CHAPTER 6 – FINAL DISCUSSION AND CONCLUDING REMARKS

6.1 Morphometric and non-metric variation combined

The reasons for using these methods of describing morphology have been discussed in Chapter 2. Relethford (1994) has found genetic and craneometric data to be in agreement and that there is limited variation in humans among major human groups. According to Sokal and Sneath (1963), there are no distinct large classes of genes affecting one group of attributes exclusively. Thus there is no theoretical reason that infracraneal, and in this case, pedal morphometric and non-metric data should not prove valuable in addressing questions concerning population relationships and the pattern and the amount of human variation. The current study suggests that the human metatarsus is variable, both metrically and in terms of non-metric traits, but not to the extent that different populations can be clearly separated. The information and conclusions drawn from these related but different analyses of morphology, are different and therefore confirm the value of using them. It has been established that the information derived from a morphometric analysis is largely dependent on the choice of variables. The key is to test, as far as possible, variables that are significant in the functional anatomy of a bone. This depends to some extent on the objective of the analysis. For example, when different species are to be investigated, the most obvious functional discrimination is that of locomotion. When a single species comprising of different subgroups is to be investigated and the broad locomotor function is known to be the same, the more subtle genetic discrimination may be the objective. This line of investigation has its limitations as other functional or potentially functional traits such as variable articular facets, tubercles or pathological
lesions may not be captured within any of the selected variables. At the same time, examining only non-metric variables do not give any indication of the extent of discrimination between groups. In the current human study, the morphometric analysis revealed the subtle but distinct discriminations between the different human subgroups, the non-metric traits revealed considerable variation within groups but broadly consistent variation between them and the identification of pathological lesions suggested differences in lifestyle.

6.1.1 The hominoid canonical discrimination

The objective of the hominoid preliminary canonical variates analysis was achieved by indicating the large scale differences between the species. Although the exact nature of the discrimination could not be determined, the broad lines of discrimination were revealing. Although the first axis held most of the canonical information, the joint information between this axis and subsequent axes was biologically meaningful. In the first metatarsal, a component of the metatarsus which plays a particularly important role in locomotion in all four species, was particularly revealing. The plot of the CV 2 “shape” related axis against the CV 1 “size” related axis, suggested that the discrimination lay in the anatomically based locomotor conclusion, clearly separating the bipedal humans from the pronograde quadrupeds. The quadrupedal apes further discriminated on the basis of terrestrial versus arboreal locomotor systems. When including the SKX 5017 hominin fossil, the fossil lay on the same line of discrimination as that of the humans. However the distance between these, suggested a discrimination between the obligate bipedalism of the humans, and
the facultative bipedalism of what is thought to be *Paranthropus robustus*. Although none of this information was new or indeed surprising, it was evident that even with a relatively simple bone in appearance, utilizing relatively few variables, the method clearly discriminates on the basis of function. Of less importance, CV 3 against CV 1 appeared to discriminate between the hominoidea of African origin on the one hand, and those from Asia on the other. On CV 4, containing less than 1% discrimination, the discrimination lay not between the groups, but in shape related sexual dimorphism within each group.

The second metatarsal, being morphologically distinct from the first, revealed a different pattern of discrimination. Here both CV 1 and CV 2 suggested largely “size” related axes. Discrimination in CV 1 lay between the groups, and CV 2 between the sexes of each group. The joint discrimination between CV 2 and CV 1 has two lines of discrimination. One revealing a geographic/genetic discrimination between the African apes and humans on the one hand, and the Asian orangutans on the other, and another, a discrimination between the sexes of each subgroup. On CV 3, containing just over 10% of the discrimination, suggested a functional locomotor discrimination between the apes on the one hand, and the apes and humans on the other. The fifth metatarsal CV 2 and CV 1 plots appeared to have two lines of discrimination. One discriminating between the African apes and humans on the one hand, and Asian orangutans on the other, and another between the sexes of the subgroups. CV 3 and CV 1 together, clearly discriminate between the humans on the one hand, and apes on the other. The three individual bones reveal discrimination that is functional and genetic to varying degrees from bone to bone. The integrated analysis
of the three bones together, reveals the genetic nature of the discrimination in all the earlier variates, discriminating largely between the African apes and humans on the one hand and the Asian orangutans on the other. By examining the scale of differences between the different hominoid species, an appreciation for the relatively subtle discrimination between human subgroups could be gained.

6.1.2 The human canonical discrimination

Corruccini (1975) discussed the relationship between modern multivariate statistical analysis and common objectives in biological anthropology. He cautions against the misuse of these techniques, especially where the inappropriate choice of variables may give artificial results in terms of size and shape. For this reason, the multivariate results in this study have been considered only in their broadest sense; general size and shape being the main consideration. Notwithstanding, as a single species was under consideration and homology was not a problem, these results are valid for the purposes of this study. The obvious differences in size found on CV 1 between the recent and ancient humans were easily explained in Chapter 4. However, the reasons for the more subtle variation in shape contained in CV 2 and CV 3 remains to a large extent uncertain. It is clear that the first and fifth metatarsals are subtly different from the second, third and fourth. These are also the bones with the comparatively greater frequency of pathological changes. These affect firstly the medial (cranial) column of the foot, being mobile and adaptive, and secondly the lateral (caudal) column, being more rigid and less adaptive. As discussed in Chapter 4, these subtle variations in morphology may be due to a number of reasons. These
are genetic, some possibly influenced by epigenetic traits, function or pathological osseous modification; most probably a combination of all these factors.

6.1.3 The non-metric analysis

Even though the trends in variation of morphological traits between the groups were very similar, the reasons for these may be two-fold. The first, may suggest that variation of these traits are inherent in humans, and the second, change in function may result in variation of certain traits. Even though there is no conclusive evidence to support the second notion, it does not exclude the possibility that a particular variant may be associated with a change in function. The sample sizes were relatively small, and changes in function do not necessarily result in “pathology”.

Of all the results obtained, the pathological changes should be interpreted with the greatest caution. Firstly, the fact that a metrical analysis was undertaken, excluded pathological changes that obscure landmarks for measurement. Secondly, the identification and description of pathological changes are somewhat ambiguous. Thirdly, the manifestation of osseous modification does not necessarily indicate that the individual was symptomatic or had metatarsal dysfunction. Many of these changes may represent inherent variation or occur as a natural result of ageing. However, the results do reveal the relationships of the frequency of changes between the bones, and do so broadly consistently between the groups. The first metatarsal is dominant, followed by the fifth. This is important in the sense that the dominance of first metatarsal pathology is not purely as a result of footwear and modern substrates. The inherent functional role of the first ray predisposes it to pathological changes; the
samples in this study strongly suggest that modern lifestyles involving footwear and variable modern substrates increase the incidence of these changes.

6.2 To what extent were the objectives of the study fulfilled?

The five metatarsal elements were comprehensively analyzed, both metrically and non-metrically. The following was concluded in terms of the working hypotheses described in Chapter 1:

1.) The general patterns of morphological discrimination between the metatarsals of the human subgroups are very subtle. The non-metric traits are very variable, but do not discriminate between any of the subgroups. The first hypothesis is therefore accepted.

2.) There are no obvious correlations between morphological features and pathological changes. The second hypothesis is therefore rejected.

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

Unfortunately the pre-pastoral subgroup was relatively small, dates spread over almost 8 000 years with no significant numbers belonging to any particular temporal period. In addition, a number of these specimens were not dated with absolute accuracy; for example, the “Wilton culture” from the Matjies River Rock Shelter (Louw, 1960) existed over approximately a 5 000 year period. Stratigraphy has shown
the chronological time depth of the site, but not the exact date BP of each individual. Because of this, no investigation into variation within the pre-pastoral Holocene period could be carried out. It should be noted, that these people were separated both chronologically and geographically and by no means represent a single population.

6.3 Future projects

This project only included four groups of humans, although genetically distinct, were all from the African continent. It is suggested that a future study should include more distantly related groups of humans, extant apes and hominin fossils. It would also be revealing to, in addition to a prehistoric Khoisan group, also include a historic Khoisan group. It would be revealing to know the extent to which extant apes and extinct hominines vary in terms of the discrete traits found in modern humans. For example, the proximal articular surface of the first metatarsal appears very similar in all the hominoidea (Clarke & Tobias, 1995), but the extent of variation within the non-human species is as yet unknown. Unfortunately, due to the paucity of the fossil record, this component of a future study cannot be comprehensively dealt with, at least not until more complete hominin metatarsal specimens are discovered. There are many more undated South African pre-pastoral specimens in a number of locations. In future these will have absolute dates, as well as being accurately sexed. This would allow for a more comprehensive analysis of pre-pastoral populations, for example geometric means plotted against time. Regrettably, at the time of writing, repatriation of many of these Holocene specimens is being planned. Should this be the case, any future studies of these samples would be unlikely.
6.4 Concluding remarks

The influence of modern lifestyles has been presumed to have a dramatic effect on foot function, potentially resulting in an increase in pathological changes. Comparing the metatarsal morphology of three recent human groups with a pre-pastoral human group reveals similar morphological variation, primarily as a result of genetics. However, the recent groups present with greater osteological modification than the pre-pastoral group. Presuming that similar morphology yields similar function, the most obvious variable between the groups is that of lifestyle. As both recent and ancient groups present with similar patterns of pathological changes, but notable differences in frequency, these changes are, at least in part, as a result of subtle variation in function and to a greater extent as a result of differences in lifestyle.
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