MATHEMATICAL REPRESENTATION AND ANALYSIS OF ARTICULAR SURFACES: APPLICATION TO THE FUNCTIONAL ANATOMY AND PALAEO-ANTHROPOLOGY OF THE ANKLE JOINT

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ABSTRACT

This thesis is a study of quantifiable variation in the geometric shape of the superior articular surface of the talus of higher primates, with special reference to fossil tali of Plio-Pleistocene hominids.

The geometric shapes of articular surfaces are closely related to synovial joint functions since they are the primary determinants of the types of articular displacements between adjoining bones and also must be adapted to withstand transarticular forces. Therefore, the description of the three-dimensional shapes of synovial joints is an important aspect of the study of the relationship between positional behaviour and limb bone and joint morphology in primates, both living and extinct. The Structuro-Functional Classification of Synovial Articular Units of MacConaill (1973) has been adopted as the basis of this study. The four structural types of articular unit in this classification, unmodified ovoid, modified ovoid, unmodified sellar and modified sellar, represent general shapes of articular surfaces. Within each type, there may be considerable variation in form in different species which might be reflected in significant functional differences. A theoretical basis for the study of such variation in articular surface form is proposed. This is based on the concept of three 'levels of articular surface variation' in homologous synovial joints: major qualitative differences, minor qualitative/quantitative differences, and fine quantitative differences. Variation at the latter two levels needs to be studied by the quantification of articular surface morphology.

Numerous features of synovial joint shape may be quantified through the representation of articular surfaces by mathematical models, from which characteristics of surface curvature, as well as other related parameters, can easily be calculated. Articular surfaces are initially undefined other than their general description in terms of MacConaill's classification and must be measured in order to be represented and analysed mathematically. A method of measurement of Cartesian coordinates and subsequent surface-fitting has been devised and used in the present study of the superior articular surface of the talus, a male modified sellar surface, of baboons, great apes, modern humans and early hominids. The six hominid fossil tali measured are: OH 8 from Olduvai Gorge, TM 1517 from Kromdraai, KNM ER-813 from East Turkana, AL 288-1as from Hadar, Stw 88 and Stw 102 from Sterkfontein. Anatomical descriptions of the latter two specimens appear for the first time.

For the talar samples of the extant species of higher primates, primary and calculated curvature variables, used to describe trochlear surface shape, were computed and variation in their values was analysed statistically. Despite considerable intraspecific variation and overlap between the values of some of the variables in the samples measured, marked similarities and differences in the form of the trochlear surface between certain of the higher primate species, and also between males and females of some species, have been identified. In the general shape of the trochlear surface and its relative anteroposterior and mediolateral curvatures, modern humans and male gorillas appear to be very similar to each other. The tali of baboons, orangutans, chimpanzees and the female gorilla are similar to each other, especially in features of relative mediolateral curvature of the trochlear surface. However, in relative anteroposterior curvature, baboons and male orangutans are at opposite ends of the spectrum, the former with a highly curved surface and the latter with very gentle curvature in the anteroposterior direction. Where possible, explanations for the differences in trochlear form, in terms of variation in positional behaviour, foot use and body size, have been proffered.

The values of the curvature variables for each of the six early hominid tali were compared with those of the samples of extant hominoids - modern humans, gorillas, chimpanzees and orangutans. The results of this thesis appear to demonstrate the presence in the fossil tali of a combination of both human-like and ape-like features of trochlear surface form. Some of the fossils, like OH 8 and TM 1517, are generally more reminiscent of the chimpanzee and orangutan tali, whilst others, such as KNM ER-813 and Stw 88, are more like the modern human bone. The results of this thesis tend to support the hypothesis that there was a significant component of arboreal climbing in the positional behaviour of certain early hominids, the case for this being strongest for OH 8 and TM 1517, less strong for AL 288 and Stw 102, and weakest for KNM ER-813 and Stw 88.

DECLARATION

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

Peter Christie

2nd day of MAY, 1990.

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CHAPTER 1. INTRODUCTION

1.1. PRIMATE POSITIONAL BEHAVIOUR AND THE SHAPE OF SYNOVIAL ARTICULAR SURFACES

In the past two decades, behavioural studies of the daily activity patterns of primates in their natural environment have revealed that previously held locomotor classifications are too rigid and underestimate the variety of a species' motor activities. As Prost wrote (1980, p.188), "*Typological categories ... submerge the distinction we need and blurr* [sic] *the similarities we seek.*" In closely related species or genera, differences in general locomotor behaviour, or in the function of a particular anatomical region, might be defined by quantifiable differences of degree rather than of kind. These may be represented by Oxnard's useful concept of a linear continuum or, for broader comparisons between more distantly related groups of primates, a star-shaped spectrum (Oxnard, 1975a, 1984). Extremes of locomotor function, such as bipedalism, slow climbing, leaping or brachiation, would be located at the ends of the arms of the star, whereas more generalized function would be towards the centre. The locomotor classification of a species would be denoted by a "*relatively fuzzy, indeterminate position*" in the body or in one of the arms of the star (Oxnard, 1984, p.105).

The term **positional behaviour** was created by Prost (1965) to accommodate the concept that a primate's daily activity consists of relatively static postural activities as well as the more dynamic locomotor behaviours. In fact the postural activities, which do not involve much or any displacement of the body with respect to the animal's environment, appear to consume by far the greater proportion of the daily cycle (75 per cent in olive baboons (Rose, 1977)). Locomotor activities have long been considered of vital importance in the study of form-function relationships but it is possible that adaptations for postural activities may also be significant.

An animal's positional behaviour in the wild may be quantified. For example, Rose (1977) has defined the totality of a primate species' positional repertoire (that of *Papio anubis*) in terms of the range of postural and locomotor activities, such as sitting, lying down, standing, walking, running, climbing and leaping. Furthermore, through many hours of observation, he has recorded the relative amounts of time each animal spent performing such behaviours. Similar methods have been used in numerous studies of the positional behaviour of other primate species (Morbeck, 1975; Fleagle, 1976a; Mittermeier and Fleagle, 1976; Rose, 1979; Fleagle and Mittermeier, 1980).

To describe primate positional behaviour, Prost (1975, 1980) has sought to quantify the relative position and displacements of body segments, as well as their contacts with the substrate. From cine recordings, he has derived measures of the angles and ranges of motion of joints of the limbs and trunk during various positional activities.

In the laboratory, characteristics of primate positional behaviour may be quantified by various techniques including: electromyography (reviewed by Tuttle *et al*, 1979; Stern and Susman, 1981); cineradiography (Jenkins, 1972; Jenkins *et al*, 1978); gait analysis (Vilensky, 1983); force plate analysis (Kimura *et al*, 1977); and biomechanical motion analysis (Wells and Wood, 1975; Yamazaki *et al*, 1979; Yamazaki and Ishida, 1984).

It is axiomatic that differences in primate positional behaviour are correlated with variability in musculoskeletal anatomy. Muscle, bone and joint morphologies of a species reflect the function, as well as evolutionary history, of its musculoskeletal system. The precise nature of the function of the musculoskeletal system, or a part of it, and the exact relationship between form and function in extant species of primates are subject to different interpretations by morphologists. It is assumed, however, that the significance of a musculoskeletal trait may be analysed with respect to concepts of mechanics and that a number of traits may be considered together as form-function complexes. The form-function complexes may be combined in the concept of the total morphological pattern of an anatomical region (Clark, 1964; Tobias, 1985). The biological role of the form-function complexes or the total morphological pattern (their role in positional behaviour and its interaction with the environment) might then be postulated for a species (Szalay and Drawhorn, 1980).

In a fossil species, whose positional behaviour is not available for study, inferences about locomotor details are rather more difficult, as they must be based on interpretations of form-function relationships in extant species postulated to be closely related to the fossil form. The underlying assumption is that associations between morphology and function in extant animals are valid also for those now extinct (Fleagle, 1979). Studies of postcranial anatomy of fossil primates are complicated further by the fact that:

1. with the noteworthy exception of footprints, only the bone tissue component of the musculoskeletal system is preserved,
2. usually only one or a few components of the skeleton of an individual are recovered, and
3. often a fossilized bone is fragmentary, deformed or cracked.

As Preuschoft has stated (1978), "*fossils provide us with little more than the shapes of bones, or sometimes only parts of bones.*" Very often the parts of the postcranial skeleton which are preserved as fossils are either the extremities of long bones, or smaller manual and pedal elements which bear articular surfaces (more specifically, the subchondral surfaces of synovial joints). The geometric shapes of articular surfaces are closely related to joint functions since they are the primary determinants of the types of articular displacements between adjoining bones (MacConaill, 1973) and also must be adapted to withstand transarticular forces (Preuschoft, 1978). According to Fleagle (1979), "*articular surfaces probably provide more direct evidence about movement during locomotion than do other parts of the bone.*" Therefore, the description of the three-dimensional shapes of synovial joints is an important aspect of the study of the relationship between positional behaviour and limb-bone and joint morphology in primates, both living and extinct.

If articular surface shape represents an adaptation to the function of a joint, the idea of articular function must be examined. The concept of the function of a joint may be interpreted differently by various workers but in general may be considered to be a complex interrelationship of,

1. the articular displacements which occur to allow relative movements of articulating bones,
2. prevention or limitation of unwanted articular displacements (by joint shape as well as by ligaments), and
3. the mechanical requirements of joint motions such as resistance to compressive and/or bending stresses.

The complicated circular interrelationship of these factors can be illustrated: if one section of an articular surface is changed in shape (for example, by the addition of more subchondral bony tissue to a localized area) to better resist stress, then the change in shape might cause an alteration in the articular displacements and associated movements of bones, which change might further affect the pattern of stresses which the joint must now resist.

To understand the nature of articular shape as an adaptation for joint function, it is necessary to examine the possible factors which might ultimately determine the adult form of articular surfaces. Clearly the important factors may be:

1. the genetically-determined growth processes of bone and cartilage, and
2. localized responses of bone-forming tissue to stresses, the well-known plasticity of bone.

Articular shape may be seen as a product of a combination of:

1. **phylogenetic processes**, in the sense that the genetically-determined growth is a result of evolutionary mechanisms such as natural selection, and
2. **ontogenetic processes** of bone remodelling in response to immediate patterns of stresses.

The relative importance of phylogenetic versus ontogenetic processes in the final determination of bone and joint shape is debatable. Two contrasting views or hypotheses may be invoked (Preuschoft, 1979). The traditional phylogenetic hypothesis is based on the premise that anatomical structures determine the function of the locomotor system. Variability of structure within a species permits variability of function. Evolutionary mechanisms act on variability of function and an adaptative form of the anatomical structure is selected. The ontogenetic hypothesis is based on a premise which is the reverse of that of the phylogenetic hypothesis: the function of the locomotor system determines the form of its anatomical structures. This is based on the principle that skeletal shape can be changed by gravitational and muscular forces through remodelling of bone to best resist stresses. The relative merit of either hypothesis in the explanation of the origin or adaptation of articular surface shape, with respect to function in any particular synovial joint, is an intriguing question. However, a resolution of the question is not necessary for the interpretation of correlation between articular surface morphology and function. The concept that joint surface shape governs the nature of articular displacements within the joint is examined in more detail in section 1.2. The view that articular surface shape and orientation are adapted for the resistance of stresses generated during positional behaviour is considered in section 1.3.

1.2. ARTICULAR MECHANICS AND THE GENERAL SHAPE OF ARTICULAR SURFACES

This section is a brief description of the movements of bones at synovial joints, the displacements of articular surfaces which underlie such movements and the significance of surface shape to such displacements. This account has been constructed largely from the numerous publications of M.A. MacConaill (1946a,b,c, 1950, 1953, 1964, 1966a,b). A more complete summary of his work may be found in MacConaill and Basmajian (1969) and in the Arthrology chapter (pp. 419-503) of **Gray's Anatomy**, 36th edition (Williams and Warwick, 1980) which draws heavily upon MacConaill's writings.

1.2.1. Osteokinematics

The movements of bones, rather the movement of one bone relative to another at a synovial joint, have been traditionally described in textbooks of anatomy [illegible] belonging to one of four categories:

1. Rotation - usually as in medial and lateral rotation of a long bone, where a point on a bone rotates about its longitudinal (or 'mechanical') axis. A bone may, however, rotate about the mechanical axis of another bone as, for example, the atlas rotating around the dens of C2.

2. Angular movements - the opening and closing of an angle of which the arms are surfaces of body parts and the apex is a synovial joint. Flexion and extension are angular movements in opposite directions, usually referred to the sagittal plane, while abduction and adduction are equivalent movements in the coronal plane.

3. Translation (or gliding) - simple sliding of one surface on another with little or no axial rotation or angular movement.

4. Circumduction - a movement combining angular movements, such that a long bone moves within an approximately conical space.

MacConaill has suggested that all individual movements of bones are one of or a combination of two basic bone movements:

1. **spin** is a rotation about the mechanical axis of the bone;

2. **swing** is any movement which is not a pure spin.

There are two types of swing movement, (a) pure swing which is not accompanied by any spin, and (b) impure swing which is accompanied by some spin. All swings occur along curved lines; during a swing, any point on the bone traces a curved rather than straight line. In a pure swing with no accompanying spin, the curved path is the shortest one possible and is called a chord. Thus a pure swing is also termed a chordal swing. During an impure swing, the point on the bone does not traverse the shortest possible curved path but moves along an arc. An impure swing is thus called an arcuate swing[1].

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[1] In earlier publications, MacConaill (1946a,b,c, 1950) used the terms cardinal movement (= chordal swing) and circumduction (= arcuate swing).

1.2.2. Arthrokinematics

As MacConaill has written, it is axiomatic that "*all movements of bones take place at specific joints and are to be referred to these joints*" (MacConaill, 1966, p.70). In other words, all *movements of bones* relative to each other at a synovial joint correspond to *displacements of articular surfaces* relative to each other within that joint.

The General Shape of Articular Surfaces

The nature of displacements of con-articular surfaces (one surface relative to its counterpart) within a synovial joint is determined primarily by the shapes of the surfaces involved. As was pointed out by Walmsley (1928) and later in more detail by MacConaill (1946a,b,c, 1953), articular surfaces are never completely flat nor are they of constant curvature (as in surfaces of revolution such as the sphere and pseudosphere). MacConaill has argued persuasively that all articular surfaces are variations of two types of curved surface, **ovoid** or **sellar**. As its name implies, the ovoid surface is most often like part of the shell of a hen's egg in that its curvature is not constant from point to point but varies in magnitude. The ovoid surfaces of synovial joints are either concave in all directions (in this case termed the female member of the articular unit) or convex in all directions (male surface). At any point on the surface, there is a maximum curvature and a minimum curvature, at right angles to each other. These **principal curvatures**, λ_1 and λ_2, are both negative in the male ovoid surface and both positive in the female. At all points on the ovoid surface, the product of the principal curvatures, the Gaussian curvature (K), is positive ($K = \lambda_1\lambda_2$).

Like ovoid surfaces, the sellar surfaces of synovial joints commonly have curvatures which vary in magnitude from point to point. By contrast, sellar surfaces are concave in one direction (positive principal curvature), but convex in the perpendicular direction (negative principal curvature). The female member of the articular unit is defined as the smaller of the two and is reciprocally curved with respect to the larger male surface. Since the product of the principal curvatures is negative for both male and female members, the sellar surface has negative Gaussian curvature.

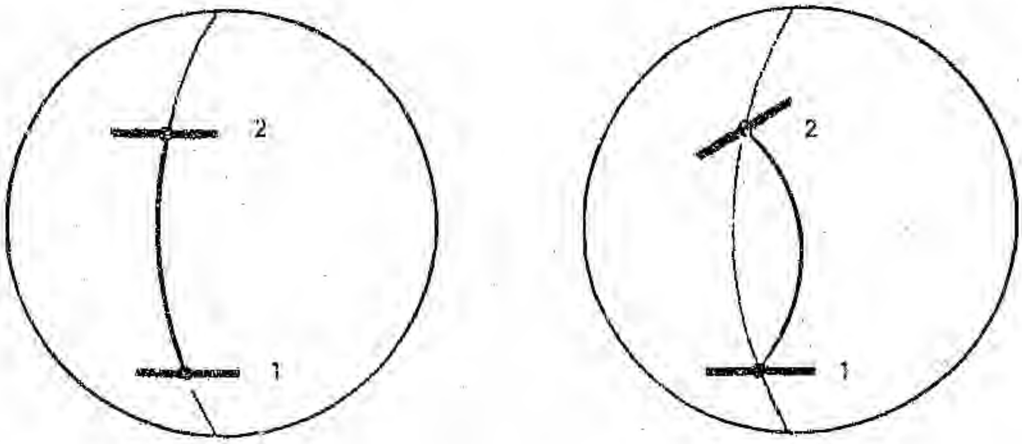
In summary: male ovoid : $K > 0; \lambda_1 < 0, \lambda_2 < 0$
female ovoid : $K > 0; \lambda_1 > 0, \lambda_2 > 0$
male and female sellar: $K < 0; \lambda_1 > 0, \lambda_2 < 0$
or $K < 0; \lambda_1 < 0, \lambda_2 > 0$

Types of Articular Surface Displacements

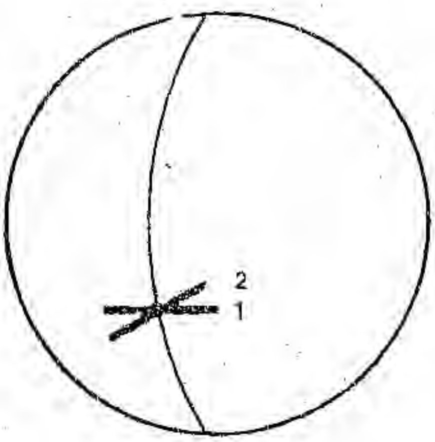
Spins (rotations) and swings of bones correspond in the main to two types of articular displacements: spin and slide. For convenience, the articular displacements may be viewed in terms of one mobile surface moving relative to a fixed surface.

Spin is a rotation of one articular surface relative to the other, about an axis normal to the surface. A point on the moving surface traverses a circular path on the 'fixed' surface. Rotations may occur independently of other displacements or may depend upon an accompanying slide.

Slide is a translation of one surface across the other. A point on the moving surface traces a path between two points on the 'fixed' surface. The path followed is always curved due to the curvature of articular surfaces. It may be either a chord, the shortest possible path between the two points, or an arc, "*any line between two points, everywhere concave towards the chord between them*" (MacConaill, 1953, p.291). Thus, like swings of bones, there are chordal and arcuate slides of articular surfaces (Figure 1). A single chordal slide produces no spin of the moving articular surface. During an arcuate slide, the moving surface *necessarily*



A. Chordal Slide (C)   B. Arcuate Slide (A)



C. Adjunct Rotation (R)

Figure 1. A. The horizontal bar, which represents a line on a female ovoid articular surface, has made a chordal slide from position 1 to position 2 on the male surface. It has not undergone a rotation.
B. In an arcuate slide from 1 to 2, the bar has rotated counterclockwise. The amount of monodal conjunct rotation is proportional to the length of the slide.
C. Without undergoing a slide, the bar has rotated counterclockwise from position 1 to 2. This is an adjunct rotation. (Drawn after MacConaill, 1964, p.561)

undergoes an axial rotation of which the magnitude is equal to the sum of the two angles formed between the arc and the ends of its chord. This rotation of the moving surface, occurring only in conjunction with its arcuate slide across the fixed surface, is called **monodal conjunct rotation**.[2] It is to be contrasted to **adjunct rotation** which can be independent of any other articular displacement (Figure 1). At a joint which allows an arcuate slide as well as independent rotation, adjunct rotation might serve to magnify or counteract the conjunct rotation.

Other possible displacements which might occur together with slides are roll, and slight compression or distraction of the con-articular surfaces. 'Roll' is a rolling (in the male surface) or rocking (in the female surface) displacement of the moving surface on the 'fixed' surface such that, in the absence of slide, there would be a one-to-one correspondence of points on the two surfaces. Roll depends upon the lack of congruence of articular surfaces. The works of Walmsley and of MacConaill have revealed that the male and female surfaces of synovial joints are more or less incongruous throughout most of the joint's range of motion. They become close-fitting usually in only one position, characteristic for each particular joint, in which there is not only maximal surface contact but also maximum tension of the joint ligaments (they are taut rather than merely tight). MacConaill has called this the **close-packed position** (CPP). Roll occurs in conjunction with a slide and the two types of displacement are supplementary in that they both swing the bone in the same direction.

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[2] A conjunct rotation is also the ineluctable result of two or more distinct and successive chordal slides.

Compression or distraction of joint surfaces may occur in extremes of movement. For example, in the CPP, which is commonly full extension of a joint (MacConaill, 1964), con-articular surfaces are pressed together firmly by the tautness of articular ligaments. At the extreme of movement opposite to the CPP, there may occur a slight distraction of the articular surfaces (Sammarco, 1977).

Comparative Dynamics of Ovoid and Sellar Surfaces

Numerous examples from human anatomy have been used by MacConaill to illustrate an interesting difference in the form-function relationship between sellar and ovoid articular surfaces. Articular units characteristically have sellar surfaces where monodal conjunct rotation is a habitual movement. The most easily understood example is perhaps the movement of the thumb during 'opposition'. From the neutral position, in which the ventral surface (pulp) of the thumb makes a right angle with the same surfaces of the fingers, the pollicial metacarpal undergoes an arcuate swing (in traditional anatomical terms, a combination of flexion and abduction) at the end of which the pulpal surface of the thumb faces those of the fingers, the angle between the opposed surfaces approaching 180°. The intra-articular displacement which brings about this swing is an arcuate slide with conjunct rotation of the basal metacarpal surface on the con-articular trapezial surface. The magnitude of rotation is proportional to the progressive length of the slide. The mating surfaces involved are sellar.

A further example provided by MacConaill (1946b, p.234) is a comparison of circumduction of the thumb at the (sellar) carpometacarpal joint with circumduction of the index finger at the (ovoid) metacarpo-phalangeal joint. Although the two joints are not homologous, the movements are analogous and are produced by arcuate slides of the same length. Clearly, congruent rotation during circumduction of the thumb is considerably greater than that during the same movement of the index.

A careful comparison of the shape of the zygapophyseal articular surfaces of lumbar and thoracic vertebrae provides an example of serially homologous joints which have differently shaped surfaces corresponding to different magnitudes of conjunct rotation. Lateral flexion of the lumbar spine involves rotation about an axis perpendicular to the zygapophyseal articular surface. MacConaill states "*the amount of this rotation between any two lumbar vertebrae is surprisingly great in view of the normal close interlocking of the articular surfaces involved. The sellar nature of these surfaces is, of course, best appreciated upon fresh, cartilage-covered specimens*" (MacConaill, 1953, p.292). There is very little if any lateral flexion in the thoracic spine and the lack of conjunct rotation between thoracic zygapophyseal surfaces is reflected by their ovoid shape.

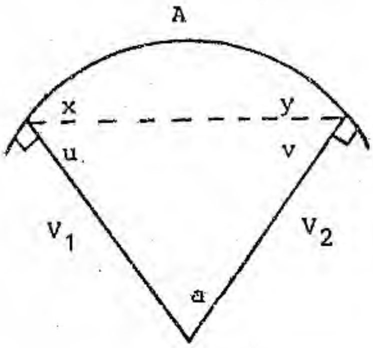
During pronation-supination of the foot, the lateral joints of the subtalar skeleton show conjunct rotation relative to one another. This is an example of **congruent rotation** in which two or more bones in a sequence rotate in the same direction contemporaneously (MacConaill, 1964). The degrees of rotation of the bones may be different from each other, in what MacConaill (1950) has called a "*gradient of angular velocity*". During congruent rotation, joints serially rotate at progressively greater or lesser rates (e.g. amount per overall movement). In the lateral joints of the foot, rotation of the calcaneus is "*conveyed to other parts of the lamina pedis in decreasing measure as we pass forwards*" (MacConaill and Basmajian, 1969, p.75). There is considerable conjunct rotation at the calcaneocuboid joint, a lesser but still appreciable amount at the cubometatarsal joint, and very little rotation at the metatarsophalangeal joint. The surface shapes of the respective articular units are sellar, planar (lightly curved ovoid) and ovoid.

The preceding examples of sellar con-articular surfaces, associated with arcuate slides (swings) which have significant conjunct rotations, illustrate a general difference with respect to intra-articular displacements between ovoid and sellar surfaces. This difference is based on (and predictable from) the general geometry of curved surfaces. Over arcuate slides of equal length and polar angle, the amount of conjunct rotation produced will be greater on a sellar surface than on an ovoid. The detailed proof of this statement may be found in MacConaill (1946b) and MacConaill and Basmajian (1969, p.309), but may be considered briefly here by reference to Figure 2.

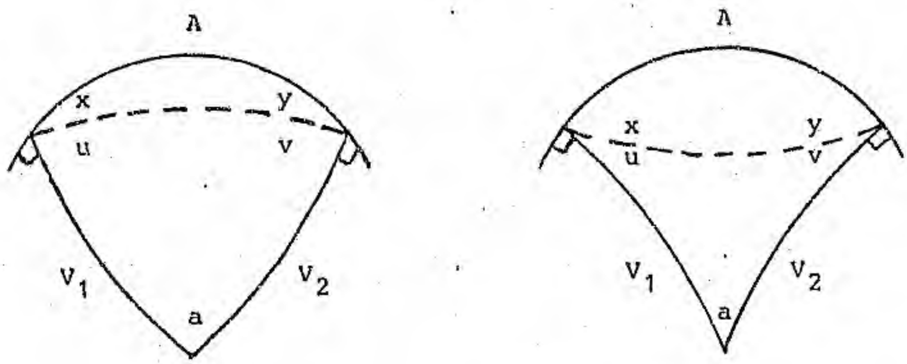
Figure 2 illustrates an arc (A) of equal length and polar angle (a) drawn on (i) a plane surface, (ii) an ovoid surface, and (iii) a sellar surface. In each case, its chord is represented by a dotted line. V_1 and V_2 are two chords which intersect the arc at a constant angle ($x + u = y + v = 90^\circ$). The magnitude of conjunct rotation of arc A on each surface is equal to the sum of the angles it makes with its respective chord ($x + y$). This sum is equal to the difference between:

1. the sum of the three angles of the three-sided figure bounded by V_1, V_2 and A ($(x + u) + (y + v) + a$), and
2. the sum of the three angles of the triangle bounded by V_1, V_2 and the chord ($u + v + a$).

On each type of surface, the first sum is the same since a is constant, and $(x + u)$ and $(y + v)$ add up to 180°. The second sum, on the other hand, is not the same on each surface but is exactly 180° on a plane surface, greater than 180° on an ovoid surface ($180^\circ + P$), and less than 180° on a sellar surface ($180^\circ - N$), where N and P are positive numbers of degrees. This is a fundamental characteristic of non-Euclidean geometry: in spherical (ovoid)



(i) Plane



(ii) Ovoid

(iii) Sellar

Figure 2. See text for details (drawn after MacConaill, 1946b, p.232).

geometry the angle sum of a triangle is always greater than 180°, while in hyberbolic (sellar) geometry the angle sum of a triangle is always less than 180°. Thus $x + y$, the magnitude of conjunct rotation, on the three surfaces is:

(i) plane: $(180° + a) - 180° = a$
(ii) ovoid: $(180° + a) - (180° + P) = a - P$
(iii) sellar: $(180° + a) - (180° - N) = a + N$

This general proof provides the theoretical basis of MacConaill's statement (1946b, p.234): "*Clearly, the more efficient saddle surface is employed in forming that joint at which conjunct (as distinct from independent) rotation is a chief aim. The amount of work performed by the musculature which moves one part upon the other at a joint is proportional to the linear distance over which the displacement is carried out upon the articular surface. Other things being equal, a given quantity of work done upon the moving part will bring about a greater conjunct rotation at a saddle joint than at one of the ovoid type.*"

Gauss's formula on integral curvature (Coxeter, 1969, p.372) ensures that, all other things being equal, the quantities N and P will increase as the curvature of the surface increases in magnitude. With respect to Figure 2, on a sellar surface as curvature increases in magnitude, the values of x and y will increase at the expense of u and v respectively. On an ovoid surface, x and y will decrease and u and v increase with greater surface curvature. Thus it follows that for an arc of given length and polar angle, the magnitude of conjunct rotation, $x + y$, will be greater on a sellar surface with greater magnitude of curvature than on one of lesser absolute curvature. Conversely an arc of the same length and polar angle will have less conjunct rotation on a more highly curved ovoid surface than on an ovoid of lesser curvature.

The possible functional or physiological importance of monodal conjunct rotation in arcuate slides might be:

1. to swing and rotate a bone to a desired position in space by a single composite movement (MacConaill and Basmajian, 1969), which does not require a "*division of consciousness*" between the swing of the bone and its rotation (MacConaill , 1946a, p.198),

2. to bring a joint to its stable close-packed position by a tightening of the articular ligaments,

3. to maintain healthy articular cartilage. MacConaill (1953) has postulated that an arcuate slide of one articular surface relative to another follows, as closely as possible, a path of "*minimal shear stress*" and thus helps to prevent wear of the cartilage.

1.3. ARTICULAR SURFACE SHAPE AND ORIENTATION AS ADAPTATIONS TO MECHANICAL STRESSES

Preuschoft (1970, 1971, 1978, 1979) has championed the concept that the functions of the musculoskeletal system are the determinants of its shape. He has used (1979, p.269) a precise, but restricted, definition of the function of the parts of the locomotor apparatus, "*their function is to sustain stresses*". Anatomical structures react to compressive, tensile and bending stresses by changing shape or orientation in order to best resist the stresses with a minimum of tissue. The morphology of a bone thus can be seen as an adaptation to the great forces acting habitually on it under normal conditions. This hypothesis is based on the principle that the shapes of bones can be changed, during the lifetime of a vertebrate animal, by gravitational and muscular forces acting on the skeleton since, under high levels of mechanical stress, bone remodels itself to best resist the stresses.

Amtmann (1979) and Frost (1985) have reviewed processes of postnatal growth of long bones, such as longitudinal increase and angular remodelling owing to differential epiphyseal growth and cross-sectional remodelling as a result of resorption and deposition of cortical bone, which contribute to the determination of the adult form of the skeleton. The experiments discussed by Amtmann and Frost have shown that the patterns of stress in the bones have considerable effects on the postnatal growth processes.

Presumably, by the same histological mechanisms discussed by Amtmann and Frost, subchondral bone can be remodelled in direct response to forces acting upon the articular surface, with the result that articular surface shape would become well-adapted for the resistance of habitual or critically high levels of stress. Bullough (1981) reviewed evidence that there occurs remodelling of subchondral bone by continuous endochondral ossification long after longitudinal growth ceases and claimed that processes of bone remodelling maintain the geometrical shapes of articular ends which most evenly distribute load imposed on them. According to him, "*Articular surfaces, as well as the rest of the bone, are in steady state, reflecting feedback interdependent with mechanical stress.*"

Certainly the latter concept is implicit in examples given by Preuschoft (1970) of marked differences of articular surface curvature and orientation of lower limb joints between apes and modern humans. He stated a fundamental principle (p.224), "*As long as no motion occurs, the force acting on a joint must always be perpendicular to the joint surfaces. If it is not, the force breaks down into a component perpendicular and a component parallel to the surface.*" If large enough, the latter component would cause serious damage to the capsular and ligamentous structures of the joint. One corollary of Preuschoft's fundamental principle is that: in general, an articular surface will be oriented normal to the resultant of gravitational and muscular forces acting on the surface. As an example, he gives the *facies articularis talaris posterior* of the calcaneus. In the horizontal plane, the resultant of the forces exerted on that surface by the flexor tendons of the medial three pedal digits is on average directed more medially, away from the long axis of the foot, in great apes than in humans due to the more divergent pongid hallux. Consequently, the posterior subtalar articular surface of the ape calcaneus is oriented more medially than that of the human heel bone.

Furthermore, the same resultant of forces may assume a greater variety of horizontal directions in the ape foot since the hallux may be placed in more positions of relative abduction. To ensure that the resultant is perpendicular to the articular surface no matter the amount of hallucial abduction, the *facies articularis talaris posterior* is more greatly curved, in the horizontal plane, in the ape foot than in the human where very little variation of the direction of the resultant is possible. Thus Preuschoft provides another corollary of his fundamental principle: if a resultant of forces acting on an articular surface may assume a wide range of directions, that surface will likely be highly curved (Figure 3).

Preuschoft (1970, p.224) stated that, "*In many cases it is not possible to explain subtle peculiarities of shape mechanically, because we are not familiar enough with the acting forces.*" It may, however, be fruitful to attempt an explanation of quantifiable differences in the orientation and relative curvature of synovial articular surfaces by a detailed consideration of the forces which might act on them during different positional activities.

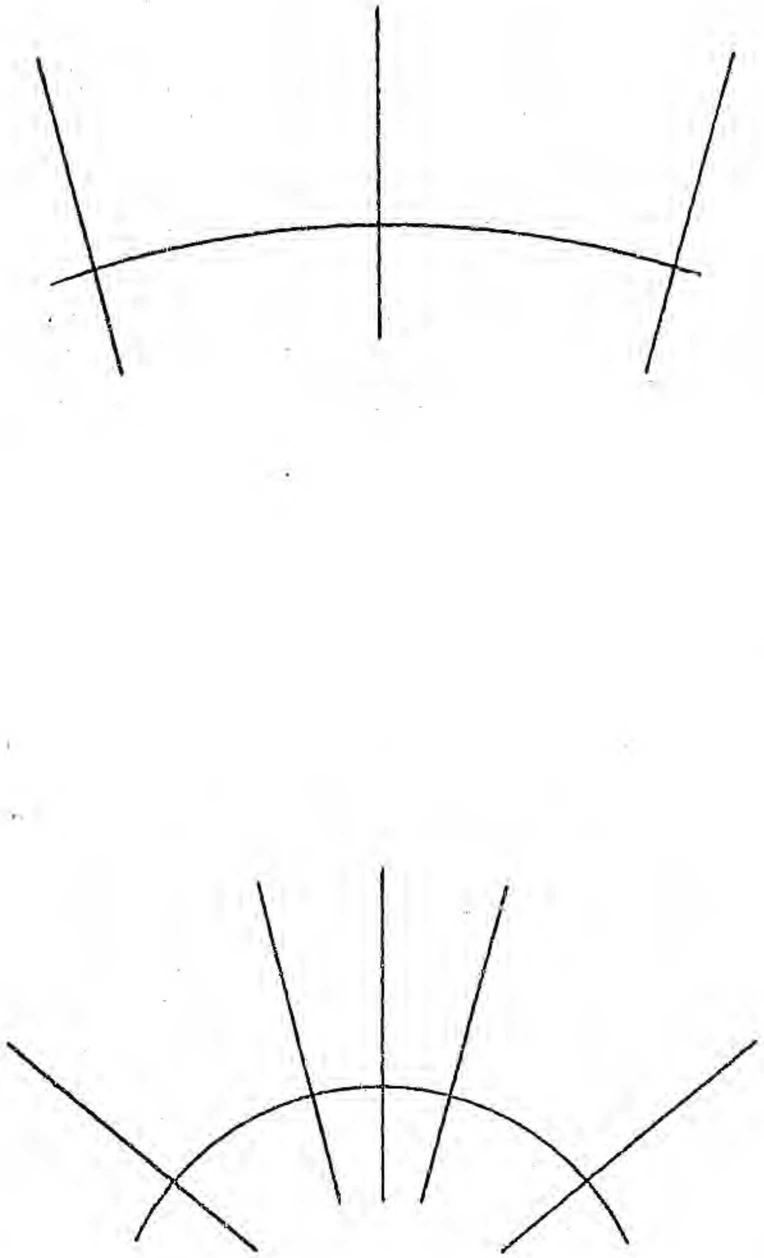


Figure 3. The curved lines represent outlines of articular surfaces. The one above is relatively flat, whilst that below is highly curved. The straight lines represent resultants of forces, all of which are perpendicular to the articular surface. In the more highly curved surface, the resultants may assume a much wider range of directions.

CHAPTER 2. CLASSIFICATION AND MATHEMATICAL REPRESENTATION OF SYNOVIAL ARTICULAR SURFACES

2.1. CLASSIFICATION OF SYNOVIAL JOINTS

Traditional classifications of synovial joints have been based both on the general shape of their articular surfaces (corresponding to parts of simple geometrical forms) and on the general type of movement permitted (for example: Grant, 1958; Breathnach, 1965; Williams and Warwick, 1980) Usually recognized are the following six classes[1] of syn[illegible]s which are listed with the general form of their artic[illegible] and [illegible] approximate type of movement allowed:

1. **Plane** (*articulatio plana*) - pa[illegible] plane - simple gliding movements.

2. **Hinge** (*ginglymus*) - parts of a cylinder or cone - hinge-like movements about a single joint axis.

3. **Pivot** (*articulatio trochoidea*) - parts of a cylinder - rotation about a single joint axis.

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[1] The terms within rounded brackets are the internationally recognized names of the classes of synovial joints whilst those within squared brackets are official synonyms or alternatives (Nomina Anatomica, 1983). A seventh class of synovial joint is **Bicondylar** (*articulatio bicondylaris*) which is in effect a double form of one of the other six joint classes.

4. **Spheroidal** (*articulatio spheroidea* [*cotylica*]) - part of a sphere which fits into either a spheroidal or ellipsoid socket - rotations about many axes.

5. **Ellipsoid** (*articulatio ellipsoidea* [*condylaris*]) - parts of an ellipsoid - rotation in two directions about perpendicular joint axes.

6. **Sellar** (*articulatio sellaris*) - parts of a hyperbolic saddle - rotation in two directions about perpendicular joint axes plus axial rotation.

Such a general classification of synovial joints can be most useful for didactic purposes but is not adequate for more detailed studies of relationships between articular morphology and function. As is evident from the work of Walmsley and MacConaill referred to in the previous chapter, the surfaces which constitute articular units or complexes are rarely, if ever, parts of simple geometrical forms. MacConaill's detailed studies of the kinematics of synovial joints led to his 1973 "**Structuro-Functional Classification of Synovial Articular Units.**"

MacConaill's Structural Classification

In this classification, articular units (pairs of surfaces articulating with each other within a synovial joint) are primarily either ovoid or sellar, but each of these types may be further divided into an unmodified and modified form. The following are descriptions of the four structural types of articular units (illustrated in Figure 4):

1. **Unmodified ovoid** - the principal curvatures of the surfaces are nearly of equal value and thus the surfaces are approximately parts of spheres. Axial rotation *independent* of any other movement is permitted. Examples of unmodified ovoid articular units in human anatomy are the hip and shoulder joints and the radiohumeral unit of the elbow. All other ovoid units are of the modified type.

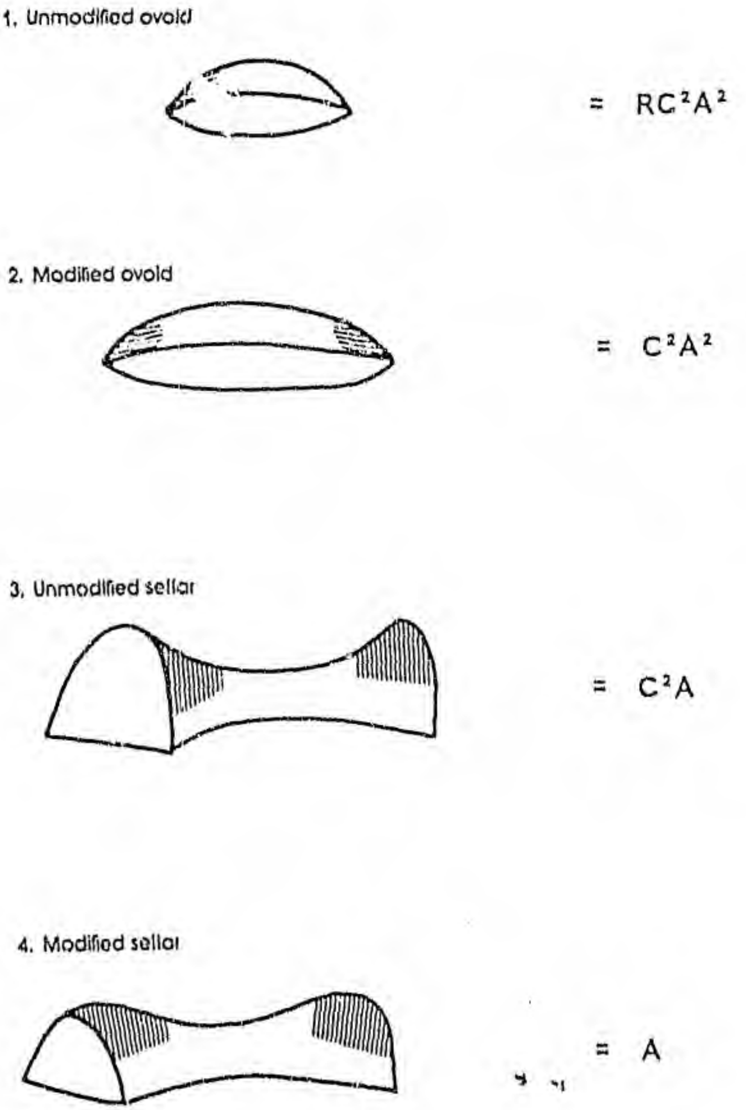

Figure 4. On the left, the four structural classes of articular surface (male surfaces only). On the right, the formulae of the four equivalent functional classes (MacConaill, 1973).

2. **Modified ovoid** - the principal curvatures of the surfaces are sufficiently different in value that the surfaces do not approximate to parts of spheres and independent rotation is not permitted. The metacarpophalangeal joints are excellent examples.

3. **Unmodified sellar** - the surfaces are convex in one direction and concave in the perpendicular direction. The first carpometacarpal joint is the classic example of an unmodified sellar unit.

4. **Modified sellar** - the surfaces have central sellar regions bounded on two opposite sides by margins which are either convex in all directions (male modified sellar) or concave in all directions (female modified sellar). This, the most complicated of the four types of articular unit, consists of both sellar and ovoid surface components. Examples of modified sellar units are the interphalangeal joints, the ulnohumeral unit of the elbow and the tibiotalar unit (excluding malleolar surfaces) of the ankle joint.

Functional Classification of MacConaill

An articular unit may be classified also according to the combination of types of displacements of one surface relative to the other (by convention, the female surface moving relative to the male). The five types of displacement permissible between members of an articular unit are: chordal slide (C), bichordal slide (two chordal slides at right angles to each other, C^2), arcuate slide (A), biarcuate slide (two distinct arcuate slides, A^2) and independent (adjunct) rotation (R). The functional classification of articular units is into four possible combinations of displacements determined by theory and experiment:

A, C^2A, C^2A^2, and RC^2A^2 .

MacConaill has determined also that there exists the following one-to-one correspondence between the four structural types of articular units and the four functional classes:

1. **Unmodified ovoid** = RC^2A^2

2. Modified ovoid = C^2A^2
3. Unmodified sellar = C^2A
4. Modified sellar = A

2.2. SHAPE VARIATION WITHIN STRUCTURO-FUNCTIONAL CLASSES OF ARTICULAR UNITS

MacConaill's "Structuro-Functional Classification of Synovial Articular Units" (1973) crystallized his previous studies of joint structure and mechanics and provided a theoretical framework on which to construct form-function analyses of synovial joints and joint complexes. This approach has been recognized as being very useful in the study of the relationship between articular morphology and positional behaviour of primates (Ziemer, 1978; Lewis, 1980a; Szalay and Dagosto, 1980).

Ziemer (1978) based her study of the functional morphology of the woolly monkey forelimb on MacConaill's classification. She described the shape of each forelimb articular unit in terms of the four structural types and correlated shape with potential and observed function. In each of the forelimb joints, potential articular displacements (and associated swings of articulating bones) were postulated based on the structuro-functional classification of the articular unit. The postulated movements of the bones were verified by manipulation of osteoligamentous preparations, and ranges of the joint motions were measured. Ziemer noted also the close-packed position of each joint, as well as limitations of movement caused by restraint by ligaments or bony or articular surfaces. Ziemer's form-function analysis was confined largely to the woolly monkey, although she did make general comparisons of that species' articular morphology and ranges of joint motion with those of other primates, such as modern humans, apes and New and Old World monkeys. A systematic comparison of joint shape differences, either among numerous woolly monkey individuals (for example, male-female differences) or between different species, and any attempt to quantify such morphological variation, were beyond the scope of her monograph.

2.2.1. The Concept of 'Levels of Articular Shape Variation' in Studies of Primate Morphology

MacConaill's classification has been adopted as the basis for the methods proposed in this thesis for the mathematical representation and analysis of synovial articular surfaces. The four structural classes of articular unit represent general shapes of the surfaces. Within each class, there may be considerable variation in form in different species which might be reflected in significant functional differences.

I believe that variations in the geometrical shape of homologous articular surfaces may conveniently be considered at three levels, the distinction between levels being not necessarily very marked:

1. **Major qualitative differences** - Differences in the shape of homologous articular surfaces between primate species, which have different patterns of positional behaviour, may be obvious from visual inspection and may, with greater or lesser success, be described verbally. This may be possible especially if broad comparisons of major differences between taxa are involved. These major (discontinuous) variations, often between different structural classes of articular units, can be related to functional differences without the need to resort to quantification. Such differences could be quantified if so desired.

2. **Minor qualitative/quantitative differences** - Often morphological variation takes the form of less obvious qualitative differences, usually variations of a single structural type, which can be better expressed and compared as quantitative differences. Description

of articular surfaces by relative terms, often rather ambiguous, could be supplanted by descriptions which use MacConaill's more precise terminology (1973). These might be enhanced by more detailed verbal descriptions of localized areas of the surface and be supported by quantification of traits such as local curvatures.

3. **Fine quantitative differences** - Subtle, gradational differences in articular shape, always variations of a single structural type, are not easily (or are poorly) described in qualitative terms. These should be considered to be elements in a spectrum of continuous variation and need to be quantified in order to be compared by statistical tests (Corruccini, 1978a). For example, this type of fine morphological variation might be found among species which have quite similar positional behaviours, between males and females of a single species, or at progressive ontogenetic stages within a species. Variation at this level may be subtle yet important. According to Szalay (1981), " *... often minor morphological changes can have profound consequences, and subsequently major adaptive significance*."

The study by Szalay and Dagosto (1980) of elbow joint morphology in primitive eutherians and primates provided an example of **major qualitative differences** in articular surface shape. The humero-ulnar articular unit (trochlea) in primitive eutherians is shaped like a small conical helix, whereas in primates it has an elongated cylindrical shape. The capitulum is spindle-shaped in primitive eutherians and spherical in primates. The gross morphological differences in elbow morphology reflect quite different functions. In eutherians, the helical form of the humero-ulnar articulation maintains the ulna in the sagittal plane, while the humerus is adducted, elevated and medially rotated in the propulsive phase of quadrupedal locomotion. Lateral stability of the elbow is aided by the elliptical form of the humeroradial articulation. By contrast, in the primate elbow, lateral stability is provided by the trochlea, while the spherical humeroradial articulation facilitates rotational movements of the forearm. Ziemer (1978) gave another example of different trochlear shapes, in this case using MacConaill's (1973) terminology. The humero-ulnar trochlea of the woolly monkey is an unmodified sellar unit, which permits the movements of flexion-extension and abduction-adduction, whereas that of modern humans is a modified sellar unit, which allows only flexion-extension associated with conjunct rotation.

An example of **major qualitative differences** in a hind limb joint is provided by the different ankle joint morphologies between certain arboreal and terrestrial marsupials. Lewis (1980a) described the tibial facet of the talus of a primitive arboreal marsupial, an Australian phalanger, as a broad area with no clear delineation between a superior and malleolar facies. The large weight-bearing fibular facet is splayed out laterally. This morphological pattern provides ample rotational mobility of the ankle at the expense of stability. Lewis reported that, in the terrestrial kangaroo and bandicoot, the homologous joint surfaces have been remodelled into a trochlea, as the talus is wedged between the medial and lateral malleoli. This pattern provides stability during terrestrial locomotion with consequent reduction in joint mobility.

The vast majority of studies of the relationship between form and function of primate joints probably deal with articular surface variation of the second level, **minor qualitative/quantitative differences**. Here again the elbow joint provides a prime example. Fleagle (1983, p.317) pointed out that the elbow is "*the skeletal region that has been analyzed most exhaustedly* [sic] *for the fossil apes*". For that reason it has been thoroughly studied also in extant primate groups. He summarized morphological differences found by numerous investigators in the elbow region of higher primates. The following are Fleagle's descriptions of pertinent features of humeral trochlear shape in different extent groups and fossil species:

New World Monkeys - relatively generalized trochlear form with a "*slight medial lip anteriorly, inferiorly, and posteriorly*" and a "*relatively low lip posterolaterally*".

Old World Monkeys - the "*medial lip of the trochlea is pronounced anteriorly and inferiorly, but not posteriorly. Posteriorly, there is a pronounced lateral lip ...*"

Pongids and Humans - there is a "*deep trochlea, with distinctive margins both medially and laterally extending almost 270° around the articular surface and divided by a deep gutter*". Elsewhere (Fleagle and Kay, 1983; Fleagle and Simons, 1978, 1980), he has used the descriptive term 'spool-shaped' to describe the pongid/human form of trochlea, a term used also by Rose (1983) and Szalay and Dagosto (1980).

Gibbons - the same form as pongids and humans except that the "*trochlear 'guttering' is less marked than in pongids*".

The term 'spool-shaped' appears frequently in descriptions of the humeral trochlea of Oligocene and Miocene fossil apes. According to Fleagle and Simons (1978, 1982) and Fleagle (1983), the broad shallow trochlea with "*distinct but not flaring distal-medial and posterolateral lips*" characteristic of *Aegyptopithecus zeuxis* and *Propliopithecus chirobates* resembles most closely that of "*generalized arboreal quadrupedal New World monkeys*". Trochlear form in these two fossil hominoids differs considerably from that of cercopithecoids and does not have the distinctive 'spool-shape' of modern apes and humans. Fleagle and Simons (1978) and Rose (1983) described trochlear morphology of the early Miocene species *Proconsul africanus* as 'spool-shaped'. Fleagle (1983) avoided the term in his description of the *P. africanus* trochlea, and instead called it 'chimpanzee-like'. He went on to say (p.320), "*This* *development of a lateral trochlear margin and the associated "gutter" between that and the medial lip is particularly pronounced in* P. africanus. ...P. africanus *looks more like a living ape than does any other early Miocene or Oligocene hominoid*." Rose (1983, p.407) made 'spool-shaped' a comparative term when he said that late Miocene humeri from Rudabanya, Hungary and the Potwar plateau, Pakistan have "*an even broader and more spool-shaped trochlea*" than early Miocene specimens.

In anatomical descriptions of articular surfaces, the use of terms of analogy such as 'trochlea', 'gutter', or 'spool-shaped', as well as descriptive adjectives, is not only unavoidable but can be evocative and most helpful. In comparative studies, however, the use of descriptive terms such as 'spool-shaped trochlea', 'flaring medial-distal lip', 'pronounced lateral border', or 'prominent medial edge' can be ambiguous, and therefore confusing, when the morphologies of homologous regions in different species are not markedly different but appear to grade into one another - when variation cannot be considered discontinuous but takes the form of fine quantitative differences. Many other examples of the use of such terms in reference to other joint surfaces can be cited. The femoral head has been said to be 'less spherical' in leaping or cursorial quadrupedal primates than in arboreal quadrupeds or suspensory forms (Fleagle, 1983). In a comparative study of the skeletal anatomy of two sympatric species of Malaysian leaf-monkeys, *Presbytis obscura* and *Presbytis melalophos*, which differed in locomotor behaviour, Fleagle (1976b) noted that the humeral head was "*more rounded and globular in* P. melalophos" than in *P. obscura*. He correlated this anatomical feature with the former monkey's greater use of armswinging and brachiating in the forest understory. In his 1983 review, Fleagle described the humeral head of *Pliopithecus vindobonensis* as "*much less globular than in extant hominoids*". Walker and Pickford (1983) described the radial notch of the ulna of *P. africanus* as "*not deeply-excavated into the coronoid as in Old World Monkeys and apes*". Fleagle (1983) used the same descriptive term 'not excavated', seemingly as a term to connote discontinuous variation, when contrasting the radial notch of *Aegyptopithecus* with that of cercopithecoids and terrestrial quadrupeds.

Jenkins and Fleagle (1975) attempted to identify features of wrist morphology related to knuckle-walking abilities in African apes. They compared African ape locomotion with that of Asian apes and suggested a rough gradation of positional behaviour from that of the largely terrestrial gorilla to the more arboreal chimpanzee, to the slow climbing orangutan, to the brachiating gibbon. Among the conclusions from their study of articular morphology was the postulation (*op. cit.*, p.223) that "*the proximal carpal joint in* Pongo *and* Hylobates *may represent an adaptive shift toward a ball-and-socket mechanism, specifically for providing additional rotatory capability. The African apes, like the cercopithecoids, retain a less specialized biaxial joint.*" In MacConaill's terminology (1973), this might be called a shift from a modified ovoid type of articulation, in which the principal curvatures are markedly unequal, towards an unmodified ovoid with very nearly equal principal curvatures. This recognition of graded, continuous variation in articular surface morphology (**fine quantitative differences**), correlated, even roughly, with gradation of locomotor behaviour, cries out for some manner of quantification and statistical analysis. In the same volume, Tuttle expressed a realization of this when he wrote, "*The considerable challenges of quantification and biomechanical explanation of these features*[2]

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[2] Tuttle was referring to those features of wrist morphology discussed by Jenkins and Fleagle (1975).

await the application and development of innovative research strategies and techniques ..." (Tuttle, 1975, p.209).

Corruccini (1978a) attempted to quantify such continuous variation in higher primates by devising thirty measurements of bony and articular features of wrist bones which were analyzed by standard multivariate statistical procedures. He did not measure articular surface curvatures directly, but instead relied on linear measures of the diameter to an estimated point of maximum curvature, or the maximum depth of a curved surface. The proposed shift from a biaxial proximal carpal joint in African apes to a ball-and-socket form in Asian apes can be reflected only indirectly and approximately by three of his linear measurements. They are:

Number 20. Maximum anteroposterior diameter of the scaphoid facet on the radius.

Number 21. Maximum depth of mediolateral curvature of the distal radius perpendicular to a plane across the distal ulnar facet and the radial styloid process.

Number 22. Mediolateral breadth of the distal radial carpal articular surface, from the midpoint of the distal radio-ulnar facet to the lateral extreme extent of articular surface in the region of the radial styloid process.

Measurement number 21 is an approximation of the average curvature in only one 'axis' of the joint, not necessarily in the direction of a principal curvature, while the other two measurements are the maximum extents of the articular surface in perpendicular directions. Alone or in combination, linear measures, such as these three of the radiocarpal joint, can describe only very approximately the geometric shapes of articular surfaces.

In my opinion, descriptions of articular surfaces or units given in comparative studies of extant and fossil primates could best be expressed by:

1. the adoption of the terminology of MacConaill's classification (1973),

2. the description in words of variations within a structural class of articular surface, and

3. for further analysis of within- or between-taxon variation in three-dimensional articular shape, the quantification of variation within a structural class.

The latter suggestion was hinted at by Szalay and Dagosto (1980, p.39), "*It is obvious that in the analysis of joints, the shapes of articulating surfaces are more sensitive indicators of both habitual (or at least possible) movements, and phylogeny, than are the relative sizes of these surfaces ... Of course, it is desirable and should be possible to express these complex shapes in terms of mathematics, making detailed statistical comparisons between taxa possible.*"

I believe that numerous characteristics of synovial joint shape could be quantified through the representation of articular surfaces by mathematical models. Gross differences between, or more subtle variation in geometric shape within, each of the four structural classes of articular unit could be quantified and then analysed statistically, by the use of characteristics of surface curvature, either local or global, as well as other related parameters. Surface curvatures can easily be calculated from a mathematical model which best represents the articular surface. Selection of particular characteristics may be hypothesis-specific and would relate to presumed form-function relationships under study in a particular synovial joint or articular unit. At present, such a method for the quantification and analysis of morphological characteristics of articular shape is perhaps most applicable to studies of between-taxon variation of the second level mentioned above, namely **minor qualitative/quantitative differences.**

Methods of mathematical representation of synovial articular surfaces are discussed in the following section.

2.3. MATHEMATICAL REPRESENTATION OF ARTICULAR SURFACES

The surface of a geometrical object (or part of the object) can be considered as an array or **manifold of related points** in a three-dimensional Cartesian space, any point being defined by Cartesian coordinates (x,y,z) (Duncan and Mair, 1983). Such surfaces can be defined mathematically in three ways, each describing the internal relationship between points on the surface (Dubrovin *et al*, 1984):

1. explicitly $z = f(x,y)$
2. implicitly $F(x,y,z) = 0$
3. parametrically $x = x(u,v)$, $y = y(u,v)$, $z = z(u,v)$.

The surfaces which constitute articular units appear to be continuous surfaces of second-order smoothness (Duncan and Mair, 1983). Here 'second-order' signifies that the curvature does not change abruptly anywhere on the surface. For example, a cylinder surmounted by a hemisphere of the same radius is smooth, but not second-order smooth, because the curvature changes abruptly at the seam. Most articular surfaces may conveniently be defined explicitly, that is, by the simplest mathematical expression, $z = f(x,y)$. For this representation it is necessary that the articular surface be oriented with respect to the Cartesian axis system so that it is not 'folded' or 'undercut', i.e. that no more than one value of z exists for any (x,y) position. Such an orientation would be impossible for the complete articular surface of the femoral head, which is commonly regarded as being approximately two-thirds of a sphere, and therefore an explicit representation of the entire articular surface is impossible.

The first three structural types of articular surface, unmodified and modified ovoid and unmodified sellar (MacConaill, 1973), can have both male and female members represented by **quadric surfaces**. These are the mathematically simplest non-plane surfaces, and their equations, whether explicit or implicit, involve terms of total degree at most two in x, y, and z (e.g. x^2, y^2 or z^2). Any plane cross-section of a quadric surface is a conic section, i.e. a parabola, hyperbola or ellipse. If the articular surface is small enough for an explicit representation to be possible, then the quadric surface representing it will be a paraboloid, with equation of the form:

$$z = a + bx + cy + dx^2 + exy + fy^2 .$$

The quadric surface will be unmodified sellar (hyperbolic paraboloid) if the discriminant $e^2 - 4df$ is positive, and ovoid (elliptic paraboloid) if the discriminant is negative. An ovoid will be unmodified if $4(d - f)^2 + e^2$ is small, and modified if $4(d - f)^2 + e^2$ is large (Figure 5).

For more extensive articular surfaces, to obtain a satisfactory fit it may be necessary to use an implicitly defined quadric surface. This more general form allows hyperboloids or ellipsoids, as well as paraboloids, and is essential if one wishes to represent a folded or undercut surface, such as the entire articular surface of the femoral head. Such a quadric surface has the implicit equation $F(x,y,z) = 0$, where $F(x,y,z)$ involves second-degree terms in z, as well as in x and y:

$$a + bx + cy + dz + ex^2 + fy^2 + gz^2 + hxy + kxz + myz = 0.$$

The fourth structural type of articular unit, modified sellar, is somewhat more complex in that its male and female surfaces both consist of a central sellar region bounded on two opposite sides by ovoid areas. A typical profile of a modified sellar surface sectioned in the y-axis would reveal three turning points. To describe such a curve, a fourth-degree polynomial is necessary.

$$z = a + bx + cy + dx^2 + exy + fy^2$$

1. Unmodified ovoid

$e^2 - 4df$ is negative

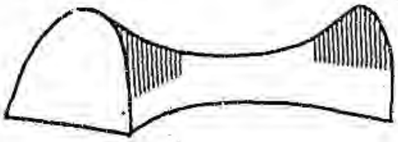
$4(d - f)^2 + e^2$ is small

2. Modified ovoid

$e^2 - 4df$ is negative

$4(d - f)^2 + e^2$ is large

3. Unmodified sellar



$e^2 - 4df$ is positive

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4. Modified sellar

$$z = a + bx + cy + dx^2 + exy + fy^2 + gx^2y + hxy^2 + ky^3 + mx^2y^2 + nxy^3 + py^4 + qx^2y^3 + rxy^4 + sx^2y^4$$

Figure 5. On the left, MacConaill's (1973) four structural classes of articular surface (male surfaces only). On the right, the mathematical equations proposed in section 3 of this chapter as models for the surfaces.

A typical profile sectioned in the x-axis has only one turning point and requires only a second-degree polynomial for its description. A modified sellar surface, either male or female, can thus be described explicitly by a polynomial in x and y containing all terms up to the degree four in y and degree two in x (Figure 5):

$$z = a + bx + cy + dx^2 + exy + fy^2 + gx^2y + hxy^2 + ky^3 + mx^2y^2 + nxy^3 + py^4 + qx^2y^3 + rxy^4 + sx^2y^4.$$

Articular surfaces are initially undefined other than by their general description in terms of MacConaill's classification and must be measured in order to be represented and analysed mathematically. Since it is technically impossible to measure all points on a surface, a method of measurement of Cartesian coordinates of a finite number of closely-spaced points, followed by surface-fitting, can be adopted to derive a polynomial equation which represents the geometrical shape of the articular surface. The equation, derived by the least-squares method, contains values for the coefficients, a, b, c, etc., for which the mathematical surface conforms most closely to the measured points. The resulting equation also allows the coordinate values of intermediate, unmeasured points to be determined, since for any given (x,y) position a z-value can be computed. This method of measurement and surface-fitting has been used in the present study of the superior facet of the trochlea tali of baboons, great apes, modern humans and early hominids (see 6.1 for more details of the methodology).

Alternative Methods of Measurement of Cartesian Coordinates and of Mathematical Modelling of Articular Surfaces

Alternative methods exist for both procedures involved in the mathematical representation of articular surfaces:

1. the measurement of Cartesian coordinates of surface points, and
2. the fitting to the coordinates of a mathematical model.

Mechanical, radiographic, optical and sonic techniques of three-dimensional coordinate measurement are possible. Computer-controlled coordinate measuring machines, like that used in the present study (see 6.1.1.2), can be programmed to take measurements of *z*-coordinates automatically over an *x,y* grid tailored for a particular joint surface. Usually a spherical-tip contact probe is used, but a non-contact laser probe might be attached to more advanced machines. Scherrer and Hillberry (1979) also have used a coordinate measuring machine for the direct measurement of points on articular surfaces, those of the shoulder joint of a dog. More simple three-dimensional measuring devices have been described by Armstrong *et al* (1979) and Wismans *et al* (1980).

An indirect method of obtaining (*x,y,z*) coordinates from ankle joint surfaces was reported by Palfrey and Ziemer (1978). They cut thin coronal and sagittal sections of casts of the surfaces, traced the surface outlines, measured two-dimensional coordinates of selected points, and then made three-dimensional reconstructions with a computer. Siu *et al* (1986) cut serial sections of actual articular ends, the distal humerus, proximal tibia and first metatarsal head, with a bone milling saw. From photographs of the sections, they digitized *y,z* values of points on the outline of the articular surface and calculated the *x* values from the number of the section.

The 'cutting' of sections of a joint surface, both *in vitro* and *in vivo*, might be accomplished by the techniques of computed tomography (CT). The (*x,y,z*) coordinates of points on an articular surface could be derived from a series of closely-spaced (e.g. 1-2 mm) high resolution CT scans (see Vannier *et al* (1985) for some anthropological applications of CT).

Stereophotogrammetry may be used for the three-dimensional analyses of anatomical structures (Duncan and Mair, 1983). Ghosh (1983) and Huiskes *et al* (1985) have described close-range stereophotogrammetric techniques to derive (x,y,z) coordinates of articular surfaces of the human knee joint.

Moiré contourography is another optical method which might be used to measure Cartesian coordinates of articular surfaces. Details of the photographic techniques involved in this method can be found in Takasaki (1970, 1973), Wijk (1980), and Duncan and Mair (1983).

Ultrasound has been employed by Rushfeldt *et al* (1981) to obtain three-dimensional coordinates of points on the human acetabular articular surface.

Alternative methods of mathematical representation of surfaces by analytical surface development were discussed in detail by Duncan and Mair (1983). One such development, the use of Coon's bicubic surface patches, was utilized by Scherrer and Hillberry (1979) to represent the humeral and glenoid surfaces of a canine shoulder joint and by Huiskes *et al* (1985) in their study of the geometry of the human knee joint.

CHAPTER 3. POSITIONAL BEHAVIOUR AND FUNCTIONAL ANATOMY OF THE FOOT AND ANKLE OF HIGHER PRIMATES[1]

3.1. POSITIONAL BEHAVIOUR AND FUNCTION OF THE FOOT AND ANKLE - GENERAL CONSIDERATIONS

There appears to be very little detailed information about the use of the foot and ankle joint in non-human primate positional behaviour. Conroy and Rose (1983) have discussed general morphological adaptations of the foot related to functional differences in higher primates. The feet of non-human Anthropoidea show primary adaptations for locomotor and postural activities associated with an arboreal environment. The major activities identified by Conroy and Rose are: 1. quadrupedal running and walking on horizontal branches, 2. climbing among branches of different sizes and orientations, 3. suspension, and 4. leaping. A primate species will have a positional behaviour pattern in which

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[1] The term 'higher primate' should be read as a synonym for 'anthropoid'. The latter word may be used, as an adjective, to express the concept of 'man-like', or, as a noun, for a creature with a general human-like form. Thus one may read: "*the anthropoid apes*". Simpson (1945) adopted **Anthropoidea, Mivart 1864** for the name of the suborder of Primates which included the living and extinct monkeys, apes and hominids (including modern humans) The word 'anthropoid' then should be used only as an informal reference to a member of, or group within, the suborder. This is how I use 'anthropoid' in this thesis.

any or all of these activities is represented but with different relative quantitative emphasis on them. For some species, such as baboons, chimpanzees and gorillas, terrestrial quadrupedalism is a major component of their positional behaviour. Yet even for these species, arboreal activities, or those that resemble them such as rock cliff climbing, remain important elements of the overall pattern of positional behaviour. Among anthropoids, variations in morphological features of the foot and ankle joint are associated with the differences in relative emphasis on the types of activities mentioned above, in the patterns of positional behaviour among the different species. A marked difference in body size between taxa, and also between males and females of a single species, is a complicating factor

There has been much confusion surrounding the names of the movements of the human foot, as a whole, and this becomes a problem when the same terminology is applied to the study of the feet of arboreal primates. Traditionally, plantar-dorsiflexion, inversion-eversion and adduction-abduction have been used to describe rotations of the human foot about axes in the three anatomical planes. However, the axes of rotation of the joints of the foot are not aligned with the anatomical planes. Thus motion of the subtalar joint complex, in one direction, involves components of dorsiflexion, abduction and eversion, whilst, in the opposite direction, involves plantar flexion, adduction and inversion. Traditionally, the former composite movement was called pronation and the latter was termed supination. Most text-book accounts today state that eversion (dorsiflexion-abduction-pronation) and inversion (plantar flexion-adduction-supination) are the composite movements of the foot. Furthermore, many anatomists consider pronation and eversion, like supination and inversion, to be synonymous.

MacConaill and Basmajian (1969) argued that eversion-inversion should be used only when the foot was off the ground and free to move relative to the leg. Pronation-supination should be used for the twisting and untwisting of the foot when it is on the ground and bearing body weight.

Lewis (1980b, 1981) has discussed the movements of the foot in humans and in arboreal primates. He preferred to reserve the terms eversion and inversion for the movement, perhaps better stated as the articular displacements, which occurs at the subtalar joint complex. Pronation and supination were used to describe the movement of the fore-foot relative to the hind-foot which occurs at the transverse tarsal joint complex. Lewis (1980b) introduced the terms endo- and exorotation to describe the inward and outward rotations of the calcaneus relative to the stationary cuboid. Further, he adopted the terminology of MacConaill and Basmajian (1969) to describe movements of the subtalar skeleton as a whole. Thus, the subtalar skeleton is 'twisted' by pronation or by endorotation of the heel and 'untwisted' by supination or by exorotation. Although somewhat complicated, the terminology proposed by Lewis, which describes the movements at joint complexes within the foot, may be used whether the foot is on the ground bearing weight, grasping a branch, or held free of the substrate.

In the following accounts of the function of the feet of higher primates, I have attempted to follow Lewis in the use of the terms eversion-inversion and pronation-supination. However, the reader should bear in mind that many authors use these terms without a clear explanation whether they refer to articular displacements in the hind-foot, fore-foot, or both combined.

The remainder of this section consists of summaries of the positional behaviour and functional anatomy of the foot in baboons, African apes, orangutans and modern humans.

3.1.1. Baboons

3.1.1.1. Positional Behaviour

Numerous classifications have been devised to provide a basis on which to make comparisons of the positional behaviour, or more specifically locomotion, of primates. Three examples are those of Napier and Napier (1967), Rose (1973) and Langdon (1986). According to Napier and Napier (1967), baboons may be placed in their category **Quadrupedalism, sub-type = Ground running and walking, (Activity = climbing, ground running)**. The appropriate categories of the other two authors are similar to that of the Napiers:

Rose (1973) -**Terrestrial quadrupedalism, ground standing and walking**

Langdon (1986) - **Quadrupedal runners and walkers**

Among cercopithecids in this category, there is a continuum from more arboreal to more terrestrial forms. The large bodied baboons can be considered to be near the terrestrial end of such a continuum. The chacma baboon is the largest of the 'savanna' baboon species (Napier and Napier, 1967). According to Hill (1970) and Anderson (1982), they are widely, but sporadically, distributed over Southern Africa in habitats which range from sea level to 3000 meters in altitude. To the chacma baboon of the highveld, Anderson has given the name 'mountain' baboon in order to distinguish it ecologically from the 'desert' and 'savanna' types. Chacma baboons usually favour hilly or rocky terrain but have been observed also to inhabit dense bush (Bolwig, 1959).

Most of their waking hours are spent on the ground as they follow a meandering daily route of foraging activity (the search for food and its consumption). Stolz (1969) followed two chacma troops in the Northern Transvaal and calculated a mean daily route 8 km long, with a range of 2.4 to 14.5 km. His estimate presumably did not include vertical travel associated with the climbing of trees or cliffs. Hall (1962a) measured daily travel of similar distance for troops in the Cape Peninsula and South West Africa. Hall further identified various modes of terrestrial progression used by chacma baboons. They include a slow walk and, at higher speeds, canter and gallop similar to horses. The usual standing postures of baboons are quadrupedal or tripedal, but bipedal postures are not uncommon.

Rose (1973, p.351) pointed out that "*Even the most terrestrial primates are not exempt from the demands of the arboreal environment.*" The rigid categorization of baboons as 'terrestrial runners and walkers' tends to play down the importance of climbing activities in their overall positional behaviour. Chacma baboons climb mainly to reach safe sleeping sites which are usually located on steep cliffs in mountainous areas but may be also in tall trees (Bolwig, 1959; DeVore and Hall, 1965; Stolz, 1969; Stolz and Saayman, 1970). They have been observed to climb trees also to gain access to food sources (Hall, 1962a) and to avoid or retreat from a predator or other presumed threat. Males will climb a tree, scan the surrounding terrain and issue the characteristic 'bahoo' call (Saayman, 1971; personal observations). Hall (1962a, p.217) emphasized the climbing and descending ability of the chacma baboon: "*climbing speed and surefootedness up or down steep rockfaces are remarkable.*"

A further use of the prehensile foot occurs during copulation when the male mounts the female by grasping her calves with his feet (Bolwig, 1959; Hall, 1962b).

3.1.1.2. Functional Anatomy of the Foot

Langdon (1986) considered the functional anatomy of the feet of Anthropoidea and, in contrast to his eight classes of higher primate positional behaviour, delineated four categories of foot use: climbing, suspension, running, and human bipedalism. The baboon foot can be placed in his running category. Langdon discussed the salient general features of the running foot. It is a relatively long foot with short toes and forms an effective rigid lever for rapid and efficient locomotion. Intrinsic joint mobility is reduced and stresses travel along the long axis of the foot (also see Pocock, 1925; Wells, 1931).

According to Conroy and Rose (1983, p.352), the cercopithecid running type of foot requires a "*nice balance between grasping, load bearing, and lever action*". Grasping is accomplished mainly by the lateral digits, in what these authors called a 'diagonal flexion grip'. Langdon (1986, p.66) has termed this a 'plantar grasp' as opposed to the 'hallucial grasp' in which the hallux is brought in opposition to the lateral digits. Joints of the foot and ankle become close-packed in dorsiflexion, inversion and supination and provide effective load bearing mechanisms by which load is distributed between the heel and forefoot during foot placement, and by the forefoot during the propulsive part of the stance phase. The general cercopithecid foot is adapted for "*above-branch quadrupedalism, during which parasagittal movements of the limb joints are generally more important than marked rotatory movements*" (Conroy and Rose, 1983, p.353). There are then less need for 'pre-set inversion' for foot placement and less conjunct rotation of the leg relative to the foot during the stance phase.

3.1.2. African apes (Chimpanzees and Gorillas)

3.1.2.1. Positional Behaviour

Napier and Napier (1967) - **Modified brachiation (Activity = chimpanzee type of brachiation)**

Rose (1973) - **Terrestrial quadrupedalism, knuckle-walking**

Langdon (1986) - **Knuckle-walking**

The locomotor classification of Napier and Napier (1967) is clearly an inadequate categorization or general description of

African ape positional behaviour, in the light of present knowledge, since it places too little emphasis on terrestrial progression. The term 'knuckle-walking' is certainly appropriate for gorillas who spend only 10 to 20 per cent of their waking hours in trees (Schaller, 1963). Male gorillas especially are limited in their arboreal activities by their great body size. Schaller (1963) found that adult males climb trees infrequently. Adult females climb to a height of 3 metres twice as frequently as adult males and juveniles do so more than four times as often. In general, adult gorillas are adept, if slow and cautious, climbers. In trees with branches and irregularities of the trunk, they grasp with both hands and feet.

Schaller (1965) reported the range of daily ground travel of one mountain gorilla troup to be between 91.4 and 1828.8 metres with an average of 531 metres. Two other groups averaged 378.6 and 663.5 metres per day. The main mode of terrestrial progression is knuckle-walking, and when running, gorillas continue to support themselves on the middle phalanges of the hands. Although the fore-limbs bear much body weight during terrestrial locomotion, forward propulsion is provided mainly by the action of the hind-limbs - hip extension and ankle plantar flexion (Tuttle, 1970). Schaller (1963) further reported that bipedal locomotion was rare even though gorillas spent approximately one-third of the day "*in a vertical position on their hindlimbs with their hands freed for such tasks as feeding and grooming*".

Chimpanzees have a considerably smaller body size than gorillas and arboreal activities, such as foraging, locomotion, resting and sleeping, make up a larger component of their positional behaviour, approximately 50 to 75 per cent of their daily activity (Goodall, 1965; Reynolds and Reynolds, 1965). Common arboreal locomotor activities include quadrupedal walking and running and vertical climbing, with feet and hands used to grasp supports. To climb vertical trunks which do not provide good supports, chimpanzees grasp around the trunk with their long arms and hands whilst the lower limbs provide most of the "*upward thrust, the feet being placed on the side of the tree nearest the chimpanzee, small toes one side, big toes the other*" (Reynolds, 1965, p.59). Arm swinging, suspension of the body by the feet, and short horizontal or vertical jumps are occasional arboreal activities.

Horizontal travel usually takes place on the ground and, when food sources are not localized, chimpanzees may range each day over an area of several square kilometres (Reynolds and Reynolds, 1965). Knuckle-walking, with the feet in a plantigrade position, is the common mode of slow terrestrial locomotion. A rapid run and a gallop are used occasionally over short distances and bipedal walking is a rare occurrence (Reynolds and Reynolds, 1965). Kortlandt (1975, p.362) noted a "*staggering diversity of quadrupedal, tripedal and "2½-pedal" types of ground-walking techniques* ", as well as "*seven distinct modes of bipedal gait*".

3.1.2.2. Functional Anatomy of the Foot

Langdon (1986) placed the African ape feet into his climbing category of foot use and mentioned the significant general features of the climbing foot. It is modified for vertical climbing, grasping and weight bearing abilities. The great mobility of the joints of the tarsus, especially the transverse tarsal joint, allows the foot to become accommodated to variable orientations of the substrate (Gomberg, 1985). In vertical climbing, the foot is held in a position of inversion and supination. Forces originate at the base of the hallux and the medial part of the foot and travel posterolaterally to the ankle. According to Conroy and Rose (1983, p.356), the foot of African apes has a large range of inversion-eversion which is "*associated both with precise foot placement and* *foot movement after placement, . combination with a powerful transverse pincer grip between the hallux and lateral digits.*"

The function of the chimpanzee foot during the stance phase of knuckle-walking has been summarized by Tuttle (1970) and Langdon (1986). The heel and posterior part of the sole make first contact with the substrate. Subsequently, since the foot is slightly inverted, body weight passes to the lateral side of the sole. As dorsiflexion proceeds and body weight moves anteriorly, the relatively mobile transverse tarsal joint becomes hyperextended. Before the foot is lifted from the ground, the proximal phalanges hyperextend and body weight transfers medially to the head of the second metatarsal. Usually the lateral four toes are kept in a flexed position and do not bear weight effectively. Tuttle (1970, p.180) has stated that the "*pattern of knuckle-walking in gorillas is very similar to that of chimpanzees.*"

Preuschoft (1970) has discussed the various forces acting on the lower limbs of African apes and modern humans. Owing to the varus position of the pongid hind limb, the prolongation of the ground reaction force, which reacts to body weight, passes medial to the ankle and medial border of the foot. However, he rebutted the concept that body weight is transmitted disproportionately to the medial part of the talus in the ape foot. He pointed out that the resultant of forces of muscular pull, which is larger in magnitude than the ground reaction force, is directed more to the lateral part of the trochlea tali which "*in pongids covers a larger area than the medial*" (p.275). Furthermore, Wood (1973) has inferred that the "*axis of weight transmission*" in the pongid ankle is more lateral than in the ankle of quadrupedal cercopithecoids.

3.1.3. Orangutans

3.1.3.1. Positional Behaviour

Napier and Napier (1967) - **Modified brachiation, orangutan type of brachiation**

Rose (1973) did not observe orangutans and thus did not classify their positional behaviour.

Langdon (1986) - **Large-bodied quadrumanous climber**

Like their African ape classification, the Napiers' description of orangutan locomotion is clearly inadequate since there is not sufficient emphasis on the use of the hind limbs in arboreal locomotion. Carpenter and Durham (1969) realized this and introduced the concept of **suspensory** behaviour to describe better the positional activities of orangutans "*while being supported by a superstratum*". Orangutans, whose habitat is primary rain forest, appear to spend as much of their waking time in trees as gorillas spend on the ground. Unlike chimpanzees and gorillas, they "*habitually traverse the canopy when moving from one locality to another*" (Tuttle, 1970, p.182). The large body size of orangutans demands a cautious mode of arboreal locomotion, termed quadrumanous climbing, rather than the arm-swinging implied by the term brachiation. They grasp supports with both hands and feet with a more or less equal contribution by all four limbs (Conroy and Rose, 1983). Tuttle (1977, p.285) reported that quadrumanous climbing includes, or is supplemented by, acrobatic activities such as "*cautious bridging, vertical ascents and descents, hoisting, hauling, and occasional pedal assisted arm-swinging and quadrupedal suspensory movement between branches*". Suspensory postures also involve secure grips with the hands and feet.

In orangutans, the mode of terrestrial locomotion appears to be less stereotyped than that of the African apes in that there are variable positions of the hands and feet. Weight is supported on the fore-limbs mainly by the balled fists but occasionally also by the knuckles. In the feet, weight is borne on the lateral aspects of the soles and the toes are usually kept in a flexed position (Tuttle, 1970). The foot is said to roll under the body weight during the stance phase.

3.1.3.2. Functional Anatomy of the Foot

The orangutan foot represents Langdon's (1986) **suspension** category of foot use. The great mobility of the foot joints is a sacrifice of efficient weight bearing in favour of a secure suspensory grasp. The orangutan is unique among primates for the extreme reduction in length of the hallux (Midlo, 1934; Tuttle and Rogers, 1966). Orangutans thus do not use a 'hallucial' grasp but instead grip, in a hook-like fashion, with the long curved phalanges of the lateral four pedal digits.

The foot is said to be held in permanent 'supination' owing to the marked flattening of the medial part of the trochlea tali (Morton, 1924). During terrestrial walking, the permanent 'supination' of the foot restricts the area of the sole which may contact the substrate and body weight is borne mainly on the lateral aspect of the foot with little support from the small hallux or lateral digits (Tuttle, 1970).

3.1.4. Modern Humans

3.1.4.1. Positional Behaviour

Napier and Napier (1967) - **Bipedalism (Activity = striding)**
Rose (1973) classified only quadrupedal primates.
Langdon (1986) - **Obligate Biped**

Modern human locomotion is essentially completely terrestrial. Tree or vertical rock climbing, while perhaps significant in some populations, is generally of minimal importance. Human locomotion on a relatively level substrate consists of a walking 'stride', at very slow to rapid speed, or running. Walking and running over uneven terrain, soft substrates, or up and down inclines, require greater muscular activity (Durnin and Passmore, 1967; MacConaill and Basmajian, 1969, p.259-60). Bipedal postures include standing and squatting. The latter position assumes great importance in some populations and results in distinct morphological features of the ankle, knee and hip joints.

3.1.4.2. Functional Anatomy of the Foot

According to Langdon (1986), the **human bipedal** type of foot resembles behaviourally the **running** foot of Old World monkeys. Significant morphological differences between the two foot types, especially in the human foot the fixed adduction of the hallux, restricted mobility of the tarsal joints and the development of arches, are associated with the much larger body size and bipedal stance and gait of modern humans.

Human bipedal walking has been studied extensively, usually under laboratory conditions which provide an evenly flat horizontal substrate (Levens *et al*, 1948; Saunders *et al*, 1953; Eberhart *et al*, 1954; Wright *et al*, 1964; Gray and Basmajian, 1968; Hutton *et al*, 1982). The function of the foot during the stance phase of the walking cycle is reasonably well-known. At **HEEL STRIKE**, when the contralateral foot is still supporting body weight, the posterolateral part of the ipsilateral foot makes contact with the substrate. There is a tendency for quick plantar flexion which appears to be resisted by eccentric contraction of the dorsiflexor, tibialis anterior. The tibia rotates internally and eversion occurs at the subtalar joint complex. At **FULL FOOT** and the first part of **MID-STANCE**, dorsiflexion at the ankle begins and body weight is distributed quickly from the heel to the fore-foot. Internal rotation of the tibia and subtalar eversion have reached their maximum extents. Later in **MID-STANCE**, as dorsiflexion continues, external rotation of the tibia and inversion of the subtalar joint begin. The position of the foot changes gradually from eversion and pronation to inversion and supination. As the plantar flexors, especially triceps surae, contract, plantar flexion commences at the ankle joint. At **HEEL OFF**, the powerful plantar flexors continue to contract and the body moves forward and upward as the heel is lifted from the substrate. Inversion at the subtalar joint and supination of the fore-foot continue as body weight moves onto the heads of the metatarsals. At this point in normal walking, the other foot makes contact with the substrate. In the final stage of the stance phase, **TOE OFF**, the metatarsal heads lose touch with the substrate and only the hallucial distal phalanx maintains contact.

3.2. THE TALOCRURAL JOINT AND SUPERIOR ARTICULAR SURFACE OF THE TALUS IN HIGHER PRIMATES

3.2.1. General Description

In higher primates, the talus occupies an important position, anatomically and functionally, in the hind limb. As the bone which is the link between the leg and the foot, it contains articular surfaces which form parts of three synovial joint complexes; the talocrural, or ankle, joint, the subtalar joint complex, and the transverse tarsal joint complex.

The primate talocrural joint may be considered to be comprised of three articular units. The largest unit, the tibiotalar articulation, has the superior articular surface of the talus (trochlear surface) and the inferior articular surface of the tibia as its male and female members respectively (*sensu* MacConaill, 1973). The other two units are the tibial and fibular malleolar articulations with the corresponding facets on the medial and lateral sides of the talus. The articular cartilage of the former unit is continuous with that of the latter two units.

Lewis (1980a) has stated that the basic form of the trochlear surface in arboreal primates (and probably all higher primates) is that of a male modified sellar surface. The reciprocally-shaped inferior tibial surface is of the female modified sellar form. In the trochlear surface, a central sellar area (the trochlear groove) is bounded on its medial and lateral sides by areas of ovoid surface (the medial and lateral crests). The articular displacement permitted at a modified sellar unit is a single arcuate movement which, in the ankle joint, consists of an anteroposterior swing with a conjunct mediolateral spin. The movements of the tibia and talus which take place at the primate ankle joint are plantar-dorsiflexion with conjunct mediolateral rotation. If the foot is fixed in a relatively immobile position during the stance phase, the leg undergoes a medial rotation during dorsiflexion and lateral rotation during plantar flexion. The non-uniformity of the trochlear surface in the mediolateral direction (convex-concave-convex) effectively prevents abduction-adduction (Ziemer, 1978). In the close-packed position of extreme dorsiflexion, the anterior edge of the distal tibia abuts on the dorsal surface of the talar neck, the medial malleolar articular surface fits snugly into the cup-shaped anterior extension of the corresponding surface on the medial face of the talus, and the conjunct medial rotation of the tibia and fibula makes taut the lateral ligaments of the ankle joint. Lewis (1980a, p.539) has discussed the functional implications of these articular displacements in the feet of arboreal primates, "*Whilst the movement is easiest to visualize as that of the tibia on talus, in the reality of the arboreal setting, it would be better to think of movement of the foot relative to the leg. In the final close-packed dorsiflexed position the foot is laterally rotated* (*or abducted*) *on the leg and its sole is inverted. Whether the foot is then involved in grasping a horizontal support during quadrupedal locomotion, or a vertical* *support during vertical climbing, weight is clearly largely directed down through the medial malleolus into the receptive cup-like articular surface.*"

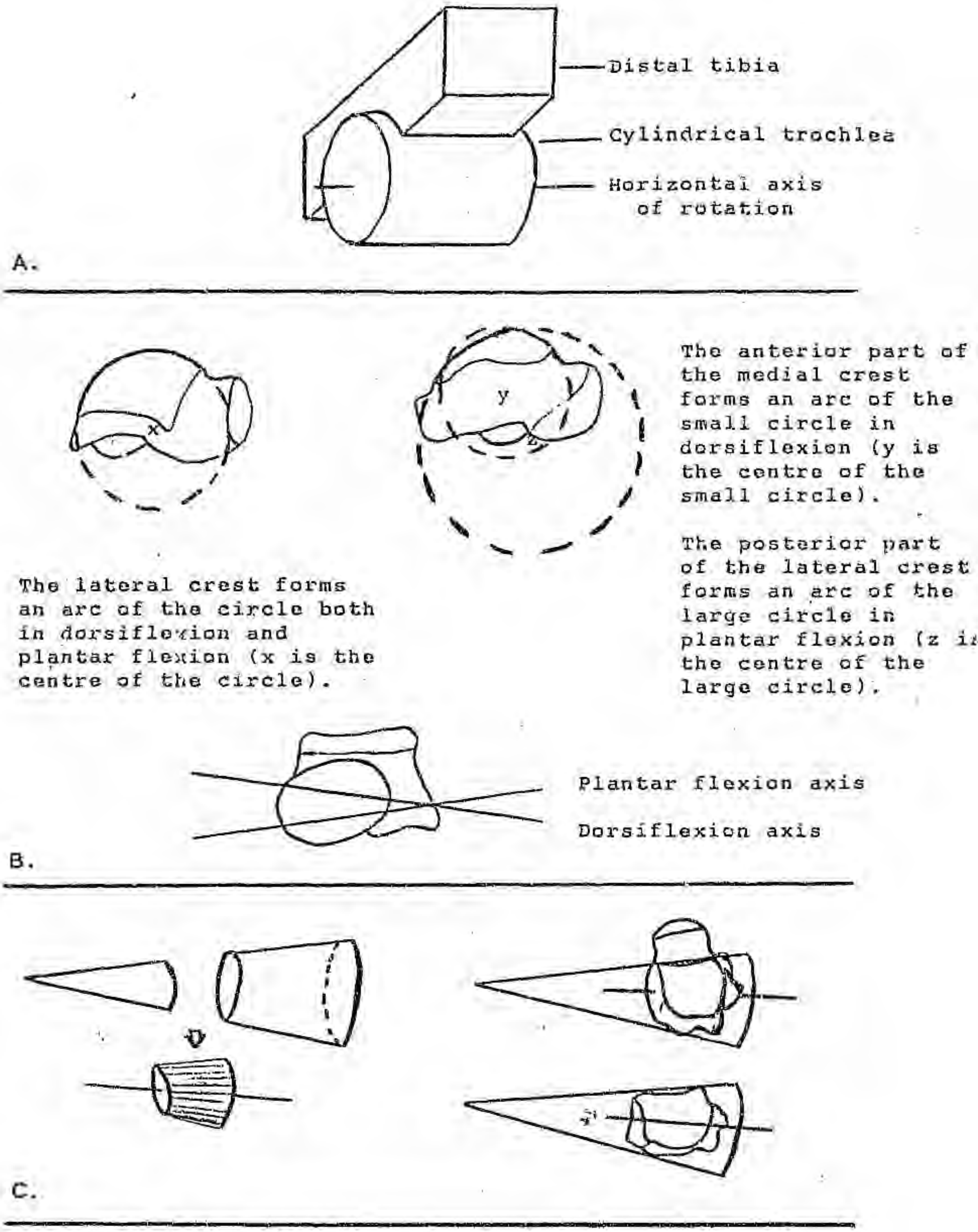
According to Conroy and Rose (1983), the movement of plantar-dorsiflexion at the talocrural joint of non-human anthropoids is associated with placement of the foot on the substrate and subsequent passage of the body over the foot during the stance phase of locomotor activity. They stated further that, in any particular species, "*The exact form of the joint also provides a variable inversion set to the foot as a whole, the extent of which may vary during dorsiflexion, as may the extent of conjunct abduction of the foot as a whole. These movements affect foot orientation prior to placement and also movements of the leg on the foot during the stance phase.*"

Since the articular displacements which occur at the talocrural joint are not strictly in a single plane, the axis of rotation of the ankle should change constantly during the excursion of the joint. However, it may probably be represented as a relatively tight bundle of axes and an average (or theoretical) axis could be envisaged. In theory, the position of the axis of rotation (or revolution) would depend upon variations in shape within this class of articular unit. It should be possible to predict the position of such an axis of the ankle joint from the shape of the trochlear surface.

In 2.1, the traditional classification of synovial joints was described in which articular surfaces were compared with idealized geometrical shapes. Such models have been applied to descriptions of the human ankle joint. The simplest description of the human talocrural joint is phrased in terms of analogy, both structural and functional, to a cylinder rotating within a reciprocally shaped structure (for example, Kapandji, 1970, pp.142-3). The only movement possible at such an articulation would be plantar-dorsiflexion in a single plane (the sagittal), in other words, a rotation about a stationary axis which, in the coronal plane, is horizontal and parallel to a tangent to the joint surface (Figure 6.A).

Barnett and Napier (1952) postulated, on theoretical grounds, that the ankle joint had one axis in plantar flexion and another in dorsiflexion. They based their hypothesis on the finding that the lateral crest of the trochlea was the arc of a circle whereas the medial crest was part of an ellipse. Two different circular profiles could be fitted to the outline of the medial crest and thus there existed two axes situated at the centres of the circles (Figure 6.B). Barnett (1955) saw the trochlea as part of a screw (for example, a left-handed screw in the left foot). In a screw, the axis is stationary and anteroposterior rotation is accompanied by mediolateral translation along the axis. Obviously referring to his earlier paper with Napier, Barnett admitted that his analogy with a screw was imperfect since the axis of rotation is not stationary.

Inman (1976) attributed the finding by Barnett and Napier of an elliptical medial trochlear profile to a geometrical illusion. If a cylinder, or cone, is sectioned perpendicular to its axis, the resulting outline will be that of a circle. If the section is oblique to the axis, an elliptical outline will be made. Inman found empirically that, in human tali, the plane of the lateral malleolar facet was always close to perpendicular to the ankle axis of motion, whereas the plane of the medial malleolar facet was almost always oblique to the axis. Furthermore, he found that both the lateral and medial crests, if sectioned perpendicularly to the joint axis, could be approximated closely to circles in 80 per cent of the human tali under study. Since the medial arc was almost always of a circle of smaller radius than the lateral arc, he used the analogy of a frustum of a cone to describe the general form



The lateral crest forms an arc of the circle both in dorsiflexion and plantar flexion (x is the centre of the circle).

The anterior part of the medial crest forms an arc of the small circle in dorsiflexion (y is the centre of the small circle).

The posterior part of the lateral crest forms an arc of the large circle in plantar flexion (z i the centre of the large circle).

Figure 6. A. The cylindrical model of the trochlea tali.
After Kapandji (1970).
B. Plantar flexion and dorsiflexion axes of rotation.
After Barnett and Napier (1952).
C. The conical analogy of Inman (1976). A right talus.

of the trochlea tali (Figure 6.C). In this analogy, the articular displacement which takes place at the ankle joint consists of a rotation about an axis which is virtually stationary yet is oblique in the coronal plane. The axis passes close to the tips of the medial and lateral malleoli. The obliquity of the axis of rotation results in a mediolateral rotation of the tibia during plantar-dorsiflexion.

In MacConaill's classification (1973), the human talotibial articular unit, that is the talocrural joint minus the malleolar ariculations, is of the modified sellar type as in other primates. The articular displacement allowed at a modified sellar unit is a single arcuate movement which comprises an anteroposterior slide accompanied by a conjunct mediolateral spin (see 2.1). A conjunct rotation of the tibia on the talus is seen also in the stance phase of human locomotion. Although of lesser magnitude than in non-human primates, such rotation at the talocrural joint is associated with a larger mediolateral rotation of the leg relative to the foot which takes place at the subtalar joint (Lewis, 1980a,b; Inman, 1976).

3.2.2. Patterns of Variation in the Shape of the Trochlea Tali in Higher Primates

The recognition by Langdon (1986) of four functional types of foot in higher primates poses the question whether there may be corresponding structural types of talocrural joint. If so, significant differences in the shape of the trochlea tali in representative species may reflect such structural types. In order to identify structural types of talocrural joint, which correspond to Langdon's **running, climbing, suspension,** and **human bipedalism** classes of foot use, it would be necessary to find, between species representative of Langdon's classes, differences in the geometric shape of the trochlea tali, or distal tibial articular surface, which are sufficient in magnitude and consistent. By the term consistent is meant that intraspecific variation in trochlear shape is reasonably small and overlap between species is not great.

A number of studies have documented or discussed general interspecific differences in the shape of the trochlea tali in monkeys, apes and humans. In a larger discussion of the TM 1517 talus from Kromdraai, Clark (1947) contrasted the coronal outlines of the trochlear surface in modern humans and great apes. He noted (p.322) that, in the chimpanzee and gorilla, the coronal trochlear outline is asymmetrical, in that it is "*flattened medially, and laterally slopes gradually upwards to the lateral border*". In the human talus, the same outline is more symmetrical with "*even curvature from side to side*" (Figure 7). Robinson (1972) confirmed Clark's observation of a trochlear profile more symmetrical in modern humans than in apes. He attributed this to the fact that the medial ridge of the trochlea is "*built up*" compared with that of the chimpanzee, a feature pointed out earlier by Elftman and Manter (1935). With regard to trochlear shape, Lewis (1980a,c) mentioned the raised medial margin of the trochlea and almost vertical orientation of the malleolar facets as the main features which distinguish the human talus from those of arboreal primates, in particular the great apes.

Conroy and Rose (1983) stated that, in the talus of arboreal quadrupedal primates in general, the "*lateral side of the trochlea is higher than the medial side*" (p.350) and, in cercopithecids especially, the talus has "*a quite pronounced lateral trochlear margin*" (p.354).

Fleagle (1976b) described a marked difference in coronal outline of the trochlear articular surface in the tali of two species of arboreal *Presbytis* monkeys. In *P. melalophos*, whose positional behaviour has a large component of leaping between small branches, the trochlear coronal profile is symmetrical, with the medial and

Figure 7. Coronal outlines of the trochlea tali of the chimpanzee, gorilla and modern humans. Posterior views of right tali. After Clark (1947).

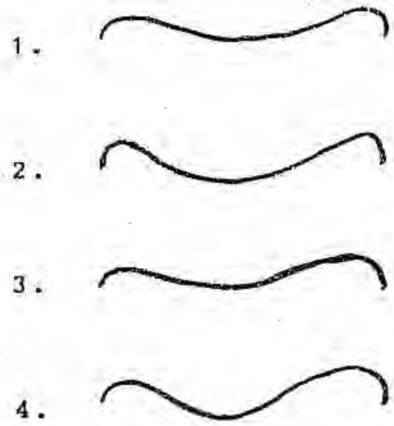


Figure 8. Different forms of curvature, in the coronal plane, of the superior articular surface of the talus, found by Sewell (1904) in approximately 1000 Egyptian tali. Numbers 1 and 2 are variations of Sewell's more common 'concave' type, (80%), while numbers 3 and 4 represent his 'concavo-convex' type (20%).

lateral margins approximately equal in height. By contrast, the trochlear profile in *P. obscura*, an arboreal quadrupedal walker/runner, is markedly asymmetrical, with the medial margin much lower than the lateral margin.

Numerous attempts have been made to quantify interspecific variation in the form of the trochlea tali among higher primates, usually as part of studies of the talus as a whole. Day and Wood (1968) used seven characters, *viz.* three angles and four indices of linear dimensions, in a multivariate study of talar form in modern and fossil humans, chimpanzees, gorillas and early hominids (OH 8 and TM 1517). Only one of their seven features, the trochlear length/breadth index, related to trochlear shape and then only very generally.

Of the talar measurements listed by Conroy (1976), only the widths of the anterior and the posterior parts of the trochlea can indicate the shape of the trochlea tali, again only in general terms.

Lisowski *et al* (1974) devised fourteen linear and two angular measures for a multivariate study of the talus in four species of monkeys, the gibbon, the great apes, modern humans and individual fossil specimens. The following eight parameters,[2] which were transformed logarithmically before statistical analysis, related to the trochlea tali:

1. Maximum medial height - the projected height from the standard basal talar plane, in which the posterior and lateral tubercles and the most inferior point on the talar head are in a horizontal plane, to the highest point on the medial margin of the trochlear surface.

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[2] The measurement names and numbers are those used by Lisowski *et al* (1974).

2. Maximum lateral height - the projected height from the standard basal talar plane to the highest point on the lateral margin of the trochlear surface.

3. Trochlear cord [sic] - the distance between the intersection of the median trochlear arc,[3] in the median sagittal talar plane, and the anterior and posterior margins of the trochlear surface respectively, in the coronal plane.

4. Transverse trochlear breadth - the distance between the medial and lateral margins of the trochlear surface taken in the transverse talar plane, that which passes through the tip of the lateral tubercle perpendicular to the median sagittal and standard basal talar planes.

5. Anterior trochlear breadth - the maximum distance between the margins of the trochlear surface parallel to the transverse talar plane.

6. Posterior trochlear breadth - the minimum posterior distance, taken parallel to the transverse talar plane, between the margins of the trochlear surface, with the exclusion of the intermediate facet.

11. Maximum median height - the projected height from the standard basal plane to the highest point on the median trochlear arc.

12. Maximum trochlear height - the perpendicular distance between the highest point on the median trochlear arc and the trochlear cord [sic].

The latter two metrical characters, along with six others, were not used in the definitive multivariate analysis. The maximum

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[3] In the paper by Lisowski *et al* (1974), the term 'median' refers to a line situated midway, in the coronal plane, between the medial and lateral margins of the trochlear surface. Thus, the median sagittal talar plane "*divides the trochlea into a medial and lateral half*".

medial, lateral and median heights (measurement numbers 1, 2 and 11) do not necessarily reflect characteristics of shape intrinsic to the trochlear surface. They are taken from the standard basal talar plane, the position of which depends upon the relative development of the lateral and posterior tubercles and the inferior surface of the talar head. The magnitude of the measurements may be affected by variations in those three bony features, as well as by the greater or lesser development of the medial and lateral crests of the trochlear articular surface. This cautionary note applies also to the observation of Elftman and Manter (1935) and later workers that the medial margin of the trochlea in the human talus is 'built up' or 'elevated'.

Latimer *et al* (1987) have argued that "*ankle anatomy and function are sufficiently dissimilar between African apes and modern humans to allow recognition of the major evolutionary changes related to the transition from quadrupedality to bipedality*". They have applied the conical analogy of Inman (1976), discussed in 3.2.1, to the study of the form and function of the talocrural joint in modern humans, chimpanzees and gorillas (and the australopithecine fossils from Hadar). To these authors, the differences between the conical African ape trochlea tali and that of modern humans, although marked, are of degree rather than kind. Measurements which they have adopted to compare the shape of the trochlea tali in pongids and modern humans are:

1. The angle between a line through the supratalar joint space and the line of the approximate axis of rotation of the talocrural joint, the latter estimated by a method similar to that of Inman (1976). The angle was measured directly from anteroposterior radiographs. The value of the angle doubled is the apical angle of the cone, a frustum of which represents the talar trochlea.
2. An angle subtended by the circular arc formed by the lateral crest of the superior articular surface of the talus. The angle

is formed by two radii drawn from the approximate axis of rotation to the anterior and posterior extents of the articular surface of the lateral crest. However, this angle will vary according to both the radius of curvature of the presumed circular lateral crest and the length of the chord between the anterior and posterior extents of the articular arc. In effect, this angle is better a measure, obtained from the talus alone, of the range of ankle joint excursion, in the sagittal plane, rather than a measure of variation in the shape of the trochlea tali.

To date, the most complete attempt to describe the geometric shape of the higher primate trochlea tali was part of the larger study by Langdon (1986) of the pedal bones and joints of extant primates and Miocene fossil species. He used fifteen direct measurements of talar characteristics, *viz.* thirteen linear dimensions and two angles, plus seventeen parameters (mainly indices) derived from the direct measures. The direct measurements were taken while the talus was "*oriented according to the sagittal plane approximated by the superior part of the fibular malleolar facet and the alignment of the most superior points on the lateral crest and the talar head in a transverse plane*". The reference position of the talus which Langdon employed was different from that used by Lisowski *et al* (1974), in which the talus was positioned according to the standard basal talar plane. The following five direct measurements[4] refer to trochlear morphology:

TA1. Trochlear breadth - the direct distance between the most superior points of the trochlear crests.

TA4. Lateral crest length - the length of the chord between the most anterior and the most posterior points of the superior articular surface along the lateral crest.

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[4] The measurement names and numbers are those of Langdon (1986).

TA5. Trochlear depth - the maximum depth of the trochlear groove measured perpendicularly from the line of trochlear breadth (TA1).
TA6. Trochlear asymmetry - the difference in maximum height of the lateral and medial trochlear crests projected from a line perpendicular to the plane of the lateral malleolar articular surface.
TA7. Lateral crest height - the maximum height of the lateral crest above, and perpendicular to, the line of lateral crest length (TA4).

Among numerous indices, which were derived from the direct measurements and devised in order to represent different aspects of the shape of the trochlear surface, were:

TAARCHT. The index of lateral crest height and lateral crest length.

TAARCHT = 100×TA7/TA4

TARADIUS. The radius (in 0.1 mm) of the arc of the lateral trochlear crest.

$TARADIUS = TA7/2 + (TA4)^2/8 \times TA7$

TAANGLE. The angle (in units of 0.01 radians) described by the trochlear arc (= the arc of the lateral trochlear crest).

TAANGLE = 100×2arcsin(TA4/2×TARADIUS)

TADEPTH. The index of trochlear depth and trochlear breadth.

TADEPTH = 100×TA5/TA1

TAASYM. The index of trochlear asymmetry and trochlear breadth.

TAASYM = 100×TA6/TA1

Although both interspecific and intraspecific variation was quantified in the metrical studies mentioned above, greater emphasis has been placed on the interspecific differences in talar morphology, including trochlear form, as related to gross functional differences in foot use. Intraspecific variation in the shape of the superior articular surface of the talus has been documented in modern humans. In a series of approximately one thousand tali of ancient Egyptians, Sewell (1904) distinguished two types of mediolateral curvature of the trochlear facet (Figure 8). In the first type, which he termed 'concave', there is "*a simple shallow concavity, which differs in degree to some considerable extent in individual bones, being much deeper in some than in others*". The concave type of trochlear surface occurred in about 80 per cent of the tali studied by Sewell. The remaining Egyptian tali had a mediolateral curvature of the second type, 'concavo-convex', which is "*concave internally and finally convex externally, the degree of curvature again varying in different bones*".

The [illegible] outlines of the trochlear surface illustrated in Figure 8 have been traced carefully from a figure in Sewell's paper. They show that even the "*two different types*" of mediolateral curvature of this surface identified and named by Sewell (and variations within his types) are subtly different versions of a modified sellar surface. However, certain extreme variants of the concave type, with sharply defined medial and lateral crests, may approach the form of a quadric surface as represented by the unmodified sellar class of articular surface (see Chapter 2).

Schmidt (1981, pp. 28-29 and 33-34) has illustrated individual differences, in modern human tali, in the anteroposterior curvature and in types of mediolateral curvature of the trochlear facet Again these can be seen as subtle variations in the form of a male modified sellar surface.

In my opinion, numerous possible variations in shape may be identified within a male modified sellar surface, such as the superior articular surface of the primate talus. For example, there may be:

1. greater or lesser average anteroposterior curvature of the facet, in other words, a greater angle of arc per unit of length.

2. greater or lesser mediolateral curvature in the regions of the medial crest, the sellar area, and the lateral crest. A more highly curved sellar region may indicate a deeper trochlear groove.

3. greater or lesser relative A-P and M-L lengths, as expressed by an index of the two measures.

4. a greater or lesser ratio of average A-P curvatures of the medial and lateral crests. This ratio may indicate a more or less conical shape of the trochlear surface.

5. differences in the ratio of average A-P curvatures of the medial and lateral crests in relation to the M-L length may provide an estimate of the slope of the theoretical joint axis of rotation relative to a coronal tangent to the superior articular surface.

6. variation in the relative position, in the coronal plane, of the saddle point, the deepest point (or point of maximum curvature) in the sellar region. This may indicate also the relative areas of the medial and lateral parts of the trochlear surface.

7. differences in the sharpness of definition of the medial and lateral crests.

8. the more or less vertical orientation of the malleolar facets.

Variations in all or some of these features of the articular surface may be related generally or more specifically to the functional anatomy of the joint.

The methods devised for the present study (described in Chapter 6) are able to provide quantification of most of the geometric shape characteristics of a male modified sellar surface mentioned above. The values of the shape characteristics have been used for statistical analyses of inter- and intraspecific variation in the form of the talar trochlea, a male modified sellar articular surface, of the higher primates described in the next chapter.

CHAPTER 4. MATERIALS

4.1. MODERN HUMAN SAMPLES

Tali with specimen numbers HD1-20 (HD = Human Dry) were dissected from embalmed cadavers used for the teaching of gross anatomy in the Department of Anatomy, University of the Witwatersrand. The individuals from which tali HD1-20 were removed for study were all male South African Negroes ranging in stated age from 35 to 70 years. In each case, the leg and foot from which the specimen was removed were previously undissected and showed no sign of deformity. When freed from ligamentous attachments, each talus was inspected for undue desiccation of the articular cartilage: if the cartilage had been too dry, the specimen would have been rejected from the study. The specimens chosen were immersed in a 10 per cent formol saline preserving fluid (pH7)[1] and stored for a minimum of seven days.

The tali, HD1-20, were skeletonized (boiled, scraped, dried and defatted), care being taken to retain their identity by keeping them in individually labelled cloth bags. One further dried talus (HD21), selected from the Raymond Dart Collection of Human Skeletons, Department of Anatomy, University of the Witwatersrand, was from a male S.A. Negro with a stated age of 50 years.

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[1] 18000 mℓ distilled water, 2000 mℓ formaldehyde, 390 mℓ 0.1N sodium hydroxide (10 gm sodium hydroxide/litre distilled water), 180 gm sodium chloride.

An additional twenty female and twenty male dried tali were selected from the Dart Collection. The individuals from whom these forty bones derived were all S.A. Negroes ranging in stated age from 25 to 39 years. For each talus from a female, a matching specimen was chosen from a male of the same stated age (and tribe, where known). The twenty female tali were assigned numbers HD41-60 and the male tali HD71-90.

Eleven dried tali from juvenile humans were selected from the Dart Collection and were assigned numbers HJ1-11 (HJ = Human Juvenile). The five males and six females were all S.A. Negroes ranging in stated age from 12 to 15 years.

The seventy-two human tali without articular cartilage were measured by the procedure described in 6.1.1.1.

The primary samples of modern human tali are summarized in Table 1.

4.2. BABOON SAMPLES

Tali with specimen numbers PD1-20 (PD = *Papio* Dry) were dissected from male chacma baboons (*Papio ursinus*) sacrificed at the end of experiments conducted by a researcher in the Department of Surgery, University of the Witwatersrand. These baboons were captured in the Vaalwater district, Transvaal, South Africa. They were kept initially in quarantine facilities of the Central Animal Service, University of the Witwatersrand and later in the Central Animal Unit at the Medical School. The cages in which the baboons were housed measure 900×900×1200 mm.

Eighteen of the twenty males were adult as judged by complete eruption of all four M3's. One of the subadult individuals (PC15) had all four M2's fully erupted, whilst the second (PC9) was more advanced, showing the M3's just above the gingival level.

SAMPLE NUMBER	SPECIMEN NUMBERS	N =	DESCRIPTION OF SAMPLE	SEX	AGE RANGE	SIDE
H1	HD71-90	20	Human tali from young adult males.	Males	25 to 39 years	10 R, 10 L
H2	HD41-60	20	Human tali from young adult females.	Females	25 to 39 years	10 R, 10 L
H3	HD1-6,8-21	20	Human tali from older adult males.	Males	42 to 70 years	10 R, 10 L
H4	HJ1-11	11	Human tali from juvenile males and females.	5 males, 6 females	12 to 15 years	Left

Table 1. Primary Samples of Modern Human Tali.

SAMPLE NUMBER	SPECIMEN NUMBERS	N =	DESCRIPTION OF SAMPLE	SEX	AGE RANGE	SIDE
P1	PD1-8, 10-14, 16-20,25,26	20	Tali from adult male baboons.	Males	Adults	10 R, 10 L
P2	PD31-50	20	Tali from adult female baboons.	Females	Adults	10 R, 10 L

Table 2. Primary Samples of Chacma Baboon Tali.

The mean weight at death of the twenty baboons was 22.1 kg with an observed range of 13.9 to 30.0 kg.

Removal of the talus was usually accomplished within minutes of death but if this was not possible, the cadaver was refrigerated and the foot dissected within twenty-four hours. Once removed, each talus was immediately immersed in a 10 per cent formol saline preserving fluid and stored for a minimum of five days.

The twenty tali were individually skeletonized. Two additional tali from adult male chacma baboons were selected from the non-human skeletal collection of the Department of Anatomy, University of the Witwatersrand, and assigned specimen numbers PD25 and PD26.

Twenty tali of adult female chacma baboons were selected from the Anatomy Department Collection and assigned numbers PD31-50. These individuals were adjudged adult based on full eruption of all four M3's.

The forty-two baboon tali without articular cartilage were measured by the procedure of 6.1.1.1.

The primary samples of chacma baboon tali are summarized in Table 2.

4.3. PONGID SAMPLES

Fifteen tali of great apes (ten African apes and five Asian apes) were selected from skeletal collections of the Anatomy Department, the Zoology Museum, and the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, and of the Transvaal Museum, Pretoria. Seven of the African ape tali were from gorillas (*Gorilla gorilla*) of which six were stated or adjudged to be males and the other a female. Six of the gorillas were adults on the evidence of full eruption of all four M3's and the other was assumed to be an adult based on overall size of the talus. The gorilla tali were assigned specimen numbers GD1-7 (GD = Gorilla Dry).

The other three African ape tali were from chimpanzees (*Pan troglodytes*), one male and two females. Two of the chimpanzees were adults while the third was a subadult since the M3's and C's were not fully erupted. The tali from these individuals were assigned numbers CD1-3 (CD = Chimpanzee Dry).

The five Asian ape tali were from orangutans (*Pongo pygmaeus*) of which three were stated or adjudged to be males and the other two females. All five individuals were adults based on dental eruption. Specimen numbers OD1-5 were given to these tali (OD = Orangutan Dry).

The fifteen pongid tali were measured by the procedure of 6.1.1.2.

The primary samples of pongid tali are summarized in Table 3.

4.4. EARLY HOMINID SPECIMENS

Casts of the following six early hominid fossil tali were measured by the procedure of 6.1.1.2:

1. OH 8 from Bed I, Olduvai Gorge
2. TM 1517 from Member 3 Kromdraai B East
3. KNM ER-813 from Upper Member, Koobi Fora, East Turkana
4. AL 288-1as from Kada Hadar Member, Hadar
5. Stw 88 from Member 5, Sterkfontein
6. Stw 102 from Member 5, Sterkfontein

The original specimens of the three South African tali (2,5 and 6) and that from Hadar have also been studied. The author was able to examine only casts of the Olduvai and East Turkana fossils.

Brief descriptions and discussions of the provenance, taxonomic status and functional anatomy of the first four tali are included in chapter 5. Anatomical descriptions of the two tali from

SAMPLE NUMBER	SPECIMEN NUMBERS	N =	DESCRIPTION OF SAMPLE	SEX	AGE RANGE	SIDE
AF1	GD1-7, CD1-3	10	Tali from male and female gorillas and chimpanzees (African apes)	7 males, 3 females	9 adults, 1 subadult	7 R, 3 L
AF2	GD1-6	6	Tali from adult male gorillas	Males	Adults	3 R, 3 L
AS1	OD1-5	5	Tali from adult male and female orangutans	3 males, 2 females	Adults	3 R, 2 L

Table 3. Primary Samples of African and Asian Ape Tali.

Sterkfontein have not been published. They are included in chapter 5, along with discussion of the provenance and provisional taxonomic status of these two fossils.

CHAPTER 5. DESCRIPTION AND DISCUSSION OF EARLY HOMINID TALI

The six early hominid tali which form part of the materials for this study are discussed under the following topics:

1. Provenance, date of deposit, and association with other hominid fossils.
2. Brief description with emphasis on the trochlea tali. Casts of the first four tali and the computer plots of their trochlear surfaces are illustrated in Figure 9. References to the original, or more complete, anatomical descriptions of these fossils are provided. As anatomical descriptions of the two tali from Sterkfontein have not been published, they are included here for the first time.
3. Taxonomic status.
4. Functional inferences from the talus (and associated foot or leg bones).

As the talus of the Olduvai Hominid 8 foot is the most studied and controversial specimen, I begin with it. Controversy surrounding its reconstruction and the different functional inferences drawn from its morphology have had a strong bearing on the study of other early hominid tali.

5.1. OLDUVAI HOMINID 8 (OH 8)

5.1.1. The OH 8 talus was recovered from level 3 site FLKNN I in Middle Bed I at Olduvai Gorge, Tanzania (M.D. Leakey, 1971) and the original announcement of its discovery was by L.S.B. Leakey (1960). FLKNN is an occupation surface just above Tuff 1B dated

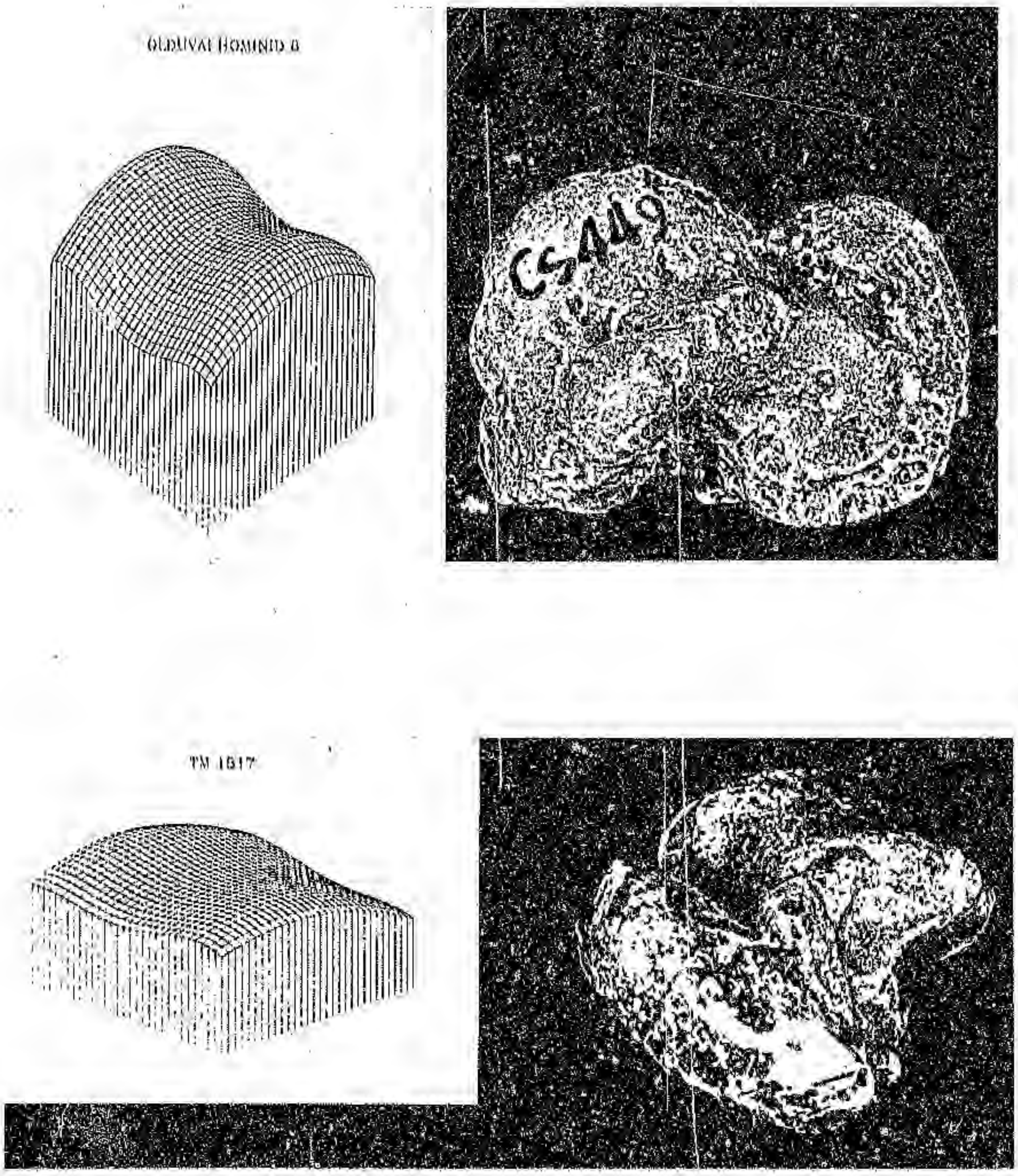

Figure 9. A. Early hominid tali from Olduvai Gorge (OH 8) and Kromdraai (TM 1517) (medial view, larger than natural size).

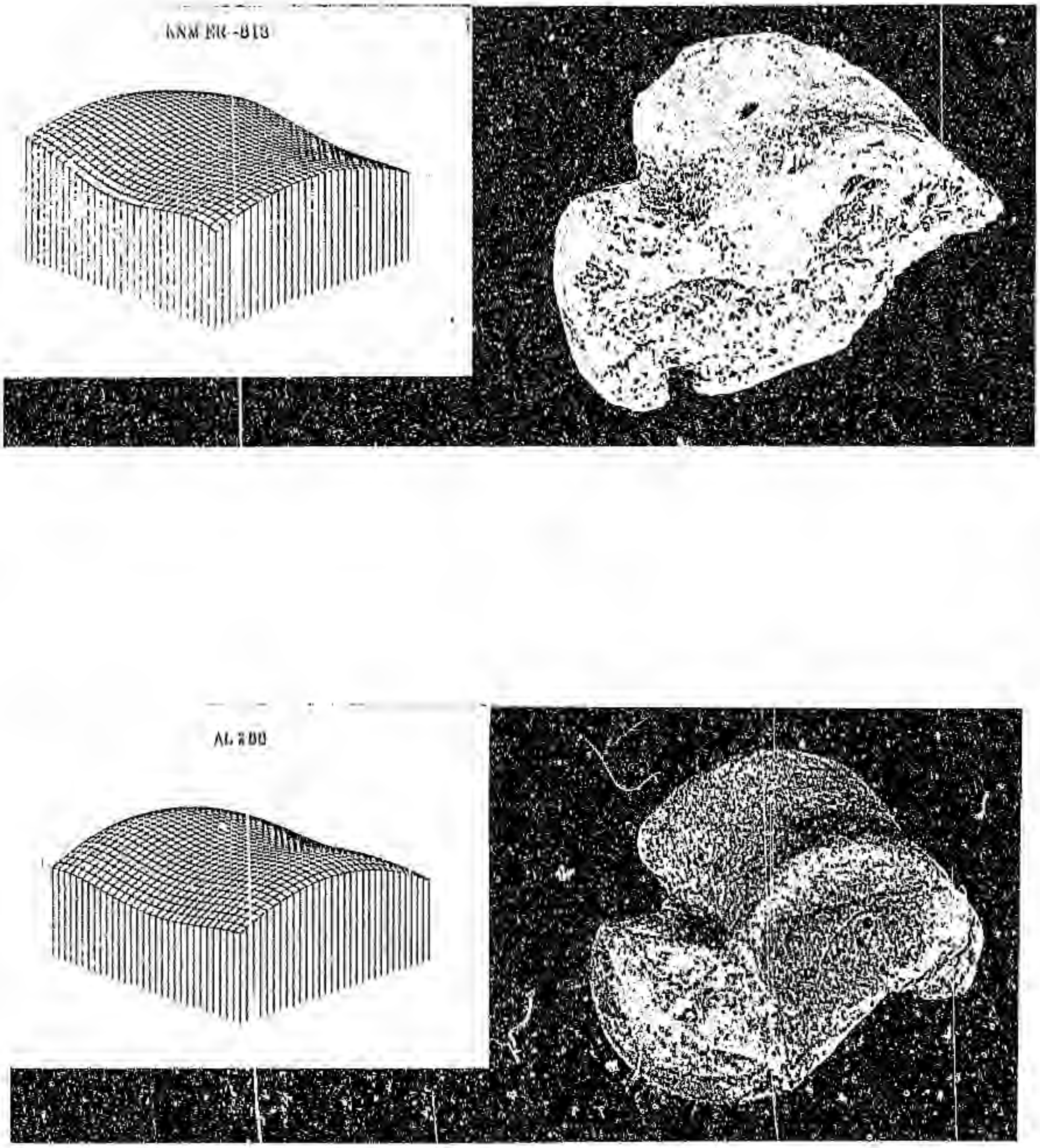

Figure 9. B. Early hominid tali from East Turkana (KNM ER-813) and Hadar (AL 288) (medial view, larger than natural size).

radiometrically at 1.79 Myr ±0.3 B.P. (Hay, 1976). The talus was found with eleven other tarsal and metatarsal bones (some incomplete) which together constitute the greater part of a single left foot. Other hominid fossils at site FLKNN I included two parietals and other skull fragments, a clavicle, numerous finger and hand bones, a molar tooth and a mandible with dentition (L.S.B. Leakey, 1960, 1961; L.S.B. Leakey *et al*, 1964). L.S.B. Leakey originally believed that the OH 8 foot belonged to the same juvenile individual represented by the mandible (at death, 12 years old by modern human standards). He stated (1961), "*The new mandible can be regarded, almost certainly, as belonging with the two parietals, the foot bones, some of the hand bones, and one of the clavicles.*" Day and Napier (1964) dissociated the foot from the juvenile remains and referred to it as that of an adult. This attribution was presumably based on their diagnosis of pathological features of the lateral tarsals as age-related arthritis. In a 1964 paper, L.S.B. Leakey *et al* described Olduvai Hominid 8 as "*an adult individual ... represented by two complete proximal phalanges, a fragment of a rather heavily worn tooth (premolar or molar), and a set of foot-bones ...*", and also "*probably the clavicle found at this site ....*" According to M.D. Leakey (1971), OH-8 is represented by the twelve foot bones, a proximal metacarpal and three finger phalanges, a radial shaft, one clavicle, and probably a broken molar. Wood (1974a) mentioned only the two proximal phalanges as part of OH 8 and said that there was no reason to associate OH 8 with the juvenile remains (OH 7). More recently, Susman and Stern (1982) have proffered a cogent argument that the OH 8 foot represents the same juvenile individual as the OH 7 jaw, skull fragments and hand skeleton. To these authors, the supposed arthritic features were the result of some trauma to the foot in childhood. They estimated its age at death to have been 13.6 to 13.9 years by modern human female standards, their conclusion being based on relative fusion of phalangeal (hand) and metatarsal (foot) epiphyses. This argument, however, has not convinced Day (1985), "*the foot is fully adult (indeed arthritic); it is clearly not associated with the juvenile hand material.*" White and Suwa (1987) have cautioned that a more detailed morphological study of the distal metatarsal ends is needed before the hypothesis of Susman and Stern can be accepted.

5.1.2. The original brief description of the OH 8 talus and associated tarsals and metatarsals was by Day and Napier (1964). The small left talus, considered in more detail by Day and Wood (1968), is undistorted and well-preserved except where bone is missing from the posterior and inferior parts of the lateral malleolar facet and lateral tubercle, as well as from the posteromedial part of the posterior calcaneal facet. The superior trochlear facies has numerous pits said to be imprints of a scavenger's teeth (M.D. Leakey, 1971). Large flakes of subchondral bone are missing from the medial and lateral trochlear margins.

The trochlea was described by Day and Napier (1964) as being 'well grooved', which means that the central sellar part of the modified sellar trochlear surface is highly curved mediolaterally. The deepest part of the groove appears to be more towards the medial edge of the trochlea. They also reported that the medial and lateral trochlear borders had virtually identical radii of anteroposterior curvature and from this inferred that the axis of the talocrural joint was stationary yet oriented in the same direction as in modern humans. It may be added that the ankle axis should also be horizontal to the trochlear plane if the radii of curvature are identical.

5.1.3. Leakey *et al* (1964) created a new species of *Homo*, *Homo habilis*, to accommodate most of the hominid fossils from site FLKNN

I and from certain other Olduvai localities. They believed that the morphology of these fossils consistently diverged from that of East and South African australopithecines toward a more human pattern. The affinities of the fossil foot bones were, according to Day and Napier (1964), clearly with those of *Homo sapiens*. Olduvai Hominid 8 was included as a paratype (OH 7 was the holotype) of the new species and has since been widely cited as clear evidence of the presence of upright stance and bipedal propulsive, if not fully striding, gait in the earliest species of man (Napier, 1964; Lovejoy, 1975, 1978; Susman, 1983).

On the other hand, since shortly after the first description of the OH 8 foot, alternative interpretations of its morphology emphasized purported ape-like or 'unique' features and consequently the question has been raised of whether this foot could indeed be classified as that of a member of the genus *Homo* (Lisowski, 1967; Lisowski *et al*, 1974, 1976; Oxnard and Lisowski, 1980; Lewis, 1980c, 1981; Oxnard, 1984; Wood, 1974a). Wood (1974a) noted similarities between the OH 8 talus and that from Kromdraai (TM 1517) (also see Day and Wood, 1968). Further he believed these two tali to be markedly different from an East Turkana talus (KNM ER-813), contemporaneous with OH 8, which he had found to be very similar to modern human tali (Wood, 1974b, 1974c). For these reasons, he concluded, "*it is a reasonable suggestion to attribute OH 8 to the genus* Australopithecus" (Wood, 1974a), and "*the Olduvai foot would be more correctly assigned to* Australopithecus boisei" (Wood, 1974b). Lewis (1980c) was just as emphatic, "*It is clear that the OH 8 foot cannot be considered to belong to the genus* Homo; *it is reasonable, however, to attribute it to the genus* Australopithecus."

5.1.4. Since the initial description of the OH 8 foot by Day and Napier (1964), workers have recognized in it a combination of morphological features, some apparently very like those of the foot of modern humans, but others rather non-human. In retrospect, one is able to trace different paths of interpretation of OH 8 morphology. Some workers have emphasized the importance of the human-like features whereas others have paid more attention to those that are ape-like or indeed considered to be unique. To the former authors, the human-like 'derived' features are most significant in that they indicate a fundamental reorganization of the foot for the demands of bipedal locomotion. Any conservative ape-like characters are either relatively unimportant (primitive) features retained from a non-bipedal ancestor, or, indicate that the 'perfected, striding' gait of modern humans had not quite been attained. To the latter authors, the primitive ape-like or unique features are most significant. These traits indicate either that, although some form of bipedal locomotion was clearly used, there was still a considerable and important reliance on arboreal limbing, or, that uniqueness of morphology likely indicates a mosaic pattern of positional behaviours, both bipedal and arboreal, unlike that seen in extant hominoids.

Day and Napier (1964) were certainly impressed by features they considered *sapiens*-like. They found a metatarsal robusticity pattern, with a very robust MT-5, which resembled modern humans but was different from that of gorillas. They did, however, worry about the MT-3 being more robust than MT-4. From the presence of an articular facet between the first and second metatarsal bases, they inferred absence of the hallucial divergence which characterizes the grasping foot of non-human primates. When articulated with each other, the distal tarsal bones were found to be aligned in a well-curved transverse arch obviously supported strongly by ligaments and tendons which left definite markings on the plantar surfaces of the bones. The calcaneus was positioned beneath the talus and the sustentaculum tali was horizontal as in modern humans. Day and Napier found the talus to be somewhat less human-like and quite similar to the Kromdraai talus. Their conclusion was that the OH 8 individual certainly possessed "*the structural requirements of an upright stance and a fully bipedal gait*" but added the caveat that the "*unique striding gait of* Homo sapiens *had not yet been achieved*".

The implication that the Olduvai talus possessed a number of unexpectedly non-human characteristics, especially a large horizontal neck angle and small torsion angle (Lisowski, 1967), led to a comparative metrical study of tali of modern humans, African apes and four fossil tali of which two were the Olduvai and Kromdraai specimens (Day and Wood, 1968). These authors utilized three angular measures[1] and four indices (based on five linear measurements) which they thought to be closely related to the functional anatomy of the talus and foot. The parameters chosen provided good discrimination between African apes and modern humans. Results of canonical analysis showed that OH 8 was intermediate between humans and apes on the first axis and separate from both groups on the second axis. The conclusion about the OH 8 talus was that its morphology was unlike either that of bipedal striding humans or that of quadrupedal African apes. In general, however, to these authors OH 8 talar morphology (even an apparently large ape-like horizontal neck angle) did not preclude the presence of an adducted hallux nor human-like transverse and longitudinal arches. The original conclusion of Day and Napier (1964), that the OH 8 individual walked bipedally but not with a striding gait, was confirmed.

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[1] A fourth angle, of head/neck orientation, was considered separately from the other seven parameters.

The biomechanical study of Preuschoft (1971) reinforced the significance of bipedal adaptation in the OH 8 foot. He correlated metatarsal and tarsal morphology with theoretical patterns of stress imposed on the foot during locomotion in modern humans and apes and interpreted characters of the Olduvai foot accordingly. He postulated that the long toe flexors of OH 8 were rather weakly developed relative to those of apes and that the fossil bones were not those of a prehensile foot. Archibald *et al* (1972) returned to the question of relative metatarsal robusticity in OH 8 and concluded that the pattern present was a variation occasionally found in the modern human foot. The relatively robust MT-5 and slender MT-2 distinguished the Olduvai foot from that of African apes and indicated to these authors a human-like striding gait.

An early criticism of the conclusions drawn by Day and Wood (1968) was by Oxnard (1972) who suggested that the previous authors had not made use of all the information from their statistical analyses. He reinterpreted their results and concluded that, rather than the OH 8 talus being morphologically intermediate between those of modern humans and African apes, it was instead uniquely different from both groups, more so than apes and humans are distinct from each other. A more complete multivariate metrical analysis of primate tali, with more talar measurements and a much larger comparative sample, followed from Oxnard and his co-workers (Lisowski *et al*, 1974). As part of this large study, the two familiar angles of the talar neck plus six linear dimensions of the talar body were measured in modern humans, the great apes, gibbons, four genera of monkeys, and numerous fossil specimens including OH 8. These eight measurements were transformed logarithmically to decrease the effect of overall talar size on variance of the dimensions. From multivariate analysis of the talar measurements, the authors concluded that OH 8 differed markedly from both modern humans and African apes. Its closest morphological relationship was with the Kromdraai talus and those of Miocene fossil apes and, amongst extant primates, the orangutan. They postulated that the talar shape of these early hominid tali reflected pedal function related to acrobatic arboreal climbing similar to, but probably less ponderous than, that seen in *Pongo*. Lisowski *et al* (1974) were careful to add that they were not suggesting comparably close genetic relationships between the fossil specimens and orangutans. With respect to OH 8, they entertained a number of possible explanations: (a) its talar features are an evolutionary legacy of acrobatic arboreal climbing in an immediate ancestor, and/or, (b) the Olduvai hominid was clearly adapted for arboreal locomotion and when bipedal locomotion was used this was not of a form as advanced as in modern man but perhaps resembled chimpanzee bipedalism.

Oxnard and Lisowski (1980) further assaulted the traditional view of OH 8, this time by examining the question of transverse and longitudinal arches in the reconstructed Olduvai foot. They rearticulated casts of OH 8, as well as tarsals and metatarsals of modern humans and great apes, in order to find most- and least-arched arrangements governed by variation in the amount of interlocking of adjoining bones. They concluded that the arches seen by them in the Olduvai foot were more like those of African ape feet than those of the highly-arched human and orangutan feet. This was especially so in the shape of the transverse arch which is flattened laterally in OH 8 and chimpanzees and gorillas. Previous findings of human-like longitudinal and transverse arches in the Olduvai foot were attributed by them to misalignment of the bones during reconstruction of the foot.

Contrary to the view of Oxnard and Lisowski (1980), Lamy (1986) concluded, from a study of the talonavicular region of pongids and hominids, that there "*is good evidence for the presence of a human longitudinal plantar arch*" in the Olduvai foot.

Lewis (1980c) studied the Olduvai foot as part of a morphological examination of articular form and function in primates. He came to conclusions about the foot which were similar to those of Oxnard and co-workers but was critical of their multivariate studies: "*it is inherent in the technique that it is virtually impossible to unravel the causal morphological factors.*" Lewis (1980c, 1981) found that OH 8 hindfoot morphology was conservative and reminiscent of that of great apes, especially the chimpanzee. This was most apparent in the subtalar joint complex; the OH 8 subtalar articular surfaces lack the drastic remodelling characteristic of modern humans and the orientation of the compromise joint axis has consequently remained ape-like. Lewis did note that the medial part of the forefoot has a more human-like appearance which reflects somewhat diminished abduction of the hallux, undoubtedly an adaptation for bipedal locomotion. He believed though that the human-like adduction usually attributed to the Olduvai foot is an overestimation and that some grasping ability was present.

Lovejoy (1975, 1978) has cast doubt on the relationship between a large horizontal neck angle and hallucial divergence. Furthermore, he has played down the significance of other presumed non-human features of the Olduvai talus and maintains that they fall within the range of variation of modern humans.

The multivariate statistical analyses of Oxnard and Lisowski, and the conclusions drawn therefrom, were criticized by Howell *et al* (1978). In general their objections centre around the inability of the chosen measurements to describe adequately complex shapes and to emphasize the most important functional aspects of a bone, especially movement potentials of a joint. Furthermore, specific results of the analysis were not referred back to the bony anatomy. The latter complaint was discussed also by Corruccini (1978b).

Susman and Stern (1982) listed features of the OH-8 foot which clearly indicated to them "*a derived, bipedal morphology*". They found, however, that the OH 7 hand, which they believe belonged to the same juvenile individual as the foot, has features of the powerful grasping hands of extant apes. They concluded that, "*a significant component of climbing was present in the locomotor behaviour of small Pliocene-Pleistocene hominids well beyond the point at which they became habitual bipeds.*"

It is unlikely that consensus will be reached on the type and frequency of such climbing, or on the morphological features which might have been the result of this component of early hominid positional behaviour (see also the discussion of AL 288-1as in 5.4.4.4). Lovejoy (1975) has cautioned that the full range of variation of modern human skeletal anatomy (and presumably non-human primate anatomy) should be considered when interpreting the morphology of fossil specimens. One might add that variation in skeletal form, as well as being between adult members of a species, might also exist between stages of an ontogenetic series. This point may become important if a fossil specimen is not adult, as suggested for OH 8 by Susman and Stern (1982). To my knowledge, all comparisons of the Olduvai foot have been with adult human and pongid individuals.

5.2. TM 1517, KROMDRAAI

5.2.1. The TM 1517 talus was recovered from a block of breccia from Kromdraai, South Africa (Broom, 1946). The discovery of the talus and associated specimens was discussed by Robinson (1972) and has been reviewed more recently by Day and Thornton (1986). The breccia block contained also parts of a robust hominid skull, fragments of a distal humerus and proximal ulna, and numerous other small postcranial bones or fragments. These remains have long been considered to belong to a single individual hominid but this has been questioned recently by Day (1985) and Day and Thornton (1986). On the basis of faunal dating, Vrba (1985, p.197; her Figure 1) has estimated that the Kromdraai B East Member 3, to which belonged the TM 1517 breccia block, should be dated to approximately 2 Myr B.P.

5.2.2. The most complete descriptions of the Kromdraai talus are by Clark (1947) and Robinson (1972). The inferior surface of the talus is badly damaged with about half of the bone missing. The superior part is, however, well preserved especially the broad trochlea tali. However, a small part of the posterolateral region of the articular surface is mi[illegible]

Clark (1947) remarked on a co[illegible] lar features which indicated to him *"a general cons[illegible] bone somewhat intermediate between that of man and* [illegible] *inoids"*. The salient features of the Kromdraai talus mentioned by Clark (1947) and Robinson (1972) are: a relatively broad superior articular surface which, in coronal section, has a symmetrical contour; a vertically oriented tibial malleolar facet; a fibular malleolar facet limited in vertical extent; a short, wide talar neck; a large horizontal neck angle; and a talonavicular articular surface of the head which is remarkably extensive mediolaterally.

5.2.3. Broom (1938) created a new genus and species, *Paranthropus robustus*, to accommodate the TM 1517 partial skull. Since he later associated the talus with the skull fragments (Broom, 1946), that bone is included as part of the holotype of *P. robustus*. Day and Thornton (1986) reassigned many of the postcranial bones to fossil baboon species but the taxonomic fate of the talus, after their reassessment, remains unclear. The last paragraph on page 98 of Day and Thornton (1986) included in the holotype only the cranial, mandibular, and dental remains plus the distal humerus, proximal ulna, and terminal hallucial phalanx. All other bones belonged to baboons. I assume that the exclusion of the talus from the holotype was a printing er.

At present, authors are divided on the use of *Paranthropus* or *Australopithecus* as the generic name for *robustus*. I shall use *Australopithecus* in this work.

5.2.4. Much of the literature published over the past quarter of a century which dealt with functional interpretations of the Olduvai foot is relevant also to the Kromdraai talus. A similarity between the two tali was noted early on (Day and Napier, 1964) especially in their possession of a combination of human-like and ape-like features. In the metrical studies mentioned previously (Lisowski, 1967; Day and Wood, 1968; Lisowski *et al*, 1974), results for the Kromdraai talus were much the same as for OH 8.

In discussions of the TM 1517 talus, Clark (1947) and Robinson (1972) focussed their attention on two interesting characters: the human-like symmetrical contour of the trochlea in the coronal plane, and the unusual breadth of the neck and talonavicular facet. Clark described the coronal trochlear outline of the australopithecine talus as having rather even curvature of both the medial and lateral crests. This was in contrast to the asymmetrical contours of the African ape talus, in which the superior facies is "*somewhat flattened medially, and laterally slopes gradually upwards to the lateral border*". Clark, citing Morton (1926), noted the relationship of the asymmetry of the ape trochlea with the more medially oriented subtalar articulations in the pongid foot, and suggested that this morphological trait was associated with transmission of body weight more to the medial side of the talus. The symmetrical profile in the modern human and robust australopithecine talus indicated "*a more even distribution in the transmission of body weight*".

As noted in the previous chapter, Preuschoft (1970) has disputed the idea that body weight is transmitted disproportionately to the medial part of the talus in the ape foot. Although, as a result of the varus position of the pongid hind limb, the ground reaction force may be directed medially, the larger resultant of muscular pull acts on the lateral part of the trochlea which "*in pongids covers a larger area than the medial*" (p.275).

In his description of the Kromdraai talus, Clark remarked upon the relatively very wide neck which is associated with an unusually great mediolateral extent of the talonavicular articular surface. The medial extension mirrors the morphology of the pongid talar head whilst the lateral extension is similar to the condition in the modern human talus. Furthermore, the relatively gentle curvature of the articular facet resembles that of the modern human and large-bodied gorilla but not the more hemispherical articular surface of the chimpanzee talus. Clark inferred that the gentle curvature of the TM 1517 talar head provided stability in the transmission of the robust australopithecine body weight to the forefoot, and the great mediolateral length of the talonavicular facet allowed for transference of the load directly forward but also rather medially as in the ape foot. To Clark, this suggested the presence of a somewhat divergent hallux in the robust australopithecine foot which could also have been used for "*grasping purposes*" and yet could be adducted "*for use in the human posture of standing and walking*". In agreement with Clark, Robinson believed that the foot of the Kromdraai individual "*was considerably more efficient for erectly bipedal posture and locomotion than are pongid feet*" and yet retained "*rather definitely apelike functional characteristics*" associated with the human-like ones.

5.3. KNM ER-813, EAST TURKANA

5.3.1. The KNM ER-813 talus and an associated fragment of tibial shaft were recovered from the Upper Member of the Koobi Fora formation at East Turkana, Kenya (R.E.F. Leakey, 1972). The site of discovery lies between the Koobi Fora Tuff above, dated radiometrically at 1.57 ±0.00 Myr B.P. (Fitch *et al*, 1974) and the KBS Tuff below, with a date of 1.89 ±0.01 Myr B.P. (McDougall *et al*, 1980).

5.3.2. The first description of the KNM ER-813 talus is in Leakey and Wood (1973). It is a reasonably complete right talus which is missing bone from the medial part of the head and posterolateral surface of the talar body. A large flake of subchondral bone is missing from the anterior part of the lateral border of the trochlea tali and the posterior half of that border is even more damaged. Leakey and Wood comment on the trochlear surface, "*The antero-posterior groove is centrally placed, so the medial and lateral margins are symmetrical. in contrast to their relative asymmetry as seen, for example, in Olduvai Hominid 8.*"

5.3.3. From the announcement of its discovery and first description, KNM ER-813 has been attributed to the genus *Homo*. Wood (1974c) cautiously suggested that it might belong to *H. erectus* since two contemporaneous femoral shafts (ER-737 and 803) were similar to *erectus* femora from Olduvai Gorge and China.

5.3.4. Using the same seven parameters as in Day and Wood (1968), Wood (1974c) found in a multivariate analysis that the fossil talus was closely aligned with modern human tali (not significantly different from modern San tali) and far removed from those of all the non-human primates measured. He concluded that probably th locomotor pattern of the ER-813 individual was "*like that of modern man*".

5.4. AL 288-1as, HADAR

5.4.1. The AL 288-1as talus was recovered from the Kada Hadar Member, Hadar, Ethiopia (Johanson and Taieb, 1976). The site of discovery is situated between the BKT-2 tuff above and the Kadada Moumou basalt (KMB) below. Walter and Aronson (1982) dated BKT-2 and KMB at 2.9 and 3.6 Myr B.P. respectively. Brown (1982) correlated volcanic tuffs and fossil faunas at East Turkana, Omo and Hadar and concluded that the lowest fossil-bearing deposits at the latter site were no older than 3.3 Myr B.P.

The talus is part of the 40 per cent complete skeleton popularly known as "Lucy" (Johanson *et al*, 1982). A distal tibia and fibula are associated with the talus, the three bones comprising a well-preserved ankle joint. The only other foot bones in the AL 288-1 skeleton are a proximal and intermediate phalanx.

5.4.2. AL 288-1as, a well-preserved, complete right talus, was described in Johanson *et al* (1982), where the superior articular surface is stated to be "*moderately grooved*". In a prior description of this bone (Christie, 1979), I noted that, "*The deepest part of the trochlear groove is situated slightly to the medial side since the lateral convex portion is wider than the medial.*"

5.4.3. Johanson *et al* (1978) published what they considered to be "*a distinctive suite of morphological traits distinguishing the Laetolil and Hadar remains from other hominid taxa*" and proposed the name *Australopithecus afarensis* for these fossils. Tobias

(1980) critically examined the claim that morphological features of the Hadar and Laetoli assemblages were sufficiently distinct from the South African gracile australopithecines. His counterproposal was to consider the Laetoli and Hadar fossils as subspecies of *A. africanus*, *A. africanus afarensis* and *A. africanus aethiopicus* respectively.

In the decade after its proposal, the nomen *Australopithecus afarensis* has generally been accepted into use by palaeoanthropologists. In this thesis, I shall use *A. afarensis* when referring to postcranial fossils from the Hadar Formation.

5.4.4. The Hadar talus and other crural and pedal fossils have been the focus of considerable debate about the presumed positional behaviour of *A. afarensis* (see Lewin, 1983). While the AL 288-1 partial skeleton has clear adaptations for bipedal locomotion, it exhibits also numerous features which are distinct from the homologous human morphology in the direction of the great apes. Such 'primitive' features are also present in other Hadar postcranial bones. Stern and Susman (1983) and Susman *et al* (1984) published detailed discussions of the anatomy of the hand, scapula, pelvis, proximal femur, knee, ankle and foot of *A. afarensis*. Their main conclusion was that arboreality was a significant component of the positional behaviour of this species. The Hadar hominids were "*vitally dependent on the trees for protection and/or sustenance*", so much so that "*morphological adaptations permitting adept movement in trees were maintained*". Susman *et al* (1984, p.137) clarified their conception of the climbing activities of *A. afarensis*, "*we suggest that these early hominids climbed vertical trunks with their forefoot (and at times midfoot also) applied to the surface, and that on the smaller supports, while they grasped with their toes, they emphasized use of their powerful hands. The sort of foot postures we envision for* afarensis *during* *vertical climbing are those common to all primates when they are on large trunks, viz. the foot is applied to the surface and the hallux is not necessarily opposed to the lateral toes.*" An arboreal component of the *A. afarensis* positional behaviour had been suggested previously by Senut (1980), Tardieu (1981) and Tuttle (1981).

A further, more tentative conclusion of Stern and Susman (1983) and Susman *et al* (1984) was that the bipedal terrestrial locomotion practised by *A. afarensis* was distinct from that of modern humans, more so in the small-bodied individuals (presumably females) than in the larger ones (presumably males). From their studies of elbow and knee morphology, Senut (1981) and Tardieu (1981, 1983) also have concluded that two locomotor patterns are evident in the Hadar postcranial fossil assemblages, but they attribute this to the presence of two different species (the results of the studies of these authors are summarized in English in Senut and Tardieu, 1985). Zihlman (1985) also has discussed the possible presence of two species of hominid at Hadar. Olson (1985) has concluded, from his study of the cranial morphology of the Hadar fossils, that there were two hominid taxa at that site.

The major points of morphological evidence from the ankle and foot of *A. afarensis* which led Stern and Susman (1983) and Susman *et al* (1984) to their conclusions may be summarized:

1. In AL 288, the posterior tilt, in the sagittal plane, of the distal tibial articular surface and the shape and orientation of the facet on the distal fibula conferred on the ankle joint a "*plantarflexion set*" similar to that in apes where it is probably "*useful in reaching for branches with the feet and in hindlimb suspension*". The articular features associated with the 'plantar flexion set' are not as marked in the larger Hadar fibulae as in Lucy's small fibula (AL 288-1at), and are not present at all in

the large tibiae, in which the distal tibial articular surface is inclined anteriorly.

2. To compensate for the plantar flexion set of the pongid and AL 288 ankle, the lateral margin of the talar trochlear surface is prolonged distally (=anteriorly) to provide for adequate dorsiflexion. In the modern human talus, the same margin "*appears truncated*" by comparison.

3. The proximal phalanges of the AL 333-115 foot have a "*strikingly pongid morphology*" in that they are long, slender and curved in the sagittal plane. The relative lengths of the proximal phalanges are not, however, as great as in extant apes, whereas the relative curvatures of the proximal phalanges of digits 2, 3 and 4 of AL 333-115 and that of Lucy (Al 288-1y) are as much as in chimpanzees and bonobos (pygmy chimpanzees). The two AL 333-115 intermediate phalanges are longer relative to their proximal phalanges than in modern humans. According to Stern and Susman (1983), long, curved phalanges are correlated with the grasping function of the foot in the arboreal positional behaviours of non-human primates. Susman *et al* (1984) have suggested that, while the *afarensis* toes were not as long as ape toes, the Hadar hominids could probably grasp with their feet as effectively as human children do with their hands.

4. The morphology of the AL 333-115 first metatarsophalangeal joint was apparently more mobile than that of modern humans which requires mediolateral stability at the end of the stance phase of walking. In the human foot, stability of this joint is provided by a relatively broad, flat articular surface on the metatarsal head. The same surface in the Hadar foot is said by Susman *et al* (1984, p.137) to be convex mediolaterally.

5. The articular surface of the medial cuneiform (AL 333-28) for the first metatarsal was described by Latimer *et al* (1982, p.704) as "*markedly convex*". To Stern and Susman (p.306), this was "*a*

nonhuman feature and one which characterizes primates with divergent halluces." A later judgement was that this facet is intermediate in curvature between those of "*a typical chimpanzee and a typical human*" (Susman *et al*, 1984, p.137).

6. That the Hadar calcanei, like those of apes, have a very large peroneal trochlea indicates that the peroneal musculature was "*suited to a role different from that in modern humans and like the role in apes*" (Stern and Susman, 1983, p.308). Deloison (1985) has found that the Hadar calcaneal morphology shows a combination of human- and ape-like traits.

Early interpretations of the Hadar postcranial fossils by the discoverer and his colleagues have placed great emphasis on the clear skeletal adaptations for bipedalism (for example, Johanson and Edey, 1981). The original description of the new species stated mildly that the "*pelvic region and lower limbs indicate adaptation to bipedal locomotion*" (Johanson *et al*, 1978, p.8). Three years later, this view had become [illegible] emphatic, "*By 3.7 Myr the hominid postcranial skeleton was fully adapted to a striding, bipedal form of locomotion*" (White *et al*, 1981, p.452). Nonhuman-like features of the *A. afarensis* foot material have been acknowledged and described by Johanson's colleagues (Latimer in Johanson, Taieb and Coppens, 1982, p.385; Latimer *et al*, 1982; Gomberg and Latimer, 1984; Latimer, 1984). However, they have preferred to consider such features as phylogenetic retentions of more pongid-like characters which, while indicative of arboreal adaptations in recent ancestors, in *A. afarensis* neither interfered with the function of the foot in terrestrial bipedalism nor were particularly useful as adaptations for grasping in an arboreal environment. To Latimer (1984), "*Characters incommensurate with a modern human model such as phalangeal length and curvature are trending away from the pongid condition indicating the relaxation of selection for climbing.*" He and his coworkers further believe that the anatomical features recognized as adaptations for bipedalism constitute "*mechanical constraints against climbing*", and that this "*strongly implies that arboreal behavior in* A. afarensis *was, if not absent, behaviorally and adaptively insignificant*" (Latimer *et al*, 1987, p.174).

As part of their comparative analysis of the talocrural joint in the African apes and modern humans (mentioned in 3.2.2), Latimer *et al* (1987) discussed the morphology of AL 288-1as in light of the inferred anatomical and functional differences between the extant pongids and hominids. They found that the angle between a line through the supratalar joint space and the line of the approximate axis of rotation of the ankle joint (see 3.2.2) was a good discriminator between African apes and modern humans, and was related clearly to the differing demands of quadrupedalism and bipedalism. To these authors, this angle, and other morphological features of the distal tibia, fibula and talus, align AL 288 and the other Hadar hominids with modern humans, with respect to fully bipedal locomotion, and argue against adaptation for arboreality. Any features of ankle joint anatomy or function in which Lucy resembles more closely chimpanzees have been ascribed to the small body size of that early hominid.

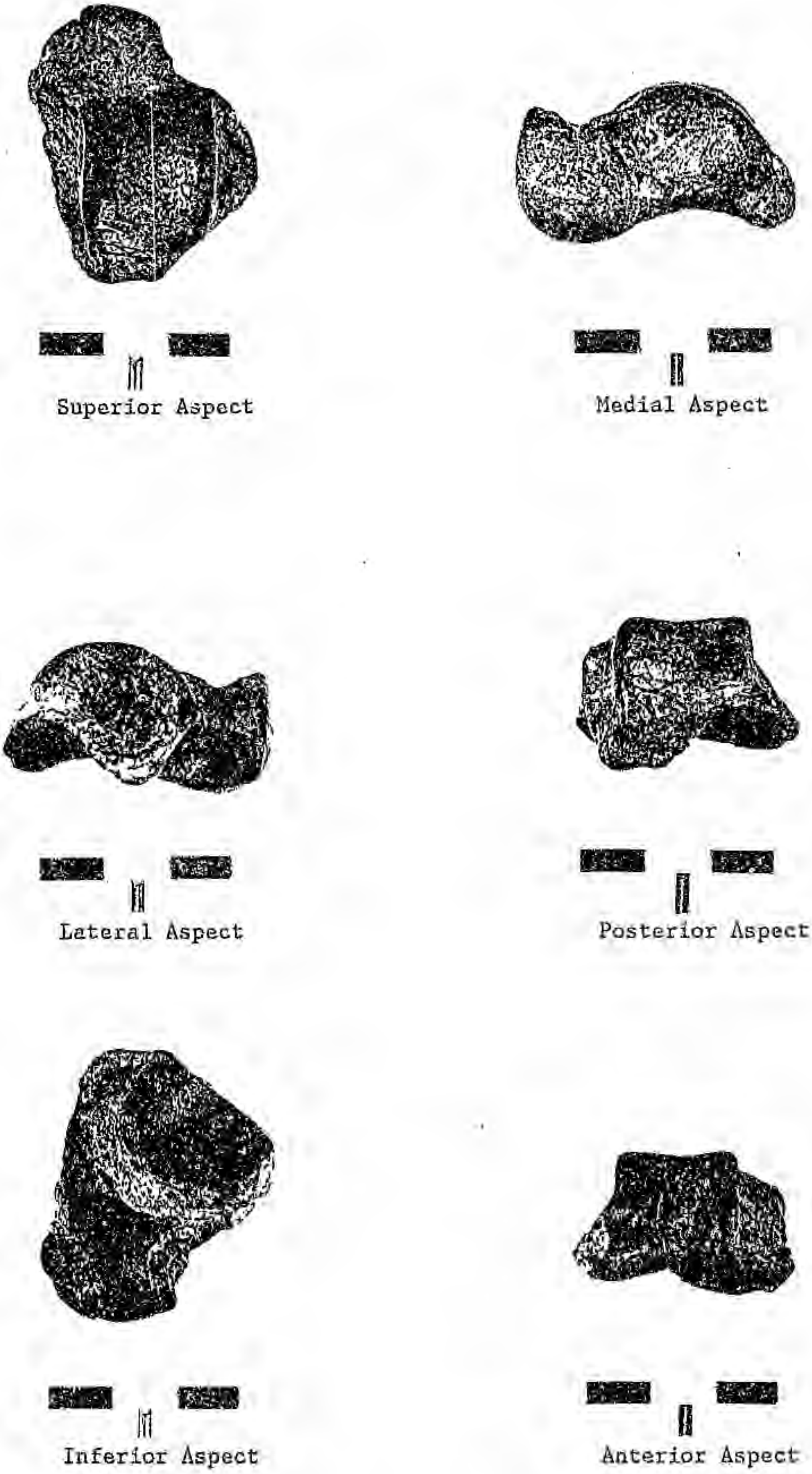
Further, Latimer *et al* (1987) have taken issue with Stern and Susman (1983) with regard to the latter's description of a 'plantar flexion set' in the ankle of extant pongids and Al 288. They measured the range of dorsi-plantar flexion in chimpanzees, gorillas, modern humans and AL 288 by radiography and also by manipulation of the talus and distal tibia. In the AL 288 ankle, the maximum extent of joint motion in the sagittal plane was found to be greater than the mean for chimpanzees, which in turn was significantly greater than in both humans and gorillas. They further asserted that "*this excursionary advantage occurred not in the direction of relative plantar flexion, but rather toward* *relative dorsiflexion*." The last statement is difficult to assess as any measurement of plantar or dorsiflexion separately from the other must be relative to an arbitrary neutral position of the foot (or talus) with respect to the distal tibia and/or fibula. Such a reference position does not appear to have been defined by Latimer *et al* (1987) nor by Stern and Susman (1983). The former authors placed little functional significance on the posterior inclination of the AL 288 distal tibia and considered it part of normal variation in *A. afarensis*. In support of their conclusion they noted that both posterior and anterior inclinations of the surface may be seen in the tibiae of African apes. Unfortunately, they did not mention whether they were able to find a tibia with posterior inclination among modern humans.

Latimer (1983, 1984) has not accepted the claim that the ventrally curved proximal phalanges of the Hadar foot were necessarily adaptations for arboreal climbing. He interpreted the phalangeal curvature as a response to large dorsoplantar bending stresses which might occur in either arboreal or terrestrial locomotion.

5.5. Stw 88, STERKFONTEIN

5.5.1. The Stw 88 talus, illustrated in Figure 10, was discovered *in situ* in breccia of Member 5, Sterkfontein (Square R/59' 12'3" - 13'3"). The age of the Member 5 deposit is not known with certainty since the identified fauna might have included an admixture of faunal materials from Members 4 and/or 6. The presence of *Homo habilis*, however, provides probable maximum and minimum estimates of approximately 2.3 and 1.6 Myr B.P. (Tobias, 1987).

5.5.2. *Preservation* - Stw 88 is an almost complete right talus. It is well-preserved except for a large part of the medial side



Superior Aspect

Medial Aspect

Lateral Aspect

Posterior Aspect

Inferior Aspect

Anterior Aspect

Figure 10. A right talus, Stw 88, assigned to *Homo habilis* from Member 5, Sterkfontein (natural size)

of the head which is missing. The inferomedial region of the articular surface of the head is cracked and depressed. The rest of the bone is undamaged. At the time of description, the bone had not been completely cleaned. Matrix partly filled the sulcus tali and a very thin matrix layer adhered to the posterior part of the superior articular surface. This thin layer did not alter the shape of the surface.

Superior Aspect - The superior articular surface is only very slightly wider anteriorly than posteriorly. The trochlear groove is shallow and its deepest point is situated medially. The articular surface of the medial crest is continued anteriorly onto the talar neck, as is that of the lateral crest but to a lesser degree. The triangular facet for the posterior talofibular ligament is evident but not very distinct. On the superior surface of the talar neck, the trochlear process for the talonavicular ligament is small.

Medial Aspect - The medial malleolar articular surface is perpendicular to the plane of the superior surface (in other words, it is oriented relatively vertically). It extends anteriorly well beyond the anterior edge of the superior surface and medially onto the neck and forms a large cup-shaped 'socket' for the medial malleolus. This 'socket' is associated with the anterior extension of the superior articular surface onto the talar neck, which in modern humans is termed the medial squatting facet.

Lateral Aspect - The lateral malleolar articular surface is relatively extensive in the supero-inferior and anteroposterior directions. In the coronal plane, its superior part is rather flat and is oriented perpendicularly to the plane of the superior surface. The inferior part is markedly concave and the facet extends well onto the prominent lateral process. In the anteroposterior direction, the inferior part of the facet is concave.

Posterior Aspect - There is a distinct groove for the posterior talofibular ligament. The groove for the tendon of flexor hallucis longus is shallow.

Inferior Aspect - The posterior calcaneal articular surface is oval-shaped and there is no 'waisting'. In the direction of its long axis, this facet is markedly concave, but is only very slightly concave along the perpendicular direction. The long narrow middle calcaneal facet is coextensive with the anterior calcaneal surface. The border between the two surfaces is marked by a rounded but definite change of contour. In its posterior half, the middle calcaneal facet is concave inferiorly, while in the posterior half, it is convex inferiorly. The anterior calcaneal surface is flattened anteroposteriorly and very slightly convex mediolaterally. The sulcus tali was not completely clear of matrix at the time of description.

Anterior Aspect - Approximately one-half to one-third of the talar head is missing. The articular surface of the head appears to have had the shape of a wide oval and its inferolateral border is clearly demarcated from the anterior calcaneal facet by a change of surface contour.

5.5.3. The Stw 88 talus and Stw 102, which is considered below, have been assigned provisionally to *Homo habilis*. Member 5 at Sterkfontein has to date yielded cranial and dental remains attributable only to *H. habilis*. Other early hominid sites in Africa which contain the earliest species of *Homo* have yielded also robust australopithecine fossils. One would expect the breccia of Member 5 in time to yield bones attributable to *A. robustus* and the possibility thus exists that Stw 88 or 102 might then need to be reassigned.

5.6. Stw 102, STERKFONTEIN

5.6.1. The Stw 102 talus, illustrated in Figure 11, was recovered *in situ* from Member 5, Sterkfontein (Square X/47 3'11" - 4'11").

5.6.2. *Preservation* - Stw 102 is a right talus which lacks almost all of the neck and head. Preservation of the rest of the specimen is fair and there is considerable weathering of surface bone in some areas. Much of the lateral crest of the superior articular surface and the superior part of the lateral malleolar facet are damaged. The anterior part of the medial malleolar facet is missing.

Superior Aspect - The anterior breadth of the superior articular surface would have been significantly greater than the posterior breadth. The trochlear groove is moderately deep and its deepest point is situated slightly more towards the medial crest than towards the lateral. There is a suggestion of a prominent trochlear process for the talonavicular ligament on the talar neck.

Medial Aspect - The medial malleolar articular surface is perpendicular to the plane of the superior surface. It appears that this surface, in the undamaged bone, would have extended anteriorly and medially onto the neck as a 'cup-shaped socket' similar to that of Stw 88. This is suggested by the orientation of a small tongue of subchondral bone from the antero-inferior part of the facet.

Lateral Aspect - Only the inferior part of the lateral malleolar facet is present. It is concave in the supero-inferior direction and convex anteroposteriorly. This articular surface does not appear to extend onto the lateral process.

Posterior Aspect - The groove for the tendon of flexor hallucis longus is badly eroded. The lateral tubercle is large.

Inferior Aspect - The posterior calcaneal articular surface is oval-shaped and there is no 'waisting'. In the direction of its

Superior Aspect

Medial Aspect

Lateral Aspect

Posterior Aspect

Inferior Aspect

Anterior Aspect

Figure 11. A right talus, Stw 102, assigned to *Homo habilis* from Member 5, Sterkfontein (natural size)

long axis, this facet is markedly concave, but is only very slightly concave along the perpendicular direction. The sulcus tali is deep. Only the posterior part of the middle calcaneal facet is present. The anterior calcaneal and talar head articular surfaces are missing.

5.6.3. The provisional systematic status of Stw 102 is the same as that of Stw 88 (see 5.5.3).

CHAPTER 6. METHODS

6.1. METHODS OF MEASUREMENT AND MATHEMATICAL REPRESENTATION OF THE TROCHLEAR ARTICULAR SURFACE

6.1.1. Method of Obtaining Cartesian Coordinates of Points on the Articular Surface

6.1.1.1. Computer Numerical Control Milling Machine

A three-axis computer numerical control (CNC) milling machine modified to permit automated measurement (see Appendix and Figure 12) was used to find Cartesian coordinates of points on the trochlear surface of the talus. Normally this machine performs programmed cutting operations on a base material such as metal and can produce elaborate shapes sculpted to fine tolerances. The material to be milled is mounted on the machine's motor-driven table which is able to move in the x (horizontal) and z (vertical) axes in preset intervals of as little as one micrometre (0.001 mm). The particular cutting device in use is attached to a mounting head which similarly moves in the y (horizontal) axis. Thus the digital computer controlling the machine can be programmed to position the cutting edge at any point in Cartesian space or group of points in succession.

To perform automated measurements rather than cutting operations, an anatomical specimen was mounted onto the movable table while a digital length transducer was fitted to the mounting head of the y-axis (Appendix). The transducer has a spherical-tip vertical probe which moves in the z-axis and gives a digital readout consisting of the z-coordinate position of the centre of

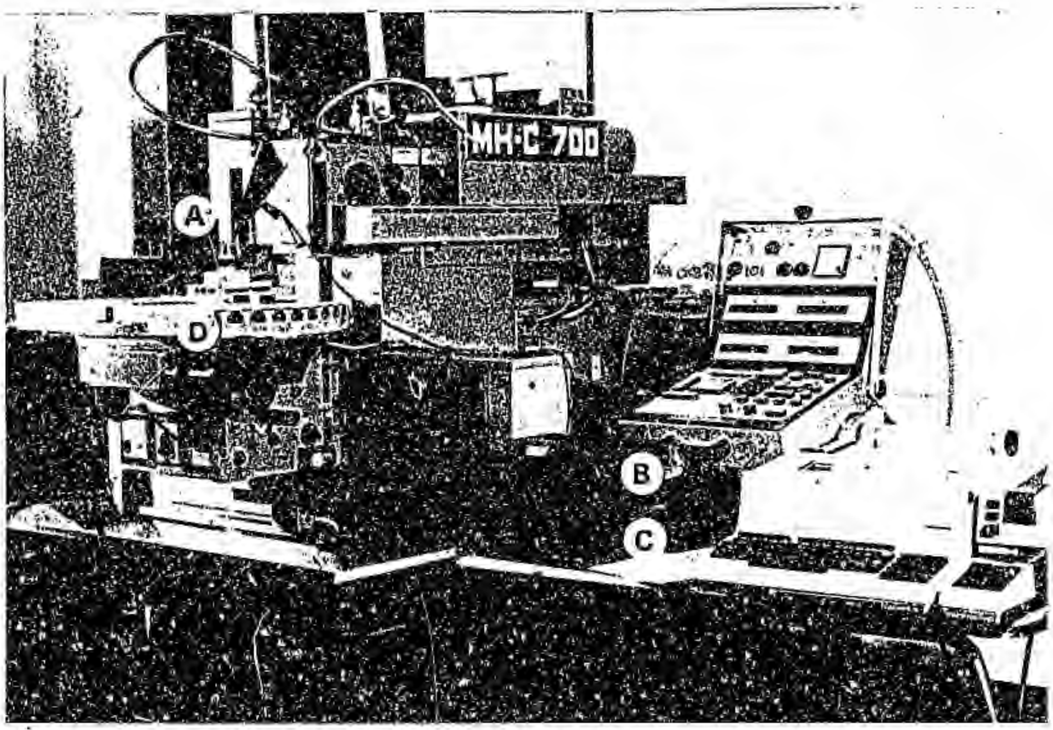


Figure 12. Computer numerical control milling machine modified by the attachment of:
(A) Digital length transducer,
(B) Printer,
(C) Display monitor.
(D) indicates the machine's movable table.

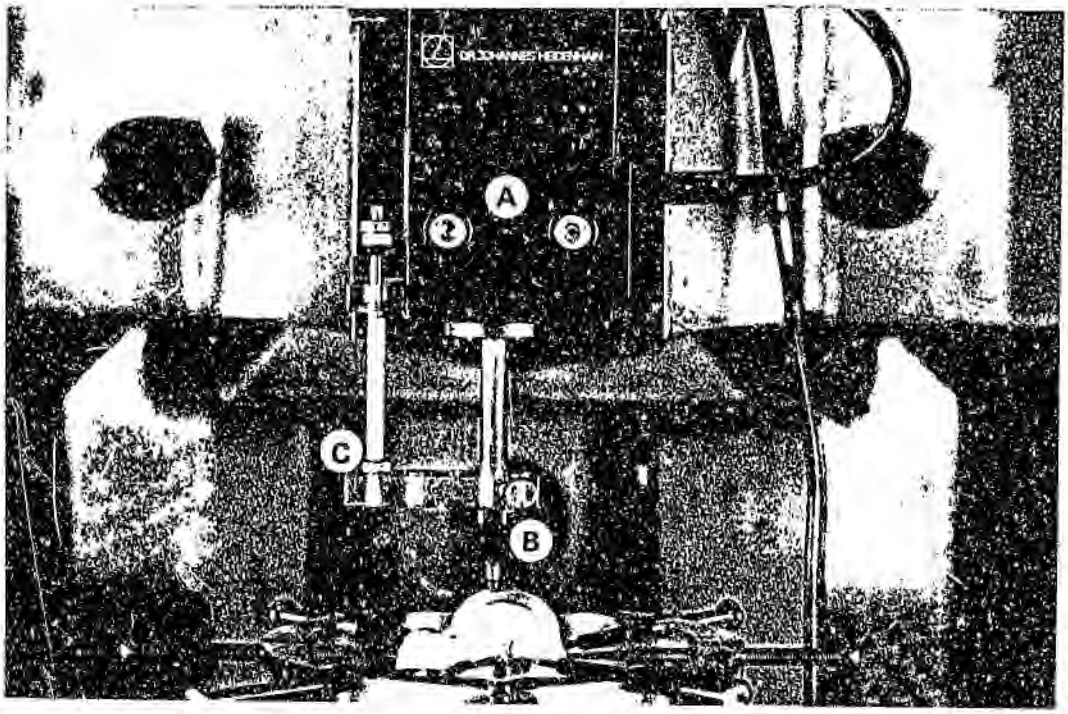


Figure 13. (A) Digital length transducer,
(B) Probe with spherical tip,
(C) Vertical guiding device.

the spherical tip (diameter = 3.175 mm). At any given position on a programmed *x*,*y* horizontal grid, the table ascended in the *z*-axis to a constant height. As the table was raised to its predetermined height, it brought the articular surface into contact with the probe and moved the spherical tip to a *z*-coordinate position, the value depending upon the character of the surface curvature at that (*x*,*y*) position (Figure 13). As each point on the grid was measured, the value of the *z*-coordinate was printed onto paper.

The 11×11 point *x*,*y* grid was programmed so that the maximum length and width of the trochlear articular surface were covered. Since this surface is not perfectly rectangular, some points sampled fell outside the boundaries of the articular cartilage and the values for these points were not included for analysis. Therefore the data set for each specimen consisted of *x*, *y* and *z*-coordinates of between 84 and 111 of the 121 points sampled.

In order to compare data sets of coordinate points from specimens which differed in structure, size and position (right or left side), it was necessary prior to measurement to mount each specimen in a standard reference (or datum) position. In other words, each bone had to be in an equivalent position with respect to the three anatomical planes (coronal = *y*,*z*; sagittal = *x*,*z*; transverse = *x*,*y*). For this purpose, mounting guides and holders were devised and built and a set procedure was followed for each specimen.

To hold a talus firmly attached to the table of the CNC milling machine and so that it would not deflect under the force of the probe (F = 0.510 N), the bone was fixed inside a perspex ring by eight pins threaded radially through the ring so that they could be tightened by hand. The ring in turn was screwed to a flat perspex sheet hinged to another perspex sheet clamped to the machine table. The hinge was parallel with the *x*-axis of the machine (Figure 14). When the bone was 'pinned' inside the ring, it was

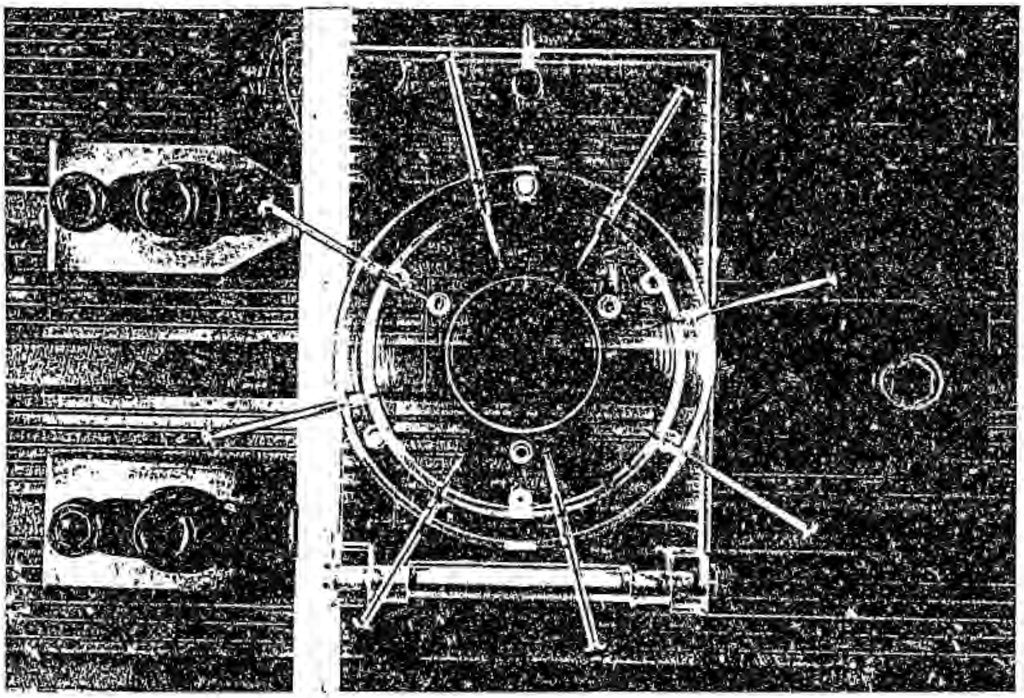


Figure 14. Perspex specimen holder clamped to the milling machine table.

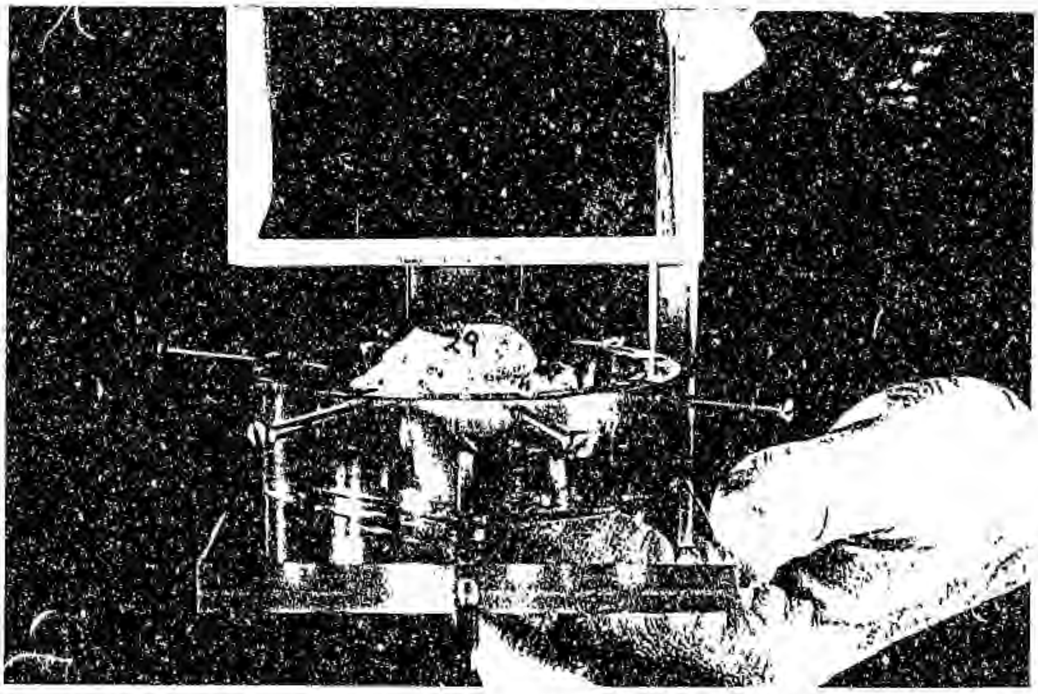


Figure 15. Alignment of the talus in the reference position prior to securing it with pins.

at the same time carefully positioned relative to the coronal and sagittal planes.

The first step in mounting the specimen was to position the medial and lateral edges of the trochlear surface snugly against one of three perspex V-blocks of different sizes, which had been glued to a square aluminium block, the face of which was positioned parallel to the *x*-axis of the machine. The ring-bearing perspex sheet was swung up to a roughly vertical position and the talus within the ring was held against the V-block such that the arms of the V made contact with the lateral and medial curvatures of the trochlear surface (Figure 15). In this position, the approximate theoretical axis of the surface was exactly parallel to the coronal plane (the *y*-axis of the machine) and thus perpendicular to the sagittal plane. While the medial and lateral edges of the trochlear surface were touching the V-block, the talus was rotated so that the antero-inferior and postero-inferior points (relative to the anatomical position) of the lateral malleolar facet were aligned visually with the edge of the perspex ring. Thus both points were in a line parallel to the transverse plane (*x*,*y* plane of the machine). As the bone was held firmly in this position by one person, another began to tighten diametrically opposed pins, two at a time, until the points just pierced the bone surface. With all eight pins tightened, the specimen was invariably held immobile within the ring (Figure 16).

With the specimen mounted securely and fixed relative to the *x* and *y* axes of the machine, one further adjustment of its position was necessary. This was to set the talus so that the approximate theoretical axis of the trochlear surface was parallel to the transverse plane (the *x*,*y* plane of the machine represented by the surface of the movable table). In this way, all measurements of the z-coordinate would be taken perpendicular to the theoretical surface axis. A consideration of the geometrical properties of a

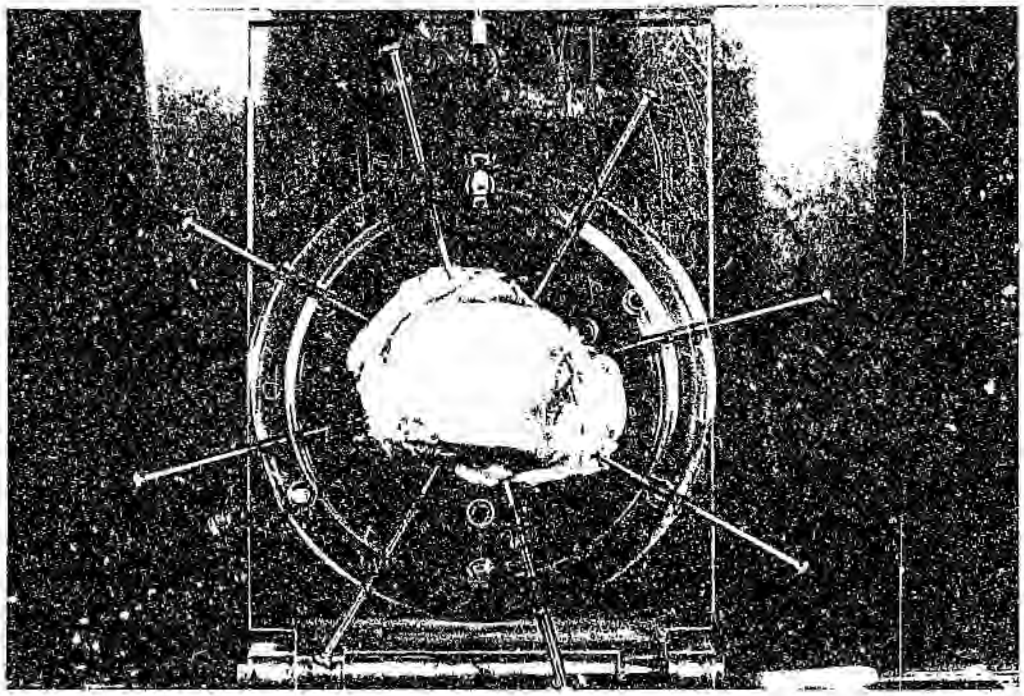


Figure 16. Talus securely mounted in the perspex specimen holder.

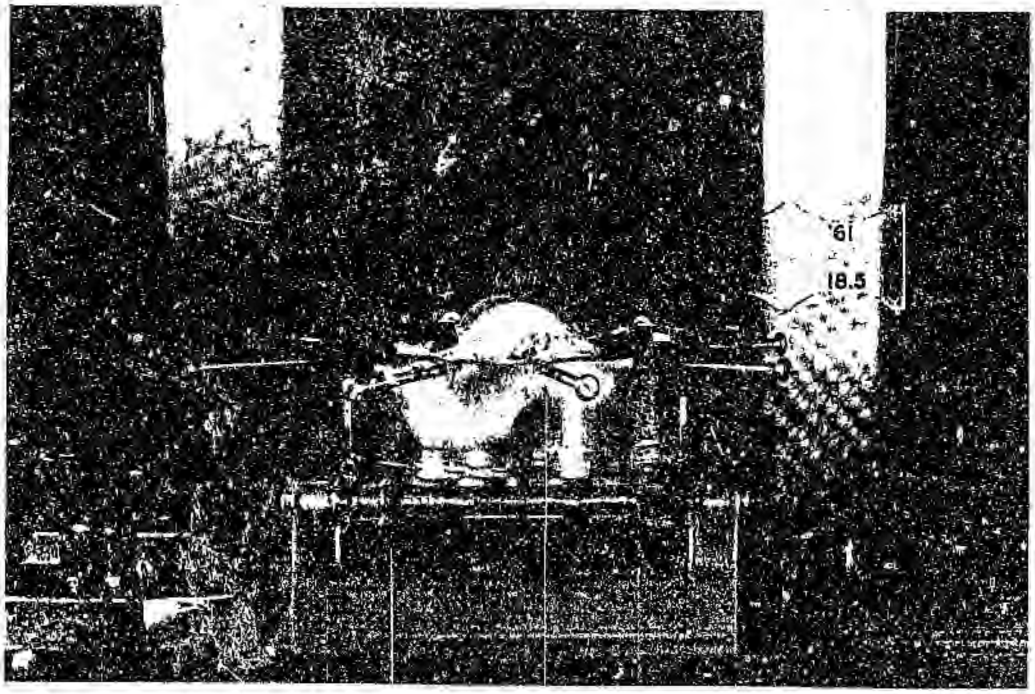


Figure 17. Measurement of the radii of the circular profiles of the medial and lateral trochlear margins.

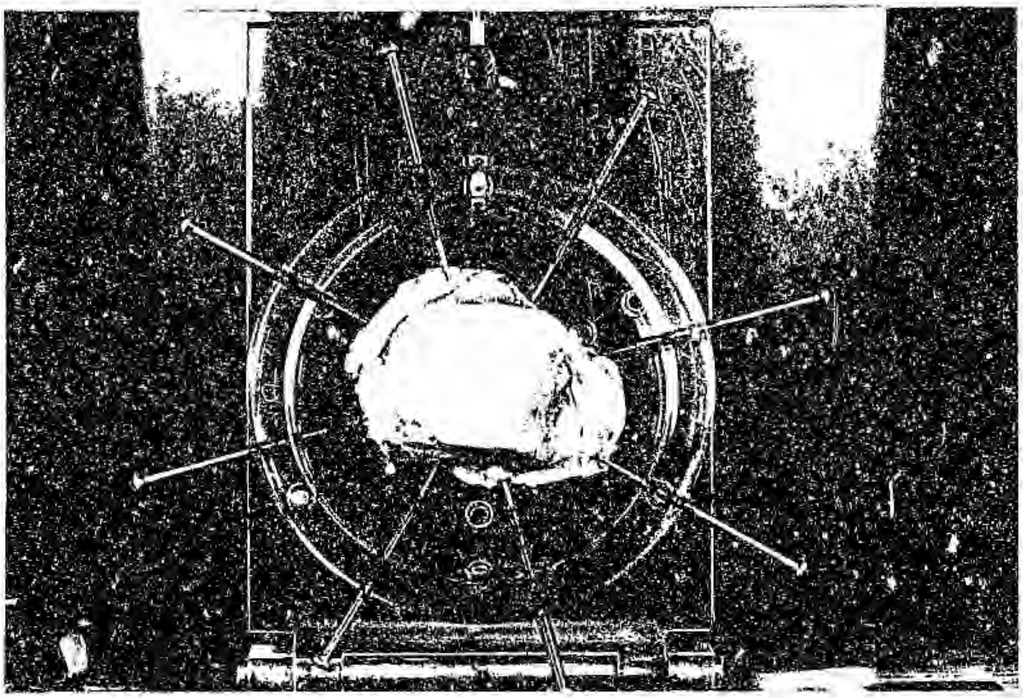


Figure 16. Talus securely mounted in the perspex specimen holder.

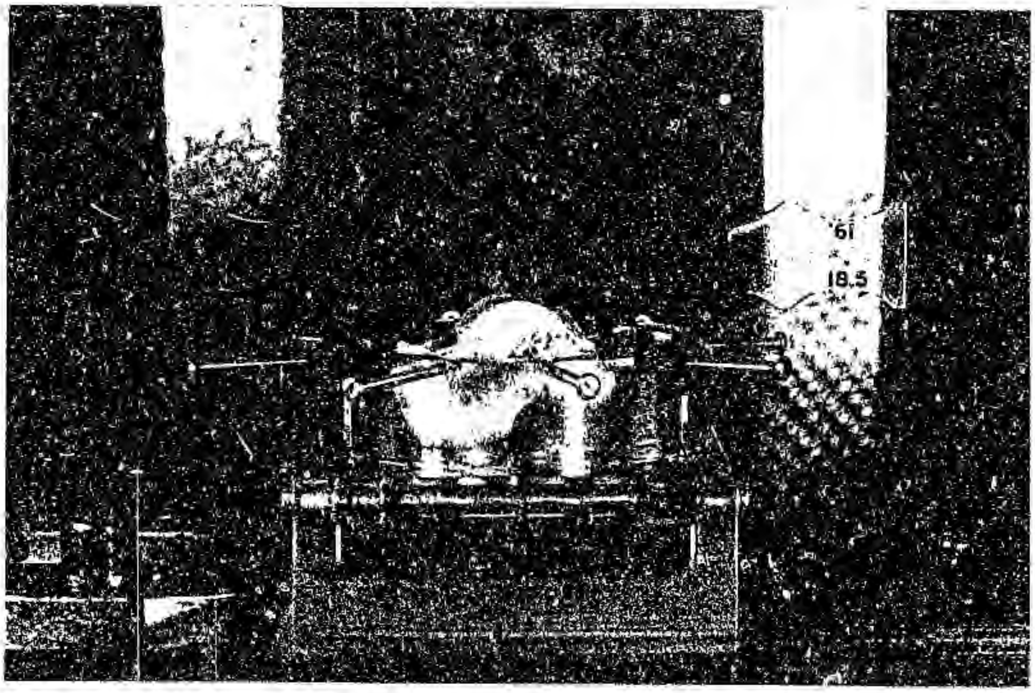


Figure 17. Measurement of the radii of the circular profiles of the medial and lateral trochlear margins.

cone or cylinder will illustrate the importance of this precaution. If a cone or cylinder is sliced perpendicular to its axis, the resulting section will always be a circle, the mid-point of which lies on the axis. If on the other hand the slice is oblique to the axis, the section will be an ellipse. Therefore to obtain mathematically precise representation of the surface curvatures (in the analogy, circles rather than ellipses), it was necessary to sample the z-dimensions of the surface perpendicular to the axis.

The approximate theoretical axis of the trochlear surface was made parallel to the *x*,*y* plane by the following procedure:

It was assumed that the trochlear surface could be represented approximately by a frustum of a cone (Inman, 1976, p.19) or a cylinder. In either case, the approximate axis could be located by finding the mid-points of the circular profiles which form the medial and lateral borders of the surface. To find the mid-points, the radii of the two circular profiles were measured to the nearest 0.5 mm with a perspex radius gauge held successively against the crests of the medial and lateral orders parallel to the *x*,*y* plane and the *x*-axis of the machine (Figure 17). To set the two mid-points of the circles (and thus the axis) at the same level in the z direction (ie. parallel to the *x*,*y* plane), the highest point of the border having the greater radius was positioned higher than the corresponding point of the other border by a value equal to the difference between the two radii. For example, if the lateral border had a radius of 21.5 mm and the medial radius was 17.5 mm, the highest point laterally was set 4.0 mm higher than the medial apex. This adjustment was made by raising or lowering the ring-bearing perspex sheet hinged to the sheet fastened to the table. Fine adjustment was made easy by turning a set-screw (Figure 18).

To position the lateral and medial borders at the difference between the two radii, first the highest point on the lateral

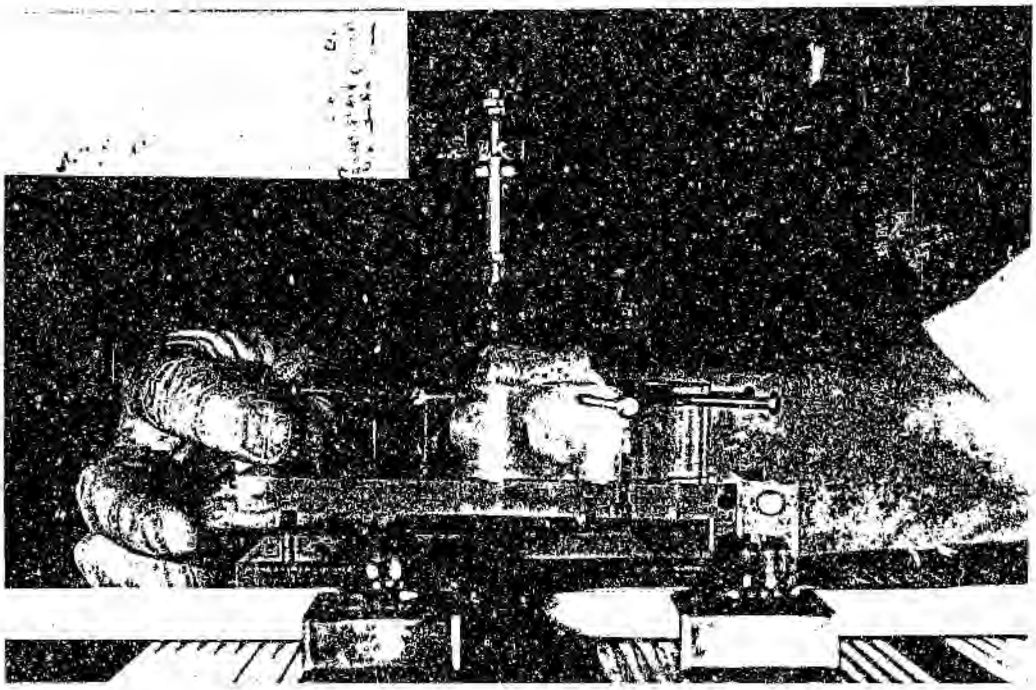


Figure 18. Fine adjustment of the position of the lateral and medial vertices in the z-axis.

border was found by sliding the spherical-tip of the probe in the x-axis and the y-axis. As the changing values of the z-coordinate were shown on the digital display monitor (Appendix), it was possible to determine the highest point in either direction. The x-coördinate of the lateral apex was fixed as the position of the theoretical axis, the probe was moved along the y-axis to the medial border and then the highest point in the y-direction was found. If the difference between the vertices medially and laterally deviated from the desired difference, the necessary fine adjustment was made and the new setting was checked by moving back and forth from the medial to the lateral border. Eventually it was possible to position the borders at the desired difference within a sufficiently small margin of error.

After the last adjustment had been made, the talus was in its reference position ready to be measured. The CNC machine was programmed to sample and measure z-coordinates of the trochlear surface over a rectangular 11×11 point grid (numbered -5 to +5 in the x and y-axes). The orientation of this grid with respect to the position of the (x,y) points was constant whether the talus was from the right or the left foot. Furthermore, the bone was always mounted so that the lateral border of the trochlear surface was toward the x_{+5} line whilst the x_{-5} line ran along the medial edge. For a right talus, the origin point of the grid (x_{-5}, y_{-5}) was near the anteromedial corner of the articular surface whereas, for the left talus, it was near the posteromedial corner. The programme was written in parametric form so that the spacing between grid points in the x and y directions could be easily changed for each specimen. To calculate the size of an 11×11 point grid which would cover the full extent of the trochlear articular surface, the maximum anteroposterior and mediolateral lengths of the surface were measured to the nearest 0.5 mm with a pair of vernier calipers. Since there were ten spaces between points in the x and

y directions, the anteroposterior and mediolateral lengths were divided by ten and the CNC machine was programmed with these parameters.

The origin point of the x,y grid (x_{-5}, y_{-5}) was found in the following manner:

The previously determined highest point on the lateral border was taken as x_0, y_{+4} (x_0 representing the x-coordinate of the approximate theoretical axis) and from that point, the probe was moved in the x direction one-half the maximum anteroposterior distance (ie. to x_{-5}). For a right talus, the direction of this movement was anterior but for a left talus, the same direction was posterior. The probe was then moved medially nine-tenths of the maximum mediolateral distance (to y_{-5}). From this x_{-5}, y_{-5} position, z-coordinates were measured along the grid one x-line after another (x_{-5} to x_{+5}).

As each (x,y) grid point was sampled, the value of the z-coordinate of the centre of the probe tip (in millimetres to three decimal places) was automatically printed on paper along with the (x,y) point number. The output from the linear transducer to the printer (Appendix) was triggered by a LED and photo-diode combination mounted on the vertical column of the machine which detected the position of an adjustable blade fitted to the movable table. For each specimen, the blade was adjusted so that, as the table reached its programmed height, the light circuit was broken and the photo-diode sent a signal to the printer. A digital delay circuit between the photo-diode and printer (set for a two-second delay) ensured that the transducer was sampled only after the table and the anatomical specimen had become stationary.

Those (x,y) grid points which did not fall on the trochlear articular surface were identified and recorded on each specimen's data sheet as the measurements were taken. The x,y and z values of sampled points which were on the articular surface were later manually put in to main-frame computer storage while the values of points not on the surface were ignored.

For each specimen, the values of x- and y-coordinates were changed from integers of -5 to +5 to millimetres by multiplying them respectively by the x- and y-grid spacing.

6.1.1.2. Three-Dimensional Coordinate Measuring Centre

A three-dimensional coordinate measuring centre was used to find Cartesian coordinates of points on the trochlear articular surface of the talus. The measuring centre consisted of a travelling-bridge-configuration measuring machine fitted with a spherical-tip omnidirectional probe (tip diameter = 1.994 mm) and a minicomputer machine control and data handling system (Appendix and Figure 19). The granite base of the measuring machine provides a flat surface (x,y plane) for the attachment of specimens and supports a bridge which traverses the x-axis. A carriage which is supported by and moves along the cross-bar of the bridge in the y-axis contains a vertically-oriented square ram which provides movement in the z-direction. The electronic probe is attached to a measuring head at the lower end of the ram. The minicomputer which controls movement of the machine axes can be programmed to position the centre of the spherical tip of the probe at any point in Cartesian space or any group of points in succession. In automated measurement of the z-coordinates of points, at given (x,y) positions on the surface of a specimen, the probe moves in the z-axis until the spherical tip touches the surface (Figure 20). Upon contact, the x,y,z-coordinates of the centre of the tip are recorded in computer memory, the probe's travel in the z-direction is reversed and it moves on to sample the next point.

Prior to the measurement of points on the trochlear surface, each specimen was mounted in a standard reference position by the procedure described in 6.1.1.1, though with one modification. In

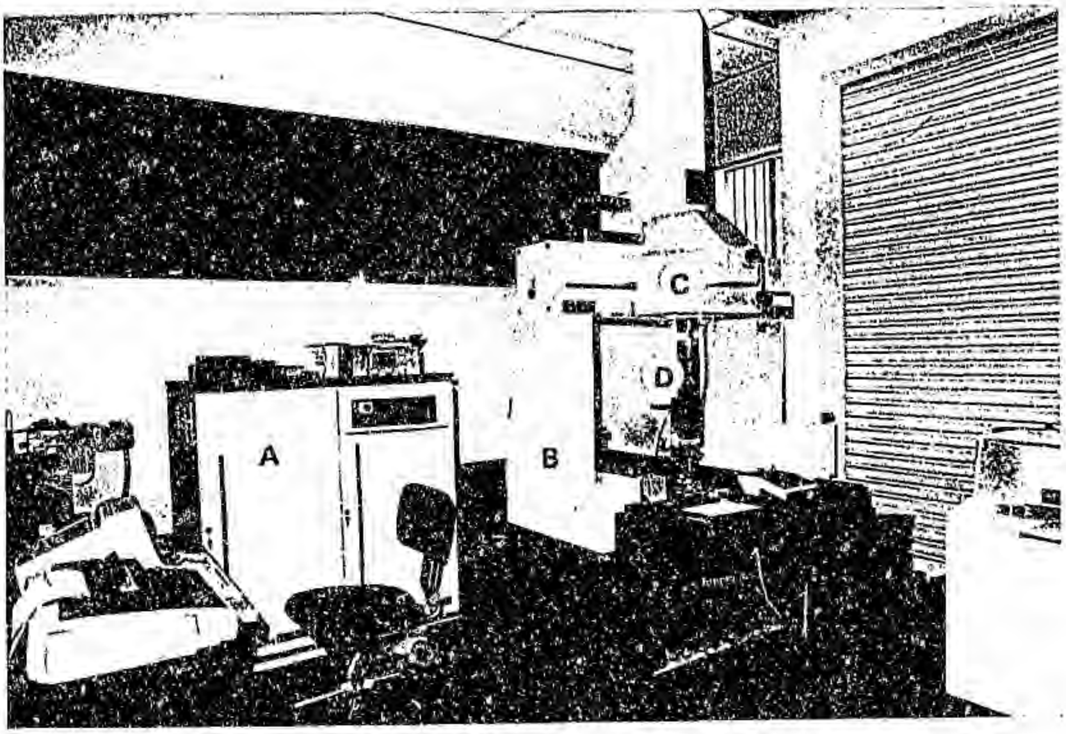


Figure 19. Three-dimensional coordinate measuring centre.
(A) Minicomputer which controls the measuring machine
(B) Travelling bridge (x-axis)
(C) Horizontal carriage (y-axis)
(D) Vertical ram (z-axis)

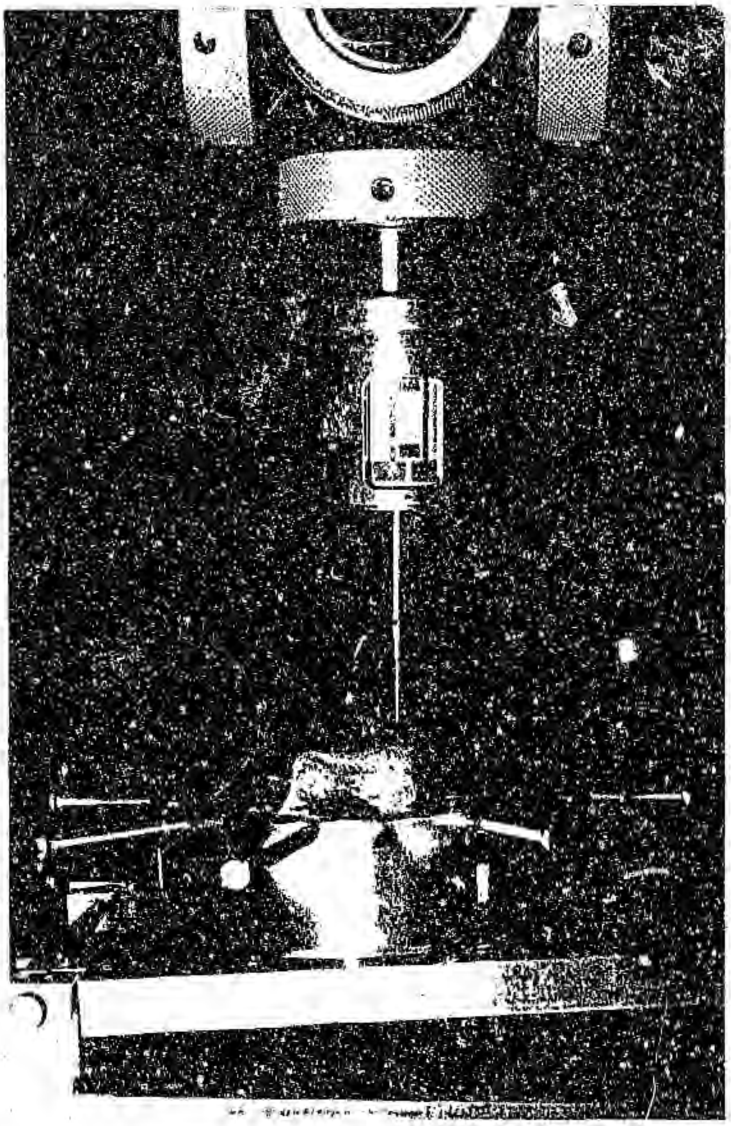


Figure 20. Probe with spherical tip about to make contact with the superior articular surface of the talus.

the procedure of 6.1.1.1, the talus was set so that the approximate theoretical axis of the trochlear surface was parallel to the transverse plane. This ensured that measurements of z-coordinates were taken perpendicular to the surface axis. This was accomplished by physically positioning the talus by means of a set screw, so that the highest point on the lateral margin of the trochlea was higher (or lower) than the medial apex by a value equal to the difference between the medial and lateral radii.

For specimens which were measured by the coordinate measuring machine, this part of the procedure was done in the following manner:

Once a talus was mounted securely in the perspex ring, the set screw was used to position it so that the lateral trochlear margin was higher or lower than the medial by approximately the appropriate distance, the difference in value between the radii of the lateral and medial crests. The probe tip was positioned over the apparent summit of the lateral border and the machine then ran a pre-programmed operation to find the highest point in the *x*-axis. The probe touched first one point then another point adjacent to the first in the positive *x*-direction. If the second point was higher in the z-axis than the preceding point, the machine went on to another point further in the positive *x*-direction. If the second point was found to be lower than the first, the probe was moved in the negative *x*-direction beyond the first point to sample a third point. If this third point was higher than the first, the machine proceeded to another point further in the negative *x*-direction. However, if the third point was lower than the first, the probe reversed direction to sample another point between the first and third. From then on the machine continued the iterative process whereby it moved the probe further in the same *x*-direction if a point sampled was higher than its predecessor, but if the point was found to be lower than that preceding it the probe was reversed to a position between them. In this manner, the probe narrowed in upon the apex in decreasing increments of x until final comparison between adjacent high points was in 0.05 mm steps. After the highest point in x had been located, the machine performed the same operation to find, at that x value, the highest point in y. This point was then taken to be the vertex of the lateral trochlear margin and was assigned coordinates $x = 0$, $y = +4$ times the y-grid spacing ((x,y) in mm equivalent to (x_0, y_{+4}) on an 11×11 point grid). The probe was then positioned over the medial trochlear margin at the same x value and the machine found there the highest point in y.

When the y,z-coordinates of the medial and lateral vertices were known, the minicomputer calculated the angle of rotation necessary to position the tangent to both vertices parallel to the x,y plane of the machine. It then calculated the angle of rotation necessary to separate the two highest points in the z-axis by a value equal to the difference between the medial and lateral radii (as measured with a radius gauge). In this case, however, the rotation of the talus was not done physically by means of the set screw as in the procedure described in 6.1.1.1. Instead, the computer controlling the machine axes instructed the probe, when traversing the 11×11 point grid, to descend in a z-axis which was perpendicular to the theoretical axis of the trochlear surface rather than to the surface of the granite table.

After the last adjustment had been made by the computer, the specimen was effectively in the same reference position as described in 6.1.1.1 and was ready for measurement. The x and y spacing of the rectangular grid and its origin point ($x = -5$ times the x-grid spacing, $y = -5$ times the y-grid spacing) were calculated as before. As each grid point was sampled, the x,y and z-coordinate values of the centre of the probe tip (in millimetres to three decimal places) were stored in the minicomputer memory and printed on paper. Those points which were not on the trochlear articular surface were identified and recorded on each specimen's data sheet as the measurements were made. The x,y,z values of points which were on the articular surface were later manually put in to main-frame computer storage while the values of other points were ignored.

6.1.2. Method of Fitting a Theoretical Surface to Measured Cartesian Coordinates

In the standard reference position, the trochlear surfaces of all tali (right and left) were measured from the medial to the lateral edges along the positive y-axis. Left tali were measured from posterior to anterior in the positive x-axis, whereas right tali were measured from anterior to posterior. For comparative purposes, all right tali were changed into left-sided specimens by the transformation:

$$x_{\text{new}} = -x_{\text{measured}}$$

For each talus, Cartesian coordinates of the trochlear surface were used to derive by least-squares a surface equation of the general form[1]:

$$z = a + bx + cy + dx^2 + exy + fy^2 + gx^2y + hxy^2 + ky^3 + mx^2y^2 + nxy^3 + py^4 + qx^2y^3 + rxy^4 + sx^2y^4.$$

This equation was chosen specifically for the trochlear surface since it provides the best fit of the male surface of a modified sellar joint (see 2.3).

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[1] In order that rounding-off errors be minimized, the values of Cartesian coordinates were changed from mm to cm. The computer program used to derive the surface equation was the General Linear Models Procedure (PROC GLM) of SAS (SAS Institute Inc., 1982).

The general function chosen as a model for the fitted surface provided accurate descriptions of the trochleae of all tali measured. The r-square value (i.e. the square of the correlation coefficient) for each specimen indicates how much variation in the z-coordinate measurements can be accounted for by the particular surface equation. The closer r-square is to 1, the better is the model's fit. The range in r-square values of all specimens was 0.9544 to 0.9985. In other words, the goodness of fit of the mathematical model to the measured Cartesian coordinates was never less than 95.4 per cent and most often was greater than 98 per cent.

Figure 21.A illustrates a human trochlear articular surface derived from a surface equation used to fit measured Cartesian coordinates.

6.1.3. Method of Calculating Corrected Cartesian Coordinates and Fitting a Theoretical Surface to the Corrected Coordinates

The polynomial equation derived from measured Cartesian coordinates does not represent a manifold of points on the trochlear articular surface, since the values of coordinates were actually recorded at the centre of the spherical tip of the probe. Thus the equation fitted points on a measured surface parallel to and slightly larger than the true trochlear surface (Figure 22). Corrected coordinates, those of points on the articular surface touched by the exterior of the probe's spherical tip, were calculated in the following manner:

$\mathbf{r}_{\text{true}} = \mathbf{r}_{\text{measured}} - a\mathbf{n}$

where $\mathbf{r} = (x,y,z)$

a = radius of the spherical tip of the probe

$\mathbf{n}$ = unit normal vector.

This equation represents the fact that the true and measured surfaces are parallel at a distance a apart. The vector $\mathbf{n}$ has constant magnitude 1 but variable direction and represents the common

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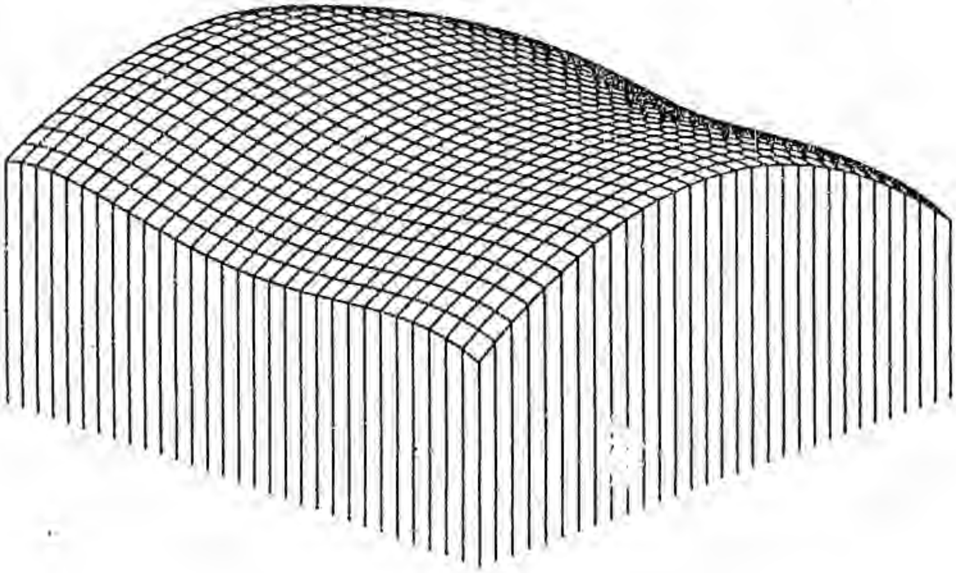


B. HUMAN CORRECTED

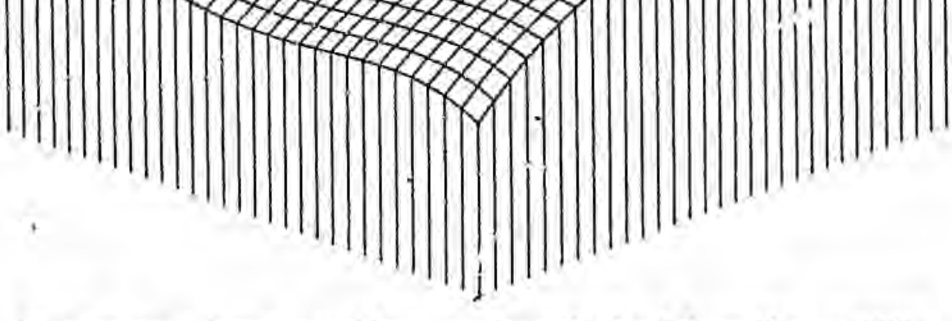
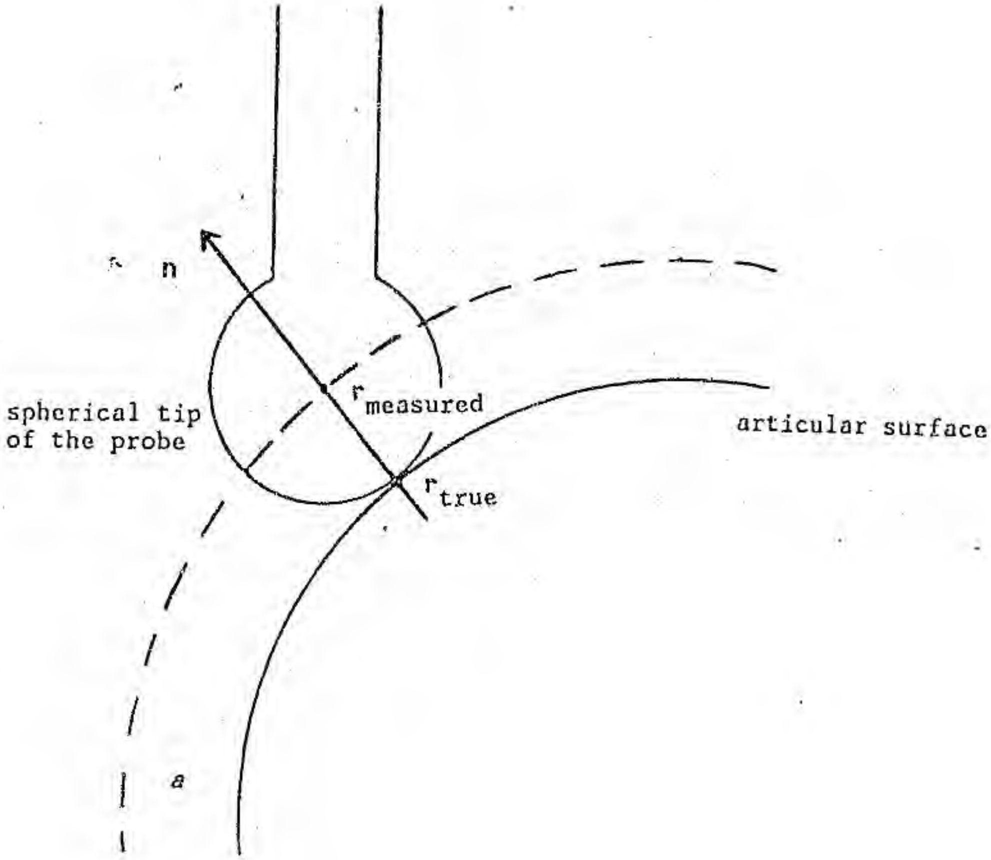


Figure 21. A. Plot of a human trochlear surface derived from the equation fitted to measured Cartesian coordinates.
B. Plot of the trochlear surface of the same talus derived from the equation fitted to corrected Cartesian coordinates.



$$r_{true} = r_{measured} - a\mathbf{n}$$

where $r = (x,y,z)$

a = radius of the spherical tip of the probe

$\mathbf{n}$ = unit normal vector.

Figure 22. The formula for the correction of measured Cartesian coordinates (see text for details).

perpendicular to both surfaces (at the points $\mathbf{r}_{\text{measured}}$ and $\mathbf{r}_{\text{true}}$ respectively). From standard results in partial differentiation:

$$n = (-z_x \, , \, -z_y \, , \, 1)/\sqrt{z_x^2+z_y^2+1}$$

where z_x and z_y are the partial derivatives of z with respect to x and y.

Once corrected Cartesian coordinates had been computed for each specimen, they were used to derive, by the method given in 6.1.2, a new surface equation of the same general form. Figure 21.B illustrates the trochlear surface of the same talus as in Figure 21.A derived from the equation fitted to the corrected Cartesian coordinates.

The use of a non-contact laser probe, now available for use with advanced three-dimensional coordinate machines, instead of the usual spherical-tip probe, would obviate the need for the correction of measured Cartesian coordinates.

6.2. METHODS OF MATHEMATICAL ANALYSIS OF THE TROCHLEAR ARTICULAR SURFACE

6.2.1. Introduction

A modified sellar surface consists of a central sellar region bounded on two sides by areas of ovoid surface. Although the equation presented in 6.1.2. is a mathematical representation of the entire modified sellar surface, this class of articular surface may be divided naturally into three regions for purposes of mathematical analysis and statistical comparison. In the case of the superior articular surface of the talus, I have loosely delineated the medial crest (ovoid), the trochlear groove (the central sellar region), and the lateral crest (ovoid) as the three regions of the surface suitable for mathematical analysis. The exact lines of transition between the trochlear groove and the crests on either side are not clearly defined, but this is not very important as the following analysis concentrates on the areas around the points of simultaneous maximum curvature of each of the three sections. These points are situated close to the centre of each section rather than near to the transitional area.

The trochlear articular surface as a whole may be compared among different specimens, or each of the three regions may be considered separately. The shape of each section may be analysed in terms of the curvatures, or radii of curvature, in the mediolateral and anteroposterior directions. The curvature at a point on a section of a surface is the reciprocal of the radius of that section at that particular point. The analogy of a sphere may illustrate this point: the larger is the radius of the sphere, the less is the surface curvature. Clearly, the surface of a ping pong ball is more highly curved than that of a tennis ball. The variables chosen for analysis could be either the curvatures (or radii of curvature) in both directions at any point, or the average of curvatures (or average radius of curvature) of a number of points. On the medial and lateral crests (ovoid areas), the curvatures in the mediolateral and anteroposterior directions will be downward (or negative), whilst in the saddle region, the anteroposterior curvature will be downward (negative) and the mediolateral curvature upward (positive). Characteristics of the overall shape of the superior articular surface of the talus such as its general conical nature, the relative mediolateral position and accentuation of the trochlear groove, may be analysed by the comparison of curvatures of the different sections. The variables described in 6.2.4 have been devised to describe and quantify variations in shape of the trochlear surface in general, and in its three regions, among the higher primate tali discussed in chapter 4.

6.2.2. Estimations of an Axis of Rotation of the Superior Articular Surface of the Talus

Ideally, a mathematical analysis of the trochlear surface would make use of parameters of surface curvature which will not be affected by any errors in the choice of x and y-axes of the measurement grid of each specimen. Instead, a reference axis intrinsic to the morphology of the articular surface should be used, for example the axis of rotation. This assumes, however, that such an axis can be defined reliably and is relatively stationary. In this preliminary analysis of characteristics of trochlear surface curvature, I wished to measure averages of curvatures in the anteroposterior and mediolateral directions (eg. perpendicular and parallel to an estimated axis of rotation of the trochlear surface).

In the setting-up of each specimen prior to measurement, an approximate axis of rotation was estimated by the use of the V-block method described in 6.1.1.1. Thus the estimated rotation axis was set as the y-axis of the measurement grid and the x-axis was perpendicular to it.

The results of a second method of estimation of the theoretical axis of rotation were compared with those of the V-block technique. The centres of curvature of twenty-five points on the central saddle section of the trochlear surface were calculated. A best-fit line through the centres was found by the least-squares method. For each talus, the orientation of the best-fit line in the horizontal plane was compared with the orientation of the y-axis. The two axes were found, in all cases, to be within a few degrees of each other.

Preliminary mathematical analysis of the trochlear surface was technically easier if the x and y-grid axes were used as the reference directions rather than the best-fit line, found by the second method of estimation, and its perpendicular. Since both the *y*-grid axis and the axis determined from the centres of curvature of twenty-five points were, in effect, estimations based on surface curvature, and apparently neither was a significantly better estimator than the other since they were very close in value, the primary curvature variables described in the following section were calculated in relation to the *x* and *y*-grid axes.

6.2.3. Method of finding (Xmed,Ymed), (Xsel,Ysel) and (Xlat,Ylat)

The primary curvature variables used to describe trochlear surface shape are reciprocals of the averages of curvatures at points on the surface spaced in relation to (Xmed,Ymed), (Xsel,Ysel), (Xlat,Ylat), which are the (x,y) coordinates of the three points of simultaneous maximum curvature in *x* and *y* located respectively on the medial crest, in the saddle region, and on the lateral crest of the trochlear surface. For each talus, these three points were found by an iterative computer procedure analogous to the Newton-Raphson method. Starting at an estimated point in each of the three regions, the computer alternately finds the point of maximum curvature in *x* without changing *y* and vice versa.

6.2.4. Variables which Describe Characteristics of Trochlear Surface Shape

6.2.4.1. Primary Curvature Variables

The variables described in this section are illustrated in Figure 23.

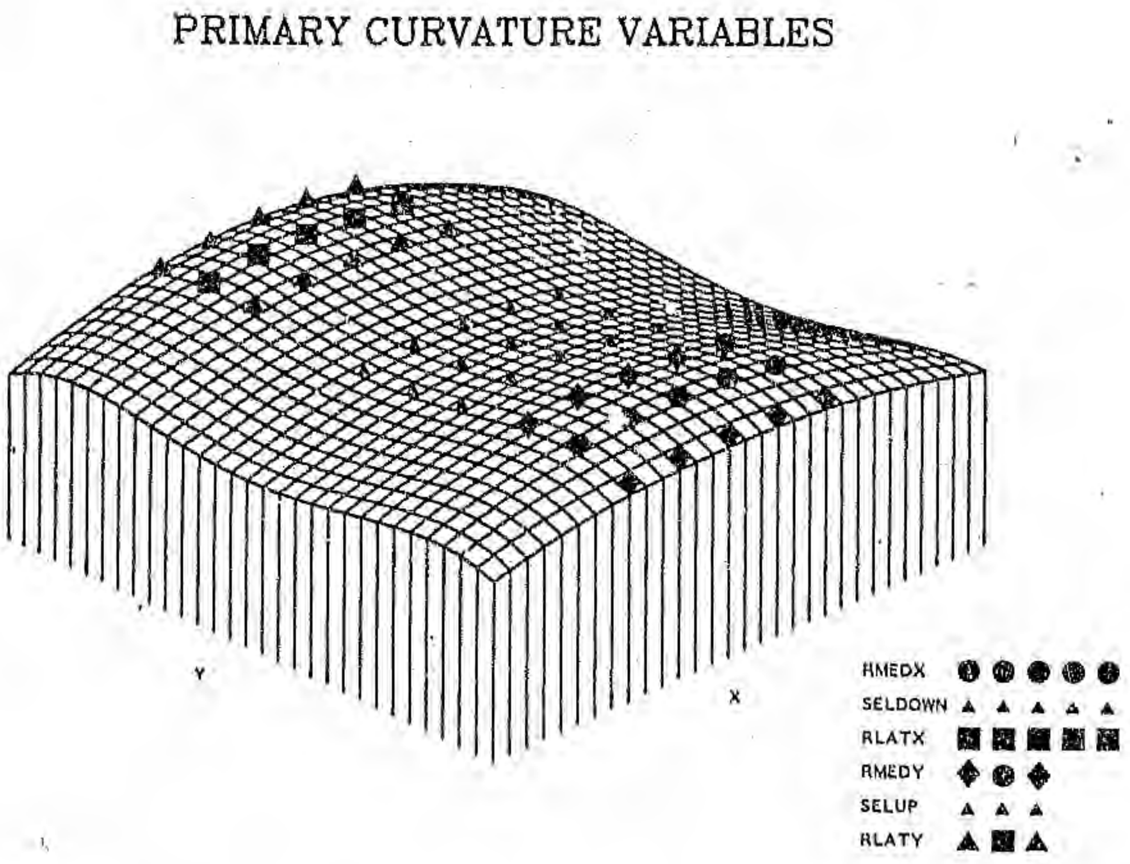


Figure 23. Primary curvature variables.
RSELX is the middle one of the three rows of five points which constitute SELDOWN.
RSELY is the middle one of the five rows of three points which constitute SELUP.

1. **RMEDX** - Radius of curvature of the **MED**ial crest parallel to the **X**-axis.

a) Reciprocal of the average of downward curvatures parallel to the *x*-axis calculated at five points, X = Xmed - 2 × X-grid spacing, Xmed - 1 × X-grid spacing, Xmed, Xmed + 1 × X-grid spacing, Xmed + 2 × X-grid spacing, at Y = Ymed.

b) A measure of the average radius of curvature of the central part (40 per cent of the maximum length in *x*) of a sagittal section through the medial crest of the trochlear surface at its point of maximum curvature in the coronal plane (Xmed,Ymed).

2. **RSELX** - Radius of curvature of the **SEL**lar region parallel to the **X**-axis.

a) Reciprocal of the average of downward curvatures parallel to the *x*-axis calculated at five points, X = Xsel - 2 × X-grid spacing, Xsel - 1 × X-grid spacing, Xsel, Xsel + 1 × X-grid spacing, Xsel + 2 × X-grid spacing, at Y = Ysel.

b) A measure of the average radius of curvature of the central part (40 per cent of the maximum length in *x*) of a sagittal section through the saddle region of the trochlear surface at its point of maximum curvature in the coronal plane (Xsel,Ysel).

3. **SELDOWN** - **SEL**lar region, **DOWN**ward curvature.

a) Reciprocal of the average of the downward principal curvatures (curvature parallel to the direction of maximum curvature, and thus not necessarily parallel to the *x*-axis) at fifteen grid points, X = Xsel - 2 × X-grid spacing, Xsel - 1 × X-grid spacing, Xsel, Xsel + 1 × X-grid spacing, Xsel + 2 × X-grid spacing, at each of the following positions: Y = Ysel - 1 × Y-grid spacing, Ysel, Ysel + 1 × Y-grid spacing.

b) A measure of the average radius of downward curvature (approximately in the sagittal plane) of the central part of the trochlear saddle (central both in the sagittal and coronal planes).

4. **RLATX** - Radius of curvature of the **LAT**eral crest parallel to the **X**-axis.

a) Reciprocal of the average of downward curvatures parallel to the *x*-axis calculated at five points, X = Xlat - 2 × X-grid spacing, Xlat - 1 × X-grid spacing, Xlat, Xlat + 1 × X-grid spacing, Xlat + 2 × X-grid spacing, at Y = Ylat.

b) A measure of the average radius of curvature of the central part (40 per cent of the maximum length in *x*) of a sagittal section through the lateral crest of the trochlear surface at its point of maximum curvature in the coronal plane (Xlat,Ylat).

5. **RMEDY** - **R**adius of curvature of the **MED**ial crest parallel to the **Y**-axis.

a) Reciprocal of the average of the downward curvatures parallel to the *y*-axis at fifteen points, X = Xmed - 2 × X-grid spacing, Xmed - 1 × X-grid spacing, Xmed, Xmed + 1 × X-grid spacing, Xmed + 2 × X-grid spacing, at each of Y = Ymed - 1 × Y-grid spacing, Ymed, Ymed + 1 × Y-grid spacing.

b) A measure of the average radius of curvature of a coronal section through the medial crest of the trochlear surface.

6. **RSELY** - Radius of curvature of the **SEL**lar region parallel to the **Y**-axis.

a) Reciprocal of the average of the upward curvatures parallel to the *y*-axis at three points, Y = Ysel - 1 × Y-grid spacing, Ysel, Ysel + 1 × Y-grid spacing, at X = Xsel.

b) A measure of the average radius of curvature of the central part (20 per cent of the maximum length in y) of a coronal section through the saddle region of the trochlear surface.

7. **SELUP** - **SEL**lar region, **UP**ward curvature.

a) Reciprocal of the average of the upward principal curvatures at fifteen grid points, X = Xsel - 2 × X-grid spacing, Xsel - 1 × X-grid spacing, Xsel, Xsel + 1 × X-grid spacing, Xsel + 2 × X-grid spacing, at each of Y = Ysel - 1 × Y-grid spacing, Ysel, Ysel + 1 × Y-grid spacing.

b) A measure of the average radius of upward curvature (approximately in the coronal plane) of the central part of the trochlear saddle (central both in the sagittal and coronal planes).

8. **RLATY** - Radius of curvature of the LATeral crest parallel to the Y-axis.

a) Reciprocal of the average of the downward curvatures parallel to the y-axis at fifteen grid points, X = Xlat - 2 × X-grid spacing, Xlat - 1 × X-grid spacing, Xlat, Xlat + 1 × X-grid spacing, Xlat + 2 × X-grid spacing, at each of Y = Ylat - 1 × Y-grid spacing, Ylat, Ylat + 1 × Y-grid spacing.

b) A measure of the average radius of curvature of a coronal section through the lateral crest of the trochlear surface.

The eight primary curvature variables, and the coordinates of the three points of simultaneous maximum curvature, were normalized to take account of simple size differences of the superior articular surfaces of the higher primate tali. The values of the variables were divided by the square root of the product of the x and y-grid spacings, $\sqrt{(dX \times dY)}$.

The values of six of the eight primary curvature variables, *viz*. RMEDX, RSELX, SELDOWN, RLATX, RMEDY AND RLATY, are all negative, since they are the reciprocals of the averages of downward curvature. RSELY and SELUP are reciprocals of upward curvature and their values are positive. For all eight variables, the absolute value, that is the magnitude irrespective of the sign, will indicate the amount of surface curvature; the larger the absolute value, the less the curvature and *vice versa* (radius = reciprocal of surface curvature).

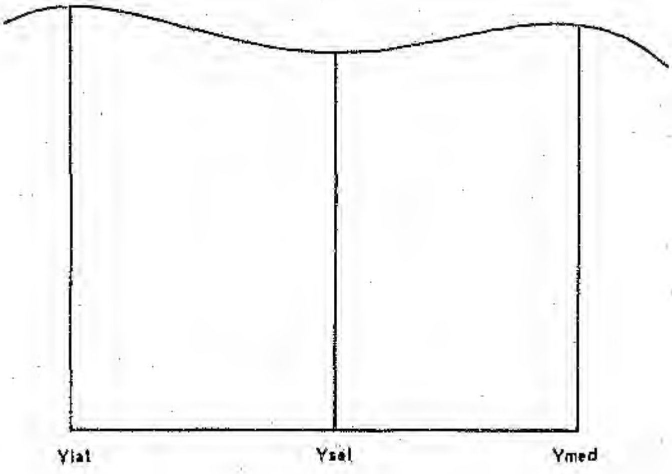
The variables RSELX and SELDOWN are very similar in that they measure the same area of the saddle region of the trochlear surface in approximately the same direction. The same holds for RSELY and SELUP. In both cases, the former variable is calculated from curvatures, parallel to either the x or y-axis, at five points on the surface, whereas the latter variable is calculated from principal curvatures at fifteen surface points. In fact, it was found that the values for RSELX and SELDOWN, and RSELY and SELUP, were virtually equal in each specimen. Therefore, only SELDOWN and SELUP, those variables derived each from fifteen points, were utilized by themselves in the statistical comparisons. However, RSELX and RSELY, each derived from five points, were used in the calculation of indices, in conjunction with the other four variables each calculated from five surface points.

6.2.4.2. Variables Calculated from the Primary Curvature Variables

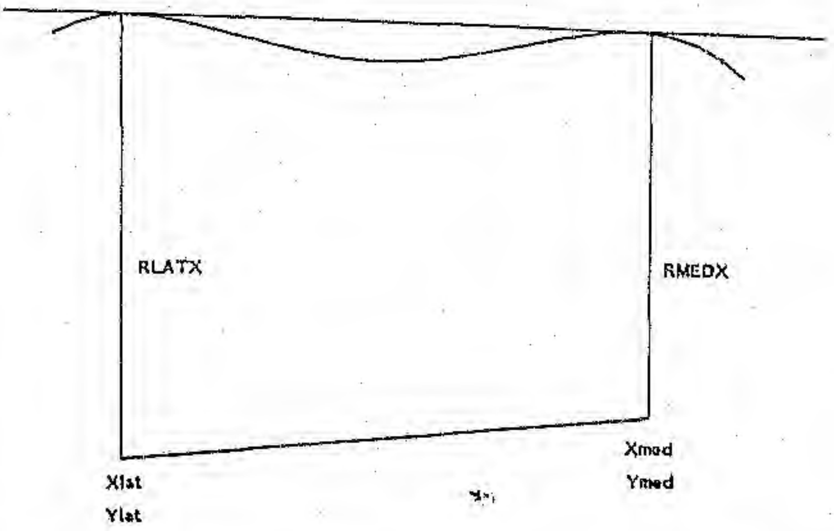
Two further variables considered to describe trochlear surface shape have been calculated from normalized primary curvature variables and the normalized coordinates, (Xmed,Ymed), (Xsel,Ysel), and (Xlat,Ylat). They are illustrated in Figure 24.

1. **POSSEL** - **POS**ition of the point of maximum curvature in the **SEL**lar region.

a). **POSSEL** = Ysel - (Ymed + Ylat) × 0.5



A. $POSSEL = Ysel - (Ymed + Ylat) \times 0.5$



B. $SLOPE = (RLATX - RMEDX) / \sqrt{(Xlat - Xmed)^2 + (Ylat - Ymed)^2}$

Figure 24. Variables calculated from the primary curvature variables.
A. POSSEL
B. SLOPE

b) A measure of the average position, in the coronal plane, of the point of maximum coronal curvature of the saddle region relative to the position of the points of maximum coronal curvature of the medial and lateral crests.

A value of 0 for POSSEL indicates that the point of maximum coronal curvature of the saddle is, on average, midway between the medial and lateral crests. The greater the absolute value of POSSEL, the further the point of maximum curvature is from the midpoint between the crests. A negative value means that it is closer to the medial crest, and a positive value indicates that it is closer to the lateral crest.

2. SLOPE

a) $\mathrm{SLOPE} = (\mathrm{RLATX} - \mathrm{RMEDX}) / \sqrt{(\mathrm{Xlat} - \mathrm{Xmed})^2 + (\mathrm{Ylat} - \mathrm{Ymed})^2}$

b) A relative measure of the orientation, in the coronal plane, of an approximate axis of the central part (in the sagittal plane) of the trochlear surface.

A value of 0 for SLOPE would indicate that the approximate axis is horizontal, in the coronal plane. In other words, it is parallel to a tangent to the medial and lateral crests. In that case, the trochlear surface would have the general shape of a cylinder. The greater the absolute value of this variable, the more the approximate axis diverges from a horizontal position. Thus, the trochlear surface would have the general shape of a cone. A negative value means that the axis points somewhat superiorly, from lateral to medial (the cone tapers from lateral to medial). A positive value indicates a more or less inferior orientation, from lateral to medial (the cone tapers from medial to lateral).

The final nine calculated variables are indices of the normalized primary curvature variables. There are three indices of the primary variables of anteroposterior curvature (X) and three of mediolateral curvature (Y). The last three indices are of the average anteroposterior and mediolateral curvatures of the medial crest, sellar region and lateral crest of the trochlear surface.

3. **RMEDX/RLATX** - Like SLOPE, this variable is a measure of the general conical or cylindrical nature of the trochlea tali. However, unlike SLOPE, this index does not take into account the distance between the lateral and medial crests (the crests may be compared with the two sections of a cone, or cylinder, for which the radii are measured). If the value of RMEDX/RLATX = 1, the surface has a general cylindrical nature. If the value < 1, the surface has a general conical nature, the cone tapering from lateral to medial. If the value > 1, the surface has a general conical nature and the cone tapers from medial to lateral.

4. **RMEDX/RSELX**
5. **RLATX/RSELX**
6. **RMEDY/RLATY**
7. **RMEDY/RSELY**
8. **RLATY/RSELY**
9. **RMEDX/RMEDY**
10. **SELDOWN/SELUP**
11. **RLATX/RLATY**

6.3. METHODS OF STATISTICAL ANALYSIS

The samples of tali of extant higher primates measured in this study are listed in Tables 1, 2 and 3 (pages 69 and 72). All comparisons are between samples of tali which had been macerated prior to measurement and thus were without articular cartilage present (dry specimens).

Comparisons of samples have been grouped according to the concept of 'Levels of Articular Shape Variation' proposed in 2.2.1. The first of these is a comparison of samples expected to have Minor Qualitative/Quantitative Differences in the form of the superior articular surface of the talus. These are the samples of the higher primates with different positional behaviours and in different categories of foot use (see 3.1 and Langdon, 1986). They are listed here along with the respective types of positional behaviour and categories of foot use:

1. Baboons (quadrupedal runners and walkers; running).
2. African apes - gorillas and chimpanzees (knuckle-walkers; climbing).
3. Orangutans (large-bodied quadrumanous climber; suspension).
4. Modern humans (obligate biped; human bipedal).

Since gorillas and chimpanzees have been placed in the same categories of positional behaviour and foot use, and since the sample size of each is very small in this study, the two species have been lumped together into the sample, African apes (AF1), for this statistical analysis. However, as tali from male gorillas constitute the largest component of AF1, they have been considered also as a distinct sample (AF2).

Results of comparisons between the primates expected to have Minor Qualitative/Quantitative Differences in talar form are presented in chapter 7. In section 7.1, a variable by variable analysis, the mean, the standard deviation (SD), and the maximum and minimum values of each sample are presented, and the means ±SD of each sample are illustrated graphically in Figures 25-41.[2]

---

[2] The standard deviation assumes that the samples are normally distributed about the mean, which may not necessarily be true when sample sizes are small.

For each variable, differences between the means of the samples were assessed by the Wilcoxon test for statistical significance. A non-parametric method was used because the sample sizes were too small to justify the assumption of normal distribution. The following is a list of the pair-wise comparisons:

1. Baboons (adult M + F) vs Modern Humans (young adults M + F)
   - Samples: P1+P2 vs H1+H2

2.a. Baboons (adult M + F) vs African Apes
   - Samples: P1+P2 vs AF1

b. Baboons (adult M + F) vs Male Gorillas
   - Samples: P1+P2 vs AF2

3. Baboons (adult M + F) vs Orangutans
   - Samples: P1+P2 vs AS1

4. Orangutans vs Modern Humans (young adults M + F)
   - Samples: AS1 vs H1+H2

5.a. Orangutans vs African Apes
   - Samples: AS1 vs AF1

b. Orangutans vs Male Gorillas
   - Samples: AS1 vs AF2

6.a. African Apes vs Modern Humans (young adults M + F)
   - Samples: AF1 vs H1+H2

b. Male Gorillas vs Humans (younger adult M + F)
   - Samples: AF2 vs H1+H2

c. Male Gorillas vs Humans (younger adult males)
   - Samples: AF2 vs H1

d. Male Gorillas vs Humans (younger adult females)
   - Samples: AF2 vs H2

Section 7.2 is a summary of the variables found to be significantly different between the samples of extant higher primates. Section 7.3 is a discussion of the general patterns of anteroposterior and mediolateral curvature of the trochlear surface in each of the higher primate species.

The second major comparison in the present study is between samples expected to have only Fine Quantitative Differences in talar form. The tali from baboons and modern humans were analysed according to possible within-species variation owing to sexual dimorphism, age, and side (right vs left).[3] The following is a list of pair-wise comparisons of samples by the Wilcoxon test for significant differences between means:

A. Sexual Dimorphism

1.a. Modern Humans - young adult females vs young adult males
- Samples: H2 vs H1

b. Modern Humans - juvenile females vs juvenile males
- Samples: H4, M vs F

2. Baboons - adult females vs adult males
- Samples: P2 vs P1

B. Ontogenetic (Age Group) Differences

1. Modern Humans - young adults (M + F) vs juveniles (M + F)

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[3] Since no tali from juvenile, or very old, baboons were available for study, the analysis of differences in trochlear form owing to age was restricted to modern human tali.

- Samples: H1+H2 vs H4

2. Modern Humans - younger adult males vs older adult males
    - Samples: H1 vs H3

C. Side Differences

1. Modern Humans - young adults (M + F), Right vs Left
    - Samples: H1+H2, R vs L

2.a. Baboons - adults (M + F), Right vs Left
    - Samples: P1+P2, R vs L

b. Baboons - adult males, Right vs Left
    - Samples: P1, R vs L

c. Baboons - adult females, Right vs Left
    - Samples: P2, R vs L

Results of the analyses of the baboon and modern human tali with respect to sexual dimorphism, age and side are presented in chapter 8.

The final series of analyses consists of the interpolation of the six early hominid tali, discussed in chapter 5, into univariate analyses of the tali of extant hominoids, *viz.* great apes and modern humans (adults and juveniles). The results are presented in chapter 9; section 9.1 is a variable by variable analysis similar to that of 7.1 and section 9.2 is a discussion of general patterns of anteroposterior and mediolateral curvature of the trochlear surfaces of the fossil tali, along the same lines as 7.3.

CHAPTER 7. UNIVARIATE ANALYSIS OF THE SAMPLES OF EXTANT HIGHER PRIMATES (EXPECTED MINOR QUALITATIVE/QUANTITATIVE DIFFERENCES)

7.1. VARIABLE BY VARIABLE ANALYSIS

There are four main samples of higher primates: modern humans, African apes, orangutans, and baboons. The African ape sample is heterogeneous and somewhat unbalanced in that it is composed of six male gorillas, one female gorilla, and three chimpanzees. Therefore, although this sample has been considered as one for the statistical comparisons, it also has been decomposed into male gorillas, chimpanzees and female gorilla to examine in which variables gorilla-chimpanzee differences and male-female gorilla differences might occur.

For each of the main primate samples, and for the three components of the African ape sample, the values of the primary curvature variables. and of POSSEL and SLOPE, are listed as: mean, standard deviation (SD), minimum and maximum values.

For each of the six primary curvature variables and eleven calculated variables, the mean ±SD of the four main primate samples, and the major component of the African apes, *viz.* male gorillas, is illustrated graphically in Figures 25-41. For any of the primary curvature variables, the sign of a value indicates only whether the curvature is downward or upward and is irrelevant to the relative amount of curvature. If the absolute value of a variable is large, then the area of articular surface has a gentle curvature (in other words, it does not bend as sharply) and *vice versa*. However, the sign of the values of SLOPE and POSSEL is important since the values may fall on either side of zero. The significance of the sign in these two variables was discussed in 6.2.4.2.

7.1.1. RMEDX - A measure of the average curvature, in the anteroposterior direction, of the medial crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-5.085	1.470	-12.063	-3.157
AFRICAN APES	10	-6.206	1.927	-9.588	-3.512
ORANGUTANS	5	-6.231	1.905	-9.050	-4.308
BABOONS	40	-4.990	0.609	-6.752	-4.029
MALE GORILLAS	6	-5.011	1.246	-6.614	-3.512
CHIMPANZEES	3	-8.215	1.358	-9.588	-6.873
FEMALE GORILLA	1	-7.348			

Preliminary examination of the above results for RMEDX (also see Figure 25) for the four species of extant higher primates suggests two pairings; modern humans and baboons, with on average a smaller radius of curvature (by analogy, the radius of a circle) of the medial crest (approximately -5.0), and the African apes and orangutans, with a considerably larger radius of curvature of the medial crest (approximately -6.2). However, three complicating factors must be taken into account. First, when the African ap sample is decomposed into male gorillas (6), female gorilla (1), and chimpanzees (3), it is seen that the largest component, the sample of male gorillas, has a mean value of RMEDX almost identical to those of the modern human and baboon tali. Clearly the chimpanzees, male and female, and the female gorilla have values for this variable which are much larger than the means for the humans, baboons and male gorillas. They are even somewhat larger than the mean for orangutans. Secondly, when the small orangutan sample is separated into three males and two females, there appears

```
                                                            RMEDX

                   |                                                                                                   |
MODERN HUMAN       |  |-------------------------- H ---------------------------|                                       |
AFRICAN APE        |                |----------------------------------- A -----------------------------------|        |
MALE GORILLA       |     |---------------------- G -----------------------|                                            |
ORANGUTAN          |                |----------------------------------- O -----------------------------------|        |
BABOONS            |                 |---------- B ----------|                                                         |
                   |                                                                                                   |
                   |___________________________________________________________________________________________________|
                 -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
```

Figure 25. RMEDX - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                                            SELDOWN

                   |                                                                                                   |
MODERN HUMAN       |                                     |------ H ------|                                             |
AFRICAN APE        |                                    |------- A -------|                                            |
MALE GORILLA       |                                |--------- G ---------|                                            |
ORANGUTAN          |                                              |----------- O -----------|                          |
BABOON             |                    |--- B ---|                                                                    |
                   |                                                                                                   |
                   |___________________________________________________________________________________________________|
                 -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
```

Figure 26. SELDOWN - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                                   RMEDX

                    |                                                                                                    |
MODERN HUMAN        |   |--------------------------- H ---------------------------|                                      |
AFRICAN APE         |                 |----------------------------------- A ------------------------------------|       |
MALE GORILLA        |      |---------------------- G -----------------------|                                            |
ORANGUTAN           |                 |----------------------------------- O ------------------------------------|       |
BABOONS             |                  |---------- B ----------|                                                         |
                    |____________________________________________________________________________________________________|
                  -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
```

Figure 25. RMEDX - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                                  SELDOWN

                    |                                                                                                    |
MODERN HUMAN        |                                      |------ H ------|                                             |
AFRICAN APE         |                                     |------- A -------|                                            |
MALE GORILLA        |                                 |--------- G ---------|                                            |
ORANGUTAN           |                                               |----------- O -----------|                          |
BABOON              |                      |--- B ---|                                                                   |
                    |____________________________________________________________________________________________________|
                  -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
```

Figure 26. SELDOWN - Samples of Extant Primates (Mean ±Standard Deviation).

a suggestion of sexual dimorphism in RMEDX for this Asian ape. The males have relatively large absolute values, -7.057, -9.050, -5.963, whereas the values of the females are comparatively low, -4.309, -4.776, and closer to the means of the humans, baboons and male gorillas. The measurement of much larger samples of the species of apes would give a clearer view of possible sexual dimorphism within species and differences between the ape taxa hinted at by the present results. Thirdly, there appears to be considerable variability in the amount of anteroposterior curvature of the medial crest of the trochlear surface in all the groups measured, except for the baboons (and the three chimpanzees). The variability appears to be much larger in RMEDX than in SELDOWN and RLATX, the other two variables which reflect curvature in the anteroposterior direction, for all the samples, but especially modern humans, African apes and male gorillas, and orangutans. This large variation is seen in Figure 25 as large standard deviations and extensive overlap between the samples.

Despite the seemingly large differences between the means of the orangutan-African ape pairing and the modern human-baboon-male gorilla group, none of the pair-wise comparisons by the Wilcoxon test revealed statistically significant differences between samples. This is most likely due to the apparently large within-sample variability.

As measured by the present techniques, the average anteroposterior curvature of the medial crest of the trochlear surface appears not to be a good or reliable discriminator between the tali of higher primates examined in this study.

7.1.2. SELDOWN - A measure of the average curvature, in the anteroposterior direction, of the trochlear groove.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-5.812	0.392	-6.702	-5.179
AFRICAN APES	10	-5.794	0.447	-6.689	-5.152
ORANGUTANS	5	-6.489	0.648	-7.262	-5.797
BABOONS	40	-4.865	0.270	-5.464	-4.292
MALE GORILLAS	6	-5.712	0.550	-6.689	-5.152
CHIMPANZEES	3	-5.923	0.303	-6.112	-5.574
FEMALE GORILLA	1	-5.900			

Of all the samples of higher primate tali studied, baboons have the greatest relative anteroposterior curvature of the trochlear groove (the results for SELDOWN are illustrated in Figure 26). The modern human and African ape tali have much the same relative curvature in this region of the trochlea tali and the average radii of curvature are larger than that of the baboon tali. All subgroups of the African ape sample have very similar mean values of SELDOWN. The orangutan tali have the least relative curvature of the trochlear groove as reflected by the large mean value of SELDOWN. In this feature, there is no apparent difference between the tali of male and female orangutans.

Within samples, there appears to be very little variation in the values of SELDOWN; the variability of each sample appears to be much lower than in the other primary curvature variables. For this reason, the Wilcoxon test revealed that the large differences between the mean of the baboon sample and those of the modern human, African ape and orangutan samples were significantly different. The orangutan sample was found to be significantly different from the other samples despite the apparent overlap with the African apes and humans. The latter two samples were not significantly different from each other in this trochlear feature.

7.1.3. RLATX - A measure of the average curvature, in the anteroposterior direction, of the lateral crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-5.255	0.720	-7.062	-4.151
AFRICAN APES	10	-5.741	0.365	-6.270	-5.058
ORANGUTANS	5	-6.378	0.752	-7.062	-5.163
BABOONS	40	-4.770	0.336	-5.669	-4.005
MALE GORILLA	6	-5.733	0.294	-6.106	-5.385
CHIMPANZEES	3	-5.580	0.452	-5.851	-5.058
FEMALE GORILLA	1	-6.270			

The pattern of values for RLATX (Figure 27), the third variable which reflects relative curvature in the anteroposterior (X) direction, is similar to the pattern seen for SELDOWN. The average baboon talus has the most highly curved lateral crest. The average human talus has less relative curvature of this crest than the baboon talus but is intermediate in value between the latter and the African ape ankle bones. Again the orangutan talus is, on average, the least curved anteroposteriorly with no apparent difference between males and females. Within the African ape sample, there is little difference in this feature between male gorillas and chimpanzees. However, the female gorilla talus has a lateral crest with low relative curvature, in fact lower than all of the male gorilla tali. In this regard, the female gorilla talus is more similar to the average orangutan talus.

The amount of variation appears to be relatively small in the samples of baboons and African apes but is somewhat higher in modern humans and orangutans. Indeed there appears to be considerable overlap in the distribution of values of RLATX between the human and baboon samples on the one hand and the human, African ape and orangutan samples on the other. Despite such overlap, the Wilcoxon test revealed significant differences between certain of

```
                                                  RLATX

MODERN HUMAN      |                    |------------ H ------------|                                                  |
AFRICAN APE       |                                     |----- A -----|                                               |
MALE GORILLA      |                                      |---- G ----|                                                |
ORANGUTAN         |                                         |------------- O -------------|                           |
BABOON            |                 |----- B -----|                                                                   |
                  |---------------------------------------------------------------------------------------------------|
                -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
```

Figure 27. RLATX - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                                  RMEDY

MODERN HUMAN      |                             |--------- H ---------|                                               |
AFRICAN APE       |     |---------------------------------- A ----------------------------------|                     |
MALE GORILLA      |            |-------------------------------------- G -------------------------------------|       |
ORANGUTAN         |        |---------- O ----------|                                                                  |
BABOON            |               |------- B -------|                                                                 |
                  |---------------------------------------------------------------------------------------------------|
                -2.0         -2.5        -3.0         -3.5        -4.0         -4.5        -5.0         -5.5        -6.0
```

Figure 28. RMEDY - Samples of Extant Primates (Mean ±Standard Deviation).

the higher primate groups. In this curvature variable, the differences between the baboon sample and the other primate samples were statistically significant. The modern human sample was significantly different also from the orangutan and African ape samples. However, closer examination of the human-African ape comparison reveals that the significant difference between the samples is due, in the main, to a dissimilarity between the human and chimpanzee tali in this trochlear feature. In fact, the male gorilla tali are not significantly different from the male human tali alone and were found to be significantly different from the female human tali only at the 10% level of significance (p=0.0552). The orangutan tali were not significantly different from those of male gorillas and differed from the whole African ape sample only at the 10% level.

7.1.4. RMEDY - A measure of the average curvature, in the mediolateral direction, of the medial crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-3.649	0.459	-5.000	-2.842
AFRICAN APES	10	-3.670	1.456	-6.443	-2.074
ORANGUTANS	5	-2.854	0.516	-3.417	-2.366
BABOONS	40	-3.002	0.387	-4.235	-2.517
MALE GORILLAS	6	-4.115	1.601	-6.443	-2.682
CHIMPANZEES	3	-2.508	0.425	-2.923	-2.074
FEMALE GORILLA	1	-4.484			

Examination of the graphic representation of the results for RMEDY (Figure 28) suggests that there are two pairings: baboons and orangutans, with a relatively small radius of mediolateral curvature of the medial crest, and modern humans and African apes, with on average a larger radius of such curvature. The great amount of variability in this metrical character in the African ape sample is striking, although this appears to be the case only for the male gorilla component. It is further evident that, in this feature, the chimpanzee tali resemble the average orangutan talus more closely than that of the gorilla (or indeed modern humans). However, it should be noted that the value of the chimpanzee tali is close to the lower range of the tali of male gorillas.

Statistically significant differences were found between the baboon and modern human samples, and between the orangutan and modern human tali. If a larger sample of chimpanzee tali were to correspond to the pattern of the three tali measured here, a significant difference would presumably be found also between chimpanzees and modern humans. The problem of the large variability of the gorilla sample requires further examination.

7.1.5. SELUP - A measure of the average curvature, in the mediolateral direction, of the trochlear groove.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	11.743	3.836	6.671	27.778
AFRICAN APES	10	12.376	7.997	6.345	29.940
ORANGUTANS	5	6.247	2.587	4.163	10.194
BABOONS	40	5.745	0.795	4.706	8.333
MALE GORILLAS	6	13.842	8.722	6.549	29.940
CHIMPANZEES	3	6.492	0.131	6.345	6.596
FEMALE GORILLA	1	21.231			

The graphic representation of the distribution of values of this primary curvature variable (Figure 29) reveals a pattern quite similar to that of RMEDY. The baboon sample is paired with the group of orangutan tali, both with small average radii of curvature. The tali of modern humans and of the African ape sample as a whole appear to have a more gentle mediolateral curvature of the trochlear groove. However, also in this feature, there is a sharp distinction between the chimpanzee component of the African apes

```
                                        SELUP

MODERN HUMAN      |                                       |----------------- H -----------------|                                 |
AFRICAN APE       |                     |-------------------------------------- A --------------------------------------|         |
MALE GORILLA      |                             |-------------------------------------- G --------------------------------------| |
ORANGUTAN         |                 |----------- O -----------|                                                                   |
BABOON            |                       |-- B --|                                                                               |
                  |---------------------------------------------------------------------------------------------------------------|
                 0.0          2 5         5.0         7.5         10.0        12.5        15.0         17.5        20.0
```

Figure 29. SELUP - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                        RLATY

MODERN HUMAN      |                                           |------------- H -------------|                              |
AFRICAN APE       |                          |------------------------------- A -------------------------------|           |
MALE GORILLA      |                               |-------------------------------- G --------------------------------|    |
ORANGUTAN         |     |---------------- O ----------------|                                                              |
BABOON            |               |------- B -------|                                                                      |
                  |--------------------------------------------------------------------------------------------------------|
                 -1.8                    -2.3                     -2.8                    -3.3                     -3.8
```

Figure 30. RLATY - Samples of Extant Primates (Mean ±Standard Deviation).

and the gorilla subgroup (male and female). Again, the chimpanzee talus more closely resembles that of the orangutan (and the baboon). The apparently very large variability of the male gorilla sample is striking but one must note also that the SD's of the orangutan and modern human sample are relatively large.

In this trochlear feature, the baboon talus is significantly different from the modern human and African ape (that is, the gorilla) talus. Whereas the orangutan talus was found to be significantly different from that of modern humans at the 5% level, the difference between it and the African ape (gorilla) talus was only significant at the 10% level. Even though the means of the two samples, orangutans and African apes (gorillas), are quite far apart in value, the great variability about the means of the two samples precludes a finding of statistically significant difference. The comment concerning the probable significant difference between a large sample of chimpanzee tali and modern human tali for RMEDY may be applied also for SELUP.

7.1.6. RLATY - A measure of the average curvature, in the mediolateral direction, of the lateral crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-2.973	0.307	-3.576	-2.254
AFRICAN APES	10	-3.000	0.666	-4.198	-2.294
ORANGUTANS	5	-2.279	0.365	-2.859	-1.862
BABOONS	40	-2.303	0.182	-2.807	-1.915
MALE GORILLAS	6	-3.125	0.680	-4.198	-2.455
CHIMPANZEES	[illegible]	-2.472	0.179	-2.653	-2.294
FEMALE GORILLA	1	-3.833			

The graphic representation of the distribution of values of RLATY (Figure 30) reveals a pattern which resembles closely those of RMEDX and SELUP. Again, the baboon sample is paired with the orangutan sample, both with small average radii of curvature. The tali of modern humans and of the African ape sample as a whole appear to have a more gentle mediolateral curvature of the lateral crest. However, once again in this feature, there is a sharp distinction between the chimpanzee component of the African apes and the gorilla subgroup (male and female). As in the previous two measures of mediolateral curvature, the chimpanzee talus more closely resembles that of the orangutan (and the baboon). The amount of variation of the male gorilla sample, and thus African apes as a whole, does not appear to be as large as in RMEDY and SELUP yet still is greater than in the samples of the other higher primates.

In this trochlear feature, the baboon talus is significantly different from the modern human and African ape (gorilla) talus. The orangutan talus was found to be significantly different from that of modern humans. The difference between the orangutan and African ape (gorilla) talus was only significant at the 10% level, once again likely to be due to the variability of the value of this metrical feature in the two samples. Also in RLATY, there is the suggestion that statistically significant differences would be found between large samples of tali of chimpanzees and modern humans (and probably between chimpanzees and gorillas).

7.1.7. POSSEL - A measure of the position, in the coronal plane, of the trochlear groove relative to the medial and lateral crests of the trochlear surface.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-0.126	0.091	-0.275	0.162
AFRICAN APES	10	0.173	0.319	-0.161	1.004
ORANGUTANS	5	-0.277	0.138	-0.453	-0.140
BABOONS	40	-0.218	0.140	-0.502	0.142
MALE GORILLAS	6	0.244	0.390	-0.039	1.004
CHIMPANZEES	3	0.064	0.199	-0.161	0.221
FEMALE GORILLA	1	0.072			

The graphic representation of the distribution of values of POSSEL (Figure 31) is quite reminiscent of the distributions of RMEDY, SELUP and RLATY. There is a pairing of the baboon and orangutan samples, both with, on average, the trochlear groove positioned in the coronal plane closer to the medial crest than the lateral. The modern human tali also have the trochlear groove slightly closer to the medial crest. By contrast, the tali of the male gorilla subgroup of African apes have an average position of the trochlear groove rather closer to the lateral crest than to the medial. Once again, however, the large variability of this feature in the male gorilla tali must be noted. The trochlear groove in the chimpanzee tali, and in that of the female gorilla, is generally closer to the midway point between the crests in the coronal plane.

Statistically significant differences were found between the baboon and modern human samples, and between the orangutan and modern human tali. The marked difference between the orangutan tali and those of the African apes (mainly the male gorillas) was significant, as was the equivalent difference between the baboon sample and the African apes (male gorillas). Furthermore, the

```
                                                            POSSEL

                  |                                                                                                              |
MODERN HUMAN      |                        |------- H -------|                                                                   |
AFRICAN APE       |                              |------------------------------ A ------------------------------|               |
MALE GORILLA      |                              |------------------------------------- G -------------------------------------| |
ORANGUTAN         |   |------------ O ------------|                                                                              |
BABOON            |         |------------ B ------------|                                                                        |
                  |--------------------------------------------------------------------------------------------------------------|
                      -0.4      -0.3      -0.2      -0.1       0.0       0.1       0.2       0.3       0.4       0.5       0.6
```

Figure 31. POSSEL - Samples of Extant Primates (Mean ±Standard Deviation).

African ape sample (male gorillas) was found to be significantly different from the sample of modern humans.

7.1.8. SLOPE - A measure of the orientation, in the coronal plane, of an approximate axis of the trochlear surface.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
MODERN HUMANS	40	-0.017	0.157	-0.328	0.693
AFRICAN APES	10	0.076	0.244	-0.203	0.481
ORANGUTANS	5	-0.016	0.192	-0.291	0.245
BABOONS	40	0.026	0.091	-0.112	0.276
MALE GORILLAS	6	-0.074	0.123	-0.203	0.103
CHIMPANZEES	3	0.362	0.199	0.132	0.481
FEMALE GORILLA	1	0.118			

The graphic representation of SLOPE (Figure 32) emphasizes the large range of values about the means in each of the higher primate samples. It is evident also that, among the samples, there is considerable overlap in the distribution of values. The exception to this is the small subgroup of chimpanzee tali (not shown separately in Figure 32). As in RMEDX, one of the two primary curvature variables used to calculate SLOPE, the chimpanzee tali are clearly different in this feature from the male gorilla bones, indeed there are no overlapping values; the minimum value for the chimpanzees (0.132) is greater than the maximum value of the male gorillas (0.103). The female gorilla value is midway between the male gorilla maximum and the chimpanzee minimum. Clearly for the variable SLOPE, as for RMEDX, the union of gorilla and chimpanzee tali as a single sample, African apes, is not justified.

The human, orangutan and male gorilla tali have mean values for SLOPE which are negative, indicating an average theoretical axis which slopes superiorly from the lateral to medial side of the talus. No significant difference was found between these three samples. As in RMEDX, there is a suggestion of sexual dimorphism

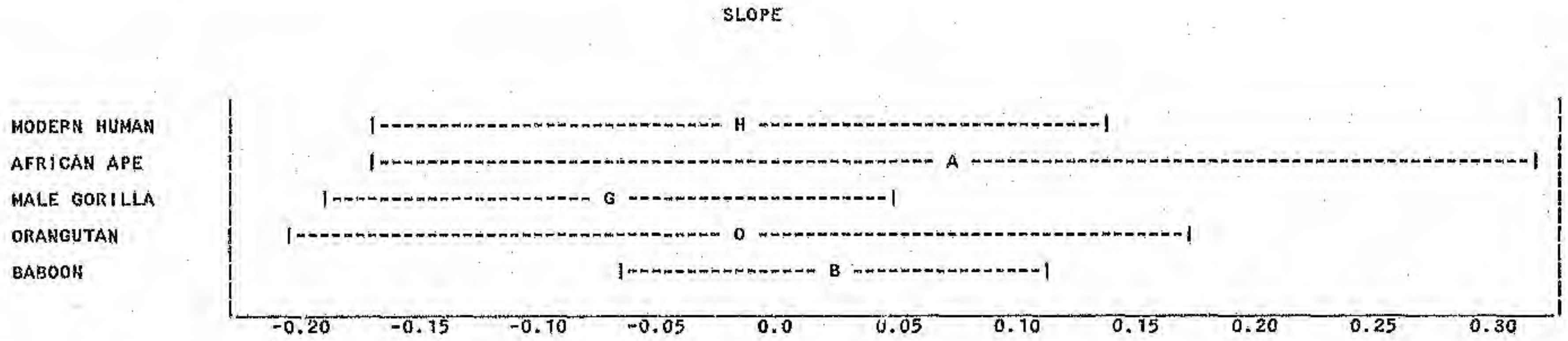

Figure 32. SLOPE - Samples of Extant Primates (Mean ±Standard Deviation).

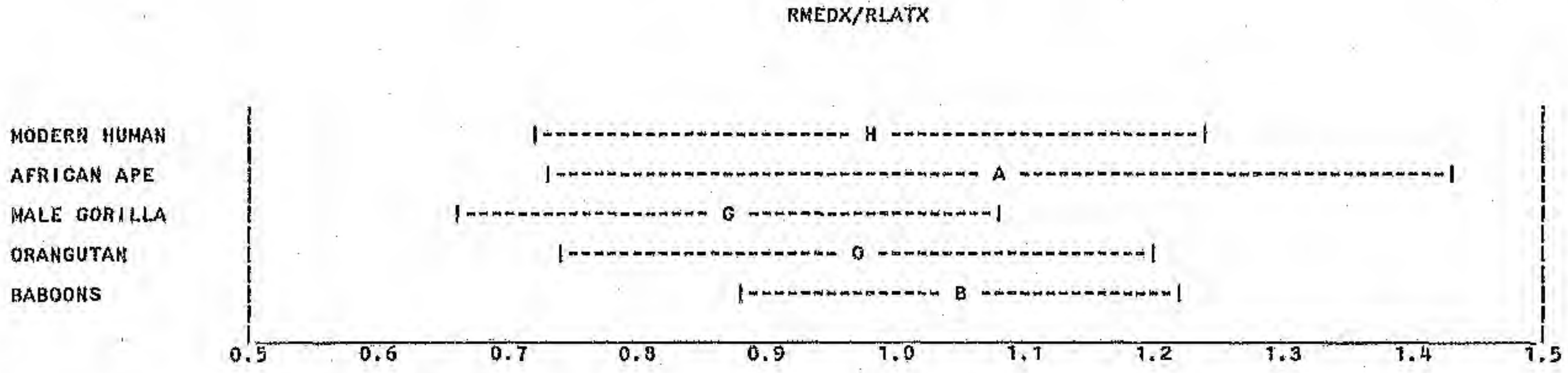

Figure 33. RMEDX/RLATX - Samples of Extant Primates (Mean ±Standard Deviation).

in the orangutan sample. Again the values for the two female tali do not overlap the values of the three male tali and are closer to the mean values of the human and male gorilla bones. The baboon and chimpanzee tali had mean values which were positive, an indication of an average theoretical axis which slopes inferiorly from lateral to medial (the same general orientation occurred in the female gorilla talus). The baboon sample was found to be significantly different at the 5% level from the modern human sample, despite the apparent overlap in the distributions of their values for this variable, and was significantly different from the male gorilla tali at the 10% level (p=0.0564). These findings appear to be contradictory since the mean value of the baboon tali is closer to that of the human sample than to the male gorilla mean. This is likely to be due to the small number of tali in the latter sample (N=6) and illustrates the problem of the use of small and grossly unequal sample sizes.

7.1.9. Indices of Primary Variables of Anteroposterior Curvature (X)

Since RMEDX/RLATX is very similar to SLOPE (the former does not take into account the distance between the medial and lateral crests), it was expected that the results for this index would be very similar to those of SLOPE. A comparison of the graphic representation of the two variables (Figures 32 and 33) reveals indeed that they have virtually identical patterns of distribution and overlap among samples.

The pattern of distribution of values for RMEDX/RSELX (Figure 34) is similar to that of RMEDX and SLOPE. The notable difference is that the mean for the modern human tali is very close to the male gorilla mean rather than to the orangutan mean. The effect of the apparent difference between male and female orangutan tali

```
                                                  RMEDX/RSELX

                  |                                                                                                   |
MODERN HUMAN      |             |---------------------- H ----------------------|                                     |
AFRICAN APE       |                        |----------------------------- A -----------------------------|            |
MALE GORILLA      |                   |-------------- G --------------|                                               |
ORANGUTAN         |                     |----------------------- O -----------------------|                           |
BABOON            |                                       |------------ B ------------|                               |
                  |---------------------------------------------------------------------------------------------------|
                 0.5       0.6       0.7       0.8       0.9       1.0       1.1       1.2       1.3       1.4       1.5
```

Figure 34. RMEDX/RSELX - Samples of Extant Primates (Mean ±Standard Deviation).

```
                                                  RLATX/RSELX

                  |                                                                                                   |
MODERN HUMAN      |                           |----------- H -----------|                                             |
AFRICAN APE       |                                        |------ A ------|                                          |
MALE GORILLA      |                                        |------- G -------|                                        |
ORANGUTAN         |                                        |------ O ------|                                          |
BABOON            |                                        |------ B ------|                                          |
                  |---------------------------------------------------------------------------------------------------|
                 0.5       0.6       0.7       0.8       0.9       1.0       1.1       1.2       1.3       1.4       1.5
```

Figure 35. RLATX/RSELX - Samples of Extant Primates (Mean ±Standard Deviation).

seen in RMEDX is apparent in the values of this index. The female values (0.670 and 0.821) are lower than the three male values (0.975, 1.035 and 1.327).

In RLATX/RSELX, there is a clear grouping of the male gorilla, orangutan and baboon samples, all with means approximately equal to 1 (Figure 35). The modern human sample has the lowest mean value (0.910) whilst the mean of the small chimpanzee sample (0.943) lies in a position intermediate between those of the humans and the male gorillas.

In all three indices, the sample of baboon tali was found to be significantly different from the modern human sample.

7.1.10. Indices of Primary Variables of Mediolateral Curvature (Y)

The distributions of the variables which reflect relative curvature in the mediolateral (Y) direction, *viz.* RMEDY, SELUP (equivalent to RSELY) and RLATY, showed a common general pattern. The orangutan, baboon and chimpanzee samples were grouped together at a distance from the pairing of modern humans and male gorillas. RMEDY/RLATY, an index of the average mediolateral curvatures of the medial and lateral crests of the trochlear surface, tends to lump the samples together (Figure 36). The ratio of medial crest curvature to lateral crest curvature, in the mediolateral direction, is similar in each sample.

The patterns of distribution of values of the other two indices, RMEDY/RSELY and RLATY/RSELY (Figures 37 and 38), appear to retain the form of the distributions of the individual primary curvature variables in the mediolateral direction (Y). The orangutan and baboon samples are again paired with each other in contrast to the pairing of the samples of humans and male gorillas. A notable difference for RMEDY/RSELY is that the chimpanzee tali ($\bar{x}=-0.347$), previously aligned with the orangutan and baboon bones,

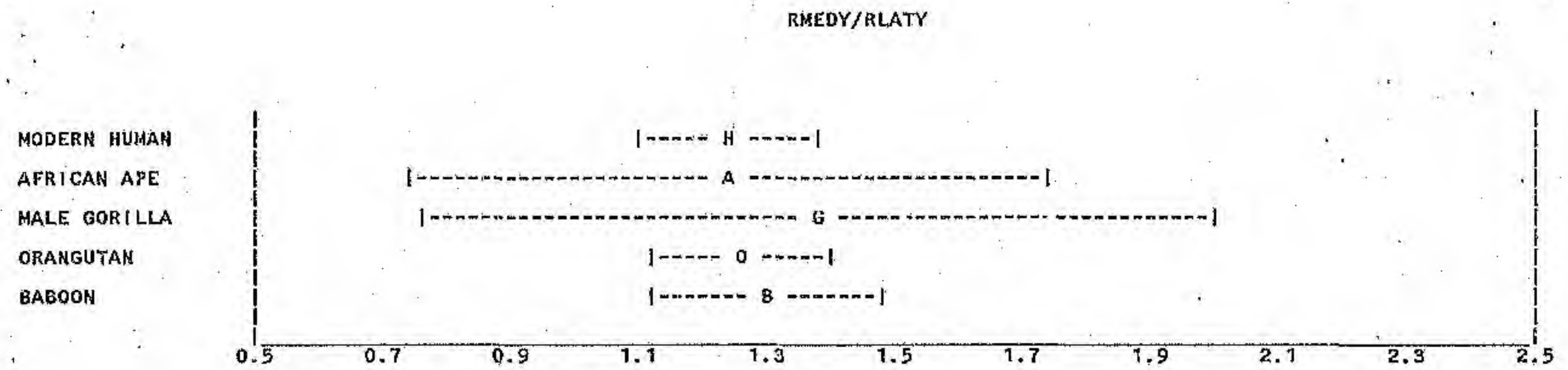

Figure 36. RMEDY/RLATY - Samples of Extant Primates (Mean ±Standard Deviation).

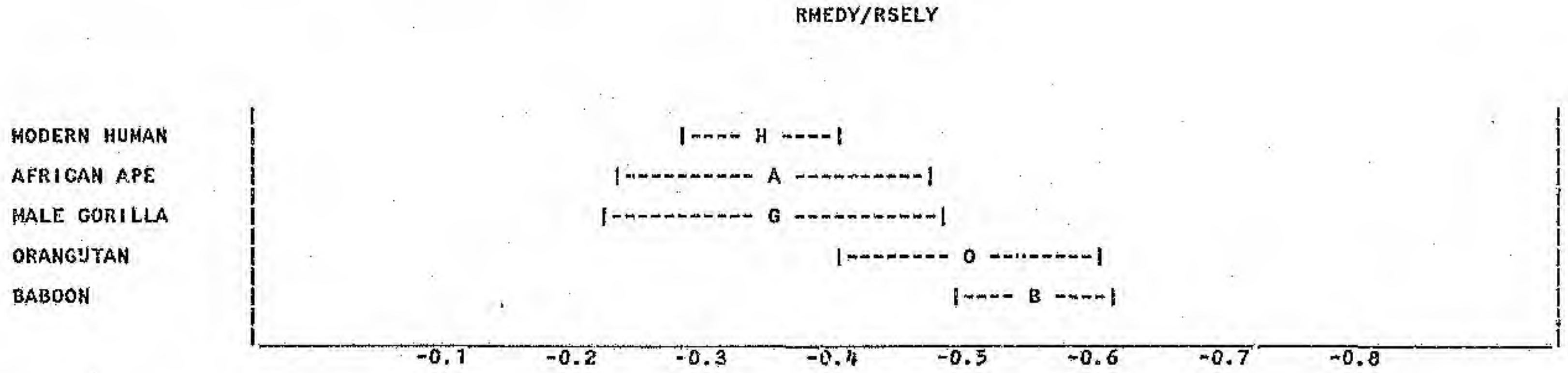

Figure 37. RMEDY/RSELY - Samples of Extant Primates (Mean ±Standard Deviation).

RLATY/RSELY

```
                  |                                                                                                   |
MODERN HUMAN      |                       |--------- H ---------|                                                     |
AFRICAN APE       |                |--------------------- A ---------------------|                                    |
MALE GORILLA      |          |---------------------- G ----------------------|                                        |
ORANGUTAN         |                                         |----------------- O -----------------|                   |
BABOON            |                                                       |------ B ------|                           |
                  |___________________________________________________________________________________________________|
                 0.1                 0.2                 0.3                 0.4                 0.5                 0.6
```

Figure 38. RLATY/RSELY - Samples of Extant Primates (Mean ±Standard Deviation).

RMEDX/RMEDY

```
                  |                                                                                                   |
MODERN HUMAN      |                    |--------- H ---------|                                                        |
AFRICAN APE       |                |------------------------------- A -------------------------------|                |
MALE GORILLA      |             |---------------- G ----------------|                                                 |
ORANGUTAN         |                                     |---------------- O ----------------|                         |
BABOON            |                               |------- B -------|                                                 |
                  |___________________________________________________________________________________________________|
                      0.5         0.9         1.3         1.7         2.1         2.5         2.9         3.3
```

Figure 39. RMEDX/RMEDY - Samples of Extant Primates (Mean ±Standard Deviation).

are very close in value to the male gorilla tali. However, for RLATY/RSELY, the chimpanzee values are closer to the orangutan and baboon means rather than to those of the male gorillas and modern humans.

In both RMEDY/RSELY and RLATY/RSELY, the sample of modern human tali was significantly different from both the baboon and orangutan samples.

7.1.11. Indices of Average Anteroposterior (X) and Mediolateral (Y) Curvatures of the Medial Crest, Sellar Region and Lateral Crest of the Trochlear Surface

The patterns of distribution of values of the indices of average anteroposterior and mediolateral curvatures of the medial crest (RMEDX/RMEDY), sellar region (SELDOWN/SELUP) and lateral crest (RLATX/RLATY) of the trochlear surface are very similar (Figures 39, 40 and 41). There is a pairing of the modern human and male gorilla samples; their means are close in value, although the male gorilla group has a larger SD. The mean of the orangutan sample is clearly separated from the human and male gorilla means but there may be some overlap between the values of the former and latter samples. The mean value of the African ape sample is inflated by the high values of the chimpanzee tali, which are closer to the orangutan and baboon means than to that of the male gorilla tali. The average baboon talus is intermediate in value between the human-gorilla pairing and that of the orangutans and chimpanzees.

In each of the indices, the sample of modern human tali was found to be significantly different from the baboon and orangutan samples.

The orangutan and chimpanzee tali have, on average, the greatest asymmetry of anteroposterior and mediolateral curvatures

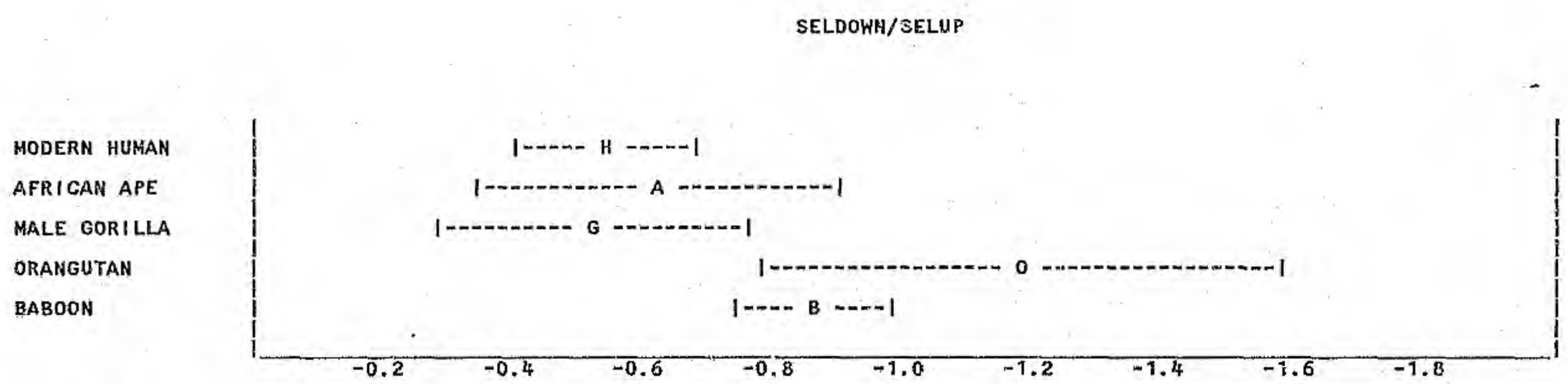

Figure 40. SELDOWN/SELUP - Samples of Extant Primates (Mean ±Standard Deviation).

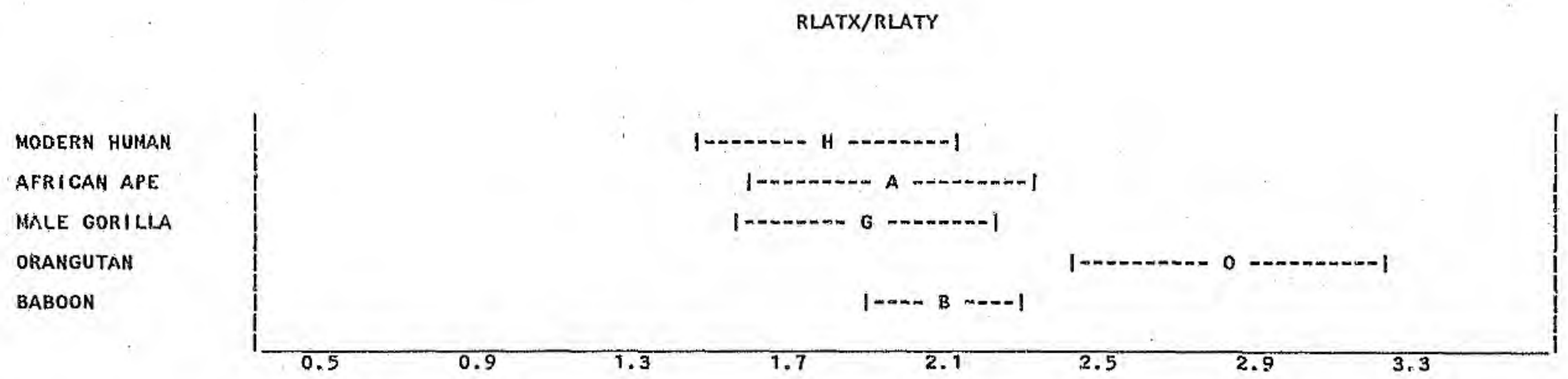

Figure 41. RLATX/RLATY - Samples of Extant Primates (Mean ±Standard Deviation).

of the medial crest. In the sellar region, it is the average human and male gorilla tali which show the greatest asymmetry in anteroposterior and mediolateral curvatures; the means of those two samples are further from 1 than the means of the baboon, chimpanzee and orangutan bones. The absolute value of the orangutan mean is much higher than those of the other samples; it is the only mean with value > 1, which indicates that the anteroposterior curvature is less than the curvature in the mediolateral direction. The orangutan sample, which has a mean value for RLATX/RLATY markedly larger than that of any of the other groups, has the greatest asymmetry of anteroposterior and mediolateral curvatures of the lateral crest.

7.2. SUMMARY OF WILCOXON COMPARISONS OF THE SAMPLES OF EXTANT PRIMATES

The following are pair-wise comparisons of the samples of extant primates measured in the present study. The primary curvature variables and calculated variables which were found to be significantly different between samples are listed. The features found to be different only at the 10% level of significance are in italics.

7.2.1.	Baboons	vs Modern Humans	SELDOWN	p = 0.0000
	N = 40	N = 40	RLATX	p = 0.0022
			RMEDY	p = 0.0000
			SELUP	p = 0.0000
			RLATY	p = 0.0000
			SLOPE	p = 0.0286
			POSSEL	p = 0.0013
			RMEDX/RSELX	p = 0.0000
			RMEDX/RLATX	p = 0.0323

RLATX/RSELX p = 0.0011

RMEDY/RSELY p = 0.0000

RLATY/RSELY p = 0.0000

RMEDX/RMEDY p = 0.0001

RLATX/RLATY p = 0.0000

SELDOWN/SELUP p = 0.0000

RMEDY/RLATY p = 0.0574

Of all the pair-wise comparisons of the samples of extant primates, that of baboons versus modern humans revealed by far the most characteristics which were significantly different. In fact, only RMEDX, an apparently highly variable feature in the samples, was not significantly different. The index RMEDY/RLATY was different only at the 10% level of significance. It should be noted that the two samples were significantly different both in the average amounts of relative curvature in different regions of the trochlear surface (primary curvature variables) and in the indices of relative curvature of the regions (which reflect aspects of overall shape of the surface).

7.2.2.

a. Baboons	vs African Apes	SELDOWN	p = 0.0000
N = 40	N = 10	RLATX	p = 0.0000
		SELUP	p = 0.0000
		RLATY	p = 0.0001
		POSSEL	p = 0.0000
		RMEDY/RSELY	p = 0.0000
		RMEDY/RLATY	p = 0.0359
		RLATY/RSELY	p = 0.0007
		SELDOWN/SELUP	p = 0.0148

b. Baboons	vs Male Gorillas	SELDOWN	p = 0.0003
N = 40	N = 6	RLATX	p = 0.0001

SELUP $p = 0.0003$

RLATX $p = 0.0003$

POSSEL $p = 0.0002$

RMEDX/RSELX $p = 0.0138$

RMEDY/RSELY $p = 0.0002$

RLATY/RSELY $p = 0.0021$

SELDOWN/SELUP $p = 0.0012$

RMEDY $p = 0.0930$

SLOPE $p = 0.0564$

RMEDX/RLATX $p = 0.0564$

After the modern human sample, that of male gorillas was found to differ most in trochlear form (as judged by the number of feature found to be significantly different) from the baboons. This is not surprising in view of the similarity between the tali of modern humans and male gorillas (see 8.2.6). Only the medial crest of the trochlear surface seems to have similar relative curvatures; RMEDX and the index, RMEDX/RMEDY, are not significantly different and RMEDY is only just different at the 10% level of significance.

The baboon sample was found to be significantly different from the African ape sample as a whole in slightly fewer variables and indices than from the male gorilla component. This is due to the chimpanzee tali, and to a lesser degree the single female gorilla bone, which were usually found to be more similar in form to the baboon tali than to those of the male gorillas.

7.2.3. Baboons vs Orangutans

$N = 40$ $N = 5$

SELDOWN $p = 0.0003$

RLATX $p = 0.0007$

RLATX/RLATY $p = 0.0016$

RMEDX/RMEDY $p = 0.0533$

SELDOWN/SELUP $p = 0.0863$

Of all the hominoid tali considered in this study, the average orangutan talus appeared to be most similar to that of the baboon, based on the number of variables found to be significantly different between the two samples. The former was found to be significantly different from the latter in only two of the primary curvature variables. However, since both of these are measures of relative anteroposterior curvature, the two samples must be considered to differ considerably in general curvature in the anteroposterior direction (see also 8.3.7). One of the indices of anteroposterior and mediolateral curvatures, RLATX/RLATY, was different at the 5% level of significance, whilst the other two indices were significantly different only at the 10% level.

7.2.4. Orangutans vs Modern Humans

N = 5 N = 40

SELDOWN p = 0.0346
RLATX p = 0.0103
RMEDY p = 0.0051
SELUP p = 0.0029
RLATY p = 0.0029
POSSEL p = 0.0218
RMEDY/RSELY p = 0.0026
RLATY/RSELY p = 0.0079
RMEDX/RMEDY p = 0.0029
RLATX/RLATY p = 0.0008
SELDOWN/SELUP p = 0.0026

Since the average baboon and orangutan tali were found to be similar in trochlear form, it is not surprising that the orangutan sample was significantly different from the modern human sample in so many features. In fact, the two samples were significantly different in all primary curvature variables, except RMEDX (which is a poor discriminator in general), two ratios of mediolateral curvature, and the three indices of anteroposterior-mediolateral curvature. No significant differences were found in the indices of anteroposterior curvature.

7.2.5.

a. Orangutans	vs African Apes	RLATY	p = 0.0321
N = 5	N = 10	POSSEL	p = 0.0040
		RMEDY/RSELY	p = 0.0321
		RLATX/RLATY	p = 0.0120
		SELDOWN/SELUP	p = 0.0433
		SELDOWN	*p = 0.0982*
		RLATX	*p = 0.0758*
		SELUP	*p = 0.0758*

b. Orangutans	vs Male Gorillas	RLATY	p = 0.0358
N = 5	N = 6	POSSEL	p = 0.0081
		RLATX/RLATY	p = 0.0456
		SELDOWN/SELUP	p = 0.0358
		SELDOWN	*p = 0.0828*
		SELUP	*p = 0.0552*
		RMEDY/RSELY	*p = 0.0552*
		RMEDY/RMEDY	*p = 0.0828*

The orangutan sample was found to be significantly different at the 5% level from the African ape sample in only one of the primary curvature variables and four of the calculated variables. Only one primary and three calculated variables separated the orangutan and male gorilla tali at the same level of significance. At the 10% level, a further three variables were significantly different in the orangutan-African ape comparison, and a further four variables were significantly different between orangutans and male gorillas. This apparent similarity of the orangutan trochlear surface with those of African apes and especially male gorillas is surprising in view of the previous findings that the orangutans were very similar to baboons, and that baboons were significantly different from the African apes/male gorillas in numerous trochlear features. The male gorilla sample was found to have a large amount of variation in most of the variables considered in this study. Therefore, there was a large overlap in values in most of the variables with the orangutan sample and thus no finding of statistical significance. It is likely that larger samples of the pongid tali would facilitate more reliable statistical tests of differences in the variables used here.

7.2.6.

a. African Apes vs Modern Humans	RLATX	p = 0.0282
N = 10 N = 40	POSSEL	p = 0.0001
	RMEDX/RSELX	p = 0.0404
	RMEDX/RMEDY	p = 0.0381
	RLATX/RSELX	*p = 0.0509*
	RMEDY/RLATY	*p = 0.0919*

b. Male Gorillas vs Modern Humans	POSSEL	p = 0.0005
N = 6 N = 40	*RLATX*	*p = 0.0995*
	RLATX/RSELX	*p = 0.0868*

c. Male Gorillas vs Male Humans	POSSEL	p = 0.0026
N = 6 N = 20		

d. Male Gorillas vs Female Humans	POSSEL	p = 0.0005
N = 6 N = 20	RLATX/RSELX	p = 0.0479
	RLATX	*p = 0.0552*

As judged by the number of significantly different trochlear features, the modern human tali appear to be most similar to the male gorilla tali. Only POSSEL was found to be different at the 5% level of significance. RLATX and RLATX/RSELX were only just different at the 10% level. The latter ratio is though significantly different at the 5% level in a comparison of the male gorillas and modern human females.

The African ape sample as a whole had more features significantly different from modern humans. This is due to the lumping of the chimpanzee tali, and that of the female gorilla, with the larger male gorilla sample. It seems likely that a much larger sample of chimpanzee bones would be significantly different from those of male gorilla and humans, if the larger chimpanzee sample followed the pattern of the three tali measured in this study.

7.2.7. Summary

Of the talar samples considered in this section, those of the male humans and male gorillas are most similar to each other. The female human bones are slightly less similar to those of the male gorillas.

The greatest dissimilarity between samples was between the modern human tali (both males and females combined) and those of the baboons. The male gorilla tali were slightly less dissimilar to the baboon bones than were those of modern humans.

Of the extant hominoid samples measured in this study, that of the orangutan tali was found to be closest to the baboon sample. The three chimpanzee tali were not included, as a discrete sample, in the Wilcoxon analysis. However, it seems that they generally appear to make the combined sample of African apes more dissimilar to that of modern humans than is the sample of male gorillas alone. Thus, the chimpanzee tali appear to differ significantly from the male gorilla bones (and from those of modern humans) and resemble more closely the tali of orangutans and baboons.

7.3. SAMPLE BY SAMPLE ANALYSIS

7.3.1. Baboons

7.3.1.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females	
RMEDX	-4.990	-5.081	-4.898	
SELDOWN	-4.865	-5.004	-4.726	s.d. $p = 0.0013$
RLATX	-4.770	-4.837	-4.704	

b. Proportions

Adult Males & Females		Males	Females	
RMEDX/RLATX	1.054	1.057	1.050	
RMEDX/RSELX	1.037	1.020	1.053	
RLATX/RSELX	0.991	0.971	1.010	s.d. $p = 0.0903$
SLOPE	0.026	0.029	0.023	

The above results indicate that, in the average baboon talus, there is the following general pattern of anteroposterior curvature of the trochlear surface: the medial crest region is slightly less highly curved than the sellar region which is, in turn, less highly curved than the lateral crest. This pattern is reflected also in the proportions of the surface, *viz.* RMEDX/RSELX and RMEDX/RLATX > 1, whilst RLATX/RSELX < 1. This general pattern is the same, both in the primary curvature variables and the proportions, in the separate samples of male and female baboons. On average, the tali of females have a trochlear surface with slightly greater anteroposterior curvature, but only in SELDOWN is the difference statistically significant. The only proportion which is significantly different (only at the 10% level) between males and females is RLATX/RSELX.

The values of the measures & proportions of anteroposterior curvature of the trochlear surface suggest that, in the average baboon talus, the surface is shaped like a cone with a gradual taper laterally. This suggestion is unexpected since visual inspection of the baboon tali and the estimation of the radii of the medial and lateral crests made prior to measurement of the Cartesian coordinates of the surface gave the opposite impression; the medial crest usually appeared to be more highly curved than the lateral Possible reasons for this apparently contradictory finding are posited in the following chapter, Discussion.

7.3.1.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females	
RMEDY	-3.002	-3.034	-2.970	
SELUP	5.745	5.941	5.549	
RLATY	-2.303	-2.405	-2.201	s.d. $p = 0.0005$

b. Proportions

Adult Males & Females		Males	Females	
RMEDY/RLATY	1.308	1.261	1.355	s.d. $p = 0.0155$
RMEDY/RSELY	-0.547	-0.535	-0.558	s.d. $p = 0.0123$
RLATY/RSELY	-0.420	-0.426	-0.414	

The general pattern of mediolateral curvature of the baboon trochlear surface, which is consistent in samples of both male and female tali, is that the lateral crest is somewhat more highly curved than the medial crest and both crests are approximately two times as highly curved as the sellar region. As in the anteroposterior dimensions, the tali of female baboons are on average more highly curved mediolaterally than the male tali. However, only RLATY is significantly different between males and females. There is an indication of a slight difference in the proportions of the trochlear surface between males and females since both RMEDY/RLATY and RMEDY/RSELY are significantly different.

7.3.2. Modern Humans

7.3.2.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females
RMEDX	-5.085	-4.691	-5.480
SELDOWN	-5.812	-5.778	-5.846
RLATX	-5.255	-5.347	-5.163

b. Proportions

Adult Males & Females		Males	Females	
RMEDX/RLATX	0.977	0.898	1.056	s.d. p = 0.0639
RMEDX/RSELX	0.878	0.816	0.939	
RLATX/RSELX	0.910	0.934	0.887	
SLOPE	-0.017	-0.068	0.033	s.d. p = 0.0337

In the average modern human talus, the general pattern of anteroposterior curvature of the trochlear surface is different from that of the average baboon talus. The medial crest region is slightly more highly curved than the lateral crest area, and both of these are, in turn, more highly curved than the sellar region. This pattern is reflected also in the proportions of the surface, *viz.* each of RMEDX/RSELX, RLATX/RSELX and RMEDX/RLATX < 1, and a negative value for SLOPE. However, whilst this pattern is the same, both in the primary curvature variables and the proportions, in the average male talus, it is slightly different in the female bones. The average female trochlear surface has the medial crest slightly less curved, in the anteroposterior direction, than the lateral crest. This is reflected in a value of RMEDX/RLATX > 1, and a positive value of SLOPE. Thus, the average male trochlear surface is shaped more like a cone which tapers from lateral to medial, whilst the female surface resembles a cone which tapers mediolaterally. Females are significantly different from males in the variables, RMEDX/RLATX (at the 10% level) and SLOPE (at the 5% level). The analogy of a cone does not hold when one considers the relative anteroposterior curvature in the sellar region. A strictly conical shape would have the value of the curvature in the sellar region intermediate between the values of the medial and lateral crest curvatures.

7.3.2.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females
RMEDY	-3.649	-3.713	-3.585
SELUP	11.743	11.246	11.980
RLATY	-2.973	-3.024	-2.923

b. Proportions

Adult Males & Females		Males	Females
RMEDY/RLATY	1.232	1.234	1.230
RMEDY/RSELY	-0.335	-0.339	-0.332
RLATY/RSELY	-0.275	-0.279	-0.271

The general pattern of mediolateral curvature of the average modern human trochlear surface, which is consistent in both male and female tali, is that the lateral crest is somewhat more highly curved than the medial crest and both crests are approximately three to four times as highly curved as the sellar region. There are no significant differences between males and females in the primary variables, or proportions, of mediolateral curvature of the trochlear surface.

7.3.3. Gorillas

7.3.3.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables

	Males	Female
RMEDX	-5.011	-7.348
SELDOWN	-5.712	-5.900
RLATX	-5.733	-6.270

b. Proportions

	Males	Female
RMEDX/RLATX	0.874	1.172
RMEDX/RSELX	0.864	1.240
RLATX/RSELX	1.001	1.058
SLOPE	-0.074	0.118

The trochlear surface of the average male gorilla talus has a medial crest region which is rather more highly curved than both the lateral crest and sellar areas, whereas the latter two have virtually identical curvatures (RLATX/RSELX = 1.001). Thus, the average male trochlear surface is shaped roughly like a cone which tapers from lateral to medial. The trochlear surface of the single talus of a female gorilla is rather different from the pattern just described. In the female trochlear surface, the medial crest is more gently curved, in the anteroposterior direction, than the lateral crest, which is slightly less curved than the sellar region. This is reflected in the indices, RMEDX/RLATX = 1.172, RLATX/RSELX = 1.058, and a positive value of SLOPE. The main difference between the female trochlear surface and that of the average male gorilla talus lies more in the variable, RMEDX, the value of which is very large for the female bone. However, it should be borne in mind that this variable was found to have a very large amount of variation in all the samples, except baboons (see 3.1.1.).

7.3.3.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables

	Males	Female
RMEDY	-4.115	-4.484
SELUP	13.842	21.231
RLATY	-3.125	-3.833

b. Proportions

	Males	Female
RMEDY/RLATY	1.371	1.170
RMEDY/RSELY	-0.347	-0.214
RLATY/RSELY	-0.275	-0.183

The general pattern of mediolateral curvature of the average male gorilla trochlear surface is very similar to that seen in the modern human tali; the lateral crest is somewhat more highly curved than the medial crest and both crests are approximately three to four times as highly curved as the sellar region. Although the values of the proportions of mediolateral curvature of the male gorilla trochlear surface are not much different from those of the average human talus, the respective values of the three normalized primary curvature variables indicate that the surface of the gorilla bone is slightly more gently curved. However, none of the differences was found to be statistically significant (see 3.2.6). The single female gorilla talus is notable for the very flat mediolateral curvature of the saddle region.

7.3.4. Chimpanzees

7.3.4.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables

RMEDX	-8.215
SELDOWN	-5.923
RLATX	-5.580

b. Proportions

RMEDX/RLATX	1.478
RMEDX/RSELX	1.392
RLATX/RSELX	0.943
SLOPE	0.362

The trochlear surface of the average chimpanzee talus has a distinct pattern of anteroposterior curvature; the medial crest curvature is much gentler than that of the sellar region, which is slight., less highly curved than the lateral crest. This indicates a general shape which is markedly conical, tapering from medial to lateral; RMEDX/RLATX = 1.478, and SLOPE has a very large absolute value.

7.3.4.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables

RMEDY	-2.508
SELUP	6.492
RLATY	-2.472

b. Proportions

RMEDY/RLATY	1.023
RMEDY/RSELY	-0.400
RLATY/RSELY	-0.395

The mediolateral curvatures of the medial and lateral crests of the average chimpanzee trochlear surface are roughly equal in value and both are approximately two and a half times more highly curved than the sellar region.

7.3.5. Orangutans

7.3.5.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females
RMEDX	-6.231	-7.357	-4.543
SELDOWN	-6.489	-6.679	-6.205
RLATX	-6.378	-6.652	-5.967

b. Proportions

Adult Males & Females		Males	Females
RMEDX/RLATX	0.972	1.099	0.781
RMEDX/RSELX	0.966	1.112	0.745
RLATX/RSELX	0.995	1.012	0.970
SLOPE	-0.016	0.088	-0.171

In the general pattern of anteroposterior curvature of the trochlear surface, the average orangutan talus (males and females combined) most closely approaches a cylindrical shape. In fact, the average curvature of the medial crest is slight greater than that of the lateral crest, which is again slightly greater than that of the sellar region. The differences between the curvature values are so small, however, that the indices are very close to a value of 1. Furthermore, the absolute value of SLOPE is very small, which indicates a nearly horizontal joint axis (as would be found in a cylinder). However, this picture is rather misleading since, in 8.3.1, it was found that the three male tali differ from the two female tali in RMEDX, and all indices which include that variable, with the possible exception of RMEDX/RMEDY. In fact, the values for RMEDX of the male tali do not overlap with those of the female bones, which suggests that a larger sample of orangutan tali might exhibit clear sexual dimorphism in this trochlear feature. Therefore, the average values of the primary curvature variables and proportions have been given separately above for males and females.

The general pattern of anteroposterior curvatures of the male trochlear surface has the medial crest with less curvature than the sellar region, which is only very slightly less curved than the lateral crest region. Thus the surface has the shape of a cone which tapers gradually from medial to lateral. The male orangutan tali have the relatively gentlest anteroposterior curvatures of any of the primate samples studied here.

The female trochlear surface has the medial crest more highly curved than the lateral, which is slightly more highly curved than the sellar region. Thus this surface resembles more a cone which tapers markedly from lateral to medial. However, as in the male human trochlear surface, the analogy of a cone appears to be imperfect owing to the sellar curvature being relatively greater than that medially or laterally.

7.3.5.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables

Adult Males & Females		Males	Females
RMEDY	-2.854	-3.060	-2.545
SELUP	6.247	7.434	4.467
RLATY	-2.279	-2.445	-2.030

b. Proportions

Adult Males & Females		Males	Females
RMEDY/RLATY	1.254	1.252	1.258
RMEDY/RSELY	-0.501	-0.444	-0.585
RLATY/RSELY	-0.403	-0.361	-0.466

The general pattern of mediolateral curvature of the average orangutan trochlear surface is similar to the pattern seen in baboons. The lateral crest is somewhat more highly curved than the medial crest and both crests are approximately two to three times as highly curved as the sellar region. In general, the trochlear surfaces of the male tali are more gently curved mediolaterally than those of the female bones, especially in the sellar region. The female orangutans have the relatively highest mediolateral curvatures of all the talar samples measured. In this regard, they are similar to the tali of baboons and chimpanzees and differ from those of modern humans and gorillas.

7.3.6. Summary

7.3.6.1. Anteroposterior Curvature of the Trochlear Surface

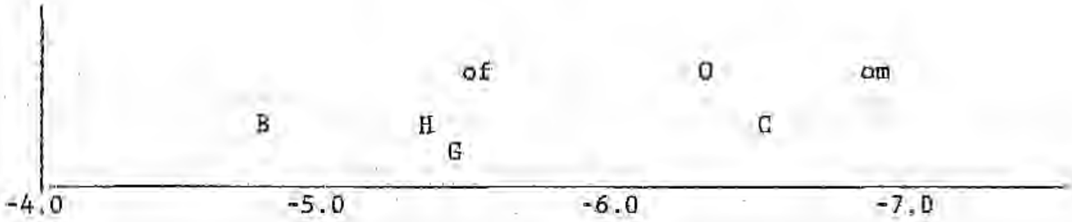

Figure 42. Average of Sample Means of RMEDX, SELDOWN and RLATX. Samples of Extant Primates (B = baboons, H = modern humans, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans).

Figure 42 is a graphic comparison of the samples of extant primates with respect to the amount of general relative anteroposterior curvature of the trochlear surface, as judged by the average of the sample means of RMEDX, SELDOWN and RLATX. The baboon tali are well-separated from the other samples and, on average, have the trochlear surface which is most highly curved in the anteroposterior direction. The chimpanzee and orangutan tali have trochlear surfaces with relatively gentle anteroposterior curvatures. However, it appears that, although this statement is true for the male orangutan bones, it does not hold for the tali of females. Their position is similar to the tali of the modern human and male gorilla samples, with general anteroposterior curvature intermediate between that of the baboons and those of the chimpanzees and male orangutans.

7.3.6.2. Mediolateral Curvature of the Trochlear Surface

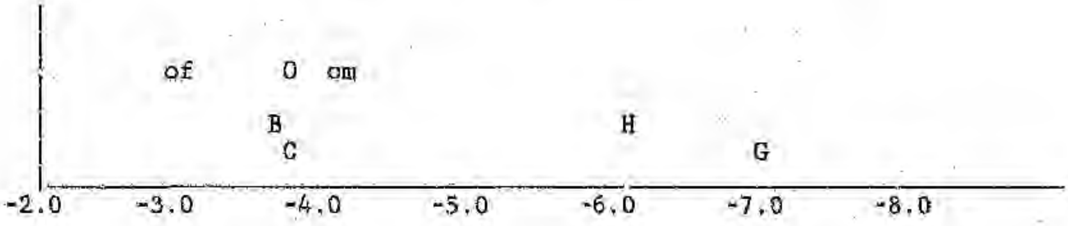

Figure 43. Average of Sample Means of RMEDY, SELUP and RLATY. Samples of Extant Primates (B = baboons, H = modern humans, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans).

Figure 43 is a graphic comparison of the samples of extant primates with respect to the amount of general relative mediolateral curvature of the trochlear surface, as judged by the average of the sample means of RMEDY, SELUP and RLATY. The baboon sample is virtually indistinguishable from the chimpanzee and combined male-female orangutan samples, all with trochlear surfaces relatively highly-curved in the mediolateral direction. In contrast, the average tali of modern humans and male gorillas have trochlear surfaces with relatively gentle mediolateral curvature.

CHAPTER 8. SEXUAL DIMORPHISM, AGE GROUP AND RIGHT-LEFT COMPARISONS OF THE SUPERIOR ARTICULAR SURFACE OF THE TALUS IN BABOONS AND MODERN HUMANS (EXPECTED FINE QUANTITATIVE DIFFERENCES)

The following are pair-wise comparisons of samples of tali of baboons and modern humans measured in the present study. The comparisons are grouped according to possible fine quantitative differences in trochlear form due to gender, age and side. The primary curvature variables and calculated variables which were found, by the Wilcoxon test, to be significantly different between samples are listed. The features found to be different only at the 10% level of significance are in italics.

8.1. SEXUAL DIMORPHISM

8.1.1. Modern Humans

a. Adult Females	vs	Adult Males	SLOPE	p = 0.0337
			RMEDX/RLATX	*p = 0.0639*
N = 20		N = 20	*POSSEL*	*p = 0.0962*

The only trochlear feature found to be significantly different at the 5% level between the human male and female tali was the calculated variable, SLOPE. The mean of the female tali = 0.033, which indicates that the trochlear surface of the average female talus is shaped somewhat like a cone which tapers from medial to lateral. The mean for SLOPE of the male bones = -0.068, which indicates that the surface is shaped more like a cone which tapers from lateral to medial (see 7.3.2). The index RMEDX/RLATX (which is similar to SLOPE) and POSSEL were significantly different only at the 10% level.

b. Juvenile Females vs Juvenile Males NO SIGNIFICANT DIFFERENCES
N = 6 N = 5

No significant differences were found between the small samples of tali from juvenile males and females, aged 12 to 15 years.

8.1.2. Baboons

Adult Females	vs	Adult Males	SELDOWN	$p = 0.0013$
N = 20		N = 20	RLATY	$p = 0.0005$
			POSSEL	$p = 0.0$[illegible]
			RMEDY/RSELY	$p = 0.0123$
			RMEDY/RLATY	$p = 0.0155$
			RLATX/RSELX	$p = 0.0909$
			RLATX/RLATY	$p = 0.0909$

Unlike the modern human tali which exhibited little sexual dimorphism in trochlear form, the ankle bones from male and female baboons measured in this study exhibited significant differences in numerous variables which reflect trochlear shape. Specifically, the male and female baboon tali differed at the 5% level in two primary curvature variables, SELDOWN and RLATY (in both, the female bones have significantly greater relative curvature; see 7.3.1), and three of the calculated variables. Two indices, RLATX/RSELX and RLATX/RLATY, were different only at the 10% level of significance.

8.2. ONTOGENETIC (AGE GROUP) DIFFERENCES

8.2.1. Modern Humans

a. Young Adults (Male/Female) N = 40
vs Juveniles (Male/Female) N = 11

POSSEL	p = 0.0170
RMEDY/RLATY	p = 0.0404
RLATX/RSELX	*p = 0.0652*

b. Younger Adult Males N = 20 vs
Older Adult Males N = 20

SELUP	p = 0.0385
RMEDX/RSELX	p = 0.0275
RMEDX/RMEDY	p = 0.0275
RMEDX	*p = 0.0565*
RLATY	*p = 0.0764*
SELDOWN/SELUP	*p = 0.0679*

The small sample of tali from juvenile humans, boys and girls between 12 and 15 years of age, differed at the 5% level of significance from the sample of tali from adult humans, males and females 25 to 39 years old, in only two of the calculated variables, POSSEL and RMEDY/RLATY. For POSSEL, the young adult tali had a mean = -0.126, whilst the mean of the juvenile tali = -0.221. Thus, in the average juvenile talus, the trochlear groove is situated, in the coronal plane, closer to the medial crest than it is in the average young adult talus. A further calculated variable was significantly different at the 10% level.

A second comparison of samples of humans in different age groups was made between young adult males, 25 to 39 years of age, and older adult males, 42 to 70 years old. These two samples differed at the 5% level in one primary curvature variable, SELUP, and two indices, RMEDX/RSELX and RMEDX/RMEDY. The sellar region of the trochlear surface of the average younger adult talus is less highly curved in the mediolateral direction than the homologous region of the average older adult talus (for SELUP, the mean of the younger adult sample = 11.506, and for the older adult sample = 9.988). The samples differed at the 10% level in a further three trochlear characters. It is interesting that the two variables significantly different (at the 5% level) between the juvenile and young adult tali were not the same as any of the three variables which differed, at the same level of significance, between the young adult males and the older group.

8.3. SIDE DIFFERENCES

8.3.1. Modern Humans

Younger Adults (Male/Female)

Right vs Left RMEDX/RSELX $p = 0.0360$
N = 20 N = 20

Only one variable, the index RMEDX/RSELX, was found to differ significantly between right and left tali of the modern human sample.

8.3.2. Baboons

a. Adults (Male/Female)

Right vs Left SELDOWN $p = 0.0098$
N = 20 N = 20 *RMEDY* $p = 0.0962$

b. Adult Males

Right vs Left RMEDX $p = 0.0451$
N = 10 N = 10

c. Adult Females

Right	vs	Left	SELDOWN	p = 0.0013
N = 10		N = 10	RMEDY	p = 0.0452
			RMEDX/RSELX	*p = 0.0890*

Like the modern human sample, the baboon tali do not appear to differ much according to the side of the body from which they came. Right and left tali from the baboon sample of males and females were found to differ significantly at the 5% level only in one primary curvature variable, and in another at the 10% level. However, in view of the sexual dimorphism in trochlear form seen in the baboon tali, right-left comparisons were made separately for tali of males and females. The right and left tali from males were significantly different only in RMEDX (the mean of the right tali = -5.296 and the mean of the left tali = -4.867). Thus, the medial crest of the average right talus appears to be significantly less curved than that of the average left talus. The right and left tali from females instead differed in more than one feature: SELDOWN and RMEDY, the two variables which were significantly different in the comparison of the whole baboon sample, were significantly different at the 5% level. For SELDOWN, the mean of the right tali = -4.867 whilst the mean of the left tali = -4.583; the sellar region of the average right talus is significantly less highly curved, in the anteroposterior direction, than in the average left talus. For RMEDY, the mean of the right tali = -2.968 whilst the mean of the left tali = -2.972; thus the medial crest region of the average right talus is slightly, but significantly, more highly curved, in the mediolateral direction, than in the average left talus. RMEDX/RSELX was different at the 10% level of significance.

CHAPTER 9. INTERPOLATION OF EARLY HOMINID FOSSIL TALI INTO THE UNIVARIATE ANALYSES OF MODERN HUMANS AND GREAT APES (PONGIDAE)

9.1. VARIABLE BY VARIABLE ANALYSIS

For comparison with the fossil tali, there are five main samples of higher primates: modern human adults, modern human juveniles, male gorillas, chimpanzees, and orangutans. The African ape sample, which was analysed in 7.1, is heterogeneous and somewhat unbalanced in that it is composed of six male gorillas, one female gorilla, and three chimpanzees. Therefore, although this sample had been considered as one for the statistical comparisons in 7.1, here it has been decomposed into male gorillas, chimpanzees (and female gorilla) since apparently significant differences between male gorillas and chimpanzees were found to occur. For certain of the variables and indices, there was a suggestion of sexual dimorphism in the orangutan sample. Apparently significant differences between males and females of this species are mentioned here for comparison with the fossils. For each of the main primate samples, the values of the primary curvature variables are listed as: mean, standard deviation (SD), minimum and maximum values. Also listed are the appropriate values of each of the six fossil tali. For any of the primary curvature variables, the sign of a value indicates only whether the curvature is downward or upward and is irrelevant to the relative amount of curvature. If the absolute value of a variable is large, then the area of articular surface has a gentle curvature (in other words, it does not bend as sharply) and *vice versa*. However, the sign of the values of

SLOPE and POSSEL is important since the values may fall on either side of zero. The significance of the sign in these two variables was discussed in 6.2.4.2.

For each of the five main primate samples, the mean ±SD is illustrated graphically in Figures 44-60. In each of the figures, the individual fossil values have been interpolated (OH = OH 8, TM = TM 1517, ER = KNM ER-813, AL = AL 288-1as, Stw 88, Stw 102). In comparisons with the samples of extant primates, the values for any variable of the fossil tali are often mentioned with respect to their position on either side of the relevant sample mean and in relation to the point one SD from the mean. Thus a fossil value may lie within, or without, the first upper, or lower, SD from the mean of a particular sample. Alternatively, the value may lie close to the limit of the first upper or lower SD. Except for SLOPE and POSSEL, in which the positive or negative sign of a value has a specific meaning, the first upper SD refers to absolute values larger than the mean, and *vice versa* for the first lower SD.

9.1.1. RMEDX - A measure of the average curvature, in the anteroposterior direction, of the medial crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-5.085	1.470	-12.063	-3.157
HUMAN-JUVENILE	11	-5.015	1.074	-7.734	-3.583
MALE GORILLAS	6	-5.011	1.246	-6.614	-3.512
FEMALE GORILLA	1	-7.348			
CHIMPANZEES	3	-8.215	1.358	-9.588	-6.873
ORANGUTANS	5	-6.231	1.905	-9.050	-4.308
OH 8		-7.008			
TM 1517		-7.843			
KNM ER-813		-5.459			
AL 288-1as		-5.423			
Stw 88		-5.365			
Stw 102		-5.432			

Stw 88, Stw 102, KNM ER-813 and AL 288-1as have virtually the same amount of relative anteroposterior curvature of the medial crest, their values for RMEDX are almost identical (Figure 44). In this feature, these four fossil tali are very similar to the average human (adult and juvenile) and gorilla tali. On the other hand, OH 8 has considerably less relative anteroposterior curvature of the medial crest and is closest in value to the mean of the three male orangutan tali ($\bar{x}$=-7.36, in contrast to the mean of the two female orangutan bones $\bar{x}$=-4.54) and the value for the single female gorilla talus. TM 1517 has the most gently curved medial crest region of the six fossils and falls between the male orangutan mean (and female gorilla value) and that of the three chimpanzee tali. Both the Olduvai and Kromdraai tali fall well without one SD from the modern human mean.

9.1.2. SELDOWN - A measure of the average curvature, in the anteroposterior direction, of the trochlear groove.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-5.812	0.392	-6.702	-5.179
HUMAN-JUVENILE	11	-5.733	0.614	-6.859	-4.963
MALE GORILLAS	6	-5.712	0.550	-6.689	-5.152
FEMALE GORILLA	1	-5.900			
CHIMPANZEES	3	-5.923	0.303	-6.112	-5.574
ORANGUTANS	5	-6.489	0.648	-7.262	-5.797
OH 8		-6.165			
TM 1517		-7.003			
KNM ER-813		-6.177			
AL 288-1as		-5.322			
Stw 88		-5.441			
Stw 102		-6.238			

Stw 88 and AL 288-1as are close to each other in the value of SELDOWN and, of the six fossil tali, have the greatest relative anteroposterior curvature of the trochlear groove (Figure 45). They are separated from the modern human mean by approximately one

```
                                                            RMEDX


                                                    Stw
                                                    102

                                                   Stw
                                                   88
                  |                                                                                                    |
                  |                                 AL                                                                 |
                  |                                                                                                    |
                  |                                  ER             OH      TM                                         |
HUMAN - ADULT     |                 |------------ H ------------|                                                      |
HUMAN - JUVENILE  |                  |--------- J ---------|                                                           |
MALE GORILLA      |                 |---------- G ----------|                                                          |
CHIMPANZEE        |                                               |------------ C ------------|                        |
ORANGUTAN         |                      |----------------- O -----------------|                                       |
                  |____________________________________________________________________________________________________|
                -2.0      -3.0      -4.0      -5.0      -6.0      -7.0      -8.0      -9.0     -10.0     -11.0     -12.0
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Figure 44. RMEDX - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

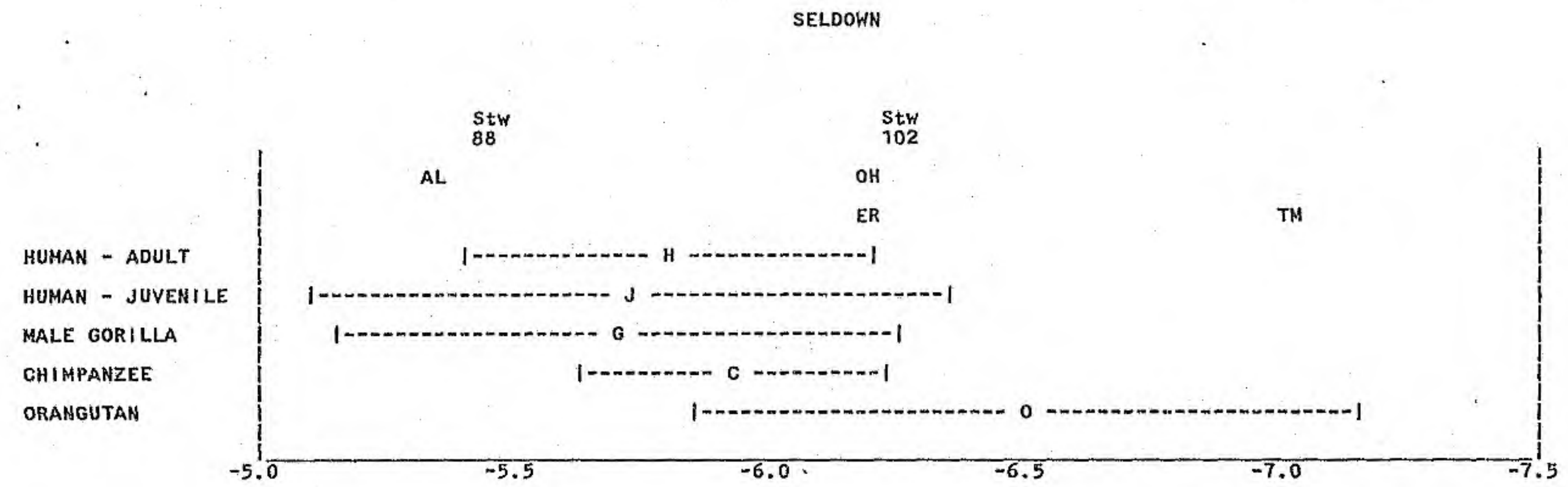

Figure 45. SELDOWN - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

SD but fall within one SD of the juvenile human and male gorilla means. OH 8, KNM ER-813 and Stw 102 have roughly the same relative curvature which is greater than that of the average tali of adult and juvenile humans, male gorillas and chimpanzees. Their values lie close to the upper first SD from the respective means of those extant primate samples. However, those three fossil tali also fall well within the lower first SD of the variable orangutan sample. TM 1517, again the outlying fossil specimen, has much less relative anteroposterior curvature of the sellar region than the other fossil tali and most of the extant hominoid bones. Its value is close to the upper first SD of the orangutan sample.

9.1.3. RLATX - A measure of the average curvature, in the anteroposterior direction, of the lateral crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-5.255	0.720	-7.062	-4.151
HUMAN-JUVENILE	11	-5.551	0.672	-6.378	-4.254
MALE GORILLA	6	-5.733	0.294	-6.106	-5.385
FEMALE GORILLA	1	-6.270			
CHIMPANZEES	3	-5.580	0.452	-5.851	-5.058
ORANGUTANS	5	-6.378	0.752	-7.062	-5.163
OH 8		-5.540			
TM 1517		-6.223			
KNM ER-813		-5.869			
AL 288-1as		-5.139			
Stw 88		-5.453			
Stw 102		-4.403			

The low absolute value for RLATX of Stw 102 suggests that this fossil has a lateral crest which is very highly curved in the anteroposterior direction. In fact, most of the articular surface of the lateral crest of this specimen is missing, due to *post mortem* damage, and the estimate of relative curvature seems not to be reliable. AL 288-1as, Stw 88 and OH 8 cluster around the adult modern human mean, the latter two being very close in value to the means of the juvenile human and chimpanzee samples (Figure 46). KNM ER-813 is within the upper first SD of the samples of humans (adults and juveniles), male gorillas and chimpanzees. As in the previous two measures of relative anteroposterior curvature of the trochlear surface, TM 1517 is again closest to the mean of orangutans, with the least amount of relative curvature of the six fossil tali. The Kromdraai talus also has virtually the same value as the female gorilla bone.

9.1.4. RMEDY - A measure of the average curvature, in the mediolateral direction, of the medial crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-3.649	0.459	-5.000	-2.842
HUMAN-JUVENILE	11	-3.899	0.506	-5.181	-3.278
MALE GORILLAS	6	-4.115	1.601	-6.443	-2.682
FEMALE GORILLA	1	-4.484			
CHIMPANZEES	3	-2.508	0.425	-2.923	-2.074
ORANGUTANS	5	-2.854	0.516	-3.417	-2.366
OH 8		-2.406			
TM 1517		-2.992			
KNM ER-813		-2.977			
AL 288-1as		-2.939			
Stw 88		-3.855			
Stw 102		-2.888			

Of the six fossil tali, Stw 88 has the least amount of mediolateral curvature of the medial crest. In this feature, it is well-separated from the other fossils and lies very close to the means of adult and juvenile humans (Figure 47). Stw 102, AL 288-1as, KNM ER-813 and TM 1517 have virtually the same amount of mediolateral curvature, with values for RMEDY which are very close to the mean of the orangutan tali. The values of these four fossils lie outside of the lower first SD of the modern human sample. Of

```
                                                           RLATX

                                   Stw                 Stw
                  |                102                 88                                                           |
                  |                                      OH            TM                                            |
                  |                              AL             ER                                                   |
HUMAN - ADULT     |                    |------------ H ------------|                                                 |
HUMAN - JUVENILE  |                           |----------- J -----------|                                            |
MALE GORILLA      |                                      '---- G ----|                                               |
CHIMPANZEE        |                                |------- C -------|                                               |
ORANGUTAN         |                                         |------------- O ------------|                           |
                  |__________________________________________________________________________________________________|
                -3.5      -4.0      -4.5      -5.0      -5.5      -6.0      -6.5      -7.0      -7.5      -8.0      -8.5
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Figure 46. RLATX - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

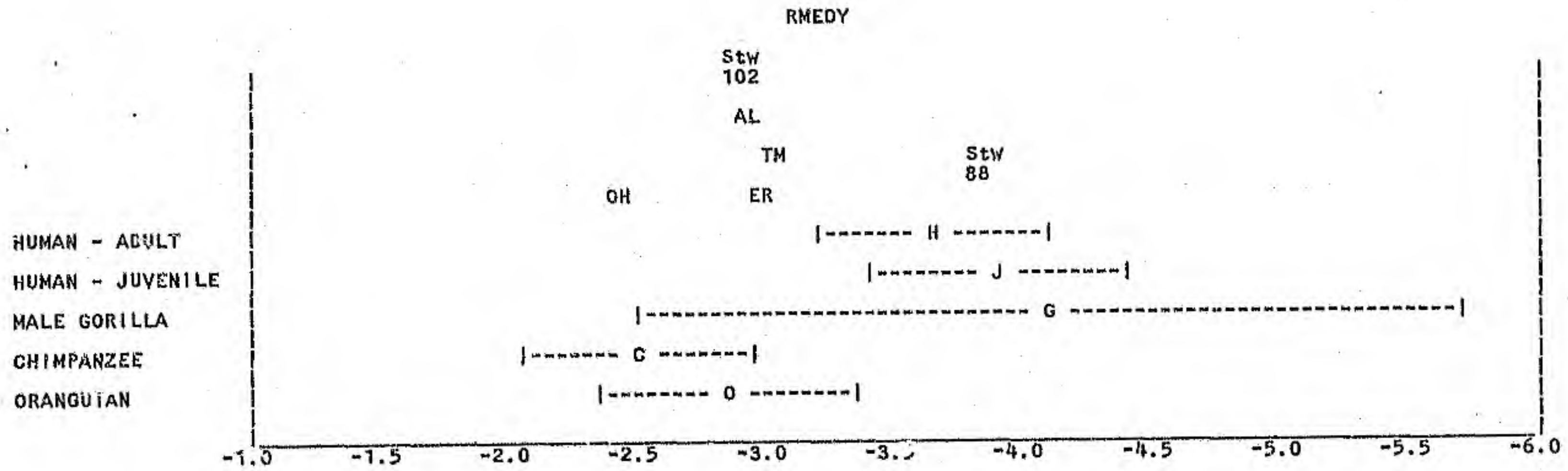

Figure 47. RMEDY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

the fossils, OH 8 has the greatest relative mediolateral curvature of the medial crest and is similar, in this feature, to the average chimpanzee talus. Its value is also just within the lower first SD of the orangutan sample.

9.1.5. SELUP - A measure of the average curvature, in the mediolateral direction, of the trochlear groove.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	11.743	3.836	6.671	27.778
HUMAN-JUVENILE	11	11.363	1.884	7.949	14.245
MALE GORILLAS	6	13.842	8.722	6.549	29.940
FEMALE GORILLA	1	21.231			
CHIMPANZEES	3	6.492	0.131	6.345	6.596
ORANGUTANS	5	6.247	2.587	4.163	10.194
OH 8		4.924			
TM 1517		6.730			
KNM ER-813		5.801			
AL 288-1as		7.657			
Stw 88		10.741			
Stw 102		6.579			

The pattern of distribution of values of the fossil tali for SELUP (Figure 48) is similar to that of the previous variable, RMEDY. Stw 88 has markedly less mediolateral curvature of the sellar region than the other fossil tali and again is closest to the means of the juvenile and adult human tali. The values of the other five fossils fall outside of one SD from the human mean and cluster about the orangutan and chimpanzee means. Again in this feature, OH 8 has higher mediolateral curvature than the other fossil tali; indeed, it has a smaller radius of curvature than the minimum values of all the samples of extant primates measured in this study except that of orangutans.

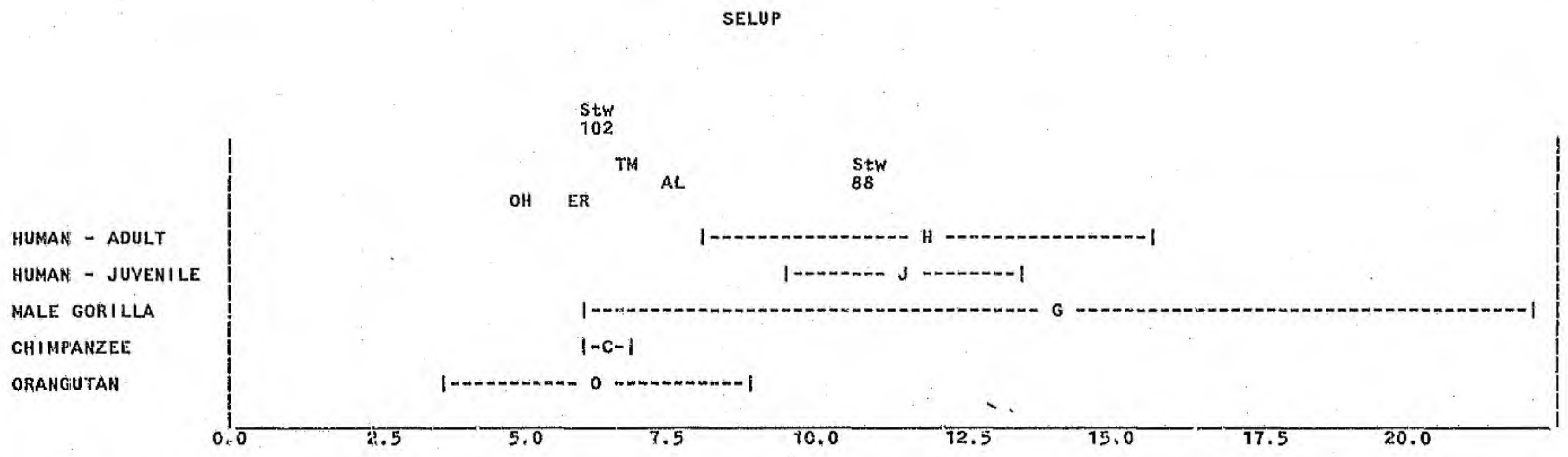

Figure 48. SELUP - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

9.1.6. RLATY - A measure of the average curvature, in the mediolateral direction, of the lateral crest of the trochlear surface of the talus.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-2.973	0.307	-3.574	-2.254
HUMAN-JUVENILE	11	-2.867	0.297	-3.282	-2.307
MALE GORILLAS	6	-3.125	0.680	-4.198	-2.455
FEMALE GORILLA	1	-3.833			
CHIMPANZEES	3	-2.472	0.179	-2.653	-2.294
ORANGUTANS	5	-2.279	0.365	-2.859	-1.862
OH 8		-2.252			
TM 1517		-2.419			
KNM ER-813		-2.086			
AL 288-1as		-2.727			
Stw 88		-2.346			
Stw 102		-2.699			

Of the six fossil tali, AL 288-1as and Stw 102 have the most gentle mediolateral curvature of the lateral crest, although they are not as gently curved as the average adult and juvenile human and male gorilla tali. In fact both values are just within the lower first SD of the adult human sample (Figure 49). The estimation of mediolateral curvature for Stw 102 is, however, not considered accurate since there is considerable damage to the lateral crest region of this fossil. The value for RLATY of TM 1517 is virtually identical to the mean of the chimpanzee tali, although it is also well within one SD from the orangutan mean. OH 8 and Stw 88 have lateral crests which are relatively highly curved in the mediolateral direction and are most similar, in this feature, to the average orangutan talus. KNM ER-813 is the outlying fossil specimen with an apperent, very small radius of mediolateral curvature of the lateral crest. However, since this region has some *post mortem* damage, the value for RLATY may not be completely reliable.

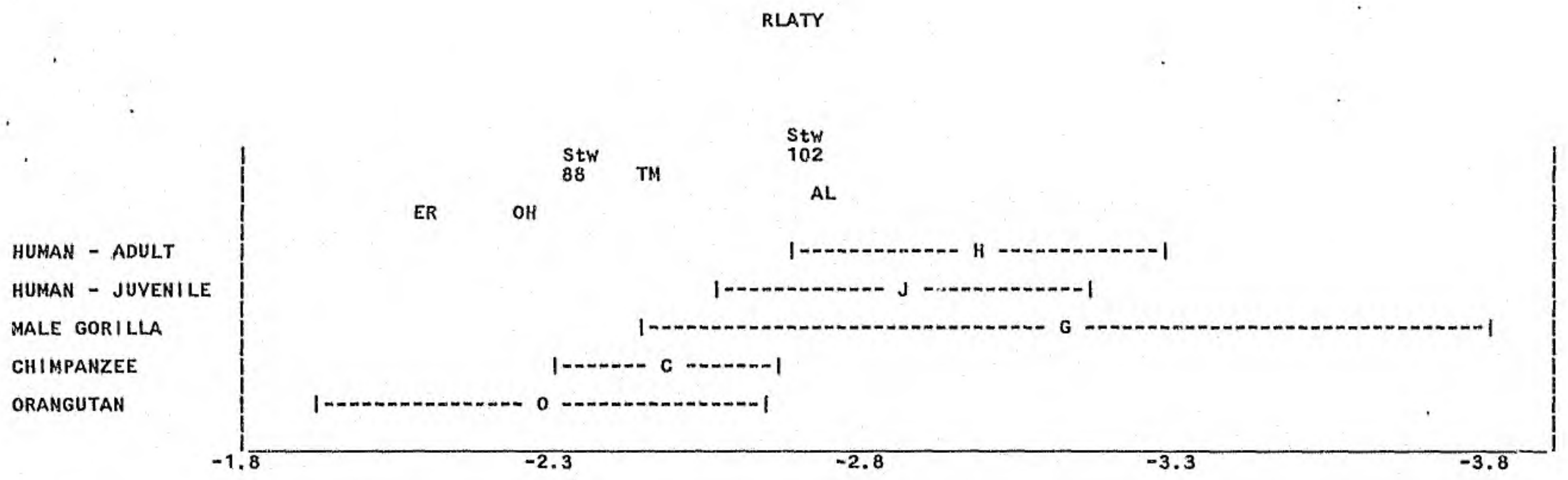

Figure 49. RLATY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

9.1.7. POSSEL - A measure of the position, in the coronal plane, of the trochlear groove relative to the medial and lateral crests of the trochlear surface.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-0.126	0.091	-0.275	0.162
HUMAN-JUVENILE	11	-0.221	0.103	-0.370	-0.087
MALE GORILLAS	6	0.244	0.390	-0.039	1.004
FEMALE GORILLA	1	0.072			
CHIMPANZEES	3	0.064	0.199	-0.161	0.221
ORANGUTANS	5	-0.277	0.138	-0.453	-0.140
OH 8		-0.095			
TM 1517		-0.303			
KNM ER-813		-0.496			
AL 288-1as		-0.028			
Stw 88		-0.341			
Stw 102		-0.115			

Of the six fossil specimens, the Hadar talus has the trochlear groove positioned closest to midway between the medial and lateral crests. Its value for POSSEL is closest to 0 and lies one SD from the modern human mean but well within the lower first SD's of the rather variable chimpanzee and male gorilla samples (Figure 50). OH 8 and Stw 102 are closest to the mean of the adult human sample. However, the usual caution is made concerning the value of Stw 102 since the damage to the lateral crest makes the calculation of the point of maximum mediolateral curvature of the lateral crest unreliable. The Kromdraai talus again most closely resembles the average orangutan talus whereas Stw 88 is in the lower first SD of the orangutan sample with the trochlear groove situated even more toward the medial crest. The latter two fossil specimens are near the value which is one SD from the mean of the juvenile human tali. KNM ER-813 is the outlying fossil specimen, as in the previous variable, apparently with the trochlear groove situated relatively close to the medial crest. As in the case of Stw 102, though, the articular surface missing from the lateral crest may

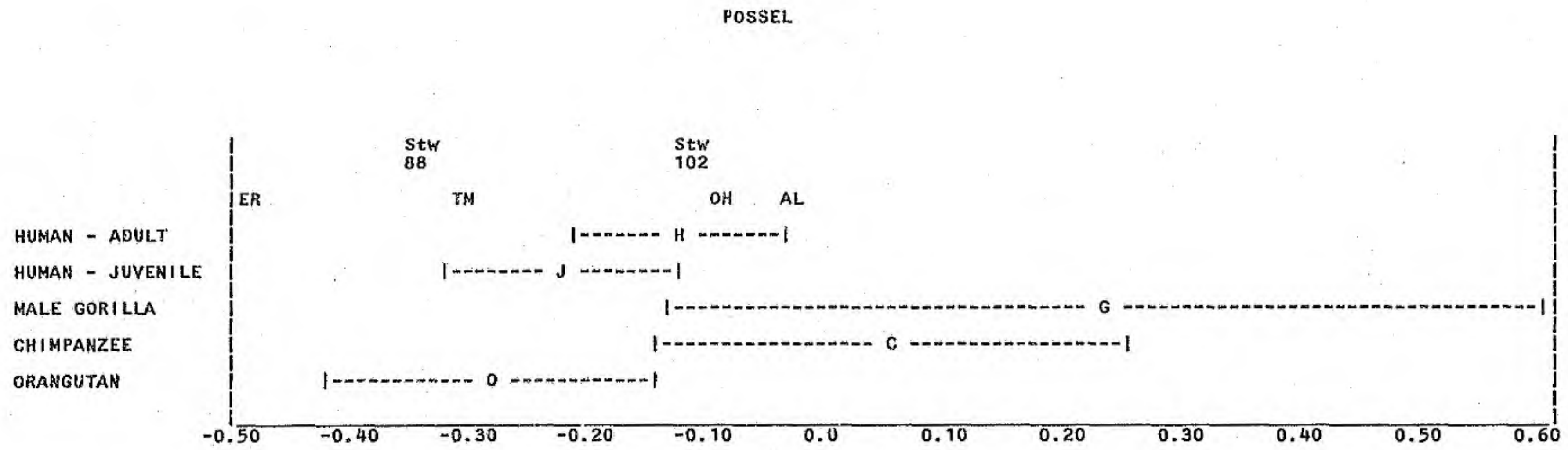

Figure 50. POSSEL - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

have resulted in an inaccurate calculation of the point of maximum mediolateral curvature of that region.

9.1.8. SLOPE - A measure of the orientation, in the coronal plane, of an approximate axis of the trochlear surface.

SAMPLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
HUMAN-ADULT	40	-0.017	0.157	-0.328	0.693
HUMAN-JUVENILE	11	-0.058	0.112	-0.240	0.204
MALE GORILLAS	6	-0.074	0.123	-0.203	0.103
FEMALE GORILLA	1	0.118			
CHIMPANZEES	3	0.362	0.199	0.132	0.481
ORANGUTANS	5	-0.016	0.192	-0.291	0.245
OH 8		0.189			
TM 1517		0.191			
KNM ER-813		-0.047			
AL 288-1as		0.033			
Stw 88		-0.011			
Stw 102		0.116			

The values for SLOPE of KNM ER-813, Stw 88 and AL 288-1as range closely around the means of the samples of adult humans and orangutans (Figure 51). The value of Stw 102 is not considered to be an accurate reflection of this feature since the calculation of SLOPE incorporates RLATX, the estimation of which was thought to be inaccurate due to the missing articular surface of the lateral crest (see 9.1.3). TM 1517 and OH 8, which have virtually identical values for SLOPE, are well-separated from the other fossil specimens and are roughly intermediate between the average orangutan, male gorilla and modern human tali, on the one hand, and the average chimpanzee talus on the other.

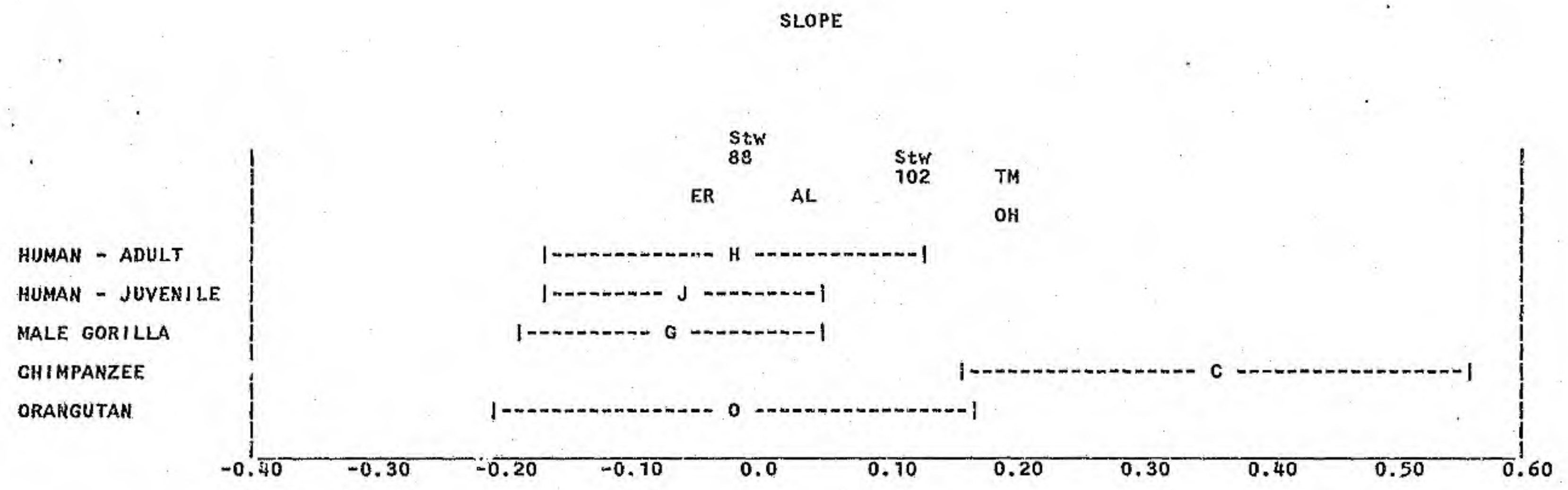

Figure 51. SLOPE - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

9.1.9. Indices of Primary Variables of Anteroposterior Curvature (X)

Since RMEDX/RLATX is very similar to SLOPE (the former does not take into account the distance between the medial and lateral crests), it was expected that the results for this index would be very similar to those of SLOPE. A comparison of the graphic representation of the two variables (Figures 51 and 52) reveals indeed that they have virtually identical patterns of distribution of the extant primate samples and the relative positions of the fossil specimens.

RMEDX/RSELX is the one index of anteroposterior curvatures which does not include RLATX. Thus it is of especial importance in the comparison with extant primate samples of Stw 102 and KNM ER-813, the two fossil specimens which have damage in the lateral crest region. In the values of this index, those two fossil tali are virtually identical to the means of the adult and juvenile human tali and the sample of male gorillas (Figure 53). Stw 88 and AL 288-1as are closest to the mean of the orangutan sample (there is a suggestion of orangutan sexual dimorphism in this feature) but well within one SD from the modern human mean. The values of TM 1517 and OH 8 are close to the mean of the three male orangutan tali ($\overline{X}$=1.112, in contrast to the mean of the two female tali, $\overline{X}$=0.746) and also near the value of the upper first SD of the modern human mean.

The value of Stw 102 for RLATX/RSELX (Figure 54) is not considered to be an accurate reflection of this feature since the calculation of the primary curvature variable, RLATX, was thought to be unreliable due to the missing articular surface of the lateral crest (see 9.1.3). TM 1517 and OH 8 are closest in value to the average adult human talus. KNM ER-813 has virtually the same value as the mean of the chimpanzee tali, whilst AL 288-1as is

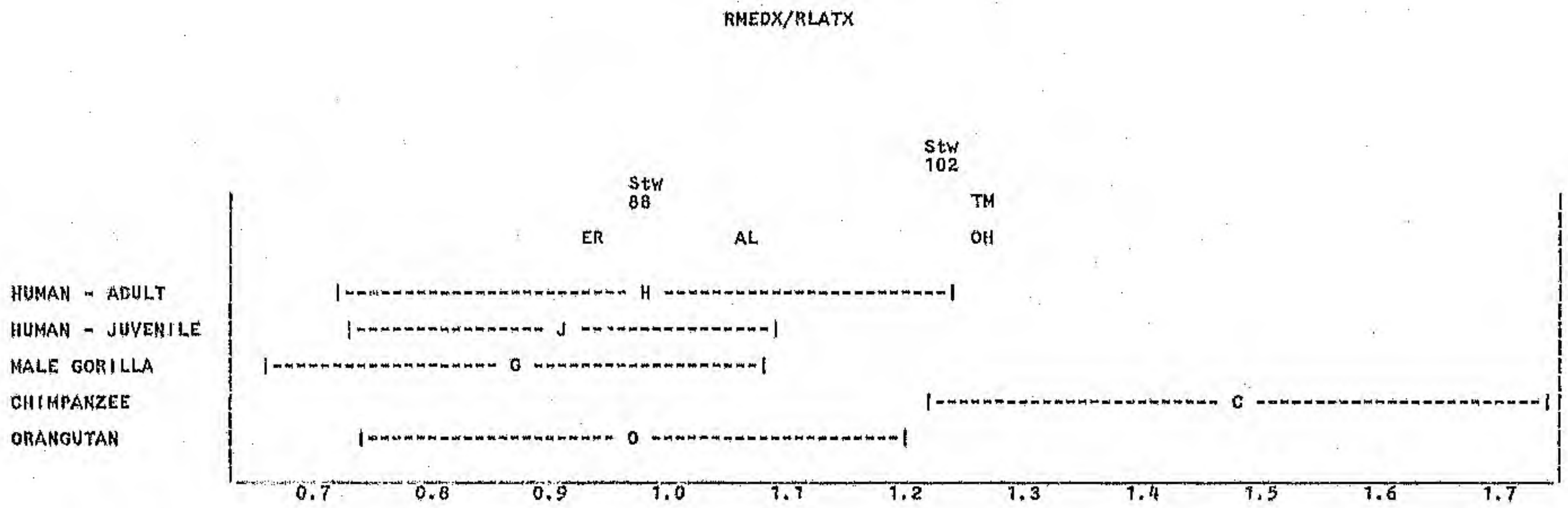

Figure 52. RMEDX/RLATX - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

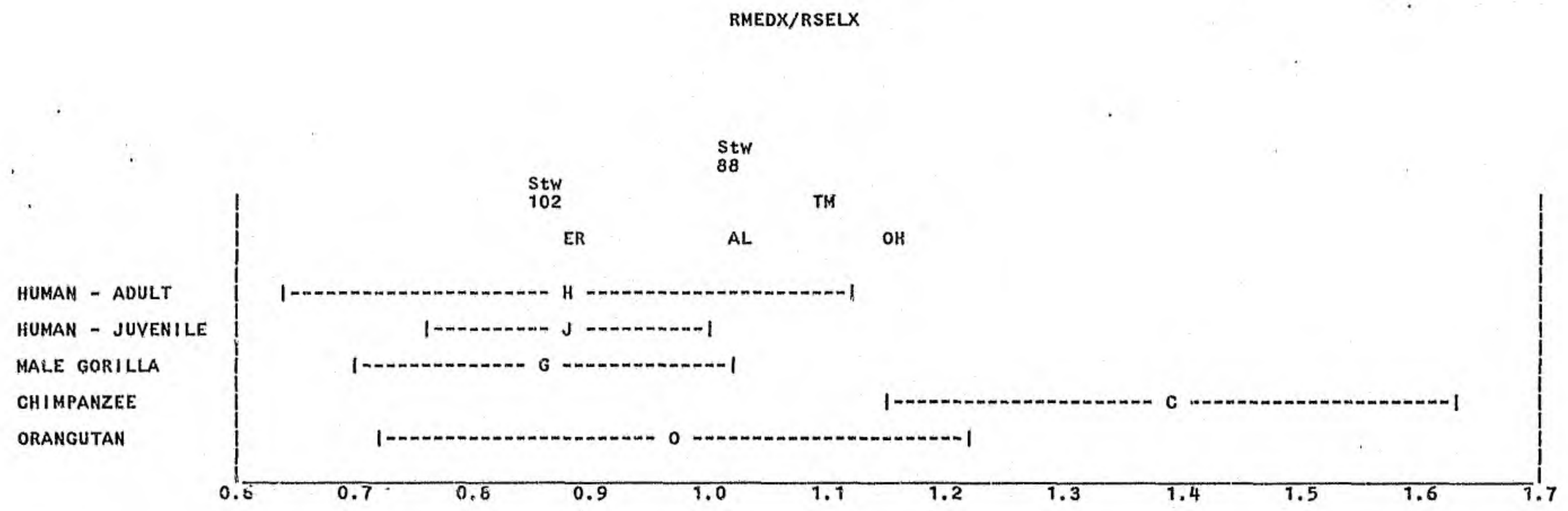

Figure 53. RMEDX/RSELX - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

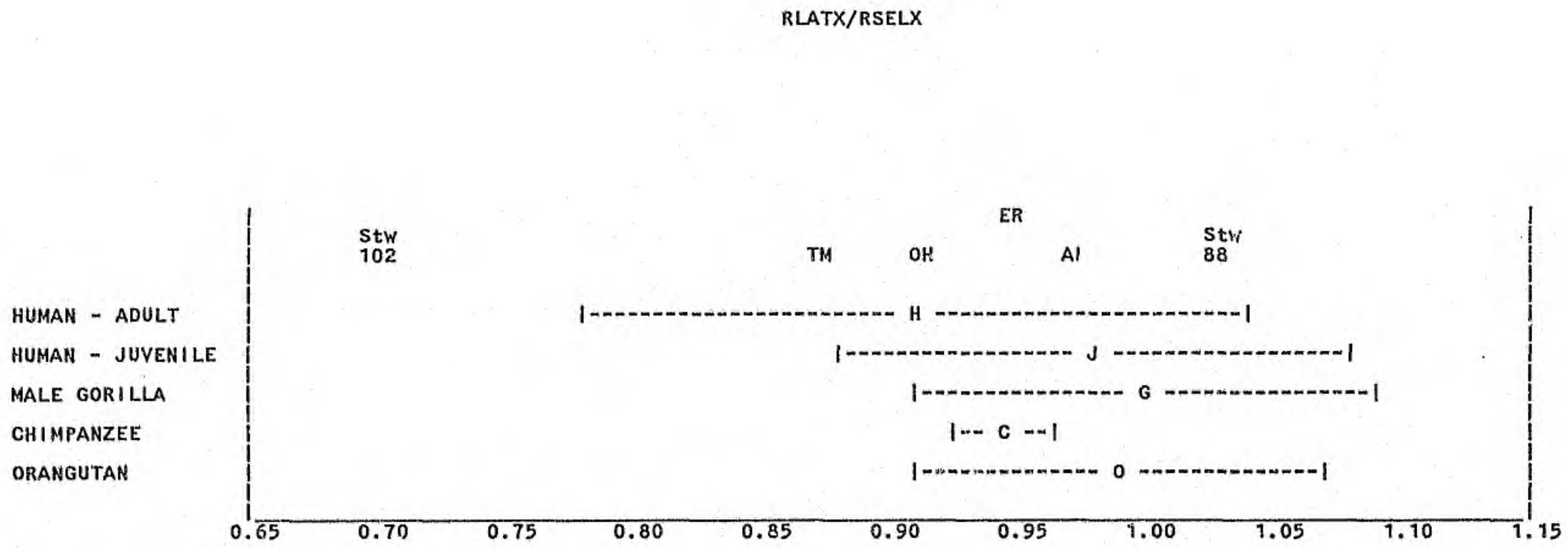

Figure 54. RLATX/RSELX - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

intermediate between the chimpanzee and orangutan means but closest to the mean of the juvenile human sample. However, the latter two fossil tali are also well within one SD from the mean of the rather variable sample of adult human tali. Stw 88 has the highest value for this index among the fossils and is approximately one SD from the adult human mean. It is also comfortably within one SD of the means of the samples of juvenile humans, male gorillas and orangutans.

9.1.10. Indices of Primary Variables of Mediolateral Curvature (Y)

KNM ER-813 was found to have a value of the primary curvature variable, RLATY, which was quite different from the other fossil tali and from the average values of the samples of extant primates. It was suggested that this result may not be reliable due to the damage to parts of the articular surface of the lateral crest. Therefore, the value for the index RMEDY/RLATY of t[illegible]ssil talus may likewise be inaccurate (Figure 55). The same proviso holds in the consideration of Stw 102 for which the damage to the lateral crests is even more extensive than in the East Turkana talus. The Hadar and Olduvai tali are close in value to the average chimpanzee talus, although both are separated from the adult human and orangutan means by one SD. TM 1517 has a value for RMEDY/RLATY which is virtually identical to the means of the adult human and orangutan samples. Stw 88 appears to be unique among the fossil tali in having a large amount of asymmetry in the mediolateral curvatures of the medial and lateral crests, and is unlike the average condition of any of the extant primate samples. Its value is just outside the upper first SD of the juvenile human sample but well within the greatly variable male gorilla sample.

RMEDY/RSELY is the one index of mediolateral curvatures which does not include RLATY. Thus it is of especial importance in the

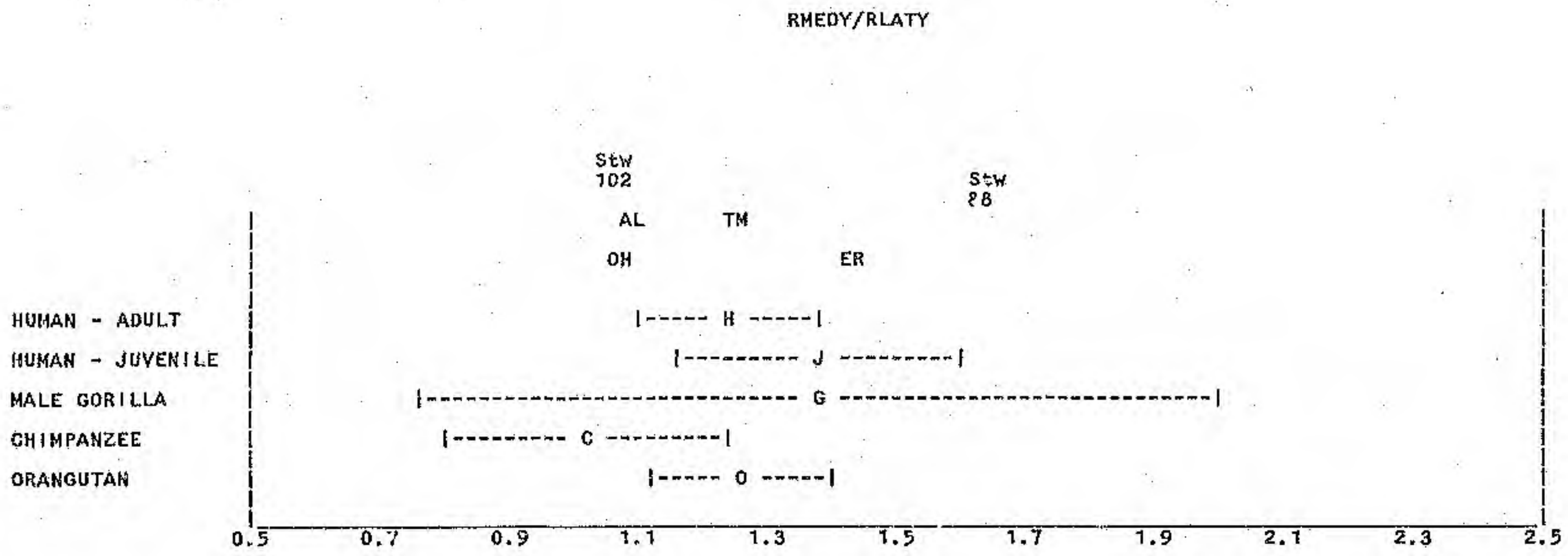

Figure 55. RMEDY/RLATY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

comparison with extant primate samples of Stw 102 and KNM ER-813, the two fossil specimens which have damage in the lateral crest region. In the value of this index, KNM ER-813, along with OH 8, is very close to the combined sample of male and female orangutans (Figure 56). However, there is a suggestion of orangutan sexual dimorphism in this feature; the mean of the three tali from males is -0.444 in contrast to -0.586 for the bones from female orangutans. Stw 102 has almost the same value as TM 1517 and the two are well separated from the means of adult and juvenile humans and male gorillas. These two fossils are closest in value to the female orangutan mean and well within one SD from the mean of the chimpanzee tali. The value of the Hadar specimen is virtually identical to the chimpanzee mean and lies at the upper first SD of the adult and juvenile human samples. In this index, Stw 88 is the closest of the fossil tali to the average human talus and yet is equally close to the chimpanzee and male gorilla means.

In the index, RLATY/RSELY, Stw 88 is again closer to the average human (adult and juvenile) and male gorilla tali than to the average chimpanzee or orangutan bones (Figure 57). Its value is close to the lower first SD of the two human samples. The values of AL 288-1as, TM 1517 and KNM ER-813 are well outside the upper first SD of the adult human sample and are closer to the means of the chimpanzee and orangutan tali. They are well within the lower first SD of the orangutan sample and close to the limit of that of the chimpanzee bones. In this index, Stw 102 appears to be very close to the average tali of chimpanzees and orangutans. However, consideration of that bone and the East Turkana specimen is subject to the same cautionary note as in RMEDX/RLATY due to the respective conditions of their lateral crests. OH 8 is the outlying fossil specimen in this index and is near the limit of the upper first SD of the orangutan sample.

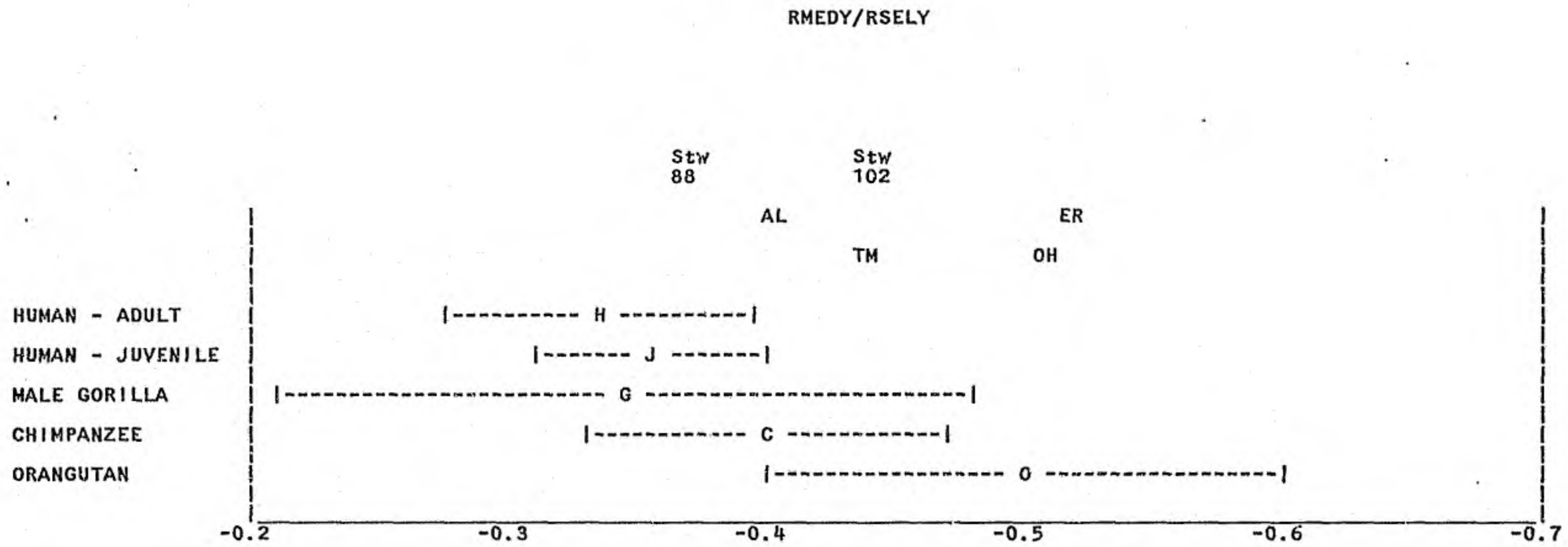

Figure 56. RMEDY/RSELY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

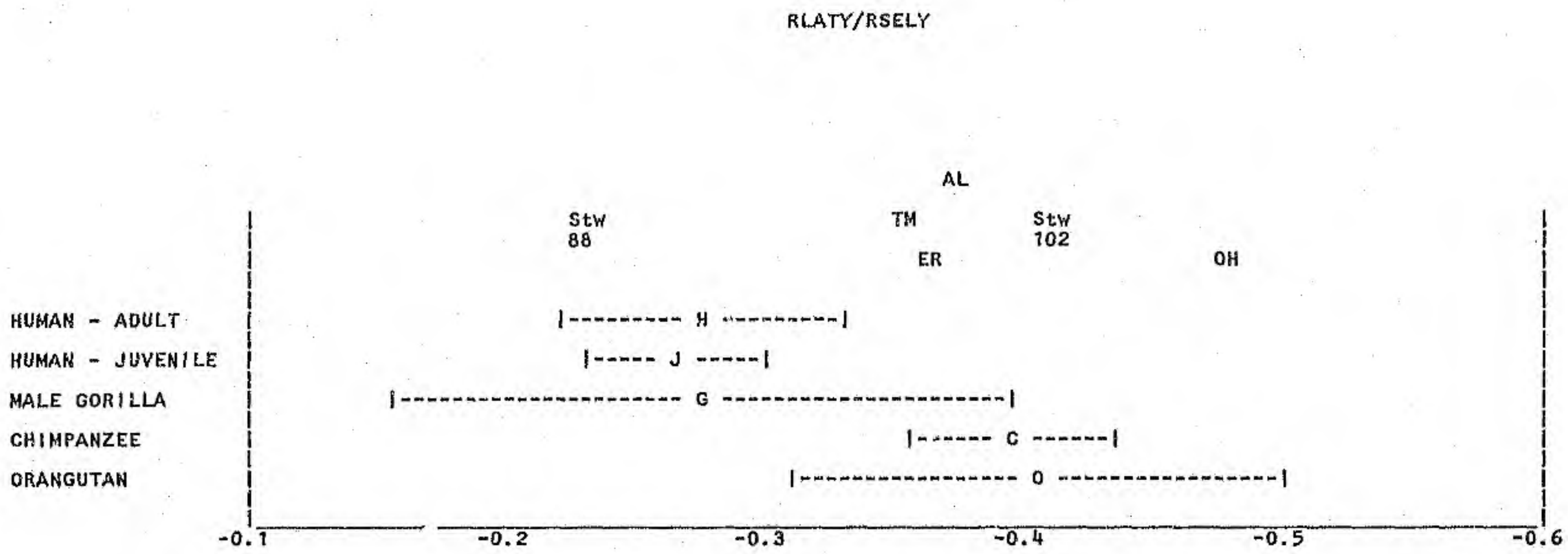

Figure 57. RLATY/RSELY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

9.1.11. Indices of Average Anteroposterior (X) and Mediolateral (Y) Curvatures of the Medial Crest, Sellar Region and Lateral Crest of the Trochlear Surface

In RMEDX/RMEDY, the index of relative anteroposterior and mediolateral curvatures of the medial crest, Stw 88 is virtually indistinguishable from the average tali of modern humans, both adult and juveniles, and male gorillas (Figure 58). Stw 102, AL 288-1as and KNM ER-813 are closest in value to the mean of the two female orangutan tali ($\bar{x}$=1.793, in contrast to the mean of the three male orangutan tali, 2.464) and are just outside of the upper first SD of the adult human sample. The tali from Kromdraai and Olduvai are closer in value to the chimpanzee and male orangutan bones.

In SELDOWN/SELUP, the index of average anteroposterior and mediolateral curvatures of the sellar region, Stw 88 again is closest to the means of the modern human and male gorilla tali (Figure 59). The value of the Hadar specimen is at the limit of the upper first SD of the adult human sample. Stw 102 is close in value to the chimpanzee mean, whilst TM 1517 and KNM ER-813 are intermediate between the chimpanzee and orangutan means. Among the fossil specimens, OH 8 has the highest absolute value for this index and lies close to the mean of the orangutan sample.

Stw 102 and KNM ER-813 lie at the extremes of the range of values of the fossil tali for RLATX/RLATY, the index of average anteroposterior and mediolateral curvatures of the lateral crest (Figure 60). However, the values for these two specimens must be considered to be unreliable due to the damage to their articular surfaces in the region of the lateral crest. AL 288-1as lies closest to the means of the male gorilla, adult human and juvenile human samples. Stw 88 is just inside the upper first SD of the juvenile human sample but closest in value to the chimpanzee mean.

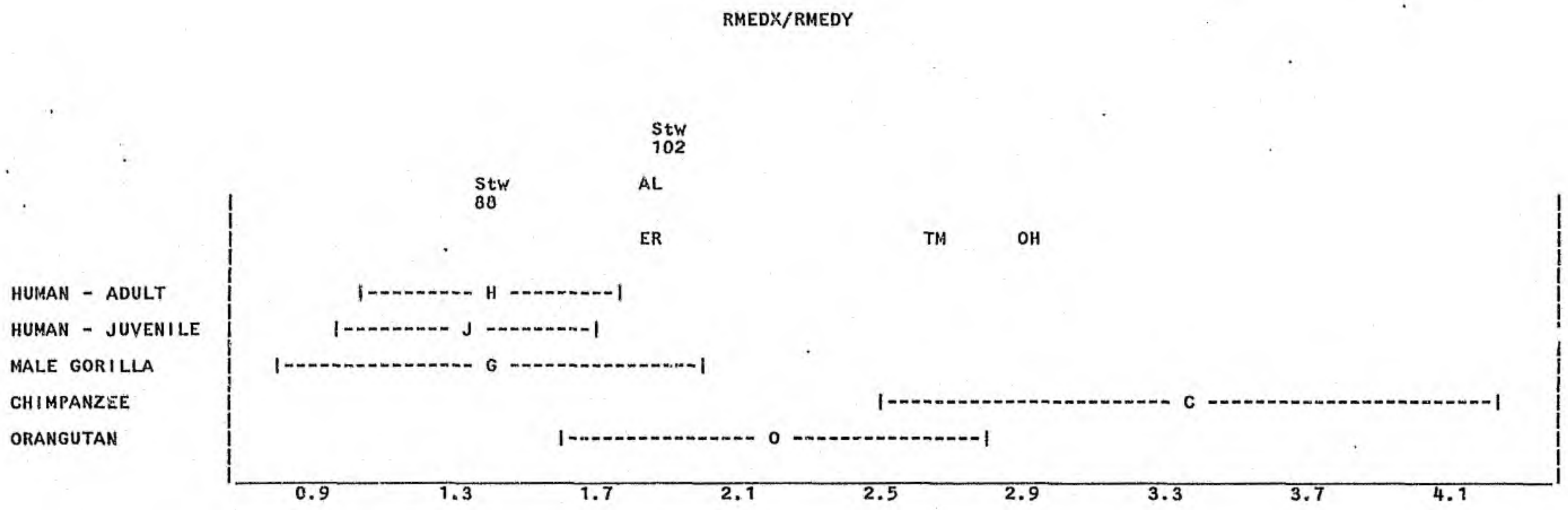

Figure 58. RMEDX/RMEDY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

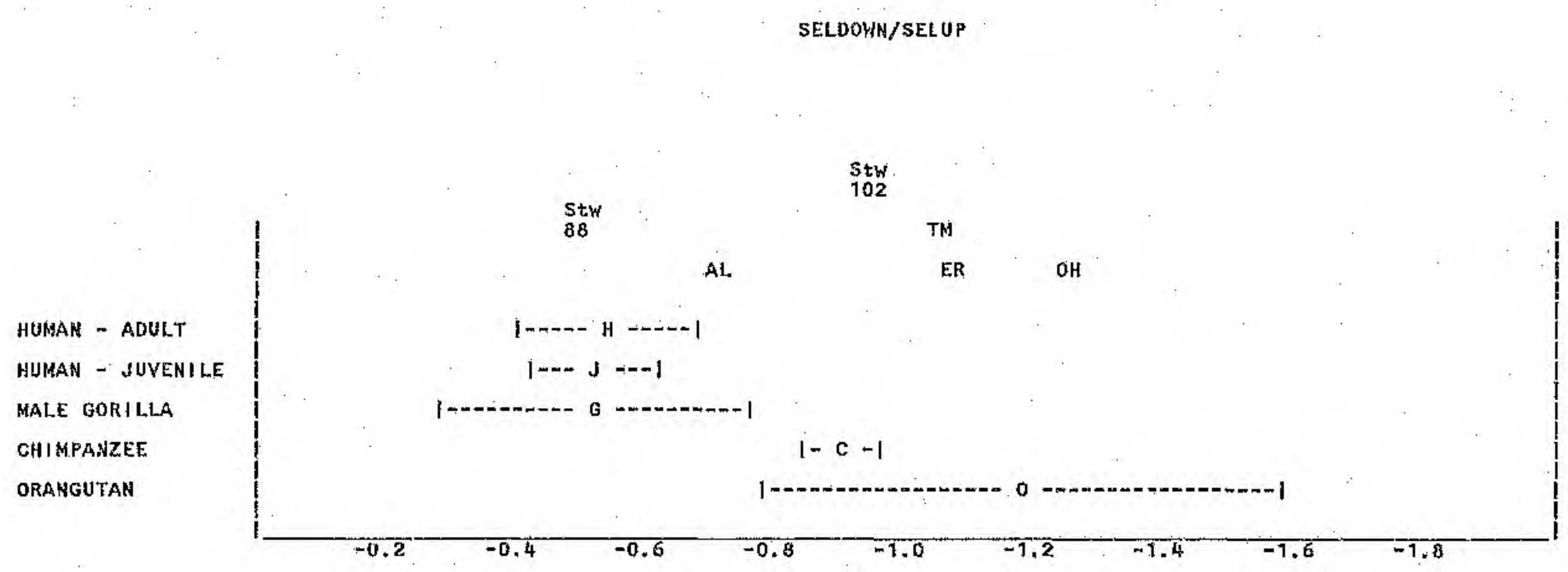

Figure 59. SELDOWN/SELUP - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

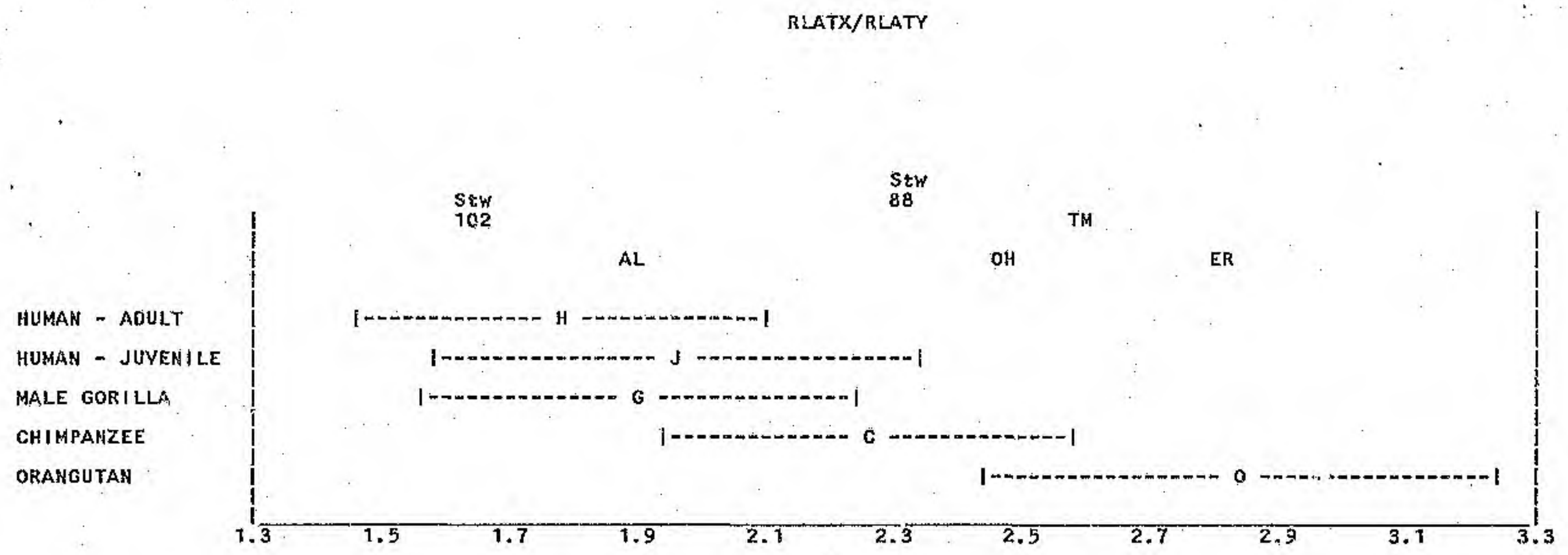

Figure 60. RLATX/RLATY - Samples of Modern Humans and Great Apes (Mean ±Standard Deviation) and Fossil Specimens.

The values of OH 8 and TM 1517 are well separated from the average adult and juvenile tali and are roughly intermediate between the chimpanzee and orangutan means. The Olduvai specimen is well within one SD from the chimpanzee mean and just at the limit of the lower first SD of the orangutan sample. The talus from Kromdraai is at the limit of the upper first SD of the chimpanzee sample and well inside the lower first SD of the sample of orangutan bones.

9.2. FOSSIL SPECIMEN BY SPECIMEN ANALYSIS

9.2.1. OH 8

9.2.1.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDX	-7.008	RMEDX/RLATX	1.265
SELDOWN	-6.165	RMEDX/RSELX	1.152
RLATX	-5.540	RLATX/RSELX	0.911
		SLOPE	0.189

The trochlear surface of OH 8 has the following pattern of anteroposterior curvature: the medial crest region is less highly curved than the sellar region which is, in turn, somewhat less highly curved than the lateral crest. This pattern is reflected also in the proportions of the surface, *viz.* RMEDX/RLATX and RMEDX/RSELX > 1, whilst RLATX/RSELX < 1. Thus, the values of the proportions of anteroposterior curvature of the trochlear surface of OH 8 suggest that it is shaped like a cone which tapers laterally. When compared with the average patterns of anteroposterior curvature of the tali of extant hominoids studied in this thesis, that of OH 8 most closely resembles the average of the three chimpanzee tali. However, the average chimpanzee talus has a relatively somewhat more gently curved medial crest region, and the difference in relative curvature between the medial crest and either the sellar region or lateral crest is greater. In view of the claim by Susman and Stern that OH 8 represents a *Homo habilis* individual approximately 13-14 years of age, the tali of juvenile humans were included in this study specifically for comparison with the specimen from Olduvai. It is notable that, in anteroposterior curvature, OH 8 resembles the average juvenile talus even less than that of the adult humans Only in RLATX, is OH 8 very close to the mean of the juvenile human sample.

9.2.1.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDY	-2.406	RMEDY/RLATY	1.069
SELUP	4.924	RMEDY/RSELY	-0.505
RLATY	-2.252	RLATY/RSELY	-0.473

The mediolateral curvatures of the medial and lateral crests of the trochlear surface of OH 8 are roughly equal in value and both are slightly more than two times more highly curved than the sellar region. Again it is the average chimpanzee talus which OH 8 most closely resembles, especially in the relative curvatures of the medial and lateral crests. In relative curvature and proportions, the trochlear surface of the Olduvai talus resembles slightly less that of the average orangutan ankle bone. The general pattern of mediolateral curvature of the trochlear surface of OH 8, as in its anteroposterior curvature, is quite unlike the juvenile human pattern.

9.2.2. TM 1517

9.2.2.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables　　b. Proportions

RMEDX	-7.843	RMEDX/RLATX	1.261
SELDOWN	-7.003	RMEDX/RSELX	1.095
RLATX	-6.223	RLATX/RSELX	0.864
		SLOPE	0.191

In the general pattern of anteroposterior curvature, the trochlear surface of TM 1517 most closely resembles that of OH 8, among the fossil specimens, and that of the average chimpanzee, among extant hominoids. Although the Kromdraai talus has somewhat more gentle anteroposterior curvature of the trochlea than OH 8, the indices of anteroposterior curvature are very close in value. Compared with the average chimpanzee trochlear surface, that of TM 1517 has a medial crest with slightly greater anteroposterior curvature whilst the sellar and lateral crest regions have considerably gentler anteroposterior curvature.

9.2.2.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables　　b. Proportions

RMEDY	-2.992	RMEDY/RLATY	1.237
SELUP	6.730	RMEDY/RSELY	-0.435
RLATY	-2.419	RLATY/RSELY	-0.352

The trochlear surface of TM 1517 is almost identical to the average of three male orangutan tali in both relative mediolateral curvatures and proportions. The lateral crest is somewhat more highly curved than the medial crest and both crests are two to three times more highly curved than the sellar region. In its mediolateral curvature and proportions, TM 1517 is also similar to the average chimpanzee talus except that the medial crest of the fossil talus is more gently curved. The trochlear surface of TM 1517 is generally less highly curved mediolaterally than the surface of OH 8, especially in the medial crest and sellar regions.

9.2.3. KNM ER-813

9.2.3.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDX	-5.459	RMEDX/RLATX	0.930
SELDOWN	-6.177	RMEDX/RSELX	0.880
RLATX	-5.869	RLATX/RSELX	0.946
		SLOPE	-0.047

The general pattern of anteroposterior curvature of the trochlear surface of KNM ER-813 is the following: the medial crest region is slightly more highly curved than the lateral crest, and both are more highly curved than the sellar area. This general pattern is reflected also in the proportions of the surface, *viz.* each of RMEDX/RSELX, RLATX/RSELX and RMEDX/RLATX < 1, and a negative value for SLOPE. Thus the trochlear surface of the East Turkana talus resembles the average modern human trochlear surface, especially those of adult males and juveniles, in that it is shaped more like a cone which tapers from lateral to medial. However, as pointed out in 7.3.2.1, the analogy of a cone does not strictly apply since the anteroposterior curvature of the sellar region is less than that of either of the crests rather than intermediate in value between them.

9.2.3.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDY	-2.977	RMEDY/RLATY	1.427
SELUP	5.801	RMEDY/RSELY	-0.517
RLATY	-2.086	RLATY/RSELY	-0.362

The mediolateral curvatures of the medial and lateral crests of the trochlear surface of KNM ER-813 are markedly unequal in value, the former being much more gently curved than the latter. The sellar region is almost twice as gently curved as the medial crest and three times as gently curved as the lateral crest. In the pattern of mediolateral curvature of the trochlear surface, the fossil talus resembles the average orangutan bone more closely than the human tali, either adult males or females or juveniles. This is mainly due to the relatively highly curved sellar area which has approximately twice as much curvature as the same region of the human tali. However, relative curvatures of the medial and lateral crests of the East Turkana talus are also somewhat greater than those of the human bones.

9.2.4. AL 288-1as

9.2.4.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDX	-5.423	RMEDX/RLATX	1.055
SELDOWN	-5.322	RMEDX/RSELX	1.024
RLATX	-5.139	RLATX/RSELX	0.970
		SLOPE	0.033

The general pattern of anteroposterior curvature of the trochlear surface of AL 288-1as is that of a cone which tapers from medial to lateral. Thus both RMEDX/RSELX and RMEDX/RLATX > 1, and SLOPE has a positive value. In the values of the primary curvature variables and proportions, the Hadar talus resembles very closely that of the average adult human female.

9.2.4.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDY	-2.939	RMEDY/RLATY	1.078
SELUP	7.657	RMEDY/RSELY	-0.402
RLATY	-2.727	RLATY/RSELY	-0.373

The mediolateral curvatures of the medial and lateral crests of the trochlear surface of AL 288-1as are roughly equal in value and both are approximately two and a half times more highly curved than the sellar region. The Hadar talus most closely resembles the average chimpanzee talus; the values of the proportions of mediolateral curvature are very similar, whereas the trochlear surface of the fossil talus is somewhat less curved in the mediolateral direction than that of the average chimpanzee ankle bone. The values of the primary curvature variables of AL 288-1as are actually very close to those of the average male orangutan talus, despite the great difference in absolute body size.

9.2.5. Stw 88

9.2.5.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDX	-5.365	RMEDX/RLATX	0.984
SELDOWN	-5.441	RMEDX/RSELX	1.016
RLATX	-5.453	RLATX/RSELX	1.032
		SLOPE	-0.011

The general pattern of anteroposterior curvature of the trochlear surface of Stw 88 is that of a cone which tapers gently from lateral to sellar to medial. In fact, the conical shape is almost cylindrical - RMEDX/RLATX, RMEDX/RSELX and RLATX/RSELX are almost equal to 1, and SLOPE is almost equal to 0. Thus Stw 88 is not unlike the average male orangutan talus in its almost cylindrical proportions, whilst its values of relative anteroposterior curvature are closer to those of the average modern human talus.

9.2.5.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDY	-3.355	RMEDY/RLATY	1.643
SELUP	10.741	RMEDY/RSELY	-0.368
RLATY	-2.346	RLATY/RSELY	-0.224

In the primary variables of mediolateral curvature, Stw 88 most closely resembles the average talus of modern humans, especially that of adult females. However, the value of RMEDY/RLATY (1.643) is higher than all the sample means of the extant primates and fossil specimens measured in this study. The lateral crest of Stw 88 is relatively highly curved and, in this feature, is more like the average chimpanzee or orangutan talus than the modern human one.

9.2.6. Stw 102

9.2.6.1. Anteroposterior Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDX	-5.432	RMEDX/RLATX	1.234
SELDOWN	-6.238	RMEDX/RSELX	0.863
RLATX	-4.403	RLATX/RSELX	0.699
		SLOPE	0.116

Analysis of the general pattern of anteroposterior curvature of the trochlear surface of Stw 102 is bedevilled by the severe damage to the lateral crest region - most of the anterior part of the articular surface of the lateral crest is missing. The absolute value of RLATX is very low and it appears that relative curvature of the whole lateral crest has not been estimated very satisfactorily from points on the posterior part of the crest alone. Therefore, only the values of RMEDX, SELDOWN and RMEDX/RSELX are reliable. In these three variables, Stw 102 is close to the average modern human talus, especially of adult females, and not unlike the talus of male gorillas.

9.2.6.2. Mediolateral Curvature of the Trochlear Surface

a. Primary Curvature Variables		b. Proportions	
RMEDY	-2.888	RMEDY/RLATY	1.070
SELUP	6.579	RMEDY/RSELY	-0.442
RLATY	-2.699	RLATY/RSELY	-0.413

Analysis of the pattern of mediolateral curvatures of Stw 102 is subject to the same restrictions as mentioned in the previous subsection. RLATY, and the two indices based on this measure, may not be used for comparison with other tali due to the damage to the lateral crest. However, in mediolateral curvature of the medial crest and sellar region, it appears that this fossil specimen more closely resembles the average chimpanzee talus, and to a lesser degree that of the orangutan, than the average modern human bones, either adult male and female or juvenile.

9.2.7. Summary

9.2.7.1. Anteroposterior Curvature of the Trochlear Surface

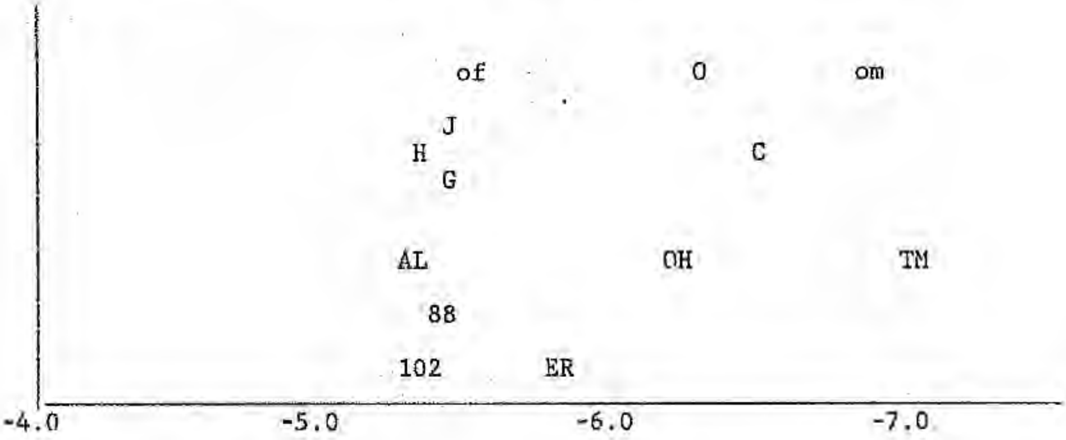

Figure 61. Average of Sample Means of RMEDX, SELDOWN and RLATX. Samples of Extant Primates (H = modern human adults, J = modern human juveniles, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans) and Fossil Specimens (OH = OH 8, TM = TM 1517, ER = KNM ER-813, AL = AL 288-1as, 88 = Stw 88, 102 = Stw 102).

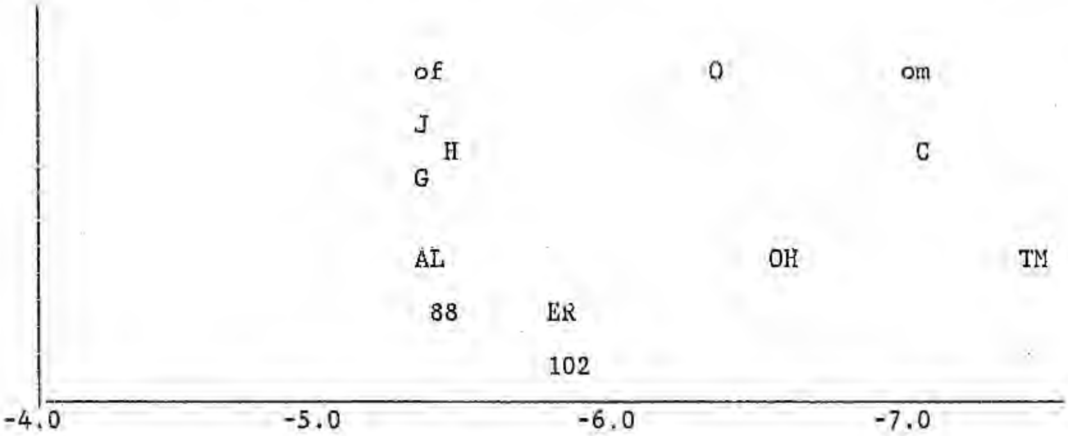

Figure 62. Average of Sample Means of RMEDX and SELDOWN. Samples of Extant Primates (H = modern human adults, J = modern human juveniles, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans) and Fossil Specimens (OH = OH 8, TM = TM 1517, ER = KNM ER-813, AL = AL 288-1as, 88 = Stw 88, 102 = Stw 102).

Figure 61 is a graphic comparison of the samples of extant hominoids and individual early hominid tali with respect to the amount of general relative anteroposterior curvature of the trochlear surface, as judged by the average of RMEDX, SELDOWN and RLATX. However, since the values of RLATX in KNM ER-813 and Stw 102 may not be reliable due to *post mortem* damage to the lateral crest, a further figure, which is based on the average of RMEDX and SELDOWN only, has been included to better assess the damaged tali with respect to the extant hominoid samples and the other fossil specimens (Figure 62).

In the first comparison (Figure 61), the Hadar talus and the two specimens from Sterkfontein are very close to each other and virtually indistinguishable from the modern human samples (both adults and juveniles), male gorillas and female orangutans. By comparison, the East Turkana talus has only slightly less general anteroposterior curvature of the trochlear surface. The talus from Olduvai Gorge is well-separated from the modern human, male gorilla and female orangutan samples and approaches the chimpanzee bones in low anteroposterior curvature. Of the early hominid bones, the Kromdraai talus has by far the least amount of general anteroposterior curvature of the trochlear surface and is most similar to the average male orangutan talus.

The second comparison (Figure 62) reveals a substantially similar pattern with the exception that Stw 102 is now virtually indistinguishable from KNM ER-813.

9.2.7.2. Mediolateral Curvature of the Trochlear Surface

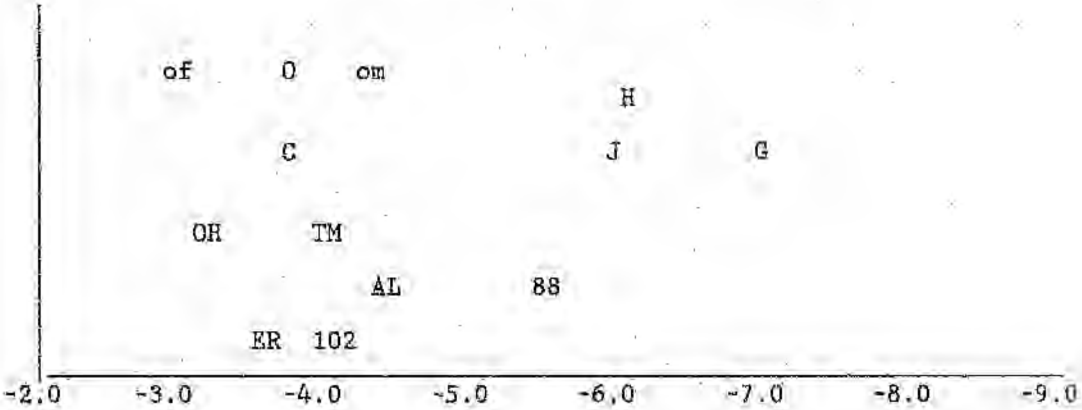

Figure 63. Average of Sample Means of RMEDY, SELUP and RLATY. Samples of Extant Primates (H = modern human adults, J = modern human juveniles, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans) and Fossil Specimens (OH = OH 8, TM = TM 1517, ER = KNM ER-813, AL = AL 288-1as, 88 = Stw 88, 102 = Stw 102).

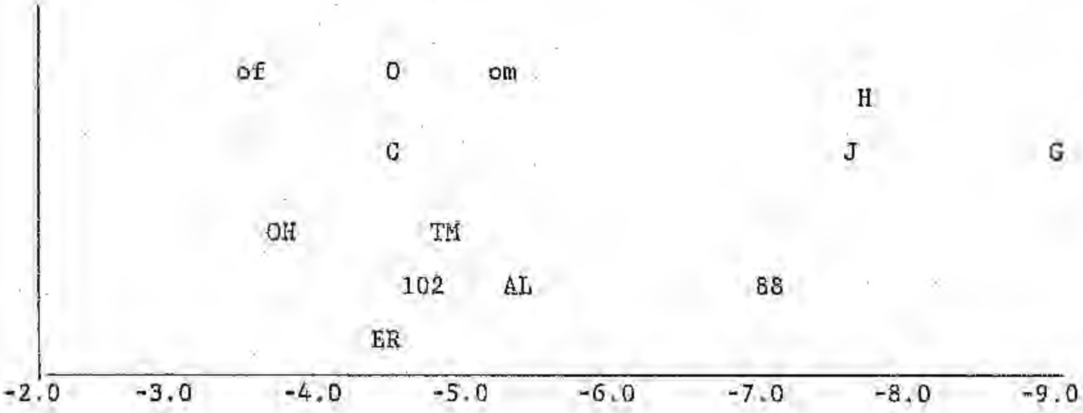

Figure 64. Average of Sample Means of RMEDY and SELUP. Samples of Extant Primates (H = modern human adults, J = modern human juveniles, G = male gorillas, C = chimpanzees, O = orangutans, of = female orangutans, om = male orangutans) and Fossil Specimens (OH = OH 8, TM = TM 1517, ER = KNM ER-813, AL = AL 288-1as, 88 = Stw 88, 102 = Stw 102).

Figure 63 is a graphic comparison of the samples of extant hominoids and individual early hominid tali with respect to the amount of general relative mediolateral curvature of the trochlear surface, as judged by the average of RMEDY, SELUP and RLATY. However, as in the previous subsection, a further figure, based on the average of RMEDY and SELUP only, is included to better assess KNM ER-813 and Stw 102 with respect to the extant hominoid samples and the other fossil specimens (Figure 64).

The two comparisons (Figures 63 and 64) have virtually identical patterns. Of the six fossil tali, Stw 88 has the most gentle relative mediolateral curvature of the trochlear surface and is most similar to the average tali of the adult and juvenile humans. The trochlear surfaces of the other early hominid tali are considerably more highly curved in the mediolateral direction and resemble more closely the surfaces of the chimpanzee and orangutan bones.

CHAPTER 10. DISCUSSION

10.1. METHODOLOGICAL CONSIDERATIONS

10.1.1. Measurement of Cartesian Coordinates and Mathematical Representation of Articular Surfaces

In this study, it was found that, for virtually every specimen, there was a high value of the goodness of fit (r-square) of the surface equation calculated as a model for the superior articular surface of the talus. However, it must be stressed that it is a goodness of fit of the surface equation initially to the Cartesian coordinates of the centre of the spherical tip of the probe used to measure points on the articular surface and then to the corrected coordinates which approximate the actual points on the surface touched by the probe. Thus the accuracy of the measured coordinates, and the subsequent corrected coordinates, is very important. In this regard, two technical considerations involved with the mechanical measurement of Cartesian coordinates (ie. by a coordinate measuring machine) must be discussed, one is the problem of the size of the spherical tip of the measuring probe, and the second is the limited number of points on a surface which are measured. Too large a probe tip and too small a number of measured points may result in an inaccurate representation of the surface, especially near the edge of the medial and lateral crests. These problems may be magnified on tali of small absolute size. This appears to be especially crucial in areas of high curvature or in areas where the curvature changes markedly in magnitude. For example, Lewis (1980a, p.537) stated that "*It is clear that* *the human talus is a derivative primate type whose main distinction is a reduction in the lateral and medial flaring of the malleolar articular surfaces. A similar remodelling has occurred in other primates e.g.* C. nictitans." This appears also to be the case in the baboon talus. More vertically oriented malleolar surfaces in the modern human and baboon tali may cause problems in the fitting of a representative surface equation. Greater error may be introduced into the mathematical representation of those areas of the human and baboon tali than in those of the ape tali where the surfaces are more gently curved (or the change in orientation is less abrupt). More careful measurement of more points, which are spaced more closely together, would likely improve the mathematical representation of the margins of the medial and lateral crests and thus improve the reliability of the overall analysis. In such instances where the curvature of an area of the articular surface is very high or changes abruptly, the procedure for calculating corrected coordinates employed in this study may not be as reliable as would be desired. These problems might be overcome by:

1. Use of a non-contact laser probe instead of a spherical-tip probe. This would obviate the need for correction of the measured coordinates, and would also allow for easier setting up of the specimens since, without any contact of the probe and the articular surface, there would be no need to hold the specimen securely to prevent displacement of the bone. However, it is not clear whether a laser probe would be effective in the measurement of cartilage-covered articular surfaces since the cartilage may not be adequately light reflective.
2. If a laser probe is not available, the use of a spherical-tip probe with the smallest possible diameter. This practice would be especially beneficial on small tali, such as those of baboons, arboreal monkeys and gibbons.

3. Measurement of many more points on the articular surface, ie. twice as many points spaced half the distance apart, especially on surfaces which are as complex as the trochlear surface, and/or the careful measurement of many points in certain areas of the surface where the curvature changes abruptly, such as the margins of the medial and lateral crests.

The techniques and equipment used in this study for the measurement of Cartesian coordinates on the superior articular surface of the talus were very complicated and not necessarily best suited for anthropological research where the measuring equipment usually must be taken to the site of the original specimens and not *vice versa*. The adoption of a simpler method of measurement of Cartesian coordinates, with sufficient precision, is obviously most desirable, especially if original fossil specimens are to be measured.

The assumption and fitting of an equation for a modified sellar surface may not be appropriate for the trochlear surface of all tali. Sewell (1904) identified a 'concave' type of trochlear surface, which type comprised 80% of Egyptian tali, and a 'concavo-convex' type, which made up the other 20% of tali. Extreme examples of the 'concave' type, with small medial and lateral crests and a large sellar region, might best be considered as unmodified sellar surfaces and be represented by an equation for a quadric surface (also see 3.2.2 and Figure 8). The goodness of fit of such an equation to the Cartesian coordinates of the articular surface may be appraised by comparing the r-square value of the new mathematical model, the equation of the quadric surface, with that of the original model, the equation chosen to represent a male modified sellar surface.

10.1.2. Mathematical Analysis of Articular Surfaces

For the initial studies of the mathematical representation and analysis of the superior articular surface of the talus, it was decided that the use of a mathematically simple, or uncomplicated, analysis would be most appropriate. Therefore, the primary curvatures chosen were the averages of curvatures calculated at numerous points in specified regions of the articular surface. However, if the relevant sections of the surface were to have rather varied curvature over the extent measured, or if the position of the sellar point of maximum curvature were to vary, in the coronal plane, from posterior to anterior (in other words, the trochlear groove were to curve markedly in the transverse plane), the average of curvatures may not be a reliable measure of geometric shape. In such an example, it may be better to look at differences in surface proportions at more, and perhaps smaller, sections of the articular surface. A case in point may be the anteroposterior curvature of the medial crest. The variable RMEDX was found to have rather high variability in most samples, which also compromises to a certain extent any of the indices which incorporate RMEDX. It is possible that the high variability of RMEDX is due to a lack of circularity of the medial crest in the anteroposterior direction. This was suggested for the modern human talus by Barnett and Napier (1952) but was refuted by Inman (1976), at least for most of the human tali studied by him. If noncircularity of the anteroposterior curvature of the medial crest is present to a marked degree, then a better method of mathematical analysis of that region is necessary. A more mathematically sophisticated analysis of the form of the superior articular surface of the talus in particular, and the general form of other articular surfaces, is expected to follow from the preliminary studies presented in this thesis.

A further illustration of the potential problems from the averaging of curvatures at numerous surface points may be the unexpected results for the index RMEDX/RLATX of the sample of baboon tali; the mean value was found to be > 1 suggesting that the general shape of the trochlear surface was that of a cone which tapered from medial to lateral. From initial crude measurements of the radii of the medial and lateral crests with a plastic radius gauge and from visual inspection (see 6.1.1.1), the impression given was just the opposite; the radius of the medial crest appeared generally to be smaller than that of the lateral. This appeared also to be the case when computer plots of the surfaces were examined; they seemed to have the same shape as the actual articular surfaces. It is possible that RMEDX may not have been calculated accurately in some of the baboon tali in which the anterior part of the medial crest changes from a region of articular surface with negative (downward) curvature to an area of surface with positive (upward) curvature towards the medial malleolar articular cup. Any points which were near the point of change from negative to positive curvature would have relatively low curvature and thus would significantly increase the average absolute value of RMEDX for that particular specimen. This may be a problem in any primate talus with a well-developed medial malleolar articular cup which alters significantly the anterior part of the medial crest of the trochlear surface. In the higher primate tali measured in this thesis, this may have affected also the values for RMEDX of the chimpanzee bones.

Prior to the statistical analyses of the samples of primate tali, the primary curvature variables of each specimen were normalized by division by the factor, $\sqrt{(dX \times dY)}$, which is the square root of the product of the x and y grid spacings. This was done to take account of simple size differences of the superior articular surfaces of the different primate tali. The intention of the normalization was to bring the trochlear surface of each bone to an equivalent size so that the relative curvatures of regions of the articular surface could be compared between primate samples, and individuals, with different overall body sizes. For this purpose, a factor which included both dX and dY was used. However, it is possible that it might have been better to normalize all primary variables of curvature in *x* by dX, and of those of curvature in *y* by dY. This would be especially beneficial if the differences between dX and dY were particularly large, which might have biased results significantly if two samples being compared had markedly different ratios of length and breadth of the trochlear surface. However, in this study it appeared that such differences were never very great. Alternative procedures of normalization of curvature variables to take account of differences in the body size of individuals, and, by implication, size variation in homologous articular surfaces, may be explored in a more sophisticated mathematical analysis to follow from the preliminary analyses included in this thesis.

An alternative refinement of the mathematical analysis, which could make use of the present techniques of coordinate measurement and surface-fitting, might be applied to the study of damaged fossil specimens, especially those with damage to either the most anterior or posterior part of a crest region only. In the two fossil tali, KNM ER-813 and Stw 102, the lateral crest region of the trochlear surface is more or less damaged. The variables RLATX and RLATY, and indices which incorporate them, are not necessarily reliable since they are calculations of average curvature over an extent of articular surface in the anteroposterior or mediolateral directions rather than curvatures of localized points. A new analysis of the samples of tali of extant primates might be made which compared the curvatures of the medial crest, the sellar and the lateral crest regions at 1. the more posterior points,

2. points midway in the anteroposterior dimension, and 3. the more anterior points. A damaged fossil, such as Stw 102 or KNM ER-813, may then be included in the analysis of the posterior and midway points only, the areas of the lateral crest where the articular cartilage is not damaged. However, a problem still remains in that it is the overall surface equation which determines the curvatures at the posterior and midway points of the lateral crest. The calculation of the overall surface equation may be inaccurate if the Cartesian coordinates for the anterior points of the lateral crest, which were not measured in the area of the damaged surface, are not present.

A further refinement of the mathematical representation and analysis of the superior articular surface of the talus may be beneficial for the study of damaged fossils, such as KNM ER-813 and Stw 102 which have articular surface missing from the lateral crest region. For example, it may be better to measure Cartesian coordinates from the articular surface of the medial and lateral crests and the sellar region separately and then to fit the appropriate surface equations to each separate region - an equation for a male modified ovoid surface to the medial and lateral crests and an equation for an unmodified sellar surface to the sellar region. In this way, the missing coordinates, from the damaged region of the surface, would not affect the best-fit surface equations of the undamaged areas of articular surface. One could then compare the undamaged regions of the trochlear surface of the incomplete fossil specimens with the homologous areas of the trochlear surfaces of the extant primate samples and other fossil tali measured in the same manner.

Finally, for a specimen in which the extent of missing articular surface is not prohibitively large, an attempt might be made to reconstruct the damaged area of the surface with plaster of Paris, or another suitable material. Cartesian coordinates of points on the reconstructed part of the surface could then be included in the mathematical representation and analysis of the articular surface.

10.1.3. Statistical Analyses of Variables of Articular Surface Shape

An unfortunate limitation of the present study is the small sample size of each of the great ape taxa which were available for measurement. It would be preferable to have tali from at least 20 individuals of each taxon with roughly equal distribution of males and females.

Furthermore, for a more complete study of the relationship between the morphology of articular surfaces of the locomotor apparatus and positional behaviour in higher primates, it would be desirable to have a larger range of comparative primate samples ie. gibbons and arboreal species of monkeys.

The possibility of poor mathematical representation of the superior articular surfaces of some tali, especially those in which areas of articular surface change markedly in curvature, was discussed in 10.1.1. A result of poor mathematical representation of a trochlear surface may be errant values of the primary curvature variables, and indices, for a specimen. This may not be significant in a large sample of tali since the mean and SD will not be too badly affected; large samples are better buffered against errant individual values. However, in a small sample, such as the chimpanzee, orangutan and male gorilla samples measured in the present study, or in single specimens, such as the fossil tali, such an event would be critical for the reliability of the results of statistical comparisons. This is a further reason for the desire to use adequate sample sizes of extant primates.

The results presented in chapters 7 and 9 indicate that some variables of trochlear surface form are clearly different between the samples of higher primates. However, even though some of the differences between sample means may be statistically significant, still there is often extensive overlap of the individual values of different samples. Thus the variation between samples is continuous and gradational, as would be expected for primate taxa with presumed Minor Qualitative/Quantitative Differences. Therefore, it may be concluded that no single feature of trochlear surface form may distinguish unequivocally between the samples of extant higher primates. It may then be advantageous to use multivariate statistical techniques to attain better discrimination between the samples. The uses, and alleged abuses, of multivariate techniques in applications to physical anthropology have been discussed in detail by Corruccini (1978), Oxnard (1984), and numerous authors in Vark and Howells (1984). Unfortunately, there are certain limitations to the use of multivariate tests for the analysis of the data from the measurements of the samples of higher primate tali in this thesis. For example, the small sizes of the samples of great ape tali rule out the assumption of multivariate normality and equality of covariance homogeneity between samples. Furthermore, the number of variables included in the analysis should be much less than the number of specimens which make up any sample (Corruccini, 1975).

Despite such reservations, preliminary multivariate studies have been made on the data which were used in the univariate analyses of chapter 7, although the results are not presented in this thesis. The results, necessarily tentative due to the limitations mentioned above, do suggest that, given adequate sample sizes and equal male-female representation, multivariate techniques would be useful in the analysis of variation in articular surface shape, and would complement the univariate analyses. More extensive studies of the potential applications of multivariate statistical techniques to measurements of articular shape, such as those presented in this thesis, may follow from the univariate statistical analyses of the present study.

10.2. VARIATIONS IN THE GEOMETRIC SHAPE OF THE SUPERIOR ARTICULAR SURFACE OF THE TALUS IN EXTANT HIGHER PRIMATES AND EARLY HOMINIDS

10.2.1. Extant Higher Primates - Minor Qualitative/Quantitative Differences Between Species Which Presumably Represent Different Categories of Positional Behaviour and Foot Use

Among the major goals of the present study were:

1. The identification of salient, and quantifiable, features of the geometric shape of a single class (*sensu* MacConaill, 1973) of synovial articular surface in higher primates, in this case the superior articular surface of the talus, a male modified sellar surface. Further, the measurement and statistical comparison of variation in the shape of the homologous surfaces among certain taxa of higher primates.
2. The correlation of significant differences in articular structure with differences in synovial joint function, be that the articular displacements which occur to allow relative movements of articulating bones or the forces acting on the joint surfaces.
3. If possible, the identification, among the primate species, of more or less discrete structural variants of the trochlear surface, which may be associated with categories of foot use (*sensu* Langdon, 1986).

The following discussion addresses the degree of success of the present study in the attainment of the goals stated above.

10.2.1.1. The first goal

Certain limitations and problems of the methodology of the present study have been discussed in 10.1. Despite such limitations, it may be said that variations in the features of the geometric shape of the superior articular surface of the talus have been measured in the higher primate taxa studied, and that significant differences in trochlear form between certain of the species, and also between males and females of some species, have been identified.

1. Anteroposterior Curvature and General Shape of the Trochlear Surface

It was found that the trochlear surface of the average baboon talus generally had much greater relative anteroposterior curvature than any of the other primate groups in this study. The differences, in the two variables SELDOWN and RLATX, between baboons and all other samples were statistically significant. The mean value for RMEDX of the baboon sample indicated that the medial crest was only slightly more highly curved than the average medial crests of the other primates and in none of the pair-wise comparisons, between baboons and another sample, was the difference statistically significant. However, it was mentioned in 10.1.2 that the value of RMEDX may not have been calculated accurately in some of the baboon tali and that the average amount of anteroposterior curvature of the medial crest may in consequence have been underestimated. This possibility also may have affected the perception of the general shape of the average baboon trochlear surface, in that the average value of RMEDX/RLATX indicated that the surface was shaped like a cone which tapered from medial to lateral. The expectation, from previous visual inspection and crude measurements of the radii of the medial and lateral crests, was that the taper of the conical surface should have been in the opposite direction.

That expectation was strengthened somewhat by the results of Langdon's (1986) index of trochlear asymmetry (TAASYM; also see 3.2.2, p.64). That index appears to be similar to SLOPE, although it is not based on direct measurements of anteroposterior curvature (or radius of curvature) of the medial and lateral crests nor, in my opinion, does it necessarily reflect differences in their respective curvatures in all specimens. Nevertheless, Langdon found that his sample of seventeen baboon tali, from different species of *Papio*, but not from *P. ursinus*, had considerably greater trochlear asymmetry, the medial crest being 'lower' than the lateral, than the great apes or modern humans.

A second one of Langdon's indices, mentioned in 3.2.2 (p.64), gave results which appear to agree with the finding of the present study regarding relatively great anteroposterior curvature of the trochlear surface in the average baboon talus. This index, TAARCHT, of lateral crest height relative to lateral crest length, appears to be a crude measure of general anteroposterior curvature of the lateral crest, and is thus similar to RLATX. The results of TAARCHT indicated that baboons had a trochlear surface more highly arched than those of the great apes or modern humans. However, it should be noted that the relationship of TAARCHT to the curvature of the arc of the lateral crest is not simple; for example, for an arc of a circle of given radius (= 1/curvature), the maximum height of the arc (a length perpendicular to the chord), which corresponds to Langdon's TA7, will not vary in a one-to-one relationship with the length of the chord, Langdon's TA4. Thus in two tali, each with identical anteroposterior curvature of the lateral crest, the one with the larger lateral crest length will have a disproportionately greater crest height.

A third index of Langdon, TARADIUS, is in fact, more similar to RLATX, although it is expressed as absolute curvature (in mm). To take account of differential body size in the higher primate taxa, Langdon normalized the values of TARADIUS by plotting them against the square root of a measure of the estimated area of the trochlear surface (TA1×TA4). He found that the radius of the arc of the lateral crest was correlated strongly with his estimator of body size, in other words, that relative anteroposterior curvature of the lateral crest, as measured by TARADIUS, was not very different among the numerous taxa of higher primates that he studied. However, it is difficult to evaluate Langdon's results for TARADIUS, normalized or not, since tests of statistical significance were not presented. Certainly, the results of the present study argue against Langdon's finding and indicate instead that significant differences in relative anteroposterior curvature of the trochlear surface, measured by a different methodology, do occur between different species of higher primates.

The relatively high anteroposterior curvature of the regions of the superior articular surface of the baboon talus implies a trochlea with an average anteroposterior arc of a circle of relatively small radius. Thus, there is a greater angle of arc per unit of length and, potentially, relatively greater excursion of the joint in the sagittal plane. Furthermore, following Preuschoft (1970; see 1.3), the resultant of forces in the sagittal plane may assume a wide range of directions on the relatively highly curved surface. For baboons, this fits well with the demands of terrestrial (or large branch) running. The more highly curved trochlear surface of baboons, relative to great apes and modern humans, also fits in with a general trend in terrestrial mammals discussed by Latimer *et al* (1987). In general, an increase in body mass is associated with a corresponding increase in trans-articular forces which, in turn, results in a lessening of anteroposterior curvature of the joint surfaces (and less range of excursion of the joint). It may be predicted that this general trend holds in male-female dimorphism in baboons, in other words, that the smaller bodied female has greater relative anteroposterior curvature of the trochlea tali than does the male of the species. In all three primary curvature variables of anteroposterior curvature, *viz.* RMEDX, SELDOWN and RLATX, the average female baboon trochlear surface is indeed more highly curved than that of the male baboon; the differences between the sexes are statistically significant in the latter two variables.

Baboons and orangutans appear to be similar in general trochlear form, as judged by the small number of variables found to be significantly different between the two samples. However, the major differences which do occur, in the relative anteroposterior curvatures of the three regions of the trochlear surface and the asymmetry of anteroposterior and mediolateral curvatures of the lateral crest, appear to be mainly between the baboon sample and the male orangutans, rather than the females. The relatively highly curved baboon trochlear surface is in clear contrast to that of the average male orangutan talus which has very gentle anteroposterior curvature. In fact, in general anteroposterior curvature of the trochlea surface, the baboon tali are somewhat more similar to those of modern humans and male gorillas (and female orangutans) than to the tali of the male orangutans (and chimpanzees). However, the relatively highly curved baboon trochlea is still significantly different from that of modern humans (and presumably male gorillas) for SELDOWN and RLATX. Also for RLATX/RLATY, the baboon tali resemble the human, male gorilla and female orangutan bones more closely than those of the male orangutans, despite the significant difference between the baboon and modern human samples for this index. The male orangutan tali have the greatest amount of asymmetry in anteroposterior and mediolateral curvatures of the lateral crest. This is due to the very gentle curvature of the lateral crest in the anteroposterior direction in the male orangutan tali (as shown by the large absolute mean value of RLATX), as opposed to the baboon tali in which the lateral crest is highly curved anteroposteriorly (a relatively small absolute value of RLATX).

The gorilla and chimpanzee have traditionally been lumped together in the same categories of positional behaviour and of foot use (see 3.1.2). However, in the present study, the average male gorilla talus was found to be more similar, in general trochlear form, to the average modern human talus than to the average of three chimpanzee tali (one male and two females) and the single female gorilla bone. This result appears to be *contra* Latimer *et al* (1987) who found, in most of the trochlear features which they measured and studied, that the chimpanzee and gorilla bones, with five males and five females in each sample, were similar to each other. Furthermore, the talar features which they measured were found to discriminate well between the African apes, on the one hand, and modern humans, on the other. This was especially so for their angle A, between a line through the supratalar joint space and the line of the estimated rotational axis of the ankle joint. Angle A of Latimer and colleagues is equivalent to the calculated variable, SLOPE, of the present study; the value of SLOPE may be changed into the value of an angle by the equation:

$$\text{angle (in degrees)} = \arctan(\text{SLOPE}).$$

Both are measures of the orientation, in the coronal plane, of an approximate axis of the trochlear surface, in other words, an estimated axis of rotation of the ankle joint. They are also indicators of the general conical or cylindrical nature of the superior articular surface of the talus. If angle A of Latimer and colleagues has a large positive value, the surface has a general conical shape, the cone tapering from lateral to medial; if the angle has a large negative value, the conical surface tapers from medial to lateral; and if the value of the angle is close to zero, the articular surface has a general cylindrical shape. The equivalent meaning of the value of SLOPE, in terms of general trochlear shape, was discussed in 6.4.2.2. Latimer *et al* (1987) found that all ten tali of each of the samples of modern humans, gorillas and chimpanzees had positive values for angle A; all trochlear surfaces were shaped like a cone which tapered from lateral to medial. This is somewhat surprising in view of the fact that Inman (1976) found that fully 20% of the human tali which he measured did not conform strictly to a conical shape (in those specimens, the anteroposterior curvature of the medial crest, but occasionally of the lateral crest also, deviated from the arc of a true circle). This raises the question of whether a larger sample of hominoid tali than that used by Latimer and co-workers might demonstrate more variation in the shape of the trochlear surface in the African ape bones. Nevertheless, those authors found that the tali of gorillas and chimpanzees were found to be significantly more cone-shaped than those of modern humans. By contrast, in the present study, the values of SLOPE were found to be rather variable within the samples of extant primates. The male gorilla talus had on average the general shape of a cone which tapered from lateral to medial. The tali of the orangutans and modern humans appeared on average to have the shape of a cone which tapered very slightly from lateral to medial, although one may say that the surface comes very close to being cylindrical. The baboon talus appeared on average to be shaped like a cone which tapered gently from medial to lateral, although this may be a false impression owing to a methodological problem as has been discussed previously. The three chimpanzee tali all seem to have the general shape of a cone which tapers markedly from medial to lateral, a result which is in strong contrast to the results of Latimer *et al* (1987). However, it should be noted that, in all of the samples mentioned, there is considerable variation about the average shapes of the trochlear surface and SLOPE did not discriminate between the modern human tali and those of the pongids studied in this thesis. Thus my measurement of a trochlear feature equivalent to angle A of Latimer *et al*, also in samples of small number, suggests that the distinction between modern humans and African apes may not be as clear as portrayed by those authors. In both studies, larger sample sizes, with equal representation of the sexes, would be preferable, and perhaps for the variable, SLOPE, or a similar measure, a more sophisticated mathematical analysis might result in greater accuracy of values, less within-taxon variability and better discrimination between samples of higher primates. For SLOPE, the main problem appears to be the high variability of RMEDX, one of the variables used to calculate SLOPE. In fact, RMEDX, a measure of the average anteroposterior curvature of the medial crest, is the main primary variable of anteroposterior curvature which distinguishes the three chimpanzee tali from those of male gorillas and modern humans; the average values of the chimpanzee bones for SELDOWN and RLATX are not far from the averages for these variables of the male gorilla and modern human samples. In each of the chimpanzee bones, the medial crest was found, by the methodology of the present study, to have relatively very gentle curvature in the anteroposterior direction. However, this was not necessarily apparent upon visual inspection of the bones. Perhaps the relatively well-developed medial malleolar articular cup apparent on the chimpanzee talus has the same effect as that suggested for the baboon talus in 10.1.2, that is, it increases the estimated radius of anteroposterior curvature of the medial crest and gives a false impression of the actual degree of surface curvature. If this was so for the chimpanzee tali, then the differences between them and the male gorilla bones, in anteroposterior curvature of the medial crest, may have been overemphasized. It is possible, then, that a more accurate measurement of RMEDX, or a more sophisticated mathematical analysis of medial crest curvature, in larger samples of chimpanzees and gorillas would reduce the potentially harmful effect of the medial malleolar articular cup on the resulting impressions of trochlear form in these species. Therefore, further study of the African ape talus, by methods similar to those of the present study but which incorporate some of the methodological improvements suggested in 10.1, may produce results which are not so contradictory to those of Latimer *et al* (1987), with respect to anteroposterior curvature and the general shape of the trochlear surface. However, as is discussed in the following subsection, there remain apparent differences in mediolateral curvature of the superior articular surface of the talus between chimpanzees and male gorillas.

In the present study, the similarity in general trochlear form between male gorillas and modern humans is striking and, yet, is unexpected in view of the seemingly different positional behaviours of these two hominoid species. An inference may be drawn that the use of the foot, as well as the magnitude, and perhaps the pattern, of trans-articular forces, are similar in modern humans and male gorillas. This perhaps may not be terribly surprising in view of the amount of semi-upright terrestrial locomotion of the male gorilla, combined with its great body size. Certainly, Morton (1924), in his study of the gorilla foot, was struck by "*the effects of terrestrial usage upon an arboreally-developed foot*", although he mentioned the apparently wide morphological variation in the several gorilla feet which were available to him. The present study appears to confirm both the human-like modifications of the trochlear surface of the talus and the relatively great range of variation in certain features in the male gorilla feet.

Latimer *et al* (1987) attributed similarities, in certain features of trochlear morphology, between gorillas and modern humans to "*the large magnitude of peak forces applied to the proximal ankle joint*" common to both relatively large-bodied species. This refers to the general trend mentioned previously in regard to the relatively high anteroposterior curvature of the baboon trochlea tali; the greater the body mass, the larger the magnitude of trans-articular forces, the less the articular surface curvature and range of joint motion. However, it should be noted that, among higher primates, the male gorilla is probably closest in mean body mass to the male orangutan, yet is not closer in trochlear form; the male orangutan has even less relative curvature in the anteroposterior direction. Therefore, it would seem that the general trend may not be applicable to animals with a large component of arboreal activities in their positional behaviour, since the pattern and magnitude of forces, even in animals of roughly the same size, may be considerably different. Indeed, Latimer *et al* (1987, p.173) cautioned against such comparisons between terrestrial bipeds and quadrupeds, on the basis that "*the loading regimes*" of the lower limb articular surfaces cannot be assumed to be identical. Such caution is perhaps even more pertinent in the comparison of essentially arboreal primates with largely terrestrial ones.

2. Mediolateral Curvature of the Trochlear Surface and Position of the Trochlear Groove in the Coronal Plane

In general mediolateral curvature of the regions of the trochlear surface, the tali of baboons and chimpanzees have virtually the same relatively high curvature, which in turn is almost the same as the orangutan sample as a whole; the male orangutans have slightly less general mediolateral curvature of the trochlear surface than the baboons and chimpanzees, whilst the female orangutans have the least average curvature. In marked contrast, the trochlear surfaces of the modern human and male gorilla tali have relatively gentle mediolateral curvatures of each of the regions of the trochlear surface; the male gorillas have slightly less mediolateral curvature in each region than modern humans, but in none of the three primary curvature variables was the difference statistically significant. Just as the relatively gentle anteroposterior curvatures of the modern human and male gorilla trochlear surfaces have been attributed largely to the great body size and consequent large magnitude of trans-articular forces acting on the talocrural joint during terrestrial locomotion in these species, so may the relatively low mediolateral curvatures be explained. In male gorillas and modern humans, most (or all, in humans) of the forces of body mass and forward propulsion are supported by the hind-limbs, and thus feet, during terrestrial locomotion. In the other primate species mentioned, relatively more of their body mass is supported by the fore-limbs and, with the possible exception of the baboons, they are less terrestrial in their positional behaviours.

As mentioned in 3.2.2, p.57, Clark (1947) made comparative descriptions, presumably from visual inspection, of the coronal (mediolateral) outlines of the superior articular surfaces of the chimpanzee, gorilla and modern human tali. Essentially, he noted that the outline in the typical chimpanzee and gorilla talus is asymmetrical, in contrast to the human ankle bone which he claimed has a more symmetrical outline with "*even curvature from side to side*". Preuschoft (1970, p.275) noted that, in the pongid talus, the lateral part of the trochlea covers a larger area than the medial, which to him was correlated with a "*greater force acting on it*". Are these descriptions of pongid and modern human morphology reflected in the results of the present study, an attempt to quantify and compare statistically inter- and intraspecific variation in such morphological features ?

If the average mediolateral outline of the modern human trochlear surface has even curvature from side to side, and is more symmetrical than the homologous outline of the pongid bone, the value of RMEDY/RLATY would be expected to be closer to 1 in modern humans than in chimpanzees or gorillas. In fact, the mean of the three chimpanzee tali is closest to 1 (1.023), with the modern human mean equal to 1.232 and male gorilla mean equal to 1.371 (but the male gorilla sample is highly variable). Hence we may conclude that the claim by Clark (1947), that the mediolateral outline of the trochlear surface is clearly more symmetrical, in the curvatures of the medial and lateral crests, in the modern human talus than in the African ape ankle bone, is not supported by the present study. On average, the human trochlear surface is less symmetrical than that of the chimpanzee and is only slightly less asymmetrical than that of the male gorilla talus.

If the mediolateral extents of the medial and lateral crests were roughly equal in the modern human talus, the value of POSSEL should perhaps be close to 0 in the modern human sample; in other words, the trochlear groove should be situated, in the coronal plane, close to the midway point between the crests. If the lateral crest were to have a greater mediolateral extent than the medial crest in the pongid talus, an inference drawn from Preuschoft's statement, the trochlear groove should be situated closer to the medial crest than to the lateral and POSSEL should then have a relatively large negative value in the chimpanzee and gorilla samples. In fact, the opposite was found - the mean of the chimpanzee tali is closest to 0 (0.064), the modern human mean of -0.126 indicates that the trochlear groove is closer to the medial crest in the average human trochlear surface and, in the average male gorilla talus, the trochlear groove appears to be situated closer to the lateral crest ($\overline{x}$=0.244). It should be noted here that POSSEL was the only trochlear feature which was found to be significantly different, at the 5% level, between the tali of male gorillas and modern humans, both males and females combined. However, it is difficult to speak about the average male gorilla talus since the variability in this feature, like many others, was found to be relatively high.

From the foregoing discussion, it may be concluded that the comments of other workers regarding relative asymmetry of the mediolateral outlines of the trochlear surface in modern humans and African apes are not supported by the findings of the present study. This appears to be the situation also with regard to the orangutan talus. For example, Morton (1924) mentioned the marked flattening of the medial part of the trochlea tali related to so-called 'permanent supination' of the orangutan foot. If, by the term 'flattening', he meant a relatively gentle curvature of the medial crest, the orangutan tali measured in the present study should have had relatively large absolute values for the variable RMEDY. In fact, on the contrary, the five orangutan tali measured in this study had a mean absolute value (2.854) lower than all other samples except that of the three chimpanzee tali (2.508). Furthermore, the medial crest was not markedly more flat (less curved) than the lateral crest. For the orangutan bones, the mean value of the index of curvatures of the medial and lateral crests, RMEDY/RLATY, was virtually the same as the means of the modern human and baboon tali. If the orangutan foot is, indeed, held in 'permanent supination', perhaps this may be attributed to the shapes of articular surfaces of the hindfoot other than those of the talocrural joint.

The variable SELUP is a measure of the average curvature, in the mediolateral direction, of the sellar region of the superior articular surface of the talus. It may be expected that a trochlear surface which has relatively greater mediolateral curvature of the sellar region would have a correspondingly deeper trochlear groove. In the present study, the depth of the trochlear groove of each specimen was not measured directly. However, Langdon (1986) measured the absolute depth of the trochlear groove (TA5) in the tali in his study and expressed trochlear depth relative to trochlear breadth (TA1) by the index TADEPTH (see 3.2.2). Langdon found that the tali of baboons and orangutans were similar in having a relatively deep trochlear groove; the groove had slightly greater relative depth in the orangutan bone than in the baboon talus, but there was quite a large amount of variability in the orangutan sample. In contrast, the tali of modern humans, gorillas and chimpanzees, which were very close together in their mean values of TADEPTH, had relatively shallow trochlear grooves; on average, the human trochlear groove had the least depth, that of gorillas slightly more depth than the human groove, and the chimpanzee trochlear groove was again slightly deeper than that of gorillas. The latter sample had somewhat large variability for this feature, but not as much as that of the orangutan sample.

The results of the present study for the variable SELUP largely agree with those for Langdon's index, TADEPTH, with the exception of the position of chimpanzees. From the results of SELUP, the orangutan and baboon samples had, on average, a trochlear groove with relatively high mediolateral curvature; however, again the orangutan sample was rather variable. The samples of modern human and male gorilla tali were characterized by a trochlear groove with, on average, relatively low mediolateral curvature. However, the values for SELUP of the three chimpanzee bones were very close to the mean of the orangutan sample, which indicates a trochlear groove with much greater relative depth than that seen in Langdon's study. A much larger sample of chimpanzee tali would perhaps give a clearer impression of this feature of the chimpanzee trochlear surface relative to the other hominoids.

The functional implications of a relatively deep trochlear groove in higher primates are not clear. Langdon (1986, p.90) suggested that a relatively deep groove would greatly increase the vertical contact between the distal tibial articular surface and the trochlear surface of the talus. This would resist undesirable motions of the joint and provide greater ankle joint stability. He mentioned that greater joint stability would be advantageous for the foot of a runner, such as the baboon, but would be less so for a climber, like the orangutan, which relies on relative joint mobility. However, if a deep trochlear groove were important for increasing ankle joint stability, one would expect that the orangutan and chimpanzee, which have relatively large components of arboreality in their positional behaviour repertoire, might have relatively shallow trochlear grooves, whereas baboons, modern humans and male gorillas, with large amounts of terrestriality, would have relatively deep grooves in the trochlear surface. Clearly, trochlear morphology does not match these expectations. Ziemer (1978) has suggested that the non-uniformity, in the mediolateral direction, of a modified sellar articular unit effectively prevents the movement - abduction-adduction. However, in the higher primate ankle joint, abduction-adduction is clearly prevented by the mortise and tenon arrangement of the joint, provided by the medial and lateral malleoli, and the strong battery of ligaments medially and laterally. It is difficult to imagine that variation in the depth of the trochlear groove has much significance in ankle joint stability. What about ankle joint mobility ? Is there a possible relationship between sellar curvature and the magnitude of conjunct axial rotation of the tibia relative to the talus in a modified sellar unit ? A theoretical relationship was mentioned previously, in 1.2.2, that, in sellar articular surfaces, the magnitude of conjunct rotation will be larger the greater is the surface curvature. One may assume that this relationship applies, not only to unmodified sellar surfaces, but also to a modified sellar surface, despite the areas of ovoid surface on either side of the sellar region which may hinder rotation. The hypothesis which follows is that the primates which have on average a relatively deep trochlear groove (with relatively high mediolateral curvature of the sellar region), such as baboons, orangutans and chimpanzees, will have relatively greater conjunct mediolateral rotation of the tibia on the talus for a given length of arcuate motion (plantar-dorsiflexion) than those species with a relatively shallow trochlear groove, such as modern humans and male gorillas. The hypothesis is testable but this must await the results of further studies which would seek to correlate variation in articular surface curvature, measured according to a methodology similar to that of the present study, with variation in the magnitudes of articular displacements and joint excursion, perhaps measured by techniques similar to those of Ziemer (1978).

In sum, the present study has been successful, at least in good part, in the goal of the quantification and statistical analysis of minor qualitative/quantitative variation in the form of the trochlear surface of the talus in extant higher primates. Despite considerable intraspecific variation and overlap of values of some of the variables used to describe trochlear shape, marked similarities and differences in the shape of the superior articular surface of the talus between the primate spcies have been identified.

10.2.1.2. The second goal.

For many of the features of trochlear shape considered in the present study, variation in the feature between different primate taxa, or between males and females (or adults and juveniles) of the same species, has been associated with suggested differences in articular movements or in forces acting on the joint surfaces owing to differences in the positional behaviours or average body size of the respective primate groups. However, other apparent differences in the structure of the trochlear surface may not, at this stage, be associated clearly with functional differences.

Such clear associations between form and function are most desirable as bases for hypotheses concerning the fossilized remains of the postcranial skeleton of higher primates, but must await the results of future attempts to isolate and define more precisely the functional and mechanical differences between the ankle joints of the different taxa, or between males and females of the same species (see 10.3 for further discussion of future avenues of form-function studies).

10.2.1.3. The third goal.

From the results of the present study, it has been possible to gain an impression of the general shape and relative curvature of the average superior articular surface of the talus of each of the species of higher primate studied and, where marked sexual dimorphism occurs, of the average male and female trochlear surfaces (see 7.3). Furthermore, the amount of variation from the average trochlear surface in each primate group and the degree of overlap, in the values of the variables, between the groups have been quantified. The question which remains is - can more-or-less discrete structural variants of the trochlear surface, and potentially the talocrural joint, which correspond to classes of foot use of Langdon (1986), be identified, according to criteria proposed in 3.2.2 ? It was suggested that, in order to identify such structural variants, it would be necessary to find differences in the shape of the trochlear surface which were sufficient in magnitude and consistent, in that there was relatively little intraspecific variation and only moderate overlap between species.

The study of features of the geometric shape of the superior articular surface of the talus, by the methodology utilized in this thesis, has resulted in probably too much intraspecific variation, and overlap between the values of the samples measured, to allow the resolution of the desired structural variants of trochlear surface. This may be attributed to genuine similarities in trochlear form and curvature, especially with regard to the extant hominoids. Certainly, Langdon (1986) found considerable overlap, in the values of many of his measures of trochlear morphology, between the samples of modern humans, chimpanzees, gorillas and orangutans. Indeed, he was led to the conclusion that his study "*revealed few indicators of foot function within the talocrural joint*" of extant anthropoids, such indicators being more apparent in the subtalar and other joints of the foot. It is also possible that certain limitations of the present methodology, discussed in 10.1, may have resulted in a de-emphasis of the differences in trochlear morphology between the different species. However, despite such apparently large variation and overlap of values, from the relatively simple mathematical analysis of the homologous articular surfaces, certain features of trochlear form have been found to differ significantly between some of the primate groups, either different species or genders. Where possible, functional explanations or, at least, correlation with differences in positional behaviour, foot use or body size, have been proffered (10.2.1.1).

From the classification of foot use in primates by Langdon (1986), certain similarities and differences in trochlear structure, between the taxa studied in this thesis, were expected. For example, among the species of extant hominoids, it was expected that chimpanzees would be most similar in trochlear form to gorillas, since they occupy the same categories of positional behaviour and foot use. Contrary to expectation, male gorillas appear to be more like modern humans in the form of the trochlear surface. The differences between the tali of male gorillas and chimpanzees found in the present study correlate with the differences in the relative percentages of their daily activities spent in arboreal (climbing) activities as opposed to the terrestrial component of positional behaviour (see 3.1.2). The large-bodied male gorilla especially is limited in its arboreal repertoire. What about female gorillas ? In this study of the form of the superior articular surface of the talus, the single female gorilla specimen was found to be more like the chimpanzee and orangutan tali than that of the male gorillas. It is interesting that Latimer *et al* (1987, p.172) stated that "*the tali of female gorillas more closely resemble those of chimpanzees ... than those of their much-bulkier male counterparts*". If the single female gorilla talus in this study is indeed representative of female gorillas in general, the apparent sexual dimorphism in trochlear form in gorillas may be due to the greater amount of climbing activity by females than by males (Schaller (1963) found that adult females climb twice as frequently as adult males), or solely by the difference in average body size and concomitant trans-articular forces, or by other functional/morphological differences between female and male gorillas which may affect the shape of the talus, or by various combinations of some or all of these factors. There has been a suggestion that the forces acting on the talus are not only different in magnitude but also act differently in male and female gorillas. For example, from comparison of relative sizes of articular surfaces in the feet of male and female gorillas, Gomberg and Morbeck (1983) have inferred that "*body weight passes more medially through the lower leg and foot*" in the larger-bodied male. The results of the present study suggest that the chimpanzee and female gorilla may be better representatives of Langdon's (1986) category of climbing foot use than is the male gorilla. In fact, both the chimpanzee and female gorilla appeared to be more similar to the orangutan, a suspensory climber, than to the male gorilla.

According to Langdon (1986), the human bipedal type of foot resembles behaviourally the Old World monkey running type of foot, with any morphological differences between the two due to the much larger body size of the humans. The results of the present study of the superior articular surface of the talus emphasize the morphological differences between the baboon and modern human ankle joints. The sample of modern human tali differed significantly from the baboon sample in more variables of trochlear form than from any of the pongid samples. It is not clear, however, whether such differences are due solely to the comparative body sizes, or whether baboons are perhaps not the best example of a running type of foot. They are usually described as being highly terrestrial but perhaps the need to adapt the foot to uneven and rather hilly terrain, as well as to the demands of climbing activities (e.g. cliffs and trees), are important aspects of baboon foot use. In addition to the effects of a marked difference in body size, adaptations in the baboon foot for the latter activities may contribute to the apparently marked morphological differences between the baboon foot and that of modern humans. However, it is possible that the present study does not measure features of trochlear form which may be most similar between baboons and modern humans, for example, the height and sharpness of the medial and lateral trochlear margins (as distinct from the crests). Problems of the measurement of Cartesian coordinates in areas of very high curvature, such as the margins of the trochlear surface in human and baboon tali, have been referred to in 10.1.1. Alternatively, the importance of overall body size differences and associated transarticular forces, may obscure any functional similarities between species in the same, or similar, classes of foot use. This general hypothesis is testable; for example, among numerous primate species within a single category of foot use, or positional behaviour, but of significantly different body size. Do they have similar articular surface form, in other words, are they more similar to each other than to species of comparable body size but of different foot use ?

The finding of a relative lack of similarity in trochlear form between primates in the same, or similar, class of foot use or positional behaviour suggests that, as positional behaviour categories may, in their inherent rigidity, mislead about the complexity of the locomotor and postural repertoire (the 'linear continuum' or 'spectrum' of Oxnard (1975a, 1984) may be a more useful concept), so categories of foot use (Langdon, 1986) or my intended structural variants of trochlear surface (or talocrural joint) may be concepts which also are too restrictive. Langdon (p.67) suggested this when he stated that the four behaviours which are the names of his foot use categories "*represent the directions of specialization observed, although it is clear that this really represents a spectrum*". Variation in morphology may be too subtle among primate taxa, and perhaps in some species there is too much intraspecific variation in certain features, for categories of trochlear morphology to be constructed. However, it is possible that further studies along the lines of this thesis, but with perhaps more accurate measurement and mathematical representation of the articular surface and a more sophisticated mathematical analysis of articular morphology (including the use of multivariate statistical techniques), will allow a more refined categorization of potential structural variants of the trochlear surface, and other articular facets, of the primate talus. It is further hoped that this may be accompanied by studies which will isolate and define more clearly differences in the use of the foot and ankle among higher primate taxa, and which may lead to a redefinition, or broadening of the concept, of categories of foot use as suggested by Langdon (1986).

10.2.2. Fine Quantitative Differences Within Species Owing to Sexual Dimorphism, Ontogenetic (Age Group) and Side (Right vs Left) Differences

One of the sequelae of the first major goal of the present study mentioned in 10.2.1. is the elucidation of subtle variation in the form of the superior articular surface of the talus within a species, what I have called in 2.2.1 the level of 'fine quantitative differences'. The samples of tali of modern humans and baboons have been examined for such differences owing to sexual dimorphism and right *versus* left side. The modern human tali have been analysed further for differences in trochlear form owing to different age groups. The possible inference of sexual dimorphism in the average shapes of the trochlear surface in orangutans and gorillas also is discussed below.

10.2.2.1. Sexual Dimorphism

In 10.2.1, a general trend among terrestrial mammals, mentioned by Latimer *et al* (1987), for increase in body size to be accompanied by a lessening of anteroposterior curvature of the trochlear surface and a smaller range of joint excursion, was discussed. Does such a trend operate only at the level of different taxa or also within a species with a difference in average body size between males and females ? The tali of male and female humans might have been expected to show such differences in articular curvature. However, none of the variables of relative anteroposterior curvature, nor any of mediolateral curvature, were found to be significantly different between males and females in the sample of modern human tali. The only variable found to differ significantly was SLOPE, a measure of the orientation of the estimated joint axis, and thus of the general shape of the surface. On average, the trochlear surface of females was shaped somewhat like a cone which tapered from medial to lateral, whilst the shape of the trochlear surface of the average male talus was that of a cone which tapered from lateral to medial.

Baboons are among the most highly dimorphic species of primates. The adult male baboon is, on average, about twice the size (has twice the body mass) of the adult female. It is not surprising then that males and females of the chacma baboon differed in many more features of trochlear form than was found in the modern human sample. Two of the variables were of relative articular curvature, *viz.* the anteroposterior curvature of the sellar region (SELDOWN) and the mediolateral curvature of the lateral crest (RLATY); in both regions, the female surface had on average the greater relative curvature. According to the results of POSSEL, the trochlear groove was positioned, in the coronal plane, closer to the medial crest on average in the female talus than in the male bone (the female mean = -0.313 and the male mean = -0.124). The other two variables found to be significantly different at the 5% level were indices of mediolateral curvatures.

The sample of orangutan tali measured in this study consisted only of five bones, three from males and two from females. However, there was a suggestion from this small sample that trochlear morphology in males and females of this Asian ape differs significantly in some features (see 7.3.5). The veracity of this suggestion must be confirmed by further studies of articular surface curvature in a larger sample of orangutan tali. The same stricture is true for the suggestion of sexual dimorphism in trochlear form in the talus of gorillas, which was represented in the present study by six male bones and only one from the smaller-bodied female.

Once statistically significant differences in articular surface shape between males and females of a species are found, a perplexing question remains - can the morphological differences be accounted for by body size difference alone, or may differences in positional behaviour and the use of the foot be invoked as well ? Certainly, differences in mean body size between males and females of a species are readily apparent from visual inspection and may be quantified by measurement of body mass. Quantitative differences, between males and females of a species, in components of the positional behaviour repertoire may be recorded by the methods currently utilized in the study of such behaviour (see 1.1). However, differences between males and females of a species, in foot use, or in the forces acting on the foot, would most likely be quite subtle and are less readily apparent. Special techniques of measurement of locomotor function would probably be necessary for the elucidation of such differences, especially in non-human primates. However, a correlation between differences in trochlear morphology and differences in positional behaviour, and preferably also subtle differences in foot use, is necessary to explain significant variation in articular form, owing to sexual dimorphism, by more than body size difference alone.

10.2.2.2. Ontogenetic (Age Group) Differences

Throughout childhood, puberty and adolescence, there occurs, in synovial joints, a remodelling of cartilage and subchondral bone. This is associated with a steady increase in body size, which is quite marked during the growth spurt. There may occur also, during the development from childhood to early adulthood, subtle changes in locomotor function, alterations in the orientation of articular surfaces through epiphyseal growth, and changes in the pattern of forces acting on the limb joints (see 1.3). Therefore, it is to be expected that the geometric shape of articular surfaces of the talocrural joint, and other joints of the foot, will change throughout this period of maturation. If such alterations in articular form are significant, it should be possible to identify them, by the methods of the present study, in samples of tali from different age groups of juveniles.

For this thesis, the tali of only one age group of immature modern humans were chosen (12 to 15 years of age). Those tali were included mainly for a comparison with the OH 8 talus, in view of the claim by Susman and Stern (1982) that the fossil bone represents a *Homo habilis* individual of 13.6 to 13.9 years, by modern human standards. Significant differences, between the tali of the juvenile humans and those of young adults, were found in two variables at the 5% level of significance and another at the 10% level (see 8.2.1). These differences provide, at least, a tentative suggestion that there may be identifiable, that is, marked and consistent, changes in trochlear form in the growth of modern humans from childhood to adulthood. Such changes might be followed in an ontogenetic series of five or six talar samples, each two to three years of age range, from childhood to early adulthood. Thus, it may be possible to construct a quantifiable pattern of growth of a hypothetical average human trochlear surface, or indeed any other articular surface. If such changes of articular surface form are shown to occur, it is possible that they may be correlated with changes, perhaps subtle ones, in locomotor function, for example, the range of joint excursion or a change in the pattern of trans-articular forces owing to an alteration in the varus/valgus position of the knee or the angle of he neck of the femur, and/or increases in body mass, especially during the growth spurt. If appropriate osteological samples were available, a similar study of an ontogenetic series of apes could be made.

Bone remodelling does not end upon the cessation of epiphyseal growth. Bullough (1981) reported that the remodelling of the articular ends of limb bones occurs throughout the life of an individual (see 1.3). Therefore, it is to be expected that age changes in the shape of the joint surfaces may be identified in samples of bones from adults of progressively older age groups. In fact, Bullough (1981) stated that roentgenograms of the ankles of young and old adults illustrate that the joints of the old persons are clearly different from those of the young healthy adults; for example, the mortise, formed by the distal tibia and fibula, is deeper and more angular in the older individual. Further, Bullough quoted A. Ogston (Journal of Anatomy and Physiology 12:503, 1878) thus, "*the general surfaces of senile joints are flatter and not so full and plump in their curves; the grooves of articulation with opposing bones are deeper and more marked and the different shapes of the articular surfaces are such that they are readily recognizable by the eye*".

In the present study, a sample of twenty tali from male humans, aged 25 to 39 years, was compared with the same number of bones from males in the age range, 42 to 70 years. Significant differences were found in three variables at the 5% level of significance, one primary curvature variable and two indices, and in a further three variables at the 10% level (see 8.2.1). The general expectation, based on the claims of Bullough and Ogston, of less highly curved articular surfaces in the tali of the older individuals was not met; on average, the sellar region and the lateral crest of the more mature bones were more highly curved, in the mediolateral direction, than in the average young adult bone, whilst the opposite was found for the anteroposterior curvature of the medial crest.

The observations of Bullough and Ogston, with regard to differences in trochlear surface form and curvature between tali from young and old individuals in their population samples, are contradictory to the findings of the present study of tali of South African Negroes. Nevertheless, that such differences have been observed and, in the present study, quantified, suggests that it may be possible to document in larger osteological samples a pattern of marked, consistent trochlear surface remodelling, from early adulthood to advanced age, in a hypothetical human talus, or indeed different patterns in hypothetical trochlear surfaces of different human populations. The methodology for such a study would be similar to that for the study of ontogenetic changes from childhood to early adulthood mentioned previously: namely, the measurement of tali from numerous samples, each perhaps of five years age range. It would be interesting to note whether any changes in articular surface shape occur steadily from early to late adulthood, or whether articular form remains in a morphological equilibrium until a certain 'threshold' age is reached, following which surface remodelling takes place relatively rapidly.

10.2.2.3. Side Differences

Compared with variations in articular morphology owing to gender and age group differences, significant differences in the shape of joint surfaces between the right and left hind limbs of primates are more difficult to explain. In this regard, the null hypothesis states that, since there is general bilateral symmetry of the mammalian body, there should be no asymmetry of homologous parts from the right and left sides, given equal uses of the parts. However, in view of the plastic nature of bone (in that remodelling of long bone shafts and articular ends may occur throughout the life of an individual), it is to be expected that consistent differential use of the right or left limb may result over time in significant morphological differences, such as in articular surface form, between homologous anatomical parts from the two sides. Alternatively, it is reasonable to infer asymmetry of function of homologous synovial joints from observed significant right-left differences in articular morphology. However, it must be cautioned that this begs the question of a clear association between morphological and functional asymmetry; other factors, such as differential blood supply during growth, may play a role in the unequal development of anatomical parts. Nevertheless, potential marked differences in the shape of the trochlear surfaces of right and left tali from the same individuals may be identified by the methods of quantification used in the present study. Are such morphological differences, according to right or left side, expected in the tali of the species of higher primates studied in this thesis, based on observations of differential hind limb use ? It appears that the concept of 'footedness', analogous to that of handedness, has been overlooked to date in studies of the positional behaviour of non-human primates. In modern humans, evidence for asymmetry of foot use inevitably depends on one's confidence in the criterion us [illegible] limb preference; can it be established reliably by [illegible] wear on the shoes, by which foot is used to kick a bal [illegible] leads when a person begins to stride from a stand [illegible], *et cetera* ? Furthermore, evidence for consistent asymmetry [illegible] foot length is contradictory; attempts to associate observed differences in foot length with handedness in males and females (Levy and Levy, 1978) have been met with counter-claims that the foot length asymmetry is in the opposite direction (Mascie-Taylor and McManus, 1981) or that no significant difference in the lengths of the right and left feet exists (Peters *et al*, 1981; Yanowitz *et al*, 1981; Means and Walters, 1982).

Despite a lack of clear expectations with regard to right-left differences in the shape of the trochlea tali, comparison of the tali from different sides was made in samples from modern humans and baboons. In both species, little difference in trochlear form between bones from right and left feet was found; significant differences were found in only one index, in the human sample, and, in the baboon sample as a whole, in two primary curvature variables (one each at the 5% and 10% levels). Analysis of sub-samples of tali from female and male baboons suggested that right-left differences may be greater in the females.

It is perhaps not surprising that little right-left asymmetry of trochlear form was found in the tali of largely terrestrial primates, such as modern humans and baboons. It is possible that 'footedness' is more common in arboreal climbers, who may use the feet in a manner more similar to their hands, than in terrestrial primates, such as modern humans and baboons. Unfortunately, the present study has not addressed the possibility of marked side differences in the feet of arboreal primates since sample sizes were not sufficiently large to allow the assessment of the degree of right-left asymmetry in the form of the trochlear surfaces of the tali of chimpanzees and orangutans. It is hoped that future studies of large samples of pongid bones will resolve this question. Furthermore, the possibility of differential hind limb and foot use in arboreal primates may be examined by detailed studies of positional behaviour which include the record of whether the right or left limb was used for a particular movement or task.

10.2.3. Early Hominid Fossil Tali

10.2.3.1. Olduvai Hominid 8 (OH 8)

If the claim by Susman and Stern (1982), that the OH 8 talus is that of an immature *Homo habilis* individual, is correct, then it is appropriate that the bone be compared with tali from juvenile individuals of modern humans and apes. A comparison of OH 8 with a small sample of juvenile human tali in the age range, 12 to 15 years, forms part of the present study. Does the Olduvai talus resemble the ankle bone of juvenile humans in the form of the superior articular surface of the talus ? The results presented in 9.2.1 suggest that the trochlear form of the Olduvai talus is less similar to that of the average juvenile human talus than to that of the adult modern human bone. However, it should be noted that the fossil bone does not particularly resemble the average adult human talus in the shape of the articular surface, but appears to be closer to that of the chimpanzee, in both anteroposterior and mediolateral curvature. For this reason, a comparison of the fossil bone with juvenile pongid tali is most desirable (see 10.2.2.2), although it may eventuate that, as with modern humans, the juvenile tali of apes are not particularly dissimilar to the tali of the corresponding adult specimens. Based on the results of the present study, it is not possible to comment further concerning the question of whether the Olduvai talus is that of an adult or juvenile individual.

As mentioned in 5.1, Day and Napier (1964) concluded that the affinities of the OH 8 foot, as a whole, were clearly with *Homo sapiens*, but that the talus was somewhat less human-like and similar to TM 1517 from Kromdraai. For example, they described the talar trochlea as being well grooved, with the deepest point of the groove situated more towards the medial crest, and with medial and lateral borders of roughly equal radii of anteroposterior curvature. In the results of the present study, these features should be reflected respectively by a relatively low absolute value of SELUP, indicating relatively high mediolateral curvature of the sellar region, a negative value of POSSEL, and a value of RMEDX/RLATX close to 1 (and SLOPE close to 0 in value). In fact, OH 8 was found to have relative mediolateral curvature of the sellar region higher than any of the fossil specimens and greater than all the tali of the extant primates studied in this thesis except the orangutans. In other words, the radius of curvature of the sellar region of OH 8 was smaller than the minimum values of all other samples except the orangutans. The value for POSSEL of OH 8 was negative, indicating that the deepest point of the trochlear groove was positioned, in the coronal plane, more towards the medial crest than the lateral. However, in this feature the Olduvai talus resembles the average modern human trochlear surface more than that of any of the pongid bones. By the methodology of the present study, OH 8 was found to have a medial crest with radius of curvature greater than that of the lateral crest (RMEDX/RLATX = 1.265 and SLOPE = 0.189), in which it most closely resembles the average chimpanzee talus, among extant hominoids.

The results of this study, concerning the trochlear morphology of OH 8, are in general agreement with the conclusion by Day and Napier (1964) that the Olduvai talus is less human-like in morphology than the rest of the foot. In fact, it seems to be not just somewhat less human-like but markedly so, and like TM 1517, closer in trochlear morphology to the chimpanzee, and to a certain extent the orangutan. This conclusion accords also with the results of the morphological study of the OH 8 foot by Lewis (1980c, 1981), who found that, in the hind foot (especially the subtalar joint complex), the Olduvai foot is morphologically conservative and most reminiscent of the chimpanzee, among extant primates.

From a multivariate analysis of their talar measurements, Lisowski *et al* (1974) concluded that the Olduvai talus was closest morphologically to that of the orangutan, among extant primates, and to the Kromdraai talus (TM 1517) and those of Miocene apes, among other fossil specimens. As mentioned above, the results of the present research suggest that the OH 8 talus is closer, in trochlear form, to the chimpanzee than to the average orangutan. However, it is closer in form to the orangutan than the average modern human talus, either adult or juvenile. Comparison of the shape of the superior articular surface of the Olduvai specimen with the homologous morphology of Miocene ape tali would be interesting in light of the similarities in talar anatomy claimed by Lisowski and colleagues. Casts of some tali from Miocene deposits have been measured by the methodology of the present study but the results of their analysis have not been presented in this thesis. It is hoped that these tali may be included in a future study, which perhaps will incorporate methodological improvements mentioned in 10.1, such as a more sophisticated mathematical analysis of the articular form.

At this stage of the analysis of trochlear form, the similarity of the Olduvai talus to the chimpanzee is interesting, in view of previous suggestions of adaptations for arboreal climbing in the feet, and other parts of the skeleton, of early hominids, as well as recent suggestions that the postcranial morphology of some *H. habilis* individuals may be more primitive than had previously been thought (Johanson *et al*, 1987). However, one must also consider the possibility that morphological similarities, in the pedal skeleton, between certain early hominids and the chimpanzee are due, at least in part, to similarity in body stature and mass. It should be noted that the tali of OH 8 and TM 1517 are slightly smaller than the two tali from Sterkfontein but are slightly larger than AL 288-1as. These five fossil tali are considerably smaller than the South African Negro ankle bones and one of the chimpanzee tali measured in the present study. Only KNM ER-813 approaches the average modern human talar dimensions but is comparable in overall size also to one of the chimpanzee bones. In view of the roughly equivalent size of the tali (and presumably of overall body mass) of five of the six early hominid individuals studied in this thesis, we may conclude that the morphological differences in trochlear form found between the fossil tali in this study are not reflections of marked differences in body size. What is the effect of very small body size on the geometric shape of the superior articular surface of the talus in modern humans ? It is interesting that Wood (1974c) compared the East Turkana fossil (KNM ER-813) with the tali of San individuals. To date, only one

San talus, that of a small female, has been measured by the techniques of the present study but a comparison of that bone with those of the extant primates and early hominids has not been included in this thesis. For future studies of articular morphology of early hominids, more San bones should be measured, especially those of females, of whom some have skeletons which appear to be roughly the same size as AL 288 (Lucy) and OH 62 and tali the same size as five of the fossil specimens measured in the present study.

If future form-function studies of articular form confirm the similarities, between certain individuals of *H. habilis* and the chimpanzee, in morphological traits of the post-cranial skeleton, which may in turn be associated clearly with the demands of arboreal climbing abilities, the case for the presence of such a component of the positional behaviour of the early hominids, represented by OH 8, living about 1.8 Myr ago will be strengthened. Such claims have been made for *H. habilis* by Susman and Creel (1979) and Susman and Stern (1982).

However, there are also taxonomic implications of the similarity of OH 8 with an extant African ape, as well as with the robust australopithecine talus from Kromdraai. For example, Wood (1974a,b,c) noted that the OH 8 talus was similar to TM 1517 from Kromdraai, and that those two specimens were markedly different from KNM ER-813, which he had assigned to the genus *Homo*. He suggested that the Olduvai talus should be assigned to the East African species of robust australopithecines, *Australopithecus boisei*. In this, he was supported by Lewis (1980c). The results of the present study suggest that OH 8 is perhaps not as markedly different from KNM ER-813 (as much as can be determined in view of the damaged nature of the latter fossil specimen), but certainly it is less human-like, in trochlear morphology, than the East Turkana specimen, tending to resemble more the Kromdraai talus. Thus, the present analysis of trochlear form perhaps gives tenta-