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Morphological variation in the metatarsal bones of selected recent and pre-pastoral humans from South Africa

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CHAPTER 1 – VARIATION IN THE HUMAN METATARSUS

1.1 Background to the current study

1.1.1 Introduction

Previous studies of human pedal evolution have concentrated predominantly on osteological comparisons of different hominoid species, both extinct and extant, from the Pleio-Pleistocene to the present. Most of these studies have been conducted on the rear-foot elements (e.g. Wood, 1974; Lisowski *et al.*, 1974, 1976; Susman, 1983; Kidd, 1995), with little extensive work as yet on the metatarsal bones. It is not at present clear as to what normal variations exist, nor what abnormal variations have occurred during more recent times in the feet of contemporary humans. The intention of the current study was to investigate the general patterns of morphological variation in terms of "size" and shape", and identify morphological traits in the metatarsus of selected recent human subgroups. In addition, pre-pastoral human specimens of early South African Holocene antiquity were also studied. Pre-pastoral specimens i.e. older than 2,000 years BP (Hausman, 1982; Roberts, 1989) were selected to exclude variables such as footwear and modern substrates. In order to contextualize the scale of variation within and between the human subgroups, a morphometric preliminary study comparing selected hominoidea (*Homo sapiens, Pan troglodytes, Gorilla gorilla and Pongo pygmaeus*) utilizing existing linear metrical data was undertaken.

1.1.2 The adaptive transformation of the human foot and metatarsal variation

The evolution of the bony morphology of the human foot is a fundamental element in the adaptive transformation that produced the human lineage (Olsen & Seidel, 1983). Erect posture and a bipedal mode of locomotion changed the lifestyle of the earliest humans and freed the upper limbs from their traditional function of supporting the body and the structure of the human foot is fundamental to bipedalism. By freeing the forelimbs from locomotion it was possible for ancestral humans to use them more extensively to interact with, manipulate and modify their environment. This may have been a significant contributing factor in the evolution of the manufacture and use of complex tools which may have further resulted in specialization of the neural faculties of early hominins. The utilization of tools and the enlargement of the cerebral cortex could have also played an important role in the evolution of the human vocal tract, which allowed the evolution of more human-like language, which would have improved communication between individuals (Laitman *et al.*, 1979). Of all these evolutionary specializations that define the human species, the foot is considered to be one of the most important and is pivotal in allowing the evolution of the first of these changes - bipedalism (Morton, 1926; Morton, 1935; Jones, 1944; Day & Napier, 1964; Olsen & Seidel, 1983). Early studies of the evolution of the human foot such as that of Morton (1935), outlined three principal changes required to transform the hypothetical arboreal or terrestrial quadrupedal ape-like foot into the habitually terrestrial bipedal human foot. These are; 1) a transfer of locomotor function from the arms and hands to legs and feet, 2) an increase in the intrinsic base of support within the foot by a lowering of the heel to the ground, and

3) cessation of grasping ability whereby the foot becomes a lever for lifting and propelling the body. Regardless of its origins, over the course of hominin development, the human foot has evolved in a number of areas. These are an elaborate plantar aponeurosis, strong plantar ligaments, longitudinal arches, an enlarged musculus flexor accessorius, an adducted (non-opposable) hallux, a remodeled calcaneocuboid joint, a long tarsus, and shortened lesser toes (Susman, 1983). In all of these evolutionary adaptations, the metatarsus plays an important role in facilitating effective bipedal locomotion.

In the majority of the anatomical texts, the metatarsal components of the human foot are described as having a similar morphology. The study of the bones themselves, however, reveals frequent morphological variations from the typical description (Singh, 1960; Ajmani *et al.*, 1984). Some of these variations (in living humans) resemble features found in other hominoid species in which such features are typical. This suggests that, within the human metatarsus, some variation may result in a change in function not necessarily suited to effective human bipedalism. Ordinarily, the modern human metatarsus is structurally so well adapted to prolonged walking and standing, that deviations from its established morphology may produce debilitating clinical manifestations best described as pathological.

While morphological variants in metatarsals of human subgroups have been identified and described by Singh (1960), Sarrafian (1983), Gudas (1992), Landers (1992) and La Porta *et al.* (1994), the extent of normal variation is poorly known. Metatarsal dysfunction and bony pathologies in contemporary humans are common (Kelikian, 1965) and may well be associated with morphological variants. While

shoes and unnatural walking surfaces are a key aspect of human culture, at least in recent times, it is not clear to what extent footwear and other environmental factors such as hard unyielding surfaces have influenced foot function and subsequent pathological changes. As early as 1930, Hallisy (1930) demonstrated that great variability exists in the muscles of the human foot. Olson & Seidel (1983) state that this variability represents an evolutionary compromise between the diversity of substrates and footwear, and the need to maintain the foot's primary structural adaptation to bipedal walking and standing; there is little evidence to support this hypothesis.

1.1.3 The origins of forefoot pathology

Pathology is defined as a medical science concerned with all aspects of disease, but special reference to the essential nature, causes, and development of abnormal conditions, as well as the structural and functional changes that result from the disease process (Stedman's Concise Medical Dictionary). Palaeopathology is the study of diseases in ancient populations as revealed by skeletal remains and preserved soft tissue (Steinbock, 1976; White, 1991). Pathological changes observable in bones such as metatarsals, result from an imbalance in the normal equilibrium of bone resorption and formation. This imbalance may occur as a result of many factors, including mechanical stress, changes in blood supply, inflammation brought about by infection, hormonal, nutritional and metabolic imbalances and tumors (Mensforth *et al*., 1978*)*. Virtually every disease has a multifactorial origin, genetic endowment and environmental influences playing a role in the manifestation of pathology (Tighe &

Davies, 1984). It is clear that within the context of examining osteological material, the manifestation of pathology is usually complex, often resulting in a variation in morphology which may be difficult to differentiate from functional or epigenetic variation. A summary of the broad classification of osteological pathology is set out in Table 1.1.

In order to undertake a study of variation, it is important to be able to recognize what constitutes normal variation in morphology and what is pathological, and once identified, what the possible origins of these pathological changes are. Kelikian (1965) cited T.G. Morton as ascribing pain of the forefoot to the comparative shortness and mobility of the fifth metatarsal bone. About a century later D.J. Morton also drew attention to the brevity and hyper mobility of the first metatarsal and considered this to be the main cause of forefoot pain (Morton, 1927). Forefoot pain, or metatarsalgia, has subsequently been well documented in many texts (e.g. Kelekian, 1965; Inman & Mann, 1973; Helal & Wilson, 1988; Hetherington, 1994; McGlamry *et al.*, 1992). Of all forefoot pathologies that manifest clinically, the medial (cranial) column appears to be the most commonly affected, more particularly the first metatarsophalangeal joint (Du Vries, 1973). Kidd (1995, 1998) has suggested that the specialist modifications pertinent to human pedal structure from that of the primitive ape-like foot took place initially in the lateral (caudal) column developing a more rigid foot specifically adapted to the stresses of walking short distances bipedally. He then went on to suggest that changes to the medial (cranial) column followed later (see medial and lateral columns of the foot in Figure 1.1). This may well present a hypothesis as to some forefoot pathology being

Table 1.1: Summary of the broad classification of pathology that may manifest in pedal skeletal material.

1. Trauma	• Fracture • Artificial Deformation
2. Infectious Disease and Associated Manifestations	• Osteomyelitis • Periostitis • Tuberculosis • Treponemal Infections
3. Circulatory Disturbances and Hematopoietic Disorders	• Necrosis
4. Metabolic and Hormonal Imbalence	• Scurvy • Rickets • Osteoporosis • Endocrine Disturbances
5. Arthritis	• Osteoarthritis • Rheumatoid Arthritis • Gouty Arthritis
6. Tumours	• Primary Tumours: benign • Primary Tumours: malignant

Figure 1.1: The medial and lateral columns of the foot. The shaded area represents the more stable lateral column

of ontogenetic origin. A mild delay or arrest in ontogenetic development could lead to defects on the medial side of the foot, rendering it more ‘ape-like’. Such a pathological state would be characterized by the medial column possessing essentially ape-like characteristics; those of mobility, though in humans, as a function of abnormality (Kidd, 1998). Typical pathologies may include bunion or hallux valgus deformity (Clough & Marshall, 1985), together with a large range of motion in the talo-navicular joint. This would seem to suggest a case where ontogeny recapitulates phylogeny (Gould, 1977). Another pedal example of this evidence was found in the OH8 talus (Lisowski *et al.*, 1976; Kidd *et al.*,1996).

Occasionally atavistic features occur in the first ray, considered to be a variant of the normal first intermetatarsal angle (*metatarsus primus varus*) originally defined as ‘metatarsus ataviticus’ (Morton, 1927; Moorhead & Wobeskya, 1995). This feature resembles more closely that of the prehensile arboreal foot of the apes; in addition it reflects some of the tarsometatarsal articular features of, for example the chimpanzee, with a convex joint and extreme mediolateral orientation of the hallux (Olson & Seidel, 1983; Susman, 1983; Aiello & Dean, 1990). They are also reminiscent of the less convex joint with a more dorsoplanter orientation of early humans and pre-humans such as the Olduvai Hominin (OH8) and modern *Homo sapiens sapiens* as described by Susman (1983) (Figure 1.2). This feature certainly makes the hypothesis suggested by Kidd (1998) seem plausible when one considers that hyper mobility of the first ray appears to increase with an increase in the first intermetatarsal angle (Greenberg, 1979). These features of segmental hypermobility of the medial column are also associated with increased pronation (abduction,

Figure 1.2: The first metatarsal of chimpanzee (a), Olduvai Hominin 8 (b), and human.. After Susman (1983).

eversion and dorsiflexion) of the foot, which when excessive, has been assumed to be the underlying cause of many foot problems as expressed by, for example, Greenberg (1979).

1.1.4 The reason for the current study

The importance of this study was to determine the extent of metatarsal variation in modern humans and to place morphological and osteogenic variation into a temporal perspective of individuals that have not been influenced by contemporary variables such as footwear.

1.1.5 Objectives of the present study

The literature suggests that while morphological variants in human metatarsals are common, the extent of normal variation is poorly known. Metatarsal bone pathologies in contemporary humans are also common and may be associated with some of these morphological variants. It follows, that the extent of the influence that morphology, pathology and environment have on each other is uncertain.

The objectives of this study were essentially threefold:

1. To identify the extent of morphological metatarsal variation within and between selected human populations. The patterns of morphological variation were determined in terms of:

1.1 An assessment of general morphology by means of a morphometric analysis.

1.2 Variation in specifically identified morphological features by means of a non-metric analysis.

2. To identify any obvious pathological changes in the metatarsus, and determine if there are any correlations between these and variation in morphology.

3. To place these morphological and pathological variants into a temporal context (recent and pre-pastoral *Holocene*); and determine to what extent morphological and pathological correlates are influenced by lifestyle (shod and unshod).

In order to investigate the objectives, the following working hypotheses were proposed:

1.) The general patterns of morphological discrimination between the metatarsals of the human populations are similar.

2.) There are correlations between morphological features and pathological changes.

3.) There is a shift in the incidence of metatarsal bone pathology with the advent of the diversity of substrates and footwear.

1.2 A review of variation in the metatarsal bones

These bones represent the most significant portion of the forefoot and the structures in the forefoot most prone to osteological changes (Dagnall, 1994). A review of their typical descriptions and known variations follows:

1.2.1 General characteristics

The five metatarsal bones are described as miniature long bones; they are subdivided into a shaft and two extremities. The shaft is prismoid in form, tapers gradually from the tarsal to the phalangeal extremity, and is slightly curved longitudinally, so as to be concave below and slightly convex above (Gray, 2002). The posterior extremity or base, is generally wedge shaped, articulating by its terminal surface with the tarsal bones, and by its lateral surface with the contiguous bones with the exception of the most medial and lateral metatarsals. The anterior extremity, or head, presents a terminal rounded articular surface, oblong in shape when viewed from above, and extending further backwards on the inferior surface, more so than on the superior surface. Its sides are flattened, and present a tubercle for ligamentous attachment. Its inferior surface is grooved in the middle line for passage of the flexor tendon (Gray, 2002).

1.2.2 First metatarsal

The first ray is a functional metatarsal unit consisting of the first metatarsal and medial cuneiform bones (Hicks, 1953; Root *et al.*, 1977; D'Amico & Schuster, 1979; Sarrafian, 1983). It represents an essential functional component of the forefoot and plays a major role in the transmission of body weight during locomotion (DuVries, 1973). Morton (1924, 1927, 1928, 1935) demonstrated the importance of the first metatarsal segment in the maintenance of the medial longitudinal arch. Anatomically the first ray consists of the collective articulations between the navicular, medial cuneiform, intermediate cuneiform, and the base of the first

metatarsal (Draves, 1986; Sarrafian, 1993). This functional unit has motion that occurs at the first metatarsal medial cuneiform joint, the medial cuneiform-intermediate cuneiform joint, and the medial cuneonavicular joint (D'Amico & Schuster, 1997; Grode & McCarthy, 1980; Oldenbrook & Smith, 1979). However, the metatarso-cuneiform joint does not move much, due to muscle and ligament attachments to both the metatarsal base and medial cuneiform. The tibialus anterior inserts into both the first metatarsal base and medial cuneiform inferomedial surface (Romanes, 1989). The peroneus longus inserts into both the first metatarsal base and medial cuneiform lateral side, the important functional effects of which were investigated by Johnson and Christensen (1999). The plantar first metatarsocuneiform ligament has been described as a major component in stabilizing the first metatarsal during weight-bearing (McCarthy, 1983; Mizel, 1993). These individual joints essentially move in unison about a common axis of motion, and function as a single unit. The predominant motion of the first ray is in the sagittal plane (dorsiflexion and plantarflexion). This motion is considered an important component of the normal function of the foot during gait (Hicks, 1954; Roukis *et al*., 1996). In a classic investigation by Hicks (1953), he found minor coronal plane inversion occurring with dorsiflexion and eversion with plantarflexion. This motion was later confirmed by other investigators (Ebisui, 1968; Kelso *et al.*, 1982; Saltzman *et al.*, 1996) using various methods on cadaveric specimens. However, other investigations report contrasting first ray movements (D'Amico & Schuster, 1997; Oldenbrook & Smith, 1979). This appears to conflict with the findings by Hicks (1953), but on closer examination of the data, it becomes evident that tarsal movements induced by the

rotation of the tibia alter the net movements observed in the first ray. This is probably achieved through a coupling effect from the more proximal joints (Johnson & Christensen, 1999).

The first metatarsal bone in humans is substantially more robust than the lesser metatarsals (Archibald *et al.*, 1972). It has a base that is kidney or reniform shaped which distinguishes it from the lesser metatarsal bones (Anderson, 1962; Draves, 1986; Aiello & Dean, 1990).

1.2.2.1 Variation in the first metatarsal

The shape of the first metatarsal head may be described as "round", "square" (sometimes referred to as oblique), or "square with a central ridge" as noted by Gudas (1992), Landers (1992) and La Porta *et al.* (1994), with the round configuration being the most common (La Porta *et al.*, 1994). Illustrations of these are to be found in Chapter 2, Figure 2.6. This appears to influence the stability of the first metatarsophalangeal joint and has been associated with Hallux Abducto Valgus, Hallux Limitus and Ridgidus (Brahm, 1988; Felner & Milson, 1995; Du Vries, 1973; Landers, 1992). However, the classification of these metatarsal head shapes is somewhat subjective.

A laterally sloped first metatarsal head has been associated with congenital Hallux Abducto Valgus (Du Vries, 1973) and is also known as the "proximal articular set angle" (PASA), which when laterally sloped is associated with an increased Hallux Abductus angle (Meyer, 1979; Landers, 1992; Vittetoe *et al.*, 1994; La Porta, 1994). Even though this is essentially a radiographic measurement, Meyer (1979)

used the PASA to investigate Hallux Valgus in two ancient populations (Pecos Indian and Yugoslav peasants), taking measurements from skeletal material. It is unclear exactly how these measurements were taken and the study was inconclusive. However, the literature does suggest that some of these morphological variants appear to have functional correlates; these may predispose the first ray and related structures to pathological osteological variation.

The proximal articular surface of the first metatarsal is commonly described as kidney-shaped with the hilum lying on its lateral margin (Wood Jones, 1946). An occasional variant of the proximal articular surface is a bipartite articular surface (Singh, 1960; Ajmani *et al.*, 1984; Draves, 1986). The joint surface is sometimes divided into upper and lower halves by a narrow band of non-articular bone (Singh, 1960; Ajmani *et al.*, 1984; Aiello & Dean, 1990). Singh (1960) in a study of the metatarsals of 100 skeletons found that the typical kidney shaped area was found in only 15 specimens. In the majority (60 specimens), the medial margin of the surface was slightly indented. This encroachment on the articular area was marked in 25 specimens, thus producing two partially united, upper and lower facets. This appearance was accentuated in some specimens by the presence of a non-articular transverse ridge resulting in a separation of the articular surface into an upper and lower portion. This ridge may occur even in the absence of a notch in the medial margin. The proximal surface is usually gently concave, but in the presence of the transverse ridge, however, the concavity is no longer continuous, there being separate upper and lower concave areas. Illustrations of these variants may be found in Chapter 2, Figure 2.7.

The corresponding variation in the anterior facet of the medial cuneiform was described by Ajmani *et al.*, (1984). In a study of 100 cuneiform bones, only 31 specimens had the typical reniform description. In the same study, 6 specimens had a transverse non-articular ridge completely subdividing this surface into two separate articular surfaces. Ajmani *et al.*, (1984) interpreted this to be an accentuation of two partially united upper and lower facets, a condition observed in 49 specimens.

There is a variable facet on the lateral aspect of the base for articulation with the second metatarsal base which has also been described as an occasional articulating facet (Singh, 1960; Sarrafian, 1983; Draves, 1989; Aiello & Dean, 1990). Singh (1960) found that variation in this facet is common and classified them as a smooth facet with well defined margins, a smooth area with indefinite margins and no indication of an area for the second metatarsal. This study by Singh (1960) revealed that, of the 100 specimens, 21 had well defined margins, in 40 specimens it is represented by a smooth area with ill-defined margins and the remaining 39 bones had no indication of an area for the second metatarsal (see Chapter 2, Figure 2.8) . Romash *et al.*, (1990), in a roentgenographic study of 118 subjects described these variations of the articular facet as Type I with no articular facet (35%), Type II with transitional lateral articular facet (38%) and Type III with a well-developed lateral articular facet (27%). Wanivenhaus and Preterklieber (1989), in a study of 100 cadaveric feet, observed an intermetatarsal joint or facet in 53%, mainly in the large male metatarsals. This may be a feature of a non-opposable hallux in humans (Day & Napier, 1964). Fritz and Prieskorn (1995) using the classification by Romash *et al.* (1990), demonstrated a statistically significant difference between the presence or

absence of the articulating facet and their average first inter-metatarsal angle. This angle appears to be larger when this facet is absent.

This feature of the articulating facet is not found in any of the extant apes. However, Lewis (1980) warned that ligamentous tuberosities are found on gorilla metatarsals. These could be confused with true articular facets. It should be noted, however, that gorillas are also the apes which next to humans have the least opposable great toe (Aiello & Dean, 1990). Some of the extinct hominins, however, have what appears to be this articulating facet. The Olduvai Hominin 8, for example, has a well defined area that appears to be for articulation with the second metatarsal. Lewis (1980) suggests that even though this impression is analogous with the articular facet in humans, it is basically a ligamentous impression. Another example is that of SKX 5017 (presumed *Paranthrobus robustus*) which has a smooth area with indefinite margins, apparently a contact area for the second metatarsal.

The obliquity of the first metatarsocuneiform joint appears to influence the first intermetatarsal angle. According to Kelekian (1965) and McCrea & Lichty (1979), an increase in intermetatarsal angle occurs with an increase in obliquity. In contrast, Saragas & Becker (1995) found no linear relationship between first metatarsocuneiform angle and intermetatarsal angle. Thus, there appears to be some doubt about any correlation between these two features.

Fritz & Prieskorn (1995) suggested that the shape of the first metatarsocuneiform joint has some effect on motion of the first ray. Similarly, a curved cuneometatarsal configuration in the transverse plane instead of a transverse anterior articular surface of the medial cuneiform may be associated with instability

and hypermobility (Kelikian, 1965). Wells (1930-31), from his comparisons of the feet of Europeans, Africans and San, suggested that the anterior articular facet of the medial cuneiform was more oblique in San and Africans than in Europeans. It is unfortunate that some of these observations appear to have been used to exaggerate "racial" differences, implying that these differences represent different stages of evolution in different human subgroups. Nevertheless, the extent of variation if present will be examined in this study.

1.2.3 Second metatarsal

The second metatarsal is the longest of the five metatarsal bones. Its base is firmly wedged between the first and third cuneiforms, providing for extra stability at the articulation between the second cuneiform and the second metatarsal (Draves, 1986). The proximal triangular surface for articulation with the intermediate cuneiform shows a distinct concavity, more marked towards the lateral side. This metatarsal has two articular facets on its lateral side adjacent to its base and variably a single facet on its medial side, corresponding to the variable first metatarsal facet and the medial cuneiform (Singh, 1960; Aiello & Dean, 1990).

1.2.3.1 Variation of the second metatarsal

The medial side of the base of this bone usually shows a facet on its dorsal part, for the medial cuneiform. Singh (1960) found this facet to be very variable in size. The proximal part is either flat or slightly convex and this may be the only part present. The distal part, when present, is gently concave. The facet generally extends

up to the proximal margin of the base to become continuous with the facet for the medial cuneiform. In the study by Singh (1960), however, it is partially cut off from this area by a non-articular notch in 8 specimens and completely cut off in 4 specimens. The facet is absent in 8 specimens but one of them shows a pressure facet in this situation.

More inferiorly and distally, the medial side of the base of the second metatarsal shows a definite smooth facet, with well defined margins, for articulation with the first metatarsal in 12 specimens (Singh, 1960). An elevated area, often rough is present at this site in 57 specimens (Singh, 1960). The remaining 31 bones show no indication of contact with the first metatarsal. Nine variations of the facets on the lateral side of the base of the second metatarsal for articulation with the third metatarsal and the lateral cuneiform are described. Illustrations of these may be found in Chapter 2, Figure 2.8:

(1.) In 49 specimens there are two, dorsal and plantar, facets separated by a non-articular area. The proximal parts of both facets are beveled off. The distal areas, for the third metatarsal are always larger and better defined than the proximal areas, for the lateral cuneiform, the latter being generally small.

(2.) In 22 specimens, the plantar facet is not beveled and articulates only with the third metatarsal.

(3.) Six specimens show only the proximal beveled part of the plantar facet, there being no plantar facet for the third metatarsal.

(4.) The entire plantar facet is absent in 9 specimens.

(5.) In 3 specimens, the entire plantar facet and the proximal part of the dorsal facet are absent, a non-articular strip taking the place of the later.

(6.) In 5 specimens, the proximal beveled part of the dorsal facet is alone absent. Again it is replaced by a non-articular strip.

(7.) In one specimen the proximal beveled parts of both plantar and dorsal facets are absent. The plantar facet reaches the proximal margin of the base to become continuous with the area for the intermediate cuneiform, but the dorsal facet is separated from the later by a non-articular area.

(8.) In another specimen, the planar facet is similar to that described in (7.) above, but the entire dorsal facet is missing.

(9.) In 4 specimens, the plantar and dorsal areas for the lateral cuneiform are continuous with one another, those for the metatarsal remaining separate.

The proximal parts of the facets, for the lateral cuneiform, are always flat, but the distal parts, for the third metatarsal, are occasionally somewhat concave.

1.2.4 Third metatarsal

The third metatarsal is shorter than the second metatarsal and has an articular facet that raps around its base from the medial side of the proximal shaft adjacent to the base to the lateral side of the shaft. The facet on the lateral side of the shaft is larger than that of the medial side (Aiello & Dean, 1990). The base is also pyramidal in shape, with its apex pointing plantar-medially (Draves, 1989) and is very constant in shape being flat in contrast to the base of the second metatarsal (Singh, 1960; Sarrafian, 1983), in fact, this feature alone frequently suffices to distinguish the two

bones from one another. The shaft of this bone usually shows a slight convexity towards the medial side.

1.2.4.1 Variation of the third metatarsal

Singh (1960), did however describe three various forms of facets on the medial side of the base and two on the lateral side. The medial side of the base shows two flat facets, plantar and dorsal, for the base of the second metatarsal. Of the 100 specimens examined by Singh (1960), 57 had this configuration. The facets reach the proximal margin of the base to become continuous with the articular surface for the lateral cuneiform. The dorsal facet is always the larger of the two. The plantar facet is at times barely perceptible. Both plantar and dorsal facets are absent in two specimens. The plantar facet is absent alone in 41 specimens; in two of them the dorsal facet does not reach the proximal margin of the base from which it is separated by a non-articular strip. The lateral side of the base of this bone presents a very constant facet on its dorsal part for the fourth metatarsal. This facet is always conspicuous. In 36 specimens, it is oval and does not reach the proximal margin of the base. In 64 specimens it reaches that margin to become confluent with the area for the lateral cuneiform, and the facet has the appearance of an oval with its proximal part cut off. The facet is usually concave but may be flat (Singh, 1960).

1.2.5 Fourth metatarsal

The morphology of the base of the fourth metatarsal is quadrilateral. The proximal surface, slightly convex, articulates with the cuboid (Sarrafian, 1983). The

fourth metatarsal is generally shorter than the third, the facets on the base are of more equal size and the medial facet is frequently not contiguous with the basal (proximal) facet (Aiello & Dean, 1990).

1.2.5.1 Variation of the fourth metatarsal

Singh (1960) found three varieties of basal facets on the medial side and are to be found in Chapter 2, Figure 2.8. There is usually an oval, flat or gently concave facet on the medial side. In 61 of the 100 specimens studied by Singh (1960), there is an oval facet not reaching the proximal margin of the base, and not subdivided into two parts. The entire facet is for the metatarsal, there being no facet for the cuneiform. In 22 specimens the facet was again oval, not reaching the proximal margin of the base, but is subdivided into two parts. In 15 specimens the facet reaches the proximal margin to become continuous with the articular area for the cuboid. It is subdivide into proximal and distal parts. The proximal part of the facet, when present, is generally small. In 2 specimens no facet was seen on the medial side of the base.

The lateral side of the base of the fourth metatarsal shows a concave, somewhat triangular facet. It is always present and varies only slightly in size and shape (Singh, 1960). A constant deep notch is present in front of it, and although also found in metatarsals two and three, is the deepest in metatarsal four (Sarrafian, 1993).

1.2.6 Fifth metatarsal

Next to the first, this is the most distinctive metatarsal. The basal articular facet is at a considerable angle to the shaft axis and lateral to this facet is a large non-

articular tuberosity. The posterior part of the shaft is also compressed in the dorsoplantar plane and the lateral margin of the bone traces a markedly curved path from the metatarsal head to the tuberosity (Aiello & Dean,1990). The base of the fifth metatarsal is pyramidal to triangular in shape with its apex pointing plantar-laterally. This apex is elongated as the styloid process of the fifth metatarsal (Draves, 1989). The fifth metatarsal bone reveals few variations from typical descriptions. The shaft of the bone generally shows a well marked convexity to the medial side. Singh (1960) found that the facets for the fourth metatarsal and for the cuboid are constant in size and shape.

1.2.7 Variable mid-shaft geometry

The cross-section of human long bone diaphyses at the mid-shaft, can assume a variety of different shapes (Martin & Saller, 1957; Lazenby, 1996; Trinkaus *et al.*, 1994; Ruff *et al.*, 1994). The dynamic relationship between mechanical loading and cross-sectional geometry in long bones is well established (e.g. Radin *et al*.,1982; Currey, 1984; Martin & Burr, 1989; Hou *et al.*, 1990; Stock & Pfeifer, 2001). The metatarsals are no exception, with predominantly the second to fourth presenting with obvious variation in mid-shaft geometry (Robling & Uberlaker, 1997).

1.3 Large scale differences between selected hominoidea

In order to contextualize metatarsal bone variation within the human species, relevant comparisons to both extant apes and extinct hominins in preceding paragraphs have been made. To further understand the relationship between

morphology and the function of these bones, a review of the major differences between related hominoidea follows.

1.3.1 General comparative morphology of the metatarsal heads

In humans the articular surfaces on the heads of the metatarsals are separated from the epicondyles by a greater distance than in apes. In animals in which the closed-packed position of the metatarso- or metacarpophylangeal joint is in *flexion*, the plantar aspect of the metatarsal or metacarpal head is wide (medio-lateral dimension) and there is an obvious narrowing of the head near its dorsal margin. This configuration characterizes fingers and toes of all the apes and humans with two notable exceptions: (1) the principle *weight-bearing* fingers of the African 'knuckle walkers', in whom the metacarpal heads are the widest on their dorsal aspect (Susman, 1979) and (2) the heads of metatarsals I–IV in humans, which are also widened dorsally (Susman *et al.*, 1984). The African apes load their fingers (principle rays III and IV) with the metacarpophalangeal joints in dorsiflexion; this is the closed packed position, thus the articular surfaces are expanded medio-laterally on their dorsal aspects. Human metatarsal heads are also expanded dorsally (see comparisons with other hominoids, Figure 1.3) indicating the enhancement of dorsiflexion at toe-off and a reduced emphasis on toe flexion in human locomotion (Susman, 1983). The significance of free dorsiflexion of the toes in walking was established by Bojsen-Møller and Lamoreux (1979). However, in the first metatarsal head in both humans and the apes, the superior width of the head is generally narrower than the inferior. In the apes this difference between the superior and inferior width is marked. In the

Figure 1.3: Anterior view of the metatarsal heads I –V.

humans, the sides of the head are generally more ‘parallel’ to each other. Susman and Brain (1988), illustrate this feature by an index that compares the mediolateral diameters, superiorly and inferiorly of the first metatarsal of SKX 5017 to chimpanzees and humans. These two measurements in the fossil yield an index of 61.0. This value in humans is 84.8 (n = 12 males; S.D. = 3.62), in chimpanzees it is 69.0 (n = 15 males; S.D. = 7.8). Thus, while humans have a hallucal metatarsal that is mediolaterally broad on the dorsal (superior) surface, neither SKX 5017 nor any of the apes have a similarly broad head.

Figure 1.4 reveals that human foot-contact differs markedly from that of chimpanzees (and the other apes), which do not toe-off on the hallux (Susman, 1983). Without the human toe-off mechanism, there appears to be no need for an enlarged hallucal metatarsophalangeal joint that close-packs in the dorsiflexed position (Susman *et al.*,1984, 1985). In the chimpanzee, for example, additional dorsiflexion is achieved through a ‘midtarsal break’ (Elftman, 1944; Susman, 1983). Another feature essential for effective dorsiflexion of the metatarsophalangeal joint is the great extent to which the articular surface continues onto the dorsum of the head.

The non-human apes in contrast, do not display a similar dorsally extended articular surface; instead the dorsal-most portion of the metatarsal head of apes appears flat in profile (Susman & Brain, 1988; Aiello & Dean, 1990). Interestingly, the afore mentioned fossil, SKX 5017, displays a very human-like dorsally extended articular surface.

In the human lesser metatarsals there is also a resulting sulcus, or depression, between the head and shaft (Aiello & Dean, 1990). This relates to an increased

Figure 1.4: Foot contact sequence during bipedalism in human and chimpanzee. Arrows show the characteristic mid-tarsal break at heel lift in the chimpanzee in contrast to the more ridged mid-tarsal complex in humans and the plantar-flexed toes of the chimpanzee at push off in contrast to the dorsiflexed toes in humans. (After Susman, 1983)

potential for dorsiflexion at the metatarsophalangeal joints. This is essential to a bipedal gait where the metatarsophalangeal joint acts as a fulcrum so that the posterior part of the foot can "roll" over during the toe off phase of gait.

The transverse shape of the first metatarsal head in humans is unique among the hominoids in having a relatively flat contour from side to side when compared to the apes (Susman *et al.*, 1984; Aiello & Dean, 1990), SKX 5017 and the Hadar fossils A.L. 333-115 (Figure 1.5) which have a highly convex surface reflecting enhanced transverse plane mobility of the hallux suited to an arboreal lifestyle (Susman *et al.*,1984).

1.3.2 Orientation of the medial metatarsal-cuneiform joint

In humans this joint lies in a plane opposite to that characteristic in the apes. The medial edge of the human joint projects further posteriorly than does the lateral edge. The opposite condition characteristic of the apes accentuates the medial projection, or abduction, of the great toe in apes. The anterior articular surface of the medial cuneiform is markedly different from that of the apes with prehensile great toes (Aiello & Dean, 1990). See Figure 1.2 for a comparison of the human, chimpanzee and Olduvai hominin. Leboucq, as early as 1882, had pointed out that the divergence of the first metatarsal was due to the extreme angle made by the plane of the distal articular facet of the cuneiform bone with the long axis of the foot. Leboucq (1882) studied the shape of the innermost cuneiform in human embryos and found that in 20 millimeter specimens the tibial border of this bone was shorter than its fibular margin, which made its distal articular facet slope obliquely forward. This

Figure 1.5: Dorsal view of the metatarsal heads I – V (from left to right) in SKX 5017, A.L. 333 – 115, bonobo, modern human, and gorilla. Metatarsal head I in humans is unique among the hominoids in having a relatively flat contour from side to side, while in the apes and fossils the same surface is highly convex. (Adapted from Susman *et al.*, 1984)

in turn induced the first metatarsal to diverge inward, away from the lesser metatarsals. As development progressed, the tibial side of the cuneiform bone grew more rapidly than the fibular border, gradually straightening the plane of the distal articular facet until, in 40 millimeter embroyos it assumed the position it occupied in adults.

However, in contrast to contemporary literature, Leboucq made no attempt to correlate “bunions” with the oblique setting of the medial cuneometatrsal joint. This is an example of a form of *peramorphic heterochrony*, in which the first intermetatarsal angle in the prenatal human approaches that of the adult prehensile arboreal foot of the apes. More precisely, a morphology transcends or moves beyond adult stages of its ancestors or primitive form (Shea, 1983). In this sense “ontogeny recapitulates phylogeny”, meaning that embryonic development repeats the pattern of evolutionary history (Gould, 1977). There is evidence for *peramorphic heterochrony* in several other areas of the foot (e.g. Lisowski, 1967; Manley-Buser, 1991; Kidd, 1999). Curiously, this is not the case in some other parts of the body (e.g. the skull) where *paedomorphic heterochrony* has been reported. In this instance, the human foot is considered *gerontomorphic* and the human skull, *neotenous* (maintaining juvenile features).

McCrea & Litchy (1979) in their radiographic study, compared first intermetatarsal angles with the medial and lateral lengths of the first metatarsal. Their findings concluded that there was an increase in intermetatarsal angle when the medial first metatarsal aspect approaches or exceeds equality in length of the lateral aspect.

1.3.3 Relative robusticity of the metatarsals

Robusticity of the metatarsals is an expression of their absolute shortness and relative thickness and the dominance in relative robusticity is an important feature of bipedalism in humans. This dominance was expressed with a formula by Day & Napier (1964) in modern man as 1>5>4>3>2 which they contrasted to the Olduvai individual (OH8) with an estimated robusticity formula of 1>5>3>4>2. Day & Napier (1964) have suggested this to be either an individual variation or to represent incomplete evolution of the *Homo sapiens* pattern of metatarsal robusticity. Archibald *et al.* (1972) in their observations of both Native American and Pongid metatarsal patterns, show the former to be the most probable interpretation. Almost half of the *H. sapiens* specimens (44%) had other than the 1>5>4>3>2 pattern, showing eight distinct formula permutations. Five different formulae were obtained from *Pan troglodytes* and three from *Gorilla gorilla*. The substantial variability in metatarsal robusticity pattern characterizes both *Homo* and the apes, but in both groups a distinct gradient in relative robusticity of metatarsals 2 – 5 can be detected, and its direction is opposite in *Homo* and the other two genera (Archibald *et al*., 1972). This difference is almost certainly related to different locomotor requirements. Bipedal gait delivers a substantial load on the fifth metatarsal during weight bearing and this load shifts to the first metatarsal during toe-off (Inman & Mann, 1973).

1.3.4 Torsion of the shaft

In humans, the heads of the metatarsals have rotated in relation to their bases to lie squarely on the ground (see Figure 1.6). In apes, the head of the first metatarsal

Figure 1.6: Transverse sections through the metatarsals of a gorilla foot and a human foot.. After Morton (1922). In the gorilla metatarsus, both the bases (dotted outlines) and heads (solid outlines) are elevated in line with the transverse arch of the foot. In humans the metatarsal bases are elevated but the metatarsal heads are on the ground.

is orientated towards the other metatarsals with the second to fourth orientated toward the first. In humans, there is very little torsion in the first, with progressively more torsion from the second to fifth. The opposite occurs in the apes where there is progressively less torsion from the second to fifth allowing the forefoot to lie in an inverted position. These relationships can be seen in Figure 1.7. The human foot is unique in having both a transverse and longitudinal metatarsal arch or, more precisely, being shaped like a half dome with its hollow surfaces facing both downward and medially. Other primates have only the transverse arch, their feet being flat in the longitudinal direction. Humans, by having the metatarsal torsion increase toward the lateral side of the foot, allow for the orientation of the proximal articular surfaces to be more medially orientated from second to fifth metatarsal with the metatarsal heads in a planter grade position, arches are formed in both the sagittal and coronal planes.

1.4 A consideration of variables that influence morphology

1.4.1 The relationship between *form* and *function*

As is the case with *Wolff's Law* of bone remodeling (Wolff, 1892), the relationship between *form* and *function* is one of the most thoroughly accepted principles of biology. Thus the *form* of a biological component is closely related to its intended *function*, or functions. This also suggests that a particular function of a bone, over time, may change form (Wolff, 1892). The problem in studying the exact nature of variation and differences in the form of skeletal material, lies in that it may

Figure 1.7: Comparative series of plantar surfaces, foot skeletons, and distal view of the metatarsals, illustrating planes of flexion and directions of torsion. Each series aligned according to the functional axis of the foot. (Adapted from Morton, 1935 by Olson & Seidel, 1983).

be uncertain which came first; form or function? Form, of an epigenetic nature, may result in a particular function. That function, depending on its deviation from "normal", may in time produce modified form. Over a period of many generations, this altered form and function may in turn manifest itself as an epigenetic variant in subsequent individuals (Figure 1.8). This may present a plausible hypothesis as to the origins of some metatarsal variation in humans. Currently, it is uncertain as to what exactly constitutes normal variation. Only when this is established, can anomalies be defined.

1.4.2 The relationship between structural variability, habitual behaviours and environment

Wolff (1892), proposed a law of bone remodeling, in which bone macrostructure and microstructure adapt to their mechanical environments. Evidence has accumulated that bone structure is highly responsive to mechanical loading during life (Stock & Pfeiffer, 2001). While it has been suggested that characteristics of bone structure may be used to make inferences about behavioural patterns and intensity in past populations, the abundance of non-mechanical factors that influence bone structure complicates our ability to do so (Stock & Pfeiffer, 2001). Regardless of these complications, some osteogenic responses to mechanical loading appear to be associated with morphological variants, the interface between the foot and the technological substrate upon which it is dependent and habitual behaviour; most likely a combination of these. What is considered to be an anomaly in contemporary human feet, is often so common, that the term *anomaly* may be redefined as

Figure 1.8 : A schematic representation of the interaction between the variables influencing morphology

"atypical" in modern humans. For example, "bunions", or an abducted position of the hallux at the first metatarsophalangeal joint, is a common feature in modern habitually shod humans. It is generally believed that constrictive footwear is a major contributing factor in causing this condition. However, a predisposing morphological variant, such as an excessively adducted first metatarsal, in many cases, may determine if osseous changes develop (Lamur *et al*., 1996). The question arises as to whether the increase in the first inter-metatarsal angle was epigenetic, or acquired? Snijders *et al.*(1986) introduced a biomechanical model that assumed that forces and moments of the tendon of the flexor hallucis longus muscle at the first metatarsophalangeal joint will enhance the abducted position of the hallux, and subsequently position of the first metatarsal into an adducted position.

Modern life style involves variable walking surfaces, which may have an effect on morphology and the development of subsequent pathological changes. This compared with ancient, unshod individuals, may give an indication as to whether the lack of diversity of substrates and footwear yield similar variation as in contemporary humans. The presence or absence of relevant morphological and pathological correlates may contribute to developing a better understanding of functional variants on forefoot osteogenic changes.

1.4.3 Shod versus unshod feet

Footwear is a relatively recent development in human culture, evolving from probably simple foot coverings primarily for the protection of the feet against cold, to more elaborate devices reflecting different cultures. This has led to the habitual

wearing of footwear in some societies, even when footwear does not serve any practical purpose. Considering *Wolff's law* (Wolff, 1892), it may be assumed that with prolonged constriction and/or changes in the biomechanics of the foot, structural changes will take place. An extreme example of this is Chinese foot binding in which obvious gross deformity has occurred (Jackson, 1990). A study by Sim-Fook and Hodgson (1958) among shod and unshod Hong Kong Chinese populations mainly concentrated on defining static "deformities" of the foot, which their study concluded would develop as a result of restrictive stockings and shoes. Studies of Asian populations whose feet are habitually either unshod, in thong-type sandals or encased in non-constrictive coverings have shown increased forefoot widths when compared to those of shod populations (Ashizawa, 1997; Kusumoto *et al.*, 1996; Morioka *et al.*, 1974).

Multiple factors contribute to the complexity of shoe fit (Rossi, 1983). The arched structure of the foot may elongate with maturity; length may increase, as may width (Frey *et al.*, 1993). Similarly, shoe size may change depending on general weight gain or loss. Several anthropometric studies have indicated ethnic and/or racial differences in foot morphology (Anil *et al.*, 1997; Baba, 1975; Bernard & Stephens, 1979; Hawes *et al.*, 1994) and endorse unique shoe lasts for each population. Whilst early morphological studies made no distinction based on gender, differences have since been found and may need further exploration (Wells, 1930-31; Wunderlich & Cavenaugh, 2000). Nevertheless, it is generally accepted that, at least in western terms, female footwear with high heels and narrow toe-boxes constrict the foot and when worn habitually, result in debilitating clinical manifestations. Most

African studies have focused on foot morphology in the context of foot disorders (Barnicott & Hardy, 1955; Engle & Morton, 1931; Gottschalk *et al.*, 1980; Saragas & Becker, 1995). Specifically, hallux valgus has been examined in shod and unshod populations or related to the use of footwear (Barnett, 1962; Barnicott & Hardy, 1955; Shine, 1965). Notwithstanding that clinical manifestations could as equally be caused by altered foot function as by poor shoe fit (Schuster, 1978) or shoe biomechanics (Fuller, 1994).

A number of studies have suggested that the unshod foot is a healthier and preferable lifestyle compared to the habitually shod foot. Sensory-induced behaviour associated with the physical interaction of the plantar surface with the ground (in the unshod), or the footwear and underlying surface (in the shod) was considered by Robbins *et al.* (1988) as being an important consideration in avoidance response to heavy plantar surface loading. Robbins and Hanna (1987) reported that there was a low frequency of plantar fasciitis in barefoot populations and the high frequency of this condition in shod individuals may be associated with diminished sensory feedback as a result of footwear. Shulman (1949) concluded from a study of habitually unshod Chinese, that people who have never worn shoes have relatively few foot disorders. However, the available literature does not reveal any information on the osteological effects of shod versus unshod feet.

1.5 The pre-pastoral *Holocene* of the western and southern Cape

The coastal margins of the western and southern Cape of South Africa contain an exceptionally rich record of human occupation in the form of open-air shell

middens and cave deposits. Until about 2,000 years ago, all local inhabitants were hunter-gatherers (Hausman, 1982; Roberts, 1989; Sealy & Pfeifer, 2000; Stock & Pfeiffer, 2001). Thereafter, some people started to keep sheep and cattle, and milk and meat from domesticated animals supplemented the wild foods which they continued to collect (Parkington *et al.*, 1986). This also indicated contact with Bantu speaking people who had migrated from the north. Agriculture was not practiced in this region until after the settlement by European colonists in the mid-17th century AD. This shift to an increased dependence on plants and domesticated animals may coincide with shifts in bone mass and stature (Smith, *et al.*, 1992). Therefore the term *pre-pastoral* is used to accurately describe the early Holocene. This period also represents the South African Late Stone Age (LSA); for this purpose in the current study, these terms have been used interchangeably. These people are collectively known as Khoisan (Hausman, 1982) and are presumed to have belonged to habitually unshod forager societies.

Holocene foragers are well-suited to anthropologically relevant investigations of the relationship between general patterns of habitual behaviour and bony morphology (Stock & Pfeiffer, 2001). On the basis of ethnographic and archaeological evidence, a gender-based division of labour is assumed (Endcott, 1999). There should be less task specialization between individuals in foraging groups than are found in agricultural or horticultural societies. It can be assumed that all individuals led an active lifestyle during childhood, with some life-long participation in subsistence activities. In this context, foraging populations can be considered long-time inhabitants of their environments, and can be viewed as

relatively homogenous, both culturally and genetically. Semino *et al.* (2002) suggest that Khoisan, together with some Ethiopians, share the deepest clades of the human Y-chromosome phylogeny; arguably making these foragers a "common denominator" within the human species. Furthermore, foraging was the dominant subsistence strategy throughout most of the human past (Stock & Pfeiffer, 2001).

The Later Stone Age sample used in this study, with the exception of a single Late Pleistocene first metatarsal from Klasies river mouth (KRM 6113B), is derived from archaeological contexts from several coastal or near-coastal sites dating from 9,720 to 2000 BP (Morris, 1993; Sealy & Pfeiffer, 2000; personal examination of skeletal collections). By restricting analysis to individuals dated earlier than 2000 BP, complications relating to the pastoral dietary and behavioral shift are minimized.