Project title: Doctoral Dissertation Improvement: Fossil footprints and the dynamics of footprint formation: Implications for the evolution of human gait

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Project abstract:

Bipedalism is a fundamental modern human behavior yet many questions about its evolution in our extinct ancestors remain unanswered. Paleoanthropologists studying fossilized skeletal anatomy have analyzed these data in many different ways only to arrive at conflicting conclusions regarding when and how bipedalism evolved. New approaches are necessary to resolve this ongoing debate.

Doctoral student Kevin Hatala (The George Washington University), under the supervision of Dr. Brian Richmond, will pursue a novel approach that circumvents these problems by analyzing a new type of ‘fossilized behavior’ data, in the form of recently discovered fossil hominin footprints. With a growing sample of fossil footprints from different times throughout the Plio-Pleistocene, these data can be used to investigate the evolution of human foot anatomy and bipedal locomotion. However, before scientists can take advantage of the information stored in these footprints, we need to determine how anatomy and gait are recorded in footprints. This study will use experimental biomechanics to investigate the dynamic process of footprint formation, and will apply this knowledge to the analysis of fossil hominin footprints from Laetoli, Tanzania, Ileret, Kenya and Engare Sero, Tanzania. These analyses will directly test the hypothesis that modern humans’ anatomical and functional adaptations for bipedal locomotion were present in hominins at 3.7, 1.5, and 0.12 million years ago.

Through collaboration with the Rutgers University/National Museums of Kenya Koobi Fora Field School, this project involves extensive training of undergraduates from Kenya, South Africa, and the US. Results will be presented to scientific audiences through publications and conferences, and to the public through ongoing collaborations with the Smithsonian’s National Museum of Natural History Human Origins Program. A new archival system will be developed at the National Museums of Kenya, allowing students and other researchers to access the original three-dimensional scans of fossil footprints generated during this project.

Doctoral Dissertation Improvement: Fossil hominin footprints and the dynamics of footprint formation: Implications for the evolution of human gait.

Bipedalism is a fundamental modern human behavior but many questions regarding the evolution of bipedalism remain unanswered. Paleoanthropologists studying the anatomy of fossil hominin species have analyzed data in many different ways only to arrive at conflicting conclusions regarding when and how bipedalism evolved. The proposed study offers a novel approach to analyzing a different type of 'fossilized behavior' data, in the form of recently discovered fossil hominin footprints. Controlled biomechanical experiments on footprint formation will be conducted with habitually unshod modern human populations and with chimpanzees to develop, for the first time, a quantitative understanding of how different variables of hominin foot anatomy and bipedal gait are preserved in footprints. These results will be used to provide interpretations of implied foot anatomy and walking gait from three different fossil hominin footprint sites at Laetoli, Tanzania (dated to about 3.7 Ma, or million years ago), Ileret, Kenya (1.5 Ma), and Engare Sero, Tanzania (0.12 Ma). Evidence from these fossil footprints will be used to directly test the hypothesis that all features of a modern human-like foot anatomy and gait were present in *Australopithecus afarensis*, and foot anatomy and gait remained essentially unchanged in *Homo erectus* and later at the emergence of *Homo sapiens*. Studying these direct snapshots of anatomy and locomotion at three very different points in human evolutionary history will provide a new perspective and opportunity to evaluate long-standing questions about the evolution of human bipedalism.

Intellectual Merit

Fossil footprints are uniquely important because they not only provide records of the complete foot anatomies of extinct hominins, but also preserve direct evidence of their gaits. Recent discoveries have expanded the sample of footprints in the hominin fossil record, but these new data require innovative analytical approaches before they can shed new light on the evolution of human anatomy and locomotion. This project is transformative in its application of novel experimental methods to establish the first quantitative criteria for interpreting foot anatomy and kinetics from fossil hominin footprints. These criteria will be used to analyze the anatomy and biomechanics evidenced by three fossil hominin footprint sites, including two recently discovered sites that have yet to be analyzed in such a way. Combining rigorous experimentation with detailed quantitative analyses of foot anatomy and gait evidenced by fossil hominin footprints will offer new perspectives to inform long-standing debates regarding the evolution of human bipedalism. This, in turn, will help us understand the timing, nature, and ecological context of evolutionary changes in hominin anatomy and locomotion.

Broader Impacts

Experimental studies of habitually unshod foot morphology and function are important to clinicians and researchers in other fields, given recent enthusiasm for barefoot running. Consistent efforts will be made to disseminate experimental results to fields outside of biological anthropology.

This project also offers broader impacts within paleoanthropology. The Co-PI and PI are developing a new archival system at the National Museums of Kenya to digitally curate three-dimensional scans of fossil footprints. This will foster international collaborations by allowing students and researchers access to original data, and address a unique set of conservation issues since fossil footprint surfaces are often too large and fragile to remove from their depositional context and, once exposed, can quickly degrade.

The Co-PI and PI will continue to present results of this study to the public through their ongoing collaborations with the Smithsonian Institution' National Museum of Natural History. These efforts will include online outreach, as well as regular lectures and participation in interactive programs at the Hall of Human Origins, organized through their Education and Public Outreach department.

Through collaboration with the Rutgers University/National Museums of Kenya Koobi Fora Field School, this project will involve extensive training of undergraduate students from Kenya, South Africa, and the US in methods of paleoanthropology and experimental biomechanics. The nature of this project provides many opportunities for student training and consistent efforts will be made to recruit trainees from groups historically underrepresented in biological anthropology.

This proposal is a resubmission. In response to a number of excellent points raised by reviewers, this revised proposal now 1) incorporates a new method (custom-designed thin pressure-sensing insoles in a minimalist sock) to directly measure foot pressure distribution in a variety of compliant sediments (i.e., of varying moisture levels); 2) omits plans to collect running data on runners in the DC area, because all of the available subject pool will have likely grown up habitually shod, and instead focuses exclusively on data collection from the habitually unshod or minimally shod Daasanach; 3) provides greater detail on this study's broader impacts, including conservation and curation of fossil footprint data with the National Museums of Kenya, publishing results of broader interest in journals outside of biological anthropology, making results available to the public, strengthening international collaborations, and providing training in paleoanthropological and experimental methods to more than a dozen students, including many from underrepresented groups.

INTRODUCTION

Researchers as early as Charles Darwin (1871) have described bipedalism – the ability to walk on two legs – as an evolutionary change that defined our human lineage. Yet there is still no consensus among paleoanthropologists about its evolutionary history. Did bipedalism evolve more than once? Can we reconstruct the ancestor/descendent sequence of changes leading to the type of locomotion practiced by modern humans? Changes in anatomy between hominin species may have resulted in, or been adaptations to, different styles of locomotion in our ancestors and we know that these changes eventually led to the type of bipedalism we use today. However, the timing, nature, and ecological contexts of such changes remain largely unknown.

The genus *Australopithecus* includes species that undoubtedly used at least some degree of bipedal locomotion when traveling terrestrially. However, much debate has focused on the extent to which locomotion in *Australopithecus* was similar to that of modern humans and whether all *Australopithecus* species shared the same locomotor mode (Ward, 2002). This debate is exemplified by research on the anatomy of *Australopithecus afarensis*, a species that shows a mix of features, some consistent with terrestrial bipedalism and some with arboreal locomotion. It has been argued that the retention of anatomical traits functionally linked to arboreal locomotion provides evidence that at least some arboreal behaviors were practiced by this species, such that their locomotor repertoire differed from that of modern humans (e.g., Jungers, 1982; Stern & Susman, 1983; Susman et al., 1984; Duncan et al., 1994; Richmond, 1998; Schmitt, 2003). However, others have interpreted these retained primitive arboreal traits as non-functional 'evolutionary baggage' (e.g., Lovejoy et al., 1973; Johanson et al., 1976; Latimer & Lovejoy, 1989, 1990a, 1990b). These disagreements about the functional interpretation of the same fossil anatomy suggest that new approaches are necessary to help resolve this debate.

The species *Homo erectus* exhibits a postcranial morphology that differs from all members of the genus *Australopithecus* and closely resembles that of modern humans, supporting the hypothesis that a new postcranial body plan emerged somewhere close to 2 Ma (Wood & Richmond, 2000). Features such as increased stature, long legs, large lower limb joints, and the absence of features associated with arboreality suggest a major shift in locomotor mode compared to *Australopithecus* (Ruff et al., 1993; Richmond et al., 2002). This apparent adaptive shift is so significant that some have proposed that *H. erectus* (rather than *H. habilis*) should mark the beginning of the genus *Homo* (Wood & Collard, 1999). Many of the modern human-like locomotor features of *H. erectus* have been linked to energetic efficiency in walking and running long distances (Carrier, 1984; Bramble & Lieberman, 2004; Steudel-Numbers, 2006; Pontzer, 2007). But while several features point towards human-like locomotion, this hypothesis is called into question by morphological differences between *H. erectus* and *H. sapiens*, which may indicate different modes of bipedalism (e.g., Rose, 1984; McHenry & Brown, 2008; Simpson et al., 2008).

Footprints are usually ephemeral but a few sets of footprints made by extinct hominins have fossilized, providing unique windows into the evolutionary history of hominin locomotion. Fossil footprints preserve the only direct records of both the foot anatomy and gait of extinct hominin species, and offer a new approach to debates over the functional interpretation of fossil evidence. Such an approach has proven invaluable in reconstructing dinosaur locomotion from fossilized footprints (e.g., Gatesy et al., 1999).

However, until quite recently, hominin footprints were rare in the fossil record. The most-studied set was discovered in 1978 at Laetoli, Tanzania (Leakey & Hay, 1979). These prints show that a hominin species, most likely *Au. afarensis*, walked bipedally about 3.7 Ma (White, 1980). But since their discovery, studies have reached conflicting conclusions regarding the 'humanness' of the foot anatomy and locomotion implied by these footprints (e.g, Stern & Susman, 1983; White & Suwa, 1987; Raichlen et al., 2010).

The recent discoveries of probable *H. erectus* fossil footprints at Ileret, Kenya (about 1.5 Ma; Bennett et al., 2009) provide new data that allow for the direct comparison of the implied foot anatomy and gait of *H. erectus* and *Au. afarensis*. These data allow for the direct testing of hypotheses related to locomotor behavior before and after the extensive anatomical changes that occurred in hominins around 2 Ma. The Ileret footprints are also the first opportunity to study the foot anatomy of *H. erectus*, due to the absence of confidently assigned *H. erectus* foot bones in the fossil record.

Even more recently, one of the earliest modern human fossil footprint sites (~120 Ka) was uncovered at Engare Sero, Tanzania (Hatala et al., 2011; Richmond et al., 2011). This sample of fossil footprints presents the first opportunity for a quantitative analysis of gait among a group of early *H. sapiens*, and provides a comparative context to assess the 'humanness' of the Laetoli and Ileret footprints. Moreover, the site at Engare Sero preserves footprints of individuals who were almost certainly running, allowing us to test hypotheses regarding the way that our immediate ancestors ran (e.g., Lieberman et al., 2010).

The growing sample of fossilized hominin footprints will allow us to address long-standing debates over the evolution of bipedal gait within the hominin clade. However, before that process can begin, we need to generate a thorough understanding of the dynamic interaction between the foot and the soft sediment in which an impression is formed. **We intend to develop such an understanding by using experimental biomechanical methods to demonstrate how specific variables of foot anatomy and gait are reflected in the morphology of footprints.** Results from these experiments will be integrated with analyses of fossil footprints in order to improve our understanding of foot anatomy and bipedal gait at different points in human evolution. **This project will use evidence from fossil footprints to directly test the hypothesis that all features of a modern human-like foot anatomy and gait were present in *Australopithecus afarensis*, and foot anatomy and bipedal gait remained essentially unchanged in *Homo erectus* and *Homo sapiens*.** The approaches that will be taken include:

1) <u>*Understanding the dynamics of footprint formation.*</u>
   a. *Human experiments.* Habitually unshod subjects will be asked to walk and run through soft sediments to produce footprints. They will wear a custom-designed pressure-sensing 'sock' that will measure the dynamic distribution of pressure beneath their feet as they produce footprints in soft sediments. Aspects of foot anatomy will be measured radiographically and sediment saturation levels and mechanical properties will also be quantified. Through controlled experimentation we can, for the first time, gain an understanding of how specific anatomical and functional variables are recorded in footprint morphology. For example, **are variations in foot anatomy (e.g., divergence angle of hallux, height of longitudinal arch) discernible from footprints? Do consistent relationships exist between the distribution of plantar pressure and footprint topography? Do relationships between anatomy, gait, and footprint morphology change with variation in sediment properties?**
   b. *Comparative primate experiments.* Similar laboratory experiments are planned with chimpanzees at Stony Brook University, in order to understand how their foot anatomy and function are recorded in the footprints they produce while walking bipedally. This comparative research is critical, given hypotheses that early hominin anatomy and bipedal locomotion may have resembled modern chimpanzees. **How are differences between human and chimpanzee foot anatomy (e.g., position of hallux and presence of longitudinal arch) and foot function (distribution of plantar pressure) reflected in their footprints formed by walking through soft sediment? Do these relationships change with variation in sediment properties?**
2) <u>*The evolution of bipedal walking as inferred from fossil footprints.*</u> Fossil *Au. afarensis*, *H. erectus* and *H. sapiens* footprints will be examined in the light of results from experiments on footprint formation. **Are characteristics of a modern human-like foot anatomy (e.g., adducted hallux,**

medial longitudinal arch) and gait (e.g., toe-off through hallux) evident in *Au. afarensis*, *H. erectus*, and/or *H. sapiens* fossil footprints? What do comparisons among fossilized *Au. afarensis*, *H. erectus* and *H. sapiens* footprints tell us about similarities or differences in their foot anatomy and/or gait?

I. BACKGROUND AND RESEARCH OBJECTIVES

A) Understanding the dynamics of footprint formation

Human footprint experiments

While fossil hominin footprints provide unique opportunities for studying locomotion, they also present the complex problem of interpreting the dynamic interaction between a foot and soft sediment that results in a footprint. Some researchers have used experimental approaches to address questions about fossil footprints but much remains unknown about the quantitative relationships between anatomical, functional, and sedimentary variables, and how they can be interpreted from fossil hominin footprints.

Day and Wickens (1980) conducted one of the earliest experimental analyses of the Laetoli footprints, in which they asked modern humans to produce footprints in fine-grained sand, and then compared contour maps of these prints to the fossil footprints from Laetoli. Tuttle and colleagues (1990), who expanded on this work, opined that the use of footwear would postdate the Laetoli footprints (see Trinkaus & Shang, 2008) and that footwear would probably significantly affect foot anatomy and function (see D'Août et al., 2009). Therefore, Tuttle and colleagues (1990) used a sample of footprints made by habitually unshod Machiguenga of Peru in their comparative study of the Laetoli prints. However, neither study assessed how specific anatomical or functional variables influence footprint morphology. Instead, they relied upon gross comparisons of footprint shape to determine whether or not humans could possibly produce footprints similar in shape to those from Laetoli.

In their interpretation, Day and Wickens (1980) understood that a footprint is not a simple mirror image of foot anatomy and that the process by which the foot generates dynamic propulsive forces must also play a significant role in determining the morphology of a footprint. However, they did not directly measure those forces. Although foot pressure-sensing devices were developed long ago (Elftman, 1934), recent advances in computer technologies have made these systems exponentially more precise and practical. D'Août and colleagues (2010) were the first to relate quantified foot pressure distributions to footprint morphology. They found that a relationship did exist between foot pressure and footprint depth, although they noted (p.524) that "…the exact nature of the interaction between the dynamics of the foot and the substrate needs to be elucidated." D'Août and colleagues (2010) conceded that their study on the relationship between plantar pressure and footprint morphology would ideally utilize a "pressure sock" that could measure pressure at the foot-soft substrate interface, although no such equipment was available at that time. Since we are primarily interested in relating footprint morphology to the distribution of propulsive forces at the foot-substrate interface, the co-PI and PI have worked with Novel, a leading manufacturer of pressure-sensing equipment, to develop an innovative custom-made system that integrates an elastic sensor on the bottom of the foot with a neoprene sock. This represents the first technology that can be used to directly measure the dynamic distribution of plantar pressure at the foot-substrate interface as a subject walks through soft sediment, while minimally obstructing the natural movements of the foot. The proposed study will also include direct measurements of foot anatomy (radiographic measurement of hallux divergence angle and longitudinal arch height) and sediment properties (moisture content and resistance to deformation). **The proposed study will be the first of its kind to include quantified measures of foot anatomy, foot function, and sediment properties, so that we can understand the simultaneous effects of anatomical, functional, and sedimentary variables on footprint morphology.** By understanding how these variables both independently and together influence footprint morphology, we can use this information to better understand the foot anatomy and gait biomechanics evidenced by fossil hominin species that may have no exact modern analogue. The experiments outlined above will test the following hypotheses:

<u>H_1:</u> The distribution of pressure underneath the foot correlates with the 3D morphology of footprints when normalized for speed (footprint depth correlates with magnitude of pressure).

H$_2$: Foot morphology is correlated with 3D footprint morphology, such that differences in divergence angle of the hallux and longitudinal arch height produce different signatures in footprint shape.

H$_3$: Sediment properties (saturation level, deformative properties) significantly influence footprint shape and affect relationships between foot anatomy, kinetics, and print morphology.

Comparative primate experiments.

While modern humans are clearly the most proficient bipeds among the apes, our ability to walk bipedally is not unique. Chimpanzees, gorillas, and gibbons all engage in some degree of terrestrial bipedal locomotion. If modern humans most recently shared a common ancestor with chimpanzees (Page & Goodman, 2001) then a comparison of their bipedal locomotion is relevant to any evolutionary study. Furthermore, one prominent hypothesis in paleoanthropology suggests that early hominin postcranial anatomy is consistent with a bent-hip bent-knee compliant bipedal gait, similar to that observed in chimpanzees (Stern & Susman, 1983; Schmitt, 2003). Understanding the interaction between the anatomy, gait, and footprint morphology of chimpanzees is necessary before we can evaluate this hypothesis using fossilized early hominin footprints.

Research has focused on the differences between chimpanzees and modern humans both in terms of foot anatomy, and the biomechanics of their bipedal walking. Morton (1922, 1924) documented the anatomical differences between the feet of modern humans and chimpanzees, and specifically differences in the abduction angle of the hallux and the development of the transverse and longitudinal arches. Chimpanzees tend to have a transverse arch, similar to modern humans and other great apes, but they lack a longitudinal arch and have a more abducted hallux. As such, an adducted hallux and a longitudinal arch are considered to be features of modern human foot anatomy that differentiate us from the great apes and contribute to our strict reliance upon bipedal locomotion (Harcourt-Smith & Aiello, 2004). These features also make our pattern of bipedal walking distinct from that of chimpanzees. Elftman and Manter (1935) found differences in the patterns by which chimpanzees and modern humans distribute pressure across the foot, with the longitudinal arch and adducted hallux of modern humans encouraging a transfer of pressure to the metatarsal heads (the “ball” of the foot) during late stance phase, followed by toe-off through the hallux. In chimpanzees, pressure never shifted to the ball of the foot and propulsion was generated by the transverse tarsal joint; this can be explained by their lack of a longitudinal arch and different hallucial morphology. A similar pattern of pressure transmission was found in a study of the bipedal locomotion of bonobos (Vereecke et al., 2003). A recent analysis of *Au. afarensis* foot morphology raised new questions about the evolutionary history of hominin foot anatomy by suggesting that *Au. afarensis* may have had a longitudinal arch, which would have allowed for a modern human-like transfer of pressure across the ball of the foot and toe-off through the hallux (Ward et al., 2011). An experimental comparison of foot function and footprint formation between modern humans and chimpanzees walking bipedally will allow us to investigate how their diverse foot anatomies (e.g., hallux position and presence or lack of a longitudinal arch) and gaits (e.g., distribution of propulsive forces) are reflected in their respective footprints. **These comparative experiments will allow us to evaluate hypotheses about the presence or absence of chimpanzee-like anatomical and functional variables in fossil hominin footprints.** Specifically, they will test the following hypotheses:

> **H$_1$: Differences in foot anatomy between chimpanzees and modern humans will be evident in their footprints. Hallux divergence angle will be evident in the position of toe impressions and presence or absence of a longitudinal arch will be made clear by midfoot topography.**
>
> **H$_2$: Differences between chimpanzee and human foot function will also be discernible from their footprints. Human footprints will have relatively deeper impressions beneath the metatarsal heads because they use the “ball” of the foot to transmit propulsive forces.**

B) The evolution of bipedal walking as inferred from fossil footprints.

The potential of the information preserved within fossil footprints has been recognized since the discovery of the Laetoli footprints in 1978 (Leakey & Hay, 1979). While hard tissue evidence indicated that members of the genus *Australopithecus* were bipedal, the Laetoli prints pushed back the oldest evidence of bipedalism from 3.0 Ma to around 3.7 Ma (White, 1980). Several researchers supported the idea that these footprints reflect a modern human-like form of bipedalism (e.g., Day & Wickens, 1980; Tuttle et al., 1990; Raichlen et al., 2010; Crompton et al., 2011). However, others have argued that the Laetoli prints reflect a foot anatomy and gait that differs from, and is more primitive than, that of modern humans and more recent hominins, such as *H. erectus* (Stern & Susman, 1983; Susman et al., 1984; Deloison, 1991; Bennett et al., 2009). **This project will generate a new interpretation of the foot anatomy and gait reflected by the Laetoli prints by using 3D methods to compare them with experimentally-produced human and chimpanzee footprints and prints of other fossil hominins.**

More recently, new fossil footprint discoveries have offered the potential to provide important insights into the evolution of gait within the hominin clade. One of these was made at Ileret, Kenya, with fossil footprints dating to ~1.5 Ma (Bennett et al., 2009). This site preserves several trails of footprints as well as isolated prints. Their size suggests they were most likely made by *H. erectus* and/or possibly by large male *Paranthropus boisei* individuals. However, if the prints were made by *P. boisei* and show relatively modern morphology and gait, parsimony would suggest that these characteristics were already present in the last common ancestor of *P. boisei* and *H. erectus*. The preservation of these prints is much better than the nearby Koobi Fora footprints described by Behrensmeyer and Laporte (1981), so much so that they will allow for more accurate reconstructions of gait. These footprints, if they do represent *H. erectus*, are the only direct evidence of the foot anatomy and locomotion of that taxon, a species whose postcranial anatomy reflects a distinct shift from *Australopithecus* in terms of body form (Ruff et al., 1993; Wood & Richmond, 2000; Richmond et al., 2002). **This sample of fossil footprints from Ileret, Kenya will provide the first quantitative analysis of foot anatomy and gait in hominins at 1.5 Ma.**

Engare Sero, Tanzania is a more recent fossil footprint site that was just reported within the past year. This site preserves hundreds of fossilized footprints that date to approximately 120 Ka (Hatala et al., 2011; Richmond et al., 2011). Along with the southern African sites of Nahoon Point (~124 Ka; Jacobs & Roberts, 2009) and Langebaan Lagoon (~117 Ka; Roberts & Berger, 1997), the Engare Sero footprints represent some of the earliest direct snapshots of locomotion in anatomically modern *H. sapiens*. The 350 footprints uncovered to date at Engare Sero comprise more than 30 trackways of multiple prints. This exceeds, by two orders of magnitude, the footprint totals at Nahoon Point (3, with only 2 preserved; Roberts, 2008) and Langebaan Lagoon (3; Roberts, 2008), thus making Engare Sero the appropriate location for detailed analyses of early *H. sapiens* locomotion. In 2010, we began excavations of these footprints and intend to return to this site each summer. Footprint trails lead directly into unexcavated sediments, so the footprint sample at this site is almost certainly larger than the current totals. **The analysis of these footprints will provide comparative evidence of unshod humans that can be used to interpret the gait of earlier hominins and permit the first quantitative analysis of foot anatomy and gait in early *H. sapiens*.** Comparative analyses of fossil footprints will target the following hypotheses:

> **$\underline{H_1}$: All three sets of fossil hominin footprints will be dissimilar from those produced by chimpanzees, as they will all reflect a modern human-like foot anatomy and gait.**
>
> **$\underline{H_2}$: All three sets of fossil hominin footprints will preserve similar features of modern human-like foot anatomy (e.g., a medial longitudinal arch and adducted hallux) and gait (e.g., medial transfer of pressure and toe-off through hallux), indicating that modern human-like bipedalism has been present in hominins since 3.7 Ma.**

II. MATERIALS AND METHODS:

A) Understanding the dynamics of footprint formation.

Human footprint experiments

(IRB approval has been granted; GW IRB#031030, expires 9/11/12, will apply for extension)

Field experiments on footprint formation will be conducted with 20 consenting adult individuals (10 men, 10 women) from the Daasanach tribe living near the village of Ileret, Kenya. Anthropologists working in Ileret since the 1960s have attested that the Daasanach grew up unshod or, just within the last decade, have been minimally shod (**Fig. 1**; JWK Harris & AK Behrensmeyer, *pers. comm.*). Thus, they are not subject to the influences of modern footwear on foot development. Also, the Daasanach are local to the site of ongoing fieldwork where the 1.5 Ma fossil footprints are located. We have collected pilot data from members of this population, so they are familiar with our research team and our protocol.

Experiments will be conducted in an open clearing with ample space for subjects to reach the desired experimental speeds. A trackway measuring 125 cm long, 50 cm wide, and 15 cm deep will be dug out of the ground and filled with sediment directly excavated from the geological layer preserving the 1.5 Ma footprints at Ileret. Water will be added to the sediment in order to reconstitute a mud similar to that in which the fossil footprints were formed. It is not crucial (and nearly impossible) to know the exact saturation level of the mud in which the fossil footprints were made. However, given the high level of anatomical detail preserved in the Ileret prints, results from other experimental work would suggest that they were formed in a strong, firm mud (Allen, 1997). These experiments will be conducted across a range of sediment moisture levels, from the point at which a footprint is barely visible to the point at which footprints are so soft and distorted that preservation in the fossil record would be impossible. Moisture levels will be quantified using a digital moisture meter. Following the addition of water, a portable penetrometer, a piece of equipment that is standard in soil mechanics, will be used to obtain a quantified measure of the resistance of the sediment to deformation (pressure required to depress the sediment to a specified depth, in KPa). With measures of both saturation and resistance to deformation, we can track how these two variables interact with each other and also how they influence relationships between foot anatomy, gait, and footprint shape.

Biometric measurements will be taken from each subject. These will include standing height, heights of the shoulder, hip (greater trochanter), knee (tibial plateau), and ankle (lateral malleolus), foot length, and circumferences at the shoulders and waist. Subjects will be palpated for placement of neon-colored adhesive markers at osteological landmarks at the hip (greater trochanter), knee (tibial plateau), ankle (lateral malleolus), and foot (5th metatarsal head). Digital video of each trial will be recorded with a high-speed camera (Casio Exilim Ex-fh100) at 1000 frames/second. Neon markers will allow for digitization and analysis of kinematic data using Vicon Motus software at George Washington University (**GW**). With these data, we can analyze the effects of hip, knee, and ankle joint angles on footprint morphology.

A portable x-ray machine (already owned by GW) will be used to take lateral and dorsi-plantar radiographs of the subjects' weight-bearing feet while standing upright (following methods outlined in Cavanagh et al., 1997). The portable x-ray device will create digital outputs, which will be stored on a field laptop computer and later analyzed in the lab at GW, using freely-available NIH ImageJ software. Radiographic measurements will include the heights of the medial and lateral longitudinal arches (from lateral view), as well as hallux divergence (from dorsi-plantar view). These variables distinguish modern human feet from those of other great apes, and are particularly prevalent in debates over the evolutionary history of the human foot (for a review see Harcourt-Smith & Aiello, 2004).

Subjects will be outfitted with Novel Pedar insoles, enclosed within NRS Hydroskin neoprene socks. This apparatus is pliable and minimally obtrusive to movements of the foot, providing a snug fit that moves with the toes and all other joints of the foot. The combination of the Pedar sensor and neoprene sock is only about 2.5 mm thick. Each subject will be asked to walk and become accustomed to this sock for at least 5 minutes prior to experimentation, such that it does not affect changes to their gait. The insole will be connected by a thin wire to an interface box affixed to the subject's waist by a neoprene belt. The interface box will send a live feed of pressure data to a laptop computer via Bluetooth.

Subjects will pass over the sediment trackway at five different speeds (slow walk, normal walk, fast walk, jog, fast run; speeds quantified from video). Each subject will complete at least 3 trials at each speed (total n>300). Subjects will be asked to repeat trials until they are able to land in the sediment trackway without adjusting their gait, while maintaining a constant speed of travel throughout the trial.

After each trial, the footprint produced in the sediment trackway will be photographed in a particular manner (~15 photographs at a variety of angles and heights) that will allow for the later creation of 3-dimensional models using photogrammetric methods (see **Fig. 2**). This will be accomplished using PhotoModeler Scanner 2012 software, also in the lab at GW. Following photography, footprints will be obliterated and the mud trackway leveled, using a trowel.

Chimpanzee footprint experiments
(IACUC approval has been granted at Stony Brook University, protocol 2009-1731-R2).

The chimpanzees that will be used in this study are held at Stony Brook University (**SBU**). Approval has been granted by the institution to conduct these experiments (see attached documentation).

Experiments on the distribution of foot pressure and footprint formation will follow procedures similar to the experiments on human subjects, but slightly altered to accommodate lab research on nonhuman primates. A wooden trackway will be constructed and filled with sediment in the lab at SBU. Several 10-gallon containers of the same sediment used in the field experiments (from the fossil footprint layer at Ileret) will be shipped back to the United States for use at SBU. Length, width, and depth will be identical to the trackway used in the human experiments. A wooden platform will be built to the height of the sediment trackway. In these experiments, a meter-long plantar pressure pad (RSScan International Footscan) will rest upon the wooden trackway, approximately 0.5 meters before the sediment. Gradually-inclined ramps will lead up to and down from the platform, with enough space for the chimpanzees to reach their preferred speeds before passing over the pressure pad. The chimpanzees will be habituated to walking over this setup prior to experimentation.

Technologies like the custom-designed 'pressure sock' have yet to be developed for chimpanzee feet and doing so is not of immediate interest to industrial companies like Novel, so chimpanzee pressure data must be collected in this manner. Comparable RSScan data have already been collected with a sample of 38 Daasanach adults and can be used in any comparative analyses of the relationships between pressure and footprint morphology in humans and chimpanzees (see Preliminary Results and Hatala et al., 2012). Additionally, these comparative experiments are critical to quantify shape variation in chimpanzee footprints in order to use morphometric comparisons between human, chimpanzee, and fossil hominin footprints to address hypotheses about the evolution of human foot anatomy and gait.

The same biometric measurements taken in the human experiments will be taken from the chimpanzees. Markers will be placed at the same osteological landmarks and all trials will be recorded with a high-definition video camera for later digitization and analysis of kinematic data using Vicon Motus at GW. Each chimpanzee will conduct 10 trials at their preferred speed and up to 10 at faster speeds, depending on the trainer's ability to motivate increased speed. These speeds will be quantified after digitization. Trials will only be included if the chimpanzee continues walking at a constant speed across the full length of the platform. Following each trial, the footprints that the chimpanzee creates will be photographed for the later production of 3-dimensional models at GW.

Analysis of experimentally-produced footprints. A landmark-based approach will be used to draw comparisons between the distribution of pressure and footprint morphology for each subject at each speed. Pressure distribution maps will be saved within Novel and RSScan software, while 3D footprint models will be created in PhotoModeler Scanner 2012, then analyzed using Geomagic Qualify 2012. Landmarks will be placed at 10 different anatomical points on the pressure distribution map (within Novel and RSScan) and on the 3D footprint model (within Geomagic). These will correspond to the medial and lateral heel, lateral midfoot, metatarsal heads 1-5, hallux, and second toe. Measures of peak pressure and pressure-impulse (pressure*time) at each of these landmarks will be exported. Positional (x-y-z coordinate) data for each landmark on the 3D footprint model will be collected within Geomagic software. The plane of the ground can be easily established, since the 3D models will always include at least 10 cm of flat, undisturbed ground around the perimeter of the footprint. The flat ground will be fixed to the x-y plane, so that measurements on the z-axis will correspond to 'depth'. These data will be analyzed to test hypotheses that correlations exist between anatomical variables (e.g., arch height) and/or functional variables (e.g., peak pressures, joint angles) and footprint depth in each region of the foot. Geometric morphometric analyses will be used to examine within- and between-subject relationships between footprint shape and multiple 'predictor variables', including measures of plantar pressure, joint angles, height of the medial and lateral longitudinal arches, hallux divergence, sediment saturation level, and resistance of the sediment to deformation. Footprints will be transformed using a Procrustes fit, then principal components analyses will be conducted. Multiple regression analyses will be used to determine the influence of the "predictor variables" on the principal components that describe variation in footprint shape. This innovative approach will provide the first information about the manner and degrees by which specific anatomical, functional, and sedimentary variables influence variation in footprint shape.

B) The evolution of bipedal walking as inferred from fossil footprints.

The fossil footprint sample will consist of footprints from Laetoli, Tanzania (~3.7 Ma), Ileret, Kenya (~1.5 Ma), and Engare Sero, Tanzania (~120 Ka). Not only is it certain that these sites preserve fossil footprints of three different hominin species (due to their dates), but they also likely represent species with very different anatomies (*Au. afarensis*, *H. erectus* and *H. sapiens*).

Casts of the Laetoli prints at the National Museums of Kenya (**NMK**) preserve 11 footprints from the G1 (single individual) trackway. At Ileret, 21 footprints have been uncovered to date. These comprise two trails of two prints each, one track of four prints, one track of seven prints, and six isolated prints. The footprint layer at Engare Sero preserves 353 footprints attributable to at least 24 trackways that range in size from three to 34 prints. At both Ileret and Engare Sero, footprint trackways lead directly into sediments that are currently unexcavated, making it almost certain that additional footprints will be uncovered in subsequent field seasons. If more are found, they will be added to the study sample.

All fossil footprints will be documented using photogrammetry. This will take place in the NMK for the Laetoli prints (see attached documentation), whereas the Ileret and Engare Sero footprints will be photographed in the field (KH and BR are actively involved in fieldwork at these sites each summer). At Ileret and Engare Sero, photogrammetry will also be used to create 3D models of the entire footprint layers, a crucial step for site preservation purposes since fossil footprints are fragile and subject to degradation once uncovered. As described previously, about 15 photographs will be taken of each individual footprint. Both trackways and isolated prints will be documented, although the focus will be on footprint trails. Trails are necessary to calculate stride and step lengths, which will be important for discerning walking speed prior to any comparative analyses (Dingwall et al., 2011, 2012).

As in the experiments, PhotoModeler Scanner 2012 will be used to create 3D models from these series of images (e.g., **Fig. 2**). Landmarks will be placed at the same 10 anatomical landmarks listed previously. Multivariate statistical methods will be used to examine within- and among-site variations in terms of footprint morphologies. Geometric morphometric analyses will elucidate shape differences between the morphologies of footprints produced by *Au. afarensis*, *H. erectus*, and *H. sapiens*. Differences will be examined in light of experimental results on footprint formation, to relate morphological differences between footprints to particular characteristics of foot anatomy, gait, and possibly sedimentary differences. For example, shallower footprint depths underneath the hallux and first metatarsal head may indicate the lack of a modern human-like toe-off in which pressure is transferred to the medial portion of the foot at the end of the stance phase. Certain fossil footprints may be excluded from comparative analyses if they are too deformed and amorphous to preserve anatomical and functional details, as may occur in very saturated sediments (Allen, 1997). The experimental approach employed by this study will bring to light the influence of sediment saturation and mechanical properties on the preservation of foot anatomy and foot function in footprint shape. This will allow us to determine, for the first time, which fossil prints were preserved in mechanically similar sediments, and therefore which prints can provide justifiable anatomical and functional comparisons. We will also be able to determine if certain prints should be excluded from comparative analyses, in cases where sedimentary differences prohibit the direct comparison of preserved relics of foot anatomy and foot function.

III. PRELIMINARY RESULTS

During the 2010 and 2011 field seasons, the co-PI led a pilot study with 38 consenting adults (19 male, 19 female) from the habitually unshod Daasanach tribe at Ileret, Kenya. This study followed the protocol outlined previously, but with pressure data collected from the RSScan pressure pad rather than the custom-designed 'pressure sock', which was not yet conceived and developed. This pilot study assessed only the relationship between the distribution of plantar pressure and footprint depths across 10 regions of the foot. Data were collected from subjects walking at both normal and fast speeds.

The cumulative assessment of the correlation between pressure and depth revealed that the two were significantly correlated. Maximum pressure explained a greater amount of variance in footprint depth (Spearman's $\rho = 0.4734$) than did pressure-impulse ($\rho = 0.2741$), although both measures of plantar pressure were significantly correlated with measures of print depth ($p<0.0001$; Table 1). When data from each walking speed were analyzed separately, we found that the relationship between plantar pressure and footprint depth changed with walking speed. A stronger relationship between maximum pressure and depth existed at fast walking speeds ($\rho=0.5650$) than at normal speeds ($\rho=0.3686$) but both relationships were significant ($p<0.0001$; Table 2). The same was true of the correlations between pressure-impulse and depth at fast ($\rho=0.3788$, $p<0.0001$) and normal ($\rho=0.1616$, $p = 0.0014$) walking speeds (Table 2).

Correlation coefficients were smaller than expected, so it was thought that between-subject differences in foot anatomy may have obscured trends in the relationship between plantar pressure and footprint depth. Further analyses tested the correlation between pressure and depth for each subject independently. Significant correlations between maximum pressure and depth were found in 26 of the 38 subjects (see **Fig. 3** for demonstrative plot). Correlations between impulse and print depth only existed in 13 subjects.

This pilot study established that the distribution of plantar pressure is correlated with the topography of footprints created in the sediment that preserves the 1.5 Ma fossil footprints at Ileret. This result differed from those of D'Août and colleagues (2010) who found that the distribution of plantar pressure at the foot-pressure pad interface was not correlated with the morphology of footprints made in sand. Differences in sediment mechanics may be the most probable explanation for why the sediment from Ileret preserved footprints that were topographically linked to the distribution of pressure measured on a pressure pad but sand did not. This supports the hypothesis that relationships between foot anatomy, foot function, and footprint morphology change with sediment properties.

Most importantly, these pilot results emphasize that a multivariate approach will be most appropriate. The coefficients of correlation between pressure and footprint depth demonstrate that plantar pressure significantly influences footprint depth, but that it explains less than half of its variation. This provides further justification for the methods of the proposed study, in which we will control and quantify anatomical, functional, and sedimentary variables, and analyze their simultaneous effects on footprint shape. Furthermore, the relationship between plantar pressure and footprint morphology may be different when new methods are applied to measure pressure at the foot-substrate interface as the footprint is being produced. It is clearly necessary to gain a more accurate understanding of how specific anatomical, functional, and sedimentary variables influence footprint morphology before we can develop accurate functional interpretations of fossil hominin footprints. With such an understanding, we can use these invaluable data to inform hypotheses regarding the evolution of human foot anatomy and locomotion.

IV. SIGNIFICANCE OF PROPOSED RESEARCH

Despite general agreement that bipedalism played an integral role in human evolution, paleoanthropologists have often disagreed over the evolutionary history of this behavior in our ancestors. Those debates based on fossil anatomy alone have reached an impasse, with researchers disagreeing over the functional interpretations of the same anatomical features. Fossil footprints provide unique windows to particular events in the past, where one can directly observe the foot anatomies and locomotor behaviors of extinct hominin species. Several intriguing hominin fossil footprint sites have been uncovered in recent years, and these present a new source of data that can be used to directly test hypotheses about locomotion in the human fossil record. However, much preliminary research is necessary before we can use fossil footprints as tools for inferring foot anatomy and gait in extinct hominins. The proposed study is transformative in the degree to which it can test contentious hypotheses about the evolution of human gait, and that it will use an innovative experimental approach to analyze the dynamic processes of footprint formation with chimpanzees and habitually unshod human subjects, to understand how specific anatomical and functional variables are preserved in footprints. Experimental results will provide the first quantitative criteria for inferring anatomical and functional variables from fossil footprints. These criteria will then provide the foundation for detailed quantitative analyses of fossil hominin footprints, which will directly test hypotheses regarding the evolution of human gait. Specifically, hypotheses will be tested regarding the foot anatomies and modes of bipedal locomotion in

Au. afarensis, *H. erectus*, and early *H. sapiens*. This novel approach will provide new insight to many long-standing questions regarding the evolution of human bipedalism.

V. BROADER IMPACTS

The impacts of this project will extend beyond paleoanthropology. Research on the Daasanach will be of interest to fields such as podiatry and exercise science, given the scarcity of detailed studies of foot anatomy and function in habitually unshod/minimally shod populations. We plan to publish results from the proposed study in journals more commonly accessed by clinicians and researchers in other fields (e.g., *Foot & Ankle*, *Gait & Posture*) in addition to traditional paleoanthropological journals (e.g., *JHE*, *AJPA*), in order to disseminate our experimental results to a broader scientific community. These results will be of particular interest to clinicians given recent enthusiasm for running barefoot, or in minimalist shoes that mimic the barefoot condition (see Parks, 2010).

This project also offers broader impacts to the scientific community through our curation and conservation efforts with the National Museums of Kenya (NMK). The Co-PI and PI have developed and already initiated a novel data management plan with colleagues at the NMK to curate and conserve fossil footprint discoveries (see Data Management Plan). All 3D scans of fossil footprints generated during this study will be catalogued at the NMK and made available to other researchers and students immediately following primary publication of the data by the PI and Co-PI. These original scans are also critical for preservation purposes because, in some cases, fossil footprint surfaces are too large and fragile to be removed from the field, and can quickly degrade once they have been excavated.

Results will consistently be presented to a broader public audience. The Co-PI and the PI will continue their work with the Education and Outreach Division of the Smithsonian Institution National Museum of Natural History’s Human Origins Program. They have already presented ‘HOT (Human Origins Today) Topics’ lectures on their latest research in the Hall of Human Origins, and participated in the ‘The Scientist is In’ program, where they set up a temporary exhibit with ‘hands-on’ materials (e.g., casts) and answer questions for museum visitors. Building on recent coverage of this work (e.g., NPR in 2010, *Science* in 2011, History Channel in 2012), the Co-PI and PI will continue to work with broader media to communicate this research to the public. Following publication of original data, the Co-PI and PI will make 3-dimensional scans of fossil footprint surfaces available to the public in a view-only format on the Human Origins Program’s website.

This project will directly contribute to training Kenyan, South African and US students, including those from underrepresented groups, in scientific research and paleoanthropology. All field experiments involved in this project will be conducted in collaboration with the Koobi Fora Field School (NMK and Rutgers University). This field school always includes undergraduate students from Kenya, South Africa, and the US. Field experiments will consistently require the assistance of at least two students, and consistent efforts will be made to recruit assistants from groups underrepresented in biological anthropology. Ten undergraduates from Kenya, South Africa, and the US have already been trained as research assistants during the pilot phase of this project. One female undergraduate from GW has already been extensively trained in both the laboratory and field methods used in this project. The Co-PI and PI worked with this undergraduate trainee to design and conduct her own independent senior thesis project within the broader scope of the project outlined here. They encouraged and worked with this student to present her results at professional conferences (Dingwall et al., 2011, 2012), and are currently working with her to prepare a manuscript for submission to the Journal of Human Evolution. This trainee is now pursuing graduate studies in biological anthropology. The nature of this project provides many opportunities for training and the Co-PI and PI will inevitably recruit and train additional undergraduates.

VI. RESEARCH SCHEDULE

Summer 2012 – conduct experiments with Daasanach, continue excavations at Ileret/Engare Sero
Summer and Fall 2012 – conduct experiments with chimpanzees at Stony Brook University
Academic Year 2012-2013 – analyze experimental data, publish experimental results
Summer 2013 – continue Ileret/Engare Sero excavations, finish collecting all fossil footprint data
Academic year 2013-2014 – complete fossil footprint data analysis, write and defend dissertation

VII. FIGURES AND TABLES

Figure 1. At left, group of local Daasanach children at FwJj14E Ileret fossil footprint site. Note that all children are unshod, as is normal in this population. At right, see minimalist sandals occasionally worn by some Daasanach men for long-distance walks.

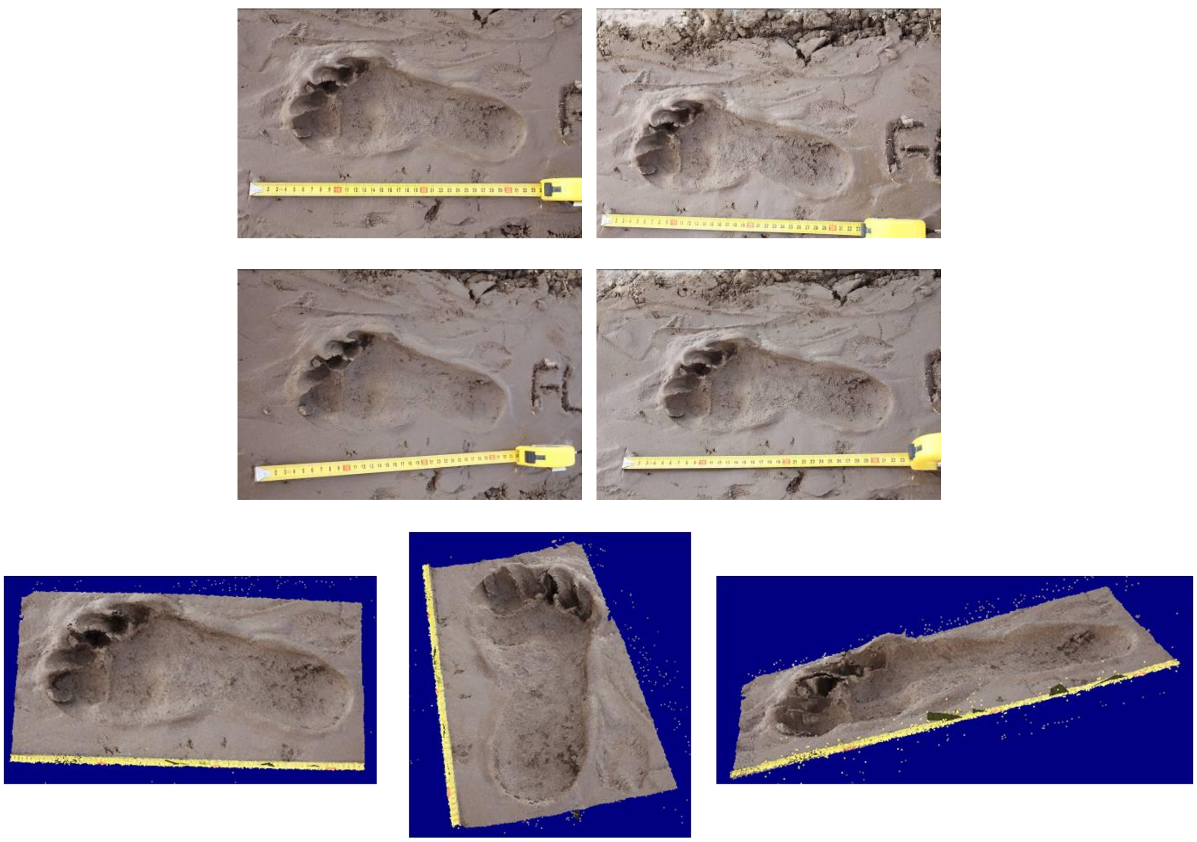

Figure 2. Four original photographs (top 2 rows) and three views of a 3-dimensional footprint model (bottom row) generated from these photographs (and more from other angles and heights) using PhotoModeler Scanner 2011.

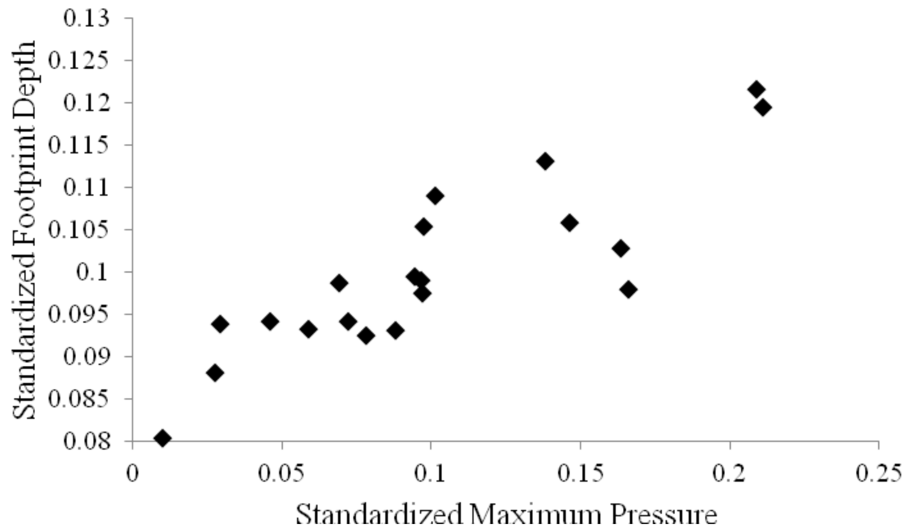

Figure 3. Sample plot showing the correlation between maximum plantar pressure and footprint depth when analyzed within the same subject. In this case, Spearman's ρ =0.8376 and p<0.0001. Because significant correlations, such as this one, were found in some subjects but not others, it will be important to quantify and evaluate the influence of other variables. The simultaneous effects of anatomical, functional, and sedimentary variables will be quantified and analyzed in the proposed study.

Correlation	Spearman's ρ	p-value
Maximum pressure & depth	0.4734	<0.0001
Pressure-impulse & depth	0.2741	<0.0001

Table 1. Correlations between standardized maximum pressures, and standardized pressure-impulse, and standardized footprint depth.

Walking Speed	Correlation	Spearman's ρ	p-value
Normal	Maximum pressure & depth	0.3686	<0.0001
	Pressure-impulse & depth	0.1616	0.0014
Fast	Maximum pressure & depth	0.5650	<0.0001
	Pressure-impulse & depth	0.3788	<0.0001

Table 2. Correlations between standardized maximum pressures, and standardized pressure-impulse, and standardized footprint depth for experimentally-produced footprints at normal and fast walking speeds.

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