



## LJMU Research Online

Wiseman, A and De Groote, I

**A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and prehistoric footprints.**

<http://researchonline.ljmu.ac.uk/id/eprint/7468/>

### Article

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Wiseman, A and De Groote, I (2017) A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and prehistoric footprints. Journal of Archaeological Science: Reports. 17. pp. 93-102. ISSN 2352-409X**

LJMU has developed [LJMU Research Online](#) for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact [researchonline@ljmu.ac.uk](mailto:researchonline@ljmu.ac.uk)

<http://researchonline.ljmu.ac.uk/>

1 **A three-dimensional geometric morphometric study of the effects of erosion on the**  
2 **morphologies of modern and prehistoric footprints.**

3 Ashleigh L A Wiseman<sup>1</sup>, Isabelle De Groot<sup>1</sup>.

4 <sup>1</sup>Research Centre in Evolutionary Anthropology and Paleoeology, Liverpool John Moores University.

5 **Contact email(s):** [A.L.Wiseman@2016.ljmu.ac.uk](mailto:A.L.Wiseman@2016.ljmu.ac.uk), [I.E.DeGroot@ljmu.ac.uk](mailto:I.E.DeGroot@ljmu.ac.uk).

6 **Author for correspondence:** Ashleigh LA Wiseman. Liverpool John Moores University,  
7 Byrom Street, Liverpool, L3 3AF, United Kingdom.

8 Introduction: Fossilised footprints have been discovered all over the world and can provide  
9 information regarding the foot size and subsequent body size estimates of the track makers or  
10 an insight into the kinematics of the foot/lower limb. After exposure, these fossils rapidly erode.  
11 It is predicted that footprint morphology is compromised after creation, prior to fossilisation  
12 and that erosion after exposure will affect the morphology of a footprint after exposure. To  
13 date, no studies have assessed if degradation prior to fossilisation and/or after fossilisation, and  
14 subsequent exposure, affects the morphology of the print, thereby affecting any measurements  
15 taken. This study aims to quantify these pre- and post-erosional processes.

16 Materials and methods: A set of experimentally generated footprints were created to test the  
17 effects of degradation of footprint morphology prior to fossilisation. In addition, Holocene  
18 footprints were recorded at Formby Point, Sefton, UK. In just over a week tidal action had  
19 completely eroded the Holocene beds. Photogrammetry was applied to the experimental human  
20 footprints and a selection of Holocene human and animal footprints. Three-dimensional  
21 Geometric Morphometric methods were utilised to estimate differences in shape and size.

22 Results: Results from the experimental footprints indicate that weather action affects the size  
23 and shape of a footprint prior to fossilisation. When the weather was dry, footprint shape and  
24 size showed little difference for two weeks, but rainfall caused significant changes. The  
25 Holocene footprints show that after fossilisation and exposure to coastal erosion, footprint  
26 rigidity is highly compromised. The human footprint borders progressively recede, increasing  
27 length and width each day. Footprint depth, often used to inform upon speed and kinematics,  
28 varied considerably in one week. Some regions becoming shallower, others increasing in depth.  
29 Similar results were found for the animal footprints, but with less significant changes in shape  
30 and size determined.

31 Conclusion: Observed significant differences in measurements result in problems for  
32 predicting stature, mass, sex, and kinematic analyses. This warrants caution when making  
33 interpretations from fossilised footprints. Rapid recording of fossilised prints from first  
34 exposure and assessing pre-fossilisation processed are necessities when recording footprint  
35 surfaces.

36 **Keywords:** fossilised footprints, geometric morphometrics, erosion, photogrammetry, 3D  
37 modelling.

38 **Conflicts of interest:** None.

## 39 1.1 Introduction

40 Fossilised hominin footprint localities have been discovered across Africa, Eurasia, Australia  
41 and the Americas (Leakey and Hay 1979; Behrensmeyer and Laporte 1981; Roberts and Berger  
42 1997; Mietto *et al.* 2003; Watson *et al.* 2005; Webb 2007; Bennett *et al.* 2009; Roberts 2009;  
43 Morse *et al.* 2013; Felstead *et al.* 2014; Aston *et al.* 2014; Masao *et al.* 2016). In lieu of skeletal  
44 material, fossil footprints can be used to infer body dimensions of the track makers (Bennett  
45 and Morse 2014). Numerous fossil and forensic-based studies have been conducted that have  
46 attempted to find a correlation between footprint measurements (e.g.; forefoot breadth, heel  
47 breadth, length, toe extremity length, etc.) and body dimensions, such as stature, body mass,  
48 hip height, sex and age (Krishan 2006; Kanchan *et al.* 2008; Avanzini *et al.* 2008; Bennett *et*  
49 *al.* 2009; Dingwall *et al.* 2013; Domjanic *et al.* 2015; Hatala *et al.* 2016a).

50 For example, stature is often predicted using the length of the foot by applying Martin's ratio  
51 of 0.15 (Martin 1914). Dependant on substrate material properties, these measurements  
52 extracted from a single trackway belonging to a single individual can vary substantially. Stature  
53 and mass predictions from just one trackway from Walvis Bay, Namibia have estimated that  
54 the individual ranged from 1.35metres to 1.73metres tall, with the individual being either  
55 malnourished or clinically obese (Bennett and Morse 2014). Evidently, slight variations in a  
56 trackway results in grossly variable biometric predictions.

57 In other locations, such as at Laetoli, Tanzania and Ileret, Kenya, the substrate material  
58 properties are much more uniform across a trackway, and biometric data that is extracted is  
59 much less variable (Bennett *et al.* 2009). Less variable measurements have resulted in  
60 numerous studies utilising these measurements to predict not only biometric data, but also  
61 kinematic data (Schmid 2004; Berge *et al.* 2006; Vaughan *et al.* 2008; Raichlen *et al.* 2008;  
62 Raichlen *et al.* 2010; Crompton *et al.* 2011; Bates *et al.* 2013; Dingwall *et al.* 2013; Bennett *et*  
63 *al.* 2016; Hatala *et al.* 2016b; Masao *et al.* 2016; Raichlen and Gordon 2017). These studies  
64 have allowed palaeoanthropologists to assess evolutionary trends in bipedal locomotion and  
65 body proportions.

66 It has been previously demonstrated that footprints are susceptible to taphonomic changes prior  
67 to diagenesis as the result of a number of variables; weather conditions, changes in surface  
68 hydrology or bioturbation (Marty *et al.* 2009; Bennett and Morse 2014). After the footprints  
69 have undergone diagenesis, and have either become exposed or excavated a number of  
70 variables can lead to the footprints becoming eroded, thus affecting footprint shape (Bennett *et*  
71 *al.* 2013). As with any archaeological material, once the fossils are uncovered and exposed to  
72 the elements they will begin to erode, with softer, lithified sediments being more susceptible  
73 to erosion (Bennett *et al.* 2013). It must be acknowledged that weather action, such as wind or  
74 rain, may affect the size and shape of a footprint in a similar manner that slight variations in  
75 substrate typology may affect a footprint (Marty *et al.* 2009; Bennett *et al.* 2013).

76 No studies to date have quantified the effects of degradation on morphology, and how this can  
77 affect measurements taken from a footprint. The current study aims to quantitatively assess the  
78 effects of taphonomy and erosion on footprint morphology through the assessment of  
79 experimental and Holocene footprints. New discoveries of human trackways at Formby Point,  
80 Merseyside has offered a unique opportunity to record a set of Holocene footprints as they  
81 rapidly eroded.

82 This study proposes that footprints are at risk of significant morphological change which will  
83 alter body size predictions at two stages. The first stage is immediately after footprint creation.  
84 The second stage is post-excavation. It is predicted that a delay in events leading to excavation  
85 and recording could result in changes in shape and size of a footprints, particularly in easily  
86 deformable softer sediments that are more susceptible to morphological changes (Bennett *et al.*  
87 2006).

88 We use a selection of experimentally generated footprints to assess changes in footprint  
89 morphology prior to fossilisation. Holocene human and animal footprints discovered along the  
90 Sefton Coast were also assessed to determine if there is any changes in shape or size per day  
91 after exposure. It is predicted that the longer a footprint is exposed then there will be a  
92 significant change in shape and size of the print. Shape change is predicted to affect  
93 measurements of the foot used to inform upon body size estimates. An improvement on  
94 understanding the effects of erosion on morphology will improve the ability to accurately  
95 assess body size estimates from future footprint sites.

## 96 **1.2 Geological and archaeological context**

97 Formby Point is located along the Sefton Coast in Merseyside, England and is characterised by  
98 silty, fine-grained sands and peat sediments, and sand dunes (Roberts *et al.* 1996) preserved in  
99 unlithified, soft-sediments (Roberts 2009; Bennett and Morse 2014). Encroaching coastlines  
100 have led to the exposure of numerous ancient sediments since the 1970s, many of which contain  
101 over 145 Holocene human trackways and animal footprints along a 4km stretch of this coastline  
102 (Huddart *et al.* 1999; Roberts 2009). The Formby Point sediments are similar to other fossilised  
103 sediment beds at Terra Amata, a site containing a Neanderthal footprints (De Lumley 1966).

104 Carbon and optically stimulated luminescence (OSL) dating of the previously excavated  
105 sediments have yielded dates from  $6650 \pm 700$  OSL BP  $\sim 3575 \pm 45$   $^{14}\text{C}$  BP (Roberts 2009).  
106 The latter date was obtained by dating roots that overlay the Holocene beds, indicating a  
107 *terminus ante quem* for the beds (Roberts *et al.* 1996; Huddart *et al.* 1999; Roberts 2009),  
108 confirming a Mesolithic age. These beds offer an interesting insight into human activity of the  
109 Late Mesolithic-Early Neolithic transition along the Sefton Coast.

110 In June 2016 three human trackways were exposed due to wave erosion at Formby Point  
111 immersed in over 700 animal footprints. Auroch, roe and red deer, crane bird, wolf/dog, and  
112 beaver footprints have been identified (Roberts *et al.* 1996; A. Burns 2017, pers. comm.). The  
113 interaction of many animal and human prints offer a glimpse into Mesolithic human activity,  
114 and even offer a unique opportunity to assess the gait dynamics of an extinct species of cattle,  
115 although this is not the focus of the current study.

116 The Holocene sediment layer was excavated by staff and students of The University of  
117 Manchester. Unfortunately, the bed was destroyed in just under two weeks after exposure due  
118 to the destructive nature of the high tide. Twice a day the sediment layer was completely  
119 immersed by high tide, with the prints only reappearing with low tide. Visually, it was possible  
120 to see the daily erosion of the footprints as the direct result of wave action (Fig.1). The sediment  
121 bed was unlithified and despite efforts to prevent human and animal interference with the  
122 footprints, tidal action still led to the destruction of the footprint bed quite rapidly due to the  
123 bed being composed of soft, easily deformable silts. Such a rapid degradation of the footprints  
124 that was noticeable by the naked eye is hypothesised to have resulted in significant

125 morphological change. Importantly, we expect that linear measurements of the foot will have  
126 changed on a daily basis. As previously discussed, these linear measurements are used to  
127 predict an individual's biometric information. Changes in these measurements are expected to  
128 produce highly variable predictions regarding body size estimations.

129 Holocene footprints have previously been exposed along the Sefton Coast (Roberts 2009), with  
130 fossilised footprints appearing at other coastal sites in the UK, such as at Happisburgh, Suffolk  
131 (Ashton *et al.* 2014). These beds containing unlithified footprints were also destroyed rapidly  
132 due to tidal action in a matter of weeks. If our study is successful in determining that  
133 morphological changes are paramount in coastal locations, particularly with footprints that are  
134 unlithified, then the biometric data that has been previously published from these sites, such as  
135 at Happisburgh (Ashton *et al.* 2014), is questionable. The sediments are variable between  
136 Formby Point and Happisburgh, but it is a fair assumption that two soft, unlithified sediment  
137 beds would have reacted similarly when exposed to the same variables: vigorous tidal action  
138 and poor weather conditions. Both of these beds deformed and were destroyed rapidly. It is  
139 expected that both sites also experienced changes in footprint morphology coinciding with the  
140 rapid destruction of the beds.

141 The rapid erosion of the footprints at Formby Point have offered a unique opportunity to  
142 quantitatively assess the effects of daily degradation on footprint morphology. If the current  
143 study is successful in determining that footprints undergo daily morphological changes, then  
144 our results will have considerable implications for future studies that assess footprint  
145 discoveries from coastal locations.

## 146 **2.1 Materials**

### 147 **2.1.1 Experimental set-up**

148 A selection of experimental footprints were created in homogenous fine-grained sand  
149 composed of rounded to sub-angular particles measuring ~0.06-0.7mm in diameter with ~20%  
150 saturation at a 40mm depth (Fig.2). Previous experiments have determined that this is the  
151 optimal saturation for footprint definition, whereby sand composition has no significant effect  
152 on morphology after saturation (D'Août *et al.* 2010; Crompton *et al.* 2011). The footprints were  
153 created inside a container with a drainage system in place. The base of the tray allowed any  
154 rainwater that saturated through the overlaying sediment to drain through to the ground to  
155 prevent the tray from flooding. Netting was placed over the footprints to prevent animal  
156 interference, but still allowed wind and rain to penetrate through.

157 The experimental prints were placed outdoors in an open area in Liverpool, Merseyside during  
158 winter. During the first 14 days the weather was dry with low wind speeds and near-freezing  
159 temperatures. There was rain and medium-to-high wind speeds during the remaining six days  
160 of the experiment. Rain resulted in small dents across the sediment to form. Footprint features  
161 progressively eroded in the final days of the experiment.

162 These experimental footprints were not created in a material that reflect any sediments  
163 belonging to fossilised beds containing footprints. We have deliberately chosen a homogenous  
164 material of uniform particle distribution and water content. The rationale for using this material  
165 is to demonstrate that footprints are susceptible to morphological change prior to becoming  
166 covered with overlaying material, a process that often leads to fossilisation (Morse *et al.* 2013).  
167 By using this homogenous material, we have avoided the problem of attempting to replicate

168 sediments from Formby Point, Ileret or Laetoli, etc. Any unlithified material (e.g., volcanic  
169 ash, fluvial or lacustrine deposits composed of silt, sand or clay of varying material properties)  
170 is expected to behave in a similar manner as the container of sand: it is expected that there will  
171 be morphological change as the direct result of weathering or coastal action. If a material can  
172 be deformed to produce a footprint with anatomical features, then the material is certainly  
173 capable of deforming as the result of weather action in the period before the material becomes  
174 covered by overlaying sediment. This must remain an important consideration when analysing  
175 fossilised footprints: any information extracted from the footprints can only be classed as  
176 relative information about the track-maker. **2.1.2 Holocene footprint data collection**

177 Three human trackways were discovered at Formby Point containing a total of seventeen  
178 complete human footprints of definite ichnology. Due to daily time constraints of the incoming  
179 high tide, only one human footprint was recorded daily and used for this study. It was the  
180 longest surviving print. Others were initially selected in addition, but were rapidly destroyed  
181 after just a few days warranting their removal from the dataset. One auroch and two roe deer  
182 footprints were also selected (Fig.3). The auroch prints offer a unique opportunity to assess the  
183 gait dynamics of an extinct species of cattle.

184 Due to a combination of excavation limitations and bad weather the human footprint was only  
185 recorded on four days out of a possible 7 days, and the animal prints were recorded on a total  
186 of five days. On the seventh day the section of bed containing the human print had completely  
187 degraded. The animal prints were destroyed the following day.

188 A DSLR D3300 Nikon camera with a macro 60mm lens of fixed zoom was used to photograph  
189 each footprint each day. Due to sporadic weather conditions (a mix of cloud cover and bright  
190 sunlight) camera settings were consistently altered to accommodate weather. The first model  
191 of the animal prints were made using a GoPro Hero4 due to time constraints of the incoming  
192 high tide.

## 193 **2.2 Methodology**

194 Photogrammetry was applied to create 3D models of each footprint daily on the licensed  
195 software Pix4D. Weather conditions during the experiments were consistent with heavy cloud  
196 cover. Conditions at Formby Point were mostly very bright, with the ground quite wet, which  
197 has reduced the resolution for two models. All photographs were taken during dry periods of  
198 the day. Model editing was completed using Avizo 9.0.

199 Footprint length was calculated by measuring the distance between the most distal point of the  
200 hallux and the most inferior point of the pternion. Length was then used to predict stature using  
201 Martin's ratio of 0.15, which has repeatedly been found to positively predict stature in modern  
202 habitually unshod populations (Martin 1914; Hrdlicka 1935; Dingwall *et al.* 2013), and has  
203 been previously applied at fossilised sediment localities such as such as Laetoli (Tuttle 1987)  
204 and Happisburgh (Ashton *et al.* 2014).

### 205 **2.2.1 Geometric morphometrics**

206 Geometric morphometrics (GM) is a suite of statistical methods employed to measure and  
207 compare patterns of similarity and differences in many objects through the process of datum  
208 acquisition, processing, analysis and visualisation of geometric information (Bookstein 1991;  
209 Slice 2005). These methods allow for morphological changes to be quantified from the

210 statistical application of landmarks (Oxnard and O'Higgins 2009). These techniques will be  
211 applied in the current study to determine if shape/size change occurs between daily models,  
212 and if this is the direct result of coastal erosion. All analyses were computed in *R*, and two *R*  
213 packages: morpho (Schlager 2017) and geomorph (Adams and Otárola-Castillo 2013).

214 A total of 44 models were landmarked, representing the experimental prints and Holocene  
215 human print. A further 15 models were landmarked, representing the animal prints. A total of  
216 20 type II landmarks were used for the human dataset and a total of 10 landmarks were used  
217 for the animal dataset (five for the first roe deer print, three for second, and three for the auroch  
218 print). All landmarks were found to be homologous between each daily model. Landmarks  
219 were digitised on 3D .ply surfaces in Avizo 9.0 (Fig.4).

220 Prior to any geometric morphometric applications, the depth of four landmarks were calculated  
221 for all experimental and Holocene human prints: the medial and lateral forefoot region at the  
222 deepest points, and the medial and lateral heel at the deepest points. The depth of these  
223 landmarks are expected to change, corresponding to increased degradation of the footprint. The  
224 landmarks that synthesised the most concave points on the medial and lateral heel and forefoot  
225 were used to calculate the linear distance across these region. Depths were thus measured using  
226 simple trigonometry for all human prints.

227 A General Procrustes Analysis (GPA) was performed, which translates and rotates each  
228 homologous landmark to the origin, whilst scaling to unit-centroid size (Zelditch *et al.* 2012).  
229 These configurations are all aligned to a single reference specimen, representing the mean  
230 shape. The resulting Procrustes coordinates compose the shape of each specimen within  
231 Kendall's shape space (Kendall 1984).

232 Shape variation was then assessed using a Principle Components Analysis (PCA), which is a  
233 non-parametric statistical technique used to examine the relationship between a set of variables  
234 by calculating the maximum distance between each individual landmark (Zelditch *et al.* 2012).  
235 Each principle component (PC) was examined to determine shape variability. Shape change  
236 was visualised by non-affine partial warp grids called thin plate splines (TPS). These grids  
237 allow for the visual representation of relative shape deformation and display landmark  
238 transformation which maps a set of GPA-aligned configuration of landmarks between a set of  
239 structures, with the grid lines representing the relative amount of bending energy between each  
240 landmark (Rohlf and Splice 1990). TPS grids were not created for the animal prints due to a  
241 reduced landmark dataset.

242 An ANOVA was computed to assess the relative amount of shape variation per day.  
243 Categorical variables were created for each landmark configuration to assist in assessing the  
244 cause of shape change. By adopting the use of categorical variables in the dataset, information  
245 about the footprints – such as the sudden appearance of holes in the surface as the direct result  
246 of rain – can be included in the analyses. Their inclusion in the dataset assigns each  
247 configuration of landmarks to a group, allowing for groups to be statistically compared. For  
248 example, group one contains two variables: the presence or absence of raindrops. This group  
249 can then be statistically compared with the second group whereby the configurations have been  
250 assigned a variable stating if the footprint has experienced a reduction in height of the  
251 landmarks relative to landmark height on day one. Subsequently, it will be possible to  
252 determine if rain action has resulted in the reduction of landmark height, and if these variables  
253 have cumulatively resulted in changes to the shape and size of a footprint.

254 Two categorical variables were developed for the experimental prints. The first describes the  
255 presence of rain drops in the bed that left small dents in the sediment towards the end of the  
256 experiment. The second describes the reduction in height of several landmarks in the forefoot  
257 region, corresponding to degradation. Two categorical variables were created for the animal  
258 prints: the presence/absence of toe ridges in the roe deer and the severe erosion of the posterior  
259 border of the auroch footprint.

260 Two categorical variables have been established for the Holocene human dataset: the grade of  
261 footprint degradation and depth. Two grades have been established for degradation: the  
262 presence and absence of the forefoot region. Footprint depth was measured at five separate  
263 points across the foot (Table.1). Two grades were established for depth based upon the  
264 significant reduction in hallux depth relative to an increasing heel depth. This is split between  
265 the first two days and the final two days for the Holocene print.

266 Finally, the relationship between footprint degradation and size was assessed by regressing log-  
267 centroid size (CS) to the first PC. Levels of significance were computed by permutation tests  
268 to a 95% confidence level, using 1000 permutations which tests the sampling distributions.  
269 Finally, morphological disparity tests were computed which performs a pairwise comparison  
270 between groups.

### 271 **3.1 Results**

#### 272 *3.1.1 Morphological change prior to fossilisation*

273 Foot length was calculated for each model (S1), with stature being predicted using Martin's  
274 ratio (Martin 1914). Different statures were produced for the models representing the final two  
275 days of the experiment, with foot length increasing as much as 6.016%.

276 PCA of the experimental prints over a period of 20 days revealed that shape variance can be  
277 explained by the first two PCs that account for more than 84% of total variance (Fig.5a). The  
278 first two axes (PC1 and PC2) can be cumulatively surmised as accounting for the observations  
279 previously accounted for in the creation of the categorical variables: the reduction in height of  
280 the toe ridges (identified in PC2) and the appearance of numerous holes as the direct result of  
281 rain/weather (identified in PC1). The maximum (PC1+) and minimum (PC1-) shape difference  
282 indicates that changes in foot length are associated with poor weather conditions, with an  
283 increased distance between anterior and posterior landmarks as ridges become shallower and  
284 less convex. As expected, weather action has cumulatively resulted in changes in shape/size of  
285 the footprint (according to PC1) and changes in footprint depth (according to PC2). This is  
286 characterised by the strong separation of negative PC scores for the final two days of the  
287 experiment and positive PC scores for the first 18 days of the experiment. The least  
288 displacement for both the experimental and Holocene prints occurs in the heel region, with  
289 shape remaining almost static with increasing erosion.

290

291 To analyse if degradation affects size, shape variability (assessed by using PC1) was regressed  
292 against log-CS for all footprints. Results indicate that size is significantly affected by  
293 degradation in the final two days of the experiment and that the null hypothesis can be rejected,  
294 and that there is a statistically significant difference in shape and size between the models, as  
295 shown by a one-way ANOVA. This is corroborated by the change in length and the change in



296 foot width for the right foot as the direct result of rain. Shape change has a significantly strong  
297 association with log-CS ( $R^2=0.57524$ ;  $P=0.002$ ), that has a weak positive correlation with  
298 weather action ( $R^2=0.22281$ ;  $P=0.002$ ).

299 A morphological disparity test found that shape change is only significantly affected by  
300 weather in the final six days of the experiment with the severe degradation of the toe ridges  
301 ( $P=0.004$ ) and the increased presence of raindrops ( $P=0.002$ ). No statistically significant  
302 shape/size change occurred in the first fourteen days of the experiment when weather remained  
303 dry. The null hypothesis can be rejected as there is a significant association between weather  
304 and shape change, as supported by a Pairwise test.

### 305 *3.1.2 Morphological change after exposure/excavation*

306 Upon visual inspection it was clear that all of the Holocene footprints selected displayed the  
307 collapse of key features of the footprints. The human footprint suffered severe degradation in  
308 the forefoot, the roe deer prints lost toe ridges, and the auroch print, which was located on the  
309 edge of the sediment bed, progressively lost the posterior region of the footprint each day  
310 alongside the erosion of the bed edge. If the bed had been discovered during the final two days  
311 of exposure then it is questionable whether the footprints would have been identified as human  
312 or animal, as the hollows that remained resembled bed damage, rather than footprints.

313 Foot length was calculated (S1). As expected, four different foot length measurements were  
314 generated, although the variance between day one and day two is only 3.8mm and is not deemed  
315 significant. Measurements from the final two days are quite different. The tip of the hallux is  
316 still easily distinguishable in the day three model, although the ridge is much less prominent.  
317 In day four a more inferior point has been identified as the tip of the hallux, although this is  
318 roughly one centimetre shorter than the first two days, and two centimetres shorter than the  
319 third day. Evidently, a large margin of error exists in determining footprint extremities after  
320 prolonged exposure.

321 Stature was then predicted using Martin's ratio. Different statures were produced in accordance  
322 with varying foot length, with the percentage increase in foot length increasing as much as  
323 6.21% with erosion.

324 PCA of the Holocene human print revealed that shape variance can be explained by the first  
325 two axes that account for more than 81% of total variance (Table 4). The first axis can be  
326 surmised as describing the significant degradation of the forefoot region and the collapse of  
327 ridges between the 2<sup>nd</sup> to 5<sup>th</sup> metatarsals that are prominent in the first two days only – these  
328 observations were previously identified during the creation of the categorical variables, and  
329 have thus informed on the major shape change of the Holocene footprint. The forefoot region  
330 becomes flat (supported by a loss of depth, as discussed in section 2.1.2), with no clear  
331 identifiable structures, with two exceptions: the hallux and the ridge surrounding the extremity  
332 of the 5<sup>th</sup> toe. This is characterised by the strong separation of individual PC scores, represented  
333 by negative PC scores for the first two days and positive PC scores for the final two days that  
334 the footprint was recorded. This division can be emphasised by the dotted line along the PC1  
335 axis (Fig.5b).

336 Variation along the second PC described changes in depth of the footprint as a whole. The  
337 hallux is seen to be decreasing in depth relative to the heel which increases depth. The depth  
338 of the lateral foot (2<sup>nd</sup> to 5<sup>th</sup> metatarsals) is found to decrease. The region under the 1<sup>st</sup>

339 metatarsal slightly decreases in depth during the first two days then increases in depth relative  
340 to the loss to the lateral border of the foot. The midfoot region (area lateral to the medial arch)  
341 remains almost static in depth, displaying the least amount of depth and shape variance across  
342 the footprint.

343 The shape differences depicted reveal that footprint shape can be warped into two different  
344 shapes, per the forefoot region. The maximum (PC1+) and minimum (PC1-) shape difference  
345 along PC1 indicates that the forefoot region becomes much more constricted as erosion  
346 increases, with a reduced height and a reduced amount of bending energy (PC1-) between each  
347 landmark. A likely cause in this displacement may be the degradation of numerous  
348 distinguishable features in this region, and a reduction in the height of numerous landmarks.  
349 Similarly, the most obvious shape change along PC2 in the experimental prints occurs in the  
350 forefoot region, explaining a reduction in the height of the toe ridge landmarks as the ridges  
351 are slowly eroded.

352 The most obvious shape change along PC2 in the print would appear to be around the head of  
353 the metatarsals. This area seems to be wider between PC2+ and PC2-, with the landmarks  
354 characterising the medial border of the foot being stretched relative to the lateral border of the  
355 foot. The lateral border of the foot becomes much less distinguishable during the last two days  
356 making this the likely cause in this displacement. The loss of the medial ridge may further  
357 explain this shape variance. This is further corroborated by the depth test which found this area  
358 lost considerable depth relative to the medial border of the foot.

359 A morphological disparity test found that shape change is significantly correlated with changes  
360 in size ( $P=0.0038$ ), with depth also significantly affected ( $P=0.00452$ ). CS is very weakly  
361 correlated to changes in depth ( $R^2=0.00723$ ). A poor  $R^2$  value may be explained by a reduced  
362 dataset ( $n=4$ ). Regardless, the null hypothesis regarding depth cannot be rejected as a positive  
363 association could not be established. Similarly, a Pairwise test was computed to establish the  
364 amount of shape change relative to footprint depth. The null hypothesis cannot be rejected as  
365 the interaction between depth and shape/size was not found to be significant ( $P>0.05$ ).

### 366 *3.1.3 Morphological change in the Holocene animal prints*

367 Shape change of the animal prints can be explained by the first three PCs that account for more  
368 than 97% of total variance (Fig.5c). The first axis can be surmised as describing the degradation  
369 of the of the auroch footprint, which was discovered at the edge of Bed III. By the second day  
370 half of the print had completely disappeared, with the lateral and medial edges of the footprint  
371 progressively eroding until its complete disappearance on the fifth day. By the third day it is  
372 no longer identifiable as a print. The loss of identifiable features of this print has resulted in  
373 the strong separation of individual PC scores along the first axis, represented by negative PC  
374 scores for the first two days and positive PC scores for the last three days.

375 Shape change along the second axis can be surmised as describing relative changes in depth.  
376 With the loss of the toes the base of the print became less convex. This loss is more evident on  
377 the fifth day, represented by negative PC scores for the first two days and a positive PC score  
378 for the final day. Variation along the third and fourth axes cumulatively describe changes in  
379 the loss of toe ridges in the roe deer footprints. The ridge between the medial and lateral toes  
380 had completely vanished by the fourth day. The borders of one of the roe deer prints are no

381 longer undercut, but are shallow and slanted. This results in a considerable lack of distinction  
382 of internal morphology.

## 383 **4.1 Discussion**

### 384 ***4.1.1 Taphonomic changes to footprint morphology prior to diagenesis***

385 GM methods were applied to quantitatively assess the effects of erosion on footprint  
386 morphology and to assess if degradation affects body proportion estimates. One Holocene  
387 human footprint, two experimental human prints and three Holocene animal prints were chosen  
388 to be recorded daily (n=59). This study was testing the hypothesis that footprint morphology  
389 will change in shape and size prior to fossilisation and after fossilisation and subsequent  
390 exposure. It was predicted that prolonged exposure will significantly affect measurements  
391 taken of the foot, thereby decreasing the accuracy of biological inferences.

392 It has been previously demonstrated that footprints undergo significant taphonomic processes  
393 prior to burial and diagenesis (Marty *et al.* 2009), that may alter the shape of a footprint thus  
394 affecting any inferences extracted, such as body proportion predictions (Bennett and Morse  
395 2014). However, to date no study has quantified morphological change due to taphonomic  
396 processes and how these changes may affect body proportion predictions.

397 The results from the current study have demonstrated that significant morphological change  
398 may occur in softer sediments prior to diagenesis, according to weather conditions. Shape and  
399 size will change significantly after rainy periods or high wind speeds. These shape/size changes  
400 have affected measurements taken of the foot (length has been used in this study as an example)  
401 thereby producing inaccurate predictions of stature. Although not the focus of this study, it can  
402 be assumed that other biological predictions will vary greatly if a footprint is exposed to  
403 adverse weather conditions prior to fossilisation. While the current study has only focused on  
404 weather action as a taphonomic variable, it is a fair assumption to say that other taphonomic  
405 processes such as bioturbation, will also affect footprint morphology.

406 The results of the current study have considerable implications for the human evolution fossil  
407 record: how accurate are previously published body proportion estimates of fossil footprints?  
408 As previously stated, by analysing the morphology of a footprint numerous inferences can be  
409 made. For example, foot parameters (such as using foot length to predict stature and foot index  
410 to predict body mass) have been used in conjunction with contemporaneous skeletal data from  
411 north-western Europe dating to 950-850Kya to assign *Homo antecessor* as the maker of the  
412 footprints from Happisburgh (Ashton *et al.* 2014). Taphonomic processes, such as changes in  
413 surface hydrology or even bioturbation, after footprint creation may have affected the shape  
414 and size of these prints, thus altering taxon assignment and body proportion predictions.  
415 Similarly, taphonomic processes of the footprints from either Laetoli or Ileret may have  
416 resulted in the hominin body proportion estimates being under- or over-estimated.

417 It is suggested that sediment beds should be inspected for evidence of weather damage,  
418 particularly in softer lithified sediments, in future fossilised bed discoveries as the surface area  
419 may have been exposed for several days prior to fossilisation, with a potential loss of  
420 information. In particular, an archaeologist should inspect the sediment bed for rain drops.

### 421 ***4.1.2 Morphological changes to a human footprint after exposure/excavation***

422 After a footprint has become covered by overlaying sediment and has begun the process of  
423 diagenesis, and subsequently exposed the print is susceptible to significant changes in shape  
424 and size, thereby affecting body size estimates. An example of how degradation can affect  
425 footprint inferences can be found in the high variance of predicted stature values presented in  
426 the current study. The first 3D model was created just under a week after the footprint was first  
427 exposed. The rapid degradation of the print after this point has significantly affected stature  
428 predictions. Shape change during the first two days is miniscule, and any analyses and  
429 subsequent results would not have produced drastically different results. As such, foot size and  
430 subsequent body size estimates can be reliably predicted in the first few days of exposure,  
431 assuming that minimal change occurred as a result of taphonomic processes prior to diagenesis.  
432 Prolonged exposure after excavation has significant implications for extracting reliable data.  
433 This problem is not unique to Formby Point, it was paramount during the excavations at  
434 Happisburgh. The Happisburgh footprints were also found on the coastline and were destroyed  
435 rapidly due to tidal action (Ashton *et al.* 2014). Any delay in recording the footprints may have  
436 resulted in stature and mass values that are not true representations of the Happisburgh  
437 hominins.

438 This has considerable implications for other footprint sites The Ileret and Koobi Fora, Kenya  
439 footprints are the oldest footprints attributable to the genus *Homo* (Bennett *et al.* 2009), and  
440 are thus of great scientific importance. The sediment bed containing the footprints are  
441 composed of fine-grained silt and sands that are unlithified and highly erodible (Bennett *et al.*  
442 2013). These sediments are quite comparable to the fine-grained sand and peaty sediments from  
443 Formby Point. Similarly, the Kenyan footprints are at threat of flooding and storm action  
444 (Bennett *et al.* 2013) – two variables that are somewhat comparable to the Formby Point  
445 sediment beds. With the exception of changes in water salinity (Formby Point is characterised  
446 by salt-water immersion and the threat of flooding at Kenya relates to non-saline lake  
447 inundation), the variables highlighted in the current study are applicable to the highly-erodible  
448 Kenyan footprints. Fortunately, the Kenyan tracks have been covered post-excavation in an  
449 attempt to geo-protect the footprints. However, if the footprints are exposed for excavation  
450 or geo-tourism during periods of stormy weather or flooding, then it is expected that the  
451 footprints will undergo significant morphological change that may affect our interpretation of  
452 the track-makers.

453 The Laetoli footprints which were formed in natrocarbonatite ash (Leakey and Hay 1979) are  
454 only partially lithified, resulting in these footprints being much more robust and firm than the  
455 unlithified footprints from Ileret (Bennett *et al.* 2013). It is expected that the Laetoli sediments  
456 will be less-susceptible to morphological change as the direct result of wind or rain action, due  
457 to much firmer substrates. However, the threat of degradation as the direct result of exposure  
458 is not redundant. Despite being much more robust and composed of a different substrate than  
459 that of Formby Point, it is expected that constant or prolonged exposure will likely result in the  
460 partially lithified Laetoli prints undergoing morphological changes. It is expected that any  
461 material that is not fully lithified and preserved will undergo significant changes in shape and  
462 size due to a number of external factors. Care should be taken for the immediate preservation  
463 of footprints of high interest, such as footprints from Laetoli. Without preservation, a footprint  
464 will continue to be subjected to considerable morphological change, and eventually the  
465 footprint may be unrecognisable. This occurred with the human footprint at Formby Point. Due  
466 to the severe degradation in the forefoot region in the Holocene human print, it is questionable

467 as to whether the print would have been declared human, if discovery was delayed. If it had  
468 been declared human, remarkable differences in footprint measurements would have been  
469 made. These measurements are used to determine body size estimates (age, sex, mass and  
470 stature). Any inferences or estimations that could be calculated from these measurements taken  
471 in the final few days would have changed drastically from those made from the first model.

472 Happisburgh is a prime example of severe degradation hampering ichnotaxonomy. Numerous  
473 hollows were excluded in the analyses of the Happisburgh footprints due to questionable  
474 ichnology; only 14 footprints out of a total of 152 could be definitively declared hominin  
475 (Ashton *et al.* 2014). These hollows could be remnants of hominin footprints whereby only the  
476 heel and border of the prints – the deepest regions that are preserved the longest – have survived,  
477 as has been observed at Formby Point (Fig.7). Alternatively, the hollows could be eroded  
478 animal footprints. Tidal erosion and a delay in recording these footprints that potentially belong  
479 to an extinct *Homo* species may have resulted in a considerable loss of data.

480 The results from the current study are a prime example of how rapidly a footprint can degrade.  
481 Within two weeks the Holocene sediment bed had completely vanished. During this time, one  
482 of the human trackways had completely eroded, with only one very deep trackway remaining  
483 *in situ*. The footprint that formed the basis of this study lay towards the west of Bed II and was  
484 the first print to be immersed by high tide. By the end of the first week Bed II had completely  
485 eroded, revealing another sediment bed below. Bed III (towards the north) was the final bed  
486 to disappear. Severe erosion in Bed III by this point made 3D modelling impossible due to the  
487 numerous pockets of water that remained during low tide. The rapid degradation of these  
488 footprints have demonstrated the pivotal need for digital recording for the preservation and  
489 future scientific investigation of these fragile fossils.

#### 490 ***4.1.3 Morphological changes in animal footprints after exposure/excavation***

491 In the current study it was demonstrated that the Holocene animal footprints also experienced  
492 a significant change in shape and size as the direct consequence of weather action. The roe deer  
493 prints, which were deeply pressed, demonstrated no significant shape change or change in size  
494 (except for the toe ridge region). This implies that lightly pressed prints are more susceptible  
495 to degradation. Prolonged exposure will affect print definition and depth.

496 The complete loss of the posterior region of the auroch print from Formby Point further raises  
497 questions regarding ichnology. By the second day the print would have been identified as  
498 damage to the bed, rather than an extinct species of cattle. Although not the focus of the current  
499 study, the auroch trackways provide a unique opportunity to study the gait dynamics of an  
500 extinct animal that could have been lost if the Formby Point prints were not rapidly recorded.  
501 Similarly, the delayed excavation at Happisburgh resulted in numerous damaged prints – poor  
502 anatomical definition has resulted in many of the Happisburgh footprints not being assigned to  
503 any taxa (Ashton *et al.* 2014) – being unidentifiable and rightly excluded from analyses.  
504 However, the loss of this data may have resulted in a lost opportunity to identify an extinct  
505 species of animal present in Britain during MIS 21/25.

506 Fortunately, better preservation resulted in the identification of numerous animal hollows  
507 within the Laetoli tracks, representing a range of extinct Pliocene species within the carnivora,  
508 equidae, suidae, and bovidae mammalian orders (Leakey and Hay 1979). However,

509 taphonomic and/or post-excavation erosion of these prints may have resulted in a warping of  
510 anatomical features. A loss of this data may have resulted in the incorrect ichnotaxonomy of  
511 the prints, or unreliable biological data of the species.

512 While rapid recording is recommended in order to extract the most reliable data, it must be  
513 acknowledged that taphonomic changes may have occurred prior to diagenesis, resulting in a  
514 loss of reliable data. Prints that display poor anatomical features are concluded to be unreliable.  
515 Prints that are deeply pressed, with clear anatomical details will undergo insignificant  
516 morphological changes in the period immediately after exposure. It is expected that clearly  
517 defined footprints will be the most reliable to inform on the track makers.

## 518 **5.1 Concluding remarks**

519 By applying GM techniques it was possible to identify the effects of erosion on footprint  
520 interpretation, particularly in softer sediments. The use of statistical techniques created a  
521 fundamental tool for the evaluation of footprint erosion. Results have shown that weather  
522 action can result in significant morphological change to a footprint prior to and after  
523 fossilisation. If a surface is free from weather damage then it may be assumed that there has  
524 been no loss of reliable data prior to fossilisation. After fossilisation and exposure a footprint  
525 will undergo considerable morphological change directly associated with weather and coastal  
526 activity. Morphology was not found to be significantly affected in the first few days after initial  
527 exposure, necessitating the need for rapid recording to provide the most accurate results,  
528 particularly in highly erodible substrates. It is recommended that inferences made on footprints  
529 that have a questionable time frame of exposure should be treated with caution. By creating  
530 high resolution 3D models rapidly these fragile fossils have been digitally preserved for further  
531 analyses.

**N.B.** Color should be used in the following figures in print:

Figure 2

Figure 3

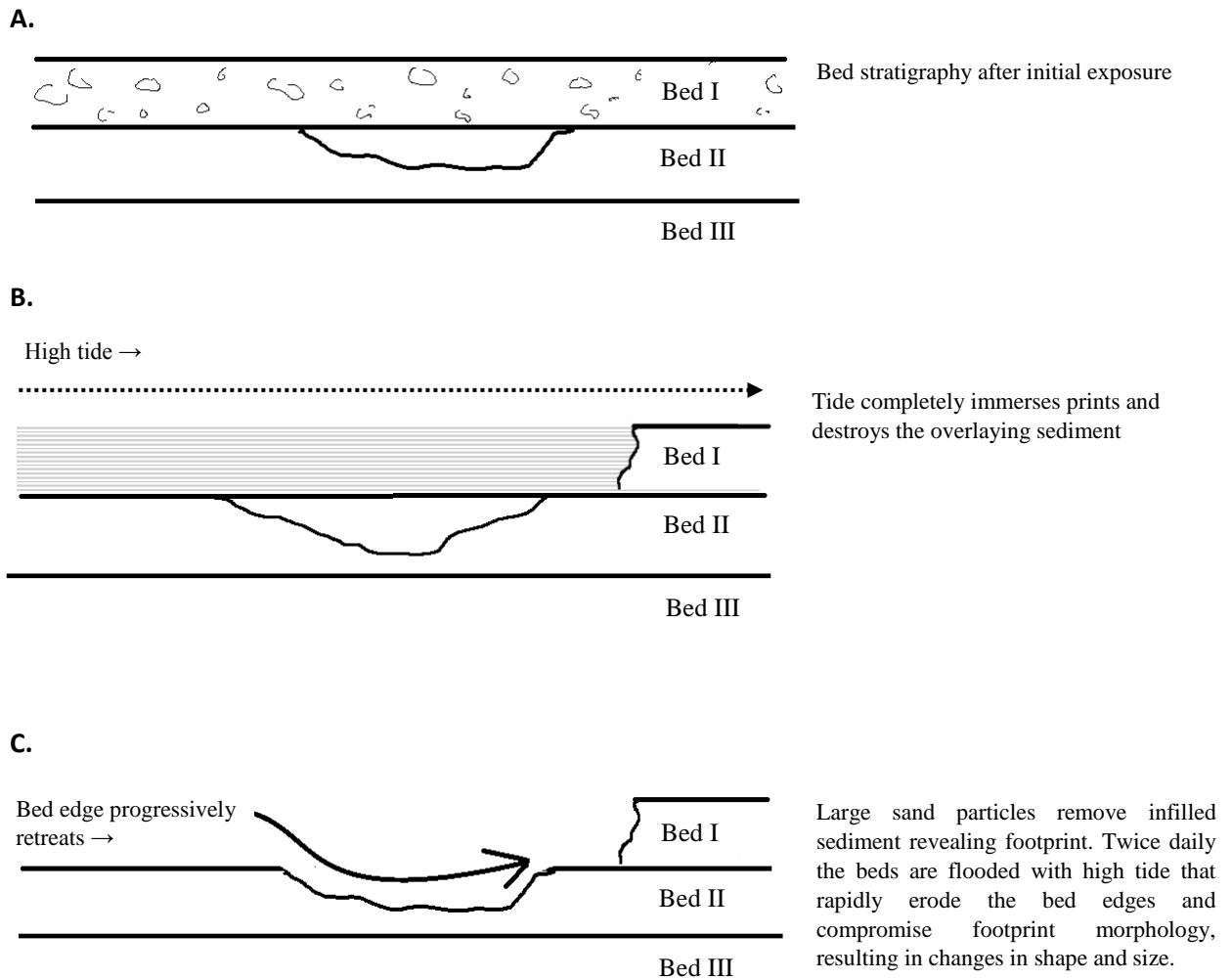
Figure 4

Figure 5

Figure 6

Figure 7

**Figure 1.** Diagram explaining the destructive nature of the high tide. Twice a day the beds were flooded by high tide which resulted in damage to the bed edges and the loss of ~60cm of the west-facing bed daily. Large sand particles and water eroded the footprint edges resulting in changes in shape and size.



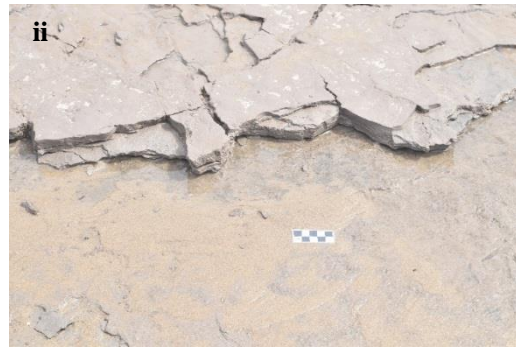


**Figure 2.** Set-up of the experimentally generated footprints on the first day of the experiment. Netting was placed over the prints each day to prevent animal interference. Photographs were taken with a camera mounted to a tripod.

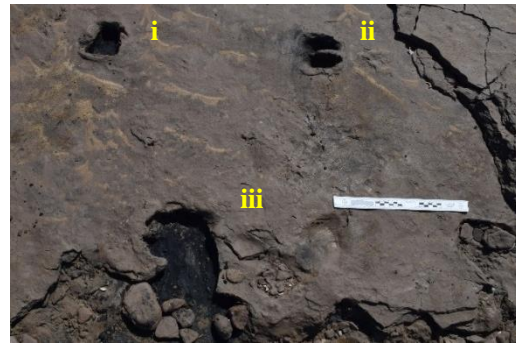


**Figure 3.** (A) High tide completely immersed the bed each day. Ai shows the incoming high tide that later reached on average 8metres high. Overlaying beds were rapidly removed by the tide, revealing lower beds below (Aii). After repeated tidal immersion, the fossilised beds were destroyed. Aiii shows the bed after just one week. Around 5metres of the west-facing bed was lost in just one week. (B) Photograph of the selected animal prints on the second day. Bi and Bii belong to roe deer. Biii belongs to auroch. Note the fragmented posterior region of the auroch print. (C) Photographs of the human print during the four days of recording, with Ci belonging to day one and Civ belonging to day four.

**A.**



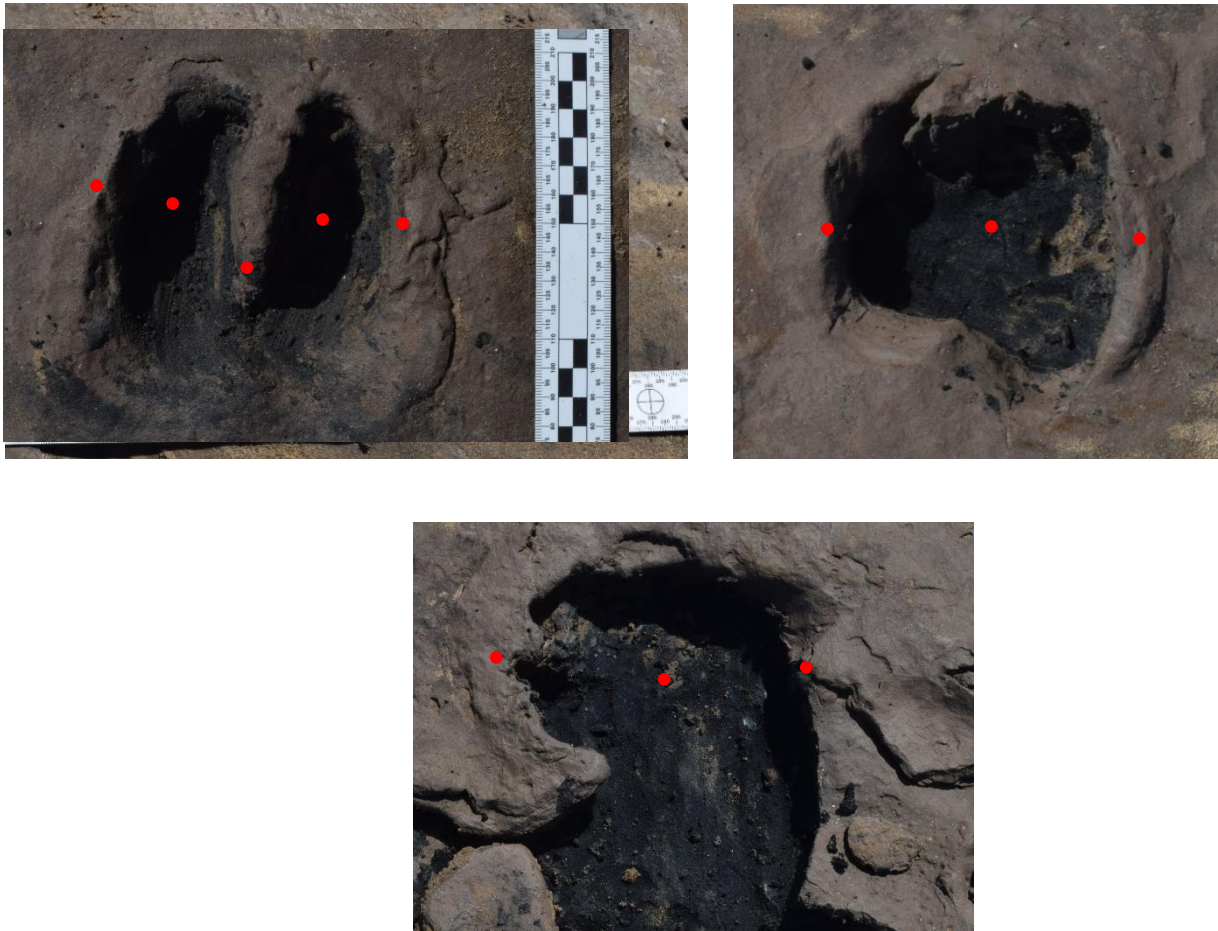
**B.**



**C.**



**Figure 4.** Landmark datasets for the human prints and animal prints. A lack of homologous landmarks in the animal dataset has resulted in a reduced landmark dataset.



**Table 1.** The depth of the Holocene human footprint at five separate locations taken from each model. Measurements are in mm. See Supporting Information 1 for experimental print measurements.

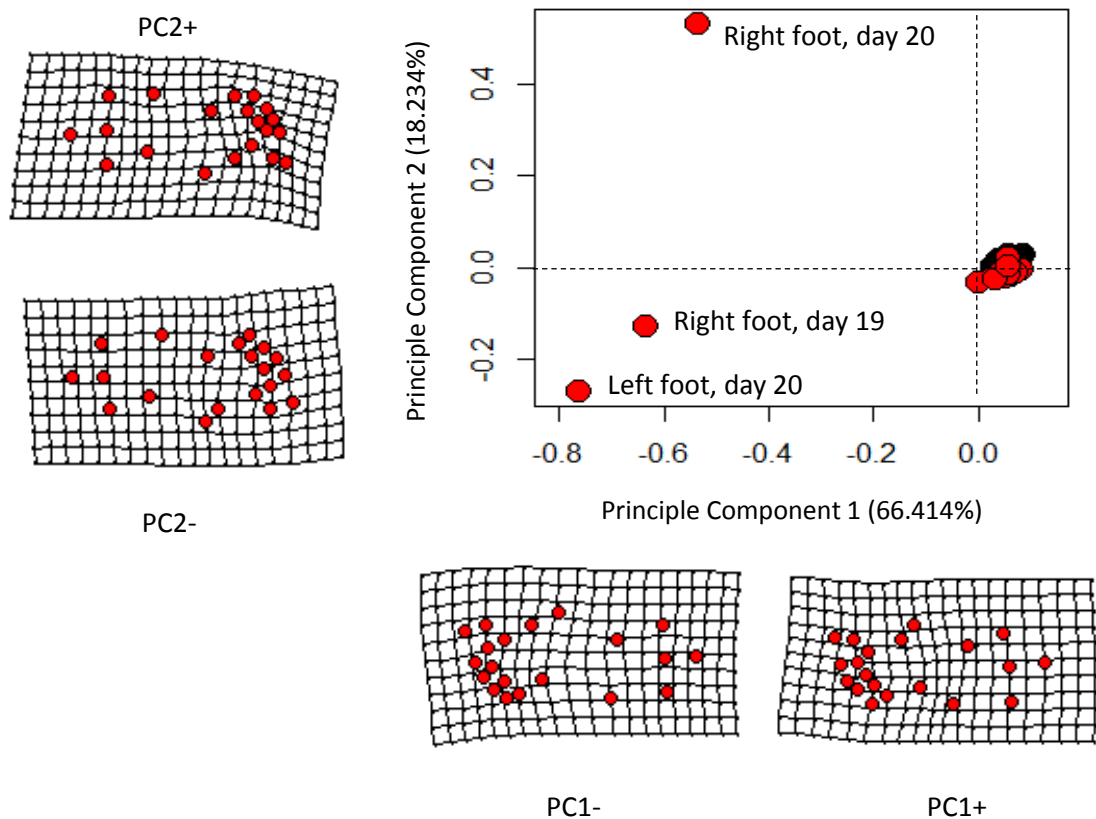
	<b>Model one</b>	<b>Model two</b>	<b>Model three</b>	<b>Model four</b>
<b>Depth of hallux</b>	15.34486	14.28583	2.656838	1.894133
<b>Depth of 2<sup>nd</sup> to 5<sup>th</sup> metatarsals</b>	19.20728	12.09233	11.39923	11.32415
<b>Depth of 1st metatarsal</b>	11.54887	8.409708	10.03207	13.9389
<b>Depth of midfoot</b>	6.422628	6.482933	8.004055	5.766013
<b>Depth of heel</b>	12.11445	16.10337	17.66635	18.48052

**Table 2.** Relative warps analysis of all footprints showing the first four principle components for the Holocene human print, the first five for the animal prints and the first 11 for the experimental prints, accounting for over 98% of variance.

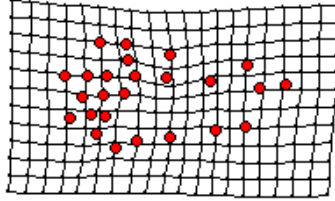
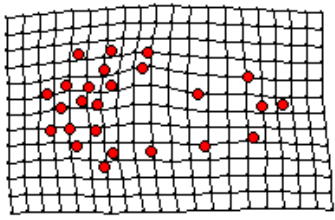
	PC	Singular value	% explained variance	Cumulative variance
<u>Fossilised human print</u>				
	1	0.07182	0.52399	0.52399
	2	0.05377	0.29370	0.81769
	3	0.04237	0.18231	1
	4	6.266E-17	0	1
<u>Animal prints</u>				
	1	0.08068	0.66746	0.66746
	2	0.04558	0.21304	0.88250
	3	0.02975	0.09079	0.97128
	4	0.01673	0.02872	1
	5	5.848E-17	0	1
<u>Experimental prints</u>				
	1	0.1932	0.6636	0.6636
	2	0.1013	0.1822	0.8458
	3	0.06836	0.08304	0.92883
	4	0.03668	0.02391	0.95274
	5	0.02638	0.01237	0.96510
	6	0.02009	0.00171	0.97227
	7	0.01599	0.00454	0.97681
	8	0.01400	0.00348	0.98030
	9	0.01231	0.00269	0.98299
	10	0.01096	0.00241	0.98513
	11	0.0106	0.0020	0.9871

**Figure 5.** A. This PCA graph illustrates the shape change in the experimental footprints (n=44). Projection of each of the experimental prints on PC1 and PC2. Red dots represent the presence of rain damage which increased in the final two days of the experiment. Black dots represent the experiments before weather damage. B. This PCA graph illustrates the shape change in Holocene human footprint (n=4). Red dots represent the presence of the forefoot. Warp grids display the maximum and minimum relative shape changes along each PC axis. Black dots represent the severe degradation of the forefoot. C. This PCA graph illustrates the shape change in Holocene animal footprints (n=5). Red dots represent the first two days of recording. Black dots represent the last days of recording when the auroch print became severely degraded.

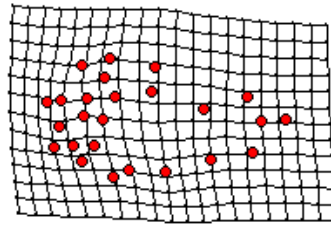
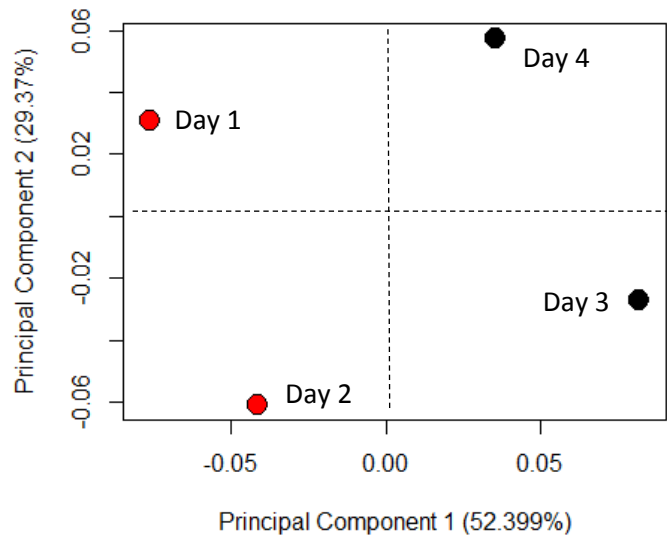
A.



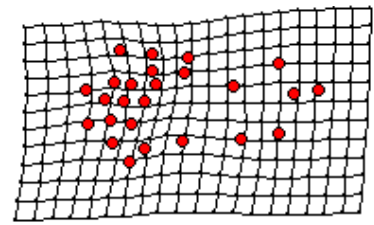
B. PC2+



PC2-

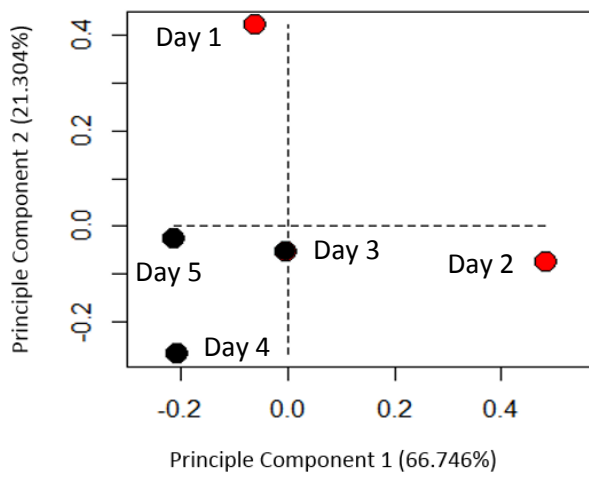


PC1-



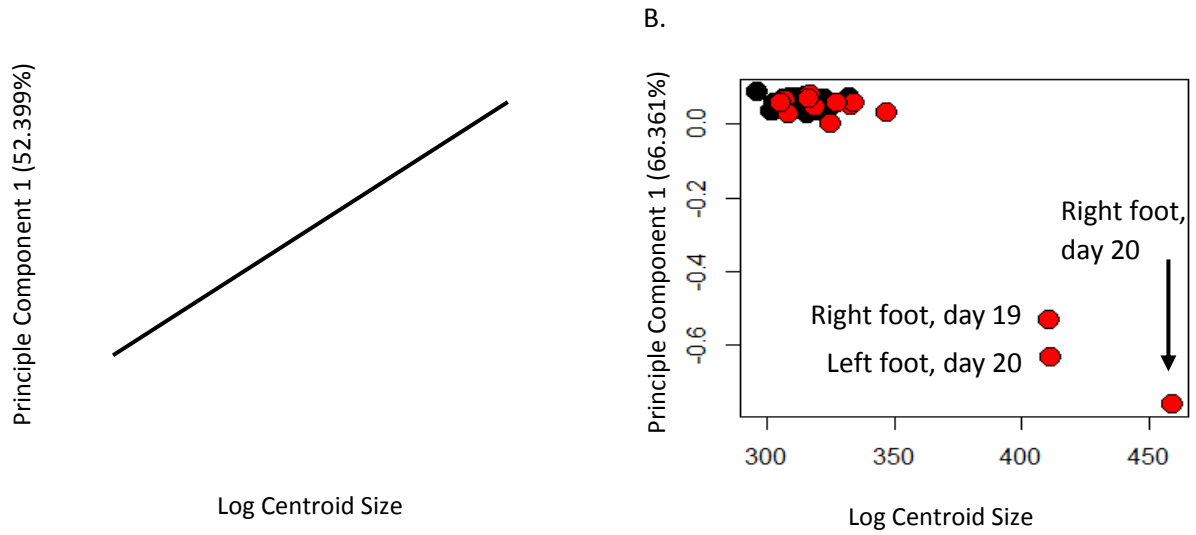
PC1+

C.





**Figure 6.** Linear regression establishing the positive relationship between centroid size and shape of the the experimental prints, as explained by PC1. Red dots represent the presence of rain damage, which increased in the final two days of the experiment. Black dots represent the experiments before weather damage, which are clustered in the graph.



**Figure 7.** Comparison of hollows from Happisburgh (top) and Formby Point (bottom). Many of the hollows that were disregarded by Ashton *et al.* (2014) that have questionable ichnology from Happisburgh could have been identified as hominin if a delay in recording had not occurred. The photograph from Formby was taken on the penultimate day of excavation. The red highlighted footprints were previously identified as human, but on this day appeared as oval hollows with no distinctive features. Photo credit: Photograph of Happisburgh sediment bed by Simon Parfitt, May 2013.



**Acknowledgements.**

The authors would like to thank the National Trust Formby and Natural England for access and permission to carry out research. We would also like to thank Simon Parfitt for use of an image taken at Happisburgh, Norfolk in May 2013.

## References

- Adams, D. C., Otárola-Castillo, E. 2012. 'geomorph: an R package for the collection and analysis of geometric morphometric shape data', *Methods in Ecology and Evolution*. 4: 393-399.
- Ashton, N., Lewis, S. G., De Groot, I., Duffy, S. R., Bates, M., Bates, R., Hoare, P., Lewis, M., Parfitt, S. A., Peglar, S., Williams, S., Williams, C., Stringer, C., 2014. 'Hominin footprints from Early Pleistocene deposits at Happisburgh, UK', *PLoS ONE* 9(2):e88329.
- Avanzini, M., Mietto, P., Panarello, A., De Angelis, M., Rolandi, G., 2008. 'The Devil's Trails: Middle Pleistocene human footprints preserved in volcanoclastic deposit of southern Italy', *An International Journal for Plant and Animal Traces* 15(3-4): 179-189.
- Bates, K. T., Savage, R., Pataky, T. C., Morse, S. A., Webster, E., Falkingham, P. L., Ren, L., Qian, Z., Collins, D., Bennett, M. R., McClymont, J., Crompton, R. H. 2013. 'Does footprint depth correlate with foot motion and pressure?', *Journal of the Royal Society Interface* 10: 20130009.
- Behrensmeyer, A. K., Laporte, L. F. 1981. 'Footprints of a Pleistocene hominid in northern Kenya', *Nature Letters* 289: 167-169.
- Bennett, M. R., Harris, J. W. K., Richmond, B. G., Braun, D., Mbau, E., Kiura, D. O., Kibunjia, M., Omuombo, C., Behrensmeyer, A. K., Huddart, Gonzalez, S., 2009. 'Early Hominin foot morphology on 1.5-million-year-old footprints from Ileret, Kenya', *Science Report* 323(5918): 1197-1201.
- Bennett, M. R., Morse, S. A., Bates, K., Crompton, R. H., 2006. 'Preserving the impossible: Conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture', *PLoS ONE* 8(4): e60755.
- Bennett, M. R., Falkingham, P., Morse, S. A., Bates, K., Crompton, R. H. 2013. 'Preserving the impossible: conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture', *PLoS ONE*
- Bennett, M. R., Morse, S. A. 2014. *Human Footprints: Fossilised Locomotion?* Springer International Publishing: London.
- Bennett, M. R., Reynolds, S. C., Morse, S. A., Budka, M. 2016. 'Laetoli's lost tracks: 3D generated mean shape and missing footprints', *Nature Scientific Reports* 6: 21916.
- Berge, M. R., Penin, X., Pelle, E., 2006. 'New interpretation of Laetoli footprints using experimental approach and Procrustes analysis: Preliminary results', *Comptes Rendus Palevol* 5(3-4): 561-569.
- Bookstein, F. L., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press: New York.
- Crompton, R. H., Pataky, T. C., Savage, R., D'Août, K., Bennett, M. R., Day, M. H., Bates, K., Morse, S., Sellers, W. I., 2011. 'Human-like external function of the foot, and fully upright gait, confirmed in the 3.66 million year old Laetoli hominin footprints by topographic statistics, experimental footprint-formation and computer simulation', *Journal of the Royal Society Interface*: doi:10.1098/rsif.2011.0258.

- D'Août, K., Meert, L., Van Gheluwe, B., De Clercq, D., Aerts, P., 2010. 'Experimentally generated footprints in sand: Analysis and consequences for the interpretation of fossil and forensic footprints', *American Journal of Physical Anthropology* 141(4): 515-525.
- De Lumley, H. 1966. 'Les fouilles de Terra Amata à Nice', *Premiers résultats Bulletin du Musée d'Anthropologie Préhistorique de Monaco* 13:29–51.
- Dingwall, H.,L., Hatala, K.,G., Wunderlich, R.,E., Richmond, B.,G., 2013. 'Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya', *Journal of Human Evolution* 64: 556–568.
- Domjanic, J., Seidler, H., Mitteroecker, P. 2015. 'A combined morphometric analysis of foot form and its association with sex, stature, and body mass', *American Journal of Physical Anthropology* 157: 582-591.
- Felstead, N. J., Gonzalez, S., Huddart, D. 2014. 'Holocene-aged human footprints from the Cuatrociénegas Basin, NE Mexico', *Journal of Archaeological Science* 42:250–259.
- Hatala, K. G., Dingwall, H. L., Wunderlich, R. E., Richmond, B. G. 2016a. 'The relationship between plantar pressure and footprint shape', *Journal of Human Evolution* 65: 21-28.
- Hatala, K. G., Wunderlich, R. E., Dingwall, H. L., Richmond, B. G. 2016b. 'Interpreting locomotor biomechanics from the morphology of human footprints', *Journal of Human Evolution* 90: 38-48.
- Hrdlička, A., 1935. 'The Pueblos. With comparative data on the bulk of the tribes of the Southwest and northern Mexico', *American Journal of Physical Anthropology* 20: 235–460.
- Huddart, D., Roberts, G., Gonzalez, S., 1999. 'Holocene human and animal footprints and their relationships with coastal environmental change, Formby Point, NW England', *Quaternary International* 55(1): 29-41.
- Kanchan, T., Menezes, R. G., Moudgil, R., Kaur, R., Kotian, M. S., Garg, R. K. 2008. 'Stature estimation from foot dimensions', *Forensic Science International* 179: 241.e1-241.e5.
- Kendall, D. G., 1984. 'Shape-manifolds, Procrustean metrics and complex projective spaces', *Bull. London Math. Soc.*, 16: 81–121.
- Krishan, K. 2006. 'Individualising characteristics of footprints in Gujjars of North India – Forensic aspects', *Forensic Science International* 169: 137-144.
- Leakey, M. D., and Hay, R. L., 1979. 'Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania', *Nature* 278: 317-323.
- Martin R (1914) *Lehrbuch der Anthropologie 2*. Jena: Fischer.
- Marty, D., Strasser, A., Meyer, C. A. 2009. 'Formation and taphonomy of human footprints in microbial mats of present-day tidal-fl at environments: implications for the study of fossil footprints', *Ichnos* 16:127–142.
- Masao, F. T., Ichumbaki, E. B., Cherin, M., B, A., Boschian, G., Iurino, D, A., Menconero, S., Moggi-Cecchi, G., 2016. 'New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins', *eLife* 5: e19568.

- Mietto, P., Avanzini, M., Rolandi, G. 2003. 'Palaeontology: Human footprints in Pleistocene volcanic ash', *Nature* 422: 133.
- Morse, S. A., Bennett, M. R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R., Crompton, R. H., 2013. 'Holocene footprints in Namibia: the influence of substrate on footprint variability', *American Journal of Physical Anthropology* 151(2): 265-279.
- Oxnard, C.E. and O'Higgins, P. (2009). 'Biology clearly needs Morphometrics? Does Morphometrics need Biology?', *Biological Theory* 4(1): 84-97.
- Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., Randall, W. M., Haas, J., 2008. 'Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics', *PLoS ONE*: 5(3): e9769.
- Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., Haas, W. R. J. 2010. 'Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics', *PLoS ONE* 5(3): e9769.
- Raichlen, D. A., Gordon, A. D. 2017. 'Interpretation of footprints from Site S confirms human-like bipedal biomechanics in Laetoli hominins', *Journal of Human Evolution* 107: 134-138.
- Roberts, G., 2009. 'Ephemeral, subfossil mammalian, avian and hominid footprints within Flandrian sediment exposures at Formby Point, Sefton Coast, North West England', *An International Journal for Plant and Animal Traces* 16(1-2): 33-48.
- Roberts, D., Berger, L. R. 1997. 'Last interglacial (c.11k kyr) human footprints from South Africa', *South African Journal of Science* 93: 349-350.
- Roberts, G., Gonzalez, S., Huddart, D., 1996. 'Intertidal Holocene footprints and their archaeological significance', *Antiquity* 70(269): 647-651.
- Rohlf, F. J., Slice, D. E., 1990. 'Extensions of the Procrustes method for the optimal superimposition of landmarks', *Syst. Zool.*, 39: 40-59.
- Schlager, S. 2017. "Morpho and Rvcg – Shape Analysis in R." In Zheng G, Li S and Szekeley G (eds.), *Statistical Shape and Deformation Analysis*, pp. 217-256. Academic Press.
- Schmid, P., 2004. 'Functional interpretation of Laetoli footprints' in Meldrum, D. J. and Hilton (ed), *From Biped and Strider: The Emergence of Modern Human Walking, Running and Resource Transport*, 49-62. Springer US, New York.
- Slice, D., E. (ed.) 2005. *Modern Morphometrics in Physical Anthropology*. Kluwer Academic/Plenum.
- Tuttle, R., 1987. 'Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1, G-2/3', in Leakey, M., D. and Harris, J., (ed), *Laetoli A Pliocene site in northern Tanzania*, 503-523. Oxford UK: Clarendon Press.
- Vaughan, C. L., Blaszczyk, M. B., 2008. 'Dynamic similarity predicts gait parameters for *Homo floresiensis* and the *Laetoli hominins*', *American Journal of Human Biology* 20(3): 312-316.
- Watson, P. J., Kennedy, M. C., Willey, P., Robbins, L., Wilson, R. C. 2005. Prehistoric footprints in Jaguar Cave, Tennessee. *Journal of Field Archaeology*, 30: 25-43.

Webb, S. 2007. 'Further research of the Willandra Lakes fossil footprints site, southeastern Australia', *Journal of Human Evolution* 52: 711-715.

Zelditch, M. L., Swiderski, D. L., Sheets, H. D., Fink, D. L., 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press: London

## Supporting Information

**Supporting Information table 1 (S1).** Measurements in centimetres taken of the foot length and the predicted stature using Martin's 0.15 ratio (Martin 1914). Percentage change difference in foot length values from the first day were calculated. Robbin's ratio of 0.14 was used for the experimental prints (EP), owing to the print maker being habitually shod. Model numbers correspond to the day that the model was made.

	Model no.	Foot length	% change in foot length	Predicted stature
<u>Formby print</u>	1	24.64	/	164.26
	2	24.64	0.01%	164.28
	3	25.75	4.42%	171.68
<u>EP left foot</u>	4	23.11	6.47%	154.05
	1	21.59	/	154.24
	2	21.46	0.62%	153.29
	3	21.37	1.06%	152.61
	4	20.64	4.40%	147.45
	5	20.56	4.78%	146.86
	6	20.99	2.80%	149.92
	7	20.54	4.87%	146.74
	8	20.30	6.02%	144.96
	9	20.79	3.74%	148.47
	10	20.98	2.86%	149.84
	11	21.21	1.76%	151.52
	12	21.32	1.26%	152.29
	13	21.62	-0.13%	154.44
	14	21.65	-0.25%	154.63
	15	21.59	0.01%	154.22
	16	22.96	-6.32%	163.99
	17	22.20	-2.79%	158.55
	18	22.07	-2.20%	157.63
19	22.19	-2.76%	158.49	
<u>EP right foot</u>	1	22.12	/	157.98
	2	21.84	1.26%	155.99
	3	21.35	3.46%	152.51
	4	21.32	3.58%	145.17
	5	20.84	5.77%	148.86
	6	20.97	5.20%	149.76
	7	21.06	4.77%	150.44
	8	21.70	1.89%	155.00
	9	22.60	-2.20%	161.45
	10	20.89	5.54%	149.22
	11	21.16	4.34%	151.13
	12	21.28	3.80%	151.97
	13	21.41	3.19%	152.94
	14	21.91	0.93%	156.51
	15	22.38	-1.19%	159.86
	16	22.94	-3.74%	163.89
	17	23.42	-5.89%	167.28
	18	22.15	-0.16%	158.23
	19	22.36	-1.08%	159.69



