The wounded forefoot – an evolutionary perspective

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The evolution of the human foot transformed the primitive, terrestrial and arboreal form of the foot into the specialised foot adapted to the bipedal mode of locomotion. However, it is thought that this transformation is not perfect and may lead to some of the foot disorders found in anatomically modern humans. In addition, modern lifestyles and footwear may contribute to pedal dysfunction, which may also result in foot ulcers, particularly in the forefoot. A basic understanding of the evolution of the human foot may help explain the aetiology of some foot wounds, thus assisting in planning the management of those disorders.

Keywords: evolution, forefoot, ulcer, callus, bipedalism

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Introduction

A human relative 'Lucy' (*Australopithecus afarensis*), who lived 3.2 million years ago in East Africa, was one of the first hominins to have a human-like footprint.[1,2] She could walk considerable distances in an erect position with her hands free to do work other than locomotion. This freeing of the hands started the rapid development of the brain in her descendants as the foot evolved from a mobile structure to one adapted to a stiff push-off mechanism during bipedal locomotion.[3-5] We may say, therefore, that this uniquely human character of cognition was rooted in the feet, making the foot one of the defining features of our lineage, representing nearly a quarter of the skeleton.[4]

This evolution of bipedalism over roughly 6 million years may give one the impression that we developed the ideal foot suitable for walking upright. In modern times, however, foot problems are very common and are thought to result from lifestyle, including unsuitable shoes, repetitive strain and injuries. Foot disorders such as bunions, plantar fasciitis, flat feet and Morton's neuroma are often considered the most common; however, wounds of the feet pose the greatest threat to limb and life, particularly in individuals with underlying systemic disorders such as diabetes.

Foot posture and foot function are associated with the presence of specific foot disorders.[6] The fact that the plantar surface of the foot is the only part of the body with constant contact with the ground (even and uneven, hard and soft); subjects it to a greater risk of injury when dysfunction occurs. The evolutionary and clinical perspectives of the foot have been considered for many years by some of the earliest scholars of evolution of the foot and attempting to understand human foot pathology, amongst them two surgeons – F Wood Jones and Dudley Morton.[7,8] Others have drawn attention to the evolutionary implications of foot disorders.[9-11] The question arises whether contemporary foot disorders, including wounds of the foot, result exclusively from modern lifestyles in which extrinsic variables play a role or are predisposed by underlying atavistic factors inherited from our extinct ancestors. Here some thoughts on the foot function, dysfunction and wounds are reviewed.

Foot function and wound formation

The human arched foot serves as a 'shock absorber' and a lever, and its relative stiffness is key to the evolution of human bipedal locomotion.[4,8,12-15] During the walking gait cycle, when the heel contacts the ground, the foot is required to be fairly stiff as it is dorsiflexed. It quickly becomes more mobile on foot flat to 'absorb' the ground reaction forces and adjust to uneven surfaces. As the stance phase of a walking gait progresses to propulsion and the heel lifts, the longitudinal arch helps convert the foot into a stiff lever allowing the heel and mid-foot to be lifted off the ground simultaneously during push-off.[15] This dynamic lever, facilitated by the longitudinal arch and plantar aponeurosis, is deployed even more extensively during bipedal running. The plantar aponeurosis and plantar ligaments are loaded immediately upon landing with the heel elevated. The medial longitudinal arch is therefore dynamic in its 'high-stiff-arch' (supination) and 'low-mobile-arch' (pronation) movements throughout stance. However, patterns and extent of arch loading and arch motion are considerably variable among individuals. This is partly due to variation in the subtalar joint axis, leading to less than ideal timing of these motions.[16,17]

Hyperpronation is a very common condition in modern humans, reminiscent of our more 'flat footed' hominin ancestors and extant great ape cousins. It is thought to be the source of a host of signs and symptoms in the foot and elsewhere. As wound care health workers and specialists, it is worth considering some of the evolutionary pressures that resulted in foot function and dysfunction. It was hypothesised that the 1.98 million-year-old *Australopithecus sediba* was a hyperpronator with several skeletal markers suggesting this.[18,19]

However, as hyperpronation appears to have been an inherent part of this extinct hominin's body plan, there are indications that its anatomy accommodated such a gait pattern to avoid injury (keeping in mind that such a creature walked bipedally, but still made considerable use of trees to move around in).[19]

In some instances, one's foot may not facilitate optimal shock absorption during foot-flat or stiff-lever action during heel-lift and toe-off. The foot mobility that we have inherited from our primate ancestors to absorb the heavy loads of walking and running bipedally may lead to debilitating injuries that compromise our locomotion and change the interface of the foot with the supporting surface. This includes increased pressures on the foot's plantar aspect exceeding the tissue's tolerance in these areas where the fibro-fatty pad of the forefoot is compressed between the metatarsal heads and the ground. This leads to intermittent compression and release on the skin, increased friction, hyperaemia, increased cell mitosis and formation of hyperkeratosis (thickened skin), commonly known as a callus. Some callus on the bottom of the foot is normal and generally not harmful, and helps prevent blisters as well as offering protection. However, once the levels of microtrauma exceed the tolerance of the tissue and underlying structures, the callus exceeds its protective thickness and takes on the role of a 'foreign body'. This becomes uncomfortable at best and subsequently painful, warning the individual that there is something untoward happening. This is either remedied by physical reduction of the callus, or offloading of weight-bearing areas by modifying gait, changing or adjusting footwear and/or using devices such as orthoses. However, when the sensory ability of the individual is compromised, the sensory warning that the callus provides to offload or change behaviour may go unheeded. Callus has been identified as a risk factor leading to severe diabetic foot ulcer; thus, it is necessary to prevent its formation. Callus formation under the first, second, and fifth metatarsal heads (MTHs) is associated with external forces (pressure and shear stress) during walking (Figure 1).[20] Murray et al. identified the factors increasing the external forces to prevent callus formation.[20] External forces and their relationship with the lower extremity joint angles and footwear size were identified as risk factors leading to callus under the metatarsal heads. More specifically, small flexion of the knee joint and large subtalar joint pronation motion resulted in callus under the first MTH.[20] For the second MTH, wearing excessively long footwear was identified and for the fifth MTH, high external force was related to tight width (narrow) footwear.[20] An effective intervention for preventing callus formation for the first MTH would involve assisting the push-off foot motion using rocker-sole footwear or gait training. For the second and fifth MTHs, wearing appropriate size footwear would be effective.[20]

Lifestyle and footwear

After our hominin relatives and ancestors left the trees to dwell on open grasslands, some of the earliest of our genus *Homo* evolved the ability to endurance run. The reasons for this are complex and beyond the scope of this paper (see Bramble and Lieberman);[13] suffice to say that we modern humans are, through evolutionary processes, inherently endurance runners. However, contemporary humans with modern lifestyles, having evolved from a hunter-gatherer and nomadic pastoralist lifestyle to a sedentary agrarian one, have lost the need to endurance run as a means of survival. This is evident in the comparison of the internal properties of the bones of apes, extinct hominins and humans.[21] Humans have the 'weakest' bones of all the primates and our extinct ancestors[21] and hunter-gatherer forbearers. Longevity among small-scale anatomically modern human populations, in particular hunter-gatherers, approaches that of industrialised populations, and non-communicable disease (diabetes, obesity, cancer and cardiovascular disease) are rare.[22] This means that small scale populations lived almost as long as industrialised ones, but without the sophisticated medical interventions responsible for extending the lives of people in modern times. Non-insulin-dependent (type 2) diabetes is so rare among small-scale populations that it is difficult to find reports of its prevalence in these groups.[23] Hunter-gatherers also have extremely low obesity and diabetes rates and high levels of physical activity.[23] In contrast, diabetes is a scourge of contemporary living and coupled with mechanical foot dysfunction, deformity and callus formation results in ulcer formation – a very serious development in a person with diabetes.[20,24]

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.[25] Modern footwear has evolved from simple foot coverings primarily for thermal protection in colder climates and mechanical protection in all environments,[25] to more elaborate devices reflecting different cultures, fashion and behaviours.[26] These factors have led to the habitual wearing of footwear in most contemporary societies, even when footwear not always serves any practical purpose. Prolonged constriction and shifts in the foot's function to accommodate the shape and form of footwear may result in structural changes. It is thought that unshod feet are generally healthier than shod.[27] A study on the pathological lesions found in the metatarsal bones of recent human groups appeared to be more severe than those found in South African hunter-gatherers from the Late Stone Age.[26] 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.[26] Studies of Asian populations whose feet were 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.[27] A study of forefoot width ratios in South African adult females suggested that a partially unshod childhood resulted in no significant increase in forefoot width.[28] Regardless, a foot 'wishes' to be in its natural width, and when footwear restricts it, it becomes problematic. In many instances, modern footwear does not match the shape of the foot, nor does the flexion area of the shoe match the flexion of the foot.[29] Having said this, footwear plays an important role in protecting the foot and there is a hypothesis that suggests from ancient Middle Stone Age trackways on the South African Cape south coast that these people may have worn some form of footwear (study in progress). The rocky coastlines would sometimes be difficult to negotiate barefoot, and an injury resulting in a wound from a sharp rock may prove fatal. Thus some form of foot protection, even in prehistoric times, is not inconceivable.

Foot deformity

Feet may become deformed as a result of external factors, such as footwear, certain foot postures, such as hyperpronation ('flat foot'), or diseases. Foot deformities may, but don't always, cause problems, such as pain and walking difficulties. As mentioned previously, footwear may play a role in causing foot deformity over time, and predisposing conditions make it more likely for foot deformity to occur. 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'.* 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. In contrast, the less convex joint with a more dorsoplantar orientation of fossil hominins such as *Homo habilis*, *Homo erectus*, and *Homo naledi* (Figure 2), is a human-like feature. It is not unusual to see humans with pathological deformity exceed the first inter-metatarsal and hallux angle values of these extinct hominins and resemble more the morphology of the apes (Figure 3). This is the type of foot prone to develop callus on the plantar surface of the first, second, and fifth metatarsal head, which in the high-risk patient, may lead to ulceration that will not heal spontaneously and threaten the limb (Figure 1). With this scenario, there is something of a 'chicken and egg' situation that is unclear. Which came first, the ill-fitting shoe, pressing the hallux laterally, causing an acquired increase in intermetatarsal angle, or the increased 'atavistic' intermetatarsal angle, causing the foot to broaden and press against the shoe? The answer is unclear, and it could be either, and probably in most cases, a combination. Either way, proof of concept finite element analysis suggests that footwear, *per se*, is an important player in the pathogenesis of hallux valgus.[30] Finally, a recent review by Thompson et al. considers the so-called 'parabola', which takes into account the cascade of differing lengths of the metatarsals defined as the intersection of an arc with the flat surface.[31] This serves as a function of the rollover motion or rocker of the foot before heel rise and provides stability and balance in standing. A further function ensures that the lever-action at the first metatarsophalangeal joint takes place so that the hallux can dorsiflex, enabling the venous pump mechanism. It is suggested that the short first metatarsal (reminiscent of the pre-human foot), is a risk factor for diabetic foot ulceration.[31]

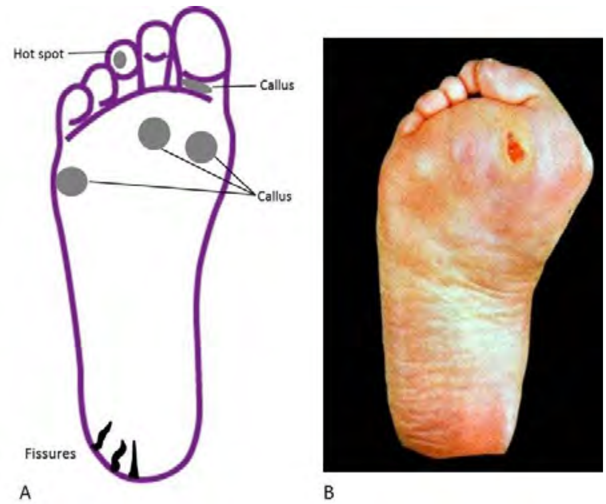

Figure 1: (A) Pressure areas on the first, second and fifth metatarsal heads where callus build-up may result in ulcer formation. (B) A classic 'bunion' foot, where the hallux valgus goes together with an increased first intermetatarsal space, making the forefoot broader and more mobile, resulting in ulcer formation under the second metatarsal head as the short first metatarsal is lifted up on ground contact. The more stable second metatarsal is subjected to pressure on the metatarsal head.

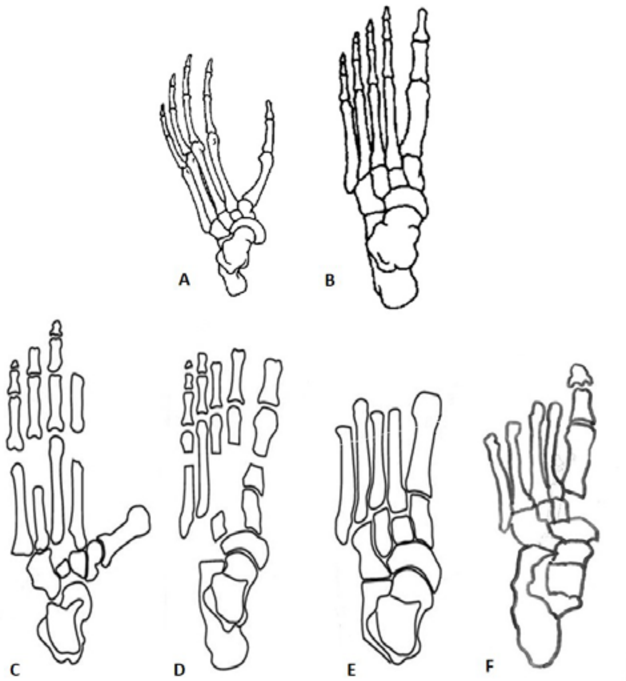

Figure 2: (A) Chimpanzee (*Pan*) foot, compared with (B), a modern human foot. The chimpanzee clearly has a wide first intermetatarsal angle and abducent hallux whereas the human has contact between the first and second metatarsal bases and small first intermetatarsal angle with a non-opposable hallux. (C) *Ardipithecus ramidus* (4.4 ma) fossil foot, characterised by retention of a widely abducent and opposable hallux.[32] (D) Representing the *Australopithecus afarensis* (3.7–3 ma) fossil foot characterised by the retention of slight hallucal abduction. (E) Representing *Homo habilis* (2.3–1.65 ma) and *Homo erectus* (1.89 ma –110 ka) fossils, characterised by a fully adducted hallux and human-like longitudinal arch. (F) The foot of *Homo naledi* (335–236 ka), flipped to represent the left side, has a predominantly modern human morphology and almost indistinguishable from a modern human foot.[33]

Figure 3: Bunion or hallux valgus as seen on a dorso-plantar x-ray view. The first intermetatarsal (angle A) is increased (> 9 degrees), and the hallux is deviated laterally (angle B). The first metatarsal head has remodelled to accommodate the angulation of the hallux, and increased its articular set angle to resemble that of an ape and some of the extinct hominins.

Discussion

Anatomically, the foot is divided into medial and lateral columns, the medial being more adaptively mobile than the lateral. Evolution has transformed the primitive, terrestrial and arboreal form of the foot into the specialised foot adapted to the bipedal mode of locomotion. This pattern has existed for more than two million years. Deviation from this adaptive pattern may result in clinical problems, including foot ulceration. Kidd[11] suggested that the specialist modifications pertinent to human pedal structure from the primitive ape-like foot took place first in the lateral column. A more rigid foot adapted for walking short distances bipedally (see also Zipfel et al.).[11,34] Then changes to the medial column followed later with the development of the medial longitudinal arch so that the foot could act as a rigid lever in the propulsive part of the gait cycle. This may well present a hypothesis as to some forefoot pathology being ontogenetic in origin.[11] A mild delay or arrest in ontogenetic development could lead to defects on the medial side of the foot, rendering it more 'ape-like' with characteristics of mobility, which in humans, may present as a function of abnormality.[11] This, together with inadequate footwear, could lead to a host of pathologies, including bunions with their sequelae of callus formation under the first metatarsal and/or second metatarsal heads depending on the metatarsal length and compensatory mechanisms of this hypermobility. Callus has been identified as a risk factor leading to severe diabetic foot ulcer; thus, it is necessary to prevent its formation. Foot structure and function, particularly abnormal subtalar joint pronation, are important aetiological factors in disordered weight-bearing and abnormal foot loading patterns resulting in callus formation in patients with and without diabetes. In 2009, for the first time in history, non-communicable diseases have become the leading cause of global mortality, which appears to be as a result of our cultural evolution in lifestyle.[35] Most recently, in 2020, for the first time, our disease-stricken world is also facing a significant communicable disease; COVID-19. More now than ever, the risk to the foot associated with comorbidities has increased significantly.[36,37]

These variables, in combination with our recent evolution to habitual bipedalism, may explain at least some of the reasons as to the increase in foot morbidity due to ulceration and subsequent amputation. A basic understanding of the evolution of the human foot can help in explaining the aetiology of some foot wounds within the context of contemporary non-communicable diseases associated with lifestyle, thus assisting in education of patients and planning management of those disorders.

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