

# Midtarsal Break Variation in Modern Humans: Functional Causes, Skeletal Correlates, and Paleontological Implications

DeSilva J.M.,<sup>1\*</sup> Bonne-Annee R.,<sup>1</sup> Swanson Z.,<sup>1</sup> Gill C.M.,<sup>1,2</sup> Sobel M.,<sup>1,3</sup> Uy J.,<sup>1,3</sup> and Gill S.V.<sup>4,5,6,7,8</sup>

<sup>1</sup>Department of Anthropology, Boston University, Boston, MA 02215

<sup>2</sup>Department of Radiology and Pappas Center for Neuro-Oncology, Massachusetts General Hospital and Harvard Medical School, Boston, MA 02114

<sup>3</sup>Department of Anthropology, University of Wisconsin-Madison, Madison, WI 53706

<sup>4</sup>Department of Occupational Therapy, Boston University, Boston, MA 02215

<sup>5</sup>Program in Rehabilitation Sciences (PhD), Boston University, Boston, MA 02215

<sup>6</sup>Department of Medicine, Boston University, Boston, MA 02118

<sup>7</sup>Undergraduate Program in Neuroscience, Boston University, Boston, MA 02215

<sup>8</sup>Department of Psychological and Brain Sciences, Boston University, Boston, MA 02215

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**ABSTRACT** Themidtarsal break was once treated as a dichotomous, non-overlapping trait present in the foot of non-human primates and absent in humans. Recent work indicates that there is considerable variation in human midfoot dorsiflexion, with some overlap with the ape foot. These findings have called into question the uniqueness of the human lateral midfoot, and the use of osteological features in fossil hominins to characterize the midfoot of our extinct ancestors. Here, we present data on plantar pressure and pedal mechanics in a large sample of adults and children ( $n = 671$ ) to test functional hypotheses concerning variation in midfoot flexibility. Lateral midfoot peak plantar pressure correlates with both sagittal plane flexion at the lateral tarsometatarsal joint, and dorsiflexion at the hallux metatarsophalangeal joint. The latter finding suggests

that midfoot laxity may compromise hallux propulsion. Multiple regression statistics indicate that a low arch and pronation of the foot explain 40% of variation in midfoot peak plantar pressure, independent of age and BMI. MRI scans on a small subset of study participants ( $n = 19$ ) reveals that curvature of the base of the 4th metatarsal correlates with lateral midfoot plantar pressure and that specific anatomies of foot bones do indeed reflect relative midfoot flexibility. However, while the shape of the base of the 4th metatarsal may reliably reflect midfoot mobility in individual hominins, given the wide range of overlapping variation in midfoot flexibility in both apes and humans, we caution against generalizing foot function in extinct hominin species until larger fossils samples are available. *Am J Phys Anthropol* 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

Fundamental to the science of functional morphology is the premise that biological form provides insight into the function of an organism. As applied to paleoanthropology, one might simply state that the shapes of bones matter. However, inferences between skeletal form and function can amount to little more than “just-so stories” unless hypotheses linking bony morphology and musculoskeletal function are tested with extant models. For instance, the interplay between loading and bone remodeling is complicated and may not always yield the expected results (Wallace et al., 2014). Similarly—and more relevant to our study—the authors of recent work on variation in the human foot have warned that skeletal anatomy may be only a “crude indication” of midfoot function in early hominins (Bates et al., 2013, p. 1).

Anatomical and functional variation that exists in modern human feet can be used to test this form: function hypothesis, and perhaps even help to reconstruct subtle differences in bipedal gait in early hominins. Thousands of human skeletons in museums all over the world have been studied by physical anthropologists, but none of us has observed or measured how the vast majority of the now skeletonized individuals walked in life. Harris and Beath (1948, p. 116) identified this problem almost 70 years ago, noting: “Even in the anatomical museum,

where abundant material for the study of structure is available, knowledge is lacking of function during life, to correlate with changes in structure which may be present.” More recently, data have been collected on gait kinematics in living humans, but rarely are there sufficient opportunities to study the bones of those individuals. The few data that are collected on the bones of these individuals (via imaging) are typically obtained only

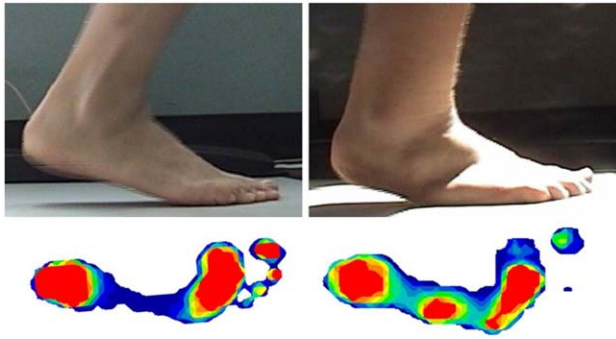
Abbreviations: CPEI, center of pressure excursion index; CSI, Chipaux-Smirak Index.

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\*Correspondence to: Jeremy M. DeSilva, Department of Anthropology, Boston University, 232 Bay State Road, #104B, Boston, MA 02215. E-mail: jdesilva@bu.edu

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**Fig. 1.** Variation in midfoot mobility in humans. Video stills of the lateral foot in a typical human with a rigid midfoot (left) and a non-symptomatic individual with hypermobility of the midfoot (right). Below are their digital footprints. Notice the high lateral midfoot pressure on the midtarsal breaker (right, from DeSilva and Gill, 2013), and the reduced pressure under the hallux. Increased kPa pressure is signified by heightened red intensity. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

when underlying pathologies are present, which hinders generalizability to form: function relationships in non-pathological individuals. Thus, the relationship between variation in skeletal form and variation in function remains poorly understood in general, and particularly in the human foot (but see advances made by Cavanagh et al., 1997; Raichlen et al., 2011; Baxter et al., 2012).

Here, we suggest that: 1) previous impediments to testing many form: function hypotheses in the human foot are significantly reduced because of advances in imaging technologies and 2) modern humans—even sedentary Western populations—are actually quite useful for testing the relationship between bony form and musculoskeletal function. Our reasoning is as follows: first, unlike most primates, humans can be easily enticed into an MRI, which visualizes both skeletal and soft tissue structures of the foot without exposing the participants to ionizing radiation (Raichlen et al., 2011; Baxter et al., 2012); and second, modern humans, perhaps because of a combination of our expanding population, relaxed selection, substrate variation, and/or our range of footwear, possess an extraordinary range of variation in foot forms. For example, there is an impressively large range of variation in longitudinal arch heights among non-pathological humans. In fact, the range of variation in shod, sedentary Western populations exceeds that which has been found in certain unshod populations (D'Aouit et al., 2009). Instead of regarding the shod, Western foot as atypical and uninformative to paleoanthropological questions, we instead propose that by extending the range of variation, Western humans provide the extremes of *pes planus* and *pes cavus* that are helpful for identifying skeletal correlates of arch height. If the shape of the talus, for example, does not significantly differ between a shod, sedentary individual with extremely high arches and one with flat feet, what hope do we have using that bone alone to determine whether or not early hominins had well-developed arches?

Similarly, as we (DeSilva and Gill, 2013) and others (Bates et al., 2013) have recently reported, modern humans display an unexpected range of midfoot mobility in the sagittal plane, and some humans even have a recognizable midtarsal break (Fig. 1). The midtarsal break, or midfoot break (DeSilva, 2010) was first recognized by

Elfman and Manter (1935) and has traditionally been characterized as dorsiflexion in the sagittal plane occurring at the calcaneocuboid joint of non-human primates. It also occurs with some frequency in pathological children, often as a result of cerebral palsy (Maurer et al., 2013). There have been two recent corrections to our anatomical and anthropological characterization of the midtarsal break. First, while some sagittal plane motion occurs at the calcaneocuboid joint, the majority of sagittal plane dorsiflexion happens laterally at the tarsometatarsal joint (Vereecke et al., 2003; DeSilva, 2010), and medially at the talonavicular joint (Thompson et al., 2014). A correlate of the finding that sagittal plane motion happens at the lateral tarsometatarsal joint is the recognition that the bases of the lateral two metatarsals—particularly the fourth metatarsal—are dorsoplantarly convex in non-human primates, but relatively flat in humans (DeSilva, 2010; Proctor, 2013; DeSilva et al., 2013). Second, though more unusual and lower in angular magnitude than other primates, some humans can consistently produce a midtarsal break (Vereecke et al., 2003; Crompton et al., 2012; DeSilva and Gill, 2013; Bates et al., 2013; Fig. 1).

These recent studies have raised important questions about the midtarsal break in humans, some of which we attempt to address in this study. What is the range of variation in midfoot mobility in non-pathological adults and in children? What anatomical (e.g., low longitudinal arch) or functional (e.g., excessive pronation) variables help explain variation in midfoot mobility both between individuals and between individual footprints of the same study subject? Does lateral midfoot mobility correlate with other aspects of the foot, such as propulsion by the hallux (see Bates et al., 2013)? Can a foot that produces a consistent midtarsal break be identified from skeletal anatomy alone?

In this study, we address some of these questions using gait kinematic and plantar pressure data collected on a large sample of children and adults ( $n = 671$ ), and a smaller subset ( $n = 19$ ) for which MRI scans were collected and aspects of foot skeletal anatomy were quantified. We hypothesized that the midtarsal break exists at the same frequency in children  $\leq 16$ -year old as in adults. Given our previous work (DeSilva and Gill, 2013), we hypothesized that BMI, arch height, and medial weight transfer all contribute to the range of variation found in midfoot mobility between different humans. Further, we expected that medial weight transfer alone helps explain variation in midfoot mobility exhibited across multiple footprints from the same individual. The recent findings of Bates et al., (2013) that lateral midfoot plantar pressure is inversely related to hallucal plantar pressure, lead to our hypothesis of a similar inverse relationship between lateral midfoot plantar pressure and dorsiflexion at the hallucal metatarsophalangeal joint during the push-off phase of walking. Finally, if there is variation in midfoot mobility in humans, and the base of the fourth metatarsal is a reliable skeletal indicator of midfoot dorsiflexion, then we hypothesized that dorsoplantar curvature of the fourth metatarsal would correlate with midfoot dorsiflexion in modern humans. Results of our findings are applied to the fossil record to infer midfoot mobility in early hominin individuals.

## MATERIALS AND METHODS

Adult individuals aged  $37.9 \pm 14.8$  years (range 17–80) ( $n = 414$ : 277 females, 137 males) and children aged

8.8 ± 3.3 years (range 1–16), ( $n = 257$ : 133 females, 124 males) participated in our study at the Boston Museum of Science as part of their *Living Laboratory* program. Sixteen was chosen as the cutoff age between juveniles and adults because ossification and fusion of the major foot elements are complete by this age in humans (Schaefer et al., 2009). The Institutional Review Boards of both Boston University and the Boston Museum of Science approved the study design (IRB numbers: 2154E and 3127E). Age was self-reported and height and body mass data were collected using a vertically positioned tape measure and a digital scale. Subjects walked barefoot at their self-selected normal walking speed down a 6.1 m long mechanized gait carpet (Gaitrite, Inc.) which collects real-time data on walking parameters, such as stride length, velocity and foot fall angle. Continuous with the gait carpet was an HR Mat VersaTek (Tekscan, Inc.) plantar pressure mat that collects high-resolution (4 sensor elements/cm<sup>2</sup>) data at 185Hz. At least two trials occurred per participant with the first trial used to calibrate the HR Mat. Plantar pressure data were synched with a video camera (Sony DCR-TRV280 Digital 8 Handycam) recording the lateral (right foot) and medial (left foot) views of the foot while it contacted the plantar pressure mat. Tekscan's video synchronization software was used to analyze the resulting video at 30 frames/second. Clear video of the lateral side of the right foot as it contacted and lifted off the HR Mat were acquired on 75 subjects for which lateral plantar pressure data were collected from that same right foot. Clear video of the medial side of the left foot as the hallucal metatarsophalangeal joint extends during toe-off was acquired on 63 subjects for which lateral plantar pressure data were collected on that same left foot. Additional details of our experimental protocol are detailed in DeSilva and Gill (2013).

Quantification of the peak lateral midfoot pressure, the angle produced at the lateral tarsometatarsal joint, the medial longitudinal arch height, and magnitude of medial weight transfer are as described in DeSilva and Gill (2013). In brief, the Tekscan research foot software module (HR Mat Research 6.51) was used to identify the maximum pressure produced along the lateral midfoot, which is quantified in kPa. Following DeSilva and Gill (2013) and Bates et al. (2013), midtarsal breakers were defined as a lateral midfoot plantar pressure in excess of 200 kPa. Video stills captured at the point of maximum dorsiflexion (identified visually) at the lateral tarsometatarsal joint were imported into Image J (NIH) and quantified as the angle formed between the plantar part of the forefoot and a line drawn along the plantar heel to the tuberosity of the 5<sup>th</sup> metatarsal, easily identified as a bulge laterally protruding from the plantolateral aspect of the midfoot. Similarly, sagittal plane motion at the hallucal metatarsophalangeal joint was quantified from video stills captured at the point when the big toe was maximally extended (identified visually). Using Image J (NIH), an angle was taken between the plantar part of the hallux in medial view and the plantar aspect of the rest of the foot defined as a straight line connecting the plantar heel to the plantar ball of the medial foot. Because skin-surface markers were not used to collect kinematic data, angular excursion data could not be collected and only angular maxima were measured. Arch height was quantified using the Chippaux-Smirak Index (CSI), which is the ratio between the minimum width of the midfoot and the maximum width of the ball of the

foot (Chippaux, 1947; Smirak, 1960). The center of pressure excursion index (CPEI) is a measure of medial weight transfer (Song et al., 1996), and is a proxy for pronation (Yoon et al., 2010; Hillstrom et al., 2013). The Tekscan research foot software module produces a center of force trajectory and a line was drawn from the starting point of the center of force (on the heel) to the final position (usually under the hallux). The furthest point along the center of trajectory arc from that straight line was identified and a line was drawn from that point to the straight line. A ratio of the two lines is the CPEI.

A second experimental protocol was used on subjects from whom MRI data were collected. Healthy young adults aged 22.3 ± 2.2 years (range 19–28) from the Boston University community were recruited for the study ( $n = 19$ : 12 females, seven males). Gait and plantar pressure data were collected at the Motor Development Laboratory (Sargent College, Boston University) in the manner described above. These data were synched with video cameras recording both lateral and medial views of the foot (left or right) while it contacted the plantar pressure mat. Unlike the Museum of Science experimental protocol, subjects repeated this walking procedure 50 times. Subjects then underwent foot MRI scanning at the Center for Biomedical Imaging at Boston University School of Medicine. Scan protocol was a proton density weighted 3D acquisition (slice thickness: 0.6 mm) on a 3 Tesla Philips Achieva scanner. Plantar pressure data were analyzed using HR Mat Research 6.51 (Tekscan, Inc.) software as described above. Since only one foot was scanned in the MRI, only plantar pressure data from that side (left or right) were analyzed in the context of foot form. Only digital pressure recordings in which the entire foot contacted the mat were used. Maximum lateral midfoot pressure for each footfall were recorded for each individual (average  $n = 13$  prints/individual) and averaged. Maximum pressure, hallucal metatarsophalangeal joint angle, lateral tarsometatarsal joint angle, arch height (CSI), and medial weight transfer (CPEI) were quantified as described above. MRI data were analyzed in OsiriX v.5.9 (Pixmeo SARL). The center of the base of the fourth metatarsal was identified as shown in Figure 2 and then quantified in ImageJ (NIH). The base was treated as a circular segment, with the dorsoplantar height as the chord, and the maximum distance between the chord and most proximal part of the base as the height of the circular segment. The ratio of the (height/chord)\*100 was calculated as a measure of base convexity as described elsewhere (DeSilva, 2010).

All statistics were calculated using SPSS v.20. Variables were tested for normality of distribution using the Shapiro-Wilk test. The Pearson's correlation was used to assess relationships between maximum lateral midfoot pressure and two normally distributed variables: 1) Intra-individual CPEI; and 2) curvature of the base of the fourth metatarsal. Non-parametric Spearman's  $\rho$  correlation statistics were used to assess relationships between the maximum lateral midfoot pressure and two non-normally distributed variables: 1) midfoot flexion angle; and 2) hallucal metatarsophalangeal joint angle. Reduced major axis regression equations (Bohonak and van der Linde, 2004) were generated to visualize the linear relationship between variables (Figs. 3–7). Residuals from these regressions were normally distributed in all cases except when regressing the angle of midfoot flexion on lateral midfoot plantar pressure and thus those data were log transformed. Multiple regression analysis was performed to test how well log age, log BMI, arch height



**Fig. 2.** 3D MPR of the foot (left). The base of the 4<sup>th</sup> metatarsal (upper left) was identified and the scans oriented in all planes such that the center of the base could be isolated and by-sectioned in lateral view (bottom left). To the right, the quantification of the curvature of the base of the 4<sup>th</sup> metatarsal is illustrated.

(CSI), and medial weight transfer (CPEI) predict maximum lateral midfoot plantar pressure.  $P < 0.05$  was used to denote significance. Data are presented as mean  $\pm$  standard deviation.

## RESULTS

Previous work by our lab group found that  $\sim 8\%$  of adult humans ( $n = 32/398$ ) possessed a midtarsal break, which was defined as lateral midfoot pressure in excess of 200 kPa, and dichotomization of the midtarsal break into either present or absent identified a high BMI, a low arch, and elevated pronation as contributing factors to a midtarsal break (DeSilva and Gill, 2013). In this study, addressing midfoot flexion as a continuous variable, we find a strong correlation between maximum lateral midfoot pressure and the angle of flexion between the elevated rearfoot and the midfoot ( $n = 75$ ,  $r = 0.83$ ,  $P < 0.001$ ). Using multiple regression statistics, arch height (CSI) and pronation (CPEI) were predictors of lateral midfoot plantar pressure ( $r = 0.63$ ,  $R^2 = 0.40$ ), independent of log age and log BMI, ( $P < 0.0001$ , both measures). Lateral midfoot pressure in adults also correlated with dorsiflexion at the hallux tarsometatarsal joint ( $n = 63$ ,  $r = 0.48$ ,  $P < 0.001$ ; Fig. 4).

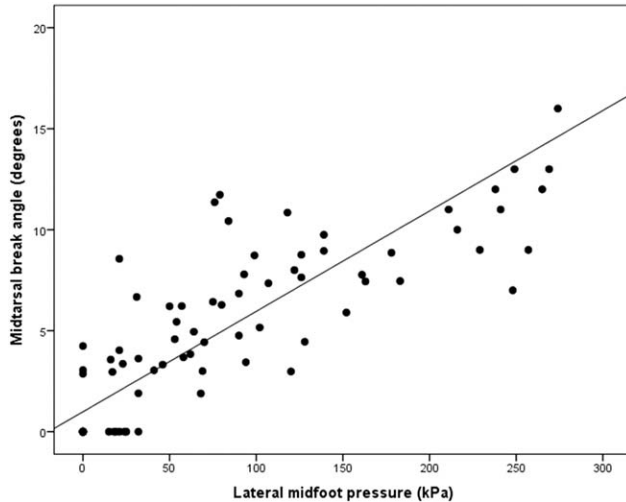
Using the 200 kPa cutoff to identify midtarsal breakers (see DeSilva and Gill, 2013; Bates et al., 2013), we identified a midtarsal break in 4% of children under 16 years old ( $n = 8/198$ ). None of the 23 participants  $< 6$  years old had lateral midfoot pressure  $> 200$  kPa, but a midtarsal break is present in 5.5% of children between 6 and 10 ( $n = 6/109$ ). A single research subject was identi-

fied as possessing the most intraindividual variation in lateral midfoot plantar pressure ( $178 \text{ kPa} \pm 53.5$ ; range 103–340 kPa;  $n = 25$  prints). In this subject, we found a correlation between lateral midfoot pressure and CPEI ( $r = 0.51$ ,  $P = 0.009$ ; Fig. 5).

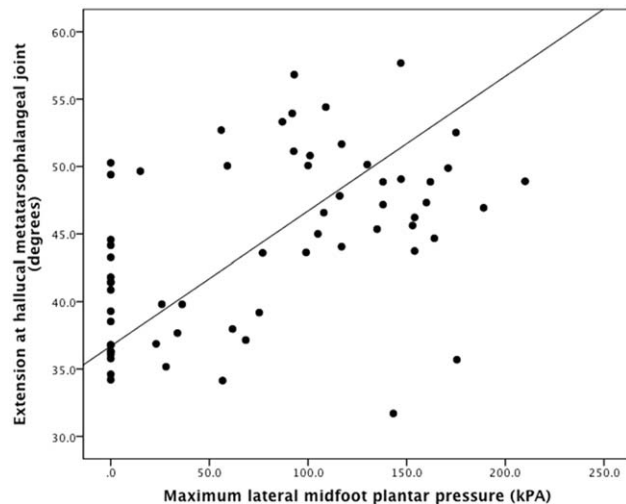
Examination of MRI scans of a subset of participants ( $n = 19$ ) revealed that the dorsoplantar curvature of the base of the fourth metatarsal was variable, with some subjects having a concave or sigmoid shape, and others a more convex shape (absolute curvature  $6.0 \pm 3.9$ ; range 0–15.9). Convexity was most obvious along the lateral aspect of the base of the metatarsal, with the medial aspect becoming flatter. There was also considerable variation in lateral midfoot pressure in these participants ( $68.9 \pm 71.8 \text{ kPa}$ ; range 0–249.9) and maximum pressure ( $124.5 \pm 102.1 \text{ kPa}$ ; range 0–358.0). Both the average ( $n = 19$ ,  $r = 0.55$ ,  $P = 0.014$ ; Fig. 6) and maximum ( $n = 19$ ,  $r = 0.70$ ,  $P = 0.001$ ; Fig. 7) lateral midfoot pressure strongly correlated with the curvature of the base of their fourth metatarsal.

## DISCUSSION

As the midtarsal break has received more attention in recent years (D'Août et al., 2002; Vereecke et al., 2003; Lovejoy et al., 2009; Crompton et al., 2010; DeSilva, 2010; Nowak et al., 2010; Crompton et al., 2012; Bates et al., 2013; DeSilva and Gill, 2013; Greiner and Ball, 2014; Thompson et al., 2014), it has become clear that this once simple and dichotomous trait is more interesting and complex than previously thought. This study adds important new contributions to our understanding



**Fig. 3.** Lateral midfoot plantar pressure is strongly correlated ( $r = 0.83$ ,  $P < 0.001$ ) with the magnitude of midfoot flexion in humans. Plantar pressure data are therefore likely to be a proxy for mobility of the midfoot.



**Fig. 4.** Subjects with high lateral midfoot plantar pressure tend to have increased dorsiflexion at the hallux metatarsophalangeal joint ( $R^2 = 0.23$ ,  $P < 0.001$ ).

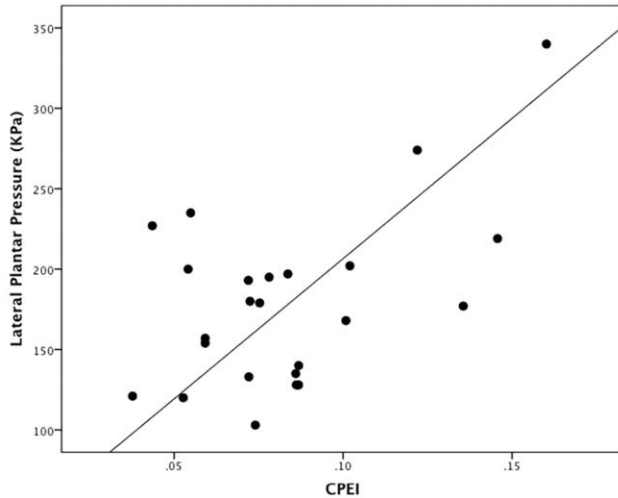
of the human midfoot and the evolutionary history of themidtarsal break. First, themidtarsal break is not a dichotomous character and instead there is a continuum of midfoot mobility found in humans, with some having a rigid lateral midfoot capable of little flexion and some with midfoot flexion that appears to overlap with that seen in non-human primates, such as chimpanzees (Bates et al., 2013). Second, we were unable to find any children <6 years-old with amidtarsal break. The reasons for this are currently unclear, but may be related to two characteristics of the juvenile foot. The presence of a more pronounced fat pad in young children (Mickle et al., 2006) may mask both the lateral midfoot plantar pressure and the midfoot flexion that would help identify amidtarsal breaker. In addition, much variability in the development of walking exists among children. Child-

ren <5 years old are still honing their walking skills (Adolph et al., 2008; Vasudevan et al., 2011). Although children between 5 and 7 years old arguably walk like adults on flat ground (Sutherland et al., 1980; Sutherland et al., 1988; Ounpuu et al., 1991), they do not walk in the same manner as adults when tasked with modifying their gait parameters to meet constraints that mimic everyday situations (e.g., crossing obstacles of varying heights) (Gill, 2011; Gill and Hung, 2012; Hung et al., 2013). Different bipedal mechanics in young children may prevent amidtarsal break, even if the midfoot is flexible in these individuals. Alternatively, these data may suggest that children are born with a more rigid midfoot and shoe wearing may result in the atrophy of muscles necessary to stiffen the lateral midfoot (see Miller et al., 2014) resulting in more adult midfoot breakers in Western shod populations than might be expected in an unshod human population.

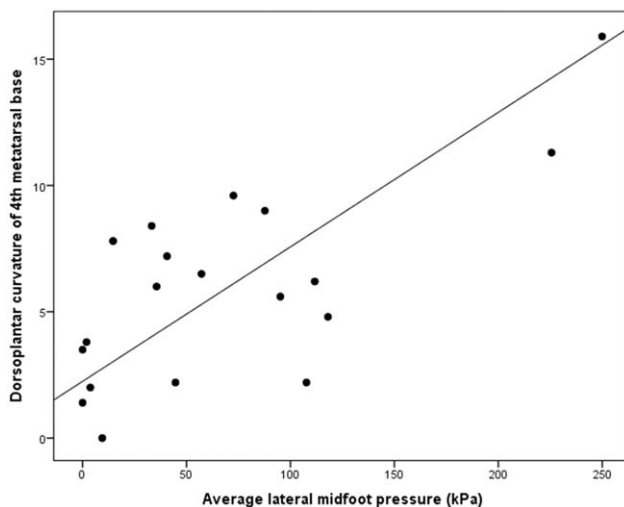
### What causes themidtarsal break in humans?

In our previous study (DeSilva and Gill, 2013), we suggested that at least three factors contribute to midfoot mobility: a high BMI, a low longitudinal arch, and pronation of the foot during the stance phase of gait. In this study, treating midfoot mobility as a continuous variable, we found that arch height and excessive pronation predicted lateral midfoot mobility independent of age and BMI. Therefore, both anatomical and functional aspects of the foot are contributing factors to midfoot laxity in humans. Lax ligaments in a flatter foot may permit lateral tarsometatarsal mobility, resisted by little else than the long plantar ligament. In addition, over-pronation of the foot during the stance phase effectively lowers the arch and loosens plantar ligaments, providing another means by which a foot, even if arched, can have midfoot mobility. This hypothesis is supported by data collected on a single individual with highly variable midfoot mobility from one walking trial to the next. Given that the individual's age, BMI, and structural arch did not change from trial-to-trial, our findings that medial weight transfer correlated with lateral midfoot pressure is evidence that the triplanar motion of pronation unlocks the bones of the foot in a manner that loosens plantar ligaments and permits mobility at the lateral tarsometatarsal joint (Elfman, 1960; Close et al., 1967).

There are two important caveats to our study. First, arch height and medial weight transfer (CPEI) explain only 40% of the variation in lateral midfoot plantar pressure in our participants, meaning that 60% of the variation is a result of other factors. We hypothesize that stiffness of plantar ligaments, such as the long plantar ligament and plantar aponeurosis, and lateral longitudinal arch supporting musculature such as the abductor digiti minimi (Reeser et al., 1983; Miller et al., 2014) may also play important roles. In addition, though strongly correlated with the midfoot angle ( $r = 0.83$ ) and therefore a very good proxy, increased lateral midfoot plantar pressure is not itself evidence of amidtarsal break. Instead, unrelated anatomies, such as a large, plantarly projecting tuberosity of the fifth metatarsal, may be producing elevated lateral midfoot plantar pressures in the absence of any actual motion at the tarsometatarsal joint. Similarly, in our single variable subject, medial weight transfer, while significant, explained only 26% of the variation in lateral midfoot plantar pressure. Thus, additional anatomical and



**Fig. 5.** Data presented here are from a single subject with highly variable lateral midfoot plantar pressures across 25 steps. Note that within the same individual, pronation (as measured by the CPEI) is correlated with ( $r = 0.51$ ,  $P < 0.009$ ) midfoot mobility.



**Fig. 6.** Linear regression (RMA) of fourth metatarsal curvature on average lateral midfoot pressure. Midfoot mobility (as assessed by lateral midfoot pressure) is correlated with ( $r = 0.55$ ,  $P < 0.014$ ) 4<sup>th</sup> metatarsal base morphology.

functional contributors to variability in midfoot mobility await proper identification and study.

Second, though we (this study) and others (Bates et al., 2013) have found that lateral midfoot plantar pressure correlates strongly with sagittal plane dorsiflexion at the lateral tarsometatarsal joint, this motion is undoubtedly multiplanar and evidence indicates that the midtarsal break has a rotational component as well (Thompson et al., 2014). As discussed shortly, the skeletal anatomy of midtarsal breakers indicates that motion at the tarsometatarsal joint is at least biplanar given that the lateral aspect of the base of the fourth metatarsal is more convex than the medial aspect. This asymmetry would result in the lateral rearfoot everting while dorsiflexing as the lateral part of the tarsometatarsal

joint rolls over a fixed medial part as the heel lifts off the substrate. A multidimensional *in vivo* examination of real-time motion at the tarsometatarsal joint in human midtarsal breakers is sorely needed.

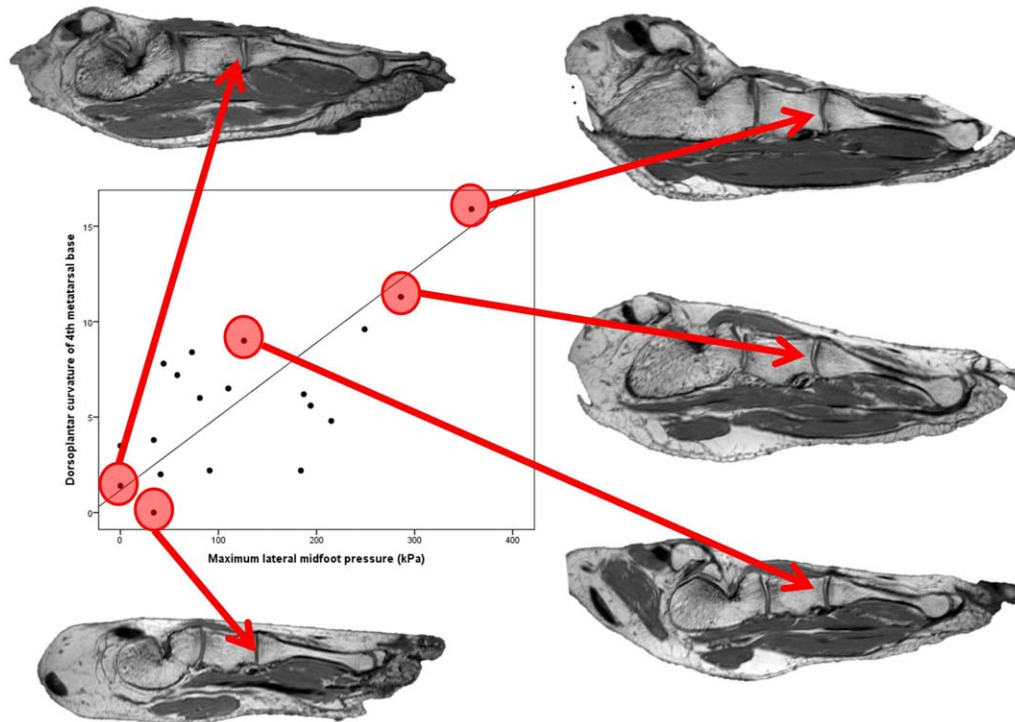
### Consequences of a midtarsal break

In DeSilva and Gill (2013), we were surprised to find that there were no statistical differences in spatiotemporal gait parameters (stride length, velocity, double support time) between subjects with and without a midtarsal break. However, Bates et al. (2013) found an inverse relationship between lateral midfoot plantar pressure and pressure under the hallux, clearly demonstrating a functional link between lateral midfoot laxity and the push-off mechanism of the human hallux. The authors suggested that tension in the plantar aponeurosis may mediate this relationship. We too examined this relationship, but instead of hallux pressure, lateral midfoot pressure correlated with a crude, uniplanar measure of dorsiflexion at the hallux metatarsophalangeal joint. Our findings agree entirely with Bates et al. (2013); increased lateral midfoot pressure correlated with increased dorsiflexion at the hallux metatarsophalangeal joint. These findings are consistent with evidence that excessive pronation minimizes the effectiveness of the plantar aponeurosis and its windlass mechanism (Kappel-Bargas et al., 1998). In addition, the mechanical advantage of peroneus longus is reduced in a pronated foot, limiting its ability to stabilize the hallux during the propulsive phase of gait (Donatelli et al., 1985; Tiberio et al., 1988). The result is hypermobility of the first ray (Glascoe et al., 1999), which reduces the effectiveness of the foot as a propulsive lever (Donatelli et al., 1996).

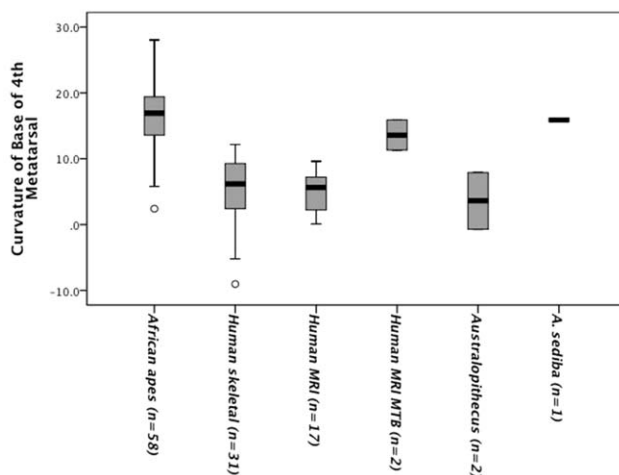
### Skeletal correlates of the midtarsal break

Previous work (DeSilva, 2010) on the midtarsal break made the following observations: 1) non-human primates have a midtarsal break, but humans do not; 2) the midtarsal break happens primarily at the lateral tarsometatarsal joint; 3) non-human primates have a more convex base of the fourth metatarsal than humans do; therefore, 4) the presence of a dorsoplantar convex fourth metatarsal base must indicate a midtarsal break. But, there is an additional step needed to complete this logic. If dorsoplantar curvature of the fourth metatarsal base can be used as an indicator of midfoot mobility, then this skeletal morphology should not only correlate with midfoot flexibility between species, but *within* them as well. Now that it is known that some humans have excessive midfoot flexibility, our species has become the ideal primate model for testing this skeletal form:midfoot function hypothesis. Our findings (Figs. 6 and 7) are strong and unambiguous: even in the context of intraindividual variation in midfoot mobility (Bates et al., 2013; this study Fig. 5), both the average and maximum lateral midfoot plantar pressure correlates with dorsoplantar convexity of the base of the fourth metatarsal. We therefore suggest that the morphology of the base of the fourth metatarsal is an exceptionally valuable osteological element for inferring midfoot mobility in fossil foot bones.

Thus, the *A. afarensis* (A.L. 333-160; Ward et al., 2011), *A. africanus* (StW 485) and Olduvai (OH 8) individuals represented by these isolated fossils can be characterized as possessing a rigid midfoot. The *A. sediba*



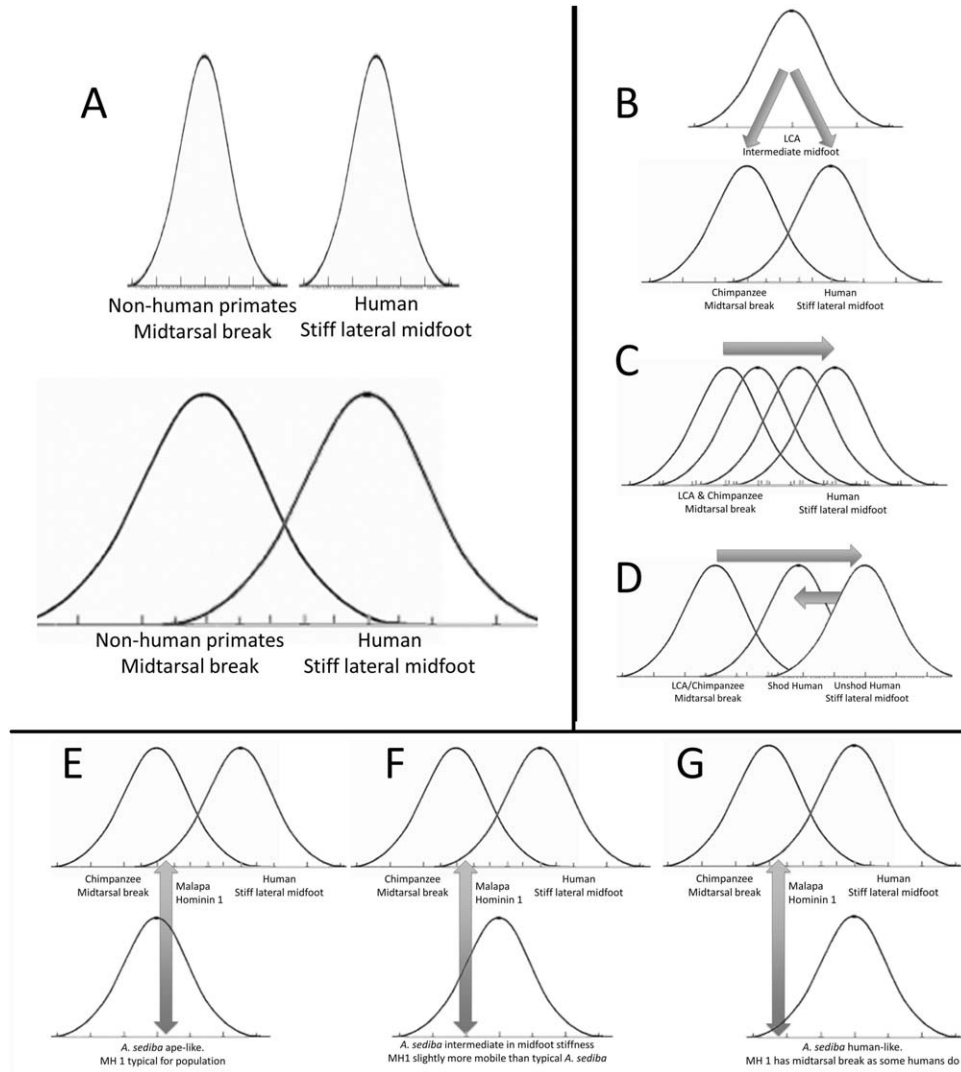
**Fig. 7.** Sagittal foot MRI representation of select subjects plotted with maximum lateral midfoot plantar pressure demonstrates that elevated midfoot mobility is associated with more convex 4<sup>th</sup> metatarsal base (arrows), whereas a flat or sigmoid shape to the base characterizes a more rigid midfoot that produces a lower peak lateral midfoot plantar pressure while walking. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]



**Fig. 8.** African apes, in general, have a hypermobile midfoot and possess a dorsoplantar convex base to the 4<sup>th</sup> metatarsal. Humans, in general, have a relatively flat 4<sup>th</sup> metatarsal base and a more rigid midfoot using data from both skeletal remains ( $n = 31$ ) and MRI scans ( $n = 17$ ). However, there is considerable variation in both foot anatomy and foot function resulting in overlap between apes and humans for fourth metatarsal base convexity. In particular, the two human midtarsal breakers assessed with MRI techniques have quite ape-like morphology to the tarsometatarsal joint. While fossil *Australopithecus* (A.L. 333-160 and StW 485) fall within the human distribution, U.W. 88-22 from *A. sediba* is shaped in a manner consistent with a midtarsal break in that individual. Whether these data are evidence of interspecific differences, or simply interindividual differences remains unclear.

individual (MH1) represented by U.W. 88-22 had a more mobile midfoot (DeSilva et al., 2013; Fig. 8). However, these data are not at odds with Bates et al. (2013) assertion that fossil foot bones may be a “crude indication” of midfoot mobility in extinct hominins. Given the overlapping range of variation in both midfoot mobility and skeletal anatomy in humans and non-human primates, it is difficult to characterize an entire species (i.e. *Australopithecus sediba*) as having a flexible midfoot and a midtarsal break given that this same anatomy exists in a reasonably large percentage of modern humans. Instead, we strongly recommend that we begin to treat these pedal elements for what they are: remains not of a monomorphic species, but of specific individuals who possessed varying midfoot mobility, within a much broader range that typified the species. Until large numbers of individuals are sampled it will remain unclear whether individual foot bones are truly representative of the entire species through space and time (contra DeSilva, 2010). For now, it is prudent to state that A.L. 333-160, StW 485, and OH 8 walked on a variably stiff lateral midfoot; not that *A. afarensis*, *A. africanus*, and *P. boisei* (or *H. habilis*) had stiff feet (though, of course, they may have). Similarly, MH1 walked on a foot that had the potential to be more mobile and produce a midtarsal break but *A. sediba* did not necessarily have a midtarsal break (though, of course, it may have).

Ultimately, these findings are consistent with a Darwinian view of gradual evolution of the human midfoot. While it was once thought that humans and non-human primates exhibited non-overlapping differences in midfoot flexibility, the results presented here and by others



**Fig. 9.** Midfoot mobility is a continuous, not dichotomous, character, best modeled as a bell curve. Since Elfman and Manter (1935), the general consensus has been that humans evolved a stiff lateral midfoot and non-human primates possessed a mobile midfoot, with little—if any—overlap between the two (A: top). It is now clear that there is both functional and morphological overlap between humans and our ape cousins (A: bottom). There are three evolutionary scenarios that might explain the current state of the human midfoot. As proposed by Lovejoy et al. (2009), the last common ancestor of humans and chimpanzees may have had a relatively stiff midfoot and that apes have evolved more flexible feet for vertical climbing, while humans have either maintained or further stiffened the lateral midfoot (B). A more traditional approach suggests that the ape foot is more primitive and the hominin foot has gradually stiffened over evolutionary time (C). A third variant on either scenario (B or C) posits that shod, sedentary Western populations of humans have more mobile feet than unshod humans and that overlap with apes is artificial and recent (D). Either way, the overlap between humans and apes compels us to treat isolated pedal fossils as individuals, rather than as typical representatives of a species with a monomorphic foot. Given that only one fourth metatarsal is currently known from *A. sediba*, scenarios E–G are all reasonable and further support for one scenario or another must await additional pedal remains from this taxon.

(Bates et al., 2013) have shown that—while still distinct—humans and our ape cousins have overlapping ranges of midfoot mobility (Fig. 9A). As shown by Bates et al. (2013) and here in this study, the evolution of a stiff midfoot may have been selectively advantageous for a biped in part by helping stabilize the hallux metatarsophalangeal joint via the windlass mechanism and/or by increasing the mechanical advantage of the peroneus longus during propulsion. As argued in the context of the *Ardipithecus ramidus* foot (Lovejoy et al., 2009), the last common ancestor of humans and chimpanzees may have possessed a more generalized, rather stiff midfoot that increased in laxity during ape evolution, and

increased in stiffness in the hominin lineage (Fig. 9B). Alternatively, *Ar. ramidus* may already be derived towards the human condition in terms of midfoot rigidity, and the last common ancestor may be more chimpanzee-like (Fig. 9C). A third variant on the evolution of the human midfoot might posit that chimpanzees and humans evolved quite different ranges of midfoot flexibility and that the overlap between apes and humans found in recent studies is a function of increased foot mobility in Western, shod humans who do not always develop the musculature necessary to maintain a stiff midfoot (see Miller et al., 2014; Fig. 9D). While these humans would still be valuable for assessing



the osteological correlates of midfoot flexibility, they would not necessarily inform our understanding of the evolutionary history of the hominin midfoot. Given these scenarios, we caution against overinterpreting isolated fossil finds (Fig. 9E–G), which alone could fall within the range of variation in modern apes, modern humans, or a hypothetical distribution of a fossil taxa in the morphospace between these two modern groups.

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