 can be accommodated within an African ape model of variability.

Chapter 7. Morphological and functional integration in the hominid hip

7.1 Introduction

The analyses presented in this chapter relate to the hypotheses concerning the consequences of absolute and relative body size (i.e., body shape) variability on the integration of morphometric and functional parameters in the pelvis and lower limb of extant and extinct hominids outlined in Chapter 2. Integration, defined in this study, refers to bivariate and multivariate covariance of dependent and independent variables. Specifically, the aim of this analysis was to examine scaling relationships of morphological (Hypothesis 4) and functional parameters of the hominid hip in geographically disparate populations known to differ substantially in body size and body shape (Hypothesis 5). Linear dimensions reflecting the spatial morphology of the hominid pelvic girdle were combined with parameters derived from 2D static functional models (e.g., Pauwels 1980; Marquet, 1985; Lovejoy & Heiple, 1972; Ruff, 1995, 1998) in order to assess hypotheses of functional equivalence and disparity in fossil hominids (Hypothesis 6).

Linear dimensions of the medio-lateral (M-L) and antero-posterior (A-P) diameters of the femoral midshaft and sub-trochanteric diaphyses were used to calculate cross-sectional area based on standard elliptical formulae (see Materials & Methods). These parameters were standardised by the appropriate sectional area to assess relative diaphyseal "robusticity" in a particular axis (i.e., M-L V's A-P relative girth). Hypothesised covariance in femoral diaphyseal shape and pelvic proportions were assessed using appropriate bivariate and multivariate statistical analyses (*Ho*5).

7.2 The "Principal determinants of pelvic form"

Sex-specific sample descriptive statistics of the raw parameters measured on appropriately preserved pelvic and femoral specimens together with those derived from the static functional model are given in Appendix III This is located in the second volume of this thesis. A comprehensive description of the model, notations used, and the calculations employed to derive hip-joint force parameters are given in Chapter 3. The "principal determinants of pelvic form" have also been described in Chapter 3 and are illustrated in Appendix 1. To briefly re-state, these linear morphological parameters define the three-dimensional form of the pelvic girdle in extant and extinct hominids, and include dimensions of the ilium, ischium, pubic ramus and sacrum. RMA and LSR bivariate regression solutions were computed between relevant variables of interest. Bi-cristal diameter was used as an independent proxy for absolute body size, and relative bi-iliac diameter (e.g., Ruff, 1991, 1994, 2000; Ruff & Walker, 1993) is defined as the primary indicator of variance in body shape. These were used as the independent variables upon which the remaining parameters were regressed, unless the investigation of a specific functional relationship was the desired objective.

A highly significant positive correlation ($p=<0.01$) exists between the height of the ilium (measured as the linear distance between the superior labrum of the acetabulum and the iliac tubercle) and the breadth of the ilium in recent humans (table 79; see Appendix I). Nonetheless, the magnitude of the correlation is highly variable (e.g., Southwest Amerindians V's Libben Amerindians). With an average correlation throughout the entire sample ranges that approximates 0.6, only 36% of the variance in iliac breadth can be explained by the variance in iliac height. The Medieval Hungarian (Magyar) sample displays excessive variability in ilium breadth with corresponding increases in the height of the iliac blade (see Fig. 135).

Pairwise comparison of the RMA slopes reveals that the Magyars display significantly less broad ilia proportional to iliac height than do Tartar or Southwest Amerindian samples ($p = < 0.05$). This likely reflects the greater ranges of variation in ilium breadth with increasing iliac height in Medieval Hungarians. RMA elevation differences between the Libben Amerindians and samples of comparable iliac proportions (i.e., Bantu, Magyars, Tartars) is a consequence of the virtual absence of a positive trend to increasing ilium breadth in this Amerindian sample (Fig. 135). No allometric changes in iliac proportions are evident in comparisons of the diminutive African Pygmies and Southeast Asian Negritos with larger bodied human samples (e.g., Bantu, Magyars, Native Americans).

When the scaling relationships of the two iliac dimensions are considered independently relative to bi-cristal diameter (maximum pelvic breadth), both are found to correlate positively (tables 80 & 81). Correlation's between iliac breadth and bi-cristal diameter are generally higher than iliac height, which is surprising given the hypothesised relationship between iliac height and degree of iliac flare. With respect to iliac height, only the Libben Amerindians display a non-significant correlation between the height of the ilium and increasing bi-cristal diameter (table 80; see Fig. 136). Considerable variability exists in the height of the ilium relative to bi-cristal diameter in both the African Bantu and Medieval Hungarian samples ($r = 0.527$ & $r = 0.482$, respectively), but also in the Southwest Amerindians ($r = 0.673$). A consequence of this is that while a general trend of increasing ilium height with increased M-L pelvic breadth exists in recent *Homo* (Fig. 136), pairwise comparisons of the RMA solutions are largely redundant. Sample slope and elevation differences are principally the product of within-sample variance, not allometric differences in iliac height.

A moderate-strong relationship exists between the A-P breadth of the ilium and the M-L breadth of the false pelvis in recent humans. The African Bantu display a significantly broader ilium relative to Bi-cristal breadth than other recent human samples of comparable such as the Magyar and Native American samples (see table 81). While notable differences exist in the relative proportions of the ilium in the African Bantu and African Pygmies (see Fig. 137), these do not reach statistical significance. The allometric implications of proportional differences in ilium breadth in these two samples is questionable, as no apparent differences exist between the African Pygmies and Medieval Hungarians (see table 81). The iliac proportions of the two Native American samples, particularly the Southwest Amerindians, are considerably smaller than samples of comparable body size (e.g., Magyars, Tartars).

While a significant positive relationship exists between the calculated degree of iliac flare (*Theta,* Lovejoy [1975]) and bi-cristal diameter, this is not of the magnitude that might have been assumed *a priori* (see Fig. 138; table 82). Approximately 20% of the variance in iliac flare in the samples can be accounted for by bi-cristal diameter. This is not particularly reassuring. Nevertheless, at a very basic level, a limited general trend of increased iliac flare (*Theta*) with increasing medio-lateral pelvic breadth in recent *Homo* exists. Interestingly, the degree of iliac flare in the African Pygmy pelvis is significantly greater than would be expected for their overall pelvic breadth relative to contemporary recent human analogues (e.g., African Bantu, Native Americans; $p=<0.001$). In contrast, iliac flare in the Medieval Hungarian samples is proportionally lower for their overall M-L pelvic proportions than comparative samples of similar overall size (e.g, Libben and Southwest Amerindians).

Prior expectations concerning purported relationships between the diameter of the acetabulum and the medio-lateral breadth of the pelvis, were that an unequivocal positive correlation should exist between these variables (e.g., McHenry & Berger, 1998*a*,*b*; Berger & Hilton-Barber, 2000; Ruff *et al.*, 1997). This is far from true in the samples included here (table 83; Fig. 139). Correlation coefficients for the African Pygmies, Australian Aborigines and Libben Amerindians do not reach statistical significance (α = 0.05)! With the exception of the Tartars, Southeast Asian Negritos and Southwest Amerindians, remaining sample correlation coefficients are uniformly low (<0.5), indicating that only approximately 20-30% of the variance in acetabulum size is explained by covariance with an independent ***bona fide*** body size proxy. Nevertheless, there is some evidence that highly significant scaling differences govern the relative size of the acetabulum in the South African Bantu and the Native American samples (see Fig. 139). Relative acetabulum size is proportionally greater in the African Bantu relative to the Southwest and Libben Amerindians.

In all cases, a significant positive correlation exists between the medio-lateral breadth of the pelvis and the linear distance between the two centres of the hip joint (table 84; see Fig. 140). With the sole exception of the Australian Aborigines (r =

0.496), the remaining correlation coefficients exceed 0.5 (table 84). While the squared regression coefficients attest to the relatively minor variance in the dependent variable explained by absolute body size, nonetheless, a general positive trend of increasing inter-acetabular distance and increased M-L hip breadth exists in recent *Homo*. With few exceptions, the African Bantu display a proportionally greater bi-acetabular diameter than do Magyars or Tartars. Magyars are especially variable in their relative inter-acetabular distance. Chief contrasts in the relative scaling of the body mass load arm in recent *Homo* (at least in these samples) are between the African Bantu and the Native American samples.

Correlation coefficients for the antero-posterior diameter of the pelvic girdle to bi-cristal diameter are presented in table 85 (see Fig. 141). All are positive, but range in magnitude from insignificant (Medieval Hungarians, Libben Amerindians), to highly significant ($p=<0.001$; African Pygmies, Tartars). While support does emerge for a general trend of a correlated increase in A-P and M-L pelvic planes in the recent hominid pelvis, considerable variability exists within individual samples (Fig. 141). In order to assess whether within-sample variance reflects sexual dimorphism, specifically manifesting proportionally larger A-P pelvic dimensions in females, gender-specific analyses were computed. Comparisons confirm that the correlation between A-P and M-L pelvic diameter is correspondingly higher in females than males (tables 86 & 87). The only notable discrepancy is the higher correlation in Southwest Amerindian males (r = 0.395 & r = 0.226, males and females, respectively). Overall, some general allometric distinctions can be identified. While there is considerable overlap between individual specimens, African Pygmies and African Bantu (males and females), generally possess significantly wider A-P pelvic proportions than the Native American samples (*p=<0.001*; RMA intercept comparisons). The remaining human samples appear to possess somewhat 'intermediate' A-P/M-L pelvic proportions relative to these extremes, however male Magyars are especially variable.

An increase in the medio-lateral breadth of the pelvis, coupled with increasing inter-acetabular distance, should mitigate an increase in the absolute length of the superior pubic ramus in hominids (e.g., Trinkaus, 1983, 1984; Rosenberg, 1988; Ruff, 1991, 1994; Ruff & Walker, 1993; Ruff, 1995; Rak & Arensburg, 1987; Rak 1990*b*, 1991). This generalisation is supported by the data presented here (see Fig. 142). A strong and highly significant correlation exists between the length of the superior pubic ramus and increasing medio-lateral pelvic breadth (*p=<0.001*). With the exception of the Libben Amerindians and Medieval Hungarians, remaining correlation coefficients are notably higher than 0.5 (table 88). While the low correlation for the Magyar sample might reflect possible sexual dimorphism in pubic ramus length, coefficients for the Libben Amerindians apparently reflects the absence of any "real" relationship between the parameters (see Fig. 142).

Pairwise comparisons of the RMA slopes detect significant scaling differences in the relative proportion of the superior pubic ramus in African Pygmies compared with the Southeast Asian Negritos and Native American samples (table 88; see Fig. 142). African Pygmies display a significantly longer superior pubic ramus relative to M-L pelvic breadth than these samples. Comparisons with relatively small-bodied Negritos are particularly enlightening in this respect. RMA elevation comparisons reveal that Australian Aborigines and perhaps Tartars possess proportionally smaller superior pubic ramii than recent humans of comparable body size (e.g., African Bantu, Magyars), although there is considerable overlap between samples. Nonetheless, there is a persuasive case that increased absolute length of the pubic ramus is a consequence of increasing medio-lateral (i.e., bi-cristal) pelvic breadth in recent *Homo*.

Relationships between the length of the superior pubic ramus and the antero-posterior diameter of the pelvic girdle are less convincing (table 89; Fig. 143). While correlation coefficients are highly significant in many cases ($p=<0.001$), they are of a demonstrably lower magnitude. Exceptions are the Australian Aborigines and Southwest Amerindians, who display a slightly better correlation of pubis length with A-P pelvic breadth. Nevertheless, quite striking contrasts emerge in some comparisons of the relative proportions of the superior pubic ramus scaled to the A-P, rather than M-L, pelvic axis. Relative length of the pubic ramus in the African Pygmies and African Bantu is proportionally short when scaled to A-P pelvic breadth, whereas it is proportionally large when scaled to M-L pelvic breadth. This most likely reflects the extreme A-P to M-L pelvic proportions in these two samples, but it is interesting to note that two possible “dimensional” constraints may influence absolute pubic ramus length in recent *Homo*.

Correlation coefficients for the medio-lateral breadth of the sacrum and bi-cristal diameter are positive and highly significant in the African Pygmy and Southeast Asian Negrito samples (table 90). Remaining correlation coefficients achieve only moderate significance, whereas the Aboriginal Australian coefficient is not significant. Libben Amerindians possess proportionally broader sacra relative to

M-L pelvic breadth than do Southwest Amerindians, Tartars and Medieval Hungarians, although considerable overlap between samples exists (see Fig. 143). Only the African Bantu display a pattern of within-sample variance suggestive of possible sexual dimorphism in relative sacrum proportions. With the exception of a few notable outliers, there exists a persuasive case for covariance of increasing medio-lateral sacral breadth and increased bi-cristal diameter in recent *Homo*.

7.3 Functional allometry of the hominid pelvis

Under the first hypothesis stated in Chapter 2, increasing body weight should lead to a concomitant increase in the inter-actebular distance and subsequent load arm (*Dw*) at the hip joint. This hypothesis is confirmed in the recent human samples included in this analysis (table 91; see Fig. 145), with the sole exception of the Aboriginal Australians (r = 0.285). Significant differences in RMA slopes exist between the Medieval Hungarians and Australian Aborigines with the African Bantu, Tartars and Southeast Asian Negritos. The latter samples display significantly increased body weight load arms [*Dw*] relative to body weight particularly the African Bantu (table 91; Fig. 145).

There has been considerable debate concerning the relative implications of proportional differences in *Dw*/*Dm* proportions and the mechanical advantage of the abductor muscles in bipedal hominids. Lovejoy and his colleagues (e.g. Lovejoy, 1975, 1978, 1988; Lovejoy, Heiple & Burstein, 1973) have proposed that an anterior pelvic configuration with relatively greater *Dw*/*Dm* proportions and relatively greater medio-lateral iliac flare would increase the mechanical advantage in the abductor muscles (*m. gluteus medius and m. gluteus minimis*). Berge (Berge, 1988) and Jungers (Jungers, 1991) have argued that increasing *Dw/Dm* proportions and M-L pelvic breadth is functionally disadvantageous, as this would increase the distance of the action line of the abductor muscles from the centre of the hip joint (Berge, 1988; Jungers, 1991). The latter view is consistent with the data calculated by Ruff in his functional assessment (Ruff, 1995, 1998).

To counteract this, a direct relationship between the increasing length of the lever arm for the abductor muscles (*Dm*) and body weight might be expected in recent *Homo*. When the pooled-sex samples were analysed, the relationship between the length of the abductor force load arm (*Dm*) and body weight were significant in a majority of samples (table 92, Fig. 146; p=<0.05). Only the African Pygmies, African Bantu and Australian Aborigines fail to display a concomitant increase of the Abductor Force lever arm with increasing body weight. When sex-specific models were computed, some interesting contrasts become apparent. In females, in addition to those samples detailed above, the relationship between *Dm* and body weight in the Libben Amerindians is not significant, whereas in males, correlation coefficients are highly significant in all cases except the Bantu and Libben Amerindians (not shown). In both the male and female analyses, African Bantu apparently possess a relatively greater biomechanical femoral neck length proportional to body weight than other human samples, particularly Native Americans.

With the exception of the African Bantu (r = 0.216), sample correlation coefficients for the abductor force lever arm [*Dm*] on the body mass load arm [*Dw*] are highly significant (p=<*0.001*; table 92). There is considerable variability within individual samples, particularly the Bantu, but also in both Native American samples (Fig. 146). This may reflect sexual dimorphism effects as noted previously. Sex-specific solutions reveal that with few exceptions (African Pygmies, Negritos, Australian Aborigines), relationships in the female sub-samples are not significant ($\alpha = 0.05$). In contrast, correlation coefficients for males are highly significant ($p=<0.001$), with the sole exception of the Bantu males (tables 93 & 94).

There appears to be a general trend to allometric correspondence of hip-joint load and lever arm proportions in recent humans. Nevertheless, this is more consistent in males rather than in females. With regards to inter-population proportional differences, Tartars have slightly less "advantageous" proportions (i.e., lower lever arm) than many humans of equivalent body size, but these comparisons did not reach statistical significance. Results of the post-hoc RMA elevation tests are reported in table 95. The considerable overlap of individual specimens and samples renders any conclusions concerning elevation differences unsound (see Fig., 147).

While *Dw* and *Dm* display moderate-good correlations with increasing body weight and with one another (Figs. 145, 146 & 147), there exists no relationship between the ratio of these variables and body weight in recent humans with the exception of the Medieval Hungarians and Southwest Amerindians (table 98; see Fig., 148). The "goodness of fit" of the regression models is not improved by the calculation of gender-specific functions (not shown). Thus, while clear sex differences in the proportions of the body weight load arm to the abductor lever arm in recent humans exists, no general allometric trend to increasing abductor moment leverage relative to the load arm with increasing body weight in recent *Homo* exists (*contra* Walker, 1993).

Similarly, with few exceptions (Bantu, Libben Amerindians), there is little convincing evidence for a proposed relationship between calculated values of abductor force (*M*) and proportions of the load arm/lever arm in recent *Homo* (table 101; see Fig. 149). Pooled-sample correlation coefficients are universally low, but positive. When sex-specific analyses are computed (tables 102 & 103), there is a notable increase in the strength of the individual correlation coefficients in females, but not males (not shown). In all analyses, regardless of significance, African Pygmies and Southeast Asian Negritos are demonstrated to possess relatively larger body mass load arm proportions for their calculated abductor force values, particularly females. It is highly likely that this manifests a morphological consequence of obstetrical demands at low body size in these populations. An alternative explanation is that this is purely an allometric consequence of greater bi-iliac breadth proportions in these samples (e.g., Ruff, 1993; see below). If this is the case, then these morphological distinctions are of little obvious functional valence.

Analyses reveal that the length of the superior pubic ramus is only moderately correlated with increasing joint reaction force (*J*) in recent humans (table 104; see Fig. 150). In general terms, there is an apparent functional relationship between the principal morphological component of the body mass load arm and increasing joint reaction force in recent *Homo*. This probably reflects an underlying correlation with increasing body size (i.e., body weight). Nevertheless, there is considerable variability, particularly within Australian Aborigines (Fig. 150). Medieval Hungarians apparently possess significantly longer superior pubic rami than do the Southwest Amerindians ($p=<0.001$), but generally, results of the pairwise comparisons of RMA solutions do not support sample specific differences that can be rigorously confirmed. The Australian Aboriginal RMA solution is likely to be heavily influenced by two negative outliers, particularly in comparisons with the African Pygmies and Southeast Asian Negritos. Nonetheless, pubic ramus length in Australians is likely to be lower relative to their estimates of *J*. This may reflect variability in lateral pelvic breadth, which is considerably lower in Australian Aborigines.

7.4 Relative size of the femoral head

Surprisingly, absolute size of the femoral head and estimated body weight is not significantly correlated in African Pygmies or Australian Aborigines (table 105; Fig. 151). In all other cases, femoral head diameter is positively correlated with body weight at a high level of significance ($p=<0.01$). The magnitude of the sample-specific correlation coefficients ranges from low to moderate, yet none are exceptional. While a general linear trend of increasing femoral head diameter with increasing body weight might be supported by the samples considered here, approximately only 20-40% of the variance in femoral head size is explained by variance in body weight.

Quite significant differences exist in relative femoral head size within *Homo*. The Native American samples possess significantly smaller proximal femoral epiphyses than other human samples ($p=<0.001$). This variability cannot be explained by allometric constraints on femoral head size, as African Pygmies and the African

Bantu possess relatively large femoral heads proportional to body mass (table 105). Indeed, relative femoral head size in these two samples is considerably greater than in the larger-bodied Medieval Hungarians ($p=<0.001$; Bantu versus Magyars), and is approximately equivalent to the Tartars. Of the samples included here, Australian Aborigines are the most variable.

Examination of sample-specific coefficients reveals a highly significant relationship between the length of the body mass load arm (*Dw*) and absolute femoral head diameter in recent *Homo* (table 106; see Fig. 152). However, while sample specific coefficients range from low to moderate (Bantu) to moderate-good (Tartars), squared coefficients indicate that approximately only 25-35% of the total variance in absolute femoral head diameter can be accounted for by covariance with the body weight load arm. It is likely that some of this unexplained variance is due to sexual dimorphism in absolute size of the proximal femoral epiphysis in recent humans (e.g., Bass, 1970; Ruff *et al.*, 1991; Ruff *et al.*, 1997). Previous analyses identified no apparent sexual dimorphism in the length of the body weight lever arm (see above). Sex-specific analyses reveal that femoral head diameter is significantly correlated with *Dw* (tables 107 & 108) in recent human males, but less so in females. While the overall scaling patterns remain similar to those of the pooled-sex analysis, there are subtle distinctions. African Bantu females do not differ significantly in the relative scaling of the femoral head from the Libben Amerindians, but comparisons with Southwest Amerindians remain significant. African Pygmies display proportionally greater proximal femoral epiphyses than other groups, and these differences are especially pronounced in females.

Correlation coefficients for the size of the femoral head on the abductor force load arm are of considerably greater magnitude than those derived from regressions of FHD on *Dm* (table 109; see Fig. 153). In recent humans, femoral head size and biomechanical femoral neck length (*Dm*) are sexually dimorphic with males displaying considerably greater mean values for each parameter. Sexual dimorphism in femoral head size is countered by correlated sexual dimorphism in *Dm*, and residual variance around the regression line is minimised. Significant differences exist in relative femoral head proportions of African Pygmies and Southeast Asian Negritos relative to the biomechanical length of the femoral neck (*Dm*). In the latter, the relative size of the femoral head is considerably smaller. Tartars display significantly enlarged femoral head proportions relative to the two Native American samples ($p=<0.001$).

A crucial theoretical prediction of the functional model (see Chapter 3) is that a change in the relationship of the body mass load arm (*Dw*) and the abductor force lever arm (*Dm*) will lead to a significant change in the magnitude of the joint reaction force (*J*) at the hip-joint. Both Jungers (Jungers, 1991) and Ruff (Ruff, 1995, 1998), have proposed that as the ratio of *Dw*/*Dm* increases, the magnitude of the joint reaction force increases concomitantly. As noted previously, this hypothesis cannot be tested by direct examination of relationships between *Dw*/*Dm* and *J*, as they are mutually dependent (see calculation of *J* in Chapter 3). However, the area (or linear approximation) of the proximal femoral articulation will be meaningfully related to the magnitude of the forces acting upon it (e.g., *W* & *J*). Thus, following the rationale of Ruff (Ruff, 1998), a positive linear relationship should exist between the absolute size of the femoral head and the ratio of *Dw*/*Dm*.

When this proposal is tested empirically (table 110; Fig. 154), the results do not corroborate prior expectations. A negative relationship exists between femoral head size and the load arm/lever arm ratio in recent *Homo*. Simply stated, as the proportions of the load arm increase relative to the length of the lever arm of the abductor muscles, the absolute size of the femoral head is reduced! Magnitudes of the coefficients range from low to moderately good, nevertheless some clear allometric distinctions can be made. African Pygmies apparently possess relatively small proximal femoral epiphyses regardless of their load arm/lever arm proportions, whereas Magyars and Tartars possess significantly greater proximal femoral epiphyses than do the African Bantu or Native Americans, although there is considerable overlap in individual samples. This pattern persists when gender-specific bivariate models are computed (see tables 111 & 112), and no significant change in the magnitude of correlation coefficients is achieved with the calculation of sex-specific functions. When AL 288-1 is introduced to the scatterplot (Blue Triangle), it is clear that her absolute femoral head size is exactly what one would predict based upon her load arm/lever arm proportions using a recent human model.

Correlation coefficients for the femoral head diameter with relative bi-iliac diameter (Bi-iliac/Stature) are relatively poor (table 113; Fig. 155). In several cases (Bantu. Magyars and Southwest Amerindians) the coefficient is not significant ($\alpha = 0.05$). This result is particularly surprising, given that both parameters are considered to reflect overall body size in hominids to such an extent that they are commonly employed in body mass estimation (e.g., McHenry, 1988, 1992*a*,*b*; Ruff, 1991, 1994; Ruff *et al.*, 1997). Moreover, relative body size is now considered to be a more reliable indicator of loading magnitude in hominid postcrania (e.g., Trinkaus, 1997; Trinkaus & Ruff, 1999*a*,*b*; Ruff 2002, 2003).

7.5 Functional Integration in the hominid lower limb

7.5.1 Femoral midshaft diaphyseal proportions

Sample-specific differences in femoral midshaft diaphyseal shape were examined using RMA regression models of area standardised medio-lateral (M-L) and antero-posterior (A-P) shaft diameters against total cross-sectional area, which was calculated using an elliptical model. In both cases, the dependent variables [FMML & FMAP] will be highly correlated with estimated cross-sectional area. This analysis seeks to examine whether observed population differences in relative medio-lateral [FMML] and antero-posterior [FMMP] diaphyseal proportions can be profitably related to differences in pelvic morphology and/or differential activity patterns (e.g., Trinkaus *et al.*, 1991, 1998; Trinkaus & Ruff, 1999*a*; Pearson, 1997; 2000). It is worth restating that area standardisation of the raw M-L and A-P diaphyseal parameters employed elliptical area as the numerator, and the diaphyseal width as the denominator. As such, an increase in the dependent (i.e., diaphyseal) variable denotes smaller, not larger, diaphyseal proportions in that particular axis.

Not surprisingly, in both series [FMML & FMAP], correlation coefficients of the dependent and independent variables are extremely strong, positive, and highly significant (p=<*0.001*; tables 116 & 117). Despite some obvious overlap between individual specimens, some notable distinctions between groups in overall femoral midshaft diaphyseal proportions emerge. The two diminutive populations, and the Southwest Amerindians and Australian Aborigines differ from remaining samples (table 116; Fig. 156) by virtue of their relatively slender medio-lateral diaphyseal proportions. In contrast, Libben Amerindian and Medieval Hungarians display proportionally greater medio-lateral diaphyseal midshaft proportions. Not surprisingly, a contradictory pattern emerges for the relative proportions of the antero-posterior diaphyseal plane (table 117; Fig. 157). As before, significant elevation differences exist between the Magyars and Libben Amerindians with all other samples with one single exception, the non-significant proportional differences between the Magyars and Tartars. Nevertheless, other pairwise comparisons of relative FMAP are generally non-significant, suggesting that variability in FMAP might be less than in FMML, and that FMML and FMAP might not be strongly correlated in all samples.

This suspicion is confirmed by analysis of the relationships between the two components of diaphyseal shape (see Fig. 158; table 118). Correlation coefficients range from negative to positive, low to high, and non-significant to highly significant. Femoral midshaft diaphyseal cross-sectional proportions of the Libben Amerindians and Medieval Hungarians are discernibly different from those seen in other humans. However, this is primarily a consequence of their extremely “narrower” relative FMAP proportions rather than their increased medio-lateral diaphyseal proportions (see Fig. 158). Diaphyseal morphology in the Bantu sample is highly variable, and may reflect some interesting gender differences in relative diaphyseal shape. Australian Aborigines display antero-posteriorly “buttressed” femoral midshaft diaphyseal proportions compared to the "intermediate" diaphyseal morphology of the Southwest Amerindians and African Bantu.

Highly significant positive correlations ($p = < 0.001$) were returned in all cases between the estimated elliptical area of the femoral diaphyseal midshaft and the body weight load arm (*Dw*) and abductor force lever arm (*Dm*). Correlation coefficients between FMArea and *Dm* were of a greater magnitude than with *Dw* (see tables 119 & 122; Figs. 159 & 160). Coefficients for the African Bantu are the lowest of all samples, whereas the African Pygmy correlation coefficients are consistently high. With respect to *Dw*, the African Bantu apparently possess relatively more "robust" femoral midshaft diaphyses than other populations of equivalent absolute size (e.g., Magyars, Native Americans; $p = < 0.001$), relative to the length of their body mass load arms. African Pygmies and Southeast Asian Negritos possess relatively greater diaphyseal area proportional to *Dw* than do Magyars ($p = < 0.001$), but not Native Americans.

A slightly different pattern of proportional differences exists when the abductor force lever arm is used as the independent variable (table 122; Fig. 160). Relative to *Dm*, Australian Aborigines, African Bantu, African Pygmies and Southeast Asian Negritos have proportionally greater femoral midshaft diaphyseal area compared with the Magyars (all samples), and Native Americans (Australians and Bantu). Tartars display significantly greater FMArea indices than their Eurasian high-latitude counterparts and both Native American samples ($p = < 0.05$, $p = < 0.001$, respectively), when expressed as a proportion of *Dm*. Elevation differences between

Bantu, Magyars and Native American samples might merely reflect elevated levels of variability in the Bantu and Magyar diaphyseal area.

In a majority of cases, relative medio-lateral diameter of the femoral midshaft is not correlated with absolute length of the body weight load arm (*Dw*). Correlation coefficients for FMML with the lever arm of the abductor muscles (*Dm*), are notably greater (table 123), and in only two samples does the magnitude of the coefficients fail to reach statistical significance (African Bantu, Tartars). The low magnitude of the correlation coefficients with *Dw* makes it difficult to interpret proportional scaling differences between samples using post-hoc comparisons. Nevertheless, it seems likely that Medieval Hungarians and Libben Amerindians differ in their FMML proportions relative to *Dw* from Australians, African Bantu and African Pygmies (Fig. 161). Despite the increased levels of significance relative to *Dw*, regressions of FMML on *Dm* reveals that if any positive trend to decreased medio-lateral "buttressing" in the femoral midshaft exists in recent *Homo*, it is generally of a low order (Fig. 162). It is difficult to interpret the bivariate relationships of the pelvic load-and-lever arms with femoral medio-lateral diaphyseal proportions as part of a cause-and-effect morphological feedback. There exists no "general functional relationship" (e.g., Rayner, 1985) between the parameters.

As in the previous analysis, magnitudes of the correlation coefficients between the relative antero-posterior diameter of the femoral midshaft and the length of the pelvic load and lever arm are higher in *Dm* than in *Dw* (tables 121 & 124). Only the African Bantu coefficient fails to reach the required order of significance in regressions of FMAP on *Dw* (table 121; see Fig. 163). Significant RMA elevation differences were detected between Libben Amerindians and the Magyar and Southwest Amerindian samples. The Libben sample is confirmed as having proportionally lower relative antero-posterior dimensions of the femoral midshaft diaphysis ($p=<0.001$), relative to *Dw*. Once again, the African Bantu are highly variable in their diaphyseal proportions. Intra-specific relationship's between FMAP and *Dm* (Fig. 164) strongly suggests a meaningful correspondence between the two parameters. Southwest Amerindians evince surprisingly "robust" FMAP indices than populations of approximately equivalent *Dm* proportions (e.g., Libben, Magyars, Tartars). Surprisingly, those populations of the highest absolute body weight (e.g., Magyars, Tartars) display relatively slender femoral midshaft A-P proportions (Fig. 164), whereas those of the Bantu are somewhat intermediate. Australian Aborigines differ from the Southwest Amerindians ($p=<0.05$) in their FMAP proportions relative to biomechanical femoral neck length (*Dm*).

Correlation coefficients for regression analyses of femoral midshaft diaphyseal area and the ratio of the "functional" pelvic parameters in recent *Homo* are uniformly low and negative (table, 125; see Fig. 165). There appears to be some general support for a limited trend of decreasing femoral midshaft cross-sectional area with increasing proportional length of the body weight load arm, but within sample variance is considerable. No increase in statistical power is achieved by computing sex-specific regression equations (not shown). African Pygmies apparently possess considerably smaller femoral midshaft diaphyseal cross-sectional areas relative to anterior pelvic proportions than other samples of equivalent *Dw*/*Dm* indices (i.e., Libben Amerindians).

In general terms, there exists a palpable negative correlation of the medio-lateral proportions of the femoral midshaft and increasing relative body weight load arm length in recent humans (table 128; Fig. 166). As before, approximately only 50% of the sample-specific coefficients reach statistical significance ($p=<0.05$), and in those only roughly 20-30% of the variance in FMML can be accounted for by variance in anterior pelvic proportions. No significant differences emerge from the sex-specific analyses. As such, only limited support emerges for the hypothesis that *Dw/Dm* proportions and relative FMML proportions are functionally related.

Similarly, while relationships between relative antero-posterior midshaft diaphyseal proportions with *Dw/Dm* follow theoretical predictions (i.e., an increase in relative A-P diameter with a proportional increase in *Dw*), correlation coefficients are modest in most cases. In only the Australian Aborigines ($r = -0.682$; $p=<0.001$), is the correlation coefficient of sufficient magnitude to suggest a meaningful relationship between the pelvic and diaphyseal parameters (table 131; Fig. 167). Interestingly, sex-specific analyses reveal that the correlation coefficient maintains its status in female Australians at least (not shown), whereas in remaining samples the correlation coefficient does not reach required levels of statistical significance ($\alpha = 0.05$). Correlation coefficients for males are slightly better, at least in that several sample-specific relationships are significant ($p=<0.05$). Surprisingly, African Pygmies display the highest relative A-P "buttressing" of the femoral midshaft, and are significantly different from Magyars and Tartars ($p=<0.001$). Australian Aborigines, who possess somewhat 'intermediate' FMAP proportions are discernibly different from the Magyar and Tartar samples.

7.5.2 Femoral sub-trochanteric diaphyseal proportions.

As before, raw medio-lateral and antero-posterior dimensions of the sub-trochanteric femoral diaphysis (taken immediately inferior to the lesser trochanter) were standardised to sub-trochanteric area (calculated using elliptical formulae). As before, higher diaphyseal indices reflect proportionally smaller, not larger dimensions in that particular plane. Not surprisingly, both standardised diaphyseal dimensions are significantly correlated with sub-trochanteric diaphyseal area [STArea]. Correlation coefficients were slightly higher with respect to antero-posterior diameter [STAP] than in medio-lateral diameter [STML]. All were highly significant ($p=<0.001$; tables 134 & 135).

Pairwise comparisons of the RMA slopes reveal that African Pygmies differ significantly in the relative scaling of their medio-lateral sub-trochanteric diaphyseal proportions from several recent human samples including Negritos, African Bantu and Magyars (see table 134). Relative M-L diaphyseal diameter in the African Pygmies is notably reduced compared to these samples (Fig. 168). In contrast, STML proportions of the Libben Amerindians are significantly strengthened relative to corresponding human samples of approximately equivalent diaphyseal area (e.g., Bantu, Australians, Southwest Amerindians). Medieval Hungarians have medio-lateral sub-trochanteric diaphyseal proportions that are roughly intermediate between those of the Bantu and Australian Aborigines, but still differ significantly from the latter ($p=<0.001$).

With respect to relative antero-posterior sub-trochanteric diaphyseal shape (see Fig. 169), African Pygmies and Southeast Asian Negritos were found to differ significantly in RMA slopes from the African Bantu ($p=<0.001$), and Australian Aborigines ($p=<0.05$). The African Pygmy slope was also observably different from the Libben Amerindians ($p=<0.05$). The two diminutive human populations possess STAP proportions that are relatively more slender than the African Bantu and Aboriginal Australians. Pairwise comparisons of RMA elevations reveal further differences in sample sub-trochanteric diaphyseal morphology. Relative STAP proportions of the Libben femora are discernibly different other samples with the exception of the African Pygmies and Southeast Asian Negritos. Southwest Amerindians also differ in their relatively slender STAP diaphyseal proportions from the African Bantu ($p=<0.001$) and Tartar ($p=<0.05$) samples, but also from the Libben Amerindians (see table 135).

Correlation coefficients for STAP on STML are detailed in table 136. Only the Tartar correlation coefficient did not reach statistical significance ($\alpha = 0.05$). Several samples (e.g., Magyars, Southwest and Libben Amerindians) display marked variability in their relative A-P sub-trochanteric proportions, some of which may be due to sexual dimorphism. In general terms, there is a trend of increasing relative STAP diameter with increasing STML diaphyseal proportions in recent *Homo* (Fig. 170). Calculation of sex-specific models does not have an observable effect upon the strength of the bivariate relationships, and only the Southwest Amerindian males exhibit an observable increase in the strength of their correlation coefficient (tables 137 & 138). Pronounced scaling differences exist between male and female Southwest Amerindians. Libben Amerindians display demonstrably A-P "flattened" sub-trochanteric diaphyses relative to many recent human samples, particularly the Bantu, Australians and Southwest Amerindians ($p=<0.001$). Medieval Hungarians also possess relatively flattened A-P sub-trochanteric diaphyses and contrast significantly with Bantu, Tartars and Australians.

With the exception of the Tartar sample (r = 0.291; n = 9), remaining correlation coefficients for femoral sub-trochanteric diaphyseal area [STArea] with the body mass load arm [*Dw*] are statistically significant (table 139). All coefficients are positive, but in only two samples (Negritos and Southwest Amerindians) is more than 35% of the variance in the dependent variable explicable by covariance with *Dw*. Thus, while a general trend of increasing femoral sub-trochanteric area with increasing length of the body mass load arm exists in recent *Homo*, this is highly variable in the samples included here (Fig. 171). Medieval Hungarians and the African Bantu display excessive levels of within-sample variability relative to the Native American samples and, moreover, slopes of the Old World samples are significantly higher ($p=<0.01$). While there is considerable overlap between individual samples, highly significant RMA elevation differences exist between the Southwest Amerindians and the Australian Aboriginal and Libben samples. Southwest Amerindians display proportionally smaller sub-trochanteric femoral diaphyseal area than these latter samples (see table 139).

A hypothesised functional relationship between the length of the body mass load arm [*Dw*] and the relative medio-lateral proportions of the sub-trochanteric femoral diaphysis is even less convincing than for proximal femoral diaphyseal area see Fig. 173). While all correlation coefficients are positive and are highly significant (*p*=<*0.05*; except the Tartars), magnitudes of the coefficients are universally low (see table 140). On average, the squared coefficient is approximately 0.16! Calculation of sex-specific models leads to an improvement in the strength of some relationships. Sex-specific correlation coefficients are discernibly higher in the African Pygmies and Southeast Asian Negritos, particularly in females. STML is significantly correlated with *Dw* in the Magyar males alone, whereas the correlation coefficient for the female Australian Aborigines attains a higher degree of statistical significance than the males.

Nonetheless, there exist some marked differences in M-L diaphyseal proportions between the samples (see Fig. 173). African Pygmies display proximal femoral diaphyses that are medio-laterally narrower compared to the Magyars and Native American samples. In the males, Tartars contrast with the Native Americans, African Bantu and Medieval Hungarians by virtue of their slender M-L sub-trochanteric diaphyses. As a general rule, female Magyars display proportionally wider M-L sub-trochanteric diaphyses relative to other human samples, although there is some degree of overlap in within-sample ranges of variation. Relationships between relative antero-posterior diameter of the sub-trochanteric diaphysis and the length of the body mass load arm [*Dw*] in recent humans are tangible, but moderate in magnitude (table 141; see Fig. 175). Approximately only 50% of the sample correlation coefficients attain a high level of statistical significance (*p*=<*0.001*), and in two samples the relationship between the two parameters is not significant (African Pygmies, Libben Amerindians). There is little to suggest that within-sample variance in the bivariate distribution is bi-modal (i.e., sexual dimorphism). At a general level, there is justifiable cause for rejecting the hypothesis that the absolute length of the body weight load arm is a major influence upon antero-posterior sub-trochanteric [STAP] diaphyseal proportions in extant *Homo*.

With the exception of the Tartar sample (r = -0.035), correlation coefficients for the femoral sub-trochanteric diaphyseal area on abductor force lever arm [*Dm*] are positive and highly significant (table 142). In all cases, the coefficients exceed 0.65. Post-hoc RMA slope and intercept tests reveal surprisingly few distinctions between individual samples (see Fig. 172; table 142). Australian Aborigines appear to have enlarged sub-trochanteric area relative to *Dm* compared with the Southeast Asian Negritos and Southwest Amerindians ($p=<0.05$). Pairwise comparisons of the Southwest and Libben Amerindians reach statistical significance ($p=<0.05$), although there is considerable overlap between the specimens.

With respect to the medio-lateral proportions of the proximal femoral diaphysis, sex-specific analyses reveal that in several samples, relationships are gender related. Only the African Pygmies and Southeast Asian Negritos evince general uniformity across the pooled-sex and sex-specific regression models (not shown). Correlation coefficients for Aboriginal Australian and Libben Amerindian males are not significant, whereas in the females, both coefficients are highly significant ($p=<0.001$). No significant relationship exists between relative femoral STML indices and *Dm* in the African Bantu, Medieval Hungarian and Southwest Amerindian females. As a result, the only proportional differences detected in the post-hoc RMA significance tests that can be considered reliable are those for the Aboriginal Australians. Australian Aborigines (particularly females), display relatively slender M-L sub-trochanteric diaphyses than Negrito, Bantu, and Native

American samples (*p=<0.001*). African Bantu and Medieval Hungarians appear excessively variable in their STML diaphyseal proportions, although there is little to suggest the contribution of underlying gender distinctions to this variance. Rather, there appears to be a surprising level of homogeneity between samples and a weak general functional relationship between the two parameters can be posited for recent *Homo*.

A similar pattern of results is obtained for the analysis of the antero-posterior sub-trochanteric dimensions regressed upon biomechanical femoral neck length [*Dm*]. In all cases, correlation coefficients are highly significant (*p=<0.001*). Nonetheless, considerable variation can be seen in the Bantu, Magyars and Native American samples (table 146; Fig. 176). Sex-specific RMA solutions were computed accordingly. As before, the magnitude of the correlation coefficients for the pooled-sample and sex-specific solutions for the African Pygmies and Southeast Asian Negritos relatively uniform (*p=<0.001*). Gender-specific relationships are less stable. With respect to the males, correlation coefficients for the Bantu, Magyars and Australian Aborigines did not reach statistical significance (α = 0.05). In females, only the Medieval Hungarians and Southeast Amerindians furnish correlation coefficients that did not reach the required level of statistical significance. Libben Amerindians display relative small STAP indices relative to *Dm* compared with the Negrito, Bantu and Southwest Amerindians (not shown).

Few recent human populations exhibit a functional relationship between femoral sub-trochanteric diaphyseal area and the index of the body mass load arm to abductor force lever arm (*Dw*/*Dm*). Only the African Pygmies, Southeast Asian

Negritos and Tartars yield correlation coefficients that are statistically significant ($p = < 0.05$; table 149). All coefficients are negative, indicating a reduction in absolute femoral sub-trochanteric diaphyseal area with a proportionally larger body weight load arm (*Dw*), but there is considerable variability in STArea both within samples, and within recent *Homo* as a whole (Fig. 177). When sex-specific analyses are computed, only females evince a general improvement in the relationships between the parameters.

Female African Pygmies, Australian Aborigines and Libben Amerindians display a significant linear relationship between the two parameters ($p = < 0.05$; see Fig. 177), whereas in males significant correlations between the pelvic and diaphyseal variables are restricted to the African Pygmies and Tartars. Little support emerges for the hypothesis that anterior pelvic proportions contribute significantly to the observed variance in sub-trochanteric diaphyseal area in recent *Homo*. Nevertheless, African Pygmies and Southeast Asian Negritos generally display relatively lower femoral sub-trochanteric diaphyseal area relative to their *Dw*/*Dm* indices than do other samples. The Southwest and Libben Amerindians also differ quantitatively in proximal femoral diaphyseal area but it is unlikely that these differences can be profitably related to differences in anterior pelvic morphology.

When the pooled-sex sample is analysed, only the African Pygmies, Southeast Asian Negritos and Australian Aborigines yield correlation coefficients for the medio-lateral (M-L) proportions of the proximal femoral diaphysis with the *Dw*/*Dm* indices (table 152; Fig. 178). All correlation coefficients are negative. Thus, at a general level, increasing relative *Dw* to *Dm* proportions is coincident with a general increase in the medio-lateral proportions of the proximal femoral diaphysis. Closer examination using sex-specific regression solutions reveals that only Australian Aborigines display significant functional relationship between the pelvic and STML in both males and females (*p=<0.05*). Highly significant correlation coefficients for the African Pygmies and Southeast Asian Negritos (*p=<0.001*) are restricted to females alone. It is unclear to what extent the strength of these relationships is due to the small effective sample sizes. Thus, with few exceptions, little support emerges for the hypothesis that a valid functional relationship exists between the medio-lateral proportions of the proximal femoral diaphysis and the load arm/lever arm proportions of the pelvis in recent *Homo*.

Correlation coefficients for the regression of relative antero-posterior (A-P) diameter of the proximal femoral diaphysis on the index of the load arm/lever arm proportions of the hip joint are relatively moderate (table, 155; see Fig. 179). Bivariate relationships of the Negrito, African Bantu and Medieval Hungarians were not significant at the $\alpha = 0.05$ level of probability. All coefficients were negative, indicating that an increase in antero-posterior proportions of the sub-trochanteric femoral diaphysis with increasing *Dw/Dm* indices. There exists, however, considerable variability within samples, particularly in the Bantu and Magyars. Sex-specific analyses reveal that a significant (*p=<0.05*) relationship between the A-P proximal femoral diaphyseal proportions exists in the male Negritos, but this remains non-significant in the Bantu and Magyars (table 155). Correlation coefficients for male Aboriginal Australians, Southwest and Libben Amerindians are also non-significant (see Fig., 179). In the female analyses, significant correlations for STAP and *Dw/Dm* were returned for the African Pygmies, Australian Aborigines and Libben Amerindians alone.

7.6 Functional morphological variation in Plio-Pleistocene fossil hominids

7.6.1 Functional models of the hominid hip

With the exception of the AL 288-1 ("Lucy") *Australopithecus afarensis* female partial skeleton, estimates of body weight (W = Mass x 9.8) for remaining Middle-Upper Pleistocene fossils fall at, or beyond, the upper size limits of recent *Homo* (Appendices III & IV; see Fig. 180). The body mass estimate for AL 288-1 was taken from Ruff (Ruff, 1998), and is considerably lower than the average for African Pygmy females. Interestingly, the body weight estimate for the Early Upper Pleistocene specimen from Skhul (Skhul IV; $W = 713.44$ N) is greater than that of the "composite" Neandertal (Neandertal; $W = 680.12$), and the Early and Later Upper Palaeolithic specimens from the Levant and Europe (see table 158). The composite Neandertal comprises bi-iliac diameter from the Kebara pelvis with average femoral length and femoral head values from available Neandertal specimens (see Appendix IV). The putative early Neandertal pelvis from the Sima de Los Huesos ([AT-1] Arsuaga *et al.*, 1999), is estimated to possess the greatest body mass of any fossil specimen included in this study. At 93.1-95.4 kg, the estimated body mass of this individual is equivalent to the calculated values for the Middle Pleistocene proximal femoral specimen from Berg Aukas, Namibia (Grine *et al.*, 1995; but see Ruff *et al.*, 1999).

This pattern of differences is replicated in calculations of estimated abductor force (*M*) and joint reaction force (*J*), with some interesting differences. In both measures (*M* & *J*), estimates for AL 288-1 fall below the recent human range of averages, whereas estimates of *M* and *J* for the Atapuerca AT-1 pelvis falls beyond the range of recent human averages (Figs. 181 & 182) and is considerably greater than in comparative fossil samples. Estimates of abductor force in the composite Neandertal individual exceed that calculated for the geologically earlier *Homo sapiens* specimen from the Levant, whereas estimates of *J* are approximately equivalent (see table 158). With the exception of the LUP specimen from the Levant (Ohalo II), values of *M* and *J* are notably smaller in the Later Pleistocene *Homo sapiens* males relative to Skhul IV.

Comparisons of the absolute length of the body weight load arm (*Dw*) in the fossil specimens reveals that the Atapuerca AT-1 and (Kebara) Neandertal possess *Dw* values that fall well beyond the upper ranges of sample-mean variation seen in recent humans (Fig. 183). The *Australopithecus afarensis* female pelvis (AL 288-1) displays a load arm that is well within recent human ranges of variation, but is considerably larger than male and female averages in samples which approximate her absolute body weight (e.g., African Pygmies and Southeast Asian Negritos). Late Upper Pleistocene hominids from the Levant and Europe also fall at the upper limits of the sample-average distributions in recent *Homo* in absolute *Dw*.

In contrast, the length of the lever arm for the abductor muscles (*Dm*) in AL 288-1 is substantially smaller than *Dw*, and is approximately equal to that seen in African Pygmy and Negrito females (Fig., 184). In apparent contradiction to the contention of Walker (Walker, 1993), biomechanical femoral neck length (*Dm*) in the composite Neandertal individual is not observably longer than in the Levantine Skhul IV specimen (see also Trinkaus, 1983). Both specimens have discernibly higher absolute *Dm* values than their geological successors in the Levant (Ohalo II) and Europe (EUP, LUP). With an absolute *Dm* value of 91.74 (estimated from the published dimension of the associated proximal femur [Femur 1] in Arsuaga *et al.*, 1999), the Atapuerca specimen differs considerably from later Eurasian Neandertals.

When the functional relationship of the body weight load arm and abductor force lever arm are considered (*Dw*/*Dm*), several interesting patterns emerge in the fossils. As several workers have previously highlighted (e.g., Stern & Susman, 1983; Lovejoy, 1988; Rak, 1990*a*; Jungers, 1991; Ruff, 1998) the AL 288-1 pelvis has an exceptionally disproportionate load arm/lever arm ratio, which clearly exceeds the typical averages seen in recent human samples (see Fig. 185). The *Dw*/*Dm* proportions are unusually high for recent and fossil *Homo sapiens* males, but not females. The *Dw*/*Dm* index of the "composite" Neandertal pelvis is exceeded by the average index of Late Upper Pleistocene females (see Fig. 185; table 158).

The extremely high index of European LUP females is a consequence of including San Teodoro 4, which has a proportionally short biomechanical femoral neck length (*Dm*) rather than a discernibly increased body weight load arm (see table 158). The *Dw*/*Dm* index of the Atapuerca AT-1 specimen falls comfortably within the recent human range of variability and is approximately equivalent to the Levantine LUP specimen from Ohalo. It is quite distinct from the Neandertal composite. If AT-1 is typical of the ancestral population, then early Eurasian Neandertals possessed an anterior pelvic load arm/lever arm configuration that differs quantitatively from both *Homo erectus* (e.g., Ruff, 1995, 1998; Ruff & Walker, 1993*b*), and later "classic" Neandertals (Howell, 1953; Brace, 1964).

There has been considerable debate concerning the functional implications of observed differences in the relative size of the femoral head in *Australopithecus* and *Homo* (e.g., Lovejoy, 1975, 1978, 1988; Lovejoy, Heiple & Burstein, 1973; Jungers, 1988, 1991; Ruff, 1998). Previous analyses (Chapters 4 & 6) have demonstrated that relative femoral head size in AL 288-1 is somewhat intermediate between extant African hominoids and recent and fossil *Homo* (see also Ruff, 1998; Gallagher, 2002; see Chapter 4). Previous analyses in this chapter have further investigated relationships between absolute femoral head size with body weight, "body shape", and also with the key functional proportions of the hip joint. Briefly re-stated, increasing load arm/lever arm proportions in recent humans leads to a decrease in absolute femoral head size and an increase in the index of relative pressure (femoral head area/body mass). Absolute and relative femoral head size decreases with an increase in *Dw*/*Dm* indices in recent *Homo*. When these findings are brought to bear on the estimated indices of relative pressure for the fossil specimens, further insights in to relative femoral head scaling in extinct hominids emerge.

Relative pressure in the femoral head of AL 288-1 (see Fig. 187) is well within the range of variability in sample-means for recent humans. However, the relative pressure index in AL 288-1 is notably greater than in African Pygmies and Southeast Asian Negritos, indicating a proportionally smaller femoral head relative to body mass (*contra* Lovejoy, Heiple & Burstein, 1973). It is exceeded only by the average value of the Southwest Amerindian females and is considerably greater than in the composite Neandertal or Eurasian Upper Palaeolithic samples. The RP (FemHead) index of AL 288-1 is exceeded by the early Neandertal specimen from Atapuerca, indicating that relative femoral head size in this individual is substantially smaller than AL 288-1, and the composite "classic" Neandertal (Fig. 187). Interestingly, the relative pressure index of the composite Neandertal (as a measure of relative femoral head size), is not observably different from several of the Eurasian Upper Palaeolithic samples but is discernibly smaller than in Skhul IV. Relative femoral head diameter in AL 288-1, AT-1 and Skhul IV is considerably smaller than in Upper Pleistocene fossil specimens.

7.6.2 Analysis of the femoral diaphyseal parameters in fossil hominids

Summary statistics for the Least Squares Regression (LSR) of the area-standardised femoral midshaft and sub-trochanteric diaphyseal parameters are presented in the following section. Male and female individuals were combined in the regression models. The resulting bivariate models were then used to estimate the relevant parameters in the fossil hominid specimens and standardised residuals were calculated accordingly. In the first instance, three dependent variables were used in the assessment of patterns of diaphyseal morphology, estimated cross-sectional area, biomechanical femoral neck length and femoral head diameter. This approach allows direct testing of the sixth hypothesis observed variance in fossil hominid femoral diaphyseal proportions likely reflect differences in anterior pelvic proportions and absolute body size, not locomotor habitus or behaviourally-mediated "activity-pattern" distinctions.

7.6.2.1 Femoral cross-sectional diaphyseal proportions

In all cases, correlation coefficients for the dependent (FMML, FMMP & STML, STAP) and independent (midshaft and proximal femoral diaphyseal cross-sectional elliptical area) variables in the recent human "macro-sample" are strongly positive and highly significant (table 159). Standardised residuals for the available fossil specimens are presented in tables 160 & 161. With respect to the femoral midshaft, only KNM-ER 737 (*Australopithecus* sp.) has femoral medio-lateral midshaft proportions that exceed the range of variability observed in the recent human "macro-sample" (Figs. 188 & 189). Previous studies (e.g., Day, 1973, 1978; Walker, 1973; McHenry & Corruccini, 1976*a*, 1978; Kennedy, 1983*a,b*, 1984; Ruff, 1995, 1998; Ruff *et al.*, 1998), suggest that australopithecine femora differ from recent *Homo* by virtue of their medio-laterally expanded and antero-posteriorly "flattened" diaphyseal profiles (i.e., the absence of a "true" *linea aspera*; see Fig. 190). Nevertheless, remaining *Australopithecus* specimens (AL 288-1 [*A. afarensis*] and Stw 99 [*A. africanus*]) apparently do not differ morphologically from femora assigned to early *Homo* (e.g., KNM-ER 1472, KNM-ER 1481 & KNM-WT 15000). Nor do they differ quantitatively from the "problematic" Trinil femora (Trinil 2 & 3 [see Fig. 190]). These findings confirm the earlier observations of Trinkaus and Long (Trinkaus & Long, 1984) and Ruff and his associates (Ruff *et al.*, 1999), that external morphological proportions of the femoral midshaft cannot be used to infer locomotor differences or taxonomic affiliation between *Australopithecus* and early *Homo*.

With respect to later hominid species (e.g., *Homo neanderthalensis* and *Homo sapiens*) few actual differences in femoral midshaft M-L & A-P proportions exist (see Fig. 191). Nevertheless, early Upper Pleistocene individuals from the Levant (Skhul IV & Qafzeh 9) can be readily distinguished from Eurasian Neandertals by virtue of their larger A-P midshaft dimensions, not relatively smaller medio-lateral dimensions (see Figs. 188 & 191). Similar morphological distinctions are observed in European Early and Later Upper Palaeolithic specimens. Relative to the EUP specimens, LUP femora are proportionally greater in the A-P plane relative to their medio-lateral dimensions (Fig. 192). While this would apparently contradict models of reduced mobility in LUP populations relative to their EUP predecessors, there is good reason to suspect that this is a size-dependent phenomenon. Absolute calculated midshaft diaphyseal cross-sectional area in LUP specimens is far greater than in their EUP forebears, which probably reflects increasing overall body mass (e.g., Holliday, 1995, 1999) in these individuals.

With few exceptions, clear distinctions in the medio-lateral (M-L) and antero-posterior (A-P) proportions of the femoral sub-trochanteric diaphysis in fossil hominids (*Australopithecus* and *Homo*) and the recent human "macro-sample" exist (see Figs. 193 & 194). The proximal femoral diaphysis of fossil specimens is apparently greater in the medio-lateral plane than in the A-P axis. Nevertheless, when standardised to cross-sectional area of the sub-trochanteric section, many Late Upper Pleistocene specimens display a reduction in the relative antero-posterior depth of the sub-trochanteric diaphysis compared with recent humans (Fig. 196). There is no evidence to suggest that Plio-Pleistocene femora attributed to *Australopithecus* differ meaningfully from specimens allocated to "early *Homo*" with respect to their sub-trochanteric diaphyseal proportions (Figs. 193, 194 & 195).

On the whole, the morphology of the Neandertal sub-trochanteric diaphysis differs quantitatively from Upper Palaeolithic *Homo sapiens* in their relatively low standardised residuals for both the M-L and A-P dimensions (see Fig. 191). Shanidar 1 is the sole exception. In contrast, several EUP specimens display marked deviations from predicted patterns based upon assumptions of morphological equivalence, including Paviland 1, Dolni Vestonice 16 and Pavlov 1 (Fig. 192). There is tentative evidence to support the view that differences in proximal femoral diaphyseal proportions of the Neandertals and Eurasian "early moderns" is restricted to the relative M-L diaphyseal proportions, not the antero-posterior axis (Figs. 189 & 192).

7.6.2.2 Scaling to biomechanical femoral neck length [*Dm*]

Correlation coefficients of the femoral midshaft and sub-trochanteric diaphyseal variables with biomechanical femoral neck length [*Dm*] range from low to moderate (see table 162; Figs. 198-207). Standardised residuals for individual fossil specimens are detailed in tables 163 & 164. All are highly significant ($p=<0.001$). Of the three femoral midshaft parameters [FMArea, FMML & FMAP], relative medio-lateral breadth of the femoral diaphysis is less strongly correlated with biomechanical neck length than is total area and relative A-P shaft depth. As in the previous analysis, the two *Australopithecus* femora (AL 288-1 and Stw 99), do not differ perceptibly in their femoral midshaft diaphyseal proportions from both recent *Homo* and Lower Pleistocene femora from Lake Turkana (KNM-ER 1472, ER 1481a & WT 15000).

While the KNM-WT 15000G femur (Walker & Leakey, 1993*b*), displays relatively smaller cross-sectional elliptical area of the femoral midshaft relative to *Australopithecus* and other early *Homo* specimens (Figs. 198-201), the antero-posterior proportions of this specimen are demonstrably different (Fig. 201). Relative A-P shaft depth of the left femur from KNM-WT 15000 is remarkably slender, possibly reflecting the sub-adult status of this individual (e.g., Smith, 1993; Leakey & Walker, 1993*b*; Ruff & Walker, 1993). When standardised residuals are calculated for the femoral midshaft diaphyseal dimensions of African Plio-Pleistocene specimens (Fig. 201), KNM-WT 15000 contrasts with other available femoral specimens, particularly in the A-P diaphyseal residual.

Eurasian Neandertals contrast with European LUP, but not EUP, specimens with respect to their femoral midshaft morphology relative to biomechanical femoral neck length. Relative to *Dm*, femoral midshaft diaphyses of European LUP hominids are remarkably "robust" and all fall well above the recent human "macro-sample" LSR regression line. These specimens differ quantitatively from the Skhul/Qafzeh specimens, Eurasian Neandertals and even EUP hominids by virtue of their relatively slender medio-lateral midshaft [FMML], not their relative antero-posterior [FMAP] shaft proportions (see Figs. 199 & 200). Standardised residual plots of the Upper Pleistocene hominids (Fig. 202), confirm this, although considerable variance in EUP diaphyseal morphology exists (compare, for example, the Dolni Vestonice femora with the Grotte des Enfants specimens).

With respect to the diaphyseal proportions of the proximal femur relative to biomechanical femoral neck length, correlation coefficients are roughly equivalent across the parameters. With the sole exception of Sts 14 (*Australopithecus africanus*), relative STArea and STAP proportions do not differ quantitatively in *Australopithecus* from those of some later Pleistocene hominids (e.g., Skhul/Qafzeh, Eurasian Neandertals). Nevertheless, australopithecine proximal femoral diaphyseal proportions are generally at, or beyond, the range of variability in the recent human "macro-sample" (see Figs. 206 & 207). Relative medio-lateral proportions of the proximal femoral diaphysis are demonstrably greater in *Australopithecus* than in recent *Homo*, however they differ discernibly from the diaphyseal proportions of later Pleistocene fossil samples (e.g., early *Homo*, Neandertals, Skhul/Qafzeh [see Fig. 204]).

Standardised residual plots confirm that differences in femoral sub-trochanteric diaphyseal morphology in *Australopithecus* and early *Homo* are a matter of degree rather than kind. Two *Australopithecus* specimens (SK 82 & SK 97) contrast with other Plio-Pleistocene femora and more closely approximate the morphological pattern seen in recent *Homo*. The proximal femoral morphology of the Sts 14 *Australopithecus africanus* femur is unique, and is probably a result of the considerable post-mortem distortion to the entire proximal epiphysis (e.g., Robinson, 1972; Day, 1973). Functional implications of the contrasting morphology of this specimen should be viewed with scepticism, although there is considerable variability within both *Australopithecus* and early *Homo* (see Figs. 206 & 207).

Relative to biomechanical femoral neck length, the greatest morphological contrasts in proximal femoral proportions in later Pleistocene specimens is between Eurasian Neandertals, Early Upper Pleistocene Levantine and Italian specimens and all European LUP specimens (see Figs. 204, 205, & 207). Relative sub-trochanteric cross-sectional area is discernibly greater in LUP and Holocene femora than in the Skhul/Qafzeh and Neandertal specimens. These hominids also contrast with the morphology observed in certain European EUP individuals (e.g., Sungir 1, La Rochette and Paviland 1). The Skhul/Qafzeh specimens and Eurasian Neandertals contrast with earlier and later *Homo* (e.g., *Homo heidelbergensis,* EUP, LUP & Holocene *Homo sapiens*) in their relatively greater M-L and A-P diaphyseal proportions (see Figs. 204, 205 & 207).

7.6.2.3 Scaling to femoral head diameter

Correlation coefficients of the proximal femoral diaphyseal parameters with femoral head diameter [FHD] in the recent human "macro-sample" are of a greater magnitude than corresponding coefficients of the femoral midshaft variables (see table 165). Standardised residuals for the fossil specimens are given in tables 166 & 167. In all cases the coefficients are highly significant (p=<*0.001*). The diaphyseal proportions of the femoral midshaft in the two *Australopithecus* specimens (AL 288-1 and Stw 99) differ notably from a majority of recent human femora by virtue of their increased cross-sectional elliptical area and their relatively greater antero-posterior proportions (Figs. 208-212). While relative cross-sectional elliptical area in the australopithecine femora is not unique, and is approached by some African Pygmy and Southeast Asian Negrito specimens, the reduced A-P diaphyseal depth of these specimens is quantitatively distinct from recent *Homo*. Standardised residuals of the Hadar and Sterkfontein hominids contrast with the morphological profiles of Lower Pleistocene specimens from Lake Turkana, particularly KNM-WT 15000 (see Fig.

211). Differences between these two samples are as great as contrasts between the "early *Homo*" specimens and the problematic Trinil 1 femur (Day, 1976, 1984, 1986*b*; Day & Molleson, 1973).

Relative to femoral head size, the proportions of the femoral midshaft diaphysis of the Eurasian Neandertal specimens contrast with Levantine Early Upper Palaeolithic femora from Skhul and Qafzeh in their relative cross-sectional elliptical area and relative medio-lateral proportions (Figs. 209, 210 & 212). While Neandertal femora do differ morphologically from European LUP and Holocene specimens, they cannot be distinguished from many European EUP specimens. Standardised residual plots reveal that the greatest contrasts in femoral midshaft diaphyseal morphology are between Neandertals and the Skhul/Qafzeh hominids (e.g., Trinkaus & Ruff, 1999*a*; Trinkaus *et al.*, 1998*a,b*), not with the European EUP specimens (see Fig. 212). As in previous analyses, distinct differences in femoral midshaft diaphyseal morphology exist between European EUP and LUP femora. The EUP femora, like the Eurasian Neandertal's, possess considerably more "robust" femoral midshaft diaphyseal proportions than the Skhul/Qafzeh or later Pleistocene samples.

The relative proportions of the australopithecine proximal femoral diaphysis differ quantitatively from that of recent *Homo*, but not from other Pleistocene samples (see Figs. 213-217). The australopithecine proximal femur is considerably more 'robust' than in recent *Homo* when relative cross-sectional elliptical area is expressed as a proportion of absolute femoral head size, however, relative M-L and A-P proportions of the diaphysis are strikingly slender. The proximal femoral morphology of *Australopithecus* is discernibly different from "early *Homo*" (see Fig. 216). In contrast to the interpretation favoured by Ruff and his associates (Ruff, Thackeray & McHenry, 1999), it is likely that these morphological differences reflect meaningful increases in diaphyseal proportions relative to femoral head size and are not merely simple allometric consequences of absolute differences in femoral head size (see Figs. 213-216).

With respect to later Pleistocene *Homo*, differences between Eurasian Neandertals and Upper Pleistocene *Homo sapiens* specimens are less equivocal for STArea and STML, than for STAP (see Figs. 213, 214 & 215). While there exist clear morphological distinctions between Neandertal femora and Qafzeh 9 with respect to sub-trochanteric femoral proportions (see also Fig. 217), these distinctions are less apparent when comparisons with Skhul IV are made. Morphological contrasts between the Neandertal's and European Early Upper Palaeolithic femora are less manifest than those with LUP specimens. However, clear differences exist in the relatively greater A-P diaphyseal proportions of the Neandertal femora relative to the EUP femora. Marked differences exist in proximal femoral diaphyseal morphology of Early and Late Upper Palaeolithic specimens (Fig. 217). LUP femora are uniformly less "robust" relative to femoral head diameter than their geological predecessors, and overall diaphyseal shape differences (M-L versus A-P) are more uniform.

7.6.3 Morphological and functional variation in the fossil hominid pelvis: Bivariate Perspectives

7.6.3.1 Principal determinants of pelvic form in the fossil hominid pelvis

Least Squares Regression (LSR) models for the regression of the Principal Determinants of Pelvic Form in the recent human "macro-sample" are detailed in table 168. Unless specifically stated, medio-lateral pelvic breadth (Bi-cristal Breadth) was used as the independent parameter in all comparisons. With respect to the proportions of the ilium, iliac height and iliac breadth (see Appendix I) are positively and significantly correlated ($p=<0.001$) with Bi-cristal breadth and with each other (see Figs. 218, 220 & 222). Standardised residuals and percentage prediction error's (IPPE's) of the individual fossil specimens from the recent human regression line are presented in table 169, and are illustrated in figures 219, 221 & 223.

Relative to medio-lateral pelvic breadth, the height and breadth of the ilium in the AL 288-1 (*Australopithecus afarensis* ["Lucy"]) pelvis are discernibly smaller than in recent and fossil *Homo*. Nevertheless, several fossil *Homo* pelvic specimens approach the morphology observed in AL 288-1 with respect to individual dimensions (e.g., Skhul IV [Ilium Ht.] & Kebara II [Ilium Br.]). While there are notable differences in the A-P proportions of the ilium relative to ilium height in *Australopithecus* relative to *Homo erectus* and *Homo heidelbergensis* (*H. rhodesiensis*) specimens, the relatively short A-P ilium of the AL 288-1 pelvis is not especially different from many European EUP specimens (Figs. 221 & 222).

Not surprisingly, the relative size of the acetabulum in the AL 288-1 pelvis is substantially smaller than in recent and fossil *Homo* relative to both bi-cristal diameter and Ilium area (Ilium Ht. x Ilium Br.). The LSR slopes, intercepts and product-moment correlation coefficients for these relationships are highly significant in the recent human "macro-sample" (table 168; Figs. 224 & 226). While the relative size of the acetabulum in the Atapuerca hominid is smaller than in Kebara and most Upper Pleistocene specimens, the hip-joint proportions are approached by the San Teodoro 4 female (Fig. 225). While this observation generally supports previous observations in this Chapter (see above) concerning the relative size of the hip joint in the Atapuerca hominid, relative scaling of the hip joint to ilium area reveals substantial variation in the relative size of the acetabulum in fossil *Homo*. Taken together, the results of these comparisons reveal that, with the exception of AL 288-1, no fossil specimens display's acetabular proportions which cannot be accommodated within the normal range of variability in recent humans (Figs. 225, 227 & 228).

As noted previously in this Chapter, Inter-acetabular distance and the length of the superior pubic ramus are highly correlated with medio-lateral pelvic breadth in recent humans (table 168; Figs. 229 & 231). Relative to Bi-cristal breadth, the proportions of the pubic ramus and bi-acetabular breadth in the *Australopithecus afarensis* female pelvis (AL 288-1 ["Lucy"]) are not unusual (Figs. 230 & 232), however, notable contrasts exist in the relative scaling of the anterior pelvic proportions in some later Pleistocene hominids. The Kebara Neandertal displays an inordinately wide inter-acetabular distance and elongate superior pubic ramus relative to *Australopithecus*, *Homo heidelbergensis* (AT-1) and the Levantine Upper Pleistocene specimen from Skhul (Skhul IV). This morphology cannot be explained by this specimen's relatively wide false pelvis, as comparisons with the EUP specimen from Grotte des Enfants 4 attest (Figs. 229 & 231; 230 & 232). Relative pubic ramus length of the Atapuerca hominid contrast's markedly with the "typical" Neandertal condition seen in the Kebara Neandertal pelvis.

Nevertheless, some interesting light on this issue emerges from consideration of the anterior pelvic proportions of the two European LUP hominids. Relative to bi-cristal diameter, the length of the superior pubic ramus in the Barma Grande 1 pelvis is actually greater than that observed in the Kebara Neandertal (Fig. 231), but relative inter-acetabular distance does not approximate that seen in the Neandertal specimen (Fig. 229). In contrast, the LUP male pelvis from Parabita displays a remarkably reduced inter-acetabular distance expressed as a proportion of Bi-cristal diameter relative to the Atapuerca AT-1 and Skhul IV specimens (Fig. 230), yet relative pubic ramus length is roughly approximate (Fig. 232). All these individuals are considered to be males, thus gender distinctions cannot account for the observed morphological distinctions in anterior-pelvic morphology. Thus, while the results of this analysis support the view that IAD and pubic ramus length are largely 'dependent' functions of M-L pelvic breadth in recent humans, there is clearly some other factor controlling the relative 'independence' of these parameters in Late Pleistocene fossil hominids.

Similarly, as noted in an earlier section of this Chapter, the correlation coefficient for antero-posterior pelvic diameter (see Appendix I) on M-L pelvic breadth are highly significant in recent *Homo* ($p=<0.001$), but this is of a reduced magnitude relative to previous dimensions. With respect to the fossil specimens, the A-P pelvic breadth in the AL 288-1 *Australopithecus afarensis* specimen is notably reduced relative to recent *Homo*, but not necessarily to fossil *Homo* (Fig. 233). Measurements from a scaled photograph of the Middle Pleistocene pelvis from Atapuerca, AT-1 (Arsuaga *et al.*, 1999) reveal that relative to M-L pelvic breadth, A-P pelvic diameter in this specimen is considerably reduced relative to both Kebara and the Early Upper Pleistocene *Homo sapiens* from Skhul IV (Figs. 233 & 234). Relative to Bi-cristal breadth, the A-P diameter of the AL 288-1 and AT-1 pelvis fall almost beyond the range of variability in the recent human "macro-sample" (Fig. 234). The A-P pelvic diameter of the Kebara Neandertal and all remaining fossil specimens, including the Parabita 1 LUP male, fall within the range of variation in recent *Homo*.

Interestingly, when the length of the superior pubic ramus is expressed as a proportion of A-P, rather than M-L, pelvic diameter, the EUP Grotte des Enfants 4 male displays a longer pubis than the Kebara Neandertal (Fig. 235). Only these specimens lie beyond the range of variability in recent *Homo*, and the LSR slope and intercept and correlation coefficient for the recent human "macro-sample" are highly significant ($p=<0.001$). The coefficient for pubis length on A-P pelvic breadth is of a higher order than that of A-P pelvic breadth on M-L pelvic breadth, and variation in Later Pleistocene hominids is considerably greater than that observed when either parameter (Pubis Length and A-P pelvic Breadth) are scaled to bi-cristal breadth. More crucially, standardised residuals for the AL 288-1, AT-1 and Kebara specimens (Fig. 236) suggests that they lie on a morphological continuum of increasing pubic ramus length with committal increases in A-P pelvic diameter (see Fig. 235).

Not surprisingly, the M-L breadth of the sacrum is highly correlated with bi-cristal breadth in the recent human "macro sample" (table 168; Fig. 237). Relative sacrum breadth in AL 288-1 and AT-1 is clearly reduced relative to that seen in recent *Homo* (Fig. 238). Nevertheless, several Upper Palaeolithic fossil specimens approach these individuals in their sacral proportions (Dolni Vestonice 15 and Arene Candide II). In contrast, Parabita II and San Teodoro 1 (both females) have relatively broad sacra compared to their Late Pleistocene male contemporaries (Figs. 237 & 238). The overall trend in Upper Pleistocene fossil specimens, including the Kebara Neandertal, is for the sacrum to be relatively narrower in proportion to overall M-L hip breadth than in it is recent humans.

7.6.3.2 Functional variation in the fossil hominid pelvis

LSR regression solutions were calculated on the recent human "macro-sample" in order to assess potential differences in the relative scaling of 'functional' parameters in the locomotor system of suitably preserved fossil hominids (see table 170). Standardised residuals and percentage prediction errors are detailed in table 171. In contrast to the results obtained in a previous section of this Chapter (Section 7.3) using individual sample parameters, a highly significant relationship exists between calculated values for the Abductor Force (see Chapter 3; Appendix III) and M-L pelvic breadth in the recent human "macro-sample" (table 170; Fig. 239). Of the fossil specimens included in this analysis, only AL 288-1 displays an inordinately low Abductor Force value relative to bi-cristal diameter (Fig. 240), although this specimen is approached by the negative standard deviation of the LUP male from Parabita (Parabita 1).

However, when calculated Abductor Force values are expressed as a proportion of Body Weight (Fig. 241), those for the AL 288-1 *Australopithecus afarensis* female falls within the range of variability in recent *Homo* and is not remarkable (Fig. 242). Similarly, the extreme negative departure of the calculated value of the Joint Reaction Force in the AL 288-1 pelvis relative to M-L pelvic breadth (Fig. 243) is likely to be a primary function of the independent (i.e., bi-cristal breadth) rather than the dependent variable (e.g., compare Figs. 240 & 244). This proposal is substantiated by an unpublished observation that relative to body mass, M-L pelvic breadth in the AL 288-1 falls 3 SD above the African Apes and is inordinately wide for an African hominoid of her "geometric size" (Gallagher, *Unpublished Observation*).

Not surprisingly, the relative length of the lever arm for the abductor muscles (BFN or *Dm* [see Appendix 1]) is highly correlated with the body mass load arm [*Dw*] in the recent human macro-sample (Table 168; Fig. 245). With respect to the anterior pelvic proportions of the AL 288-1 *Australopithecus afarensis* female, the results of this analysis confirm the overwhelming consensus view that the *Dw*/*Dm* index of this specimen are extremely different from the morphology observed in Pleistocene *Homo* (Fig. 246). This observation further confirms the earlier findings of this analysis that inter-acetabular distance (and *Dw*) are not disproportionately great in the AL 288-1 pelvis, but that biomechanical femoral neck length [*Dm*] is proportionally shorter than in Pleistocene *Homo* (e.g., Lovejoy, 1988; Jungers, 1991; Ruff, 1995, 1998). Nevertheless, there exist some individual recent human specimens with *Dw*/*Dm* proportions that are even more extreme than that seen in AL 288-1 (Fig. 245).

In contrast to the observations in an earlier section of this Chapter (Section 7.6.1), the anterior pelvic proportions of the Middle Pleistocene hominid from Atapuerca contrast notably from those of recent humans. When relative biomechanical femoral neck length [*Dm*] is expressed as a proportion of the body mass load arm [*Dw*], this individual lie's almost 2.5 SD units from the LS regression line (Fig. 246). Nonetheless, the anterior pelvic proportions of this hominid approximate those of several European Upper Palaeolithic specimens (Dolni Vestonice 13, 14, 15, Parabita 1). These individuals display a relatively greater biomechanical femoral neck length [BFN] relative to the body mass load arm [*Dw*]. However, relative BFN length in the Atapuerca hominid contrast markedly with those observed in the Levantine Early Upper Pleistocene male from Skhul (Skhul IV) and the La Ferrassie 1 Neandertal (Figs. 245 & 246). This finding furnishes unequivocal support for Trinkaus' (Trinkaus, 1983*a*) contention that the relatively long pubic ramus and wide inter-acetabular distance in Eurasian Neandertals occurred without a concomitant elongation of the femoral neck. This morphological configuration differs quantitatively and qualitatively from that hypothesised in *Homo erectus* (Ruff, 1995).

The correlation coefficient for femoral head diameter relative to the body weight load arm/lever arm proportions [*Dw*/*Dm*] in the recent human "macro-sample" is not significant at $\alpha = 0.05$ (table 170). Nevertheless, as with previous results of this Chapter, femoral head diameter decreases with increasing proportions of the body weight load arm (see Fig. 247). Considerable variability exists within the "macro-sample", some of which may reflect sexual dimorphism in both parameters. Nevertheless, there is little doubt that AL 288-1 ("Lucy") displays a disproportionately small proximal femoral epiphysis when expressed as a function of her anterior pelvic proportions (Fig. 248). Interestingly, when femoral head diameter in the Atapuerca AT-1 individual is scaled relative to it's anterior pelvic proportions the results contrast with previous observations in an earlier section of this Chapter (Section 7.6.1), which used Lovejoy and colleagues' (Lovejoy, Heiple & Burstein, 1973) index of "relative pressure". Relative femoral head diameter in the Atapuerca individual is not excessively small when compared with the Levantine "early modern" from Skhul IV and with Eurasian Later Pleistocene *Homo sapiens* specimens (Fig. 248). When expressed as a proportion of the body weight load arm/abductor force lever arm [*Dw*/*Dm*] ratio, relative femoral head size in this putative Neandertal ancestor is considerably smaller than in the La Ferrassie 1 Neandertal.

Nevertheless, a more appropriate allometric scaling approach to the relative size of the femoral head would be to directly assess deviations of individual specimens from an LSR function expressing femoral head diameter as a proportion of estimated body weight (Fig. 249). The correlation coefficient for the LS regression model in the recent human "macro-sample" is highly significant (Table 170). Relative to body weight, femoral head diameter in the AL 288-1 *Australopithecus afarensis* female lie's nearly 3 SD units below the predicted value generated by the LSR model (Fig. 250). Nevertheless, the negative deviation of AL 288-1 is exceeded by the Middle Pleistocene hominid from Atapuerca (calculated using an LSR function of FHD on acetabular diameter [Arsuaga *et al.*, 1999]). Relative to the lowest predicted body mass for this individual (93.1 kg [Arsuaga *et al.*, 1999; see Appendix III), femoral head diameter is smaller than in AL 288-1! This confirms the previous observation using used Lovejoy and colleagues' (Lovejoy, Heiple & Burstein, 1973) index of "relative pressure" (Section 7.6.1). There is no question that the Middle

Pleistocene *Homo* species sampled at Atapuerca were adapted to "habitual terrestrial bipedalism". This finding casts considerable doubt on a prevailing view (e.g., Stern & Susman, 1983; Susman *et al.*, 1984, 1985; Jungers, 1988, 1990, 1991; Ruff, 1998) that a relatively small femoral head in AL 288-1 is a *bona fide* indicator of an 'incomplete' adaptation to terrestrial bipedalism in *Australopithecus*.

Despite the general uniformity in relative femoral head size in Upper Pleistocene hominids, several specimens display unusually large or disproportionately small proximal femoral epiphyses. Relative to body weight, femoral head diameter in the LUP Barma Grande 1 and Arene Candide II hominids are extremely large, and exceed the relatively modest proximal femoral epiphysis (estimated) for the Kebara II Neandertal. In contrast, the relative size of the femoral head in the Levantine Skhul IV and the European EUP specimens from Predmosti and Grotte des Enfants (Predmosti 3 & Grotte des Enfants 4) are proportionally small.

7.6.4 Multivariate Perspectives

A Principal Components Analysis (PCA) was performed on the covariance matrix of the six raw "principal determinants of pelvic form" for the sex-specific sample means of the recent and fossil hominid groups. Three Principal Components were extracted, the first of which accounted for 79.62% of the total variance (table 172). The remaining two Components accounted for 14% and 4.37%, respectively, cumulating in a total percentage of explained variance of roughly 98%. In the re-scaled matrix, all variable loadings on the first PC are high and positive, whereas the second component is bi-polar (table 173). Non-parametric correlation coefficients of the raw variables on the PC1 scores are universally positive and are highly significant (*p=<0.001*), indicating that the first PC samples multivariate general size (e.g., Shea, 1985). Bi-acetabular diameter and the length of the superior pubic ramus are positive, whereas the height and breadth dimensions of the ilium and the antero-posterior diameter of the pelvis are negatively loaded on the second PC. Variable loadings on the third PC contrast bi-iliac diameter and ilium height (positive) with A-P pelvic breadth (negative).

A bivariate scatterplot of the component scores for PC1 and PC2 is shown in figure 251. With the sole exception of the Late Upper Palaeolithic male sample, *Homo sapiens* specimens all cluster around zero on the second component axis. In marked contrast, AL 288-1 and the Neandertal pelves score positively on PC2. The underlying morphological pattern of the two specimens is quite distinct. While both specimens are medio-laterally wide across the iliac tubercles and share a relatively wider inter-acetabular distance in proportion to the A-P pelvic plane, the AL 288-1 pelvis has an absolutely and relatively short A-P pelvic plane. In contrast, the Neandertal pelvis is roughly equivalent in its A-P/M-L pelvic proportions but does possess a relatively longer superior pubic ramus. In contrast to Neandertals and recent *Homo*, LUP males possess a relatively wide A-P pelvic breadth with no committal increase in inter-acetabular distance or pubic ramus length.

These specimens can be effectively distinguished by their locations on the third Component Axis. Positive loadings of bi-iliac diameter and iliac height and negative loading of the A-P pelvic diameter all contribute to the position of the AL 288-1 pelvis and its deviation from the Neandertal specimen. Interesting contrasts emerge from considerations of the locations of the EUP and LUP composite specimens on PC3 (see Figs. 252 & 253). A-P pelvic diameter, which loads negatively on PC3, is relatively greater in the LUP samples when expressed as a proportion of bi-cristal diameter (not shown). Both bi-iliac diameter and ilium height load positively on PC3. However, while differences in relative A-P pelvic breadth may account for the proximity of the LUP females to the Neandertals, this cannot account for the high PC scores of the LUP males on PC3, nor their proximity to the EUP males.

7.5 Summary

The aims of this chapter were to critically assess the three hypotheses relating to functional morphological integration in the hominid pelvis outlined in Chapter 2. Results of this analysis equivocally support the expectations of the fourth fypothesis. The "principal determinants of pelvic form" scale allometrically with increasing medio-lateral pelvic breadth in recent humans, although some interesting within-sample allometric phenomena are revealed. The length of the superior pubic ramus is strongly correlated with both the medio-lateral and antero-posterior pelvic planes in recent *Homo*. Anterior pelvic load arm/lever arm proportions [*Dw/Dm*] proportions can be shown to be sexually dimorphic in the African apes and recent humans and decreasing relative lever arm proportions is concomitant with a decrease in absolute and relative femoral head size.

As a general rule, results of analyses presented here furnish only limited support for, or contradict, expectations of fifth hypothesis. Larger-bodied recent human samples do display proportionally wider medio-lateral and reduced antero-posteriorly less broad midshaft and proximal femoral diaphyses than do smaller-bodied humans, supporting a size-dependent component to observed morphological variability in diaphyseal shape. Nevertheless, femoral midshaft and subtrochanteric diaphyseal areas are only moderately, and negatively correlated with increasing body mass load arm/lever arm [*Dw/Dm*] proportions in recent humans. Correlation coefficients for relative M-L and A-P indices of the femoral midshaft and subtrochanteric diaphyses with anterior pelvic proportions are generally not consistent with the expectations outlined in the fifth hypothesis, but do suggest that a moderate increase in M-L and A-P diaphyseal "robusticity" is a direct consequence of increasing proportions of the body mass load arm in *Homo*.

The results of this study provide only limited support for the sixth hypothesis that anterior hip proportions contribute significantly to observed variance in femoral midshaft and subtrochanteric diaphyseal proportions in fossil hominids. When M-L and A-P diameters of the femoral midshaft and subtrochanteric diaphysis are scaled to elliptical area and biomechanical femoral neck [*Dm*], no apparent distinctions between *Australopithecus* and "early *Homo*" femora emerge. The results of this study suggest that while considerable variability in australopithecine subtrochanteric diaphyseal morphology (relative to *Dm*) exists, M-L diaphyseal proportions of the proximal femur are not consistently different from "early *Homo*". Only KNM-WT 15000 (*Homo erectus*) displays a significant departure from australopithecine femoral morphology, probably a reflection of its subadult status. The results of this analysis support the view that differences in midshaft and proximal femoral diaphyseal proportions of Eurasian Neandertals and Upper Palaeolithic *Homo sapiens* probably reflect allometric, rather than habitual activity-related phenomena.

The wide interacetabular distance of the *Australopithecus* pelvis (AL 288-1 & Sts 14) is a demonstrable consequence of the relatively wider medio-lateral flare of the ilium, whereas in the Kebara Neandertal, IAD is both absolutely and relatively wider than in more recent humans. Allometric appraisal of the recently recovered Middle Pleistocene pelvis from Atapuerca (AT-1) reveals that the wide IAD and elongated superior pubic ramus is a probable Neandertal autapomorphy. The proposal that this morphology is meaningfully related to an overall enlargement of the M-L and A-P pelvic planes in Neandertals is plausible, although the A-P pelvic diameter in the Kebara Neandertal is not extreme. Relative femoral head size in AL 288-1, while smaller than in recent humans, appears to be a direct consequence of her relatively small body size and proportionally great load arm/lever arm proportions. Surprisingly, when considered relative to estimated body mass, femoral head size in the Atapuerca hominid is smaller than in *Australopithecus afarensis*.

Chapter 8. Discussion

8.1 Relative proportions of the epiphyses and diaphyses

Results of the univariate, bivariate and multivariate (PCA, CVA) statistical analyses reveal that the African apes possess a consistent "suite" of features relating to the relative size of the elbow joint complex (distal humerus, proximal radius), and distal radial epiphysis [DRB] that are proportionally greater compared to *Homo*. This "complex" of features is considered here as derived for the African hominids. Consensus cladograms derived from molecular and soft-tissue analyses of African hominoid systematics suggest that these features should be regarded as homoplasic, rather than synapomorphic (e.g., Ruvolo, 1997; Cela-Conde, 2001; Goodman *et al.*, 2001; Groves, 2001; Watson *et al.*, 2001; Wood and Richmond, 2000; Gibbs, 1999; Gibbs *et al.*, 2000).

The results of this study are entirely consistent with the empirical expectations of the first hypothesis of this thesis and overwhelmingly support the results of previous investigations using different standardisation procedures (Jungers, 1988*a*, 1990). Not surprisingly, comparisons of developmentally labile (e.g., Ruff, 2002, Ruff *et al.*, 1991, 1994; Trinkaus *et al.*, 1994; Martin, Burr & Sharkey, 1998; Lieberman *et al.*, 2001), upper limb skeletal tissue also confirms the proportionally greater degree of diaphyseal "robusticity" relative to *GM*ALL in the African hominoids relative to recent *Homo*. The sole inconsistency in the upper limb comparisons of the African apes and recent *Homo* concerns the relative epiphyseal and diaphyseal proportions of the ulna, which are considered here to be of reduced functional valence. This does not presuppose that there exists no "functional information content" in the proximal ulna of *Pan*, *Gorilla* and *Homo* (see below).

Interestingly, at an overall level, observed "patterns" of relative scaling in the upper and lower limb of the extant African hominoids (including within *Homo*) are consistent when both proportional ratios and bivariate regression methods are employed. This suggests that when correlations between the dependent and independent variables are strong, and sample sizes are sufficiently good, either approach can be utilised. This would 'expand' the available statistical procedures available to researchers wishing to explore allometric distinctions at lower level taxonomic and evolutionary contexts. The Geometric Mean approach favoured here (see also Reno *et al*., 2000) is a valid proxy for absolute body size.

Significant scaling differences in the upper limb of the African apes were detected. Relative to *Gorilla*, *Pan paniscus* and *Pan troglodytes* display proportionally greater proximal and distal radial epiphyses and midshaft circumferences. *Pan paniscus* displays a proportionally smaller midshaft circumference and a proportionally greater distal articular breadth of the radius than *Pan troglodytes*. All three radial dimensions and radius length are positively and significantly correlated with *GM*ALL. Without exception, *Gorilla* displays proportionally smaller radial dimensions than *Pan* relative to geometric size. RMA post-hoc significance tests confirm that the dorso-ventral breadth of the articular surface and diaphyseal proportions of the ulna is relatively greater (to *GM*ALL) in *Pan* than in *Gorilla*. There is convincing evidence that the epiphyseal and diaphyseal dimensions of the forelimb elements in *Gorilla* are consistently smaller than in *Pan*.

These findings contradict expectations of the "structural compensatory" hypothesis, under which *Gorilla* should display increasing proportional epiphyseal and diaphyseal "robusticity" in their upper limb distal segments.

A contrasting picture emerges for the relative dimensions of the humerus in both *Pan* and *Gorilla*. Correlation coefficients for the raw dimensions of the humeral epiphyseal and diaphyseal dimensions in the African ape samples are strong, positive and highly significant ($p=<0.001$), suggesting that comparisons of proportional indices and RMA regression models should yield equivalent results. Pairwise comparisons of proportional indices indicate that the distal humeral epiphysis is proportionally greater in *Gorilla* than in both species of *Pan*, whereas humeral midshaft circumference is proportionally smaller relative to *Pan troglodytes* alone. When post-hoc elevation tests of the species-specific RMA solutions are considered, only bi-epicondylar diameter emerges as being significantly greater in *Gorilla* than in *Pan*.

As terrestrial pronograde knuckle-walkers (Napier & Walker, 1967*a*,*b*; Napier & Napier, 1967; Jenkins & Fleagle, 1975; Susman, 1984*b*; Fleagle, 1988, 1998), both *Pan* and *Gorilla* habitually load their hindlimbs during locomotor activities (Kimura *et al*., 1979). Indeed, Kimura and his colleagues (Kimura *et al*., 1979), propose that the levels of force imposed on the hindlimbs are substantially greater than those imposed on the forelimbs in all Anthropoid Primates (see also Steudel, 1980*b*; Preuschoft, 1989). It is thus likely that the femoral midshaft of *Pan* and *Gorilla* is subjected to bending moments at least of an approximate magnitude to those observed in *Homo* (e.g., Koch, 1917; Preuschoft, 1971; Pauwels, 1980). Considerable variability exists in the relative scaling of the lower limb dimensions in *Pan* and *Gorilla*. While the relative proportions of the femoral midshaft are relatively homogenous in the African apes, the relative size of the proximal and distal femoral epiphyses reveal consistent contrasts. Both *Pan paniscus* and *Gorilla* display proportionally greater femoral head and femoral bicondylar breadth dimensions than *Pan troglodytes*, although significant differences in *Pan* are restricted to comparisons of relative FBB alone (p=<0.05).

Significant differences within the African apes were also detected for the relative epiphyseal and diaphyseal proportions of the tibia. Comparisons with *Pan paniscus* and *Pan troglodytes* reveal that the *Gorilla* tibia displays a proportionally greater distal articular area and a proportionally smaller midshaft circumference relative to geometric size (p=<0.001). With respect to the relative size of the proximal tibial epiphysis [PTB], male and female *Gorilla* tibiae possess proportionally greater PTB/*GM*ALL indices than *Pan troglodytes*, but comparisons with *Pan paniscus* reached significance in the males alone. More importantly, relative DTP indices are apparently positively allometric with increasing geometric size in the African hominoids, although differences between the two species of *Pan* were not significant.

Pan paniscus differs from *Pan troglodytes* in the relative size of the proximal tibial epiphysis (males only) and the tibial midshaft circumference (both sexes). Interestingly, while the relative proportions of the proximal tibial epiphysis are uniformly greater in *Pan paniscus*, the relative size of the tibial midshaft in the two species of *Pan* displays a contrasting pattern that is gender specific. Whereas *Pan* *paniscus* males display relatively greater TMC/*GM*ALL indices than *Pan troglodytes*, tibial diaphyseal proportions in *Pan paniscus* females are relatively smaller. Observations on the relative size of the tibial midshaft in the African apes contradicts prior expectations of the "structural compensatory" model, where relative TMC in *Gorilla* is predicted to be proportionally greater than in *Pan troglodytes* and *Pan paniscus*. The relatively greater proportions of the proximal and distal articular dimensions of *Gorilla* do confirm the expectations of the structural compensatory hypothesis and presumably reflect functional adaptations to increased magnitudes of compressive stress with increasing *GM*ALL in the African hominids, particularly the talo-crural joint.

The results of this analysis strongly contradict the expectations of the second hypothesis. There is no evidence to support the proposal that the relative proportions of the upper and lower limb epiphyses would display reduced levels of inter-sample variance compared with measures of diaphyseal "robusticity". No support emerges for the hypothesis that lower limb diaphyseal proportions display reduced levels of inter-sample variance compared with those of the upper limb. Significant differences were detected in pairwise comparisons of the relative size of the proximal and distal humeral epiphyses and also the proximal radial epiphyses in recent humans. Patterns of variability in the relative scaling of the humeral epiphyses are of a greater magnitude than in the radius, where only African Pygmies were found to display significantly smaller proximal radial epiphyses than remaining samples. There is limited support for an underlying allometric basis for the observed variance in the relative scaling of the upper limb epiphyses and diaphyses in recent *Homo*, but scaling patterns in the femoral and tibial epiphyses and diaphyses are less consistent with an allometric scaling model.

With respect to the upper limb variables, Australian Aborigines display relatively smaller proximal and distal humeral epiphyses and diaphyseal midshaft circumferences. This supports the previous observations of Collier (Collier, 1989) and Pearson (Pearson, 1997, 2000) who concluded that Australian Aborigines have relatively "gracile" humeral epiphyses and diaphyses proportional to humeral length. Comparisons of the relative size of the radial midshaft circumference reveal that Australian Aborigines display proportionally more "gracile" radial and ulna midshafts than do Magyar and Native American samples. The observation that Native Americans display disproportionately low, and Southeast Asian Negritos unusually elevated, radial midshaft dimensions is consistent with proposals that 'structural' and 'mechanical' factors are not exclusive governing constraints upon patterns of skeletal robusticity in the upper limb of recent *Homo* (e.g., Collier, 1989, 1993; Pearson, 1997, 1999). Following Ruff and his associates (Ruff, 1998, 2000; Ruff *et al.*, 1993, 1994; Trinkaus & Ruff, 1999*a*,*b*, 2000; Trinkaus & Churchill, 1999), who have proposed that relative scaling comparisons of skeletal tissue (i.e. joints and diaphyseal parameters) must include some measure of beam length and total load (body mass), it would be profitable to reassess patterns of epiphyseal and diaphyseal scaling in recent humans using a "relative body size" proxy as the independent parameter (Gallagher, *in prep.*).

A "mosaic" pattern of scaling differences emerges in relative epiphyseal and diaphyseal proportions of the lower limb in recent *Homo*. Emerging patterns of differential epiphyseal and diaphyseal "robusticity" in the femur and the tibia are distinct, even across contiguous functional and developmental "modules" ([e.g., the knee-joint] Lovejoy *et al.*, 1999, 2000, 2002). Significant differences in the scaling of the proximal and distal femoral epiphyses are consistent with an underlying allometric explanation in recent *Homo*. Low-latitude Australian Aborigines and African Bantu do display relatively small proximal and distal femoral epiphyses relative to high-latitude Medieval Hungarians and Libben Amerindians, whom they closely approximate in geometric size. Indeed, Australian Aborigines display a proportionally smaller proximal femoral epiphysis compared to all remaining samples (e.g., Collier, 1989; Pearson, 1997, 2000). Significant differences in the relative size of the distal femoral epiphysis in Australian and Bantu samples compared to the diminutive African Pygmies probably reflect the influence of relative, rather than absolute, body size. However, the proportionally larger distal femoral epiphyses of Native Americans relative to the Magyars suggest that factors other than structural equivalence are involved in the differential patterns of skeletal robusticity in recent *Homo*.

A contrasting picture emerges for relative epiphyseal and diaphyseal proportions in the tibia. Australian Aborigines display relatively greater proximal epiphyseal and midshaft proportions than do the Magyars. This is not consistent with previous observations for the distal femoral epiphysis, which is presumably governed by proximate epigenetic and mechanical stimuli (e.g., Lovejoy *et al.*, 1999, 2000). The observation that the Native American samples generally display proportionally greater proximal tibial epiphyses than is typical in remaining human samples is consistent with previous observations of relative scaling of the distal femoral epiphysis. As a general rule, patterns of relative epiphyseal and diaphyseal size distributions in the tibia of recent humans suggest only limited adherance to an underlying structural allometric component. This is consistent with previous studies which suggest that patterns of relative robusticity in recent and fossil hominids are more apparent in the tibia than in the femur and likely reflect a greater degree of stress-induced osteonal modelling during growth and development, and remodelling during life (Lovejoy *et al.*, 1976; Lovejoy & Trinkaus, 1980; Trinkaus & Ruff, 1999*b*;; Lieberman & Pearson, 2001; Ward *et al.*, 2003; but see Pearson, 1997).

Statistical comparison of relative epiphyseal and diaphyseal "profiles" in extant and extinct African hominoids unequivocally supports expectations of the third hypothesis that the locomotor affinities of *Australopithecus afarensis* (AL 288-1 ["Lucy"]) lie with the obligate bipedal hominids rather than with the extant African apes. The upper limb epiphyses of AL 288-1 are relatively small, although relative size of the distal humeral epiphysis is apparently "proportionally equivalent" (i.e., Isometric) for an African hominoid of her diminutive geometric size. If AL 288-1 is typical of her species, then *Australopithecus afarensis* contrasts with *Pan* and *Gorilla* who display proportionally greater distal humeral, proximal radial and distal radial epiphyses (e.g., Jungers, 1988*a*, 1990; Gallagher, *this study*). I have argued earlier that this suite of morphological distinctions should be considered functionally "derived" features for the extant African apes.

Relatively larger distal humeral and proximal radial epiphyses in *Pan* and *Gorilla* presumably manifest osteological modifications that maintain the structural integrity of the elbow joint when subjected to tensile and compressive forces during suspensory postures and weight transmission in normal terrestrial gait (Susman, 1984*b*; Fleagle, 1988, 1998). The proportionally greater distal radial epiphysis in *Pan* and *Gorilla* manifests one among many of the morphological adaptations to terrestrial pronograde knuckle walking in extant African hominoids (e.g., Tuttle, 1967, 1969*a*,*b*, 1975; Tuttle & Basmajian, 1974; Tuttle *et al.*, 1972; Jenkins & Fleagle, 1975; Jungers, 1988*a*, 1990; Richmond & Strait, 2000, 2001*a*,*b*,*c*; Richmond *et al.*, 2001; Kelly, 2001).

The absence of proportionally enlarged distal humeral and proximal radial epiphysis in *Australopithecus afarensis* raises interesting questions relating to the proposed continued reliance on arboreal substrates in this early hominid morph (e.g., Senut, 1981*a*,*b*,*c*; Senut & Tardieu, 1985; Stern, 2000; Stern & Susman, 1983; Susman *et al.*, 1984, 1985; Ward, 2002). Until the requisite data relating to force components and magnitudes acting at the elbow joint during suspensory postures in Asian and African hominoids are collected, the precise functional implications of the relatively enlarged distal humeral and proximal radial epiphyses in the African apes will remain speculative. The integration of the Asian hominoids (*Hylobates*, *Symphalangus* and *Pongo*) within the current comparative framework might qualify some aspects relating to this problem and suggest profitable avenues for future research.

The relatively enlarged distal radial epiphysis in *Pan* and *Gorilla* relative to that in *Australopithecus afarensis* and *Homo* is particularly enlightening with respect to the recent proposal that the last common ancestor of the Hominini was a terrestrial knuckle-walker (e.g., Richmond & Strait, 2000, 2001*a*,*b*,*c*; Richmond *et al.*, 2001; Kelly, 2001; see also Tuttle, 1967, 1969*a*,*b*, 1975). Richmond and Strait (Richmond

& Strait, 2000, 2001*a,b,c*; Richmond *et al.*, 2001), propose that the distal radial morphology of *Australopithecus anamensis* (KNM-ER 20419 [Heinrich *et al.*, 1993]) and *Australopithecus afarensis* (AL 288-1q,v [Johanson *et al.*, 1982]), display several morphological features (Richmond & Strait, 2000: 383-384; fig., 3), which are considered to be crucial determinants of stabilisation of the radio-carpal joint during extension in normal terrestrial knuckle-walking (e.g., Tuttle, 1967, 1969*a,b,c*, 1975; Tuttle & Basmajian, 1974; Tuttle *et al.*, 1972; Lewis, 1972, 1980, 1989; Jenkins & Fleagle, 1975; Richmond & Strait, 2000; Richmond *et al.*, 2001; Kelly, 2001).

The findings of this study are particularly relevant in light of the proposed contribution of "phyletic inertia" in the distal radius of early hominids (Dainton, 2001; Lovejoy, Heiple & Meindl, 2001; Richmond & Strait, 2001*a,b,c*). "Phylogenetic inertia remains the most plausible interpretation of the morphology we identified" (Richmond & Strait, 2001:326). The results of this study suggest that the distal radial epiphysis of *Australopithecus afarensis* had undergone significant morphological size reduction relative to the condition seen in *Pan* and *Gorilla*. The proposal that the interosseus membrane and annular ligament in the proximal and medial radio-ulnar articulation of *Homo* are morphological adaptations that are specifically related to terrestrial knuckle-walking (e.g., Kelly, 2001), is not consistent with comparative anatomical observations (Gibbs, 1999).

The relative size of the hindlimb epiphyses in AL 288-1 have been cited in conjunction with the functional implications derived from the orientation of the iliac blade as manifesting an incomplete adaptation to terrestrial bipedalism in *Australopithecus afarensis* (e.g., Stern & Susman, 1983; Susman *et al.*, 1984, 1985;

Jungers, 1988*a*). The results of this analysis confirm that relative to overall geometric size, the hindlimb epiphyses of AL 288-1 are distinctly hominid rather than hominoid. This is especially true of the components of the knee joint (Taieb *et al.*, 1976). Relative to geometric size, the femoral head of AL 288-1 is demonstrably "intermediate" between the African apes and recent humans.

8.2 Epiphyseal Geometry of the Distal Humerus and Proximal Ulna.

Morphological distinctions in the distal humerus and the proximal ulna of recent humans and the extant African apes revealed in this analysis are largely consistent with previous observations using multivariate analyses of linear metrics (e.g., Feldesman 1979, 1982; Lague & Jungers, 1996; Aiello *et al.*, 1999) and GPA of 2D landmark co-ordinates (Bacon, 2000; Mitteröcker & Gunz, 2002). The first PC of the distal humeral and proximal ulnar matrices reliably discriminates African apes, recent humans and extinct fossil hominids. With few exceptions, pairwise permutation comparisons of Procrustes chord differences of the distal humeral and proximal ulnar epiphyseal geometry are statistically significant in both *Homo* and the African apes.

The principal morphological distinctions between the African apes and recent *Homo* "explained" by PC1 and PC2 for the distal humerus and proximal ulna are summarised in table 174. Product-moment correlation coefficients reveal that the first Principal Component of the distal humerus is highly correlated with Centroid Size in the African apes, but not recent *Homo*. PC4 and PC6 also correlate significantly ($p=<0.001$) with Centroid Size in *Pan* and *Gorilla*. Morphological shape changes in the African ape distal humerus on this axis should be considered allometric (i.e., size change is correlated with a change in shape [Gould, 1966; see Chapter 1]). Further insights in to the nature of morphological shape change in the distal humerus of recent *Homo* on PC2 were accomplished by thin-plate spline ("TPS") "morphing". Morphological differences in recent humans are apparently the result of a ***uniform shape change*** manifesting an increase in the medio-lateral proportions of the distal humerus (medial epicondyle and capitulum) with a contiguous reduction in the supero-inferior (height of the capitulum and olecranon fossa) and antero-posterior proportions of the articular surface.

The sole significant shape change not explained by a medio-lateral increase in the distal humerus in recent *Homo* on PC1 is the increased anterior projection of the capitulum, although this is likely to be correlated with the increased medio-lateral proportions of the caput (i.e., an overall relative size increase) on PC2. A similar morphological generalisation characterises the shape changes in the distal humerus on PC4 in *Pan* and *Gorilla*. Increasing Centroid Size in the African ape distal humerus is correlated with an increase in height and breadth and a subsequent medial displacement of the olecranon fossa, medio-lateral expansion of the articular surface (especially the capitulum) and an increase in the medial projection and postero-superior deflection of the medial epicondyle.

Multivariate analysis (PCA, CVA) and thin-plate spline "morphing" of the distal humerus in the extant and extinct African hominoids reveals that *Australopithecus* can be distinguished from *Pan* and *Gorilla* by virtue of their medio-laterally expanded olecranon fossae, anteriorly displaced and moderately projecting medial epicondyles, and their medio-laterally expanded and increased anterior projection of the capitulum. Thin-plate spline "morphing" of the AL 322-1 (*Australopithecus afarensis*) specimen to various australopithecine distal humerii (including AL 288-1) is a valuable indicator of morphological shape variability within the genus. The AL 322-1 individual is morphologically "isolated" from the remaining australopithecine specimens on the second Principal Component, whereas KNM-ER 739 (*A. boisei*) falls at the extremes of the recent human range of variability in PC1 scores, but approximates the distribution of Eurasian Neandertals on this axis. The KNM-ER 739 distal humerus specimen does not differ from KNM-KP 271 (*Australopitheus anamensis*) or AL 288-1 (*Australopithecus afarensis*) in its position on the second Principal Component.

Relative to the KNM-KP 271 (*A. anamensis*) and AL 288-1 (*A. afarensis*) distal humerii, the AL 322-1 (*A. afarensis*) specimen displays a medio-lateral and antero-posterior reduction in overall proportions of the distal humeral epiphysis. In contradistinction to the views of Bacon (Bacon, 2000) and Wolpoff (Wolpoff, 1999), KNM-KP 271 does display a subtle anterior expansion of the capitulum, which is absent in AL 288-1. AL 288-1 (*A. afarensis*) displays a slight increase in the supero-inferior height of the capitulum and an increase in the relative projection and a distinct posterior deflection of the medial epicondyle relative to the AL 322-1 *Australopithecus afarensis* specimen. The latter "feature" is further developed in morphological shape comparisons with KNM-ER 739. Morphological shape comparisons of the AL 322-1 (*A. afarensis*) and the reputed "early *Homo*" distal humerus (KNM-ER 1504 [McHenry, 1994*b*; Bacon, 2000]) reveal a slight medio-lateral increase in the olecranon fossa and a discernible increase in the anterior projection of the capitulum.

Previously proposed morphological distinctions in the distal humerus of later Pleistocene (e.g., Middle-Upper Pleistocene) *Homo* specimens are neither as marked nor consistent as has been previously proposed (e.g., Trinkaus, 1983*a*; Churchill. 1994; Churchill & Smith, 2000; Yokley & Churchill, 2002). The Eurasian Neandertal specimens tend to cluster at, or beyond, the extreme range of recent humans on PC1, whereas the Middle Pleistocene *Homo heidelbergensis*/*Homo rhodesiensis* distal humerus from Kabwe, Zambia and the Early Upper Pleistocene specimen from Omo-Kibish ([Omo 1] Butzer *et al.*, 1969; Day & Stringer, 1982; Pearson, 1997), can be readily differentiated by their relative locations on PC1 and PC2. This is especially true of the Omo 1 distal humerus, which lies at the extremes of the recent human range of variability on the second component axis.

Relative to Kabwe, Omo 1 displays a pronounced reduction in the medio-lateral proportions of the olecranon fossa, a uniform antero-posterior expansion of the articular surface and a distinct increase in the anterior projection and inferior margin of the capitulum. These morphological shape distinctions contrast this specimen with other later Pleistocene humerii, including Neandertals and European EUP and LUP hominids. TPS "morphing" of the Kabwe 'reference' to the Feldhofer Grotto 'target' specimen reveals no discernible medio-lateral expansion of the olecranon fossa in the Neandertal holotype but does support a medial expansion and slight (but distinct) posterior deflection of the medial epicondyle. TPS "morphing" demonstrates that relative shape variability in Neandertal distal humeral morphology is of a relatively low magnitude. Relative to the Neandertal holotype, two of the Krapina specimens (Kr161 & Kr 170) display a notable increase in the supero-inferior height of the medial epicondyle and a decrease in the medio-lateral breadth of the olecranon fossa.

Both of these features correlate with the observed morphological shape changes on PC1 and PC2. No morphological shape distinctions were apparent in the comparisons of the Feldhofer and Shanidar 1 distal humerii.

Quite uniform shape changes can be recognised between the Neandertal and EUP/LUP distal humerii. These relate to a *uniform shape change* consisting of an overall increase in the supero-inferior height of the capitulum and medial epicondyle and an anterior expansion of the medial wall of the trochlea in EUP/LUP distal humerii. There is no consistent reduction in the medio-lateral proportions of the EUP/LUP medial epicondyle that would furnish support for the view that this is a "derived" morphological feature of the Neandertal distal humerus relative to *Homo sapiens* (*contra* Yokley & Churchill, 2002). While the results of this analysis support the position of Trinkaus (Trinkaus, 1983*a*: 231) that the general "robusticity", but not the degree of projection of the medial epicondyle is consistently different in Neandertals and EUP/LUP humans, this might not apply ubiquitously to comparisons with all recent humans. Indeed, the classification of the Kr 170 specimen as a *Gorilla* in the Canonical Variates Analysis is presumably related to the medial expansion and posterior deflection of the medial epicondyle in this specimen. Moreover, the contention that Neandertals do not differ in their relative articular proportions of the distal humerus from recent and fossil *Homo sapiens* specimens (e.g., Trinkaus, 1983*a*; Yokley & Churchill, 2002; *in press*) is not supported by the results of this study.

In the analysis of the proximal ulna, both PC1 and PC2 scores correlate significantly and negatively ($p=<0.001$) with Centroid Size in the "total-sample", however these axes are not correlated. In the African apes, PC2 and PC3 (but not

PC1) are significantly correlated with Centroid Size, whereas in recent *Homo*, only PC5 is significantly, and negatively, correlated with geometric size. Thus, the morphological distinctions between *Pan* and *Gorilla* on PC2 (and CV2) are allometric shape changes. No such generalisation applies to patterns of morphological shape variability in recent humans.

TPS "morphing" confirms that the principal morphological differences in the proximal ulna within *Pan* (*Pan paniscus* and *Pan troglodytes*) on PC1 involve an increase in the dorso-ventral proportions of the articular surface and the medio-lateral proportions of both the coronoid and olecranon processes. Increasing medio-lateral breadth of the coronoid process in *Homo* is contiguous with an anterior displacement and increased relative area of the radial notch. Morphological distinctions between *Pan* and *Gorilla* on PC2 involve a correlated reduction in the D-V and M-L proportions of the articular area with a correlated reduction in the medio-lateral breadth of the coronoid process and a protraction (especially of the anterior region) of the radial notch. Morphological shape changes in recent humans on PC3, which is negatively correlated with Centroid Size, involves the "relative shear" of the long axis of the olecranon process relative to the coronoid process.

Relative to AL 288-1 (*A. afarensis*), the morphology of the Middle Pleistocene *Homo* specimen from Baringo-Kapthurin ([KNM-BK 66] Solan & Day, 1992) displays a discernible reduction in the medio-lateral breadth and a slight reduction in the dorso-ventral proportions of the articular surface. Contiguous with these changes is a posterior displacement of the radial notch. There are no evident morphological distinctions in the proportions of the radial notch, the olecranon and the coronoid processes between the two specimens. These morphological distinctions relate to the loci of the two specimens on the first and second Principal Components. That AL 288-1 lies closer to the "centroid" of the recent human distribution on PC1 and PC2 is the strongest evidence that these shape changes do not manifest an evolutionary continuum in the proximal ulna towards the morphology of more recent humans.

Morphological shape differences between "archaic" humans (*Homo sp. indet*; *Homo neanderthalensis*) and "anatomically modern" humans are generally consistent with previous propositions (e.g., Churchill *et al.*, 1996; Holliday *et al.*, 1993; Pearson *et al.*, 1998; see also Groves, 1998). Neandertal ulnae can be discriminated from EUP/LUP specimens by virtue of a number of consistent morphological features. Nevertheless, the findings of this study contrast with those of Churchill and his colleagues (Churchill *et al.*, 1996), in that the Neandertal ulnae differ morphologically from the EUP and LUP individuals, but not recent humans *per se*. While the Omo-Kibish ulna does differ morphologically from the Baringo-Kapthurin specimen ([KNM-BK 66] Solan & Day, 1992) by virtue of its relatively high coronoid process relative to the olecranon and expanded radial notch (Churchill *et al.*, 1996), these same anatomical distinctions differentiate KNM-BK 66 from Neandertal ulnae (Shanidar 4 & 6). The proposal that all "archaic" specimens display a uniform morphological pattern in the proximal ulna that manifests morphological (and by inference, behavioural) stasis is inconsistent with these findings (*contra* Churchill *et al.*, 1996; Holliday *et al.*, 1993).

The principal morphological distinctions between "archaic" (i.e., Neandertal) and "modern" ulnae identified by Churchill and his associates (Churchill *et al.*, 1996:233) are highly variable in Eurasian Neandertals. TPS "morphing" of the Skhul IV specimen to the Shanidar Neandertals (Shanidar 5 & 1) reveal that differences in radial notch orientation and posterior displacement of the coronoid process are likely to be correlated with an overall decrease in D-V and M-L proportions of the articular surface in Neandertal ulnae. Moreover, relative to Skhul IV, the Shanidar specimens display a subtle *increase*, not a decrease, in the height of the coronoid process relative to the olecranon, which contrasts the Levantine Early Upper Pleistocene specimen with the European EUP/LUP hominids. Nevertheless, Neandertal ulnae can be morphologically distinguished from most EUP and LUP hominids by virtue of their relatively greater dorso-ventral and medio-laterally narrow, articular surface and coronoid process, inferior displacement of the radial notch and increased height of the coronoid relative to the olecranon. These morphological distinctions are consistent with the results of previous studies using linear metrics (e.g., Trinkaus, 1983*a*; Churchill *et al.*, 1996; Holliday *et al.*, 1993).

To what extent do the observed distinctions in distal humeral and proximal ulna morphology in the extant hominoids (*Pan*, *Gorilla* & *Homo*) reflect morphological adaptations to structural stability and range of motion of the elbow joint during locomotion? Relative to the recent humans, it would appear that the reduced proportions of the olecranon process (ulna) and fossa (humerus) in *Pan* and *Gorilla* relative to *Homo* likely reflects a reduction in the range of medio-lateral rotatory excursion permitted at the joint. Such a view is substantiated by the observation that the dorso-ventral and medio-lateral proportions of the articular notch of the ulna in *Pan* and *Gorilla* are also reduced relative to *Homo*. Surprisingly, the proportions of the radial notch in the African ape ulna are considerably reduced relative to Centroid Size than in recent humans. This suggests that the elbow joint (Distal Humerus, Proximal Ulna and Proximal Radius articulations) of *Pan* and *Gorilla* is considerably more closely "packed" with a reduced range of motion.

The comparative anatomical study of Gibbs (Gibbs, 2000) has determined that the insertions of *m. brachialis* and *m. pronator teres* on the anterior aspect of the coronoid process of the ulna and the *m. triceps* insertion on the olecranon process of the ulna are topographically equivalent throughout the Great Apes. Surprisingly, the attachment area for the triceps muscle on the olecranon process is considerably smaller than in humans, however, the action lines of the three most important muscles recruited during normal extension and pronation of the elbow joint in the hominoids are more closely aligned in *Pan* and *Gorilla* than in *Homo*. As a whole, the morphological distinctions of the elbow joint in the African apes is consistent with the hypothesis that joint excursion during loading is reduced relative to *Homo*. While these distinctions, together with the postero-superior "deflection" and subsequent expansion of the area for the insertion of the common flexor tendon on the medial epicondyle suggest clear adaptations in *Pan* and *Gorilla* to terrestrial pronograde knuckle-walking, reducing the range of excursion at the elbow joint would also be mechanically advantageous during climbing. An interesting finding is that the morphological shape distinctions in the proximal ulna of *Pan* and *Gorilla* on PC4 & PC6 are correlated with Centroid Size. These morphological changes might be consistent with a proposal of increased structural integrity of the elbow joint with increased size (both "geometric" size and Centroid Size; see above). Data on relative force moments in the elbow joint during terrestrial locomotion and climbing is required to further explore this interesting proposition.

The observed morphological distinctions in the elbow joint of *Australopithecus*, particularly the AL 288-1 female for which both elements are available, are not consistent with a proposed distinction in upper limb use in Pliocene and Lower Pleistocene hominids. Despite considerable morphological variability in distal humeral articular morphology in *Australopithecus*, there is no evidence to support the view that these hominids display structural modifications consistent with a reduced joint excursion relative to early *Homo*. Nevertheless, at present, the morphology of the elbow joint in recent humans cannot be directly related to any specific functional role. Until we include data relating to other primates, particularly *Pongo*, the sole statement beyond contention is that the distal humeral and proximal ulna geometry of *Homo* and *Australopithecus* generally differs from that of *Pan* and *Gorilla*. Nevertheless, direct comparisons of the proximal ulna in AL 288-1 and the Middle Pleistocene specimen from Baringo-Kapthurin (KNM-BK 66 [Solan & Day, 1992]) are particularly revealing, and do not suggest profound differences in elbow joint recruitment which one would expect if *Australopithecus* remained adapted to an arboreal existence. This view is supported by a recent analysis of cross-sectional diaphyseal proportions in *Australopithecus afarensis* (Ward *et al.*, 2003), which established that bending resistance in the humerus was not consistent with proposed arboreality in this species.

With respect to the Neandertal elbow joint, the morphological distinctions in the proximal ulna are consistent with proposals that, relative to Upper Pleistocene *Homo sapiens*, these hominids probably did engage in manual activities that engendered greater stresses in their elbow joint. The reduced height of the coronoid process relative to their S-I high olecranon processes, together with their reduced M-L articular proportions and relatively smaller radial notch suggest anatomical enhancements of joint stability during manual loading. Neandertal radial diaphyses are unusually curved and, relative to later hominids, their radial tuberosities (insertion on m. biceps brachii) are medially orientated and are particularly swollen (Trinkaus, 1983*a*,*b*; Churchill, 1994, 1996, 1998; Churchill *et al.*, 1996). This evidence is supported by comparative analyses of cross-sectional diaphyseal properties of the upper limb bones (humerus, radius & ulna) of Eurasian Neandertals, which display greater resistance to bending and pronounced cross-sectional shape differences relative to Upper Pleistocene modern humans that are consistent with hypothesised osteonal remodelling in response to elevated mechanical demands (Trinkaus, 1997, 2000; Trinkaus & Churchill, 1999; Trinkaus *et al.*, 1998, 1999).

8.2. Epiphyseal Geometry of the Proximal Femur

The principal morphological distinctions between recent humans and the African apes on PC1, and variation in proximal femoral geometric shape in the African apes and recent and fossil hominids on PC2 are summarised in table 175. The proximal femoral morphology of the African apes differs from recent *Homo* by virtue of the increased proportions of the greater trochanter, relatively more vertical superior surface which does not project above the trochanteric fossa, reduced biomechanical femoral neck length and more elliptical profile of the femoral head. Principal morphological shape changes on the second Principal Component appear to distinguish the majority of "archaic" fossil hominid femora (e.g., *Australopithecus*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*) from "anatomically-modern" *Homo sapiens*. These involve a notable reduction in biomechanical femoral neck length and a notable increase in the antero-posterior proportions of the greater trochanter and femoral neck, and increased relative proportions of the femoral head.

Interestingly, exploration of relative shape variation using TPS "morphing" procedures reveals that the proportional decrease in the relative length and increased antero-posterior proportions of the femoral neck are also manifest in the African apes on PC2. Additionally, increasing positive scores on PC2 in *Pan* and *Gorilla* records a contiguous increase in relative femoral head proportions in both the M-L and A-P axes. None of these morphological shape changes are *allometric*, as PC1 and PC2 are not correlated with Centroid Size in either the total, recent human, or African ape matrices. PC4 and PC6 are negatively and positively correlated with Centroid Size in the African apes alone. These axes reflect an increase in S-I depth of the greater trochanter, a reduction in femoral neck length and increasing relative proportions of the femoral neck (PC4), together with increasing A-P breadth of the greater trochanter, increasing horizontal orientation of the superior surface and increased relative femoral head size (PC6). These component axes are negatively correlated in *Pan troglodytes* and *Gorilla*.

Pairwise comparisons of the two *Australopithecus afarensis* (AL 288-1 and AL 333-3), and the Lower Pleistocene KNM-ER 1503 (*Australopithecus boisei*) specimens yield crucial insights in to patterns of morphological shape variability and evolution of the proximal femur of *Australopithecus*. Morphological differences between AL 288-1 and KNM-ER 1503 are relatively minor and are consistent with a model of locomotor stasis in *Australopithecus* (e.g., Lovejoy, 1973, 1975, 1978; Lovejoy, Heiple & Burstein, 1973; Day, 1973, 1976, 1979), whereas pronounced morphological distinctions exist between the conspecific Hadar specimens (AL 288-1 & AL 333-3). In contradistinction to the views of Stern and his colleagues (e.g., Stern, 2000; Stern & Susman, 1983; Susman *et al.*, 1984, 1985), the results of this analysis suggest that the morphology of the AL 333-3 proximal femur is apparently more "ape-like" than the relatively smaller AL 288-1 individual. AL 333-3 is far removed from AL 288-1, KNM-ER 1503 and other Lower and Middle Pleistocene hominid femora in its relative loci on PC1 and PC2, and is classified as *Pan paniscus* in the resulting CVA. Nevertheless, exploration of extreme patterns of morphological shape change on the first and second Principal Components in *Pan paniscus*, *Pan troglodytes*, and *Gorilla* reveal that these differences, however marked, are not consistent with hypothesised gender distinctions in locomotor habitus in *Australopithecus* (e.g., Lague, 2002; *contra* Stern & Susman, 1983; Susman & Stern, 1991; Susman *et al.*, 1984, 1985; Senut & Tardieu, 1985). However, until further proximal femoral specimens of *Australopithecus* are recovered, described and made available for study (e.g., Clarke, 1998), our knowledge of morphological shape variability in the proximal femur of this early hominid genus will remain limited.

Morphological comparisons of the left proximal femur of the 1.5 Myr old juvenile *Homo erectus* individual ([KNM-WT 15000G] Brown *et al.*, 1985; Walker & Leakey, 1993*a*,*b*) with relevant australopithecine specimens reveals a pattern of morphological shape change which conflicts with previous interpretations (e.g., Day, 1973, 1976, 1979; McHenry & Corruccini, 1976*a*,*b*, 1978; Aiello & Dean, 1990; Ruff, 1995, 1998; Ruff *et al.*, 1999). The most striking contrast is that no discernible differences exist in the medio-lateral (M-L) proportions of the femoral neck in *Homo erectus* and *Australopithecus*. Furthermore, relative proportions of the femoral head are demonstrably greater in *Australopithecus* (*contra* Ruff *et al.*, 1999), but consistent support emerges for the view that the femoral neck in early *Homo* is antero-posteriorly narrower than in *Australopithecus* (e.g., Day, 1973, 1976, 1979, 1986*a*,*b*; Walker & Leakey, 1993*b*; Ruff, 1995).

When absolute size differences are constrained, there is a striking resemblance in proximal femoral geometry of the KNM-WT 15000G femur and the ambiguous Trinil 1 specimen (*contra* Day, 1973, 1986*a*; Day & Molleson, 1973). Nevertheless, the Trinil 1 femur displays a moderate decrease in the M-L proportions of the femoral neck, a notable decrease in S-I proportions of the greater trochanter and increased relative size of the femoral head. These morphological distinctions also distinguish KNM-WT 15000 from, and ally the Trinil femur with, the chronologically later Middle Pleistocene specimen from Kabwe (Smith-Woodward, 1921; Pycraft *et al.*, 1928), on PC2. Relative to KNM-WT 15000, the femoral neck of the Kabwe specimen is relatively greater in its antero-posterior aspect and the femoral head is relatively larger overall. These proportional changes are consistent with the proposed evolutionary increase in body mass in "archaic" *Homo* in the Middle Pleistocene (e.g., Ruff, 1994; Ruff *et al.*, 1997; Grine *et al.*, 1995; Kappelmann, 1996).

Interestingly, comparisons of the Early Upper Pleistocene *Homo sapiens* male from the Levant ([Skhul IV] McCown & Keith, 1939) with the Kabwe and Feldhofer Grotto Neandertal reveal a similar pattern of morphological shape changes that are accentuated in Kabwe. Relative to these "archaic" *Homo* specimens, the early "anatomically-modern" human proximal femur from the Levant displays a notable reduction in the relative length of the femoral neck and an increase in the A-P and M-

L proportions of the greater trochanter. This is consummate with a re-orientation of the superior surface, which is expanded medially above the trochanteric fossa. Surprisingly, there is a relative increase in both the S-I and A-P proportions of the femoral head, which is not consistent with previous appraisals of the absolute or relative size of the femoral head in these hominids (Trinkaus, 1983*a*).

Average absolute dimensions of the proximal femoral articular surface of the two better-preserved Skhul/Qafzeh hominids (Skhul IV & Qafzeh 9) is 45.82mm, and lies 3SD units below the means of the three Kabwe femora (X = 50.49mm; SD = 1.125) and the Neandertal specimens (X = 52.18; SD = 0.997; *n*=6). Trinkaus (Trinkaus, 1983*a*) furnished comparative relative FHD/Bi-condylar femur length indices for the Eurasian Neandertals (X = 12; SD = 0.6; *n*=5), and the Skhul/Qafzeh hominids (9.5; SD = 0.4; *n*=4). Using an approximation of the length of the femur for the Kabwe E689 femur of 475mm (Kennedy, 1984:105), the index for this African "archaic" *Homo* individual is of the order of 10.15, which is close to the mean of the European Upper Palaeolithic sample (X = 10.4; SD = 0.7, n=11 [Trinkaus, 1983*a*:304). Trinkaus (Trinkaus, 1983*a*:304) concluded that relative to the Skhul/Qafzeh hominids, Eurasian Neandertals possessed a "...relatively large femoral head".

Morphological comparison of the Neandertal proximal femoral geometric configuration with suitably preserved European EUP and LUP specimens confirms the previous observations on the relative proportions of the femoral neck and femoral head seen in the Levantine Upper Pleistocene specimen. Relative to the Neandertal proximal femur, EUP and LUP hominids generally exhibit a discernible reduction in the relative length of the femoral neck, a committal increase in the relative A-P proportions of the greater trochanter and femoral neck and an overall increase in the proportions of the femoral head. Once again, these observations contrast with previous assessments of the absolute and relative size of the proximal femoral epiphysis in later Pleistocene hominids (e.g., McCown & Keith, 1938; Trinkaus, 1983*a*; Pearson, 1997). These morphological transformations are more pronounced in the LUP, rather than EUP specimens. This conflicts with proposals of a reduction in locomotor-based activity levels in the Eurasian later Pleistocene (e.g., Churchill, 1994, 1998; Pearson, 1997; Holt, 1999; Holt & Churchill, 2000; but see Holliday, 2000, 2002), if epiphyseal skeletal tissue is developmentally "constrained" (e.g., Ruff *et al.*, 1991, 1993; Lieberman *et al.*, 2001).

8.4 Functional integration in the hominid pelvis

Results of the analyses performed in Chapter 7 are consistent with expectations of the fourth hypothesis of this thesis. With few exceptions, the proportions of the ilium are highly and positively correlated with bi-iliac diameter and, with each other. Interestingly, significant scaling differences in the proportions of the ilium in recent *Homo* are apparent in ilium breadth, but not ilium height. The Native American samples display relatively less broad ilia than Old World human samples of comparable body size (e.g., Bantu, Magyars) when expressed as a proportion of medio-lateral pelvic breadth and iliac height, although there is considerable variance in the Magyar sample. Correlation coefficients for estimated relative flare of the iliac blade and bi-iliac diameter are less convincing, and are not consist with the allometric model.

The African Bantu and Medieval Hungarians display a proportionally elongated superior pubic ramus relative to their respective Old World low-latitude and high-latitude co-habitants (Australians and Tartars, respectively), suggesting that factors other than increasing lateral pelvic breadth influence the proportions of the pubic ramus in some recent humans. There is tentative evidence to support the proposal that these distinctions are an allometric consequence of a relatively greater antero-posterior pelvic plane, at least in the Bantu. However, significant scaling differences in relative inter-acetabular distance (or *Dw*) between the Bantu and Australian Aborigines may also plausibly contribute to the observed differences in relative pubic ramus length in these samples (e.g., Trinkaus, 1984*a*, 1988).

A significant finding of this study is that consistent sexual dimorphism exists in the proportions of the body weight load arm (*Dw*) to abductor force lever arm (*Dm*) of the hip joint in recent *Homo*. Furthermore, this is a function of the relatively smaller biomechanical femoral neck length (*Dm*) in human females. This confirms and expands upon the earlier observation of Jungers (Jungers, 1991) in his African Pygmy sample. Interestingly, non-parametric multiple sample comparisons of the recent human females reveals that *Dw*/*Dm* proportions do not differ statistically, at least in the samples included here, whereas in the males, variance in this index is highly significant. Available data on the anterior pelvic proportions of the African apes utilised in this study reveal that the *Dw*/*Dm* index is sexually dimorphic in the African apes (see table 176), and might well be a primitive feature of the anterior pelvic configuration in African hominids that has remained morphogenetically constrained in hominid evolution, irrespective of the adoption of bipedal gait and the obstetrical adaptations that have occurred within the past 2.5 Myrs (e.g., Rosenberg, 1988, 1992).

In contrast to the positive allometric relationship between medio-lateral hip breadth and bi-actabular diameter (or *Dw*), no convincing evidence emerges to support the an allometric relationship between biomechanical femoral neck length (*Dm*) and M-L hip proportions in recent *Homo*. The only significant observation is that the African Bantu possess a relatively larger biomechanical femoral neck proportional to bi-iliac diameter, presumably to offset their relatively enlarged inter-acetabular diameter relative to moderate iliac flare (Ruff, 1991, 1994, 1995, 1998; Ruff & Walker, 1993). Given the theoretical premise of Ruff's model (Ruff, 1995, 1998), one might reasonably expect a significant relationship to exist between increasing *Dw* and *Dm*. In order to mediate against an anterior pelvic configuration approximating that seen in *Australopithecus afarensis* ([AL 288-1] i.e., wide *Dw* and short *Dm* [Ruff, 1998: fig 3) and a consequential increase in *J*, then a linear relationship between *Dw* and *Dm* is expected. Further to this, it is a reasonable expectation that a significant positive relationship will exist between *Dw*/*Dm* and femoral head size in recent humans.

Despite the convincing allometric relationship between inter-acetabular distance (and *Dw*) with bi-iliac diameter, and the finding that *Dw* and *Dm* are significantly (and functionally) correlated, no relationship exists between the proportional index of *Dw*/*Dm* and medio-lateral hip breadth in recent *Homo*. This relationship is not generally improved when *Dw*/*Dm* is regressed upon relative bi-iliac diameter (bi-liac diameter/stature [estimated from femur length; see Chapter 3]). The hypothesis that ecogeographically-mediated evolutionary changes in relative body size (Ruff, 1991, 1993, 1994; Ruff & Walker, 1993*a*), directly moderated changes in *Dw*/*Dm* proportions of the *Homo erectus* pelvis relative to *Australopithecus* (e.g., Lovejoy *et al.*, 1973; Ruff, 1995, 1998) is not supported by a recent human prediction 'model'. Nevertheless, this does not imply that this supposition is necessarily incorrect, particularly in light of the linear relationship between increasing femoral length and *Dm* in recent and fossil hominids (Wolpoff, 1976; Ruff 1995; see Fig. 254).

In direct contradiction to theoretical expectations (e.g., Frankel & Burstein, 1970; Nordin & Frankel, 1989; Ruff, 1998) a significant ***negative*** relationship is established between the absolute size of the femoral head and increasing *Dw*/*Dm* proportions in recent humans. Visual and statistical comparisons of average "relative pressure" indices for the femoral head (Lovejoy, Heiple & Burstein, 1973), in human females reveal that these are consistently greater than in recent human males, indicating that female proximal femoral articular surfaces are ***relatively smaller when expressed as a proportion of estimated body mass***. With respect to the anterior-pelvic configuration of AL 288-1, this study furnishes little support for the conclusion that the *Dw*/*Dm* proportions of this diminutive *Australopithecus* individual "offer no obvious mechanical insights in to Lucy's relatively small femoral head." (Jungers, 1991:221). The absence of a consistent pattern of allometric relationships between femoral head size and parameters of purported functional significance in the hominid pelvis furnishes only limited support for the hypothesis that variability in this system is highly influenced by absolute or relative body size constraints. Indeed, correlation coefficients for FHD on relative body size (Ruff, 1991, 1993, 1994; Ruff & Walker,

1993) are relatively poor. This result is surprising given that Ruff and his associates (Ruff *et al.*, 1997) report an excellent correlation between body mass estimates derived from both parameters.

The functional significance of the relatively wide inter-acetabular distance and marked iliac flare in the pelvis of *Australopithecus* has been the focus of critical discussion (Lovejoy, 1973, 1975, 1978, 1988; Lovejoy *et al.*, 1973; Tague & Lovejoy, 1986; Stern & Susman, 1983; Susman *et al.*, 1984, 1985; Jungers, 1991; Rak, 1990*a*; Ruff, 1995, 1998). The most obvious explanation is that the greatly enlarged distance between the two centres of the hip joint and medio-laterally wide inlet in the AL 288-1 pelvis are related consequences of an absolutely wider M-L pelvic breadth (e.g., Stern & Susman, 1983; McHenry, 1986; Tague & Lovejoy, 1986; Rak, 1990*a*). In contrast, Rak (Rak, 1990*a*) demonstrated that the medio-lateral, but not antero-posterior, proportions of the pelvic inlet in AL 288-1 are *relatively* wider than in *Homo* and *Pan troglodytes* when scaled to body mass. Thus, Rak (Rak, 1990*a*) proposed that a relatively wider M-L pelvic inlet in *Australopithecus* served to minimise vertical displacements of the centre of mass during the swing phase of the gait cycle (Rak, 1990*a*; Inman *et al.*, 1981; Whittle, 1998; Nigg & Herzog, 1999).

There is an undeniable relationship between the inter-acetabular distance and the medio-lateral breadth of the pelvis in extant and extinct hominids, and proportions of the body mass load arm in AL 288-1 are not distinct. However, unpublished data suggests that relative to geometric size, medio-lateral hip breadth in AL 288-1 is considerably greater than in recent *Homo* and in the African apes. This confirms observations based upon the regression of M-L hip breadth and a 'linear' measure of cranio-caudal size, such as femur length or estimated stature (e.g., Jungers, 1991; Ruff, 1991, 1993, 1994; Ruff & Walker, 1993; Porter, 1995). Morphologically, this is a direct a consequence of her less antero-medially rotated iliac blade relative to recent humans (e.g., Johanson *et al.*, 1982; Lovejoy, 1988; Tague & Lovejoy, 1986; Robinson, 1972; Zuckerman *et al.*, 1973; Ashton *et al.*, 1981; Stern & Susman, 1983; Susman *et al.*, 1984; McHenry, 1975, 1986).

The principal metrical distinctions between the ilium of *Australopithecus* (AL 288-1 [Johanson *et al.*, 1982; Lovejoy, 1988; Tague & Lovejoy, 1986], Sts 14 [Robinson, 1972; Lovejoy *et al.*, 1973; McHenry, 1986], Stw 431 & Stw 441/465 [Häusler, 2001; Häusler & Berger, 2001]) and early *Homo* lie in the antero-posterior breadth of the ilium. Relative to iliac height, iliac breadth is discernibly less broad in AL 288-1 recent and fossil *Homo*. The 1.95 Myr old KNM-ER 3228 (Feibel *et al.*, 1989; Rose, 1984), is considered to be morphologically indistinguishable from *Homo erectus* ilia, including KNM-ER 1808, KNM-WT 15000, OH 28 and Arago XLIV (Day, 1971, 1982; Sigmon, 1982; Rose, 1984; Walker & Leakey, 1993*b*; Walker & Ruff, 1993; Ruff, 1995).

The projected degree of iliac flare in the reconstruction of the sub-adult KNM-WT15000 *Homo erectus* pelvis (Walker & Ruff, 1993) is relatively moderate compared to *Australopithecus* (e.g., Ruff, 1991, 1993, 1994; Walker & Ruff, 1993). This reconstruction has been criticised by J.C. Ohman and his associates (Ohman *et al.*, 1998; Ohman *et al.*, *in prep.*; Latimer & Ohman, 2001) who have argued that the cranio-caudal length of the vertebral column in this individual is abnormally short, the result of a rare developmental pathology (Latimer & Ohman, 2001; J.C. Ohman, *pers,* *comm.*). A consequence of reducing the cranio-caudal height of the vertebral column in KNM-WT 15000 is that the medio-lateral proportions of the inferior thorax and pelvic girdle are significantly increased. It is most unfortunate that this specimen may eventually contribute little reliable evidence as to the pelvic proportions of early *Homo*.

In his recent reconstruction and analysis of the fragmentary pelvis of the Stw 431 *Australopithecus africanus* partial skeleton from Sterkfontein, Häusler (Häusler, 2001) has proposed that the antero-posterior iliac proportions of this male specimen were relatively greater than in the female *Australopithecus* pelvis (AL 288-1 & Sts 14). I concur with this view but suspect that it is a consequence of an allometric increase in the total area of the ilium. Stw 431 displays an absolutely greater iliac height above the anterior horn of the acetabulum relative to Sts 14 and AL 288-1 (Stw 431 = 98.12mm; Sts 14 = 81.93mm; AL 288-1 = 83.49mm [taken perpendicular to the tubercle]). However, Häusler (Häusler, 2001) has demonstrated that the proportions of the anterior ilium relative to iliac height are greatly enlarged in Stw 431 relative to the two female specimens.

The contour of the ilium as reconstructed by Häusler (Häusler, 2001:68), does not differ significantly from appropriately re-scaled contours of the juvenile Makapansgat ilia (MLD 7 & MLD 25) and Sts 14. The medio-lateral breadth of the ilium across the superior iliac spines is slightly greater in the juvenile MLD 7 than in the adult Sts 14 and AL 288-1 specimens, suggesting that the relative degree of iliac flare in *Australopithecus* is quite variable and perhaps, developmentally more labile. If the revised geochronology of the Sterkfontein deposits is correct and

Australopithecus Member II and IV specimens are between 2.5-1.8 Myrs old (Berger *et al.*, 2002), there emerges little support for prevailing theories of a gradual evolutionary change in the locomotor morphology of this early hominid genus.

The absolute and relative reduction in medio-lateral hip breadth in *Homo erectus* suggested by the results of this analysis likely reflects the observed changes in thoracic proportions relative to AL 288-1 (e.g., Schmid, 1983, 1991; Jellema *et al.*, 1993). Nevertheless, the degree of lateral iliac flare in early *Homo* is considered to be greater in adult *Homo erectus* individuals (e.g., KNM-ER 3228, KNM-ER 1808 & OH28; [Ruff & Walker, 1993; Walker & Ruff, 1993]) than in recent humans. The recently recovered *Homo heidelbergensis* pelvis from Atapuerca ([AT 1-1] Arsuaga *et al.*, 1999), is characterised by extreme levels of iliac flare, as indicated by the relatively short bi-acetabular distance and superior pubic ramus proportional to bi-cristal diameter (Arsuaga *et al.*, 1999; see Lovejoy, 1975, 1978).

The relative proportions of the anterior pelvic region in this individual are unique, and contrast with all known fossil specimens including *Australopithecus afarensis* (AL 288-1). When the relative proportions of the antero-posterior plane of the pelvis are considered, it is clear that *Homo heidelbergensis* displays the requisite adaptations to a fully human rotational birth mechanism (e.g., Rosenberg, 1988, 1992; Ruff, 1995), even if the relative A-P breadth in this individual is slightly smaller. This morphological transformation appears to have been accomplished without considerable alteration to the overall pelvic morphology and proportions, which are reminiscent of earlier *Homo* (Arsuaga *et al.*, 1999; Day, 1971, 1982, Rose, 1984; Ruff, 1995; Walker & Ruff, 1993; Walker & Leakey, 1993*b*).

While the absolute length of the body weight lever arm (*Dw*) does not differ between the Atapuerca AT-1 and Kebara pelves, the biomechanical length of the femoral neck (*Dm*) in the associated femur (Arsuaga *et al.*, 1999) is evidently longer than in Neandertals (Trinkaus, 1983*a*; Trinkaus & Ruff, 1999*a,b*; Holliday, 1995, 1997*a,b*). The proportions of the load arm/lever arm (*Dw/Dm*) in the Atapuerca individual are lower than in the Neandertal model, and do not differ perceptibly from recent or fossil *Homo sapiens*. Upper Palaeolithic females approach Neandertals in their *Dw/Dm* index. The anterior pelvic proportions of *Australopithecus afarensis* (AL 288-1) are clearly different from later hominids, a product of their relatively short femoral neck. Surprisingly, the relative pressure index of the Atapuerca hominid is greater than in remaining fossil specimens, including Neandertals and AL 288-1.

The relative pressure index of AL 288-1 is clearly within the range of variation seen in recent *Homo*, implying that relative femoral head area in this individual was not perceptibly different from that in recent humans (e.g., Lovejoy *et al.*, 1973; Ruff, 1988, 1998; *contra* Jungers, 1991). Thus, on the basis of the traditional argument, *Homo heidelbergensis* from Atapuerca was apparently less well adapted to habitual bipedalism than *Australopithecus afarensis*! The relative size of the femoral head in Eurasian Neandertals is not observably different from Skhul IV or European Upper Pleistocene *Homo sapiens* (e.g., Ruff *et al.*, 1993; Trinkaus & Ruff, 1989*a,b*, 1999*a,b*; Holliday, 1995, 1997*a,b*).

The proposal that the elongated superior pubic ramus and inter-acetabular distance of the Neandertal pelvis is a direct consequence of a relatively enlarged M-L and A-P pelvic plane cannot be rejected. Relative to M-L pelvic breadth, IAD (*Dw*) and pubic ramus length are proportionally greater in Neandertals than in recent and fossil *Homo*. Several LUP hominids (especially the females) exceed the Kebara pelvis in their relative A-P pelvic planes (to M-L) pelvic breadth, but their pubic ramii are not especially long. Indeed, when the length of the superior pubic ramus length is scaled to the A-P breadth of the pelvis this remains especially long in Neandertal's compared with recent humans, but is relatively shorter in the AT-1 and LUP *Homo* pelves. The results of this analysis do not support Rosenberg's (Rosenberg, 1988) contention that the elongated pubic ramus in Neandertals is an allometric, rather than a selective phenomenon (e.g., Rak & Arensburg, 1987; *contra* Trinkaus, 1984, 1988), but conflict with Rak's (Rak, 1990*b*, 1991) interpretation of the proximate influences on the Kebara pubic ramus.

Nevertheless, these results are entirely consistent with Trinkaus' (Trinkaus, 1983*a*,*b*, 1984) *morphological* statements (i.e., that the anterior pelvic morphology is a hereditary, "unit" of inheritance) and the recent analysis of the Shanidar 3 thoracic proportions (Franciscus & Churchill, 2001). I view the expansion of the medio-lateral proportions of the Neandertal pelvis to be the direct result of a directed, evolutionary increase in the relative proportions of the inferior thorax (e.g., Boulé, 1911-13; McCown & Keith, 1939; Arensburg, 1991; Franciscus & Churchill, 2001). The medio-lateral proportions of the pelvis remained constant with these morphological transformations. If the Atapuerca pelvis is a probable Neandertal ancestor (e.g., Arsuaga *et al.*, 1997; 1999; but see Bischoff *et al.*, 2003), these allometric changes precipitated an increase in the inter-acetabular distance and an apparent lateral displacement of the acetabulae relative to the sagittal pelvic plane.

Results derived from bivariate assessments of "functional integration" in the lower limb of recent humans furnish only limited support for the fifth hypothesis that a "general functional relationship" would exist between the proportions of the anterior pelvis and the midshaft and proximal femoral diaphysis of recent humans. Results of comparisons of area standardised medio-lateral (M-L) and antero-posterior (A-P) dimensions of the midshaft and proximal femoral diaphyses do suggest a strong allometric component to the observed distinctions between high-latitude and low-latitude human groups, with the larger-bodied high-latitude humans display relatively greater M-L, and correspondingly reduced A-P proportions of the femoral midshaft and sub-trochanteric area cross-sections. These differences are consistent with Ruff's comparative analysis in which relative diaphyseal strength and cross-sectional polar moments of area (J) where proportionally greater to absolute body size (e.g., femur length) in Pecos Pueblo Amerindians relative to East African's (Ruff, 2000).

The theoretical proposal that increasing *Dw/Dm* proportions in recent humans would lead to concomitant increase in bending moments in the femoral midshaft and sub-trochanteric diaphyses, directly implied by fifth hypothesis of this thesis, is only partially supported by the results of this analysis. Some support emerges for a proposed functional relationship between increasing load arm/lever arm proportions and increased proportional medio-lateral bending resistance in the midshaft and proximal femoral diaphysis. However, increased *Dw/Dm* indices also correspond with an increase in the relative bending resistance of the A-P plane of the femoral midshaft and subtrochanteric sections in recent humans. Surprisingly, both midshaft and proximal femoral cross-sectional areas are negatively correlated with increasing *Dw/Dm* indices, which is not consistent with the expectation of increased bending resistance as a consequence of increasing anterior pelvic proportions (relative increase in *Dw*). Thus, the results of this study suggest that while anterior hip proportions (e.g., *Dw/Dm*) have only a limited influence upon within-sample variance in relative proportions of the femoral diaphysis in recent *Homo*, and this cannot explain the broader patterns of femoral diaphyseal shape differences (i.e., increased relative M-L proportions in high-latitude samples) in recent *Homo*.

The analyses of the femoral midshaft and diaphyseal cross-sectional proportions in fossil hominids also provide only limited support for a proposed relationship between anterior pelvi proportions (especially relative *Dm*) and observed variability in femoral midshaft and subtrochanteric diaphyseal proportions. While the comparisons confirm previous observations that femora attributed to *Australopithecus* display midshaft and subtrochanteric diaphyses that are expanded medio-laterally and flattened antero-posteriorly relative to Later Pleistocene and recent hominids (e.g., Day, 1971, 1973, 1976, 1978; Walker, 1973; McHenry & Corruccini, 1976, 1978; Ruff, 1995, 1998; Ruff *et al.*, 1999, these distinctions are less pronounced in comparisons with "early *Homo*" specimens (e.g., Ruff *et al.*, 1999). Indeed, there is considerable support emerges for Ruff's contention (Ruff, 1995, 1998; Ruff *et al.*, 1999) that the principal distinctions in femoral sub-trochanteric morphology are between "earlier" and "later" hominids (Wolpoff, 1976, 1978; *contra* Day, 1973, 1976, 1978; McHenry & Corruccini, 1976*a*,*b*, 1978).

Femoral midshaft and sub-trochanteric proportions in *Australopithecus* and early *Homo* are indistinguishable when scaled to biomechanical femoral neck length (*Dm*), which contradicts the empirical expectations of the sixth hypothesis of this thesis. The pronounced distinctions that are apparent when relative subtrochanteric proportions (particularly relative STML) of australopithecine and Early Pleistocene *Homo* specimens are expressed as a proportion of femoral head diameter (e.g., Ruff *et al.*, 1999), likely reflect the evolutionary transformation in body size and body shape that occurred with the emergence of *Homo* (e.g., McHenry, 1988, 1991, 1992*a*,*b*; 1994*b*; McHenry & Coffing, 2000; Ruff, 1991, 1993, 1995; Ruff & Walker, 1993; Aiello & Wood, 1994, 1998). These findings, together with the observed relationship between femoral length and *Dm* in recent and fossil *Homo* (Fig. 254), are consistent with the view that the observed morphological distinctions in Plio-Pleistocene hominid femora probably reflect contrasting patterns of M-L and A-P bending moments imposed by modifications in overall pelvic proportions in response to evolutionary constraints relating to increasing body mass and encephalisation, not increasing locomotor competency (Ruff, 1995, 1998; Ruff *et al.*, 1999).

With respect to later Pleistocene *Homo*, clear distinctions are apparent in the relative proportions of the femoral midshaft and sub-trochanteric diaphysis. The results of this analysis do not support the contention that the femoral midshaft proportions of Neandertals differed from European Early Upper Palaeolithic however, consistent contrasts are confirmed in the proximal femoral diaphysis of these hominids (Trinkaus, 1983*b*, 1993, 1997, Trinkaus *et al.*, 1998*a*,*b*; Ruff & Trinkaus, 1989; Sladek *et al.*, 2000; Pearson, 1997). The principal distinctions in relative M-L and A-P proportions of the femoral sub-trochanteric diaphysis of Neandertals and EUP hominids appear to be a result of relatively greater A-P diaphyseal diameters of Neandertal femora. However, it must be noted that EUP femora are highly variable in their relative proximal femoral proportions, whereas Neandertals are not. When scaled to *Dm* or femoral head diameter, Neandertals can be clearly differentiated from EUP and LUP hominids by virtue of their discernibly increased A-P, not M-L, proximal femoral proportions. However, there some notable outliers in the EUP sample exists (e.g., Paviland 1 and Pavlov 1). Femoral sub-trochanteric proportions of Eurasian Neandertals do contrast notably with available "early anatomically-modern" *Homo sapiens* femora from East Africa and the Levant (e.g., KNM-ER 999a, Skhul IV & Qafzeh 9 [e.g., Trinkaus, 1993, 1997; Trinkaus & Ruff, 1999*a*; Bräuer *et al.*, 1997).

The greatest contrasts in femoral midshaft and sub-trochanteric diaphyseal proportions in the Upper Pleistocene hominids are between the European EUP specimens with available individuals from the Levant (Skhul/Qafzeh) and European LUP hominids, not with the Neandertals. Interestingly, while the LUP specimens display consistently greater femoral midshaft and sub-trochanteric diaphyseal cross-sectional area relative to Eurasian Neandertals and European EUP hominids, their M-L and A-P proportions are considerably reduced and are more uniform. These findings suggest that attempts to infer lifestyle and activity level distinctions between EUP and LUP/Holocene hominids using approximations or actual determinants of midshaft and cross-sectional area are probably not valid (e.g., Holliday, 2002). I concur with Holliday's suggestion that differences in diaphyseal cross-sectional area in these samples principally reflect increases in body mass and changing body proportions (e.g., Holliday, 1997*b*, 1999, 2000), not differential loading histories (e.g., *contra* Holt, 1999, 2003; Holt & Churchill, 2000). This view is also supported by Ruff's (Ruff 2003) comparative analysis of relationships between cross-sectional area and cortical area in anthropoid primates.

Nevertheless, the pattern is considerably more complex than is generally admitted. Sample differences in cross-sectional M-L and A-P proportions (relative to Area, *Dm* & FHD) are consistent in comparisons of EUP and LUP hominids, and Neandertals with the Skhul/Qafzeh and LUP specimens. More crucially, considerable variability exists in the EUP hominids, and contrasts the Gravettian samples from Central Europe (Dolni Vestonice and Pavlov) with the Italian EUP hominids from the Grotte des Enfants. A substantial majority of the known LUP hominids are from Italian sites, and proposed differential activity levels based upon archaeological models of economic and settlement demography in terminal Pleistocene sites in the North European Plain (e.g., Clark, 1975; Bailey, 1983; Price, 1985, 1987; Jacobi, 1978; Constandse-Westermann & Newell, 1990) are unlikely to be applicable to coastal foraging economies (e.g., *contra* Holt, 1999, 2003; Holt & Churchill, 2000). Furthermore, Holt's insistence (Holt, 1999) that LUP/Holocene humans underwent a reduction in relative body mass coincident with a *decrease* in stature (e.g., Frayer, 1980, 1981, 1984; Jacobs, 1985*a*,*b*; Pearson, 1997, 2000; Formicola and Giannecchini, 1999) and an *increase* in bi-iliac diameter cannot be supported. Decreasing body height and increasing bi-iliac diameter leads to a significant increase in body mass (Gallagher, *unpublished observation*).

Chapter 9. Conclusions

With respect to the relative size of the epiphyseal joints and diaphyseal midshaft circumferences of the major long bones of the hominoid skeleton, results obtained in this study are largely consistent with previous observations (e.g., Jungers 1988*b*, 1990) and furnish equivocal support for the first hypothesis outlined in Chapter 2. With few exceptions, the epiphyses and diaphyses of the upper limb bones are significantly larger in the extant African apes relative to recent humans when expressed as a proportion of a valid body mass proxy (*GM*ALL). Conversely, recent humans differ from the extant African apes (*Pan* and *Gorilla*) by virtue of their relatively larger lower limb epiphyses and diaphyses, particularly in the tibia. These results support theoretical assumptions of increased skeletal tissue response to increasing mechanical load in the joints and midshaft diaphyses of the limbs in response to differential locomotor requirements.

Nevertheless, while this explanation is relatively straightforward in the case of compressive and bending forces acting in the lower limb of terrestrial bipedal hominids, it is likely that tensile stresses may be equally important in animals which utilise their forelimb in vertical climbing postures, as observed in *Pan*. Interestingly, while *Gorilla* displays a proportionally greater distal humeral epiphysis [BIEPIC] relative to *GM*ALL than *P. paniscus* or *P. troglodytes*, relative size of the epiphyseal joints and diaphyseal mid-sections of the distal segments of the upper limb (radius and ulna) are significantly greater in *Pan*. These structural distinctions probably reflect the importance of non-compressive loading regimes coincidental with an increased frequency of suspensory postures in *Pan*. Within recent *Homo*, no evidence emerges to support the second hypothesis that intra-specific variance in the relative size of the epiphyses is "constrained" (i.e., less manifest) relative to the diaphyseal parameters.

Relative to the extant African apes, *Australopithecus afarensis* (AL 288-1 "Lucy"), a "hominid" profile comprising relatively small upper limb epiphyses and relatively large lower limb epiphyses. While, the relative size of the femoral head in AL 288-1 is demonstrably smaller in AL 288-1 relative to *GM*ALL compared with recent *Homo,* relative size of the remaining available lower limb epiphyses [FBB & PTB] are not especially small. As such, the expectations outlined in the third hypothesis (see Chapter 2) are confirmed. This observation, in conjunction with the results of other analyses (e.g., Lovejoy, 1975, 1978, 1988; Lovejoy *et al.*, 1973, 2000; Ohman *et al.*, 1997; Ward *et al.*, 2003), support the contention that the lower limb skeletal anatomy of *Australopithecus afarensis* was structurally adapted to bearing compressive, bending, and tensile stresses incurred during terrestrial bipedal locomotion. Comparisons of relative epiphyseal size in the upper limb of AL 288-1 are not consistent with the emerges from the analyses of the relative size of the upper limb epiphyses in AL 288-1 in favour proposal that *Australopithecus afersnsis* maintained a significant arboral component in its locomotor repertoire. These results support the recent findings of C.V. Ward and her colleagues (Ward *et al.*, 2003) using cross-sectional diaphyseal proportions of the *A. afarensis* upper and lower limb.

Exploratory Geometric Morphometric analyses (GPA, PCA and post-hoc testing) of the distal humerus and proximal ulna landmark configurations accurately distinguish recent humans from the extant African apes, *Pan* and *Gorilla.* The projection of the medial epicondyle and the proportions of the olecranon fossa in the African ape distal humerii are not equivalent to the morphology seen in *Australopithecus*. On the whole, while subtle contrasts in the proportions of the capitulum exist in *Australopithecus* and *Homo*, there is considerable variability in capitulum morphology in either genus. No discernible morphological segregation of australopithecine distal humerii from those of later "archaic" *Homo* humerii (e.g., Neandertals) is apparent. The results obtained in this study apparently contradict previous studies using linear metrics and multivariate analyses and the recent 2D morphometric analysis of Bacon (Bacon, 2000).

Similarly, with respect to the proximal ulna, no significant morphological differences are apparent when direct comparisons of the *Australopithecus afarensis* (AL 288-1) and the Middle Pleistocene *Homo* ulnae from Baringo-Kapthurin (KNM-BK 66) were undertaken. Both specimens are far removed from the African apes (*Pan* and *Gorilla*) on the first Principal Component of the linear tangent space co-ordinates. It is highly likely that the morphological changes between Apes and hominids primarily reflect concomitant adaptations to enhanced structural stability under compressive (knuckle walking) and tensile (climbing) stresses. Previously proposed morphological shape distinctions in the elbow joint of Eurasian Neandertals and EUP & LUP hominids were confirmed for the proximal ulna, but not the distal humerus. The functional significance of the observed morphological differences in Neandertal and Pleistocene *Homo sapiens* might be related to enhanced stability of the elbow joint during arm flexion and supination of the forearm. This explanation is supported by a wealth of comparative observations of Neandertal upper limb morphology (e.g., Trinkaus, 1983*a*; Trinkaus & Churchill, 1989; Churchill, 1994, 1996, 1998; Yokely & Churchill, 2002).

Geometric Morphometric analyses of the proximal femur of African hominoids reveal a suite of morphological features that differentiate the femur of *Homo* from the African apes. These involve changes in the relative proportions of the femoral neck, femoral head and greater trochanter (see Chapter 6), support previous observations on hominid proximal femoral morphology (e.g., Lovejoy & Heiple, 1972; Robinson, 1972; McHenry & Corruccini, 1976*a*,*b*, 1978; Stern & Susman, 1983; Susman *et al*., 1984), and are apparently not allometric. Interestingly, with the sole exception of the AL 333-3 A. afarensis specimen, all remaining fossil specimens can be reliably discriminated from *Pan* and *Gorilla* on PC1. The principal distinctions in the proximal femoral morphology of recent and fossil hominids on PC2 do not support proposed locomotor distinctions between *Australopithecus* and *Homo*. Relative to recent *Homo*, the hominid fossils included her display an increase in the proportions of the femoral neck and a relatively smaller proximal femoral epiphysis.

Allometric analyses of the pelvic girdle and lower limb in recent humans revealed that the "principal determinants' of pelvic shape (see Chapter 3) increase proportionally with increasing medio-lateral pelvic breadth (and presumably with body mass) in recent *Homo*. This supports the fourth hypothesis outlined in Chapter 2. Surprisingly, there is no increase in the relative proportions of the lever arm for the abductor muscles (*Dm* [Ruff, 1995] or BFL [Lovejoy *et al*., 1973; Lovejoy, 1988]) with M-L pelvic breadth in recent *Homo*. Moreover, there is significant sexual dimorphism in the ratio of the load arm/lever arm (*Dw*/*Dm* [Ruff, 1995]) in *Gorilla*, *Pan* and *Homo*; biomechanical femoral neck length [*Dm*] is proportionally shorter in females relative to males. The proposal that a significant positive relationship would exist between the ratio of *Dw*/*Dm* and absolute femoral head size in recent humans is apparently not supported by the results obtained in this study. As the ratio of *Dw*/*Dm* increases, absolute and relative femoral head size decreases, and this might explain the relatively smaller proximal femoral epiphysis in fossil hominids whose *Dw*/*Dm* proportions exceed those seen in more recent humans (e.g., *Australopithecus*). The relatively small proximal femoral epiphysis observed in the Middle Pleistocene specimen from Atapuerca cannot be simply explained by distinctions in its anterior pelvic proportions.

Statistical comparisons of femoral midshaft and sub-trochanteric diaphyseal proportions in recent *Homo* suggests that relative medio-lateral, not relative antero-posterior, "buttressing" occurs with increased absolute and relative body size in recent humans. Moreover, calculated sectional diaphyseal area (based upon the equation for an ellipse) at the femoral midshaft and sub-trochanteric planes is negatively, not positively correlated with anterior hip proportions [*Dw*/*Dm*]. The finding that M-L and A-P diaphyseal indices were negatively correlated with the body mass load arm/lever arm proportions in recent humans indicates that a substantial level of intra and inter-sample variability in femoral shaft shape in recent humans is not a response to alterations in anterior pelvic proportions. Thus, these data provide only partial substantiation of the fifth hypothesis of this thesis.

Nevertheless, the observation that Eurasian Neandertals femora differ from Eurasian Upper Palaeolithic in their sub-trochanteric diaphyseal proportions (especially their A-P indices) suggests that their unusually wide body mass load arm (*Dw*) may have profoundly influenced the nature of immediate forces acting on the proximal diaphysis. These findings support the recent results obtained by Weaver (Weaver, 2003) in his analysis of femoro-pelvic proportions and diaphyseal morphology.

males and females (at least ten of each) in two populations displaying distinctly different body proportions.

With respect to the fossils, such data is impossible to gather. Nevertheless, skeletal collections offer the best chance of surveying differences in hominid hip form, such as those elaborated in this study. Epoxy resin casts of the available pelvic specimens in the Virchow Collection and those of the Natural History Museum in London could be constructed using 3D scanning equipment and relevant software to manufacture moulds. Three-dimensional casts of the pelvis of *Australopithecus*, *Homo erectus*, *Homo heidelbergensis* and Eurasian Neandertals can also be constructed. Strain gauges embedded in relevant areas of interest (e.g., the femoral neck, superior pubic ramus, anterior ilium and sacro-iliac buttress) could be used, in conjunction with photo-elastic stress measurement protocols, to directly quantify experimental forces in the hip joint modelled on observed force data obtained from a limited number of experimental subjects.

Recommendations for future research

The results generated by this research identify significant questions that remain to be answered by future research, in addition to some specific issues regarding further improvements to the analyses themselves.

The two-dimensional pelvic "model" commonly used in functional assessments of the hominid hip is almost certainly too simplistic and suffers from the serious drawback that forces are calculated using actual morphological parameters (see Chapter 3). The calculated forces are not independent and, as such, a proper examination of the mechanical effects of observed differences in hip joint morphology in recent and fossil humans, particularly the anterior pelvic proportions (*Dw/Dm*), cannot be addressed. There are two viable research designs that can make significant advances towards addressing this problem.

A first involves the direct assessment of the forces acting at the hip joint and the proximal and midshaft femoral diaphyses using in-vivo measurement protocols. CT examination of the pelvis and lower limb, in conjunction with a few basic anthropometric measurements can accurately capture the relevant dimensions of the pelvis in volunteer subjects. Actual forces in the hip joints can be assessed in these subjects using kinetic and kinematic measurement equipment, such as piezo-electric pressure plates to determine Joint Reaction Force and electromyography to determine Abductor Force. Unfortunately, collecting this data is expensive and time consuming and in order to carry out an informative study, we would require effective samples of

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