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Shod versus unshod: The emergence of forefoot pathology in modern humans?

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Abstract

Background: Pathologies of the metatarsal bones in contemporary humans are common yet it remains unclear from an evolutionary perspective to what extent, if any, footwear and other environmental factors such as modern substrates have contributed to the emergence of common metatarsal pathological changes.

Objectives: To investigate the frequency of metatarsal bone pathologies in contemporary and habitually unshod pre-historic people in order to ascertain whether these frequencies are affected by variation in habitual behaviour, the wearing of footwear and/or exposure to modern substrates

Method: The metatarsal elements from four human groups were examined for pathological variation. Three of these skeletal samples were from recent rural and urban shod populations (Sotho, Zulu and European) and one from habitually unshod pre-pastoral Holocene people who practiced a subsistence hunter gatherer lifestyle.

Results: The trends in the dominance of pathological lesions between the five metatarsal bones were broadly similar in all four samples. In all groups the first metatarsal presented with the greatest number of pathological lesions; more specifically, at the first metatarsal head. The Sotho and European groups presented with notably greater frequencies of pathological changes followed by the Zulu group and then the pre-pastoral.

Conclusions: The pathological lesions found in the metatarsals of the three recent human groups generally appeared to be more severe than those found in the pre-pastoral group. This result may support the hypothesis that pathological variation in the metatarsus was affected by habitual behaviour including the wearing of footwear and exposure to modern substrates.

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1. Introduction

Footwear as it is known today is a relatively recent development in human culture with archaeological evidence dating back to at least the middle Upper Paleolithic (Gravettian) in parts of Europe [1]. Modern footwear has evolved from simple foot coverings primarily for thermal protection in colder climates and mechanical protection in all environments [1], to more elaborate devices reflecting different cultures, fash-

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ion and behaviours. These forces have led to the habitual wearing of footwear in most contemporary societies, even when footwear not always serves any practical purpose. Considering Wolff's model of bone remodeling [2], it has been hypothesised that with prolonged constriction and changes in the function of the foot in order to accommodate the shape and form of footwear, structural changes may result [3].

A study by Sim-Fook and Hodgson [3] among shod and unshod Hong Kong Chinese populations supports such a hypothesis by concluding that some deformities developed as a result of restrictive stockings and shoes. Studies of Asian populations whose feet were habitually either unshod, in thong-type sandals or encased in non-constrictive coverings

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have shown increased forefoot widths when compared to those of shod populations [4–6]. A study of forefoot width ratios in South African adult females however, suggested that a partially unshod childhood resulted in no significant increase in forefoot width [7]. It is clinically accepted that Western female footwear with high heels and narrow toe-boxes constrict the foot, particularly the forefoot, and when worn habitually, may result in debilitating clinical manifestations [8–13]. Specifically, hallux valgus has been examined in shod and unshod populations and has been shown to be related to the use of footwear [8–13].

A number of studies have gone further in suggesting that a habitually unshod foot is healthier when compared to the habitually shod foot [14–16]. 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) has even been suggested by Robbins et al. [15] as being an important consideration in avoidance response to heavy plantar surface loading. Schulman [14] also concluded that people who have never worn shoes have relatively few foot disorders. Trinkaus [1] found a marked reduction in the robusticity of the lesser toes associated with the use of footwear. Surprisingly however, little is known concerning the skeletal effects of habitually unshod feet compared to habitually or variably shod feet.

Concerning clinical studies, forefoot pain, or metatarsalgia, has been extensively documented (e.g. [17-21]) and of all forefoot pathologies that manifest clinically, the medial (cranial) column appears to be the most commonly affected, more particularly the first metatarsophalangeal joint [22]. Clinical studies with and without shoes, indicate that the introduction of footwear has little effect on the basic heel to forefoot patterns of ground reaction forces (GRF) during walking [23–27]. There is, however, some evidence that the forefoot is stiffer in habitually shod individuals [28] and this loss of mobility may lead to greater incidences of forefoot pathology. Ideally, to test the hypothesis that the wearing of footwear leads to a greater incidence of forefoot pathologies, individuals and populations who remain unshod throughout their lives would be compared directly to individuals who practice habitual shodding from early in life. In addition, modern lifestyle involves variable walking surfaces, which are not found in Nature, which may contribute to an increase in pathological changes.

Finding modern populations of humans who do not wear footwear however, is practically impossible as the wearing of some type of footwear is very nearly universal across modern populations. Thus this study therefore approaches the question from an archaeological and palaeontological perspective in order to gain access to populations that would have not had access to modern footwear and remained unshod during their entire lives.

The coastal margins of the western and southern Cape of South Africa, however, contain an exceptionally rich record of human occupation in the form of open-air shell middens and cave deposits. Until about 2000 years ago,

all local inhabitants were hunter-gatherers [29–32] and are assumed, based on strong ethnological, anthropological and paleontological data, to have been habitually unshod [29–33]. Thus these early-to mid-Holocene foragers are well-suited to an investigation of the relationship between the wearing of footwear and bony morphology and pathology [32]. We have undertaken a study which compared the frequency of metatarsal pathological changes of both recent and prepastoral Holocene human samples in order to compare the form and frequency of forefoot pathologies and test the hypothesis as to whether modern footwear leads to a higher frequency of disease.

2. Materials and methods

The metatarsal elements from recent (Sotho, Zulu and European) and pre-pastoral skeletal samples were examined for pathological variation. Population groups were established based on the anatomical and clinical records associated with each individual, including the stated linguistic group as noted on the death certificate. The three recent samples were each comprised of 30 males and 30 females and the pre-pastoral sample 11 males, 10 females and 14 individuals of unknown sex. The recent human specimens were made available courtesy of the University of the Witwatersrand (Raymond Dart Collection, Johannesburg) and the ancient (pre-pastoral) specimens by the South African Museum, Cape Town and National Museum, Bloemfontein. The prepastoral humans were dated between 9720 and 2000 (¹⁴C and stable isotope) years B.P. The specimens used in this study were restricted to adults with fully fused epiphyses. Only metatarsals where landmarks for metrical mensuration were identifiable were included as this formed part of a broader study; any pathologies that resulted in the complete deformation of the bone were therefore excluded [34].

Our examinations supported the hypothesis that there is no conclusive evidence that in any given individual one foot has consistently greater pathological variation over the other [22-25]. Therefore wherever possible, the metatarsal elements of only the left feet were examined, but if the left foot elements were missing or damaged, the right side was used in order to maximize the number of archaeological specimens used in the study. Obvious pathological features or lesions were identified and an attempt was made to associate these with a suspected pathology or dysfunction where possible. A framework based on clinical descriptions of osseous modifications (albeit derived from habitually shod populations) and inferred pathomechanical implications was constructed as a guide in classifying the various lesions. Care was taken to distinguish ante mortem modification from peri and post mortem modification.

It was recognized by this study that the criteria generally used to identify and describe bony pathological changes are somewhat ambiguous. As with any morphologically variable organism, the differentiation between what constitutes

a "normal" variant and what is pathological is not always clear. Two principles were therefore applied, first, the identification of obvious and unambiguous pathological changes according to the established criteria and secondly, any obvious changes in bone that represented variation not seen in most specimens. With the archaeological material in particular, care was taken to exclude any post mortem changes that may have resulted from the immediate burial environment and problems during or after excavation [35,36]. The frequency of pathological features was examined for trends between the bones of each individual, sex and group. Twotailed Fisher's exact tests ($\alpha = 0.05$) were carried out to test for potential frequency differences between the pre-pastoral sample and Sotho, Zulu and European samples for each of the five metatarsals. Web-based software by Uitenbroek [37] was utilized to perform the statistical tests.

3. Results

The sample size and frequency for each pathological lesion from each series is presented in Table 1.

3.1. The Sotho group

The first metatarsal presented by far with the most pathological changes with 63.3% of both males and females exhibiting changes. This is followed by the fifth metatarsal where 26.6% of both males and females presented with pathological changes. In the second and third metatarsals, 20% of the males and 26.6% of the females show evidence of pathological changes. In the fourth metatarsal, 16.6% of the males and 20% of the females present with pathological changes. The dominance of the frequency of lesions in each metatarsal is expressed by the formula 1 > 5 > 2 = 3 > 4 in males, and 1 > 5 = 2 = 3 > 4 in females where 1 represents the first metatarsal, 5 the fifth and so on. By far the most common pathological changes in the Sotho group, were hypertrophy of the dorso-lateral aspect of the first metatarsal head in the females (27%) and hypertrophy of the medial and dorsomedial eminence of the first metatarsal head in males (20%). A ridge between the medial and lateral tubercles of all the metatarsals was also found to be common. The first, second and third metatarsals in females generally presented with a higher frequency of inter-tubercle ridges.

3.2. The Zulu group

The first metatarsal presented by far with the most pathological changes with 50% of the males and 23.3% of the females exhibiting some evidence of forefoot pathology. The fifth metatarsal showed the second highest frequency with 16.6% of males and 10% of females presenting with pathological changes. In the second metatarsal, 6.6% of both males and females have pathological changes. In the third metatarsal, 13.3% of the males and 10% of the females exhib-

ited pathological changes. In the fourth metatarsal, 13.3% of the males and 6% of the females present with pathological changes. The dominance of the frequency of these lesions in each metatarsal is expressed by the formula 1 > 5 > 3 = 4 > 2 in males, and 1 > 5 = 3 > 2 = 4 in females. The most common pathological changes in the Zulu group, were found in males and were hypertrophy of the dorso-medial eminence of the first metatarsal head (27%) and hypertrophy of the dorso-lateral aspect of the first metatarsal head (23.3%). Osteophytes of all the metatarsal bases are also more common in the males.

3.3. The European group

As with the other contemporary groups, the first metatarsal presented by far with the most pathological changes with, 70% of the males and 66.6% of the females showing some degree of pathology in this bone. This was followed by the third metatarsal in the males, with a pathological incidence of 20% and then the fifth and fourth metatarsals in the females, with pathological frequencies of 13.3%. European males presented with equally frequent pathological changes in the second, fourth and fifth metatarsals. In the second metatarsal, 3.3% of the females had pathological changes. In the third metatarsal 6.6% of the females presented with pathological changes. The dominance of the frequency of lesions in each metatarsal is expressed by the formula 1 > 3 > 2 = 4 = 5in males, and 1>5=4>3>2 in females. Of importance is that the European males presented with a formula that varies considerably from those of the other groups. In addition to the general types of pathological lesions found in the third metatarsal of the other groups, the European male third metatarsal commonly presented with traumatic callus formation, inter-tubercle ridging and deviation of the distal shaft.

The most common pathological changes in the European group, were hypertrophy of the dorso-medial eminence (40%) and hypertrophy of the dorso-lateral aspect (20%) of the first metatarsal head in the males. The females also have comparatively high frequencies of these lesions exhibiting a frequency of 26.7% and 16.7%, respectively. Unlike in the other groups, there were also found to be high frequencies of osteophytes on the medial articular margin of the first metatarsal head and erosion of the plantar extensions.

3.4. The pre-pastoral group

As the numbers of individuals of known sex were comparatively small, serious consideration of the differences of pathological changes between males and females could not be undertaken. Nevertheless, as in the other groups, the first metatarsal in both sexes presented with the greatest frequency of pathological changes. In the males this was followed by the fifth and second metatarsals. In the females, the fifth, fourth and second metatarsals each had an isolated pathological lesion. Neither of the sexes presented with any pathological change in the third metatarsal. The most com-

Table 1 Frequency of pathological lesions in the samples of pooled sex Zulu (N=60), Sotho (N=60), European (N=60) and Pre-pastoralists (N=35) for each area of each bone where lesions were exhibited

| Pathological lesion | Zulu | Sotho | Euro. | Pre-past. |
|--------------------------------------------------|------|-------|-------|--------------------|
| M1 head hypertrophy medial/dorso-medial eminence | 12 | 10 | 20 | 3(n=32) |
| M1 head osteophytes medial margin | 0 | 0 | 5 | 2(n=32) |
| M1 head flattening | 1 | 5 | 1 | 0 (n = 32) |
| M1 head dorsal exostosis or spur | 4 | 1 | 1 | 0 (n = 32) |
| M5 head dorsal exostosis or spur | 1 | 0 | 0 | 0(n=32) |
| M1 head dorso-lateral hypertrophy | 8 | 8 | 11 | 1(n=32) |
| M1 head-osteophytes lateral margin | 0 | 0 | 3 | 0(n=32) |
| M1 eroded crista | 3 | 2 | 7 | 3(n=32) |
| M1 eroded plantar extension | 0 | 0 | 3 | 3(n=32) |
| M2 eroded plantar extension | 0 | 0 | 5 | 0(n=32) |
| M3 eroded plantar extension | 0 | 0 | 8 | 0 (n = 30) |
| M4 eroded plantar extension | 0 | 0 | 0 | 0(n=33) |
| M5 eroded plantar extension | 0 | 0 | 0 | 0(n=32) |
| M1 osteophytes of base | 2 | 4 | 0 | 0(n=32) |
| M2 osteophytes of base | 3 | 1 | 0 | 0(n=30) |
| M3 osteophytes of base | 5 | 1 | 3 | 1(n=30) |
| M4 osteophytes of base | 5 | 2 | 2 | 1(n=33) |
| M5 osteophytes of base | 6 | 1 | 0 | 1(n=32) |
| M1 dorsal lipping of head | 1 | 5 | 0 | 1(n=32) |
| M2 dorsal lipping of head | 0 | 0 | 1 | 0(n=30) |
| M3 dorsal lipping of head | 0 | 0 | 1 | 0(n=30) |
| M4 dorsal lipping of head | 0 | 0 | 0 | 0(n=33) |
| M5 dorsal lipping of head | 1 | 1 | 0 | 0(n=32) |
| M1 irregular cortical lesions | 1 | 2 | 0 | 1(n=32) |
| M2 irregular cortical lesions | 1 | 0 | 0 | 0(n=30) |
| M3 irregular cortical lesions | 0 | 0 | 0 | 0(n=29) |
| M4 irregular cortical lesions | 1 | 0 | 0 | 0(n=33) |
| M5 irregular cortical lesions | 1 | 1 | 2 | 0(n=32) |
| M1 bone callus formation due to fracture | 0 | 1 | 1 | 1(n=32) |
| M2 bone callus formation due to fracture | 0 | 1 | 1 | 0(n=30) |
| M3 bone callus formation due to fracture | 1 | 0 | 1 | 0(n=29) |
| M4 bone callus formation due to fracture | 1 | 0 | 1 | 0(n=33) |
| M5 bone callus formation due to fracture | 0 | 0 | 1 | 0(n=32) |
| M1 periarticular bony erosions | 0 | 0 | 3 | 0(n=32) |
| M2 periarticular bony erosions | 0 | 0 | 0 | 0(n=30) |
| M3 periarticular bony erosions | 0 | 0 | 0 | 0(n=31) |
| M4 periarticular bony erosions | 0 | 0 | 0 | 0(n=33) |
| M5 periarticular bony erosions | 0 | 0 | 0 | 0(n=32) |
| M5 styloid process exostosis | 2 | 1 | 4 | 1(n=32) |
| M1 ridge between medial and lateral tubercles | 1 | 6 | 3 | 1(n=32) |
| M2 ridge between medial and lateral tubercles | 0 | 10 | 3 | 1(n=30) |
| M3 ridge between medial and lateral tubercles | 0 | 3 | 8 | 1(n=30) |
| M4 ridge between medial and lateral tubercles | 0 | 10 | 8 | 0(n=33) |
| M5 ridge between medial and lateral tubercles | 0 | 3 | 1 | 0(n=32) |
| M2 lateral deviation of distal metatarsal shaft | 0 | 7 | 1 | 0(n=30) |
| M3 lateral deviation of distal metatarsal shaft | 1 | 3 | 1 | 0(n=30) 0(n=29) |
| M4 lateral deviation of distal metatarsal shaft | 3 | 8 | 0 | 0(n=33) |
| M5 lateral deviation of distal metatarsal shaft | 2 | 0 | 0 | 0(n=32) |

mon pathological changes in both sexes were hypertrophy of the dorso-medial eminence and erosion of the plantar crista.

3.5. Comparison of the recent and pre-pastoral groups

The percentile frequencies of pathological changes between the recent and pre-pastoral groups are represented in Fig. 1. The first metatarsal presented with the most pathological changes in all four groups. Of these, the Sotho and European groups had by far the greatest frequency, the Zulu

and pre-pastoralists considerably less. This is followed by the fifth metatarsal, the greatest frequency in the Sotho, the Zulu and European groups while the pre-pastoralists exhibited lowest frequencies of pathological lesions. Broadly, the second metatarsal, third and fourth metatarsals presented with fewer pathological changes than the first and fifth. The dominance of the frequency of pathological changes in each metatarsal is expressed by the formula 1 > 5 > 2 = 3 > 4 in the Sotho, 1 > 5 > 3 > 4 > 2 in the Zulu, 1 > 5 = 4 = 3 > 2 in the European and 1 > 5 = 3 > 4 > 2 in the pre-pastoral group.

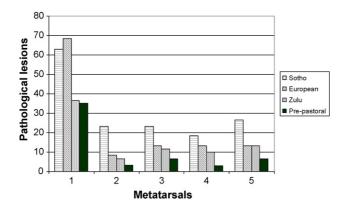


Fig. 1. Bar chart comparing the percentile frequency of pathological changes between the metatarsals of Sotho, European, Zulu and pre-pastoral samples. The sexes in all the samples are pooled.

Clearly, most pathological changes in these samples occur in the Sotho and European groups, followed by the Zulu whilst the pre-pastoralists present substantially lower frequencies. The dominance of the frequency of pathological change in the pooled recent versus the pre-pastoral groups interestingly, however, revealed a formula of 1 > 5 > 3 > 2 = 4 in both groups (Fig. 2). It is thus of particular interest to note that the foot on the pre-pastoralist group is uniformly "healthier" than the modern groups. This is particularly clear when examining the foot lateral to the first metatarsal where mid-foot pathologies are extremely rare in the unshod population and the frequency of occurrence are always below that of the shod populations.

Of the pathological changes, a few were common to all four groups. These were hypertrophy of the medial and dorso-medial eminence, dorso-lateral hypertrophy, dorsal lipping and eroded crista of the first metatarsal head, osteophytes of the bases of metatarsals three, four and five, irregular cortical lesions of the lesser metatarsal shafts and styloid process exostoses. It is therefore hypothesized that these pathologies are almost certainly not related to habitual wearing of footwear but must be due to other factors. The only pathological changes unique to the pre-pastoral and European groups were osteophytes on the medial margin and plantar extensions of the first metatarsal head and an eroded plantar extension

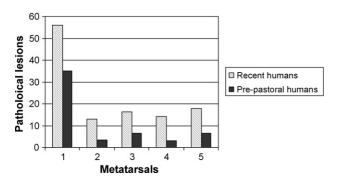


Fig. 2. Bar chart comparing the percentile frequency of pathological changes between the metatarsals of recent pooled sample (Sotho, European, and Zulu) and pre-pastoral sample.

of the first metatarsal. With the remaining pathologies, they were either absent in the pre-pastoral group or in evidence only as isolated cases of pathological lesions. It was noted, however, that the Sotho, European and pre-pastoral samples each contained isolated individuals with ridges between the tubercles of the first to third metatarsals. These lesions were not seen in the Zulu group. Notable, were the lack of obvious periarticular erosions of the metatarsal heads. The exception to this were a few cases of this condition found in the European first metatarsal head. Thus the frequency of metatarsal pathology in the first metatarsal was significantly higher in the Sotho, Zulu and European combined sample (23%) than in the pre-pastoralists (p = 0.033). The Sotho, Zulu and European combined sample was not significantly different from the pre-pastoralists for the remaining metatarsals; metatarsal two (p = 0.137), metatarsal three (p = 0.387), metatarsal four (p=0.216) and metatarsal five (p=0.121).

3.6. Trends in the frequency of lesions in the distal, shaft and proximal metatarsus

The general trends in frequency of pathological lesions in the three parts of each metatarsal for each group are represented by bar charts in Fig. 3. An examination of these trends reveals that the first metatarsal head was by far the most common site for pathological change. This follows general trends in other studies which have observed higher

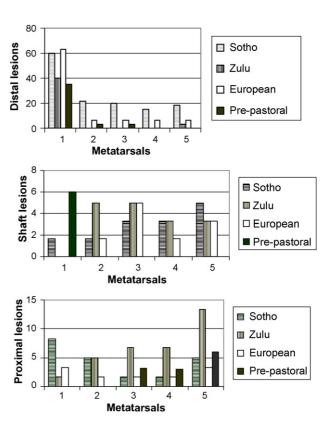


Fig. 3. Bar charts showing the comparative percentile frequency of pathological lesions in the distal, shaft and proximal parts of the metatarsals.

frequencies of distal pathologies in the mammalian skeleton [38]. In contrast, the metatarsal shafts exhibit comparatively fewer lesions with dominance in frequency bearing no clear pattern between the groups or individual bones. The recent human samples, however, had at least a few cases where the second to fifth metatarsals had some forms of shaft irregularity. In contrast, the pre-pastoral sample presented with a comparatively high frequency of first metatarsal shaft irregularity. The Sotho was the only other group to involve the first metatarsal shaft. These irregular cortexes were probably associated with either periostitis or post traumatic bone callus formation.

In all groups the proximal portions of the bones presented with some arthritic changes in generally high frequencies. The Zulu group had slightly more of these lesions compared to the other groups, with pathologies being most common in the third to fifth metatarsal shafts. However, as the samples were relatively small, particularly for the pre-pastoral group, even isolated lesions have an impact on the overall frequency of lesions. Nevertheless, it was observed that the distal articular surface and head of the first metatarsal had by far the greatest frequency of pathological changes.

4. Discussion

A study of skeletal pathological variation can only add to our understanding of modern human diversity and may prove valuable in addressing questions concerning population relationships and the pattern and amount of osteogenisis, in this case, that of the metatarsus. These, as morphologically modified bone, differ from metric and genetically discrete traits as they are mostly acquired and coincidental to other variation. The frequency of pathological changes within these samples were not necessarily representative of the pathological changes *per se*, but rather occurred within the samples that were suitable for combined metric and non-metric studies [34].

Of the pre-pastoral sample, none were excluded on the basis of pathological changes obliterating landmarks or deforming bone to such an extent that metrical measurement was not possible due to scarcity of samples, thus actually increasing the relative frequency of pathologies. In contrast, a number of individuals from each recent human sample were excluded for this reason. Thus there is no doubt that the recent human groups, although much larger in sample sizes, also presented with many more pathologies, both in frequency and extent. This applies particularly to the first metatarsal which exhibited statistically significantly higher frequencies in the recent groups.

4.1. General trends in pathological conditions

Considering the differences between the sexes of the recent groups, the Sotho generally did not show a discernable difference between males and females. The Zulu and

European males, however, exhibited a higher frequency of pathological changes than the females. In modern western cultures, it has been shown through clinical studies discussed previously that females generally have a greater tendency to foot pathology as a result of female footwear. A possible explanation for the Zulu males having a greater frequency of pathological lesions may be related to occupation, where most of the males in South Africa had a history of manual labor in mines requiring work to be done while standing. This may or may not be the case in the European males, although it is important to note that most of the females also presented with pathological changes. No immediate explanation can be given for the Sotho and European samples presenting with considerably more pathological changes than the Zulu. The European females, however, not surprisingly presented with more pathological changes in the first metatarsal head than either male Europeans or any other group—male or female. A plausible explanation for this would be that in the context of South African recent history, the European females probably tended to wear more constricting footwear.

Age does not appear to be a factor in this study, as the mean age of the Sotho males was 36 (S.D. 8) and Sotho females, 34 (S.D. 6.8). The Zulu population was by and large slightly older; the male mean age being 49 (S.D. 15) and the females, 44 (S.D. 12). Similarly the European sample mean age was 45 (S.D. 7) for the males and 51 (S.D. 11) for the females. Although the age at death of the pre-pastoral individuals is unknown, it was estimated that their mean ages fell within the range of the recent groups, and in many cases, slightly older.

It is interesting to note that the patterns of pathological variation between the groups were very similar with the first metatarsal presenting by far with the greatest frequency of bony modification, followed by the fifth metatarsal. The first ray is an important functional unit in the more mobile medial column, and the fifth ray in the more rigid lateral column resulting in greater GRF on both columns at different times during the stance phase of gait. This is an important result as it indicates that the pattern of pathology is the same across the four populations, pointing to what may be an inherent evolutionary weakness in these areas of the foot related to bipedalism—it is only the frequency and form of these pathologies that change with the pre-pastoralist group uniformly exhibiting lower frequencies and lesser magnitude of presentation.

4.2. A consideration of selected pathological lesions

An attempt was made to explain the reasons for some of the common pathological changes found in the four samples under consideration. As the samples were suitable for both metric and non-metric analyses, severe pathology thus being excluded, suggested that most, if not all these lesions were as a result of a primary mechanical aetiology. This would suggest that the broad pathological pattern may be related, at least to some extent, to habitual behaviour.

4.3. Hypertrophy of the medial/dorso-medial eminence of the first metatarsal

This represents one of the most common osseous modifications, particularly in the three recent human groups. Few of these were true "medial eminences", but rather a hypertrophy of the medial tubercle. Most were so large, that they could not be considered as normal variation in tubercle size. The pre-pastoral group rarely presented with tubercles or medial eminences that were hypertrophied. As the recent groups were presumed to have been habitually shod, pressure from footwear and associated changes in biomechanics are considered the most probable causes.

4.4. Osteophytes of the medial margin of the first metatarsal head

A few of the pre-pastoralists presented with this osseous modification which with the exception of a few Europeans, was not found in the recent samples. This suggests that there was a migration of sesamoid bones [39], and may be associated with erosion of the planter crista. The only plausible explanation for this that we can hypothesise is that the pre-pastoral foragers had a lifestyle that required constant locomotion which resulted in "wear and tear" on the first metatarsal head that differs from that as a result of footwear. The possibility, however, of a laterally deviated hallux cannot be excluded although there was no conclusive evidence for this.

4.5. Eroded crista and eroded plantar extension of the first metatarsal head

All groups presented with a few examples of eroded plantar cristas, but the pre-pastoral group presented with the highest frequency. This group also presented with the same number of eroded plantar extensions which were not present in any of the recent population samples. Grode and McCarthy [40] suggest that due to a medial deviation of the first metatarsal, there is a resulting displacement of the medial sesamoid that erodes the crista and medial plantar extension. Perhaps, even in the unshod pre-pastoralists, there may have been mechanical dysfunction of the first ray resulting in sesamoid subluxation. These lesions were completely eburnated in most instances and may simply represent normal degeneration over time.

4.6. Dorsal exostosis or lipping of the metatarsal head

Dorsal exostoses were found in all the groups studied, but to a lesser extent in the pre-pastoralists where the osteophytes were smaller than in the other three groups. This suggests that these individuals had advanced hallux limitus [41–45]. Roth [46] classifies the hallux limitus associated with these exostoses or lipping as *hallux limitus grade two*. This condition is almost certainly not caused by either the wearing of footwear

or the environment as there is also evidence of it in a non-human hominid [47] that had a bipedal gait similar to that of modern humans [47–49].

4.7. Osteophytes of the metatarsal bases

Osteophytes were found in all the groups. However, osteophytes of the base of the first and second metatarsals did not present in the pre-pastoral group. This suggests a functional adaptation due to a divergent first ray deformity, separating the base of the first metatarsal and the first and second cuneiforms [41]. In both the recent and pre-pastoral groups, individuals with osteophytes of the third to fifth metatarsal bases were found. The exact nature of their pathology remains unknown.

4.8. Fractures

All four human groups presented with isolated first metatarsal shaft callus formation due to fractures. This is usually as a result of direct trauma [50] or indirect hyperplantarflexion [51]. Only the Sotho and European groups presented with an isolated bone callus formation with each incident exhibiting on the second metatarsal shaft. This represents the most common metatarsal fracture due to its recessed and therefore stable position. The Zulu group presented with isolated bone callus of the third and fourth metatarsals of the same individual, probably as a result of direct trauma. The same occurred in a single European individual, but also involved the fifth metatarsal. No fifth metatarsal styloid fractures were detected in any of the four samples examined.

4.9. Ridge between the tubercles

A number of individuals presented with prominent ridges between the lateral and medial tubercles from predominantly the Sotho, European and pre-pastoral groups. In the Sotho and European groups, this occurred in all the metatarsals and in the pre-pastoralists in the first, second and third metatarsals. Some incidences occurred only in one bone and others in two or three bones. Notably, of these lesions only a single Zulu female presented with an inter-tubercle ridge of the first metatarsal. There are two possible explanations for these ridges. They may be as a result of metaphyseal "scarring", or as a result of habitual hyper-dorsiflexion of the metatarsophalangeal joints. In the first instance, a variation in epiphyseal ossification or damage may result in ridging. The first metatarsal has a peculiarity in growth, contrary to the classic anatomical descriptions which claim only proximal ossification from the diaphysis, there is also a common finding of a distal physis [52]. In the second instance, the development of these ridges may be a signature for lifestyle related activities. As an archaeological sample was studied, this second possibility was of particular interest.

Uberlaker [53] examined bony changes on the superior distal surface of metatarsals also in a pre-historic sample

from coastal Equador which strongly suggest that they were produced by prolonged hyperdorsiflexion of the toes, probably resulting from a habitual kneeling posture. This could be considered as a "kneeling signature", in much the same way that tibial and talar "squatting facets" strongly suggest a habitual squatting posture [54]. As these have been found in both the recent and pre-pastoral groups, inferences for specific differences related to culture or lifestyle cannot be made. This may be a good example of similar mechanical function, even under very different circumstances resulting in the same osseous modification.

4.10. Irregular hypertrophy of the cortex

Irregular cortical hypertrophy was observed in all bones excepting the third metatarsal. Whether these can be considered as truly "pathological" is unclear. It is doubtful if any of these can be associated with osteomyelitis as they were merely a slight thickening and "roughening" of the cortex, most likely as a result of periostitis. Perhaps these lesions were a response to abnormal loading of the bones over time.

4.11. Periarticular bony erosions associated with rheumatoid arthritis

Although osteophytosis was identified in individuals from every group under consideration which may have been as a result of rheumatoid arthritis, there was no conclusive evidence that this was the case. However, bony erosions associated with rheumatoid arthritis were found only in the first metatarsal of a few of the European individuals. No doubt, this degeneration of the subchondral bone will have resulted in dysfunction of the joint. When examining isolated bones, the distinction between severe rheumatoid arthritis and severe osteoarthritis is indistinguishable and can only be substantiated with evidence from other skeletal elements such as the hands.

5. Conclusion

The results presented here suggest that the unshod lifestyle of the pre-pastoral group was associated with a lower frequency of osteological modification. The influence of modern lifestyle including the use of footwear, appears to have some significant negative effect on foot function, potentially resulting in an increase in pathological changes. The recent human groups additionally presented with greater osteological modification than the pre-pastoral Holocene group. Presuming that a similar biomechanical pattern exists in both shod and unshod groups, the most obvious variable between the groups was that of footwear, lifestyle and environment. As both recent and ancient groups presented with similar patterns of pathological variation, but notable differences in frequency, these changes are interpreted, at least in part, as a result of subtle variation in function due to environment, and to a greater extent as a result of differences in habitual behaviour.

Conflict of interest

None.

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