Morphological Integration in Developing Limbs of

Homo sapiens and *Papio ursinus*

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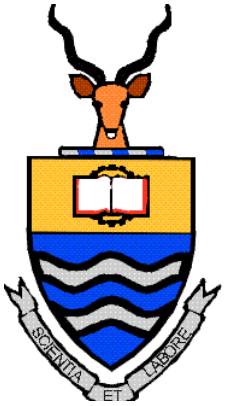
A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.



SCHOOL OF ANATOMICAL SCIENCES
UNIVERSITY OF THE WITWATERSRAND, MEDICAL SCHOOL
JOHANNESBURG

January 2008

Declaration

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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Manoj Dayal Chiba

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Abstract:

Previous studies have documented the locomotor pattern of bipedal and quadrupedal primates based on gross morphological or cross-sectional differences. Although these studies provide a measurable amount of understanding they fail to allow one to understand the emergence of these differences ontogenetically. Many researchers have opted to use genetic or epi-genetic factors as reasons for the differences. It has been suggested that the manner in which traits change may be constrained or facilitated by their levels of integration, and therefore morphological integration may be viewed as a source of evolutionary constraint.

Ontogenetic samples of 92 humans and 20 baboon skeletons were analyzed for differences and/or similarities using metric and cross-sectional geometric data, of the femur and tibia. The analysis included the computation of regression techniques, bi-variate and multivariate analysis. Contrary to expectations, results indicate no significant difference between species. This suggests that ontogenetically both humans and baboons have similar growth trajectories and the epi-genetic factors due to differing locomotory modes have minimal influences. However, both epi-genetic and genetic factors need to be explored further. Furthermore, both metrical and cross-sectional data provide a clear understanding into this pattern of morphological integration and thus should be used together in the analysis of locomotor patterns.

Dedication

To my Dad

Your constant confidence, love and dedication have always supported me through failure and success, beyond what words can express, without you this piece of work would never be complete. Thank you for clearing a difficult road Dad… You will remain my pillar of strength.

And to my late Mum,

from high above the clouds I know without you this would never be possible your support is dearly missed, your humor still remains unparallel and the faith you showed in me unknown to anyone, I say this with a tear in my eye and a sore heart … thank you with love and appreciation.

Acknowledgements

I wish to acknowledge my gratitude to the many people that have contributed towards the completion of this thesis. First, this thesis would not have been completed without the support of my supervisor, Dr Andrew Gallagher. I thank him for his guidance, astute suggestions, support and patience. He has been a model to me with his unfailing work ethic and professionalism. His friendly demeanor has made this thesis a great joy over the two years. Thank you for your time and effort.

For the financial support which made this research possible. I would like to extend my thanks to the Paleontological Scientific Trust (PAST); the team of Paleo-tours (Marianne Robinson and Dr Colin Mentor); the Centre for Health Sciences Education (CHSE) and Reproductive Health Research Unit (RHRU). Dr Kevin Kuykendall from the Fossil lab and Victoria Gibbon.

A special thanks to my loving wife Bindya Vyas for your unfailing support and dedication.

To Professor Emeritus Philip V. Tobias, for his constant chats and support in the corridors of the department. To Professor J.C Allan, for the talk and 'lecture' on statistics.

A special note of thanks must go to Dr. Mofokeng from the Johannesburg Hospital for allowing me to use the Computer Tomography Scanner. Fiona who did the scanning on

that Sunday morning. This thesis would not have been applicable had I not had access to the equipment. To Claudia Vergie, for waking up early that morning and helping Dr Gallagher and I to scan, your assistance is greatly appreciated. To Elijah Mofokeng, who always kept his door open for me to use the Raymond Dart Collection of Skeletons, and the friendly banter and constant encouragement. To Ruth Mika from the Museums Comparative collection. To the numerous technical staff and secretaries of the department of Anatomical sciences.

A special note of thanks must go to my friends, the usual suspects outside the medical school, drinking coffee and puffing away on cigarettes, in no order of importance, Altaf Khumree, Olebogeng Moeng, Janeen Jeena, Nivashnee Pather, Adhil Bhagwandeen, Elin Devereaux, Salman Khan, Yin Hlaing, Claudia Vergie, Muhammed Spocter, Brandon Billings, Victoria Gibbon, and Allan Gould.

Last but never least, to my dad (Dayal Chiba), sister (Ameeta Tribhowan), brother in law (Sahil Tribhowan) and niece (Maya-Mahima Tribhowan), thank you for the unconditional love and support.

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Special Note:

The compact disk (CD) attached with this MSc thesis contains the following supplementary data in the file names:

- CT Raw Data- Microsoft® Excel File
- Raw Metric Measurements-Microsoft® Excel File

1.1. Introduction:

The manner in which an adult bone reaches its final form is largely speculative; with the entirety of bone form being the primary focus for those interested in the human fossil record (Lovejoy *et al.,* 2002). This phenomenon of bone growth is further compounded by the lack of understanding in ontogenetic development, which according to Alemseged *et al.,* (2006), is central to the study of human evolution. In order to gain a 'holistic' understanding of bone growth, a concept that needs to be explored is that of morphological integration. Morphological integration refers to the tendency for structures to show correlated variation, because they develop in response to shared developmental processes or function in concert with other structures (Hallgrimsson *et al.,* 2002). Zelditch and Fink (1996) have proposed that organisms are not merely collections of autonomous parts; rather their parts interact with each other throughout life. These sentiments are vital as studies have shown that correlated growth and development occurs and this is further understood to be the reason for the gross morphological symmetry observed within species (e.g. Rosenburg, 2003). While many studies focus on observed correlated variation, few studies allow one to fully understand the post-natal developmental significance of these correlated changes, especially in paleo-anthropological research with particular reference to bipedality. Morphological integration may provide valuable insight into differing patterns of integration, based on differing locomotor modes between species (namely, *Homo sapiens* and *Papio ursinus*). Lumner (1939) in Jungers (1984), used mixed cross-sectional data rather than longitudinal data to assess the manner in which certain limb segments scaled

developmentally with other segments (e.g. arm versus leg); to determine if one could extrapolate growth trends in one species and thereby account for proportions in a closely related but larger species. Unfortunately, Lumner's (1939) study did not take into account the locomotor function/mode of the species with differing locomotor modes. The anthropoid species analyzed have differing habitual locomotor modes.

1.1.1 General Overview of Bone Properties

Bone is a living tissue capable of changing its structure as a result of the stresses to which it is subjected to (Snell, 2004). The growth of bone is a result of an increase in cell number, cell size and extra cellular ground substance (Buchanan and Preece, 1993). In long bones this occurs in the epiphyseal growth plate through the proliferation and hypertrophy [enlargement of an organ or part of the body due to increased size of constituent cells (MedicineNet, 2008)] of chondrocytes, synthesis of their surrounding matrix and mineralization of this cartilage under the regulation of local and distant factors. This provides one with a very basic understanding of bone growth.

Bone in its nature is made-up of compact (cortical bone) and spongy bone (trabecular/cancellous bone), figure 1. In brief summary, cortical bone is an anistropic material that is tough (Buchanan and Preece, 1993); it lies beneath the periosteum (thin membrane covering bone) and is reported to be thicker in the shaft than in the extremities (Keaveny and Hayes, 1993). Trabecular bone is relatively compliant and very heterogeneous, with this heterogeneity making the material properties very difficult to

generalize; furthermore this arrangement of trabecular bone is optimally organized to resist loads by functional activities (Huiskes, 2000). It is subsequently trabecular bone density that is often used in order to ascertain the functional activity and loading history of bones.

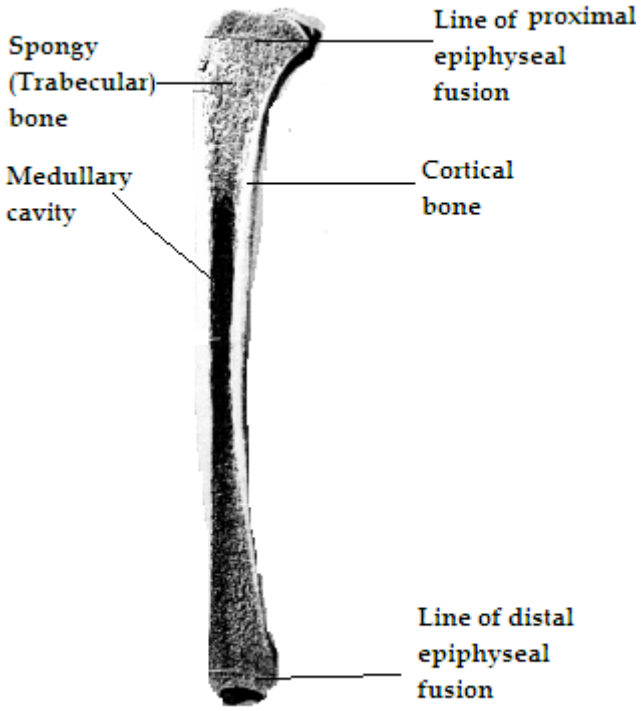


Figure 1: A left tibia sectioned through to show key bony elements on the gross anatomy of a human long bone (White and Folkens, 2000 p: 24)

1.1.2 Cross-Sectional Geometric Properties of Bone

From the preceding section it is apparent that bone is primarily made-up of cortical and trabecular bone. These constituents of bone further invoke general mechanical properties

and loading modes of bone, which include tension (i.e. force related to stretching); compression (i.e. subjection of a material to compressive stress); bending (i.e. structural element subjected to a lateral load); shearing (i.e. deformation of a material substance in which parallel internal surfaces slide past one another); torsion (i.e. twisting of an object); axial force (internal force whose resultant force is acting along the longitudinal axis of the structure) and combined loading (i.e. combination of torsion and compression primarily) (Ryan, 2002). Cross-sectional geometric properties such as size and shape of cortical and medullary areas and polar moments of area are reported to be reliable estimates in the determination of locomotor patterns (Kimura, 1994). Cortical area is defined as the area of bone consisting of cortical bone; total area is defined by the entirety of the cross-sectional area of the bone (i.e. cortical area and medullary area) and the polar moment of area being defined as the measure of ability to resist torsion (Wikipedia, 2007).

1.1.3 Genetic and Epi-genetic Factors

Lieberman *et al.,* (2004) reported that genetic and/or epi-genetic factors contribute an integral part in the moulding of a skeleton. Although, from the above conclusion it is possible to deduce that three factors are present, namely (i) genetic, (ii) epi-genetic and (iii) combination of genetic and epi-genetic; many researchers (e.g. Forwood and Burr, 1993; Nunamaker *et al.,* 1990; McLeod *et al.,* 1998 to name a few) however, have opted to use genetic or epi-genetic factors only.

Genetic factors are genetically determined constituents, which are pre-determined and are under the control of local and distant factors. These are to some extent expressed in the phenotype of an individual. In comparison to epi-genetic factors which are environmentally driven, and although possible to be seen in the phenotype are dynamic rather than static.

Bone form and the adult maintenance of it is a product of an integrated syncytial response system that is principally guided by the transduction of external loads (Nunamaker *et al.,* 1990; McLeod *et al.,* 1990 and Huiskes, 2000). However, many researchers [e.g. Bryant (1982); Javois (1984); DuBoule (1994); Shubin *et al.,* (1997); Carroll *et al.,* (2001)] have reported that external bone morphology is dictated by an integrated system of expressed gene arrays; with Rubin (1984), summating this by reporting that although the predominant responsibility of the skeleton may be to withstand the extremes of physical activity, it does not necessarily follow that the strains generated during this activity are what drives the skeleton's morphology. Furthermore, Forwood and Burr (1993 p: 90) report that "… the adult skeleton is conservation rather than acquisition…" indicating that genetic rather than epi-genetic factors are important in the morphology of final adult skeletal form. The above arguments highlight the two schools of thought, i.e. genetic and epi-genetic. However, a combination of the two (epi-genetic and genetic factors) is not a new school of thought as Lovejoy *et al.,* (2002) has identified that mechano-transduction, especially in the growing skeleton, is to provide the necessary threshold values required for implementation or maintenance of patterns of growth guided by positional

information. This conclusion indicates that both genetic and epi-genetic factors are necessary in leading up to the final growth pattern.

1.1.4 Age Effects on Bone Growth

The effect of age on the geometric properties of bone (cortical area and total area) has been reported by numerous authors (Martin and Atkinson, 1977; Ruff and Hayes, 1982; Ruff, 1992; Kimura, 1994); with older individuals showing decreased density and strength. However, this effect on bone will not be explored, as the study only considered individuals from birth to adulthood.

1.1.5 Human Evolution and Bone

From an evolutionary viewpoint, bone is not required to be designed to a mechanical optimization rule. They (bones) must be sufficiently light, adaptable to environmental factors; repairable; stiff and the strength must be adequate for daily usage without fracture (Huiskes, 2000).

Human evolution is generally associated with four key events, namely (i) terrestriality; (ii) bipedality; (iii) encephalization and (iv) culture (Lewin, 1999). The sequence in which these hallmarks have occurred is under much debate. One key feature of hominid evolution is however, bipedality. Bipedality is defined as the ability to walk upright on

two limbs; and is generally a demarcating feature of belonging to human ancestry or not. The reason for this trait evolving may have been for numerous reasons:

1. carrying (Hewes 1961, 1964, 1973; Kortlandt, 1967; Lovejoy, 1981)
2. display or warning (Livingstone 1962; Westcott, 1967; Ravey 1978)
3. new feeding adaptations (DuBrul, 1962; Jolly 1972)
4. combination of the above (Sigmon, 1971; Rose, 1976)

According to McHenry (1982), theories on the origin of bipedality are by their very nature important and speculative. They are important because they involve the first change that differentiated the hominid evolutionary lineage from the rest of the animal kingdom; and speculative because they require reconstruction of so many unknowns, especially morphology, behavior and ecology of the last common ancestor and first hominid. Paleo-anthropologists unfortunately do not have living hominids (except humans) to work with or observe, and hence have to rely on fragmentary skeletal remains in order to determine locomotory patterns. The best evidence for locomotor adaptations is given by the: (1) position of the foramen magnum; (2) shape of the spine; (3) anatomy of the pelvis; (4) anatomy of the femur; (5) anatomy of the knee; (6) anatomy of the foot and (7) arm/leg ratios. This study is based on the anatomy of the femur (4); arm/leg ratios (7) and the anatomy of the tibia. With finds such as *Australopithecus afarensis* (MVP-1 and A.L. 129-1A +B); *A. africanus* (Sts 14); *Homo neanderthalensis* (e.g. Kebara 2) and unknown species (DIK-1-1); studies into post-crania are needed in order to accurately interpret locomotion and hominid ancestry without damaging the specimens.

Ohman *et al.,* (1997) and Lovejoy *et al.* (2002) have reported that a single fossil (e.g. part of a limb bone) can serve as singular evidence of overall gait pattern. However, numerous researchers have reported dual gait patterns, i.e. non-exclusive bipedality or quadrupedality. Furthermore, the ontogenetic growth patterns of species are poorly understood, especially in highlighting differences in locomotory modes.

With all of the above in mind, technology such as Computer Tomography (CT) has been identified by numerous authors (e.g. Ruff and Leo, 1986; Beamer *et al.,* 1996; Ohman *et al.,* 1997; Lovejoy *et al.,* 2002) to be able, with correct analyses, to find similarities and differences in locomotory patterns, with regard to changes in bone architecture. Various authors [e.g. Thompson (1917); Gould (1966); Schmidt-Nielsen (1975)] have reported that body-weight places severe structural and mechanical constraints on the shape of vertebrate long bones and therefore, the thickness of the bone should be studied in its relationship to body weight or size and, in addition to the relative, rather than merely the absolute length of the bone (Schultz, 1953).

The total area of bone cross-sections is an indicator of the volume of bone substance, which also indicates resistance against axial force. In long bones axial force is usually not important from the adaptive viewpoint (Kimura, 2006); rather the polar moment of area is of greater importance (Kimura, 1974; Lanyon, 1982). In contrast Lieberman *et al.,* (2004) concludes that cross-sectional properties do not necessarily provide reliable data on the orientation of loads to which bones are subjected. If any of the above or other arguments highlighted earlier hold true, this study may provide a clear resolution in favor of one or

the other. With this study being ontogenetic in nature, in terms of bone growth, many researchers have argued that mechanical stimulus in terms of loading, may or may not influence the final adult form. Hert *et al.,* (1971) has proposed that remodeling of bone as a result of mechanical stimuli is vitally important and is not restricted to a particular stage in life, and may occur throughout life; however, the features of bone in terms of locomotion are primarily influenced during growth.

Activity patterns are apparent at the mid-shaft level (Kimura, 1974). Although this study compares gross values, and not statistically subjected to account for body size, it may provide valuable insight in testing the adaptionist paradigm of activity causing changes in bony elements.

The debate surrounding change or reasons for change in internal bone architecture continue. The differences and/or similarities in this architecture seen using CT scanning are equivocal. Lovejoy *et al.,* (2002), reports that a larger cross-sectional area medio-laterally (in the proximal femur at the neck shaft junction) indicates bipedal locomotion, and is consistently different from most ape-femora (general quadrupedal locomotion) at the same locomotion. Ohman *et al,* (1995, 1997) propose a consistent difference between bipeds and quadrupeds in the superior-inferior cortical bone distribution of the femoral neck. The argument follows that features on the proximal femur are based on alterations of the musculoskeletal anatomy (Aiello and Dean, 1990; Lovejoy *et al.,* 2002), thus indicating that the amount of usage of these muscles may indeed have some effect on the bone. Furthermore, patterns of morphological adaptations are manifested in the pelvis

and proximal femur (head and neck commonly) concerning hominid bipedality (Lovejoy, 1988). The structure of the proximal segments of limb bones (upper limbs) are more influenced by body shape (Ruff, 1994) than is the structure of the distal segment of limb bones (lower limbs), so that differences in activity alone may be more clearly discernable in the distal segments of limbs (Ruff *et al.,* 2006).

Few studies have focused on the middle and distal segments of the lower limbs. Stock (2006) reported that the relative strength of the distal limbs (e.g. femur and tibia) show a greater correlation with habitual activity patterns. Furthermore, mid-shaft robusticity is indicative of locomotory patterns (Kimura, 2006).

Although few post-cranial finds are diagnostic (in locomotory terms) [e.g. AL 129-1A + 1B, *A. afarensis* with a well-preserved knee joint to indicate bipedality (Johanson and Edgar, 2001) and the DIK 1-1 juvenile specimen with a genu valgus (Alemseged *et al.* 2006) to indicate bipedality]. This study in part hopes to address and resolve this issue of sub-adults and provide a clear resolution to ontogenetic locomotor development. Few studies have attempted to wed information on ontogenetic scaling (i.e. allometry, discussed in detail below) with functional inferences (Grand, 1972; Jungers and Fleagle, 1980; Shea, 1981). According to Jungers and Fleagle (1980), ontogenetic allometry of post-cranial elements is a valuable tool in functional morphology as information on divergent locomotor adaptations in closely related species can be extracted from a scrutiny of the specific developmental pathways that culminate in adult differences. Although Cheverud (1982b) has reported that skeptism surrounds the extrapolation of

ontogenetic allometry to evolutionary allometry, because to do so would necessarily imply that the ontogenetic vectors are not genetically correlated, no evidence of this exists.

1.1.6 Intermembral Index

The intermembral index (IMI) is a common manner in which the relative lengths of fore and hindlimbs can be compared. Humans in general have an IMI of 72, while the bonobos have an IMI of 100 and 150 for some gibbon species (Duncan, 1995).

Humans have longer lower limbs than upper limbs in comparison to most other primates (Schultz, 1953 and Jungers, 1985). Ruff (2002) has shown that certain colobines and humans do show overlapping proportions for humeri to femori comparisons. Differences interspecifically in intermembral proportions have further been reported to develop prior to birth (Buschang, 1982), and are further increased during the growth of the limbs when they are used for locomotion (Jungers and Hartmann, 1980; Buschang, 1982) and therefore, intermembral length proportions are in part dependent on normal mechanical usage of limbs (Ruff, 2003). Rollison and Martin (1981) have reported that primate limb proportions are influenced by intricate combination of body-size and locomotor specialization. However, as Aiello and Dean (1990 p: 250), have reported "…the higher IMI in the large apes is primarily from an alteration in the relationship between the lower limb length and body weight rather than upper limb length and body weight…" Many biologists have further shown that the relative lengths and robustness of the humerus are diagnostic in terms of locomotor adaptations. Cartmill (1974) has reported that in

primates the relative forelimb length increases at a faster rate than the relative hind limb indicating the mechanical pre-requisites of this mode of locomotion (quadrupedalism). The opposite trend was observed in terrestrial primates. These intermembral differences are tested in this study, in an attempt to address developmentally when these changes occur, and provide a further understanding.

With all of the above in mind, this study attempts to test the theory of adaptation on the differing locomotor patterns, with the use of CT scanning, linear measurements and formulae, from an ontogenetic viewpoint.

1.2 Allometry and Constraints

1.2.1 Allometry

In order for one to fully understand morphological integration it is important to understand the primary associated concepts', namely allometry and constraints. Allometry is a type of 'specialized' form of scaling and refers to the structural and functional consequences of differences in (or scale) among organisms of more or less similar design (Jungers, 1984). Allometry is defined as the relationship between changes in shape and overall size (Levington, 1988), and may be divided into four sub-categories, namely, (1) ontogenetic; (2) phylogenetic; (3) intraspecific and (4) interspecific (Gould, 1966). The category of importance to this study is category 1 (ontogenetic allometry). According to Gould (1966) this category is dynamic, i.e. constantly changing throughout life as individual approaches adulthood. In this context, the long bones of the body will/ or should show correlated growth throughout development in accordance with the

relationship between changes in shape and overall size. Furthermore, with the use of an allometric approach it may be possible to elucidate the differences between species, due to the functionality of functional morphology and biomechanics. While it is known that humans and baboons have differing modes of locomotion differences in the long bone growth trajectories are largely unexplored between these species.

1.2.2 Constraints

Constraints are limitations on processes and/or patterns of evolution, growth, form and function. Constraints may be phylogenetic, functional, developmental or structural (Maynard Smith *et al.,* 1985) and are evident in patterns of invariance (Lieberman *et al.,* 2000). Cheverud (1995, 1996) states that integration revealed by complex patterns of correlation and co-variation, and constraints affecting variation and in turn integration, may be analysed by examining patterns of invariance. The evidence pointing towards the existence of constraints is revealed by the use of allometry (Lieberman *et al.,* 2000).

In an attempt to use an open-minded approach to evolutionary theory, Gould (2000), has indicated that there are three major influences on the genesis of form, namely, adaptation, phylogenetic history and structural law of form. These forms may further assist in coming to logical conclusions as to the morphological integration of developing limbs.

1.3 Objective of Study:

This study will examine and test the theory of adaptation and bone remodeling due to differing modes of locomotion in *Homo sapiens* and *Papio ursinus,* from a developmental aspect, for the different lower limbs traits in question.

Null hypothesis 1: Humans and baboons show significant differences in metrical measurements due to differing locomotory modes.

Alternative hypothesis 1: Humans and baboons do not show significant differences in metrical measurements due to the locomotory modes.

Null hypothesis 2: Humans and baboons show differences in the level of significant correlations in cross-sectional properties due to the differing locomotor modes.

Alternative hypothesis 2: Humans and baboons do not show differences in the level of significant correlations in cross-sectional properties and are thus not due to the locomotor modes.

2. Materials and Methods:

2.1 Samples

Analyses are based on 126 specimens of *Homo sapiens* (n_{total}=92, n_{males}= 44, $n_{females}$=31, $n_{unknown}$=17) and *Papio ursinus* (n_{total}=20, n_{males}=12, $n_{females}$=4, $n_{unknown}$= 4), respectively. Male and female specimens were pooled, within respective species. Skeletal material was obtained from the Raymond Dart collection (humans) and the comparative collection of the Hunterian Museum (baboons), School of Anatomical Sciences, University of Witwatersrand. The human sample was exclusively African, in order to minimize the variation in body proportions that occurs between different populations groups, and is manifested during post-natal ontogeny (Eveleth and Tanner, 1990). The preservation of the specimens is relatively the same. The method of maceration is identical within both species of primate, and hence will not alter the consistency in terms of mass and hence fat content. While the age distributions are important within each species, the definition of pre and post adolescents differs between the species, based on life history parameters, and a categorical system was used to incorporate both humans and baboons, based on the relative definitions of each species. The age distributions within humans and baboons are provided in Appendix B and sub-divided into categories1 [infant- second month to end of lactation, (Bogin, 2001)], category 2 [juvenile- ages 7-10(girls) and 7-12 (boys) in humans, (Bogin, 2001) and 3-10 years in chimpanzees, (Holly-Smith *et al.,* 1994), and based on museum classification in the case baboons] and category 3 [sub-adult- 5-8 years after the onset of puberty in humans, (Bogin. 2001) and eruption of last permanent teeth

to longevity in chimpanzees, (Holly-Smith *et al.,* 1994) and museum classification in case of baboons].

2.2 Metric Measurements

In order to test the objectives previously outlined, a series of simple linear dimensions, epiphyses, diaphysis, mass, medio-lateral and antereo-posterior proportions of the femur and tibia were collected (see Appendix A, table E and table F) on individual skeletons using the Mitutoyo™ digital caliper (0.01mm precision), osteometric board (1mm precision), flexible tape measure (0.1cm precision) and a KERN® EW balance scale (0.1g precision). In addition to the aforementioned measurements, the mass of the clavicle, humerus, radius, ulna, sacrum, femur and tibia were taken. The reasons for only taking those masses were due to the inconsistency in preservation of the other skeletal elements of the body. The definitions of these measurements is listed in Singh and Bhasin (1968), von Driesch (1976), Bräuer (1988), da Silva *et al.,* (2003) and Rosenburg (2003), and were measured according to standard protocol. In baboons only individuals categorized as infants, juveniles and sub-adults were used (based on catalogue classifications). In the human sample, only individuals from 0-18 years of age were considered. Measurements were taken on the left and right sides of the skeletons.

2.3 Computer Tomography Scanning

In addition to the standard metrical measurements, left femora and tibiae were subjected to Computerized Tomography (CT) scanning on a Philips CT Brilliance ® CT scanner, at the Department of Radiography Johannesburg General Hospital. Digital images of the selected cross sections were saved for further analysis. Bones were scanned at the following locations (2mm slices, for reasons that very high resolution and smaller slices were not deemed necessary for such a project and inherently due to the constraints placed on the use of the CT scanner by the "owners"). The horizontal range used was 192cm and the vertical range of 52cm as parameters of the scan field. The reconstruction algorithm is that of expectation-maximization and the calculating of this algorithm are outlined as p (z|y, _) = p(y, z|_)/p (y|_); where y= incomplete data consisting of values of observable variables, z= missing data, p=joint probability density function and _= parameters given (Wikipedia, 2008)

1) Femur
   a) 10% - below the greater trochanter (see figure2)
   b) 50% - mid-shaft (see figure2)
   c) 90% - above the distal metaphysis (see figure 2)

2) Tibia
   a) 10% - below the tibial tuberosity (see figure 3)
   b) 50% - mid-shaft (see figure 3)
   c) 90% - above the distal metaphysis (see figure 3)

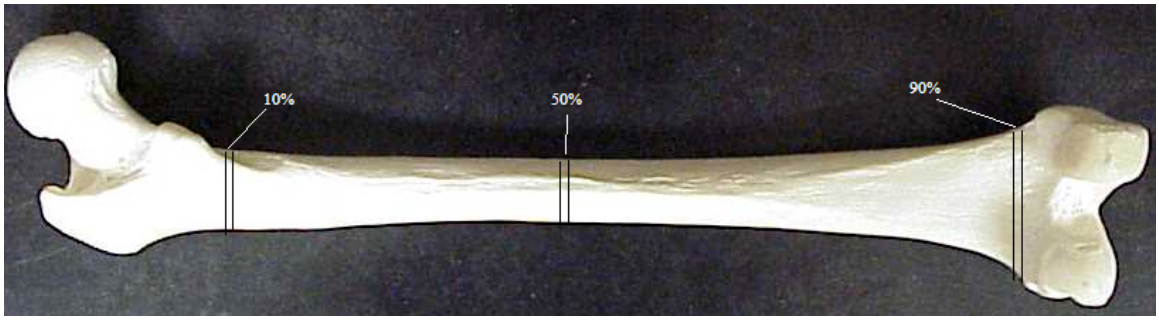


Figure 2: CT scanning markers femur

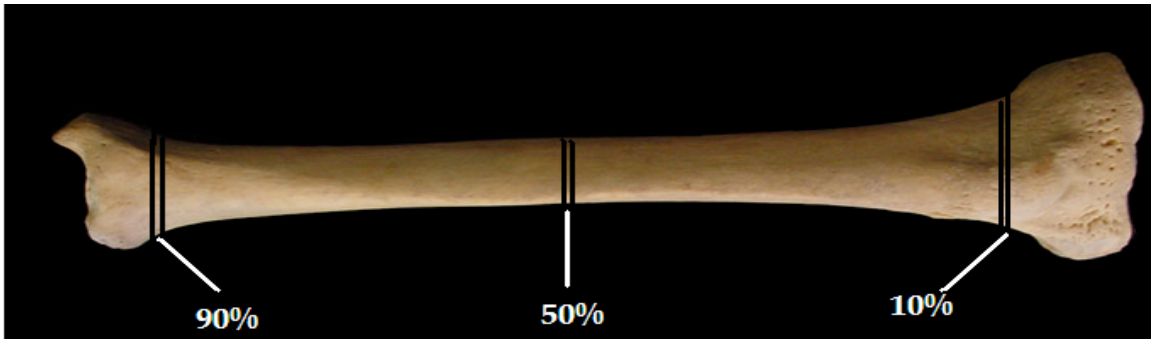


Figure 3: CT scanning markers tibia

CT scanning of the bones was conducted independent of sex of the individuals. Ontogenetically sex of the individuals, in my opinion would have very little influence on the gross CT results, and if they did have an influence, clumping of the data would be observed within each species for the sex specific specimens, (i.e. males of certain age categories would clump together and females of a certain age would clump together), however, in studies with larger samples sizes of adolescents the sex specific changes may be observed. This is however in light of there being no accounting for size differences

within each respective species. This project has accounted for the sexual size difference that may be observed by the use of ratios (see section 2.4).

Furthermore, it should be well noted that in the use of cross-sectional areas, the amount of activity undertaken by individuals measured and analyzed is an important facet in interpretation of the results during post-natal ontogeny and there is no direct way to compare activity levels (Ruff, 1999a). It is however documented, that the variation due to mechanical loading within each sample may not be great (Ruff, 1999). Furthermore, this study is constrained by small age-cohort sample sizes; therefore it was decided in order to obtain a better understanding all individuals were clumped rather than be split into the differing age-cohorts.

2.4 Statistical Methodology:

All analyses were carried out on log-transformed (base 10) data for the two species. Log transformation of data allows for the counteracting of the following problems normally associated with the use of raw data: (1) skewed data; (2) outliers and (3) unequal variations; furthermore log transformed data allows for simplification on statistical models. All data were first tested for normality, and only data that proved to be normally distributed were used in the final analysis (appendix 2).

The accuracy of measurements was determined by the calculation of Lin's concordance correlation co-efficient, P_c (Lin, 1989). Traditionally only P_c values greater than or equal

to 0.9 for the specific measurements are considered for the final analysis; however, it was decided to maintain all variables that are close to 0.9 for the specific measurements (appendix 2).

Growth curves for maximum length versus age of individuals were computed in Paleontological Statistics programme (P.A.S.T) ver. 1.18, using the von Bertalanffy growth equation. This equation is given by:

$$Y=a\ (1-be^{-cx})$$

Where a=estimation of maximum values from data set at hand; b= constant that is estimated to the line drawn; e= exponential; c= growth constant and x= time;
this is commonly used for modeling the growth of multi-celled animals (Brown and Rothery, 1993). The shape of the curves indicated the growth pattern, and when visually assessed may provide valuable information on the patterns of growth within and between species.

Allometry is only used in this project as a biological understanding and the mathematical equation associated with allometry is provided here, but the slope analysis between and within the species is given below. Allometric equation: $Y=aX^b = \log(Y) = \log(a) + b \log X$, where b= the allometric slope. Where b=1, the slope is said to be isometric; b<1, negative allometry (e.g. an increase in body size with a decrease in brain size); b>1 positive allometry (e.g. an increase in body size with an increase in brain size).

To test for significant differences, 99% and 95% significance levels were computed, between bony elements, between the two species, a Students's t-test was performed, using SPSS® version 11. This test indicates sample differences by using the means and the distribution of the sample scores around them (Clegg, 1990).

In order to investigate patterns of inter-relatedness between different variables, Pearson's correlation co-efficient was computed using P.A.S.T ver. 1.18 and SPSS ver. 11.0. Significance levels of 99% and 95% were computed. The critical values were obtained from a table of critical values in Allan (1982) and further used to delineate significance levels for the varying sample sizes for the traits. Subsequently, all the values obtained from the Pearson's correlation co-efficient were squared, in order to obtain the co-efficient of determination (R^2) which gives an indication of the amount of variation in the Y-axis that maybe explained by that in the X-axis (Matlack, 1993 and Sokal and Rohlf, 1995).

In order to be able to make logical assumptions between the two species, the size factor needed to be eliminated. It has been reported by Jouffroy and Lessertisseur (1979), that in order to eliminate size, ratios instead of absolute dimensions are used. The following formulae were used in order to determine the ratios:

1. Log Cortical Area of specific bone/Log Mass of specific bone i.e. LogCA/LogM
2. Log Total Area of specific bone/Log Mass of specific bone i.e. LogTA/LogM

3. Log Polar Moment of Area of specific bone/Log Mass of specific bone i.e. LogJ/LogM

In order to determine cortical areas (CA), total areas (TA) and polar moments of area (J), the CT scans were analyzed using ImageJ (Abramoff *et al.,* 2004) and MomentMacro (O'Neill and Ruff, 2004). Standardized Major Axis (SMA) was computed in SMATR ver. 1.0 (Falster *et al.,* 2003). In order to investigate if relationships existed between mass and CA, TA and J respectively for a specific element section, each was regressed linearly against the mass of the respective element. SMA was used to equate a line passing through the major axis of a roughly elliptic cloud of standardized data (Falster *et al.,* 2003). Therefore, the SMATR ver. 1.0 program allowed for the calculation of SMA which is well suited for the analyzing of bivariate trait relationships, giving the proportional relationship between variables. SMA, calculated on log transformed data, allows for a superior estimate for the line summarizing the relationship between two variables, as it minimizes the residual variance in both the X and Y dimensions (McArdle, 1988; Sokal and Rolhf, 1995). Slopes were first fitted across the species within each group, with a confidence interval of 95 %. In order to calculate observed relationships among groups, the statistical differences in the slope and intercept of group SMA relationships were tested. A SMA slope common to both groups was estimated and the significance of this estimate was determined by testing for significant heterogeneity among group slope estimates by permutation (Manly, 1997). The residuals were then permuted among groups 2000 times; and according to Falster *et al.,* (2003), the common slope and test statistics are recalculated after each iteration. The ability to calculate slopes

allows one to test for the intercept differences amongst species. In order to determine whether the growth rate (given by the slope m) for the two species as being homo- or heterogeneous, a comparison of slopes was performed using SMATR.

An intermembral index was further calculated according to Aiello and Dean (1990). The calculation of this index allows one to make confident assumptions on the mode of locomotion. The formula for calculating this index is:

$$\text{Intermembral Index} = \text{Forelimb length} / \text{Hindlimb length} * 100$$

Following that: Forelimb length = Humerus length + Radius length; and

Hindlimb length = Femur length + Tibia Length.

Mass of the individual elements was determined using a KERN® EW balance scale. Both sides of the above described bones were weighed, and the average calculated for each bone. Where one side was missing, the present side was taken as the average. Skeletal mass of each specimen, within each species, was further calculated by the use of the Geometric Mean (GM) in Microsoft Excel ®, in order to obtain a proxy for the individual's skeletal mass. The above mentioned mass for each bone weighed, was used in the calculation of the GM.

$$GM = \sqrt{Y_1+Y_2+Y_3\ldots..Y_n}$$

The GM is the square root of the summed product of *n* raw variables (Sokal and Rohlf, 1995). TA and CA was calculated as a ratio of mass and used for a direct comparison between species.

Exact randomization comparisons (ERC), were performed in RUNDOM Projects version 2.0 LITE (Jadwiczczak, 2003), which allowed for statistical estimates to be made, by taking random samples from the data at hand. Furthermore, the program allowed for bootstrapping which allows for one to make confident assumptions from small sample sizes about a more general population (Yu, 2003). Analysis of Variance (ANOVA) was performed using this programme as well. The ANOVA test allows one to ask the question, are there one or more significant differences anywhere among the samples? This further allows one to decipher whether the observed values might belong to the same population, regardless of group, or whether the observations in at least one of the groups seem to come from a different population. The answer to such a question lies in the calculation and comparing of the variability of values within groups to the variability of values between groups (Daniel, 1999).

In order to test if significant differences or similarities, between correlation matrices between species exist, the Mantel test was performed using XLSTAT®. This test allows one to understand if significant differences or a similarity between observed correlations occurs.

The usage of descriptive statistics (e.g. standard deviation and co-efficient of variation) is often misleading in post-natal developmental studies, as the observed variations/ results obtained from these statistical tests, are not due to sample variations (as would be seen

for specific traits in only adults for example), but rather due to a gross difference between the age of individuals.

2.4.1 Determination of Measurement Error

For each variable, within each species, on each side, was first visually assessed to determine normality, and second the resultant probability plot correlation coefficient (PPCC) value from the normality plot was further assessed to determine normality (see Appendix B for normality plots and PPCC values). The P_c values obtained are reported in table 1, and range from 0.999 (maximum length of humerus, maximum length of the femur, medio-lateral mid-shaft diameter of the left femur and the maximum length of the tibia) to 0.763 (mid-shaft circumference of the left radius)

Table 1: P_c values obtained for all variables

Bone	Variable	Pc Value Left	Pc Value Right
Femur	Maximum length	0.999	0.999
	A-P mid-shaft diameter	0.993	0.989
	M-L mid-shaft diameter	0.999	0.992
	Sub-trochanteric M-L diameter	0.996	0.995
	Sub-trochanteric A-P diameter	0.986	0.988
	M-L diameter distal shaft	0.935	0.826
	Proximal epiphyseal breadth	0.902	0.931
	S-I diameter femoral head	0.996	0.995
	A-P diameter femoral head	0.92	0.938
	Bi-condylar breadth	0.989	0.995
	Nutrient foramen distance from Proximal metaphysic	0.998	0.995
	Mass	0.996	0.998
Tibia	Maximum Length	0.999	0.999
	Proximal articular width	0.994	0.996
	A-P diameter at level of tuberosity	0.995	0.99
	M-L diameter at level of tuberosity	0.996	0.982
	M-L distal articular breadth	0.981	0.991
	A-P distal articular breadth	0.997	0.997
	A-P mid-shaft diameter	0.998	0.911
	A-P diameter at nutrient foramen	0.996	0.985
	M-L diameter at nutrient foramen	0.99	0.938
	M-L mid-shaft diameter	0.851	0.845
	Nutrient foramen distance form Proximal metaphysic	0.965	0.975
	Mass	0.997	0.999

3. Results:

3.1 Metric measurement results

The determination of Pearson's correlation co-efficient (r), for linear measurements, were computed in order to determine inter-relatedness between the variables. The significance levels computed for r-values were at 99% and 95%; however, due to the varying sample sizes the r-values differed and were taken accordingly from Allan (1982). For the baboon sample the significant r-values ranged from $r > 0.991$ to $r > 0.676$ (i.e. $r > 0.991$ for the mid-shaft circumference versus medio-lateral mid-shaft diameter and $r > 0.676$ for the nutrient foramen distance from the proximal metaphysis versus anterior-posterior diameter of the femoral head). All correlations in the baboon femur are significant at the $P<0.01$ level. In the case of the tibia in baboons, the r-values range from $r> 0.976$ to $r> 0.504$ (i.e. $r> 0.976$ for the medio-lateral mid-shaft diameter versus mid-shaft circumference and anterior-posterior mid-shaft diameter, $r>0.504$ for nutrient foramen distance from proximal metaphysis versus medio-lateral diameter at the level of the nutrient foramen). The correlations for the baboon tibia were significant at the $P<0.05$ significance level. The baboon femur correlations indicate a stronger correlation than in the tibia. This suggests a stronger coupling of variables in the femur than the tibia, due to the higher significance levels correlations.

In comparison, the human sample femur, the significant r-values ranged from $r > 0.974$ to $r > 0.019$ (i.e. $r > 0.974$ for subtrochanteric antereo-posterior diameter versus superior-inferior head diameter, $r > 0.019$ for the nutrient foramen distance from the proximal metaphysis versus medio-lateral diameter distal shaft). It is worthwhile noting that the

medio-lateral diameter of the distal shaft does not correlate significantly at P<0.01 with any of the measured variables in the femur (figure 4 and 5). For the human tibia, the r-values range from r> 0.996 to r> 0.910 (i.e. r> 0.996 for anterior-posterior diameter at the level of the nutrient foramen versus mid-shaft circumference, r> 0.910 for medio-lateral diameter at the level of the nutrient foramen versus mass). With regards to the human tibia, all correlations between the variables were significant at the P< 0.01 level. The significant correlations in the femur and tibia, excluding the medio-lateral diameter of the femur distal shaft versus all variables, are inconsistent across both species; with baboons demonstrating a P<0.05 correlation for the tibia in comparison to the P<0.01 correlations shown by the human tibia. The differences between the species with regards to significant correlations indicate that humans have a more conservative coupling between the variables than do baboons, however, the P<0.01 correlations across both species tends to indicate a constraint among the femoral variables across the species barrier.

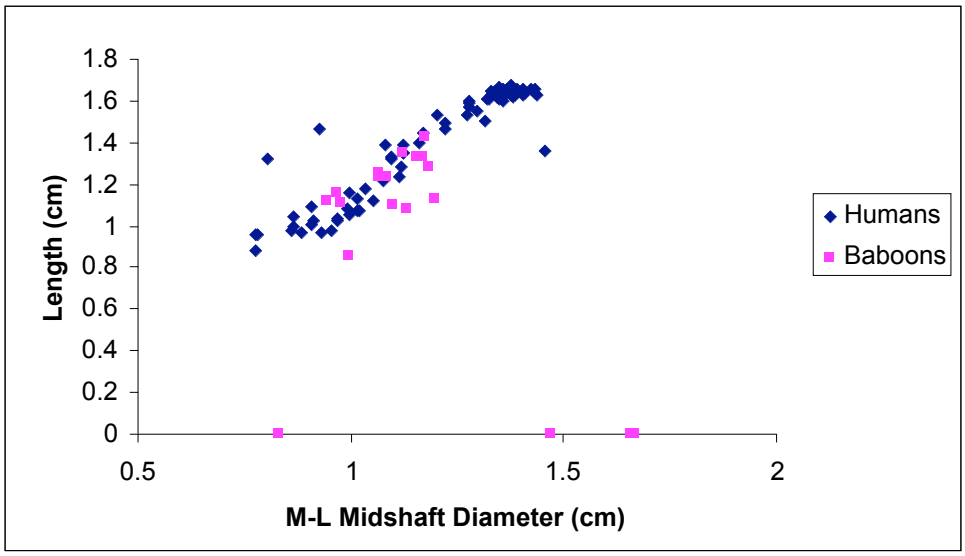


Figure 4: Log Medio-Lateral (M-L) diameter (cm) versus Log Length (cm), Femur, both species

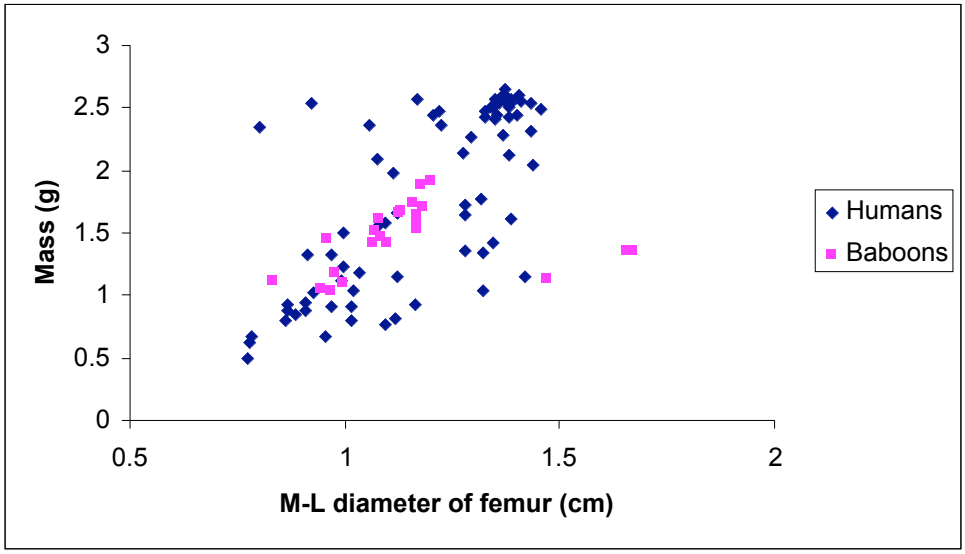


Figure 5: Medio-Lateral (M-L) diameter (cm) versus Mass (g), Femur, both species

To determine if differences or similarities in correlation matrices occurred, the Mantel test was performed. The results from the Mantel test for linear dimensions all showed that the matrices were correlated at the $P< 0.05$ level. For the femur r (human femur; baboon femur) = 0.762; while for the tibia r (human tibia; baboon tibia) = 0.984. These results indicate that the matrices between the two species are correlated, for the respective bones in question (namely, femur and tibia), see Appendix C. These results are consistent with the above findings, whereby the correlations were all significant at the $P<0.05$ level. This again indicates a possible phylogenetic constraint between the species for the variables.

The intermembral index (IMI), figure 6, allows one to make confident assumptions about the mode of locomotion. Baboons have an expected higher average IMI of 107.5 in comparison to the humans whom have an average IMI of 72.5. This trend is further observed in figure 6 below, whereby baboons on average plot above humans comparatively, and over-lap is observed during infancy. Furthermore, graphically the

differences that culminate in adult differences are observed. The graph indicates a maximum length to which baboons' hind and forelimbs grow to before stabilizing, in comparison to humans which continue to grow for an extended period before stabilizing. No statistical analyses were performed on the IMI as it alone indicates a ratio of fore-limb to hind-limb length, in order to determine which (fore-limb or hind-limb) is greater in length.

With respect to the constituents of the IMI, r (human humerus; baboon humerus) =0.673; r (human radius; baboon radius) =0.697; r (human femur; baboon femur) =0.762 and r (human tibia; baboon tibia) =0.984, the matrices are correlated at 95%,
these results are in contradiction of what is expected when one observes the intermembral indices (see figure 6, below). One would expect differences in the matrices as average differences are calculated and visually seen with respect to the intermembral index. Furthermore, in order to determine if the species have homo-or heterogeneous slopes for the IMI, a slope comparison was computed and the results indicate that the slopes are different. This indicates that the growth of the two species differs with regards to the IMI, and can be seen in figure 6. The outliers observed in figure 6 may indicate individuals that were incorrectly measured.

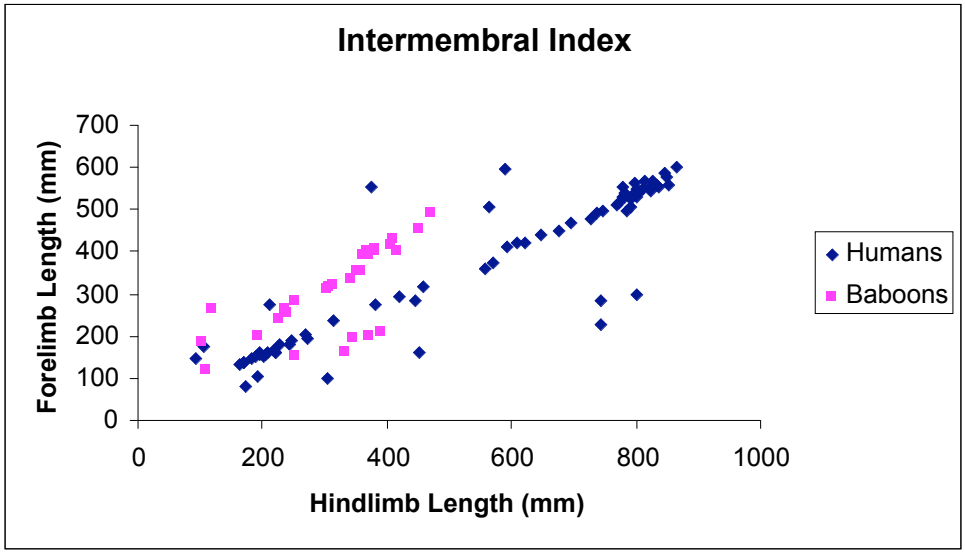


Figure 6: Intermembral Index (Forelimb length/Hindlimb length) both species

3.2 Computer Tomography Scanning results

The r-values determined for the Computer tomography (CT) scanning are presented below. These results indicate if a correlation between the specific elements and bony markers occur. The human proximal femur r-values range from 0.975 [Cortical area (CA) versus Total area (TA)] to 0.772 (length versus mass), with all r-values significant at a 99% significance level. The baboon proximal femur r-values range from 0.98 (J versus TA) to 0.44 (length versus TA); mass and length versus all bony elements (i.e. CA, TA and J) are significant at a lower significance level, i.e. 95%, in comparison to bony elements against each other, and length which correlate at a 99% significance level. These results indicate a discrepancy in the significance levels for the proximal femur

between the species, which may further indicate decoupling between the variables. The human proximal femur shows more conservative correlations while in baboons these correlations are less conserved in terms of strengthing of correlations.

In order to understand if differences or similarities between the correlation matrices occurred, again the Mantel test was used. The results of this test indicate non-significant differences between the proximal femora of both species at a 95% significance level. This is expected as all variables are significantly correlated at the 95% (although not all at the 99% significance level) significance level. This indicates that between the species there is a comparable degree of correlation. The strength of correlations is however, different once analyzed individually (see above). Mass in the CT scanning results presented in tables 2-13, are the geometric mean for the mass of the individual specimens. Mass and length versus bony markers significance levels are different in both species, with length versus TA in the baboon proximal femur being significant at the P>0.05 level. This indicates that the variables are not dependent on each other and the decreased correlations my further indicate a decoupling, though within certain limits.

Table 2: Human Proximal Femur r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.01	P<0.01
CA	0.962411		P<0.01	P<0.01	P<0.01
J	0.975551	0.970769		P<0.01	P<0.01
Mass	0.80859	0.789727	0.78197		P<0.01
Length	0.842	0.817	0.779	0.772	

Table 3: Baboon Proximal Femur r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.05	P>0.05
CA	0.973099		P<0.01	P<0.05	P<0.05
J	0.989411	0.952946		P<0.05	P<0.05
Mass	0.584844	0.609512	0.61607		P<0.01
Length	0.440	0.528	0.482	0.678	

For humans the mid-point on the femur (50%) show r-values range from 0.988 (CA versus TA) to 0.313 (length versus J), while for baboons, at the same bony marker, the values range from 0.99 (J versus TA) to 0.405 (length versus J). r-values in humans are significantly correlated at P<0.01 and P<0.05 significance levels (see table 4), with length versus J being significant at the P<0.05 level. In comparison to baboons, the correlations vary between P<0.01; P<0.05 and P>0.05 (see table 5). These trends are different to those observed in the proximal femur, with length in the baboons being correlated to a lower significance level. This indicates a further decoupling between length and bony markers at the middle (50%) femur. The results show that length varies independently from the bony markers (10%, 50% and 90%) bony elements. This is in comparison top humans whereby he P<0.01 correlations are maintained indicating a more conservative correlation between the variables. However, length versus J in humans is decreased to P<0.05, thus suggesting that in humans, these variables are less conservative and possibly more variable than in baboons.

Table 4: Human Middle Femur r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.01	P<0.01
CA	0.98828		P<0.01	P<0.01	P<0.01
J	0.981116	0.976081		P<0.01	P<0.05
Mass	0.808378	0.785708	0.775978		P<0.01
Length	0.355	0.354	0.313	0.380	

Table 5: Baboon Middle Femur r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.05	P>0.05
CA	0.967417		P<0.01	P<0.05	P>0.05
J	0.990745	0.960067		P<0.05	P>0.05
Mass	0.609769	0.548247	0.615558		P<0.01
Length	0.426	0.390	0.405	0.678	

The distal femur r-values range from 0.92 (J versus TA) to 0.158 (length versus CA) for humans and from 0.97 (J versus TA) to 0.45 (mass versus CA) in baboons. r-values for humans are significantly correlated at P<0.01; P<0.05 and P>0.05 (see table 6). In baboons correlations are significant at P<0.01 and P<0.05 level. The trend in the distal femur, in terms of common correlations is J versus TA, which is consistent across both species, a trend that is not observed at any other marker on the femur. The distal femur indicates a strengthening of correlations for baboons and weakening of correlation in humans with regards to length versus bony elements and mass. This indicates that the

length varies independently against the bony elements and further suggests a decoupling between the variables.

Table 6: Human Distal Femur r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.01	P>0.05
CA	0.844409		P<0.01	P<0.01	P>0.05
J	0.920208	0.913749		P<0.01	P>0.05
Mass	0.789794	0.770523	0.809178		P<0.05
Length	0.226	0.158	0.225	0.301	

Table 7: Baboon Distal Femur r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.05	P<0.01
CA	0.895393		P<0.01	P<0.05	P<0.05
J	0.979187	0.921652		P<0.05	P<0.01
Mass	0.613003	0.452245	0.597172		P<0.01
Length	0.599	0.579	0.618	0.903	

The proximal tibia r-values range from 0.947 (J versus TA) to 0.307 (length versus J) for humans. The baboon r-values range from 0.98 (J versus TA) to 0.28 (mass versus CA). r-values for human proximal tibia are significantly correlated at P<0.01 and P<0.05 significance level, however in baboons; the correlations significant at 99% only include the following: CA versus TA; J versus TA and J versus CA, mass versus the bony

markers show a decreased significance level at 95%. In the case of the proximal tibia, both species show the strongest r-values for J versus TA, suggesting that the two variables are interdependent for the proximal tibia in both species. Mass, however, does not correlate at the P<0.01 significance level in baboons in comparison to humans suggesting a less conservative relationship between mass and the bony elements.

Table 8: Human Proximal Tibia r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.01	P<0.01
CA	0.906223		P<0.01	P<0.01	P<0.01
J	0.947108	0.944397		P<0.01	P<0.05
Mass	0.780284	0.780306	0.741431		P<0.01
Length	0.361	0.333	0.307	0.322	

Table 9: Baboon Proximal Tibia r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.05	P<0.01
CA	0.920164		P<0.01	P<0.05	P<0.01
J	0.984122	0.898037		P<0.05	P<0.01
Mass	0.31379	0.280314	0.359261		P<0.01
Length	0.669	0.632	0.690	0.721	

Middle tibia r-values range from 0.97 (CA versus TA) to 0.148 (length versus mass), for humans, while in baboons the values range from 0.98 (J versus TA) to 0.37 (mass versus

TA). r-values are significantly correlated at 99% for bony elements versus each other, while length versus bony elements at P<0.05 and length versus mass at P>0.05 humans, while in baboons the mass versus TA, CA and J are correlated at a 95% significance level; the bony markers against each other significantly correlate at 99%. The middle tibia does not however show a common trend across both species. Mass is significantly correlated across both species (P<0.01 in humans and P<0.05 in baboons) versus bony markers indicating that mass correlates well with the bony elements and possibly changes in accordance with changes in bony elements. Length is independent of bony elements and does not influence the bony elements in humans, indicating a decoupling. This is in contrast to baboons whereby length correlates significantly at P <0.01 level with bony elements, suggesting a coupling in baboons.

Table 10: Human Middle Tibia r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.01	P<0.05
CA	0.973221		P<0.01	P<0.01	P<0.05
J	0.965126	0.954301		P<0.01	P<0.05
Mass	0.738088	0.731828	0.668955		P>0.05
Length	0.289	0.312	0.267	0.148	

Table 11: Baboon Middle Tibia r and p-values from CT analysis

	TA	CA	J	Mass	Length
TA		P<0.01	P<0.01	P<0.05	P<0.01
CA	0.97824		P<0.01	P<0.05	P<0.01
J	0.9816	0.949355		P<0.05	P<0.01
Mass	0.378276	0.383776	0.419733		P<0.01
Length	0.705	0.713	0.721	0.721	

Distal tibia r-values for humans range from 0.94 (J versus CA) to 0.615 (length versus CA). In baboons these values range from 0.91 (J versus CA) to 0.14 (mass versus CA). The human correlations are all significant at a 99% significance level, while the baboons again exhibit that mass versus TA, CA and J are correlated at a 95% significance level, the bony elements against each other are correlated at 99%. The most noticeable trend in the distal tibia is similar to that of the proximal tibia whereby the highest r-values are J versus CA, suggesting that J is influenced by CA in the distal tibia and TA in the proximal tibia. Furthermore, there is a decoupling between length and mass in the distal tibia, a trend that is not seen in the proximal and middle tibia. In baboons this disassociation between length and mass at the bony markers shows a clear decoupling and suggests length varies independently from the elements in the distal tibia.

The tibia across both species in comparison to the femur indicates an opposite trend, i.e. in the femur the common trends occur in the lowest r-values while in the tibia the common trends occur in the highest r-values. The common factor is J whether it is at the

highest or lowest r-values. This further shows that at different bony marker levels the bending moment is influenced by differing bony elements (either TA or CA).

Table 12: Human Distal Tibia r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.01	P<0.01
CA	0.840827		P<0.01	P<0.01	P<0.01
J	0.870871	0.949514		P<0.01	P<0.01
Mass	0.63343	0.677053	0.70623		P<0.01
Length	0.622	0.615	0.633	0.722	

Table 13: Baboon Distal Tibia r and p-values from CT analysis

	TA	**CA**	**J**	**Mass**	**Length**
TA		P<0.01	P<0.01	P<0.05	P>0.05
CA	0.71799		P<0.01	P<0.05	P>0.05
J	0.894659	0.911938		P<0.05	P>0.05
Mass	0.382626	0.1447	0.298143		P>0.05
Length	0.355	0.273	0.335	0.187	

A similar trend concerning the significant values is observed in both bones, with baboons showing a greater number of decreased (P<0.05) correlations than humans.

In order to understand if differences between cortical area and polar moments of area between the species occurred at all bony markers, a Student's t-test was performed and

the results indicate no significant difference between the two species for the two bony elements at all bony markers.

The bi-variate relationships between TA and CA versus mass, for both species at the specific femoral markers, figures 7-9, indicate overlap. The overlap does not allow one to be able to draw clear distinctions between the species, which is unexpected as the correlation levels calculated differ, see table 2 and 3 above; one would expect the same level of significant correlation, considering the overlap that is observed. Furthermore, this trend is not observed when humans mass increases beyond the baboon stabilizing mass, i.e. when in humans mass exceeds Log 2 grams. This shows that when mass is plotted against TA and CA there are no differences between the species. There are similar changes in the variables (e.g. increase in mass produces an associated increase in TA and CA) between the species. Furthermore, the relationship between the variables does not allow one to differentiate when the differences occur developmentally.

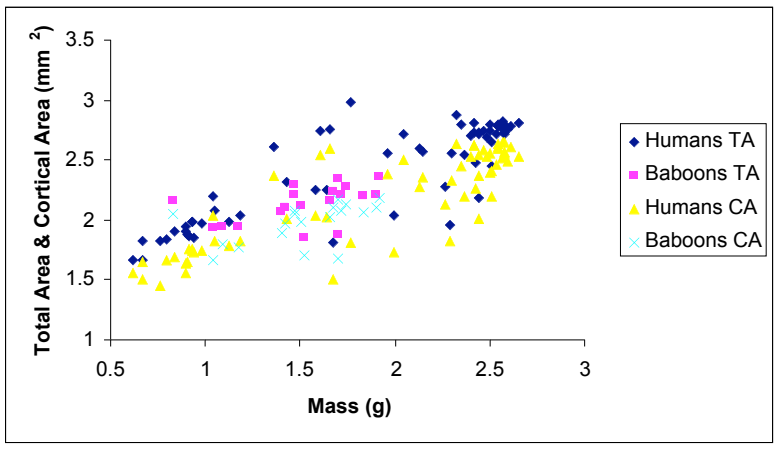


Figure 7: Log Total & Cortical Area versus Log Mass, both species proximal femur, indicating the overlap

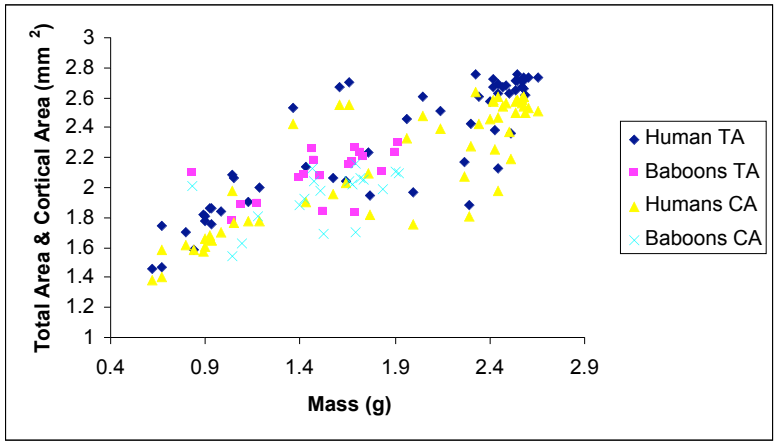


Figure 8: Log Total & Cortical Area versus Log Mass, both species middle femur, indicating the overlap

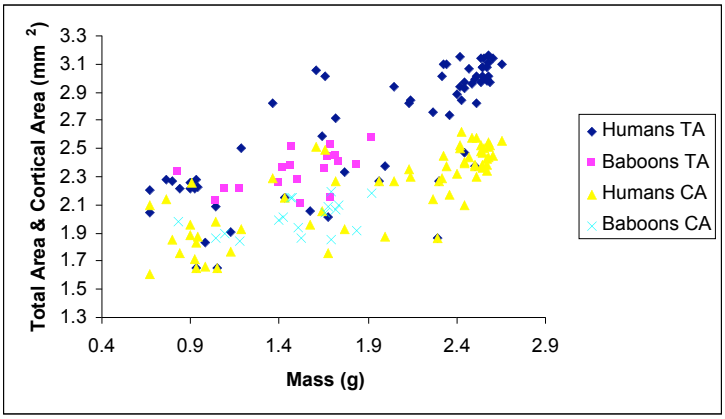


Figure 9: Log Total & Cortical Area versus Log Mass, both species distal femur, indicating the overlap

In figure 9 above, the over-lap that is observed in the above figures 7 and 8, visually appears to be decreased, allowing the clear distinctions between the individual species bony elements to be seen. These results are however, consistent with tables 6 and 7 above, whereby the bony elements versus mass are at different significance levels. This

indicates in the distal femur mass does not change similarly in both species, rather only within species.

The trends observed above for the femoral markers are observed in the tibia as well.

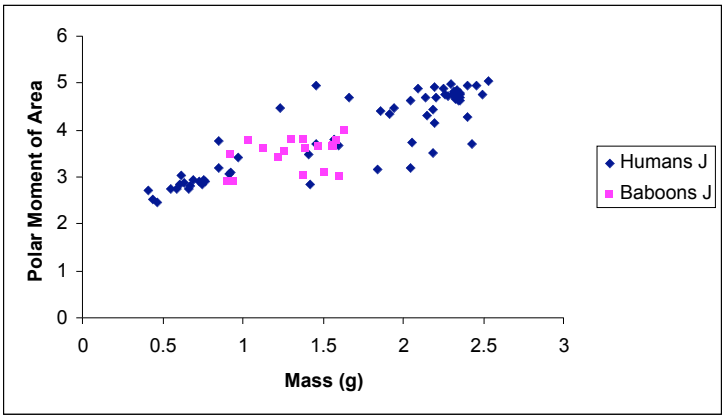


Figure 10: Log Polar Moment of Area versus Log Mass, both species Proximal Tibia

Figure 10 above shows the overlap in mass versus J for the proximal tibia, the same trend is observed for the other markers and on the tibia and femur. When mass exceeds log 2g, the overlap is not observed. Unlike with the bony elements (in this case CA and TA) versus mass for the femur, mass versus J is consistent with the same trends observed across both bones and both species; i.e. considerable over-lap. This means that J in both species developmentally shows no difference and cannot be used to distinguish between species. Furthermore, developmentally an increase in mass produces a correlated increase in J across species, suggesting that J is dependent on the mass of the individuals. These results do not indicate what is observed for r- and p-values (tables 2-13) as there are discrepancies in the p-values. This shows that the smaller baboon sample size may be an

important factor in the determination of p-values as visually no differences in the correlations are seen.

Table14: Means and Standard Deviations (Stdev.) obtained from ratio calculations for femora and tibiae, both species

	Human Femur		**Baboon Femur**		**Human Tibia**		**Baboon Tibia**	
Ratio	Mean	Stdev.	Mean	Stdev	Mean	Stdev.	Mean	Stdev
LogCA/LogM	1.124	0.496	1.117	0.22	1.089	0.562	1.078	0.207
LogTA/LogM	1.197	0.534	1.039	0.205	1.174	0.604	1.007	0.191
LogJ/LogM	1.926	0.834	1.787	0.359	1.893	0.98	1.718	0.336

Tables 14 indicate the means and standard deviations for the specified ratios. These ratios are a means of accounting for body size. The differences observed for the means above between the species are minimal (no statistical test was performed to understand if a difference occurred, see materials and methods for reasoning). From the above values, it is apparent that the spread of data (standard deviation, stdev.) is greater in humans than in baboons (again, no statistical test was performed to understand if a difference occurred, see materials and methods for reasoning). The range of means for humans tibia is from 1.089 (log CA/ logm) to 1.893 (logJ/logM), whilst in baboons the range is from 1.007

(logTA/logM) to 1.718 (logJ/logM). The corresponding tibia standard deviations range from 0.562 (log CA/ logM) to 0.98 (logJ/logM) for humans and 0.191 (LogTA/LogM) to 0.336 (LogJ/LogM). For the femur the range of means are from 1.124 (LogCA/LogM) to 1.926 (LogJ/LogM) in humans; and in the baboons they range from 1.039 (LogTA/LogM) to 1.787 (LogJ/LogM). The human standard deviation ranges from 0.496 (LogCA/LogM) to 0.834 (LogJ/LogM) and in baboons from 0.205 (LogTA/LogM) to 0.359 (LogJ/LogM). From these values, the spread of data allows one to understand that in humans the data is spread to a greater extent than in baboons with regards to both the femur and tibia; with average stdev. results being twice as large in humans as in baboons. In terms of the means (average values), this difference is minimal and averages between the two species very similar. This trend is however, unexpected considering that the stdev. differs widely between the species.

Table 15: Comparison of slopes between species for Femur Mass against TA, CA and J

	Proximal Femur	Middle Femur	Distal Femur
Total Area (TA)	P> 0.05	P< 0.05	P> 0.05
Cortical Area (CA)	P< 0.05	P> 0.05	P< 0.05
Polar Moment of Area (J)	P< 0.05	P< 0.05	P> 0.05

Tables 15 above and 16 below indicate the p-values obtained for the comparison of slopes between the two species. These p-values allow for the understanding in growth

rates between the two species. P-values < 0.05 [e.g. proximal femur cortical area (CA)] provide evidence that the slopes between the groups differ, whist the opposite is true for p > 0.05 [e.g. proximal tibia total area (TA)]. The proximal and distal femur TA; middle femur CA and distal J, indicate that the slopes between the two species are the same; while the remainder of the bony elements at the markers show that the slopes between the species is different. This indicates for certain elements the rates of growth are the same in both species, while for other elements this is not true. This further shows that the rates of change between the species can be either hetero- or homogenous for certain elements.

Table 16: Comparison of slopes between species for Tibia Mass against TA, CA and J

	Proximal Tibia	Middle Tibia	Distal Tibia
Total Area (TA)	P> 0.05	P< 0.05	P> 0.05
Cortical Area (CA)	P< 0.05	P< 0.05	P< 0.05
Polar Moment of Area (J)	P> 0.05	P> 0.05	P> 0.05

The tibia slope comparisons between the species show that the proximal and distal tibia TA and all bony markers J slopes are the same, while the remainder of the slopes differs. The trend observed between the bones is all bony markers on the femur and tibia TA have the same slopes, the distal and proximal femur and tibia CA have the same slope and the distal femur and tibia have the same slope. The only slope differences are seen in the middle CA, and proximal and middle J.

The bi-variate distributions of femoral and tibial proximal (10%), middle (50%) and distal (90%) bony elements are shown in figures 8-25. For figures 11-13, clumping data is observed for the respective species, with minimal over-lap. Human data visually lay above baboon data for many of the data points. This trend is apparent in both the femur length versus CA and tibia length versus CA. Figure 11, p-values (table 2 and 3); indicate a stronger correlation in humans than in baboons, which is visually seen as human data clusters to a greater extent than baboon data. Baboon data appears to cluster to a lesser degree in an area. However, the human data is also spread over a larger area than baboons. These visual results for the human data are inconsistent with table 2 results whereby $P<0.01$ significant correlations are observed, which means that the clusters of data may influence the results to a greater extent than previously thought, by depressing the outliers. Furthermore, the change in X and Y scales may influence what is observed meaning that the data may appear more spread visually than what is expected from the p- and r-values and an unchanged X and Y scale. Figure 12, p-values (table 4 and 5) indicate the same trend as the proximal femur, while the p-values (table 6 and 7) indicate the same level of significant correlation across both species.

{NOTE: For Figures 11-28, humans are represented by blue; and baboons by pink}

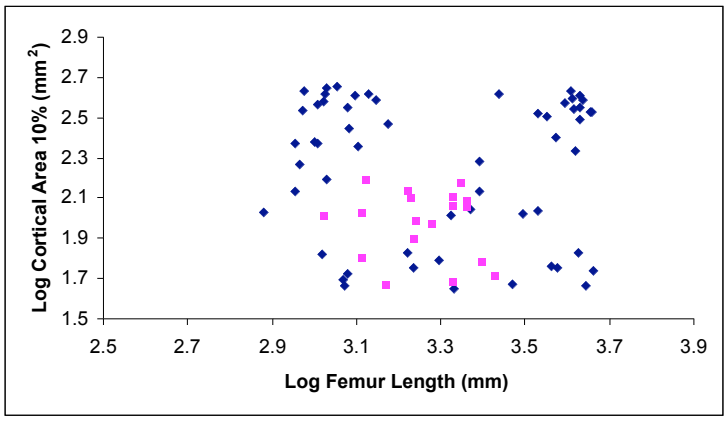


Figure11: Log Cortical Area 10% versus Log Femur Length, both species

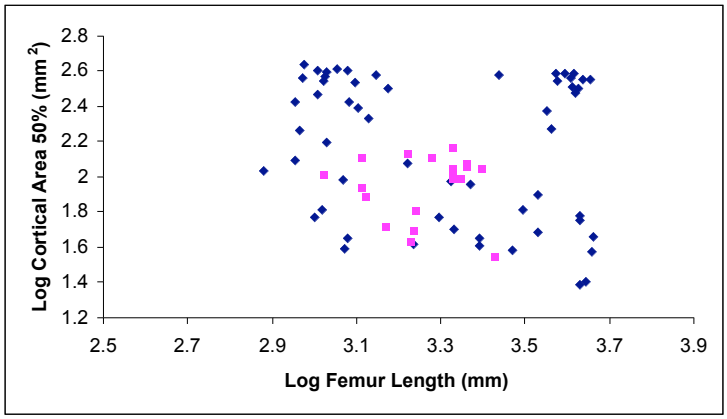


Figure 12: Log Cortical Area 50% versus Log Femur Length, both species

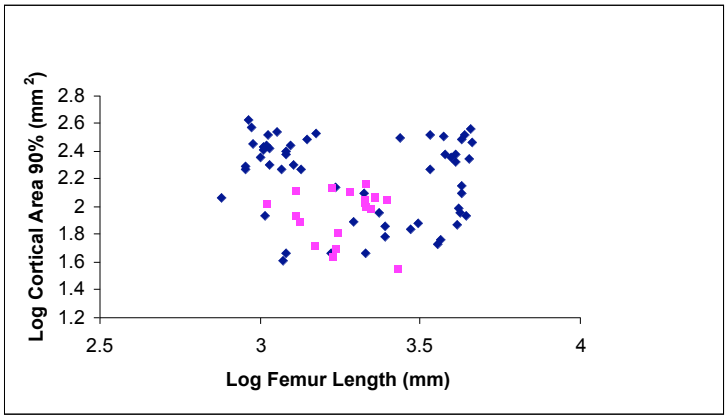


Figure 13: Cortical Area 90 % versus Log Femur Length, both species

Figure 13 above indicates the same trend as in figures 11 and 12. Figures 11 and 12 coupled with tables 2-7 indicate overlap and correlations between the variables between the species suggest coupled changes in the elements.

The tibia length versus CA, indicate the same trend as in the femur above. For the proximal tibia (figure 14); clumping of data is further observed, however, the degree of data points over-lapping is minimal. This implies that one would expect a greater degree of overlap in the data visually and the spread of data again be similar; however this is not visual observed which again may be due to the change in the X and Y scales, and may be further compounded by the smaller baboon sample size. Furthermore, as is shown in the graphs baboon proximal tibia length does not exceed log length of 3.4 mm. Figure 14 p-values (table 8 and 9); indicate the same level of significant correlation between the species. Figure 15 p-values (table 10 and 11), however, indicates a stronger correlation within baboons than in humans, while the opposite is observed for figure 16, whereby the p-values (table 12 and 13) indicate a stronger correlation in humans than baboons.

The results obtained from the above bi-variate plots are similar for figures 17-28.

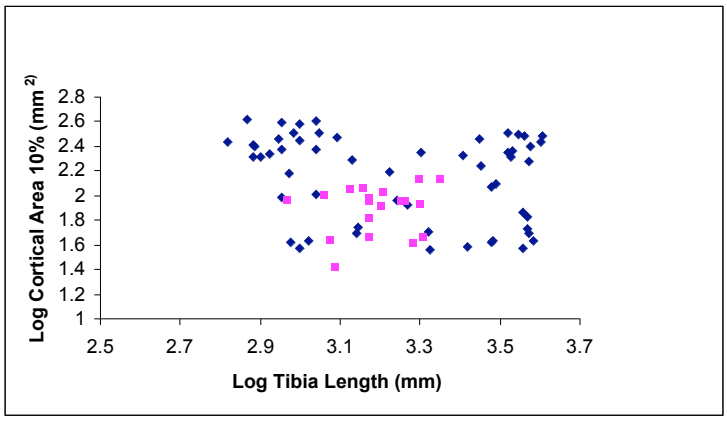


Figure 14: Log Cortical Area 10 % versus Log Tibia Length, both species

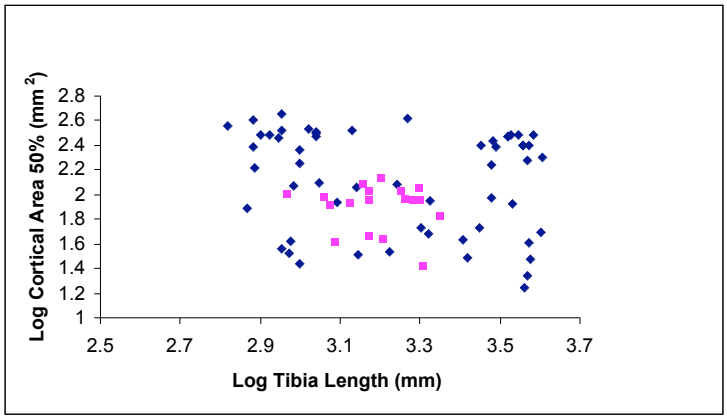


Figure 15: Log Cortical Area 50 % versus Log Tibia Length, both species

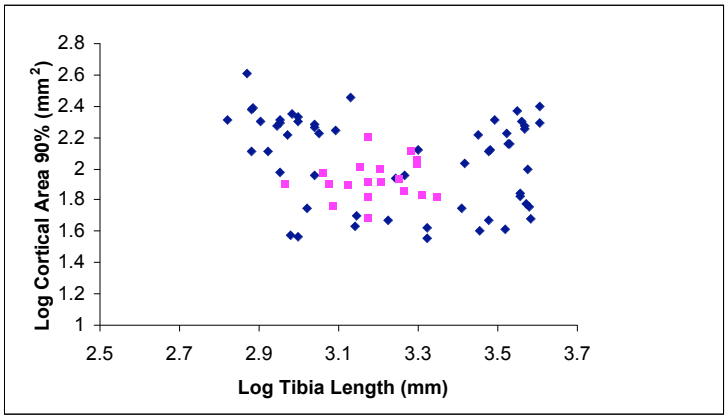


Figure 16: Log Cortical Area 90 % versus Log Tibia Length, both species

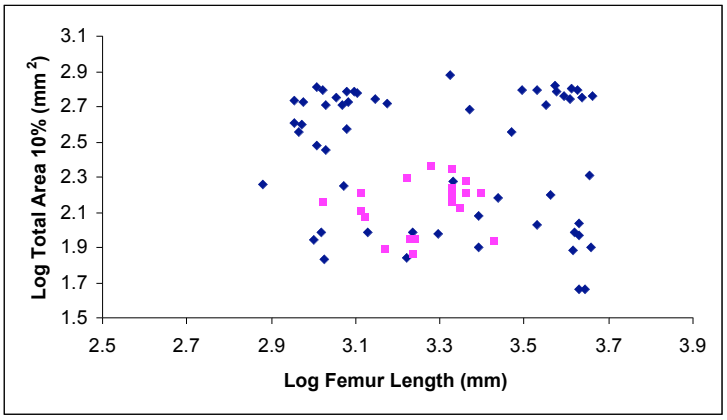


Figure 17: Log Total Area 10% versus Log Femur Length, both species

Figure 17 indicates that the same trend observed in the distal tibia versus CA, figure 16 above. Data points of humans are dispersed to a greater extent than in baboons; the p-values (table 2 and 3) indicate that the correlation between the humans is greater than in baboons. Clumping of data points for both species is observed, and over-lap between the two species is minimal. Human data points are correlated to a greater extent in the proximal and middle bony markers (i.e. $P<0.01$ compared to $P<0.05$) in comparison to baboons; however, in the distal femur length versus TA, the baboon data points are correlated to a greater extent ($P<0.01$) in comparison to humans ($P<0.05$).

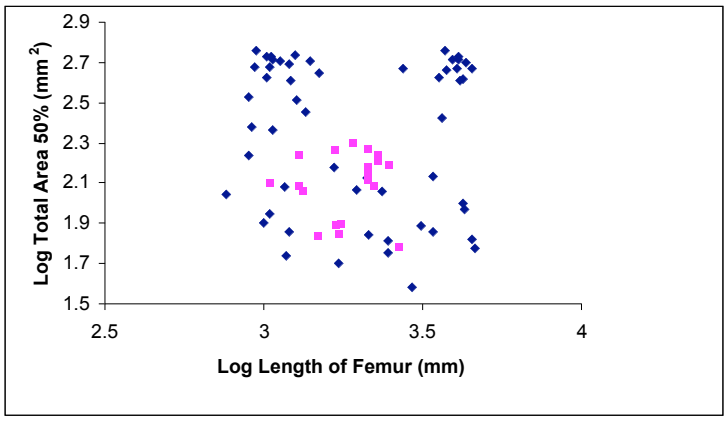


Figure 18: Log Total Area 50% versus Log Femur Length, both species

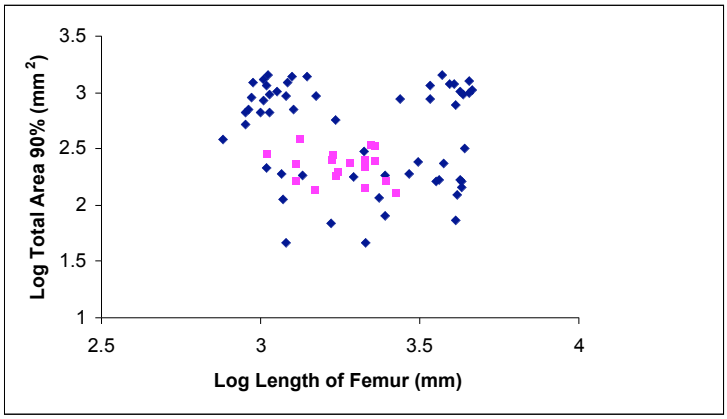


Figure 19: Log Total Area 90% versus Log Femur Length, both species

The results obtained for the tibia length versus TA at all bony markers (figures 20-22, below), is the same trend observed in the femur length versus CA (figures 11-13, above) at all bony markers.

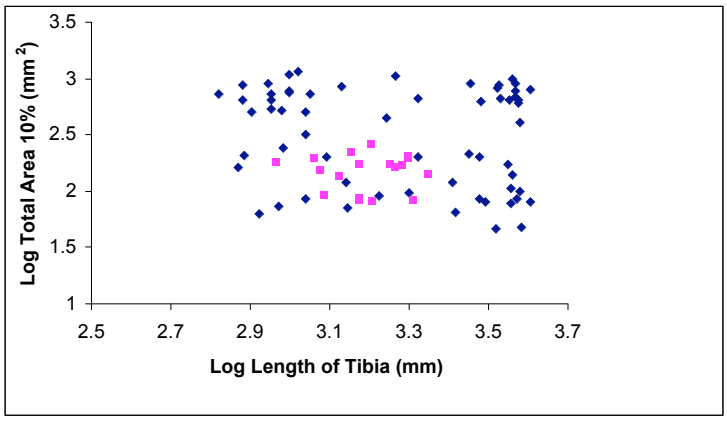


Figure 20: Log Total Area 10 % versus Log Tibia Length, both species

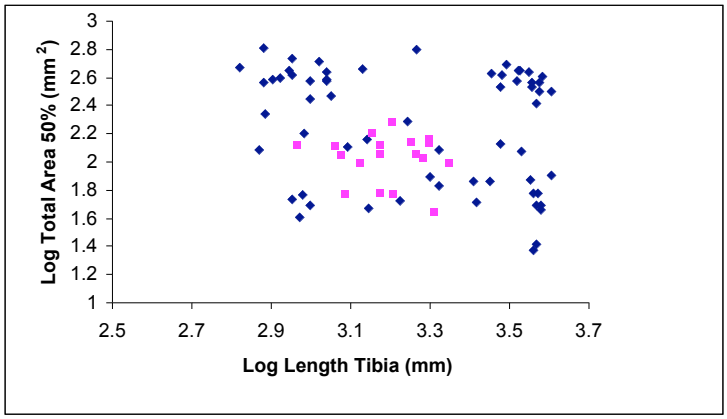


Figure 21: Log Total Area 50 % versus Log Tibia Length, both species

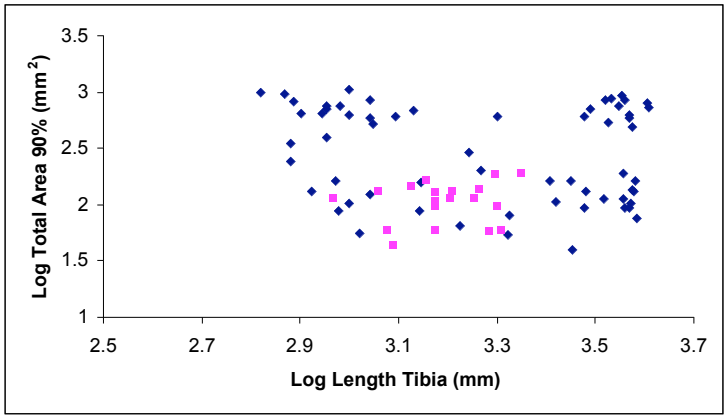


Figure 22: Log Total Area 90 % versus Log Tibia Length, both species

J versus femur length shows a similar graphic trend across all bony markers. The proximal and middle bony markers indicate a stronger human correlation ($P<0.01$) than baboon correlation ($P<0.05$); the opposite trend is observed with the distal bony marker, whereby baboon data points correlate to a greater significance level than humans ($P<0.01$ in comparison to $P<0.05$). The same trends with regards to over-lap are seen, whereby minimal over-lap is present, suggesting stronger correlations in baboons than humans.

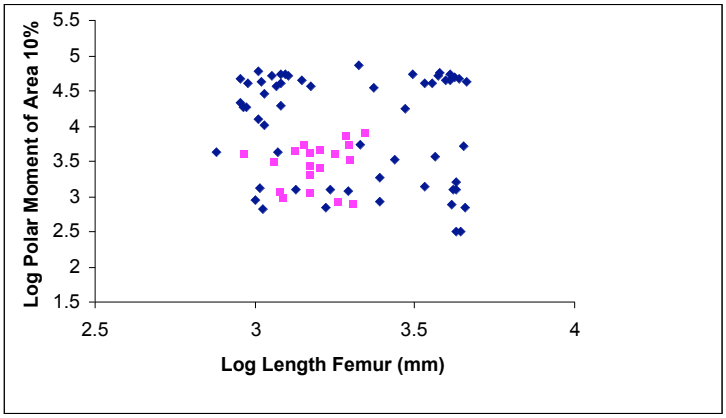


Figure 23: Log Polar Moment of Area 10% versus Log Femur Length, both species

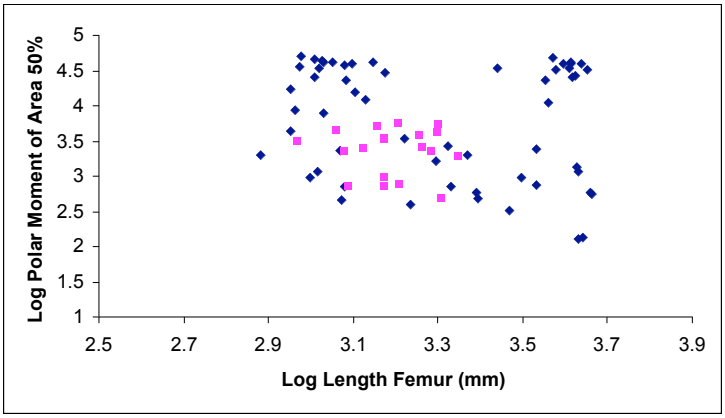


Figure 24: Log Polar Moment of Area 50% versus Log Femur Length, both species

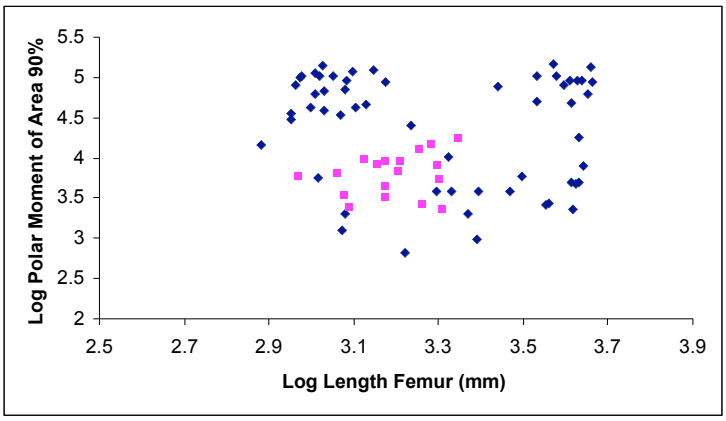


Figure 25: Log Polar Moment of Area 90% versus Log Femur Length, both species

The tibia correlation for length versus J at all bony markers is opposite to the trend for the femur length versus J. For the tibia, the proximal and middle tibia in baboons indicate a stronger correlation ($P<0.01$) in comparison to humans ($P<0.05$).

From the figures above 11-25, over-lap in data points between the species is minimal, clumping of data points within the respective species is observed; however, the humans show a greater range of distribution points in comparison to the baboons.

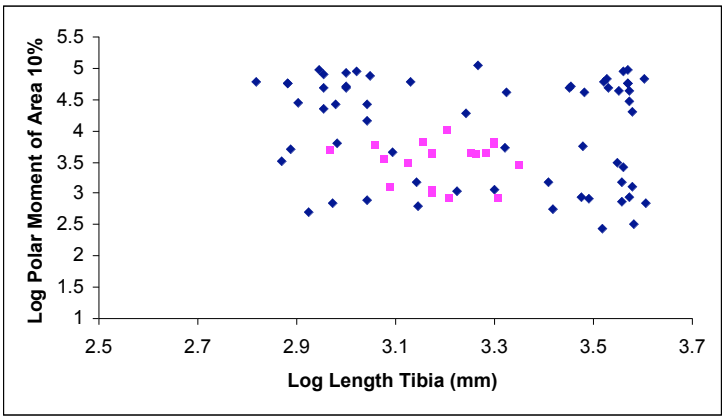


Figure 26: Log Polar Moment of Area 10% versus Log Tibia Length, both species

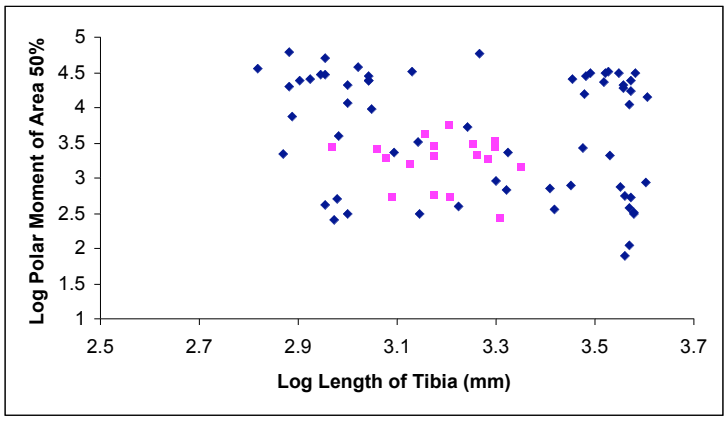


Figure 27: Log Polar Moment of Area 50% versus Log Tibia Length, both species

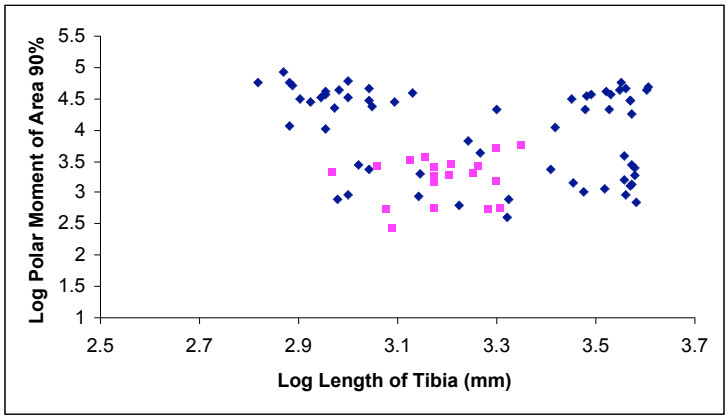


Figure 28: Log Polar Moment of Area 90% versus Log Tibia Length, both species

The Mantel test results all indicated that the matrices were correlated at the $p<0.05$ level, for all bony elements between species. The r-values ranged from 0.983 (human proximal femur; baboon proximal femur) to 0.738 (human distal tibia; baboon distal tibia), see appendix C. However, these results show that there is no difference between the two species, while p-and r-values for certain variables indicate differences in the species. The $P<0.05$ significance level may be the reason for the correlations as most variables except, length versus bony elements middle femur baboons; length versus bony elements human

distal femur; length versus mass human middle femur; length versus bony elements and mass distal tibia baboons, are significant at $P<0.05$.

4. Discussion:

The human linear dimensions show significant correlations at the $P < 0.01$ level, for most variables, except the medio-lateral (M-L) distal shaft diameter of the femur; similarly, the cross-sectional data shows significant correlations at the $P<0.01$ level, except for length versus J middle femur; length versus TA, CA and J whereby the significance level is $P<0.05$ and length versus mass ($P>0.05$) for the distal femur; length versus J (proximal tibia) and length versus all bony elements and mass (middle tibia). A similar trend is seen in the baboon sample, whereby all linear correlations for the femur are significant at a $P<0.01$ level, however these correlation are decreased to a significance level of $P<0.05$ for the tibia; in the cross-sectional data for the following, mass versus TA, CA, J on the proximal femur; length versus CA and J, result in a $P<0.05$, with length versus TA $P>0.05$; $P<0.05$ for mass versus bony elements and $P>0.05$ for length versus bony markers in the middle femur; $P<0.05$ for mass versus bony elements and length versus CA, for the distal femur; the variables not mentioned resulted in a $P<0.01$ significance level. For the baboon tibia cross-sectional data, the majority of variables were significant at $P<0.01$, except mass versus bony elements on the proximal tibia, length versus bony elements on the middle tibia, mass versus bony elements on the distal tibia. The distal tibia further showed $P>0.05$ for length versus bony markers and against mass. The rates of change in the bony elements in relation to mass in both the femur and tibia of both species are similar; furthermore, there is no significant difference between the correlation matrices. No significant difference between the species is seen for the bony elements, when ratios are used.

The correlations observed may indicate that during post-natal growth, the correlated regions within the respective bones are a under conservative genetic control (Holliday, 1997). These results are consistent with that of many earlier works (e.g. Schultz 1926), which report that genetic encoding is the reason for correlated growth. Intrinsic genetic factors may further provide evidence for the maintenance of structural integrity within regions of organisms (e.g. human femur). This may further provide evidence for allometric relationships, in that most physiological functions vary allometrically with body size (de Pontual *et al.,* 2003).

Cross-sectional bony elements correlating with each other are expected to be significantly correlated as total area (TA) and cortical area(CA) are two of the three bony elements of which bone is inherently made up of (i.e. TA = CA + MA). This equation would thus explain the significant correlations with the mass of the bones versus bony elements, as mass of bone = TA= CA + MA. Therefore, as mass depends on these elements a change in one of the elements (TA and/or CA and/or medullary area), would influence the density of the bone, resulting in a change of the mass of the bone, regardless of whether these elements are influenced due to genetic, epi-genetic or a combination of the two. However, as mass was taken as the skeletal mass of the individual specimens, this strongly indicates that mass versus bony elements is genetically determined developmentally and not influenced by epi-genetic factors; as if epi-genetic influences is the primary developmentally, the correlations would surely be different between the species due to the locomotory differences between the species.

The lack of correlations between the M-L distal shaft diameter with any other variables, may lend evidence in the femur to epi-genetic factors (e.g. mode of locomotion) influencing linear and morphological dimensions in the femur, and possibly a genetic decoupling of the variables. This then indicates that the M-L distal shaft diameter may not correlate well with the rest of the femoral variables, because it is susceptible to epi-genetic factors, by virtue of being part of the distal segment of limbs which are more energetically costly to move (Alexander, 1998; Hildebrand and Goslow, 2001), thus dependent on the rate and frequency of movement, and that it must maintain proportionally greater loads (Drapeau and Streeter, 2006) in comparison to proximal segments; therefore it (M-L distal shaft diameter) may indeed vary independently of the other variables, and be dependent on the phenomenon of locomotory pattern, exercise, amount of use/disuse and stress/strain due to body size that it is subjected to. Humans are habitually bipedal organisms, and a considerable degree of the force needed to carry out such a locomotor mode comes from the lower limbs. This indicates that the force required and thus generated by energy expenditure by the lower limb muscles, must remain within a certain set of limits (the units and range of these limits may indeed be arbitrary) in order to maintain the structural integrity of the region. This may possibly indicate that the M-L distal diameter is variable within humans (bipeds) and not for baboons (quadrupeds) for this trait (i.e. baboons show significant correlations for this variable), thus lending that it may be a reliable predictor for locomotory patterns in discerning bipedal from quadrupedal organisms; i.e. it would remain unaltered in quadrupedal organisms and show correlated growth and change but not in bipedal organisms Although, Lieberman *et al.,* (2004) has reported that epi-genetic influences are

integral role in the moulding of the post-cranial skeleton, these epi-genetic stresses may be minor; and not play an important role in bipedal apes, in such a way as to change the structure.

The nature of this study (cross-sectional) indicates that regardless of age, gender and amount of physical activity an individual may perform, it may indeed be inconsequential on the gross adult morphology. The femur of bipedal organisms (e.g. humans), is under a comparable degree of stress due to the nature of the mode of locomotion; thus this lends one to postulate that genetics rather than epi-genetic factors are important as far as gross morphology is concerned and it may be these genetic factors that maintain the integrity of the morphology and shape of bone. It is worthwhile noting that although bone undergoes considerable amounts of tension, compression, bending, shearing torsion, axial bending and combined loading through an individuals life-time, these bio-mechanical properties if undertaken in excess may cause the alteration of bone morphology; however, these properties have set-points to which a bone can withstand, and once exceeded, these may cause complete fracturing of bones, which may in turn be viewed as 'pathologies' on bone and/or observed as excess bone cell growth at the site of fracture/breakage. The set-points may be dependent on numerous factors (e.g. age, use/disuse), however, due to the nature of this study (birth to 18 years), these factors (age, use/disuse, exercise) cannot be eliminated, and therefore the set-points can be assumed to be primarily genetically determined and partly influenced by the loading history ontogenetically. It is known the baboons and humans have differing modes of locomotion, thus the sites of these bio-mechanical stresses and strains will be different; however, these changes are more likely

to be seen microscopically rather than macroscopically in the bone architecture. Thus, if the epi-genetic factors of activity are integral in the moulding of a skeleton, gross cross-sectional data analyses may not allow for one to observe this; and the trabecular architecture may indeed be more viable than is gross cross-sectional data. If indeed bone changes in accordance with activity levels (Nunamaker *et al.,* 1990; McLeod *et al.,* 1990 and Huiskes, 2000), the spongy bone is the bony element that would change. Huskies (2000), reported that the trabecular (spongy) architecture of cancellous bone is optimally structured for its load bearing function, suggesting that its formation is governed by mechanical forces. If Huiskes (2000) intended that the architecture alone is governing the bones structural integrity and not the density, this would further provide an explanation for the correlations observed, and may indicate that the epi-genetic factors are important in determining this architecture, and in turn this internal architecture may influence gross morphology; unfortunately, this study falls short in analyzing the trabecular architecture of bone. However, the density in terms of area covered, was analyzed. If, activity alone is responsible for changes in density, these differences would be observed in this study as this would be elevated in humans and not in baboons, due to the nature of locomotion; and the correlations observed may have been decreased significantly, due to this variable influence (individuals vary in amount of stress/strain put on the limbs due to locomotory differences, amount of exercise and mass of the individuals). However, the effect of coupled changes (i.e. a change in one bony element causing a change in another bony element) cannot be discarded as being due to either genetic or epi-genetic influences. Unfortunately, this study can not document the amount of use and/or disuse as it is

unknown, and thus can not provide accurate data analyses in order for one to safely conclude that indeed epi-genetic factors are integral for this variable.

The muscles of the lower limb, more specifically in the femur, use the femoral bone as a foundation, therefore if one element of the muscle changes, possibly due to use and/or disuse or simple genetic coding, these effects maybe seen on the femur itself; however, Tuttle *et al.,* 1979 has shown that muscular activity is not observed on the femoral bone itself. This further purports that genetic factors are integral and if not, the primary factor that may have any influence on gross bone morphology and therefore, not the amount of use/disuse and/or exercise. Furthermore, if the structural integrity of the femoral bone, especially femoral head, is influenced by epi-genetic factors, it may show a considerable amount of variation which may then not render it such a reliable predictor in body size.

de Pontual *et al.,* (2003), reported that most physiological functions vary allometrically with body size, then if one looks at stature, it may follow that the significant correlations, whether at $P<0.01$ or $P<0.05$, indicate that the body size, in terms of stature, are a function of allometric scaling within an organism. However, the $P>0.05$ correlations between length and mass at the bony markers indicate that decoupling between the elements due to genetic factors pre-determining length and mass of bone being influenced by internal architecture which according to Huiskes (2000) is influenced by exercise, use/disuse and age, and in contradiction to de Pontual *et al.,* (2003), not all physiological functions scale allometrically. Body size has been reported to influence many bony properties **(**Ruff, 1998); however, no significant difference between the species is seen

for the bony elements. This indicates similar responses to stress and strain in cortical bone, of both bipedal and quadrupedal organisms (though they have markedly different modes of locomotion!); which may inherently indicate a developmental and phylogenetic constraint. Indicating, that if epi-genetic factors are integral in the influencing of bony elements, these should be apparent ontogenetically after three years of age, when the different modes of locomotion are adopted between humans and baboons (Bogin, 2001). Thus, once body size is accounted for there are no differences for the bony elements, between bipedal and quadrupedal organisms. This highlights the importance of accounting for body size in analyses of data; and further reinforces the homogeneity of body size (once accounted for) across the two species and possibly across all primates for post-cranial elements, unlike is seen in the relative brain to body size in humans (Spocter, 2007).

The "clumping" of ontogenetic data, rather than splitting the individuals of both species into age-co-horts (see materials and methods for reasoning), may further lend to the differences in significance levels ($P<0.01$ in comparison to $P<0.05$). However, the results (correlations) further lend evidence to Drapeau and Streeter (2006) in that a greater stress is put on the distal segments of limbs and possibly making them more variable.

Baboons place less emphasis (in terms of stress and strain) on their lower limbs during locomotion in comparison to humans. Thereby, the laws of use and disuse and body mass influences should apply (i.e. coupling or decoupling within elements due to locomotion and/or genetic influences). However, the correlated data provides evidence for allometric

relationships between the variables. The decreased level of significance for the cross-sectional data suggests that although Tuttle *et al.,* 1979 reports that, there is very little activity in thigh muscles during bipedal locomotion; in non-habitual bipedal organisms (e.g. baboons) the activity of the thigh muscles may be elevated; and thus the activity generated differences may cause this disparity in the level of significance between the species. The smaller baboon sample size may further compound the lower significance level, as it is known that $n<30$ (pers. comm. Allan), does not statistically allow for good estimates for population representation.

The decreased levels of significance in the tibial bone (baboon distal tibia and human middle tibia) ($P>0.05$) is observed across both species. This provides clear indication that in the tibia there is an allometric decoupling of these elements. This provides further evidence that the mode of locomotion does not influence the tibia in any manner, and that evidence pertaining to locomotory modes based on mass and length vectors are primarily in the femur.

Epi-genetic factors if responsible for the moulding of skeletal elements (e.g. tibia bone), a clear difference in the growth rates (given by the slope homo- or heterogeneity, see table 15 and 16), would be observed due to differing locomotory modes. The similarities between the slopes of both species, is indicative of developmental constraint and possibly a phylogenetic constraint as well. The differences observed may in part be due to differing selective pressures and life history patterns; and these may provide a better explanation for differences in the growth rates (humans grow for an extended period in

comparison to baboons). The differences in rates of growth may hold true as shown by Kimura (1974) and Lanyon (1982), which report that differences are due to differing modes of locomotion, for certain time periods during growth, however, statistically when the ontogenetic sample is analyzed globally no differences are seen between the bony elements. This is further compounded by the lack of understanding in hominid life history patterns, locomotory modes (dual or exclusive) and the reasons for bipedalism.

The results further indicated no difference in correlation matrices, which further lends one to infer that there is a constraint between the respective species; and that there is no developmental difference between the species due to the differing locomotory modes. These (correlation matrix) results further indicate that genetic rather than epi-genetic factors pre-determine the morphology, in terms of size, shape and bony elements, of individuals within a species. These genetic factors are further displayed when one looks at the intermembral index (IMI). The constituents of the IMI indicate no difference between the matrices; however, a clear average difference is seen on the graphical plot. These results of the IMI are consistent with Aiello and Dean (1990). The overlap observed is during the stage when both humans and baboons are growing at the same rate and the body proportions are the same (Bogin, 2001). Furthermore, the intermembral index shows that the differences that culminate in adult differences are clearly discernable ontogenetically, after three years of age (human age). Holliday (1997) reported that limb proportions have remained stable through evolutionary short periods. The importance of the intermembral index ontogenetically, highlights the importance of better understanding of morphology and cross-sectional differences developmentally, which the results fall short of as the data was clumped rather than split into age co-horts.

A fossil with complete elements (i.e. to calculate intermembral index), which may not be an adult; the mode of locomotion inferred by the intermembral index may be misleading as overlap is seen in the early stages of development.

With regards to the polar moment of area (J), it is expected that humans would have higher average J values in comparison to baboons, because humans subject their lower limbs to a greater stress and strain. J correlates with all bony elements, indicating that J is influenced to a greater extent by mass and body size, which may be coupled to load, imposed by the individuals; as the correlation in baboons is significant, but the activity in the lower limbs are minimal in comparison to humans. Kimura, (1974) and Lanyon, (1982), have reported that J should be studied in an attempt to determine locomotory patterns; however, statistically there is no difference between the two species, further indicating that J is not influenced by locomotory mode but rather by CA and TA, possibly skeletal mass and body size. The lack of such a difference may indicate a phylogenetic and a developmental constraint.

The correlations of length versus markers (10%, 50% and 90%) indicate that there is no manner in which the length of a bone influences the bony properties, which may elude that epi-genetic factors influence the cross-sectional properties of bone and not length which is genetically coded for (no matter what one does height is genetically pre-determined).

From the above it is apparent that genetic factors within and between the species are the primary precursors for linear dimensions and gross cross-sectional dimensions; although many features on bone are diagnostic in determining locomotor repertoire, in the absence of such features (e.g. genu vagus), simple linear measurements and gross cross-sectional dimensions cannot determine locomotory mode, as they are genetically predetermined rather than epi- genetically.

Lieberman *et al.,* 2004 aptly concluded that cross-sectional areas do not provide reliable data on the orientation of loads, the results of this study reinforce this sentiment.

The results of this study indicate the rejection of the null hypothesis and suggest acceptance of the alternative hypothesis in that humans and baboons do not show significant differences in metrical and cross-sectional geometric properties and thus this may indicate that genetic rather than epi-genetic factors are integral.

5. Conclusion:

Understanding how an adult bone reaches its final form is largely unknown, especially in terms of being influenced by genetic or epi-genetic factors. The amount of variation in a species has been reported as being a useful precursor in determining activity patterns in species (Pearson and Lieberman, 2004). Unfortunately, the variation patterns in ontogenetic studies cannot alone assess whether the variations observed are in part due to age differences and/or activity patterns. This is further compounded by the lack of understanding of cross-sectional data differences in species with differing locomotory patterns.

The results of this study strongly suggest that there no clear discernable differences in bony elements alone being able to predict locomotory patterns. These sentiments reinforce Lieberman *et al.,* (2004) suggest that cross-sectional areas alone are unreliable. Cross-sectional data alone may prove to be unreliable, however, used in conjunction with gross-morphological characteristics that define bipedal and quadrupedal organisms, may indeed prove to be fruitious. Both genetic and epi-genetic factors play an integral role in the moulding of a skeleton towards its form in terms of locomotory pattern. Studies that indicate one or the other seem to be clear adaptionist or non-adaptionist view points; and these need to addressed as well as cautioned against, unless data testing the form-function relationships have been tested for (Pearson and Lieberman, 2004). As has been reported by Huiskes (2000), the trabecular architecture of bone may in part be the defining point in determining locomotory pattern. Density of bone once accounted for in terms of area, shows no clear differentiation between the species. Many of the correlations indicate an

intricate system of morphological integration, which indeed provides evidence towards a genetic predisposition, however, due to the lack of knowledge of activity of the measured individuals' one can not safely disregard the activity related changes that have been reported by Woo *et al.,* (1981).

A combination of epi-genetic and genetic factors [factor three (iii)] in this study takes a more conservative approach in terms of understanding locomotory patterns, and this may indeed be the only mechanism that is possible in understanding bone changes and patterns of integration. Until further evidence towards life history patterns, physiological patterns and molecular patterns emerges, factor iii may be the only logical step towards the understanding developmental pathways, in terms of stress and strain and the effects of mechanical loading. Until then, cross-sectional data alone provides minimal evidence of locomotory differences between species.

6. Future Studies:

One of the main points of the thesis makes one understand that much more work needs to be considered. It is in my opinion that studies centering around the inclusion of greater number of taxa be included, however in light of this, cross-sectional data should be used as a basis to assess the differences once more taxa are included, as it is evident that with the use of only two species, no clear evidence by the use of CT scanning and cross-sectional data analysis is possible. Furthermore, a better understanding on primate life history patterns needs to be undertaken, if we are to get a better understanding of hominids.

6. Appendix

6.1 Appendix A

Table A: Measurements, instrument, definition and reference used on Clavicle (both species)

Measurement	Instrument used	Osteometric point	Reference
Maximum Length (c1)	Osteometric board	Straight distance between acromial and sternal end	Singh and Bhasin (1968)
Vertical Diameter at mid-shaft (c2)	Sliding caliper	Anterior-posterior diameter at mid-shaft	Singh and Bhasin (1968)
Saggital diameter of mid-shaft (c3)	Sliding caliper	Superior-inferior diameter at mid-shaft	Singh and Bhasin (1968)
Mass (ca)	Scale		

Table B: Measurements, instrument, definition and reference used on Humerus (both species)

Measurement	Instrument used	Osteometric point	Reference
Maximum Length (h1)	Osteometric Board	Straight distance between head and articular surface	
M-L diameter at mid-shaft (h2)	Sliding caliper	Medio-lateral diameter at mid-shaft	
A-P diameter at mid-shaft (h3)	Sliding caliper	Anterior-posterior diameter at mid-shaft	
Mid-shaft circumference (h4)	Tape Measure	Circumference at mid-shaft	
Nutrient foramen distance from proximal metaphysis (h5)	Sliding caliper	Straight distance from nutrient foramen to proximal metaphysis	
Mass (hb)	Scale		

Table C: Measurements, instrument, definition and reference used on Radius (both species)

Measurement	Instrument used	Osteometric point	Reference
Maximum length (r1)	Osteometric Board	Straight distance between superior and inferior articular surface	
Transverse diameter at mid-shaft (r2)	Sliding caliper		
Head diameter (r3)	Sliding caliper	Diameter of head of radius	
Saggital diameter at mid-shaft (r4)	Sliding caliper		
Mid-shaft circumference (r5)	Tape measure	Circumference at mid-point	
Nutrient foramen distance from proximal metaphysis (r6)	Sliding caliper	Straight distance from nutrient foramen to proximal metaphysis	
Mass (rc)	Scale		

Table D: Measurements, instrument, definition and reference used on Ulna (both species)

Measurement	Instrument used	Osteometric point	Reference
Maximum length (u1)	Osteometric board	Straight distance from superior and inferior articular surfaces	
Olecranon-coronoid width (u2)	Sliding caliper	Straight distance between olecranon and coronoid	
M-L diameter of the olecranon process (u3)	Sliding caliper	Maximum straight Medio-lateral diameter of olecranon process	
S-I height of olecranon process (u4)	Sliding caliper	Maximum straight Superior-inferior height of olecranon process	
Trochlear width (u5)	Sliding caliper	Maximum width of trochlear	
Breadth of coronoid process (u6)	Sliding caliper	Maximum breadth of trochlear	
Height of coronoid process (u7)	Sliding caliper	Maximum height of coronoid process	
A-P diameter of mid-shaft (u8)	Sliding caliper	Straight anterior-posterior diameter of mid-shaft	
M-L mid-shaft diameter (u9)	Sliding caliper	Maximum medio-lateral mid-shaft diameter	
Nutrient foramen distance from proximal metaphysis (u10)	Sliding caliper	Maximum straight distance from nutrient foramen to proximal metaphysis	
Mass (ud)	Scale		

Table E: Measurements, instrument, definition and reference used on Femur (both species)

Measurement	Instrument used	Definition	Reference
Maximum length (F1)	Osteometric board	Straight distance between the highest point of the head and the deepest part on the lateral medial condyle	Singh and Bhasin (1968)
A-P mid-shaft diameter (F2)	Sliding caliper	Maximum antero-posterior distance in the middle	Bräuer (1988)
M-L mid-shaft diameter (F3)	Sliding caliper	Maximum medio-lateral distance in the middle	Bräuer (1988)
Sub-trochanteric medio-lateral diameter (F4)	Sliding caliper	Maximum medio-lateral distance below the lesser trochanter	Bräuer (1988)
Sub-trochanteric antero-posterior diameter (F5)	Sliding caliper	Maximum antero-posterior distance below the lesser trochanter	Bräuer (1988)
M-L diameter of the distal shaft (F6)	Sliding caliper	Maximum medio-lateral distance of distal shaft	Bräuer (1988)
Proximal epiphyseal breadth (F7)	Sliding caliper	Maximum proximal epiphyseal breadth	Bräuer (1988)
S-I diameter of the femoral head (F8)	Sliding caliper	From the highest point on the femoral head to the lowest point between the head and neck	Singh and Bhasin (1968)
A-P diameter of the femoral head (F9)	Sliding caliper	From the most lateral aspect to the medial aspect	von Driesch (1976)
Bi-condylar breadth (F10)	Sliding caliper	Maximum breadth of bicondyles	von Driesch (1976)
Nutrient foramen distance from proximal metaphysis (F11)	Sliding caliper	Distance from the nutrient foramen to the proximal metaphysis	von Driesch (1976)
Mass (Ff)	Scale		Bräuer (1988)

Table F: Measurements, instrument, definition and reference used on Tibia (both species)

Measurement	Instrument used	Definition	Reference
Maximum length (T1)	Osteometric board	Straight distance between the upper most part on the intercondylar eminence and the lowest part of the medial malleolus	Singh and Bhasin (1968)
Proximal articular width (T2)	Sliding caliper	Maximum width of proximal articular surface	Bräuer (1988)
A-P diameter @ level of tuberosity (T3)	Sliding caliper	Maximum antero-posterior diameter at the level of the tuberosity	Bräuer (1988)
M-L diameter @ level of tuberosity (T4)	Sliding caliper	Maximum medio-lateral diameter at the level of the tuberosity	Bräuer (1988)
M-L distal articular breadth (T5)	Sliding caliper	Maximum medio-lateral diameter of distal articular surface	Bräuer (1988)
A-P distal articular breadth (T6)	Sliding caliper	Maximum antero-posterior diameter of distal articular surface	Bräuer (1988)
A-P tibia mid-shaft (T7)	Sliding caliper	Maximum diameter at the middle	Bräuer (1988)
A-P diameter @ nutrient foramen (T8)	Sliding caliper	Maximum antero-posterior diameter at the level of the nutrient foramen	Bräuer (1988)
M-L diameter at nutrient foramen (T9)		Maximum medio-lateral diameter at the level of the nutrient foramen	Bräuer (1988)
M-L tibia mid-shaft (T10)	Sliding caliper	Maximum medio-lateral diameter in the middle	Bräuer (1988)
Mid-shaft circum. (T11)	Tape measure	Circumference in the middle	Singh and Bhasin (1968)
Nutrient foramen distance from proximal metaphysis (T12)	Sliding caliper	Distance from the nutrient foramen to the proximal metaphysis	Bräuer (1988)
Mass (Tg)	Scale		Bräuer (1988)

6.2 Appendix B:

Table A: Sex distribution

SEX/ SPECIES	*Homo sapiens*	*Papio ursinus*
Males	44	12
Females	31	4
Unknown	17	4
Total	92	20

6.3 Appendix C:

Baboon Femur Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

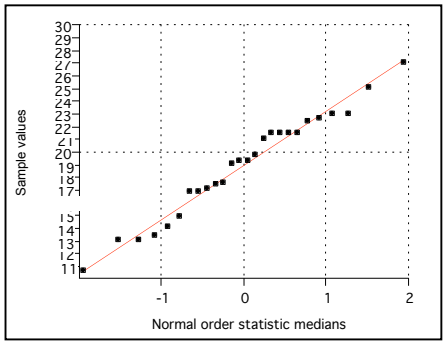


Figure Gg: Variable F1 Left side PPCC = 0.9889

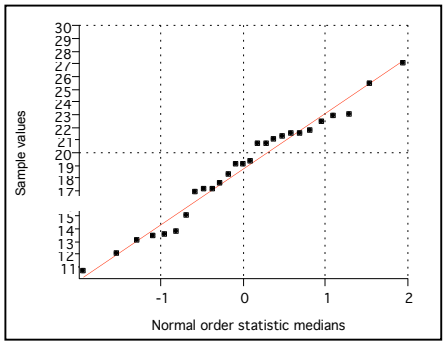


Figure Hh: Variable F1 Right side PPCC = 0.9883

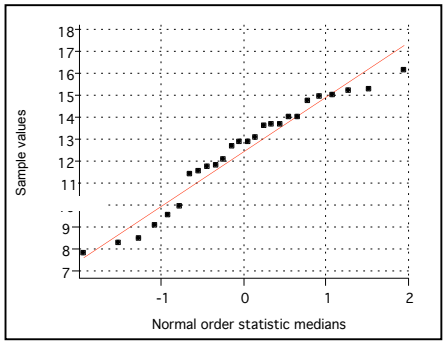


Figure Ii: Variable F2 Left side PPCC = 0.9764

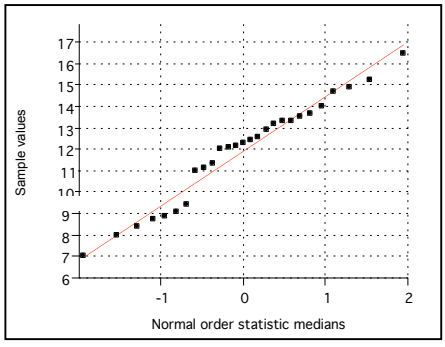


Figure Jj: Variable F2 Right side PPCC = 0.9835

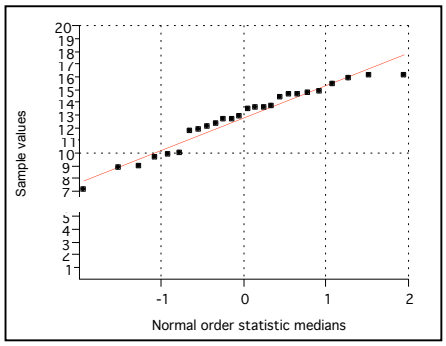


Figure Kk: Variable F3 Left side PPCC = 0.9757

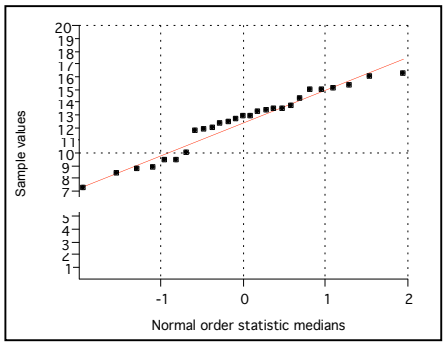


Figure Ll: Variable F3 Right side PPCC = 0.9787

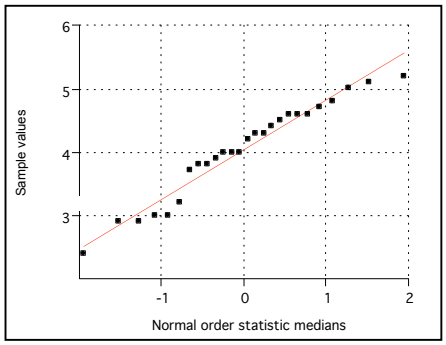


Figure Mm: Variable F4 Left side PPCC = 0.9791

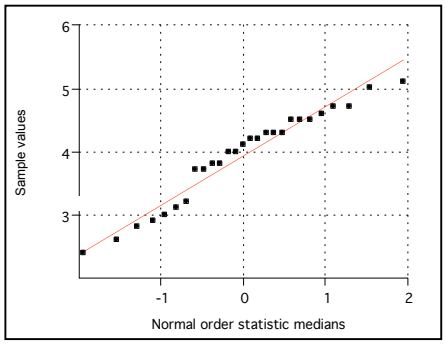


Figure Nn: Variable F4 Right side PPCC = 0.9764

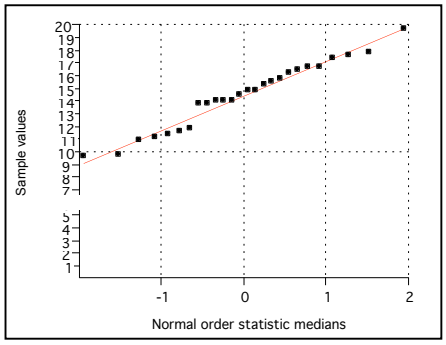


Figure Oo: Variable F5 Left side PPCC = 0.9876

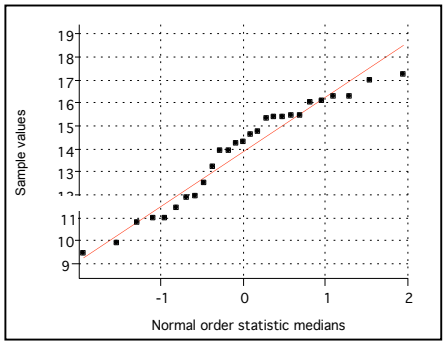


Figure Pp: Variable F5 Right side PPCC = 0.9745

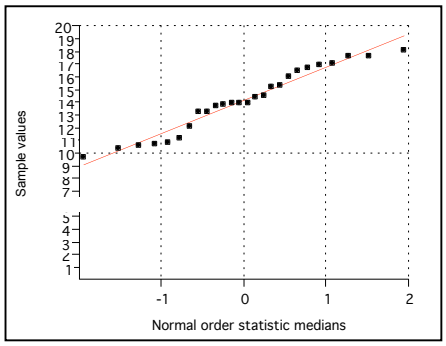


Figure Qq: Variable F6 Left side PPCC = 0.9814

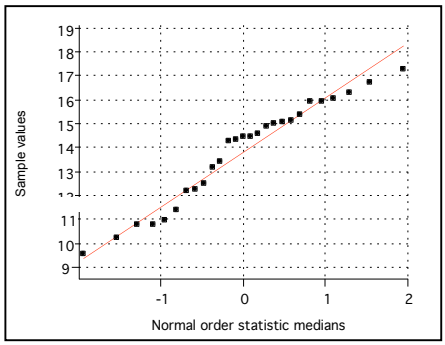


Figure Rr: Variable F6 Right side PPCC = 0.9784

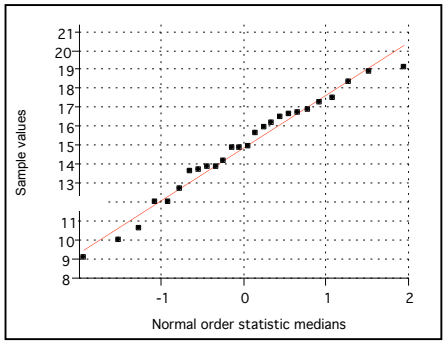


Figure Ss: Variable F7 Left side PPCC = 0.9884

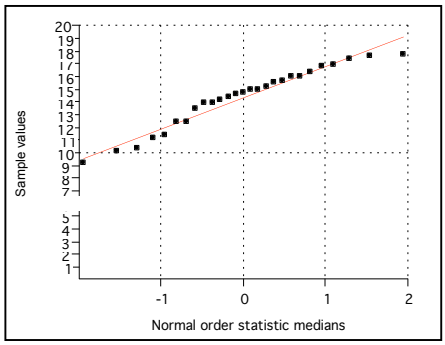


Figure Tt: Variable F7 Right side PPCC = 0.9787

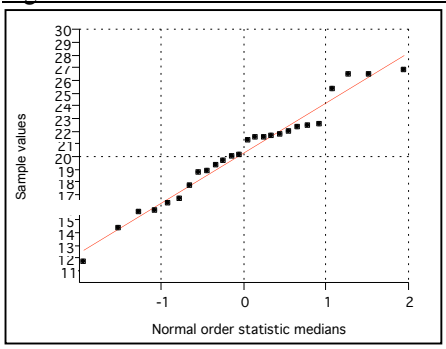


Figure Uu: Variable F8 Left side PPCC = 0.9863

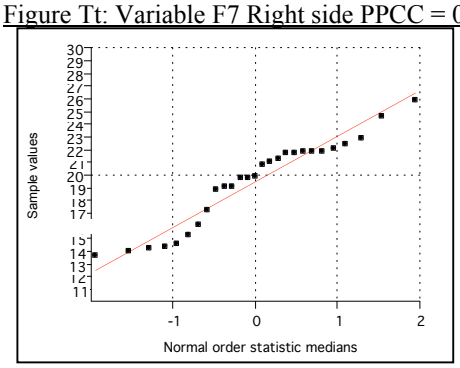


Figure Vv: Variable F8 Right side PPCC = 0.9686

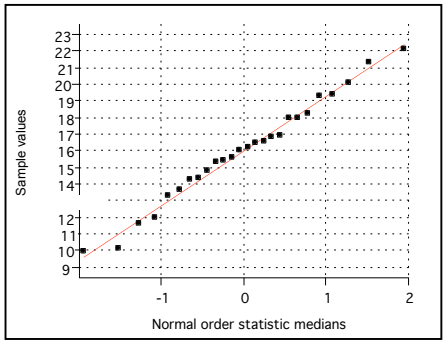


Figure Ww: Variable F9 Left side PPCC = 0.9945

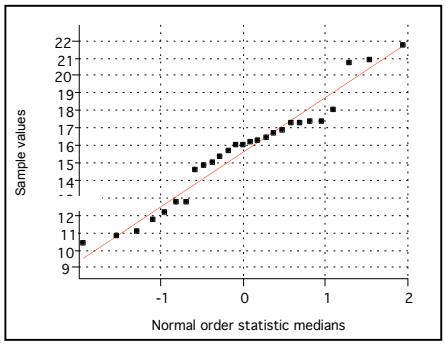


Figure Xx: Variable F9 Right side PPCC = 0.9785

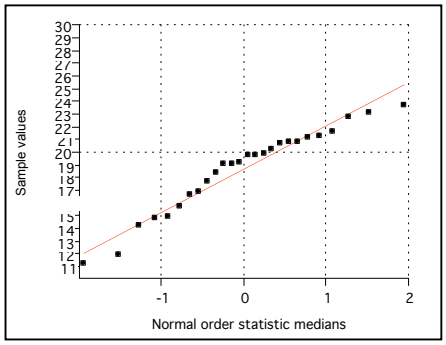


Figure Yy: Variable F10 Left side PPCC = 0.9752

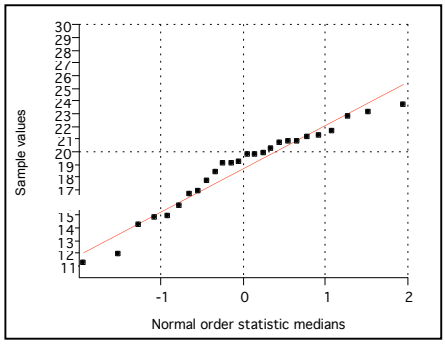


Figure Zz: Variable F10 Left side PPCC = 0.9644

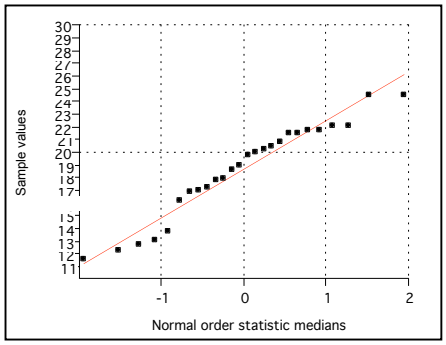


Figure a: Variable F11 Left side PPCC = 0.9767

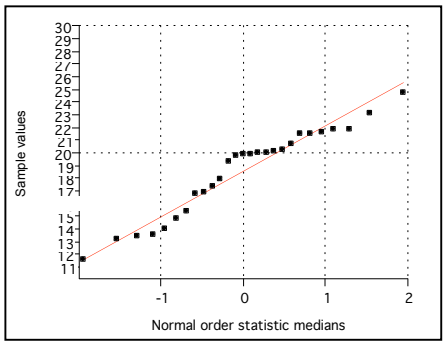


Figure b: Variable F11 Right side PPCC = 0.9721

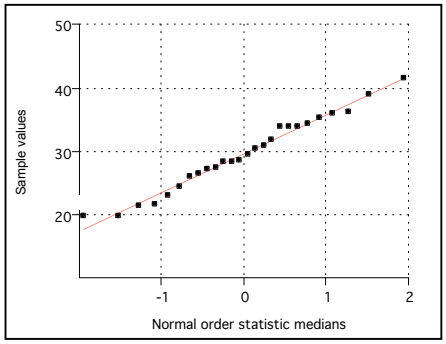


Figure c: Variable F12 Left side PPCC = 0.9918

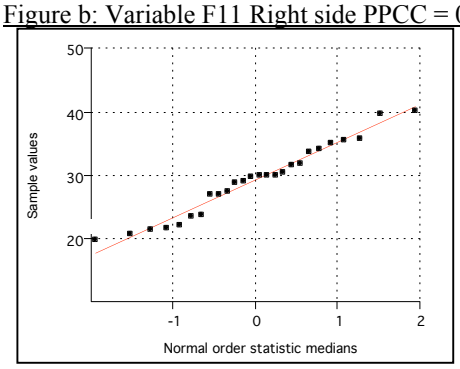


Figure d: Variable F12 Left side PPCC = 0.9874

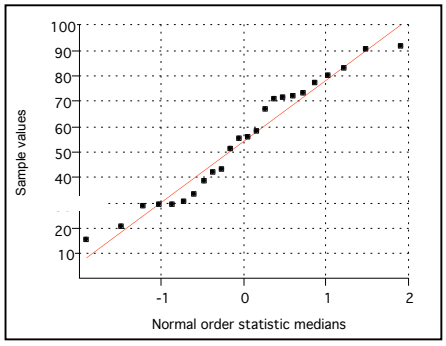


Figure e: Variable F13 Left side PPCC = 0.9818

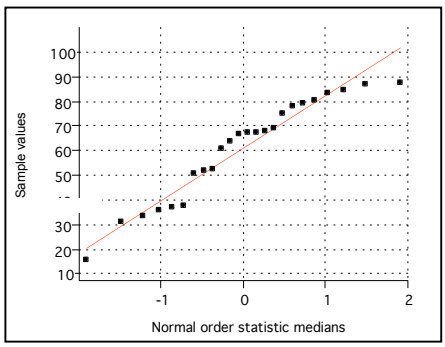


Figure F: Variable F13 Right side PPCC = 0.9713

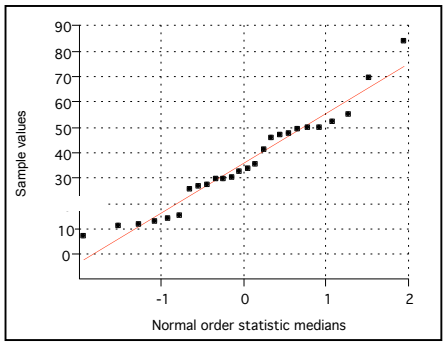


Figure g: Variable Ff Left side PPCC = 0.9769

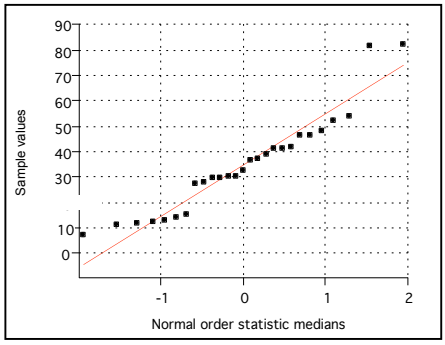


Figure f: Variable Ff Right side PPCC = 0.959

Baboon Tibia Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

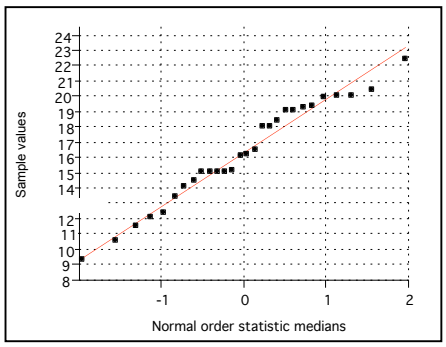


Figure g: Variable T1 Left side PPCC = 0.9863

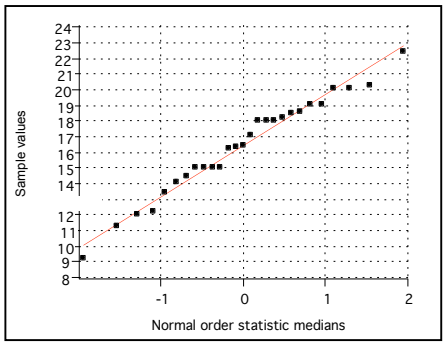


Figure h: Variable T1 Right side PPCC = 0.9881

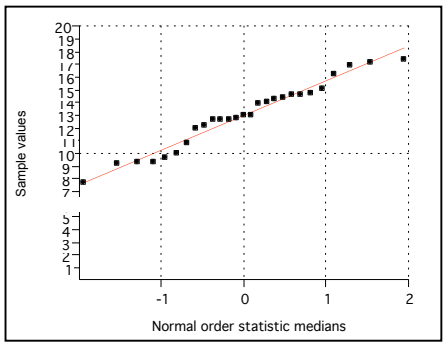


Figure i: Variable T2 Left side PPCC = 0.9798

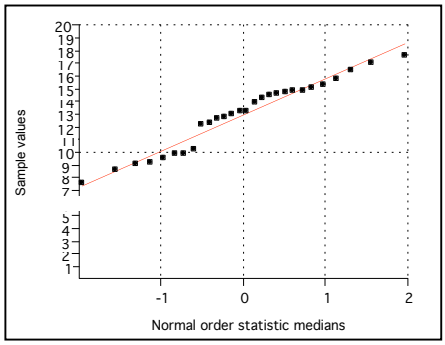


Figure j: Variable T2 Right side PPCC = 0.9858

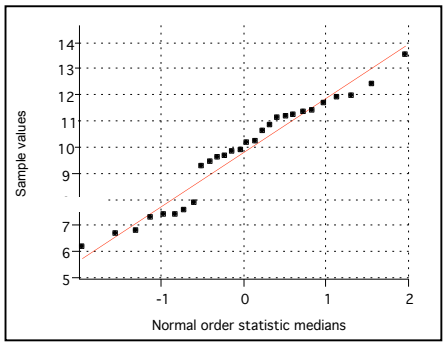


Figure k: Variable T3 Left side PPCC = 0.9786

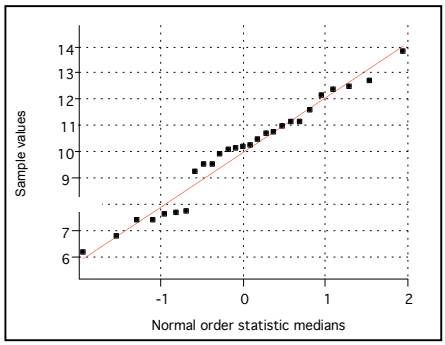


Figure l: Variable T3 Right side PPCC = 0.985

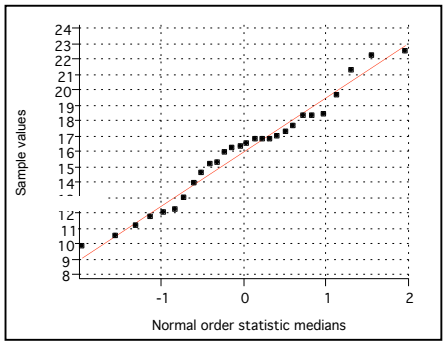


Figure m: Variable T4 Left side PPCC = 0.9881

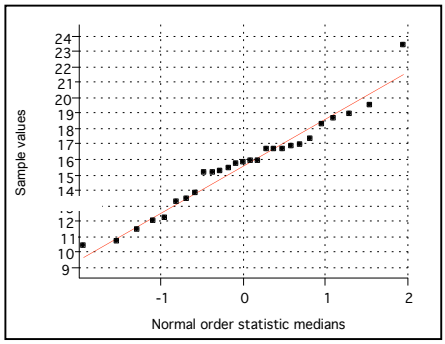


Figure n: Variable T4 Right side PPCC = 0.9793

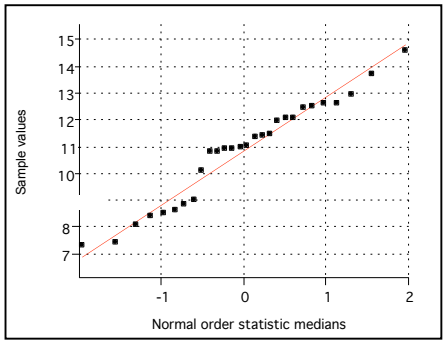


Figure o: Variable T5 Left side PPCC = 0.9804

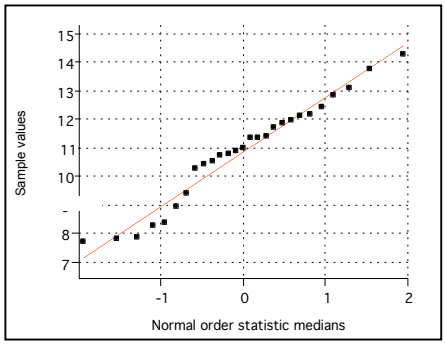


Figure p: Variable T5 Right side PPCC = 0.9831

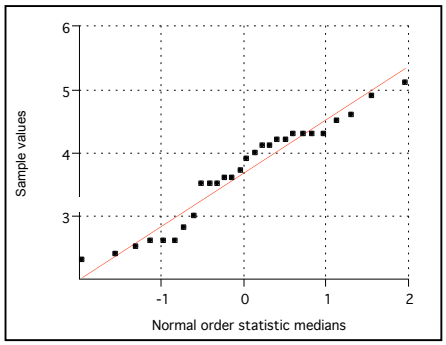


Figure q: Variable T6 Left side PPCC = 0.9746

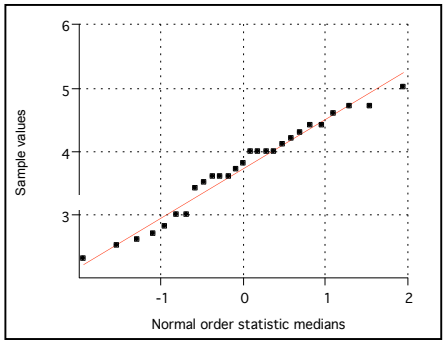


Figure r: Variable T6 Right side PPCC = 0.9864

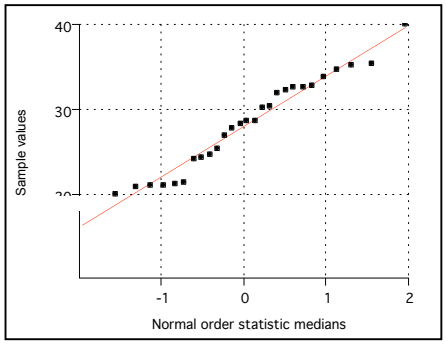


Figure s: Variable T7 Left side PPCC = 0.9826

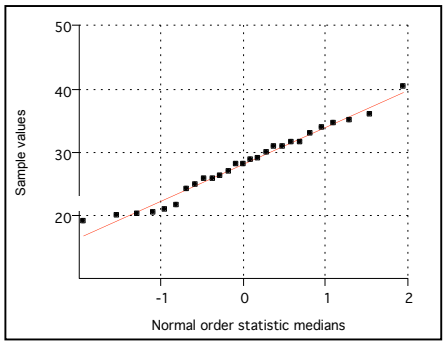


Figure t: Variable T7 Right side PPCC = 0.9894

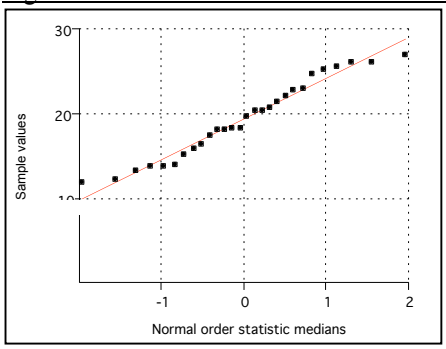


Figure u: Variable T8 Left side PPCC = 0.9849

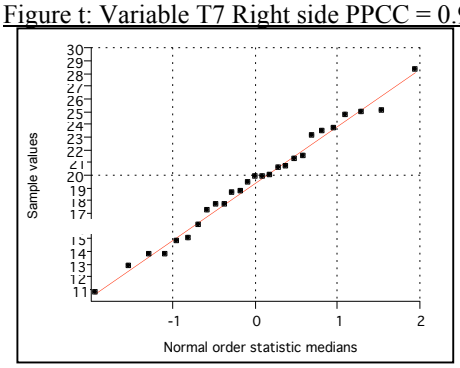


Figure v: Variable T8 Right side PPCC = 0.9947

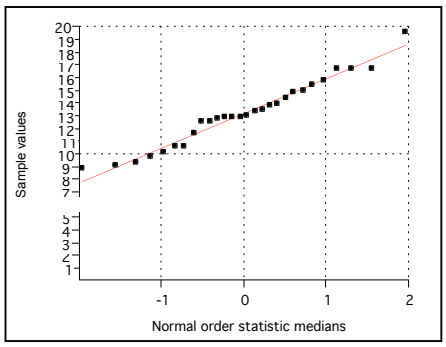


Figure w: Variable T9 Left side PPCC = 0.986

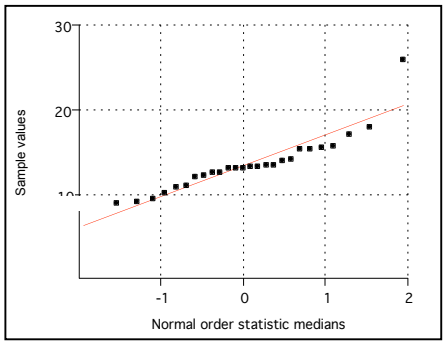
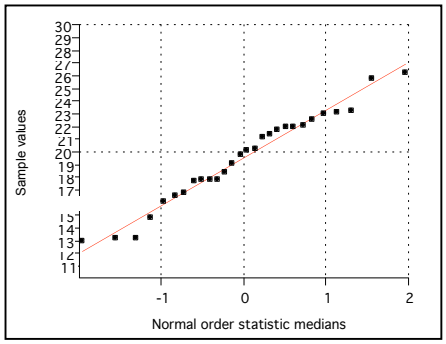


Figure x: Variable T9 Right side PPCC = 0.9158



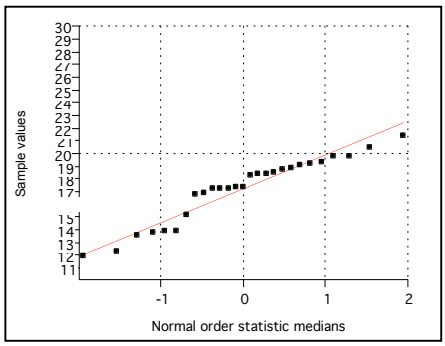


Figure y: Variable T10 Left side PPCC = 0.9871

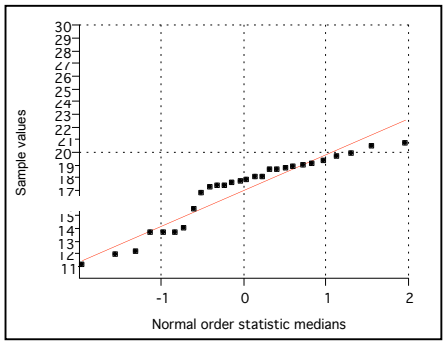


Figure z: Variable T10 Right side PPCC = 0.9762

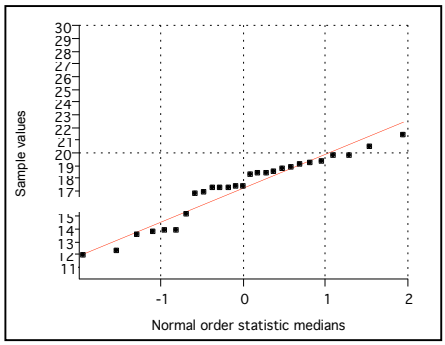


Figure a1: Variable T11 Left side PPCC = 0.9515

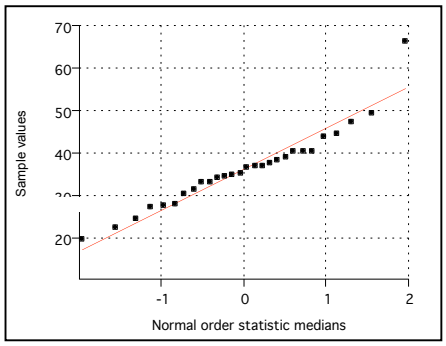


Figure a2: Variable T11 Right side PPCC = 0.9666

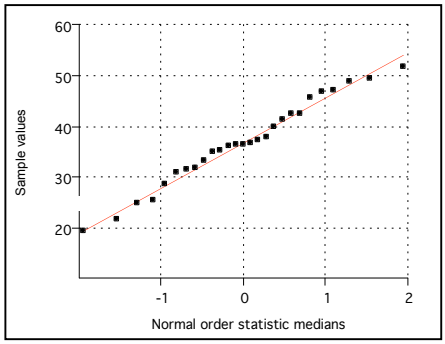


Figure a3: Variable T12 Left side PPCC = 0.9563

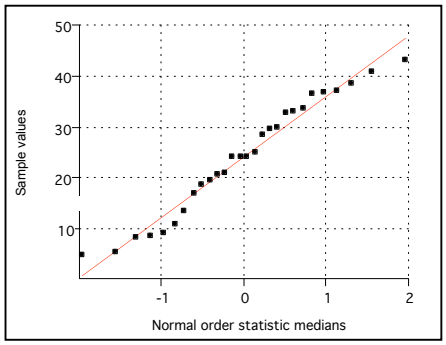


Figure a4: Variable T12 Right side PPCC = 0.9921

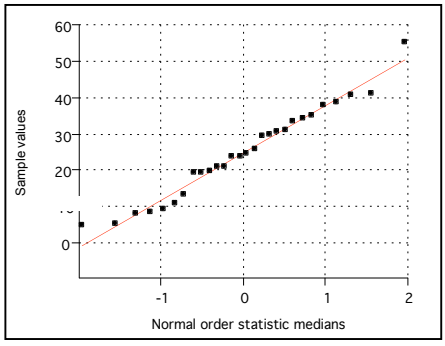


Figure a5: Variable Tg Left side PPCC = 0.9855

Figure a6: Variable Tg Right side PPCC = 0.9866

Human Clavicle Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

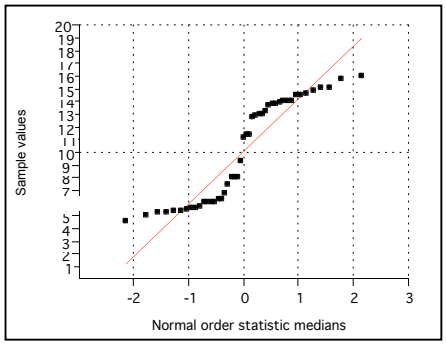


Figure b1: Variable C1 Left side PPCC = 0.9329

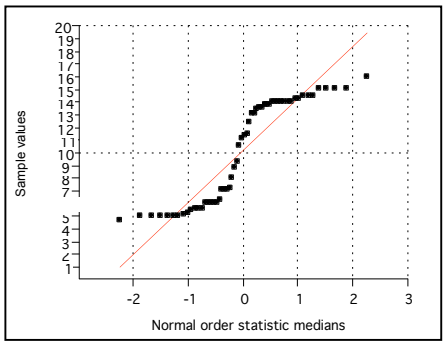


Figure b2: Variable C1 Right side PPCC = 0.9203

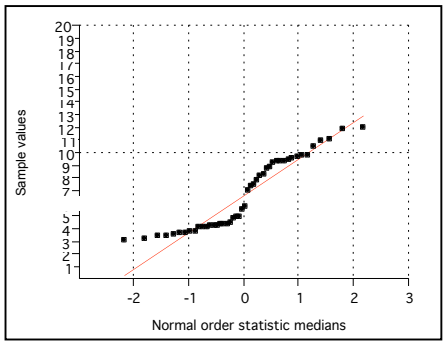


Figure b3: Variable C2 Left side PPCC = 0.9472

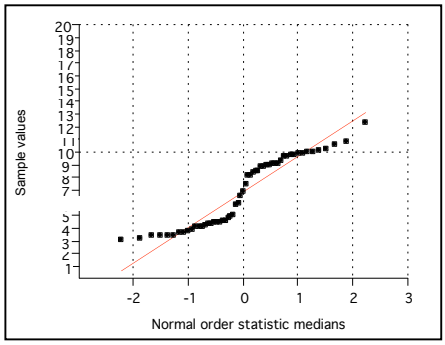


Figure b4: Variable C2 Right side PPCC = 0.9466

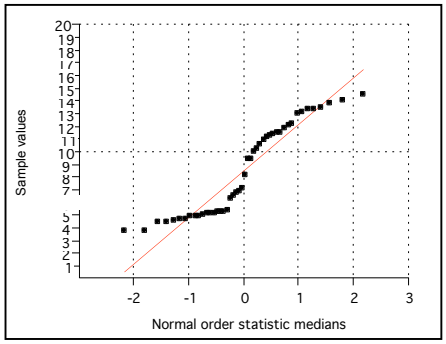


Figure b5: Variable C3 Left side PPCC = 0.9465

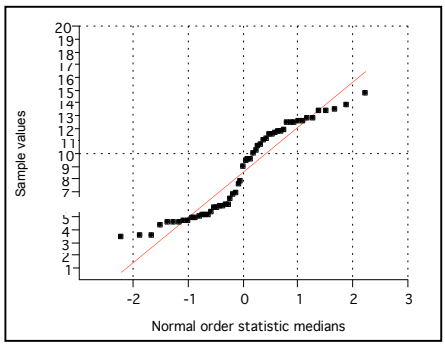


Figure b6: Variable C3 Right side PPCC = 0.9564

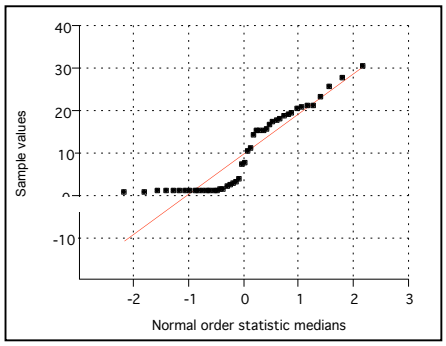


Figure b7: Variable Ca Left side PPCC = 0.9264

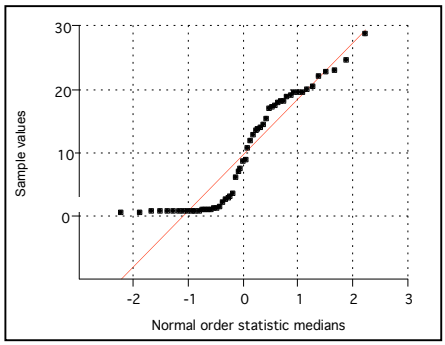


Figure b8: Variable Ca Right side PPCC = 0.9345

Human Humerus Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

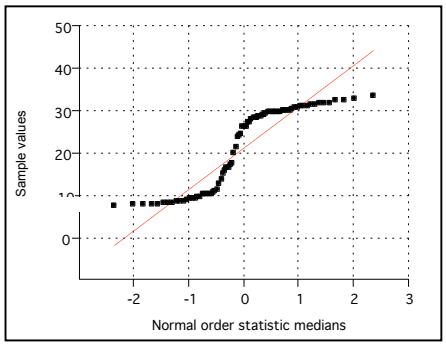


Figure c1: Variable H1 Left side PPCC = 0.9097

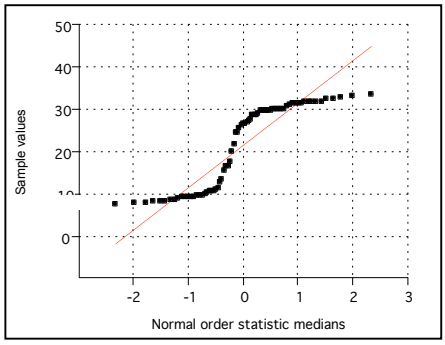


Figure c2: Variable H1 Right side PPCC = 0.9137

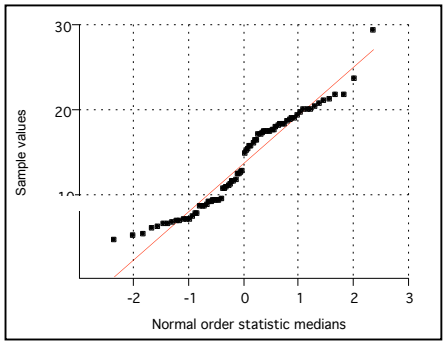


Figure c3: Variable H2 Left side PPCC = 0.9592

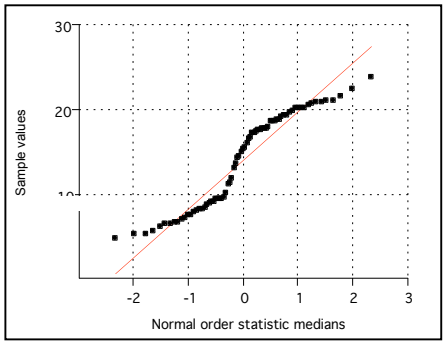


Figure c4: Variable H2 Right side PPCC = 0.9736

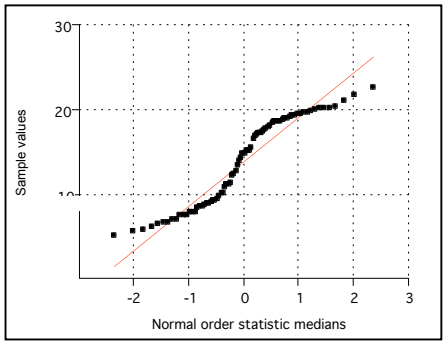


Figure c4: Variable H3 Left side PPCC = 0.9521

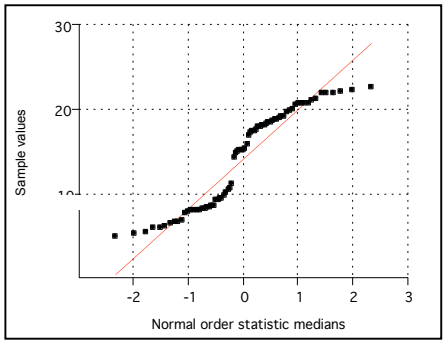


Figure c5: Variable H3 Right side PPCC = 0.9603

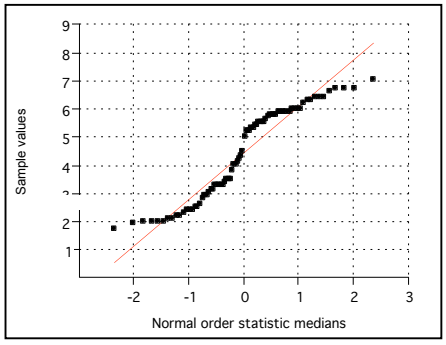


Figure c6: Variable H4 Left side PPCC = 0.9468

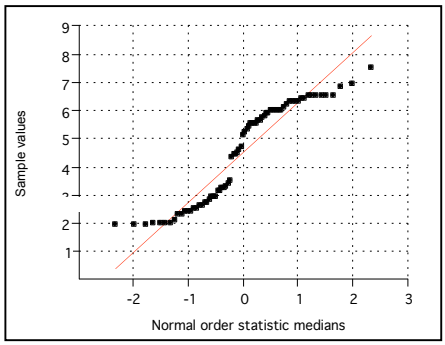


Figure c7: Variable H4 Right side PPCC = 0.9574

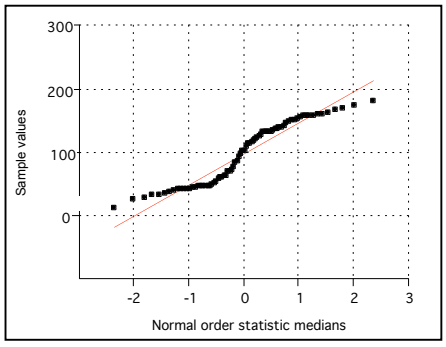


Figure c8: Variable H5 Left side PPCC = 0.9733

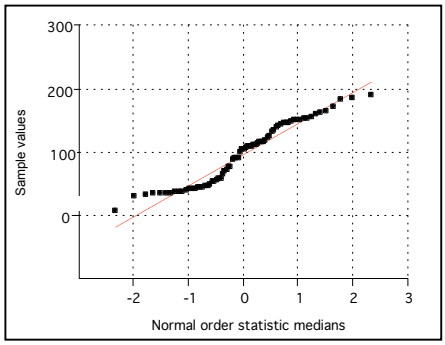


Figure c9: Variable H5 Right side PPCC = 0.9606

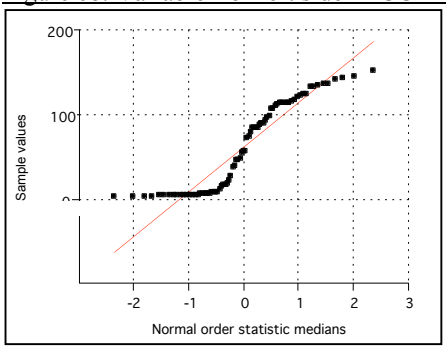


Figure c10: Variable Hb Left side PPCC = 0.9363

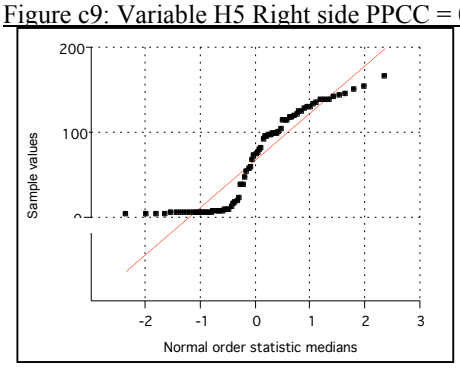


Figure c11: Variable Hb Right side PPCC = 0.9

Human Femur Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

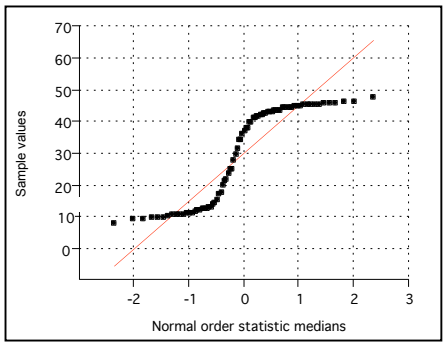


Figure g1: Variable F1 Left side PPCC = 0.9099

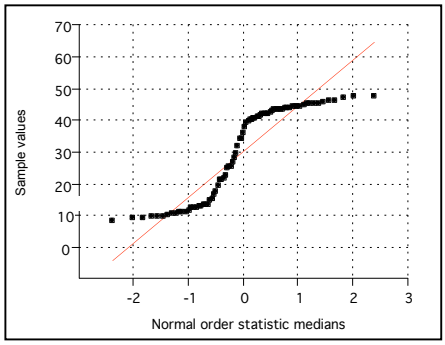


Figure g2: Variable F1 Right side PPCC = 0.9207

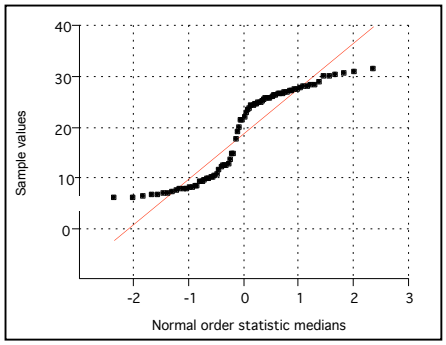


Figure g3: Variable F2 Left side PPCC = 0.9371

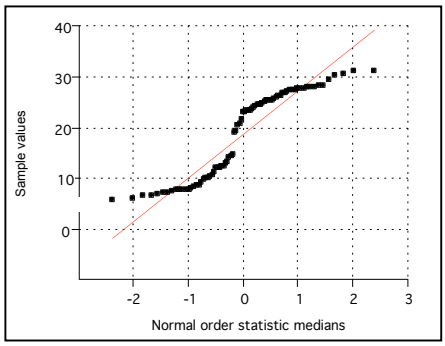


Figure g4: Variable F2 Right side PPCC = 0.9393

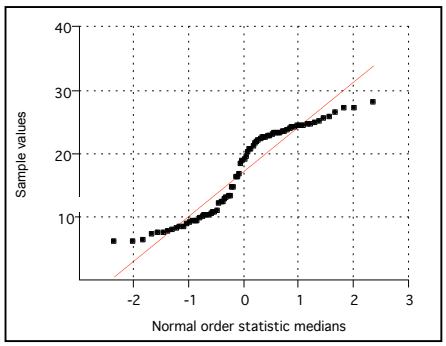


Figure g5: Variable F3 Left side PPCC = 0.9515

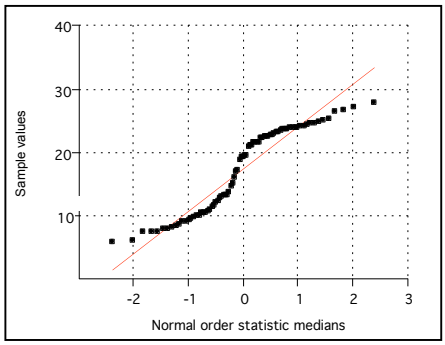


Figure g6: Variable F3 Right side PPCC = 0.9536

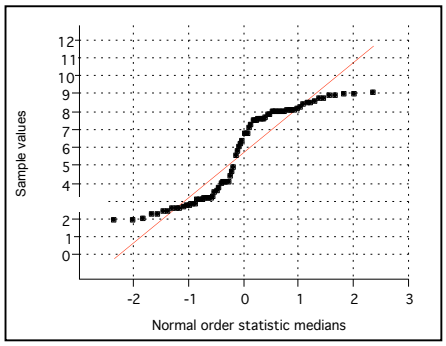


Figure g7: Variable F4 Left side PPCC = 0.9374

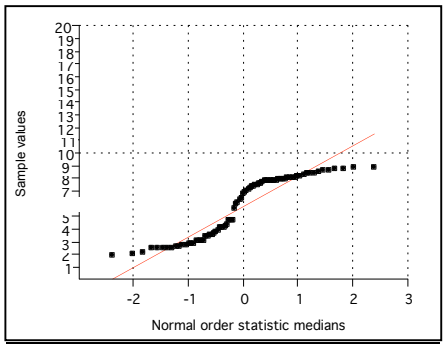


Figure g8: Variable F4 Right side PPCC = 0.9351

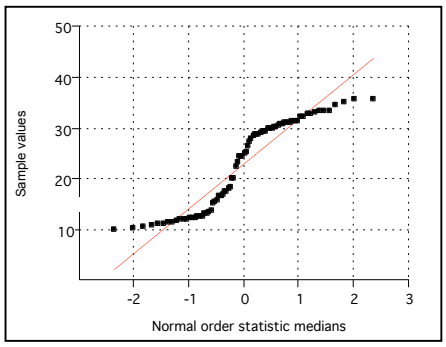


Figure g9: Variable F5 Left side PPCC = 0.9442

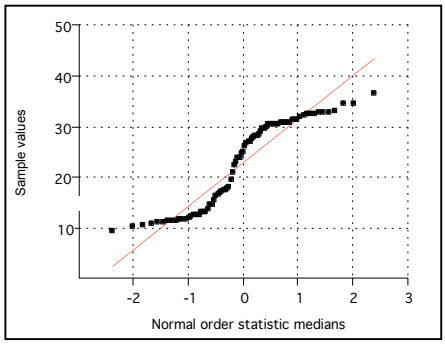


Figure g10: Variable F5 Right side PPCC = 0.944

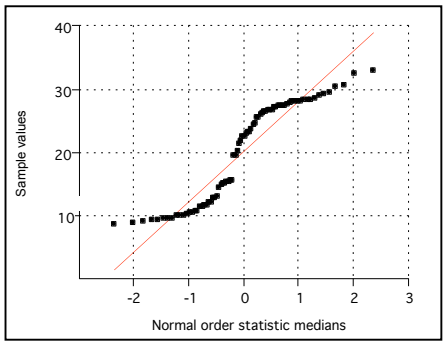


Figure g11: Variable F6 Left side PPCC = 0.9433

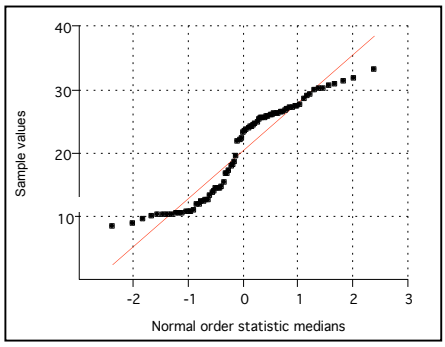


Figure g12: Variable F6 Right side PPCC = 0.9559

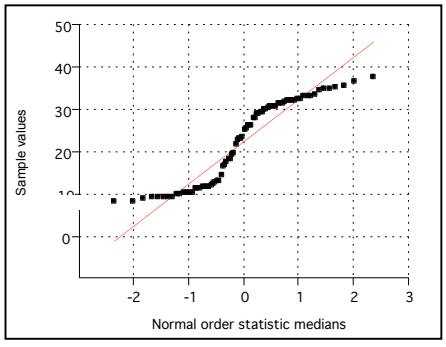


Figure g13: Variable F7 Left side PPCC = 0.9443

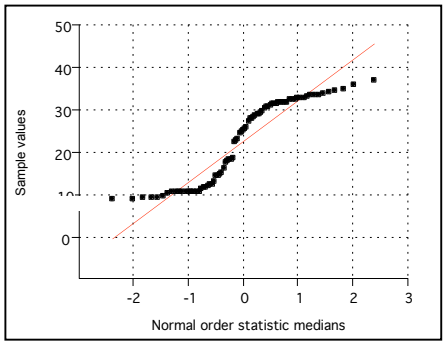


Figure g14: Variable F7 Right side PPCC = 0.9351

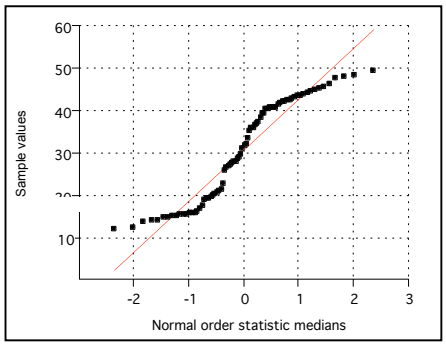


Figure g15: Variable F8 Left side PPCC = 0.9582

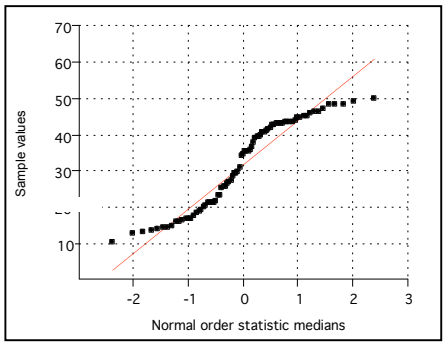


Figure g16: Variable F8 Right side PPCC = 0.9613

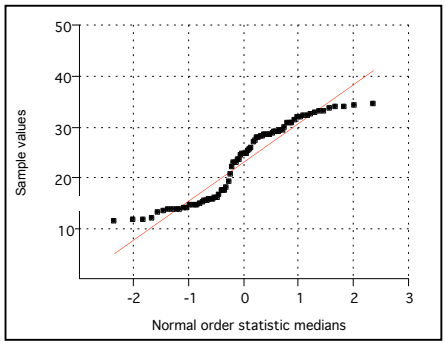


Figure g17: Variable F9 Left side PPCC = 0.9556

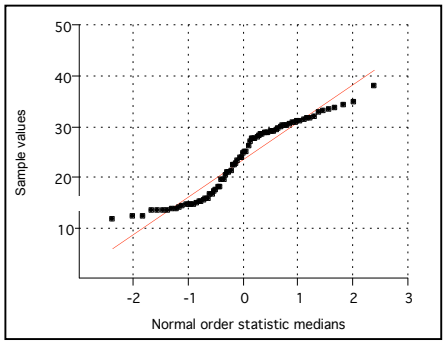


Figure g18: Variable F9 Right side PPCC = 0.9641

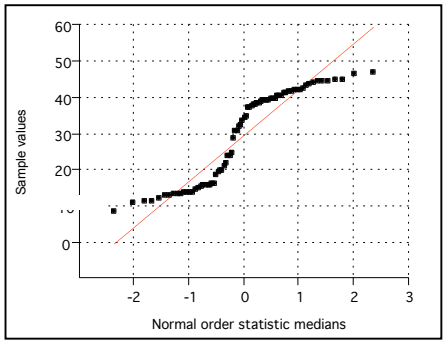


Figure g19: Variable F10 Left side PPCC = 0.9367

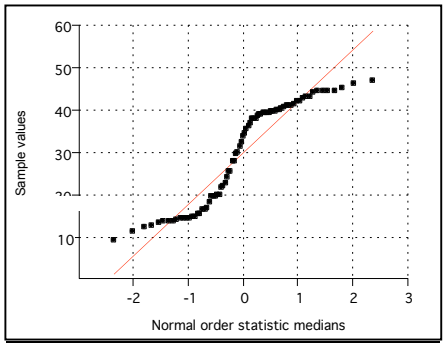


Figure g20: Variable F10 Right side PPCC = 0.9434

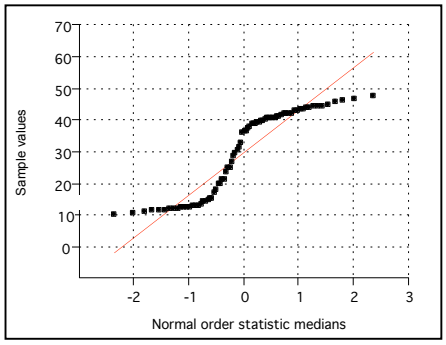


Figure g21: Variable F11 Left side PPCC = 0.928

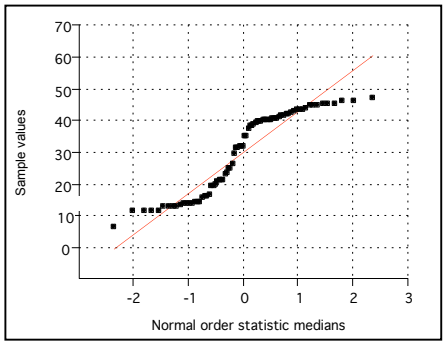


Figure g22: Variable F11 Right side PPCC = 0.9406

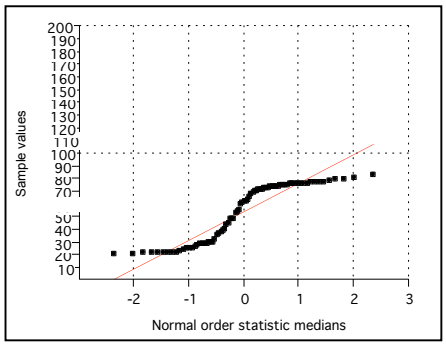


Figure g23: Variable F12 Left side PPCC = 0.928

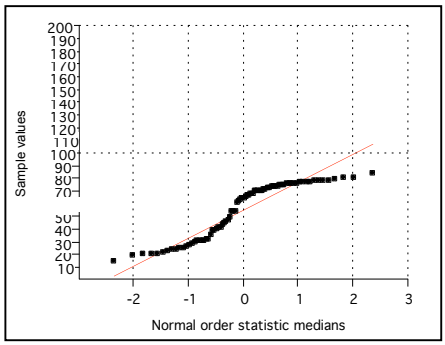


Figure g24: Variable F12 Right side PPCC = 0.9394

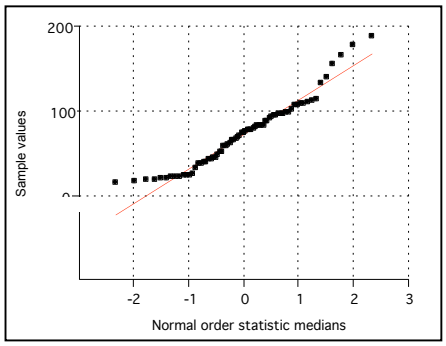


Figure g25: Variable F13 Left side PPCC = 0.9748

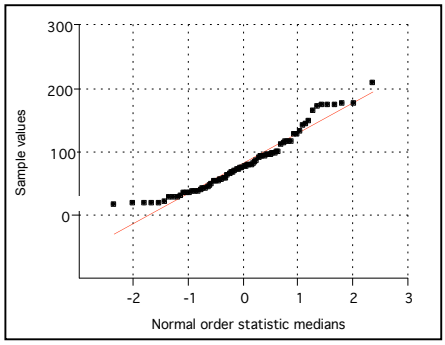


Figure g26: Variable F13 Right side PPCC = 0.9707

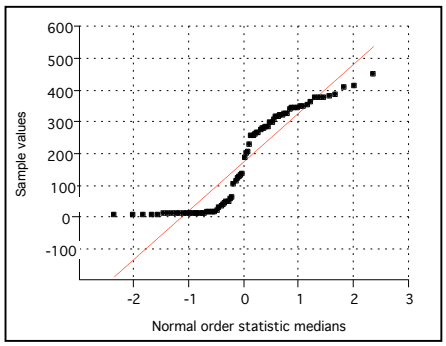


Figure g27: Variable Ff Left side PPCC = 0.9259

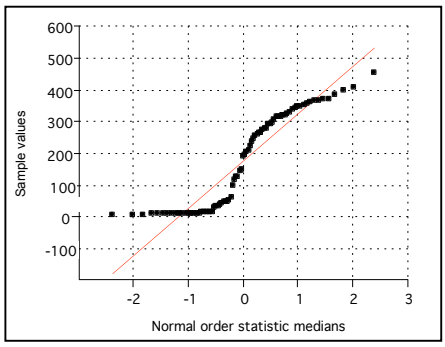


Figure g28: Variable Ff Right side PPCC = 0.9313

Human Tibia Normal Probability Plots and Probability Plot Correlation Coefficients (PPCC)

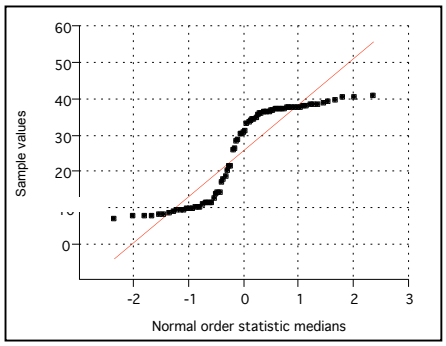


Figure h1: Variable H1 Left side PPCC = 0.9136

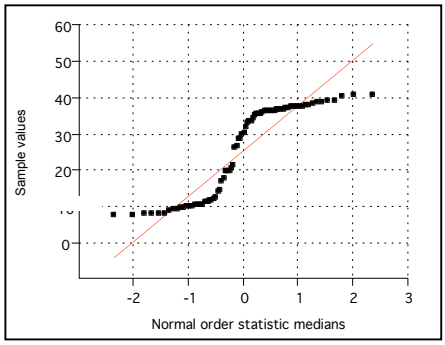


Figure h2: Variable H1 Right side PPCC = 0.915

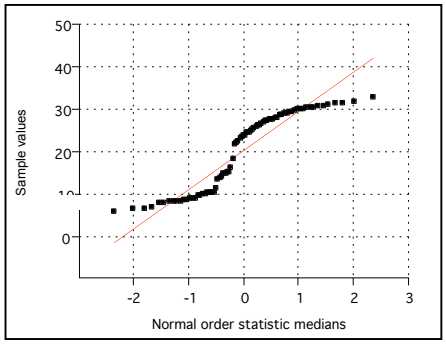


Figure h3: Variable H2 Left side PPCC = 0.9362

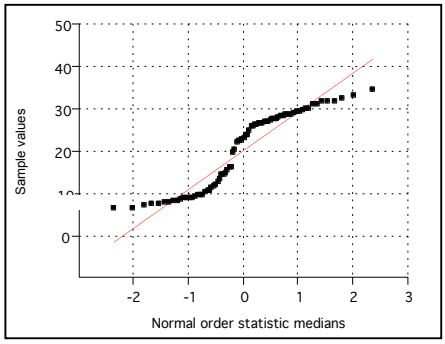


Figure h4: Variable H2 Right side PPCC = 0.9451

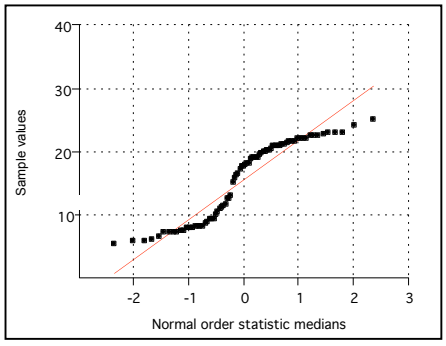


Figure h5: Variable H3 Left side PPCC = 0.946

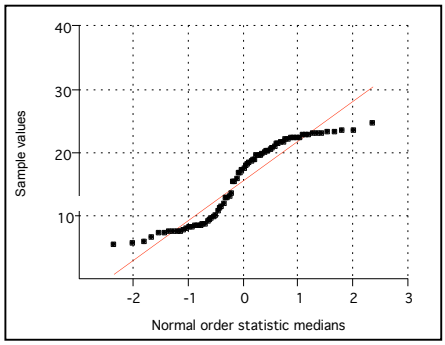


Figure h6: Variable H3 Right side PPCC = 0.9486

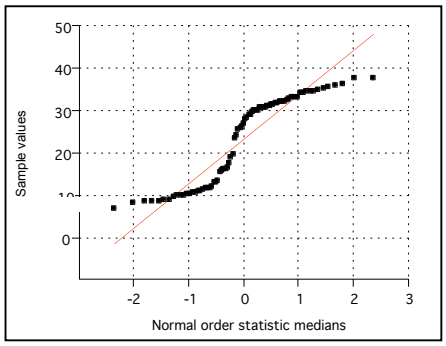


Figure h7: Variable H4 Left side PPCC = 0.9352

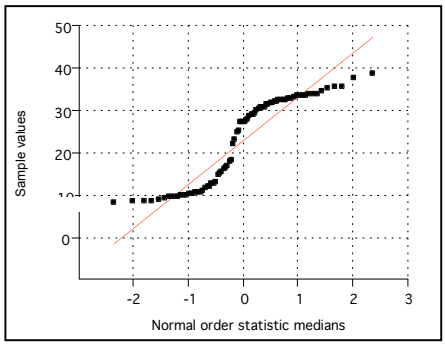


Figure h8: Variable H4 Right side PPCC = 0.9322

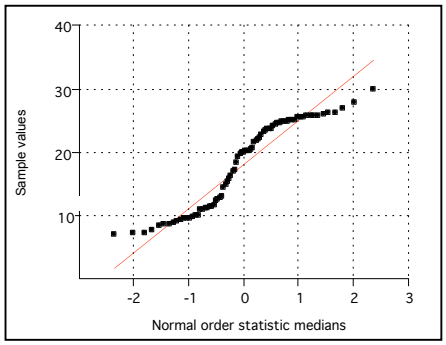


Figure h9: Variable H5 Left side PPCC = 0.9547

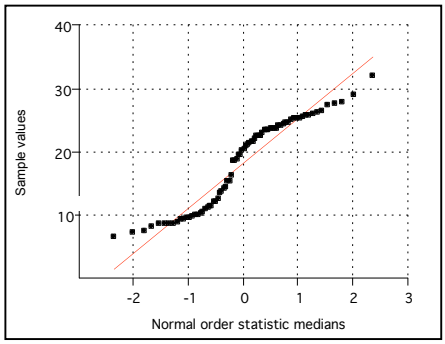


Figure h10: Variable H5 Right side PPCC = 0.96

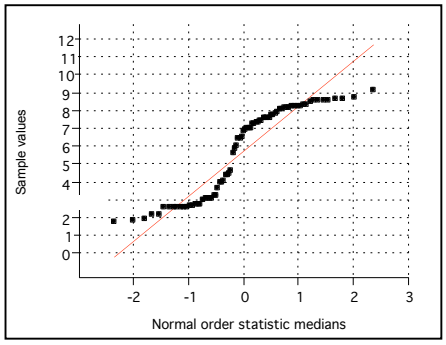


Figure h11: Variable H6 Left side PPCC = 0.9333

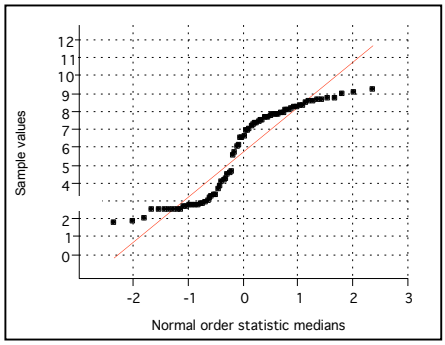


Figure h12: Variable H6 Right side PPCC = 0.9384

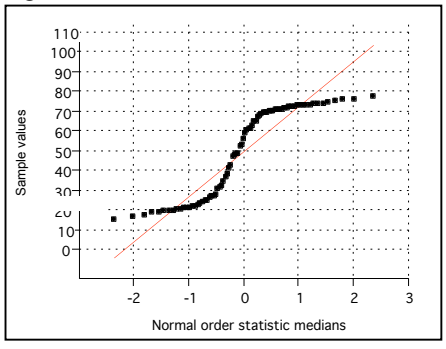


Figure h13: Variable H7 Left side PPCC = 0.9253

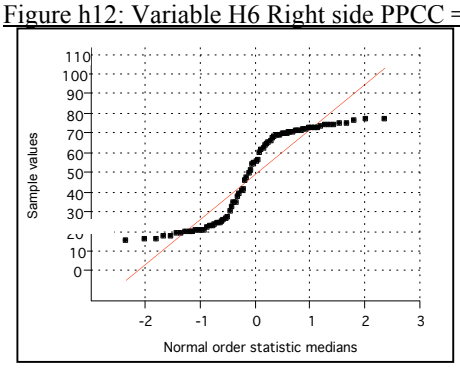


Figure h14: Variable H7 Right side PPCC = 0.9284

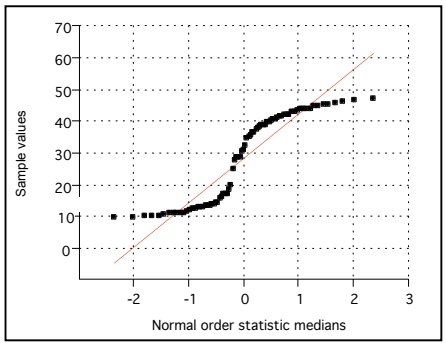


Figure h15: Variable H8 Left side PPCC = 0.9278

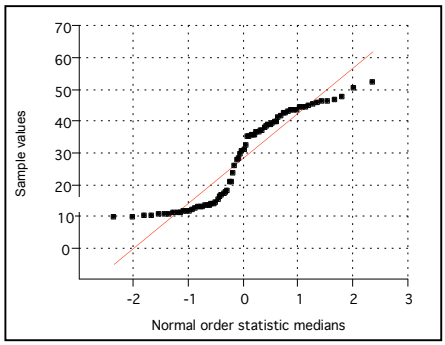


Figure h16: Variable H8 Right side PPCC = 0.9427

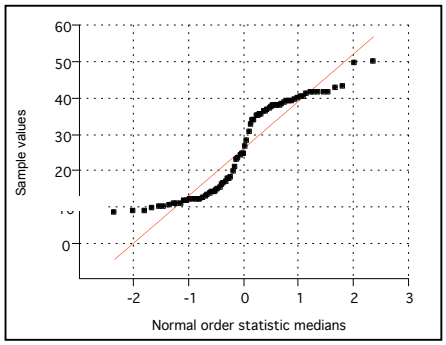


Figure h17: Variable H9 Left side PPCC = 0.9447

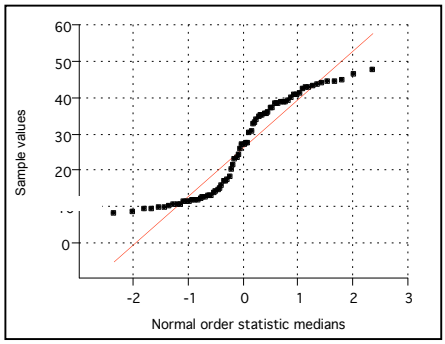


Figure h18: Variable H9 Right side PPCC = 0.9489

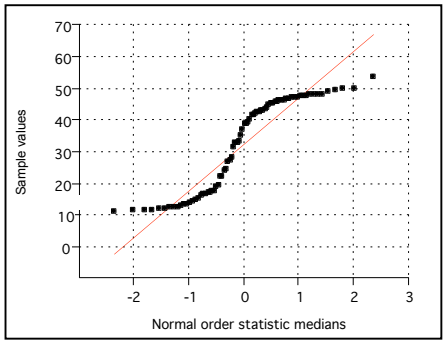


Figure h19: Variable H10 Left side PPCC = 0.9323

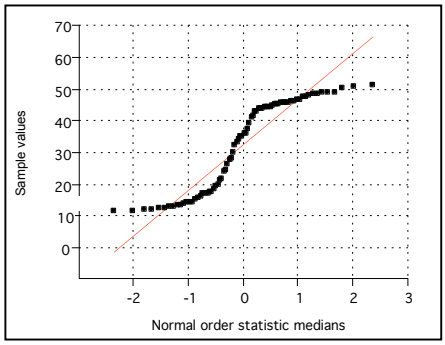


Figure h20: Variable H10 Right side PPCC = 0.9344

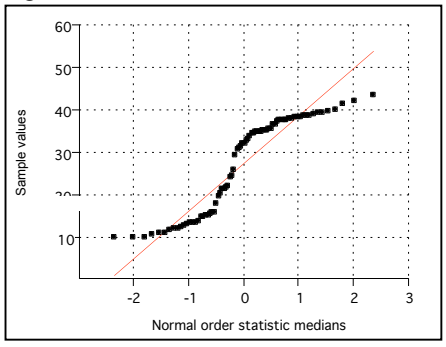


Figure h21: Variable H11 Left side PPCC = 0.9359

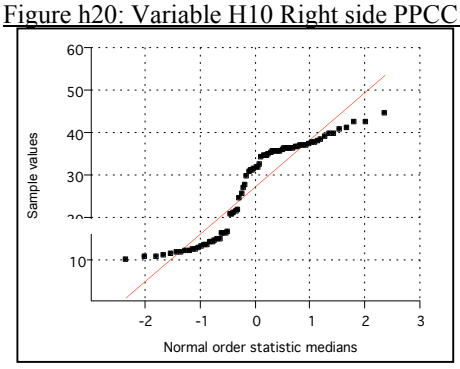


Figure h22: Variable H11 Right side PPCC = 0.9387

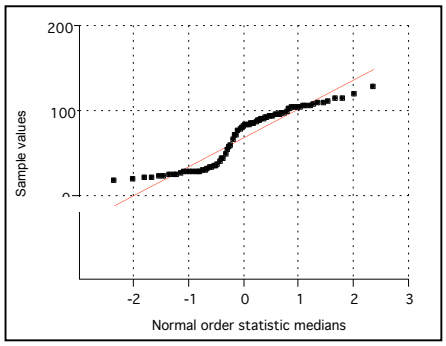


Figure h23: Variable H12 Left side PPCC = 0.9488

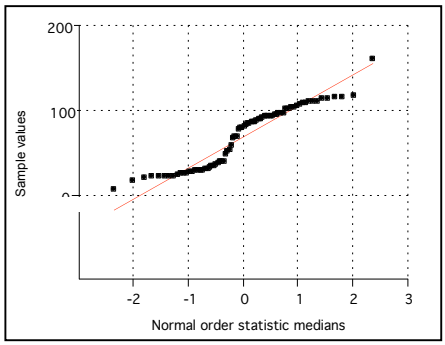


Figure h24: Variable H12 Right side PPCC = 0.9572

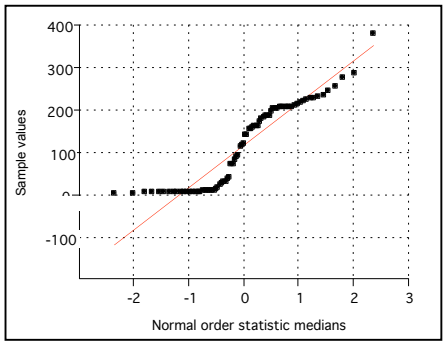


Figure h25: Variable Hg Left side PPCC = 0.9378

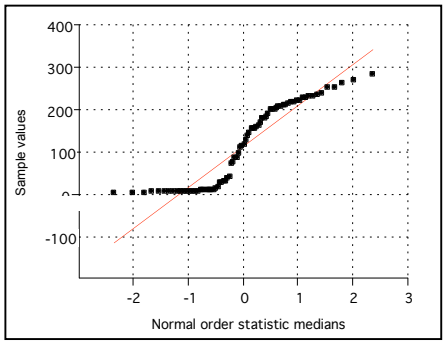


Figure h26: Variable Hg Right side PPCC = 0.9329

Appendix D

Table A: Variance-co-variance matrix for humans' humerus

	max l	M-L dms	A-P dms	mc	NFDPM	Mass
max l	92.03	49.728	49.27	15.449	394.79	469.14
M-L dms	49.728	30.569	27.928	9.089	209.5	267.16
A-P dms	49.27	27.928	29.418	8.8071	209.69	264.64
Mc	15.449	9.089	8.8071	2.812	65.724	82.195
NFDPM	394.79	209.5	209.69	65.724	2044.6	1994.7
Mass	469.14	267.16	264.64	82.195	1994.7	2818.7

Table B: Variance-co-variance matrix for baboons' humerus

	max l	M-L dms	A-P dms	mc	NFDPM	Mass
max l	13.547	7.8383	8.8646	2.5868	53.932	13.239
M-L dms	7.8383	5.3604	5.6091	1.6556	30.72	9.6789
A-P dms	8.8646	5.6091	7.7017	2.0488	36.049	5.1637
mc	2.5868	1.6556	2.0488	0.57863	10.653	1.2902
NFDPM	53.932	30.72	36.049	10.653	442.71	2.7507
Mass	15.651	12.628	8.8386	2.4226	20.217	455.94

Table C: Variance-co-variance matrix for humans' radius

	Max L	Tdms	M-L dms	Hd	Nufdpm	Mass
Max L	57.878	23.348	28.401	44.858	184.73	122.45
Tdms	23.348	10.122	11.967	18.509	74.114	50.497
M-L dms	28.401	11.967	15.175	22.547	91.408	62.6
Hd	44.858	18.509	22.547	37.618	144.23	97.054
Nufdpm	180.18	72.197	89.2	140.22	606.11	385.58
Mass	122.45	50.497	62.6	97.054	396.42	306.14

Table D: Variance-co-variance matrix for baboons' radius

	Max L	Tdms	M-L dms	Hd	Nufdpm	Mass
Max L	14.854	5.833	7.7327	11.235	32.058	24.172
Tdms	5.833	2.5839	3.0964	4.3256	13.057	8.376
M-L dms	7.7327	3.0964	4.5081	5.8925	17.854	12.471
Hd	11.235	4.3256	5.8925	9.5433	25.08	20.29
Nufdpm	32.058	13.057	17.854	25.08	96.425	50.491
Mass	23.436	8.8513	12.23	19.277	48.579	47.732

Table E: Variance-co-variance matrix for humans' femur

	MAX L	A-P MD	M-L MD	MC	SUB-TRM-LD	SUB-TROA-PD	A-P DDS	M-L DDS	PEB	S-I DFHD
MAX L	196.8	115.55	90.5	27.2	112.2	96.8	125.0	582.8	88.3	163.3
A-P MD	115.5	72.124	51.4	17.88	66.7	57.0	75.8	422.2	53.7	94.7
M-L MD	90.5	51.487	48.7	12.60	54.9	48.4	57.1	211.6	42.4	83.3
MC	27.2	17.848	12.6	27.09	23.9	29.4	31.9	78.8	29.3	47.0
SUB-TRM-LD	112.2	66.792	54.3	23.93	70.4	62.7	77.5	312.0	58.4	104.5
SUB-TROA-PD	96.8	57.019	48.42	29.47	62.78	63.3	71.8	281.7	56.2	102.4
A-P DDS	125.0	75.852	57.11	31.93	77.53	71.8	91.7	281.8	68.03	118.1
M-L DDS	582.8	422.25	211.6	78.81	312.0	281.7	281.9	4893	168.8	454.1
PEB	88.3	53.718	42.4	29.35	58.4	56.2	68.9	168.8	58.3	93.9
S-I DFHD	155.8	90.546	79.6	45.6	100.6	98.8	113.8	440.5	90.5	165.3
A-P DFHD	151.1	85.42	85.7	87.86	115.6	132.2	134.6	378.1	120.4	218.8
BB	283.8	179.08	116.7	81.05	174.1	158.6	211.0	579.0	155.6	260.1
NFDPM	404.1	254.58	147.9	150.9	248.86	221.1	334.5	-189.9	248	372.1
Mass	1958.1	1158.4	949.8	190	1116.7	922.7	1218.2	3657.8	852.4	1579.3

Table F: Variance-co-variance matrix for baboons' femur

	MAX L	A-P MD	M-L MD	MC	SUB-TRM-LD	SUB-TROA-PD	A-P DDS	M-L DDS	PEB	S-I D
MAX L	15.888	8.21	8.5094	2.6373	8.613	8.2809	8.0395	11.91	10.423	1
A-P MD	8.21	5.0666	4.9267	1.5523	5.0647	4.9756	5.1087	7.4809	6.4674	6
M-L MD	8.5094	4.9267	5.1113	1.5723	4.9837	4.8533	5.0298	7.3081	6.2296	6
MC	2.6373	1.5523	1.5723	0.49078	1.5773	1.5283	1.5802	2.3054	1.965	

SUB-TRM-LD	8.613	5.0647	4.9837	1.5773	5.9302	5.2203	5.302	8.059	6.7254	6
SUB-TROA-PD	8.2809	4.9756	4.8533	1.5283	5.2203	5.3484	5.2355	7.7146	6.6446	6
A-P DDS	8.0395	5.1087	5.0298	1.5802	5.302	5.2355	5.8513	8.1885	6.6955	6
M-L DDS	11.91	7.4809	7.3081	2.3054	8.059	7.7146	8.1885	12.274	10.066	9
PEB	10.423	6.4674	6.2296	1.965	6.7254	6.6446	6.6955	10.066	9.2722	8
S-I DFHD	10.965	6.3204	6.3243	1.984	6.6652	6.6051	6.5475	9.7125	8.2697	9
A-P DFHD	13.368	7.3644	7.492	2.3386	7.7267	7.7016	7.657	11.262	9.6072	1
BB	20.559	11.529	11.691	3.6272	12.449	12.143	12.33	17.749	15.435	1
NFDPM	51.438	31.475	32.708	10.029	33.581	32.002	31.417	50.481	44.048	3
Mass	72.92	35.092	36.106	10.964	37.562	37.222	33.799	49.55	47.15	4

Table F: Variance-co-variance matrix for humans' tibia

	MAX L	**A-P DMS**	**M-L DMS**	**A-P DNF**	**M-L DNF**	**MC**	**PAB**	**A-P DTUB**	**M-L DTUB**	**M-L DAB**	**A-P DAB**	**NFPM**
MAX L	150.96	109.06	73.948	123.76	81.875	29.787	269.36	166.67	150.76	173.41	133.75	406.09
A-P DMS	109.06	82.356	55.196	92.838	60.65	22.334	196.6	122.65	110.49	126.34	98.108	294.53
M-L DMS	73.948	55.196	38.171	62.425	41.978	15.151	132.9	83.028	75.58	85.842	66.684	200.76
A-P DNF	123.76	92.838	62.425	105.58	68.939	25.23	222.76	139.85	125.62	143.41	111.28	331.83
M-L DNF	81.875	60.65	41.978	68.939	47.121	16.671	147.71	92.596	84.128	95.416	74.444	222.5
MC	29.787	22.334	15.151	25.23	16.671	6.1025	53.628	33.467	30.236	34.501	26.723	80.601
PAB	269.36	196.6	132.9	222.76	147.71	53.628	494.04	302.53	276.39	316.1	240.29	725.17
A-P DTUB	166.67	122.65	83.028	139.85	92.596	33.467	302.53	192.8	174.23	194.01	148.61	451.2
M-L DTUB	150.76	110.49	75.58	125.62	84.128	30.236	276.39	174.23	163.39	178.02	134.25	409.65
M-L DAB	173.41	126.34	85.842	143.41	95.416	34.501	316.1	194.01	178.02	204.69	154.94	466.97
A-P DAB	133.75	98.108	66.684	111.28	74.444	26.723	240.29	148.61	134.25	154.94	122.78	360.94
NFPM	406.09	294.53	200.76	331.83	222.5	80.601	725.17	451.2	409.65	466.97	360.94	1146.2
Mass	1106.7	816.09	548.64	926.89	607.46	222.85	2034.4	1276.3	1161.8	1304.5	978.87	2998.5

Table G: Variance-co-variance matrix for baboons' tibia

	MAX L	A-P DMS	M-L DMS	A-P DNF	M-L DNF	MC	PAB	A-P DTUB	M-L DTUB	M-L DAB	A-P DAB	NFF
MAX L	11.023	7.8294	5.9244	8.5806	4.5121	2.2662	17.186	13.327	8.0666	9.1001	6.983	23.3
A-P DMS	7.8294	6.4687	4.7676	7.1645	3.8875	1.8389	12.962	10.373	6.0891	7.0431	5.716	14.1
M-L DMS	5.9244	4.7676	3.6856	5.3807	2.9788	1.3917	9.8743	7.9262	4.8121	5.296	4.3929	10.9
A-P DNF	8.5806	7.1645	5.3807	8.6899	4.4884	2.074	15.16	11.967	6.8021	7.77	6.308	13.3
M-L DNF	4.5121	3.8875	2.9788	4.4884	2.6756	1.1389	8.0814	6.2888	3.9818	4.5654	3.6745	6.9
MC	2.2662	1.8389	1.3917	2.074	1.1389	0.55164	3.8185	3.0574	1.8158	2.0529	1.6806	4.15
PAB	17.186	12.962	9.8743	15.16	8.0814	3.8185	31.883	23.122	14.378	15.378	12.076	30.7
A-P DTUB	13.327	10.373	7.9262	11.967	6.2888	3.0574	23.122	18.945	11.377	11.075	9.4273	24
M-L DTUB	8.0666	6.0891	4.8121	6.8021	3.9818	1.8158	14.378	11.377	8.4939	6.8655	5.7279	14.3
M-L DAB	9.1001	7.0431	5.296	7.77	4.5654	2.0529	15.378	11.075	6.8655	10.491	7.0707	16.7
A-P DAB	6.983	5.716	4.3929	6.308	3.6745	1.6806	12.076	9.4273	5.7279	7.0707	6.1962	13.1
NFPM	23.359	14.178	10.958	13.326	6.949	4.1588	30.749	24.12	14.377	16.716	13.128	70.9
Mass	39.25	29.835	22.723	33.357	17.966	8.7503	64.716	51.181	30.959	33.561	27.079	76.1

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