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News and Views

Interpretation of footprints from Site S confirms human-like bipedal biomechanics in Laetoli hominins

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1. Introduction

The recent discovery of additional hominin footprints at Laetoli (Masao et al., 2016) offers a rare opportunity to revisit the biomechanics of bipedalism in early hominins, a trait that was a defining event in the evolution of the human lineage (Darwin, 1871). While a great deal of work has explored how and why this hallmark trait evolved, recent debates have often focused on how best to reconstruct hominin biomechanics (Stern and Susman, 1983; Latimer and Lovejoy, 1989; Stern, 2000; Ward, 2002; Lovejoy and McCollum, 2010). Specifically, researchers have examined whether early hominins used energetically economical human-like mechanics, characterized by generally extended hindlimb joints throughout a step, or whether they used a form of bipedalism that fell somewhere between human and more flexed-limb chimpanzee-like bipedal mechanics (Stern, 2000; Lovejoy and McCollum, 2010). While much of this debate has revolved around analyses of fossil skeletal elements, ancient footprints provide another avenue to test models of hominin locomotion. Due to their age and the rarity of fossil prints, the Laetoli footprints, dated to 3.66 Ma and usually attributed to *Australopithecus afarensis*, have played a key role in discussions of the evolution of hominin bipedal

mechanics (Leakey and Hay, 1979; Stern, 2000). Recently, Masao et al. (2016) reported the discovery of several new footprints at Laetoli (Site S) that are likely contemporaneous with the original Site G prints. Here, we examine the newly discovered footprints from Laetoli Site S to determine whether aspects of their morphology linked to locomotor biomechanics resemble the prints from Site G.

Since footprints are a record, albeit imperfect, of forces generated by the motion of limbs to displace the body's center of mass (Bates et al., 2013), previous work has tried to identify key characteristics of substrate deformation that are linked to the degree of flexion or extension in lower limb joints throughout the step (Raichlen et al., 2010; Crompton et al., 2012; Hatala et al., 2016). For example, in an experimental study of footprint generation, we compared footprints made by human subjects walking through a sand trackway using both extended hindlimb joints and chimpanzee-like flexed hips and knees (bent knee bent hip or BKBH walking; Raichlen et al., 2010). We found that footprints generated during BKBH walking left deeper toe relative to heel impressions compared with normal, extended limb walking.

The difference in proportional toe depth was linked to the mechanical consequences of BKBH walking (Raichlen et al., 2010). During walking, the center of pressure (COP; the point of ground force application) moves from the heel at touchdown to the forefoot during toe-off, and the forces applied to the ground determine, to some degree, the depth of the impression under the COP (Raichlen et al., 2010; Bates et al., 2013). As the COP travels past the mid-foot the human heel rises due to the presence of a stiff longitudinal arch, and forces following heel rise deform the substrate under the toes. The COP passes the mid-foot earlier in the step in BKBH walking, leading to larger forces under the toes and relatively deeper impressions (Raichlen et al., 2010). Using data collected from topographic maps, we found that the Site G prints at Laetoli exhibit proportional toe depths more similar to extended limb walking in humans. Since *A. afarensis* likely possessed a relatively stiff arch (Ward et al., 2011), we concluded that the Site G prints were generated by a biped walking with extended, human-like mechanics.

Our analysis was confirmed by a forward dynamics simulation of footprint generation performed by Crompton et al. (2012). Their

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extensive and detailed analysis provided a major step forward in our understanding of the Laetoli prints because they modeled the anatomy of *A. afarensis* and showed that if this species was responsible for the Laetoli prints, an extended limb gait would have produced the morphology present in the fossil substrate. While these studies explicitly tested models of walking with BKBH gaits, other work has suggested differences between Laetoli hominin mechanics compared with modern humans. Hatala et al. (2016) used a detailed morphometric study of 14 footprint landmarks on human footprints collected at walking speeds to show that the Laetoli prints differ from human prints in ways that they suggest are consistent with slightly greater degrees of hip and knee flexion at touchdown. Hatala et al. (2016) also compared prints with those

made by living chimpanzees and suggested that proportional toe depth does not distinguish human prints from those of chimpanzees walking with highly flexed hips and knees, calling into question the conclusions of Crompton et al. (2012) and Raichlen et al. (2010).

Here, we perform an analysis of footprint depths in the newly discovered and reported footprints from Laetoli Site S using 3D reconstructions made available by Masao et al. (2016). We test the hypothesis that the new Site S prints show similar morphology compared with the Site G prints and are also consistent with extended limb bipedalism. We also examine our results in light of comparative data from chimpanzees presented by Hatala et al. (2016).

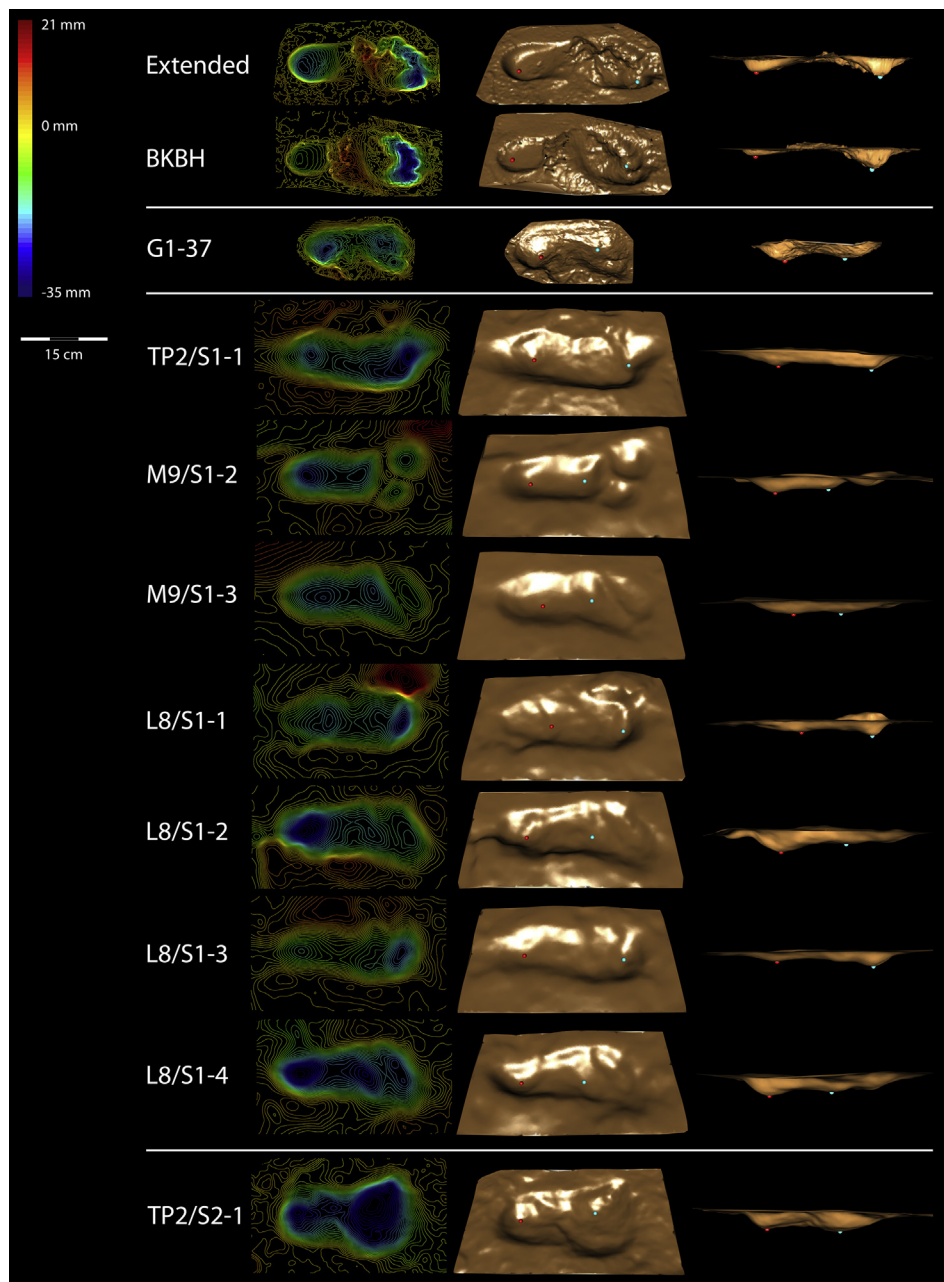


Figure 1. Contour plots and three-dimensional scans of Laetoli Site S footprints and comparative footprints. Horizontal white lines separate prints made by different individuals. The top two footprints (“Extended” and “BKBH”) are from experimental data reported in Raichlen et al. (2010); the third footprint is from the Laetoli G1 series of prints. Colored spheres denote deepest points in the hindfoot and forefoot of each print. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Methods

Footprint depth data for human subjects ($n = 8$ subjects; see [Supplementary Online Material \[SOM\] Table S1](#) for more information on experimental subjects) and the Laetoli Site G prints ($n = 8$ prints) were taken from [Raichlen et al. \(2010\)](#). Note that we used data from only the G1 trackway since the G2/3 track was likely made by two individuals, with one walking in the steps of the first hominin. Three-dimensional representations of the Laetoli Site S tracks ($n = 8$ prints) were downloaded from the MorphoSource Digital Repository (www.morphosource.org) and manipulated in R version 3.3.1 ([R Core Team, 2016](#)). Each footprint was leveled using a plane fit to 12 points surrounding each print, avoiding topographical irregularities such as erosional features and pressure mounds immediately surrounding each print. Following [Raichlen et al. \(2010\)](#), the deepest point was found in the forefoot and hindfoot of each print. Proportional toe depth was calculated slightly differently for this study. Instead of calculating it as the difference in forefoot to hindfoot depth divided by hindfoot depth (as in [Raichlen et al., 2010](#)), here we calculate proportional toe depth as follows:

$$\text{Proportional Toe Depth} = \log_{10} \left(\frac{\text{forefoot depth}}{\text{hindfoot depth}} \right)$$

This formulation of proportional toe depth produces a metric in which the magnitude of the value is independent of the choice of which measure to use as the denominator in the ratio, and it produces values that are symmetrical about zero for equal proportional differences in opposite directions (see [Smith, 1999](#) for a more complete discussion of these points). Results using this metric on the original [Raichlen et al. \(2010\)](#) data set are qualitatively indistinguishable from the results of that study (see below).

We compared proportional toe depths among footprint groups using linear mixed effects models with footprint group as a fixed effect. All linear model fits and pairwise contrasts were performed using the nlme and multcomp packages in R version 3.3.1 ([R Core Team, 2016](#)). Footprints were split into three or four groups, depending on the model: (1) experimentally produced footprints using BKBH gaits, (2) experimentally produced footprints using extended gaits, and (3) either all Laetoli footprints as a single group or separated into Site S and Site G groups. The individual producing each print was treated as a random effect in our models to take into account repeated measurements on subjects. For the purposes of these models, we assumed that the Site G prints (G1) represent a single individual. Following [Masao et al. \(2016\)](#), all prints from Site S were assigned to a single individual, with the exception of print TP2/S2-1 which was treated as being produced by a second individual. Tukey post-hoc pairwise contrasts were used to compare mean proportional toe depths for fossil footprints with the experimental data.

3. Results and discussion

Proportional toe depths in the new prints from Site S are more variable than at Site G, but are consistent with previously collected data from Site G and exhibit a similar range of variation as modern human proportional toe depths generated with extended limb mechanics ([Figs. 1 and 2](#)). Linear mixed effects models show that proportional toe depths in Laetoli prints and extended limb modern prints differ significantly from proportional toe depths in modern human BKBH prints ([Table 1](#)). However, we found no significant differences in proportional toe depths in the Laetoli prints compared with extended limb modern human prints ([Table 1](#)). These results do not change if we remove the prints from Site G that

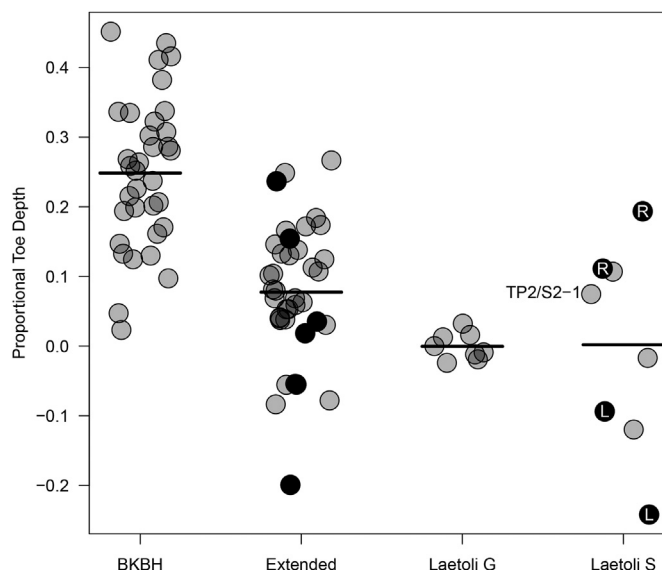


Figure 2. Comparison of proportional toe depths in Laetoli and experimentally generated footprints. Horizontal black bars denote means within each group. BKBH depths are from prints made by humans walking with a bent knee bent hip gait. Extended depths are from prints made by humans walking with an extended limb (i.e., using a normal gait). Site S and Site G depths are from Laetoli footprint trackways. Values from Laetoli Site S were collected from 3D scans of the trackways. Values from Site G and from experimentally generated prints were taken from [Raichlen et al. \(2010\)](#). Note that all Laetoli G prints were made by a single individual (series G1), and all Laetoli S prints were made by a single individual with the exception of one (TP2/S2-1). Four consecutive Site S prints (L8/S1-1 through L8/S1-4, shown as solid black circles) exhibit the highest variability in the Laetoli footprints, with the two right prints having the highest proportional toe depth and the two left prints among those with the lowest proportional toe depth. A similar range of variation is exhibited by a single modern human subject using an extended limb gait (Subject 3, denoted by black circles). R and L inside circles refer to right and left prints respectively.

Table 1
Linear mixed effects models and Tukey pairwise contrasts comparing footprints from Laetoli with experimentally generated prints in modern humans.

| | Variable | d.f. _n | d.f. _d | F(n,d) | p-value |
|---------|--------------------|-------------------|-------------------|---------|---------|
| Model 1 | Intercept | 1 | 75 | 49.01 | <0.001 |
| | Footprint groups 1 | 2 | 75 | 36.18 | <0.001 |
| Model 2 | Intercept | 1 | 74 | 43.32 | <0.001 |
| | Footprint groups 2 | 3 | 74 | 23.64 | <0.001 |
| | Comparison | Estimate | Std. Error | z value | p-value |
| Model 1 | BKBH – Extended | 0.168 | 0.022 | 7.750 | <0.001 |
| | BKBH – Laetoli | 0.246 | 0.046 | 5.310 | <0.001 |
| | Extended – Laetoli | 0.078 | 0.046 | 1.697 | 0.195 |
| Model 2 | BKBH – Extended | 0.168 | 0.022 | 7.744 | <0.001 |
| | BKBH – Site G | 0.254 | 0.069 | 3.695 | 0.001 |
| | BKBH – Site S | 0.240 | 0.061 | 3.924 | <0.001 |
| | Extended – Site G | 0.086 | 0.069 | 1.256 | 0.562 |
| | Extended – Site S | 0.072 | 0.061 | 1.178 | 0.613 |
| | Site S – Site G | 0.014 | 0.085 | 0.170 | 0.998 |

Note: Both models include subject (i.e., the individual making a footprint) as a random effect. Model 1 includes a categorical fixed effect that identifies three groups: experimentally produced footprints using an extended gait, experimentally produced prints using a BKBH gait, and all of the Laetoli footprints. Model 2 modifies the categorical fixed effect to treat footprints from Laetoli Site S and Laetoli Site G as belonging to separate groups.

[Hatala et al. \(2016\)](#) described as damaged, or if we remove prints from the M9 test pit which may be affected by a tectonic fracture that was re-cemented by calcite (see [SOM Tables S2 and S3](#) and [Masao et al., 2016](#)).

The amount of variability in proportional toe depths at Site S is noteworthy. Much of the variance is driven by differences within

the four consecutive tracks from L8. In this sequence, the right foot shows consistently larger proportional toe depths than the left foot (Fig. 1). This degree of variation within an individual is high, however Subject 3 from our modern human experiment displayed a similar degree of variation during the extended limb trials (Figs. 2 and 3). While side-to-side differences could be caused by asymmetrical limb mechanics in the L8 individual, we believe that this is unlikely. Other tracks at Site S purportedly from the same individual do not show a similar degree of side-to-side variation. Instead, it is more likely that these differences were caused by localized changes in substrate properties (e.g., moisture content) that can affect proportional toe depths (Raichlen et al., 2010).

Based on this analysis, we conclude that the footprints of the two newly discovered individuals walking at Laetoli are consistent with bipedal mechanics that included a generally extended hip and knee, although their kinematics may not necessarily be identical to the modern human pattern. If it is true that Site S and G are contemporaneous, then it would appear that by 3.66 Ma bipedal mechanics took on a more economical form of walking than the more flexed limb joints used by living chimpanzees and presumably also used by the last common ancestor of hominins and African apes.

While we recognize that our method of footprint analysis is less detailed than other recently published analyses (e.g., Crompton et al., 2012; Hatala et al., 2016), we believe it is sound and robustly reflects the way that bipedal mechanics transfer to substrate deformation. However, proportional toe depth is a valid footprint metric only when foot anatomy is roughly similar among the groups being compared. Proportional toe depths reflect limb mechanics in humans because the rigid longitudinal arch causes the heel to rise once the COP passes the metatarsal heads, which occurs earlier in stance when forces are higher during human BKBH walking as compared to walking with an extended limb (Raichlen et al., 2010). Thus, within individuals, increased hip and knee extension is generally associated with decreased toe depth (Fig. 3). Due to the mid-tarsal break in chimpanzees, a larger portion of the foot remains on the ground later in the step, even when the knee

and hip are highly flexed (Vereecke et al., 2003). We believe this anatomical difference explains why humans and chimpanzees showed similar proportional toe depths in Hatala et al.'s (2016) study. As a consequence, comparing proportional toe depths between these species will not provide an accurate reflection of comparative bipedal mechanics.

While we do not agree with their assessment of the utility of proportional toe depth, our study is unable to address the more nuanced differences in mechanics suggested by Hatala et al. (2016). Because our experimental BKBH footprint data were collected with relatively high levels of knee and hip flexion (~40° difference in mean hip and knee angle between conditions; see Raichlen et al., 2010), we cannot use our results to assess whether Hatala et al.'s (2016) more detailed analysis reflects smaller differences in hip and knee flexion in Laetoli hominins compared with modern humans. In conclusion, we suggest that the newly described footprints at Laetoli Site S, combined with prints from Site G, reflect early hominin bipedal mechanics that were largely similar to those of modern humans.

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Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.04.002>.

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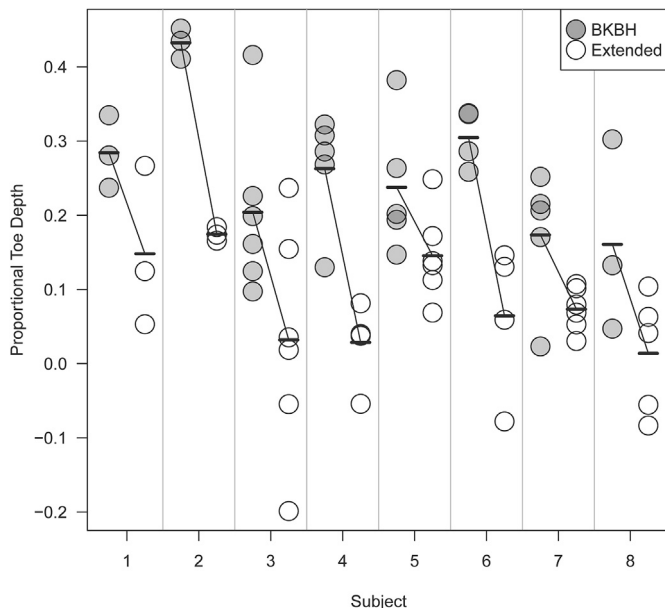


Figure 3. Proportional toe depths in individual human subjects walking with an extended limb and with BKBH gaits. Horizontal black bars denote means within each group. Note that, within individuals, walking with a flexed limb posture results in increased proportional toe depths.

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