Starting off on the Wrong Foot. Jeremy DeSilva, Boston University

Last August, close to one billion humans tuned in to the Olympic games in London. We all marveled at the human body performing seemingly impossible feats of speed, strength and agility. But, there was one performance that was different from the others. A competitor in the 400-meter sprint (one lap around the track), one of the fastest humans in the world, did not have feet. Oscar Pistorius, a South African sprinter, was born without fibulae, and before he even celebrated his first birthday, both of his legs were amputated just below the knee. Twenty-five years later, he was representing his country, using prosthetic feet to run as fast as any human on the planet. But, Pistorius' prosthetic foot looked almost nothing like the foot of his fellow sprinters. The human foot has 26 individual bones- 52 moving parts in total- that are bound together with ligaments and held stiff by the actions of the many muscles that traverse the foot or are intrinsic to the foot itself. Pistorius' blade consisted of a single moving element. His prosthetic was made of a material that was compliant and good at absorbing the high ground reaction forces incurred during "foot" strike; stiff enough for the propulsion necessary to drive the body forward; but elastic enough to bend, and recoil in a manner that put a 'kick' in his step. In engineering terms, it was an excellent "design." The question to consider, therefore, is not why Pistorius' prosthetic didn't look more like a human foot, but why our feet do not look more like Pistorius' blade.

The answer, of course, is that Pistorius' foot prosthetic was conceived in the mind of an engineer, tested in a biomechanics laboratory, and built essentially from scratch. In contrast, the human foot is the product of a very long, complex, and non-linear evolutionary history. I will argue that the human foot is not very well designed precisely because we were not designed. Interestingly, one does not have look very far to see Pistorius-like feet in the biological world. Ostriches, for example, have fused the bones of their ankle and foot into a single, rigid bone called the tarsometatarsus. They have long, thick tendons that act to store elastic energy during bipedal locomotion. The muscles used to propel the limbs are located up in the body of the bird, far away from the foot, helping to increase their stride frequency, and therefore, speed. So, why does the ostrich foot resemble Pistorius' prosthetic more than my own foot does? It is likely that the modern ostrich foot is better "designed" for bipedal walking, because it has been part of a lineage under selection for this kind of locomotion for nearly 250 million years. My lineage has been bipedal for a mere 5 million years, and prior to that, my ancestors spent millennia in the trees, evolving feet well-adapted for grasping. Even then, we can still ask why my foot doesn't look more like an ostrich foot. To put it simply, and in the vernacular of a good New Englander, "you can't get there from here."

So, where is "here" or even "there"? Understanding the evolutionary history of the human foot is critical to understanding why we could not have evolved an ostrich-like anatomy, which I contend is better "designed" than my own. Our starting point for this exercise is the early Mesozoic, 245 million years-ago, when the ancestors of modern birds (archosaurs) lived alongside the ancestors of modern mammals (therapsids). Early in the Mesozoic, the lineage leading to birds (dinosauria) had split from the ancestors of modern crocodilians, and the fossil record demonstrates quite clearly that these early dinosaurs were bipedal. Quadrupedalism re-evolved in some dinosaurs (the long-necked sauropods, for example), but the lineage starting with the earliest dinosaurs and terminating with modern ostriches is an unbroken chain of bipedal animals. If this is true, then selective pressures have been pruning and refining bird foot anatomy for bipedalism for upwards of 235 million years. Our mammalian ancestors were on a very different path.

The earliest mammals were quadrupeds, not bipeds. One major anatomical innovation in early mammals was the repositioning of the talus from a position *next to* the calcaneus, to *on top of* the calcaneus. This seemingly simple alteration transforms the foot from a structure that moves primarily in one plane (front to back sagittal motion) to one that can move in both the sagittal plane and the coronal plane. In other words, by shifting the talus on top of the calcaneus, inversion and eversion of the subtalar joint were now possible. Small mammals could now twist their foot inwards or outwards more effectively. But, this was by no means a point of no return. Terrestrial artiodactyls (deer, for example) and the distantly related perissodactyls (horses, for example) have independently shortened their ankle bones, elongated and fused their metatarsals, and reduced their pedal digits. Muscles are concentrated in the body of the animal so that mostly long, thick tendons course through the lower limb and foot. These animals have therefore independently evolved, in some ways, the Pistorius-like, blade "design". But, our primate ancestors were on a very different path.

The earliest primates were arboreal. Not only did they possess a highly mobile subtalar joint (the joint formed between the superimposed talus on the calcaneus), but they also evolved a grasping big toe. The primate foot, the raw material from which the human foot has evolved, has been under intense natural selection pressure to be a mobile, grasping appendage. Muscles within the foot itself help control the fine motions of the toes important for grasping onto branches high in the forest canopy. As Oligocene and Miocene primates diversified, our ancestors (the catarrhines and eventually the hominoids) dramatically increased body size and continued to inhabit a forest environment. Selection maintained, and if anything enhanced, the grasping abilities and mobility of the foot. For instance, the foot of *Proconsul*, an 18 million year-old hominoid, has highly mobile tarsal joints, and a large grasping big toe. While the foot of modern apes may have become even more adapted for life in the trees in the time since our lineage diverged from theirs, our starting point, the foot from which our own evolved, was a grasping, muscle-filled, mobile appendage, adapted for a life in the trees.

The human foot, therefore, is a modified ape foot. It is a highly mobile structure composed of many moving parts made more rigid by ligaments, muscles, and some subtle bony alterations. These small modifications, anatomically subtle though functionally quite important, are the biological equivalent of paper clips and duct tape. Of course, the human foot does its job quite well and natural selection has fiercely molded the foot into a functional structure that absorbs ground reaction forces, stiffens during the propulsive phase of gait and even has elastic structures, like the arch and the Achilles tendon, which may put a kick in our step. The intrinsic muscles, which previously controlled fine movements of the grasping foot, now help support the arch. If these modifications had not evolved, it is highly likely that our ancestors would have all been leopard food and humans, as we know them today, would not exist. But, because evolution acts by making small, often jerry-rigged modifications to pre-existing structures (in this case, an ape-foot), and our lineage has been bipedal for a mere 5 million years or so, one would be quite hard-pressed to call the design of our foot "intelligent". Naturally, there are medical consequences for this jerry-rigged system: ankle sprains, plantar fasciitis, collapsed arches, and all of the problems associated with excessive pronation, among many others. If our feet were well designed, would podiatry be a billion dollar industry?

It is of course quite reasonable to hypothesize that many of the foot maladies that humans develop today are simply the result of our sedentary lifestyle. Perhaps shoe-wearing has altered the 'normal' growth and development of our feet, leaving shod populations predisposed to foot pathologies? Perhaps the consequences for having foot anatomies predisposed to injury are no longer as severe as they used to be, and the harsh reality of natural selection has been relaxed? If any of these quite reasonable explanations were correct, we should see fewer, or perhaps different, foot pathologies in the human fossil record. But, we do not. Instead, the fossil record indicates that many of the very same foot maladies humans suffer from today existed in the past, and in surprisingly high frequencies, especially given how rare hominin foot fossils are.

Two of the almost 20 (10%) distal tibiae show evidence for healed ankle fractures. There is a healed ankle fracture in Kadanuumuu, the large male *Australopithecus* who lived 3.5 million years ago (Haile-Selassie et al., 2009). A small female hominin, KNM-ER 2596, also broke her ankle as a juvenile, but lived long enough for it to heal (DeSilva and Papakyrikos, 2011). The OH 35 tibia was from an individual who had suffered a severe high ankle sprain (Susman, 2008). The OH 8 foot belonged to a small hominin with age-related osteoarthritis along the lateral metatarsals and the medial ankle joint (Weiss, 2010). There is evidence that the very famous *Australopithecus* "Lucy" had asymptomatic flatfoot (DeSilva and Throckmorton, 2010). There are cases of healed stress fractures, compression fractures, and even what may be a case of hallux limitus. Most of these foot pathologies are rare or absent in modern African apes, meaning that they are pathological consequences of walking upright on a modified ape-foot.

Humans are marvellous animals, and unlike any other placental mammal, we move from place to place on our hind legs. We not only move in this odd manner, but we do it quite well, expending very little energy walking on our two legs. This efficient gait is possible because our bodies are well-balanced, with our heads, torso, hips, knees, and feet more or less in the same plane, minimizing the muscular effort necessary to keep us from toppling over. It is quite easy to look at the human form with awe. Biological anthropologists of course do this all the time, but we marvel not at a body designed from scratch, but at the power of natural selection and, in this particular case, its ability to convert a grasping foot into a propulsive one in a mere 5 million years.