

1 Footprints and human evolution: homeostasis in foot function?

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6

7 Abstract

8 Human, and hominin tracks, occur infrequently within the geological record as rare acts of
9 sedimentary preservation. They have the potential, however, to reveal important information about
10 the locomotion of our ancestors, especially when the tracks pertain to different hominin species. The
11 number of known track sites is small and in making inter-species comparisons, one has to work with
12 small track populations that are often from different depositional settings, thereby complicating our
13 interpretations of them. Here we review several key track sites of palaeoanthropological significance
14 across one of the most important evolutionary transitions (*Australopithecus* to *Homo*) which involved
15 the development of anatomy and physiology better-suited to endurance running and walking. The
16 sites include the oldest known hominin track site at Laetoli (3.66 Ma; Tanzania) and those at Ileret
17 (1.5 Ma; Kenya). Tracks from both sites are compared with modern tracks made by habitually unshod
18 individuals using a whole-foot analysis. We conclude that, contrary to some authors, foot function has
19 remained relatively unchanged, perhaps experiencing evolutionary homeostasis, for the last 3.66 Ma.
20 These data suggest that the evolutionary development of modern biomechanical locomotion pre-
21 dates the earliest human tracks and also the transition from the genus *Australopithecus* to *Homo*.

22 **Keywords:** Ichnology, vertebrate tracks, human evolution, Laetoli, Ileret

23

24 1.0 Introduction

25 Within the geological record, human footprints (tracks) occur infrequently as result of rare occurrences
26 of sedimentary preservation (Aldhouse-Green et al., 1993; Roberts et al., 1996; Allen, 1997; Avanzini
27 et al., 2008; Lockley et al., 2008; Kim et al., 2009; Schmincke et al., 2009 2010). Each set of tracks
28 holds a potential glimpse into the locomotive behaviour of the track-maker. Currently the oldest and
29 most famous hominin tracks are those at Laetoli in Tanzania made some 3.66 Ma ago, preserved in
30 volcanic ash and probably made by *Australopithecus afarensis* (Deino, 2011; Leakey and Hay, 1979;
31 Leakey and Harris, 1987; White and Suwa, 1987; Bennett et al., 2016). In 2009, details of a track site
32 close to the village of Ileret in northern Kenya were published as the second oldest hominin footprint
33 site, dating to 1.5 Ma ago (Bennett et al., 2009). These footprints are believed to have been made by

34 *Homo erectus* (Dingwall et al., 2013; Hatala et al., 2016a,b). Comparison of the Ileret and Laetoli
35 tracks has the potential, therefore, to explore the transition in locomotive style between
36 *Australopithecus*, compared with the later genus *Homo*. This is one of the most significant
37 evolutionary transitions from early habitual bipeds such as *Australopithecus afarensis* to endurance
38 walkers and runners which characterise more modern humans such as *Homo erectus* and of course
39 our own species (Bramble and Lieberman, 2004). The ability of our ancestors to walk efficiently
40 would have influenced their interaction with the landscape, the way they foraged and hunted for food,
41 gathered raw materials to use as tools, sought water, and their ability to migrate across the globe.
42 The evolutionary pressure on the foot would have been intense, and therefore it is legitimate to ask if
43 the evolution of the foot played a role in shaping human evolution as a whole across this transition, or
44 alternatively was the course of evolution, with respect to foot function, set much earlier?

45 Tracks have the advantage over fossil foot bones because not only are such bones rare in the fossil
46 record (e.g., Clarke and Tobias, 1995; Gebo and Schwartz, 2006; Ward et al., 2011; Zipfel et al.,
47 2011; Granger et al. 2015; Harcourt-Smith et al., 2015;), but in truth, fossil foot bones alone rarely
48 give an unambiguous indication of the way our early ancestors walked, since the 26 bones of the foot
49 act through a series of complicated soft tissues which are not preserved. Our aim is to explore here
50 the potential of tracks to assess the evolution, or lack of it, across the australopith to *Homo* transition.

51

52 **2.0 Methods**

53 The quantitative study of vertebrate tracks, including hominin tracks, is being transformed by the
54 increasing availability of techniques to digitally capture tracks in three-dimensions whether by optical
55 laser scanning or by digital photogrammetry (Bennett et al., 2013). All the data used here was
56 captured using a Konica-Minolta (Vi900) optical laser scanner housed in a custom built rig to support
57 the scanner horizontally and shield it from dust and excess sunlight (Bennett and Morse, 2014). The
58 data was acquired either as a consequence of direct excavation, or in the case of Laetoli, by scanning
59 first generation casts of the tracks held at the National Museums of Kenya (Nairobi). The data for the
60 Ileret track site is based on that available to the authors at the end of 2010.

61 Digital data were exported as xyz point clouds and processed within freeware written by the authors
62 (DigTrace, available from: www.DigTrace.co.uk). This integrated software package allows for the
63 creation of three-dimensional models via photogrammetry, their analysis and comparison using a
64 whole foot technique. The creation of a mean track for a population of tracks, or trackway, and the
65 comparison of two or more tracks (or means) is achieved by a whole-foot registration technique
66 (Bennett et al., 2016).

67 The registration process requires the user to denote one track in a series as a “master” with which all
68 the remaining prints are aligned by defining corresponding landmarks (matching points) on each
69 track. Selection of the master is guided by identifying which track is most anatomically complete.
70 Landmarks are placed on the basis either formally defined anatomical points or informally defined

71 points of recurrence (i.e. point matching). These landmarks can also be complemented by
72 “geometrical” landmarks, located for example between defined landmarks. DigTrace currently
73 supports three types of geometrical landmarks: line, triangle and square, where an artificial landmark
74 is inserted in the centre of gravity of each pair, triplet or quadruplet of the user-defined landmarks,
75 respectively.

76 DigTrace then computes a transformation of the source print to align it with the master, by minimising
77 the mean squared deviation between the landmark coordinates. Denoting by Y a matrix of landmark
78 coordinates for the master print (one landmark per row) and by X a matrix of corresponding landmark
79 coordinates of the print to be registered, the software calculates the transformation matrix W as an
80 approximate, optimal in the least square sense, solution to the following system of equations:

$$81 \quad Y = XW \quad (1)$$

82 DigTrace supports two types of transformation. Firstly, affine transformation, where the matrix W is
83 not constrained in any way and is calculated as:

$$84 \quad W = (X^T X)^{-1} X^T Y \quad (2)$$

85

86 where the matrix X is supplemented by a column of 1's to account for the intercept term, hence
87 allowing for translation. Secondly, rigid transformation, where the matrix W is constrained to
88 represent a valid rotation only. Denoting by $A = X_c^T Y_c$ the covariance matrix of X and Y after centering
89 (i.e. subtracting their respective centroids, which accounts for translation), the optimal transformation
90 can be calculated as:

$$91 \quad W = (A^T A)^{1/2} A^{-1} \quad (3)$$

92

93 For numerical stability this operationalised in the software using the Kabsch algorithm (Kabsch, 1976)
94 which calculates W via singular value decomposition of the covariance matrix. Once tracks are
95 aligned all the registered tracks are sampled using a grid to create mean depth and other measures of
96 central tendency for all the points on that grid.

97

98 **3.0 *Austropithecus-Homo* transition: localities and tracks**

99 **3.1 *Laetoli* – Australopithecus**

100 The most iconic of all hominin track sites is at Laetoli in northern Tanzania (S 3° 13' 29.6911", E 35°
101 11' 30.3158). This series of trackways was first discovered and excavated in the late 1970s and are
102 now dated to 3.66 Ma (Deino, 2011; Fig. 1). The site provides one of the earliest direct sources of
103 evidence for hominin bipedalism (Leakey and, Hay 1979; Leakey, 1981; Leakey and Harris, 1987;
104 Meldrum et al., 2011).

105

106 The site lies 36 km south of Olduvai Gorge and a total of 18 track sites have been found, of which
107 approximately half have been recorded (Musiba et al., 2008). The Laetoli Beds overlie Precambrian
108 basement and can be divided into a lower unit (64 m thick) that consists mainly of air-fall tuffs and
109 water-worked tuffaceous sediments, and an upper unit (44-59 m thick) of air-fall tuffs (Drake and
110 Curtis, 1987; Hay, 1987; Ditchfield and Harrison, 2011). The famous Footprint Tuff bearing the
111 hominin tracks (Leakey and Hay, 1979; Leakey and Harris, 1987) is found in the upper unit. Hay
112 (1987) interpreted the footprint tuffs as having an aeolian origin and suggested that the tephra was
113 deposited over a period of a few weeks at the transition between the dry and wet seasons. According
114 to Lockley et al. (2008), over 9,500 individual animal tracks have been recorded, of which the vast
115 majority are rabbits or hares. Other animal tracks include examples of monkeys, antelopes,
116 elephants, rhinos, three-toed horses, cats, hyenas, giraffes, guinea fowl and francolins (Leakey and
117 Harris, 1987; Musiba et al., 2008). The main hominin site (Site-G) is approximately 27 m long and
118 consists of three trackways, two of which (G-2 and G-3) are superimposed with a second track-maker
119 (G-3) walking crudely in the footsteps of the first (G-2). Due to the superimposed nature of the G-2
120 and G-3 trackways attention has largely focused on the G-1 trackway generating extensive debate
121 and analysis within an ever-growing literature (e.g. Meldrum et al., 2011). The track-maker has been
122 widely attributed to *Australopithecus afarensis* given that a small number of skeletal fragments have
123 been recovered from the Laetoli Beds and it is also the only species of hominin known from the region
124 during this time period (Suwa, 1984; Leakey and Harris, 1987; White and Suwa, 1987). This view is
125 not shared by all however, with some pointing to the possibility of a hitherto un-recorded hominin
126 species as being the potential track maker (Tuttle et al., 1990). White and Suwa (1987) suggest that
127 the track-maker for trail G-1 had a height in the range of 1.1 to 1.15 m while the G-3 track-maker was
128 slightly taller at 1.32-1.52 m. Tuttle et al. (1990) revised these estimates to 1.22 and 1.44 m
129 respectively based on their modern analogue data. Figure 2 shows a mean track computed using
130 eleven usable prints from the G1 trackway and a mean for the G3 trackway extracted from the G2-G3
131 composite (Bennett et al., 2016).

132

133 4.2 Turkana Basin- Homo

134 The Koobi Fora Formation, Turkana Basin (northern Kenya; N 3° 56' 52.9224", E 36° 11' 12.0264")
135 contains two track sites. The older at ~1.52 Ma was reported in 2009 at a site close to the village of
136 Ileret within the Okote Member of the Koobi Fora Formation (FwJj14E; Bennett et al., 2009). The
137 second site was first described by Behrensmeyer and Laporte (1981) and lies 40 km to the south.
138 FwJj14E consists of an eroding bluff of sediment capped unconformably by Holocene sediments
139 (Galana Boi Formation; Feibel et al., 1989). Excavation at various levels has found multiple track
140 surfaces and is on-going. The surfaces described here are those of 2009 excavations and are
141 located at two stratigraphic levels, with isolated hominin and animal track-bearing strata between
142 (Figs 3 and 4; cf. Hatala et al., 2016b). The sedimentary succession consists of over 9 m of fine-
143 grained, normally graded, silt and sand units (0.1 to 0.5 m) between thicker (0.5 to 2.0 m) palaeosol
144 units with at least three tuffs used for dating. Isaac and Behrensmeyer (1997) suggest that the

145 sediments around Ileret form part of a low energy fan-delta with numerous seasonally dry
146 distributaries draining into a lake which may have gradually transgressed over at least part of this
147 area. There is no evidence of this transgression at FwJ14E and track-bearing horizons consist of
148 fining-upward waning sheet flood deposits, in which course sand drapes underlying deposits (and/or
149 the previous flood cycle) fining upwards to fine silts, which appear to have been emergent but are not
150 unduly desiccated. They may be representative of either crevasse splays, or simply over-bank floods
151 on a low lying flood- or delta-plain. There has been some revision since Bennett et al. (2009) with
152 respect to the sequence of tracks (Dingwall et al. 2013; Hatala et al., 2016b). The upper track
153 horizon, and the best, consists of a number of isolated prints and one short trail of nine prints which is
154 interpreted by Dingwall et al. (2013) as being made by two individuals travelling in a similar direction
155 (Fig. 3). All the human tracks occur in association with a rich record of mammals and birds. Walking
156 speeds of between 0.45 and 2.2 ms⁻¹ made by heavy (41.5 to 60.3 kg), tall individuals (1.526-1.858
157 m) are proposed for this track (Dingwall et al. 2013). The prints were tentatively attributed by Bennett
158 et al (2009) to *Homo erectus*, although Dingwall et al. (2013) has suggested that they could have
159 been made by a male *Paranthropus boisei* (see also: Hatala et al., 2016b; Roach et al., 2016). Using
160 all the available tracks on both the upper and lower surface a mean was created (Fig. 5A). It is
161 important to note that many of the tracks show taphonomic influence particularly associated with side
162 wall suction on foot withdrawal which gives rise to long, narrow tracks with little plantar detail. The
163 impact of other animal tracks both prior to and after imprinting is clear in most prints (Fig. 4A) and also
164 adds to the noise associated with this mean. Additional tracks from this site have been excavated
165 more recently are reported by Hatala et al. (2016b) and are ascribed to predominantly male track-
166 makers probably of *Homo erectus*, potentially moving as hunting groups (Roach et al., 2016).

167 Approximately 45 km to the south of Ileret, there is a second footprint site (GaJi10), first reported by
168 Behrensmeyer and Laporte in 1981 consisting of a single trackway of poorly defined prints which is in
169 contrast to those at Ileret, and may have been imprinted subaqueously or at least in shallow water
170 (Bennett et al., 2014a). The footprint surface occurs below a prominent tuff, sampled and correlated
171 to the Akait Tuff dated to 1.435 Ma (Brown et al., 2006; Bennett et al., 2009). Re-excavation of these
172 prints by Bennett et al. (2009) uncovered four of the original seven prints. The lithofacies around
173 GaJi10 is consistent with a low energy fluvial-lacustrine system subject to both short-term seasonal
174 and millennial-scale water variations (Behrensmeyer, 1975; Lepre et al., 2007). This landscape was
175 rich in a diverse range of vertebrate and semi-aquatic fauna and has yielded a plethora of vertebrate
176 remains with aquatic and semi-aquatic fauna being more common around GaJi10 (Behrensmeyer,
177 1975; Bennett et al., 2014a).

178 The original surface excavated by Behrensmeyer and Laporte (1981) contains over 89 distinct
179 impressions (c. 12 m²) identified as the tracks of large vertebrates (hippopotami) in addition to the
180 short hominin trackway. According to Behrensmeyer and Laporte (1981) the site was covered by
181 shallow water an interpretation based in part on the presence of a wading bird track, although it is
182 possible that the hominin trackway was made at a subsequent lake low-stand. Behrensmeyer and
183 Laporte (1981) attributed the tracks to *Homo erectus*, an interpretation supported by Bennett et al.

184 (2009) upon re-excavation. Track anatomy is poor compared to the prints at Ileret perhaps reflecting
185 the sub-aqueous conditions. A second excavation on the same palaeo-surface has been excavated
186 80 metres to the south and contains over 240 individual tracks interpreted by as being formed by
187 swimming hippopotami 'punting' or bottom-walking along the bed of a shallow water body (Bennett et
188 al., 2014a). The depth of this water body is estimated at between 0.5 and 1.5 m and is a deeper
189 water equivalent to that found in the excavation further north in which the hippopotami tracks were
190 formed by normal walking (the water body being too shallow to allow swimming). This animal
191 assemblage provides a sharp contrast to that described at Ileret which is subaerial and dominated by
192 bovid, suid and equid tracks.

193

194 4.3 Modern – Homo sapiens

195 In order to provide a modern control, data was collected for 33 habitually unshod Daasanach at Ileret
196 in 2008. The individuals were asked to walk at a comfortable pace across a pre-prepared
197 experimental plot held at constant moisture content and filled with sand and silt from the backfill pile at
198 FwJj14E. The chosen moisture content was based on maximising the sediment cohesion and was
199 maintained using a simple moisture probe. The single right track was selected from the dozen or so
200 left by each individual and scanned. A mean track was then created in DigTrace (Fig. 5B).

201

202 **4.0 The *Australopithecus-Homo* transition: track comparisons**

203 Figure 6 shows unregistered and registered means for the track populations in this study. The upper
204 part of this figure shows the tracks at their relative sizes, while in the lower half of the figure the
205 influence of size has been removed. Figure 7 shows the standard deviations for the various track
206 means when registered in different combinations against each other using DigTrace. Positive and
207 negative areas of difference are highlighted by the 1 standard deviation contours, with red (+ve) and
208 blue (-ve) areas showing areas of maximum divergence between the registered mean tracks.

209 The Ileret tracks have a narrow, tapering heel consistent with a softer substrate in which foot
210 withdrawal causes side-wall suction and a decrease in width. The enhanced longitudinal asymmetry
211 (deeper ball than heel) is also a feature of softer substrate (Morse et al., 2013). The substrate first
212 holds the weight of the individual during the first phase of stance, only to fail further during the second
213 phase associated with higher plantar pressures during toe-off. The lack of clarity of toe impressions is
214 also a feature of deeper prints where foot withdrawal often modifies the impressions left by
215 phalanges. The medial longitudinal arch is also modified in softer substrates by the proximal
216 movement of sediment under rotation of the ball of the foot. The Ileret mean track is derived from a
217 highly variable and deep set of tracks which show taphonomic influences and the influence of a
218 relatively weak, fine-grained substrate with a high level of stratigraphic turbation due to animal
219 trampling and elevated pore-water content. For all these reasons, and the overall greater track depth,

220 the relationship between biomechanical pressure and depth is likely to be poor (Bates et al., 2013a).
221 It is worth noting, however, that individual track fragments not included in the mean, particularly of the
222 forefoot, provide good anatomical impressions, suggesting that the toes were similar in morphology
223 and length to those of modern humans (Bennett et al., 2009; Fig. 4C). It is our view that given the
224 data available, the mean does not remove the influence of substrate to reveal a viable track for
225 biomechanical comparison. These tracks remain important due to their association with other animals
226 and because they may say something about the activity, for example hunting, of the track-makers but
227 unless better, shallower tracks from more uniform substrate areas in terms of sedimentology than
228 biomechanical inferences should only be made, if at all, with extreme caution. Note also that the
229 tracks from Koobi Fora described by Behrensmeyer and Laporte (1981) are not included here
230 because there is insufficient anatomical detail to allow comparison. The fact that these tracks may
231 have been formed subaqueously is probably the reason for the lack of preserved detail.

232 There is a greater topological similarity between the G1/G3 and the modern Daasanach means (Figs
233 9 and 10). Both sets of tracks were made in drier substrates with more spatially, along the trackway,
234 consistent sedimentological properties. Both sets of tracks are shallower and therefore more ideal for
235 making biomechanical inferences (Bates et al., 2013a).

236 Comparing the G3 mean to the Daasanach mean the differences are restricted to a slightly variation
237 in depth along the lateral side of the modern foot. The modern foot is more impressed and may
238 reflect a subtle difference in the degree to which the longitudinal medial arch is developed in the case
239 of the G3 mean. It should be noted however, that this arch becomes slightly less pronounced as
240 substrates become firmer and the difference may therefore also reflect greater compaction of the G3
241 track in the base of the G2 track. The G1 mean has a slightly less developed arch when compared to
242 the Daasanach mean (Fig. 7), although in the case the key difference is the shape and depth of the
243 heel area; it is deeper and more elongated in the case of the G1 mean. There is a lack of clear
244 anatomical difference between the Laetoli and modern tracks therefore supporting the conclusion of
245 Crompton et al. (2011) that both sets of tracks are biomechanically similar in form.

246 Hatala et al. (2016a,c) stress the importance of medial transfer as the defining characteristic of
247 modern foot function. The implication is that this is less well developed in the Laetoli tracks (Hatala et
248 al. (2016a,c). This is consistent with the landmark based analysis of the Ileret tracks (Bennett et al.,
249 2009) who suggested that they showed a greater mechanical affinity to modern *Homo sapiens* prints
250 rather than to Laetoli. Figure 8 shows data on the deepest point in the ball area of tracks for both
251 Laetoli and a sample of modern tracks in excess of 695 individuals. What is clear from this is that
252 modern feet show a range of behaviours and the degree of medial transfer is variable within a large
253 population. This is consistent with Bates et al. (2013b) who suggested that in a small group of
254 modern humans the foot showed greater mid-foot flexibility giving rise to an effective mid-tarsal break
255 and a lack of medial transfer in some tracks. Not only does this data challenge the idea that medial
256 transfer is a defining characteristic of modern gait (cf. Hatala et al. 2016a; Fig. 8), but the Laetoli
257 tracks while showing less medial transfer, evident in the G1 and G3 means (Fig. 2), are not atypical of
258 the variability in modern foot function. The difference between the Laetoli tracks and those of modern

259 humans are small, and what variances are visible appear to focus on the degree to which the medial
260 longitudinal arch is developed, which itself appears potentially to be enhanced primarily within the
261 genus *Homo*.

262 Recent work by Hatala et al. (2016c) has added to this ongoing debate. They use 14 functionally
263 important locations across tracks to compare modern human (n= 245) and chimpanzee tracks (n=24)
264 with those of Laetoli (n=5). The different track samples were not co-registered, unlike this study and
265 that of Crompton et al. (2011), and the 14 points apparently placed by 'eye'. They used Mahalanobis
266 distances to model and compare the means of different samples, of varying sizes. The computed
267 distances show statistical differences suggesting a distinction in track morphology between the three
268 sampled populations. Hatala et al. (2016c) interpret this in terms of the Laetoli track maker (*A.*
269 *afarensis*) having a more flexed lower limb posture than is typical for modern humans. This may not
270 be as extreme as the bent knee and/or hip flexion hypothesised and debated by some (Raichen et al.
271 2010; Crompton et al., 2011). Hatala et al. (2016c) draw attention to the presence of only a moderate
272 medial weight transfer in the Laetoli tracks as further evidence of their interpretation of a more flexed
273 biomechanical motion.

274

275 **5.0 Conclusion**

276 The lack of difference in track topology, and therefore by inference biomechanical function, between
277 *Australopithecus* tracks and ones made by modern *Homo sapiens* identified in this paper may
278 suggest that foot functional anatomy over the last 3.66 Ma has remained relatively unchanged. This
279 supports the conclusions of Crompton et al. (2011), but challenges those of Hatala et al. (2016c).
280 This does not necessarily mean that the track-maker at Ileret, assumed to be *Homo erectus* (Bennett
281 et al., 2009; Dingwall et al., 2013), had a similarly modern foot function since these tracks are in the
282 author's opinion dominated by the influence of substrate. Hatala et al. (2016a) point to the medial
283 shift in the later part of stance as the defining element of modern gait, a feature that is present in the
284 Ileret tracks (Hatala et al., 2016b). Figure 8 however shows that modern human foot function has a
285 range of variability with respect to the degree of medial transfer. This variability encompasses that
286 present in all of the populations sampled here, including those at Laetoli. We do not necessarily
287 therefore agree with the conclusions of Hatala et al. (2016c) that there is sufficient distinction in the
288 degree of medial transfer to allow locomotory discrimination between the Laetoli track-maker and
289 modern humans.

290 To this we must add a word of caution implicit in this type of analysis and remember that we are in
291 practice making critical inferences about whole genera from a very limited sample of tracks! The
292 more we sample modern human foot function the more variable it appears to become (Fig. 8; Bates et
293 al., 2013b). In addition some researchers have suggested that the Laetoli track-makers may have
294 had specific pathologies or been undertaking specific behaviours leading to non-standard tracks (e.g.,
295 Tuttle et al., 1990). Ultimately we have the data that we have and while further data is always

296 desirable and might be forthcoming from Laetoli in time with new discoveries, we need to take a view,
297 at least in the interim, with what we have. Therefore as things stand we tentatively suggest, as stated
298 above, that the biomechanical differences present within the tracks sampled here are within the range
299 of variability of modern humans and are therefore left with the most parsimonious conclusion that
300 primary foot function (i.e. walking) has varied little during the last 3.66 Ma.

301 The evidence from fossil bones provides a slightly different picture, suggesting that different
302 genera/species may have slightly different locomotor repertoires (e.g., Gebo and Schwartz, 2006;
303 Harcourt-Smith et al., 2015). A combination of anatomical features suggests that both terrestrial
304 bipedality and arborealism is evident as far back as *Oreopithecus* (Szalay and Langdon, 1986; Moyà-
305 Solà et al. 1999). Lovejoy et al. (2009) suggest that the robust nature of metatarsals two and three in
306 *Ardipithecus ramidus* indicates a role in applying accelerative force in the later part of bipedal stance,
307 while an abducted hallux might have provided grip on branches, and therefore conclude that
308 locomotion involved both arboreal climbing and terrestrial bipedalism. *Australopithecus sediba* has
309 been reported by Zipfel et al. (2011) to possess ankle and foot morphology that would facilitate a
310 range of both arboreal and terrestrial bipedal locomotion and evidence for a strong Achilles tendon
311 may suggest adaptation for energy efficient terrestrial running. Furthermore the mid-foot of OH-8,
312 traditionally ascribed to *Homo habilis* is variously described as having an 'apelike' talus combined with
313 strong longitudinal arches (Day and Napier, 1964), or an un-stabilised medial mid-foot with no medial
314 arch, combined with a stabilized calcaneocuboid joint on the lateral side (Kidd et al., 1996).

315 The retention of both arboreal and terrestrial bipedal attributes within the foot can be interpreted in
316 different ways. For example, Harcourt-Smith and Aiello (2004) suggest that this range of functional
317 morphology indicates multiple paths to bipedalism (mosaic evolution) in early hominins as evidenced
318 by the anatomical mosaicism present. The alternative is to suggest that this range of functionality
319 might instead simply be due to a high degree of functional redundancy in the 26 bones and
320 associated 80+ ligaments present. Evidence presented by Bates et al. (2013b) suggests that retained
321 mid-foot mobility occurs in modern humans and amounts effectively to a mid-tarsal break in some but
322 not all steps and that there is greater overlap in foot function between hominins and great apes than is
323 often implied (see also: Wolf et al., 2004; Crompton et al., 2010, 2012).

324 One reason for the retention of this functional flexibility (or redundancy) is that unshod humans rarely
325 walk on flat and stable surfaces, but instead on uneven ground where foot flexibility is critical to
326 balanced, safe and cost-effective locomotion. Most fossil tracks (and associated laboratory studies)
327 do not account for this, since they involve walking on relatively flat surfaces, although potentially
328 muddy and slippery ones. It is therefore perhaps not surprising to find a convergence in foot
329 behaviour across different genera walking on flat terrain, especially since subtle skeletal differences in
330 the 26 bones can be compensated for by the 80+ ligaments in the foot. In the context of other terrain
331 types and foot functions the retained redundancy is not redundant at all. One could go as far as to
332 suggest that functional flexibility/redundancy in the foot is perhaps a defining and important
333 evolutionary characteristics conferring an advantage that allows for a wide range of possible motions

334 from climbing to endurance walking and/or running. This flexibility is something that we perhaps now
335 underestimate as habitually shod individuals.

336 This speaks to recent debates about the origins of hominin bipedalism and the importance of complex
337 topography (Winder et al., 2013, 2014) which challenges the more conventional arboreal hypotheses
338 (Thorpe et al., 2007, 2014a, b; Crompton et al., 2010). This remains contentious, with potentially no
339 simple, or single explanation (Wood, 2014; Allen et al., 2015), however retention of functional
340 flexibility/redundancy would allow hominins to use both arboreal and rocky refuges while evading
341 predators, as well as cope with rough and variable terrain and different types of ground surfaces.
342 These behavioural drivers may have in reality changed little over the last 3.66 Ma.

343

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352

353 **References**

354 Aldhouse-Green, S.H.R., Whittle, A.W.R., Allen, J.R.L., Caseldine, A.E., Culver, S.J., Day, M.H.,
355 Lundquist, J., Upton, D., 1993. Prehistoric human footprints from the Severn Estuary at Uskmouth
356 and Magor Pill, Gwent, Wales. *Archaeologia Cambrensis* 141, 14–55.

357 Allen, A., Crompton, R.H., Winder, I.C., D' Août, K., 2015. Walking over complex terrain: a systematic
358 review. *Footwear Science* 7(S1), S29-S30, DOI:10.1080/19424280.2015.103830

359 Allen, J.R., 1997. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, SW Britain:
360 mechanics of formation, preservation and distribution. *Philosophical Transactions of the Royal Society*
361 *B: Biological Sciences* 352, 481-518.

362 Avanzini, M., Mietto, P., Panarello, A., De Angelis, M., Rolandi, G., 2008. The Devil's Trails: Middle
363 Pleistocene human footprints preserved in a volcanoclastic deposit of Southern Italy. *Ichnos* 15, 179-
364 189.

365 Bates, K.T., Collins, D., Savage, R., McClymont, J., Webster, E., Pataky, T.C., D'Août, K., Sellers,
366 W.I., Bennett, M.R., Crompton, R.C., 2013b. The evolution of compliance in the human lateral mid-
367 foot. *Proceedings of the Royal Society of London B: Biological Sciences* 280, 20131818.

368 Bates, K.T., Savage, R., Pataky, T.C., Morse, S.A., Webster, E., Falkingham, P.L., Ren, L., Qian, Z.,
369 Collins, D., Bennett, M.R., McClymont, J., Crompton, R.H., 2013a. Does footprint depth correlate with
370 foot motion and pressure? *Journal of the Royal Society Interface* 10, 20130009.

371 Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate
372 assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology* 146, 473–
373 578.

374 Behrensmeyer, A.K., Laporte, L.F., 1981. Footprints of a Pleistocene hominid in northern Kenya.
375 *Nature* 289, 167-169.

376 Bennett, M.R., Morse, S.A., 2014. *Human Footprints: Fossilised Locomotion?* Springer, Dordrecht,
377 The Netherlands.

378 Bennett, M.R., Morse, S.A., Falkingham, P.L., 2014. Tracks made by swimming Hippopotami: An
379 example from Koobi Fora (Turkana Basin, Kenya). *Palaeogeography, Palaeoclimatology,*
380 *Palaeoecology* 409, 9-23.

381 Bennett, M.R., Reynolds, S.C., Morse, S.A., Budka, M., 2016a. Laetoli's lost tracks: 3D generated
382 mean shape and missing footprints. *Scientific Reports* 6, 21916.

383 Bennett, M.R., Falkingham, P., Morse, S.A., Bates, K.T., Crompton, R.H., 2013. Preserving the
384 Impossible: Conservation of Soft-Sediment Hominin Footprint Sites and Strategies for Three-
385 Dimensional Digital Data Capture. *PLoS One* 8: e60755.

386 Bennett, M.R., Morse, S.A., Liutkus-Pierce, C., McClymont, J., Evans, M., Crompton, R.H.,
387 Thackeray, J.F., 2014b. Exceptional preservation of children's footprints from a Holocene footprint site
388 in Namibia. *Journal of African Earth Sciences* 97, 331-341.

389 Bennett, M.R., Harris, J.W.K., Richmond, B.G., Braun, D.R., Mbua, E., Kiura, P., Olago, D., Kibunja,
390 M., Omuombo, C., Behrensmeyer, A.K., Huddart, D., Gonzalez, S., 2009. Early Hominin Foot
391 Morphology Based on 1.5 Million Year Old Footprints from Ileret, Kenya. *Science* 323, 1197-1201.

392 Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of Homo. *Nature* 432,
393 345-352.

394 Brown, F.H., Haileab, B., McDougall, I., 2006. Sequence of tuffs between the KBS Tuff and the Chari
395 Tuff in the Turkana Basin, Kenya and Ethiopia. *Journal of the Geological Society* 163, 185–204.

396 Clarke, R.J. and Tobias, P.V., 1995. Sterkfontein Member 2 foot bones of the oldest South African
397 hominid. *Science* 269, 521.

398 Crompton, R.H., Sellers, W.I., Thorpe, S.K.S., 2010. Arboreality, terrestriality and bipedalism
399 *Philosophical Transactions of the Royal Society of London B* 365, 3301-3314.

400 Crompton, R.H., Pataky, T.C., Savage, R., D'Août, K., Bennett, M.R., Day, M.H., Bates, K., Morse, S.,
401 Sellers, W.I., 2011. Human-like external function of the foot, and fully upright gait, confirmed in the
402 3.66 million year old Laetoli hominin footprints by topographic statistics, experimental footprint-
403 formation and computer simulation. *Journal of the Royal Society Interface* 9, 707-719.

404 Day, M.H., Napier, J.R., 1964. Hominid Fossils from Bed I, Olduvai Gorge, Tanganyika: Fossil Foot
405 Bones. *Nature* 201, 969-970.

406 Deino, A.L., 2011. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Laetoli, Tanzania. In: Harrison, T. (Ed.), *Paleontology and*
407 *geology of Laetoli: Human evolution in context.* Springer, Netherlands, pp. 77-97.

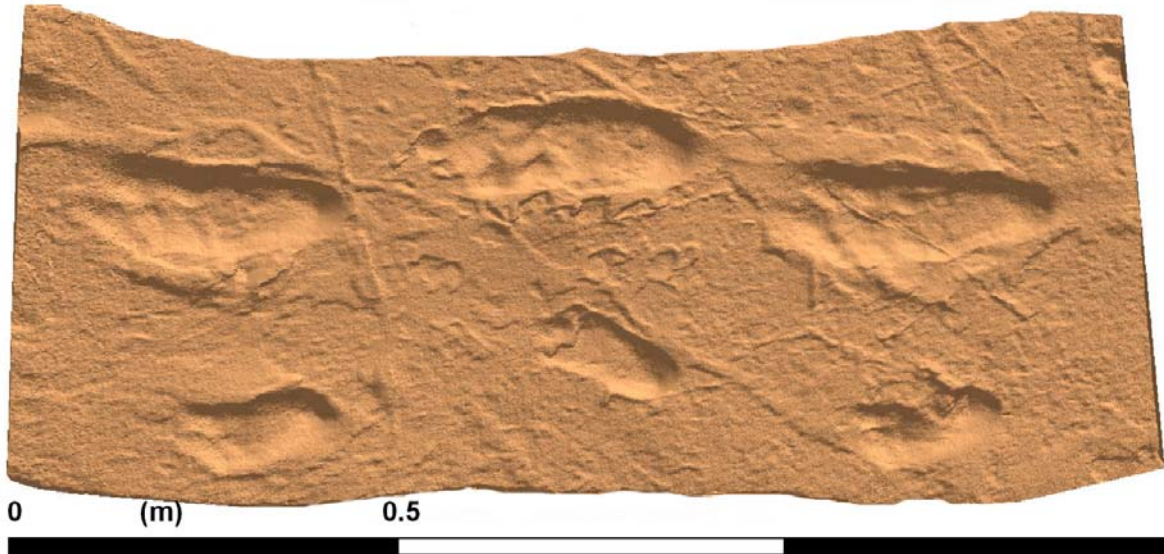
- 408 Dingwall, H.L., Hatala, K.G., Wunderlich, R.E., Richmond, B.G., 2013. Hominin stature, body mass,
409 and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya. *Journal of*
410 *Human Evolution* 64, 556-568.
- 411 Ditchfield, P., Harrison, T., 2011. Sedimentology, Lithostratigraphy and Depositional History of the
412 Laetoli Area. In: Harrison, T., (Ed.), *Paleontology and geology of Laetoli: Human evolution in context.*
413 Springer, Dordrecht, The Netherlands., pp. 47-76.
- 414 Drake, R., Curtis, G.H., 1987. Geochronology of the Laetoli fossil localities. In: Leakey, M.D., Harris,
415 J.M. (Eds.), *Laetoli: A Pliocene Site in Northern Tanzania.* Clarendon Press, Oxford, pp.48-52.
- 416 Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo
417 Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical*
418 *Anthropology* 78, 595-622.
- 419 Gebo, D.L., Schwartz, G.T., 2006. Foot bones from Omo: implications for hominid evolution.
420 *American Journal of Physical Anthropology* 129, 499-511.
- 421 Granger, D.E., Gibbon, R.J., Kuman, K., Clarke, R.J., Bruxelles, L., Caffee, M.W., 2015. New
422 cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature*
423 522, 85-88.
- 424 Harcourt-Smith, W.E., Aiello, L.C., 2004. Fossils, feet and the evolution of human bipedal locomotion.
425 *Journal of Anatomy* 204, 403-416.
- 426 Harcourt-Smith, W.E.H., Throckmorton, Z., Congdon, K.A., Zipfel, B., Deane, A.S., Drapeau, M.S.M.,
427 Churchill, S.E., Berger, L.R., DeSilva, J.M., 2015. The foot of *Homo naledi*. *Nature communications*,
428 6.
- 429 Hatala, K.G., Wunderlich, R.E., Dingwall, H.L., Richmond, B.G., 2016a. Interpreting locomotor
430 biomechanics from the morphology of human footprints. *Journal of Human Evolution* 90, 38-48.
- 431 Hatala, K.G., Roach, N.T., Ostrofsky, K.R., Wunderlich, R.E., Dingwall, H.L., Villmoare, B.A., Braun,
432 D.R., Richmond, B.G. 2016b. Footprints reveal direct evidence of group behaviour and locomotion in
433 *Homo erectus*. *Scientific Reports*, 6, 28766.
- 434 Hatala, K.G., Demes, B., Richmond, B.G., 2016c. Laetoli footprints reveal bipedal gait biomechanics
435 different from those of modern humans and chimpanzees. *Proceeding of the Royal Society B* 283,
436 20160235.
- 437 Hay, R.L., 1987. Geology of the Laetoli area. In: Leakey, M.D., Harris, J.M. (Eds.) *Laetoli: A*
438 *Pleistocene Site in Northern Tanzania.* Clarendon Press, Oxford, pp. 23-47.
- 439 Isaac, G.L.I., Behrensmeyer, A.K., 1997. Geological context and palaeoenvironments. In: Isaac, G.L.I.
440 (Ed.), *Koobi Fora Research Project, Volume 5, Plio-Pleistocene Archaeology*, Clarendon Press,
441 Oxford, pp. 12–70.
- 442 Kabsch, W., 1976. A solution for the best rotation to relate two sets of vectors. *Acta Crystallographica*
443 *Section A* 32, 922-923.
- 444 Kidd, R.S., O'Higgins, P.O., Oxnard, C.E., 1996. The OH8 foot: a reappraisal of the hindfoot utilizing a
445 multivariate analysis. *Journal of Human Evolution* 31, 269–291.
- 446 Kim, K.S., Kim, J.Y., Kim, S.H., Lee, C.Z., Lim, J.D., 2009. Preliminary report on hominid and other
447 vertebrate footprints from the Late Quaternary strata of Jeju Island, Korea. *Ichnos*, 16, 1-11.

- 448 Leakey, M.D., 1981. Tracks and tools. *Philosophical Transactions of the Royal Society of London B,*
449 *Biological Sciences* 292, 95-102.
- 450 Leakey, M.D., Harris, J.M., 1987. *Laetoli: A Pliocene Site in Northern Tanzania.* Clarendon Press,
451 Oxford, UK.
- 452 Leakey, M.D., Hay, R.L., 1979. Pliocene footprints in the Laetoli beds at Laetoli, Northern Tanzania.
453 *Nature* 278, 317.
- 454 Lepre, C.J., Quinn, R.L., Joordens, J.C., Swisher, C.C., Feibel, C.S., 2007. Plio-Pleistocene facies
455 environments from the KBS Member, Koobi Fora Formation: implications for climate controls on the
456 development of lake-margin hominin habitats in the northeast Turkana Basin (northwest Kenya).
457 *Journal of Human Evolution* 53, 504–514.
- 458 Lockley, M., Roberts, G., Kim, J.Y., 2008. In the Footprints of Our Ancestors: An Overview of the
459 Hominid Track Record. *Ichnos* 15, 106-125.
- 460 Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and
461 propulsion: the foot of *Ardipithecus ramidus*. *Science* 326, 72-72e8.
- 462 Miall, A.D., 2016. *Stratigraphy: A Modern Synthesis.* Springer International Publishing.
- 463 Meldrum, D.J., Lockley, M.G., Lucas, S.G., Musiba, C., 2011. Ichnotaxonomy of the Laetoli trackways:
464 the earliest hominin footprints. *Journal of African Earth Sciences* 60, 1-12.
- 465 Morse, S.A., Bennett, M.R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R., Crompton,
466 R.H., 2013. Holocene footprints in Namibia: the influence of substrate on footprint variability.
467 *American Journal of Physical Anthropology* 151, 265-279.
- 468 Moyà-Solà S., Köhler M., Alba D.M., 1999. Primate evolution – in and out of Africa. *Current Biology* 9,
469 547-550.
- 470 Musiba, C.M., Mabula, A., Selvaggio, M., Magori, C.C., 2008. Pliocene animal trackways at Laetoli:
471 Research and conservation potential. *Ichnos* 15, 166-178.
- 472 Pataky, T.C., Goulermas, J.Y., 2008. Pedobarographic statistical parametric mapping (pSPM): a
473 pixel-level approach to foot pressure image analysis. *Journal of Biomechanics* 41, 2136-2143.
- 474 Raichlen, D.A., Gordon, A.D., Harcourt-Smith, W.E., Foster, A.D., Haas Jr, W.R., 2010. Laetoli
475 footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS One* 5,
476 p.e9769.
- 477 Roach, N.T., Hatala, K.G., Ostrofsky, K.R., Villmoare, B., Reeves, J.S., Du, A., Braun, D.R., Harris,
478 J.W., Behrensmeyer, A.K. and Richmond, B.G., 2016. Pleistocene footprints show intensive use of
479 lake margin habitats by *Homo erectus* groups. *Scientific reports*, 6.
- 480 Roberts, G., Gonzalez, S., Huddart, D., 1996. Inter-tidal Holocene footprints and their archaeological
481 significance. *Antiquity* 70, 647–651.
- 482 Schmincke, H-U., Kutterolf, S., Perez, W., Rausch, J., Freundt, A., Strauch, W., 2009. Walking
483 through volcanic mud: the 2,100 year old Acahualinca footprints (Nicaragua). *Bulletin of Volcanology*
484 71, 479-493.
- 485 Schmincke, H-U., Rausch, J., Kutterolf, S., Freundt, A., 2010. Walking through volcanic mud: the
486 2,100 year-old Acahualinca footprints (Nicaragua) II: the Acahualinca people, environmental
487 conditions and motivation. *International Journal of Earth Science* 99, 279-292.

- 488 Scott, J.J., Renaut, R.W., Owen, R.B., 2008. Preservation and paleoenvironmental significance of a
489 footprinted surface on the Sandai Plain, Lake Bogoria, Kenya Rift Valley. *Ichnos* 15, 208-231.
- 490 Scott, J.J., Renaut, R.W., Owen, R.B., 2010. Taphonomic controls on animal tracks at saline, alkaline
491 Lake Bogoria, Kenya Rift Valley: impact of salt efflorescence and clay mineralogy. *Journal of*
492 *Sedimentary Research* 80, 639-665.
- 493 Scrivner, P.J., Bottjer, D.J., 1986. Neogene avian and mammalian tracks from Death Valley National
494 Monument, California: their context, classification and preservation. *Palaeogeography,*
495 *Palaeoclimatology, Palaeoecology* 57, 285-331.
- 496 Suwa, G., 1984. Could *Australopithecus afarensis* have made the hominid tracks at Laetoli? *Journal*
497 *of Physical Anthropology* 963, 224–225.
- 498 Szalay, F.S., Langdon, J. 1986. The foot of *Oreopithecus bambolii*: an evolutionary assessment.
499 *Journal of Human Evolution* 15, 585–621.
- 500 Thorpe, S.K., Holder, R.L. and Crompton, R.H., 2007. Origin of human bipedalism as an adaptation
501 for locomotion on flexible branches. *Science* 316, 1328-1331.
- 502 Thorpe, S.K.S., McClymont, J.M., Crompton, R.H., 2014a. The arboreal origins of human bipedalism.
503 *Antiquity* 88, 906-914.
- 504 Thorpe, S.K.S., McClymont, J.M., Crompton, R.H., 2014b. Putting flesh on to hominin bones.
505 *Antiquity* 88, 924-926.
- 506 Tuttle, R., Webb, D., Weidl, E., Baksh, M., 1990. Further progress on the Laetoli trails. *Journal of*
507 *Archaeological Science* 17, 347-362.
- 508 Ward, C.V., Kimbel, W.H., Johanson, D.C., 2011. Complete fourth metatarsal and arches in the foot
509 of *Australopithecus afarensis*. *Science* 331, 750-753.
- 510 White, T.D., Suwa, G., 1987. Hominid footprints at Laetoli: Facts and interpretations. *American*
511 *Journal of Physical Anthropology* 72, 485-514.
- 512 Winder, I.C., King, G.C.P., Maud H. Devès, M.H., Bailey, G.N., 2013. Complex topography and
513 human evolution: the missing link. *Antiquity* 87, 333–49.
- 514 Winder, I.C., King, G.C.P., Maud H. Devès, M.H., Bailey, G.N., 2014. Human bipedalism and the
515 importance of terrestriality. *Antiquity* 88, 915-916.
- 516 Wood, B., 2014. Unreasonable expectations. *Antiquity* 88, 917-918.
- 517 Wolf, P., Stacoff, A., Stüssi, E., 2004. Modelling of the passive mobility in human tarsal gears
518 implications from the literature. *The Foot* 14, 23–34.
- 519 Zipfel, B., DeSilva, J.M., Kidd, R.S., Carlson, K.J., Churchill, S.E., Berger, L.R., 2011. The foot and
520 ankle of *Australopithecus sediba*. *Science*, 333, 1417-1420.

521

522 **Figure Captions**



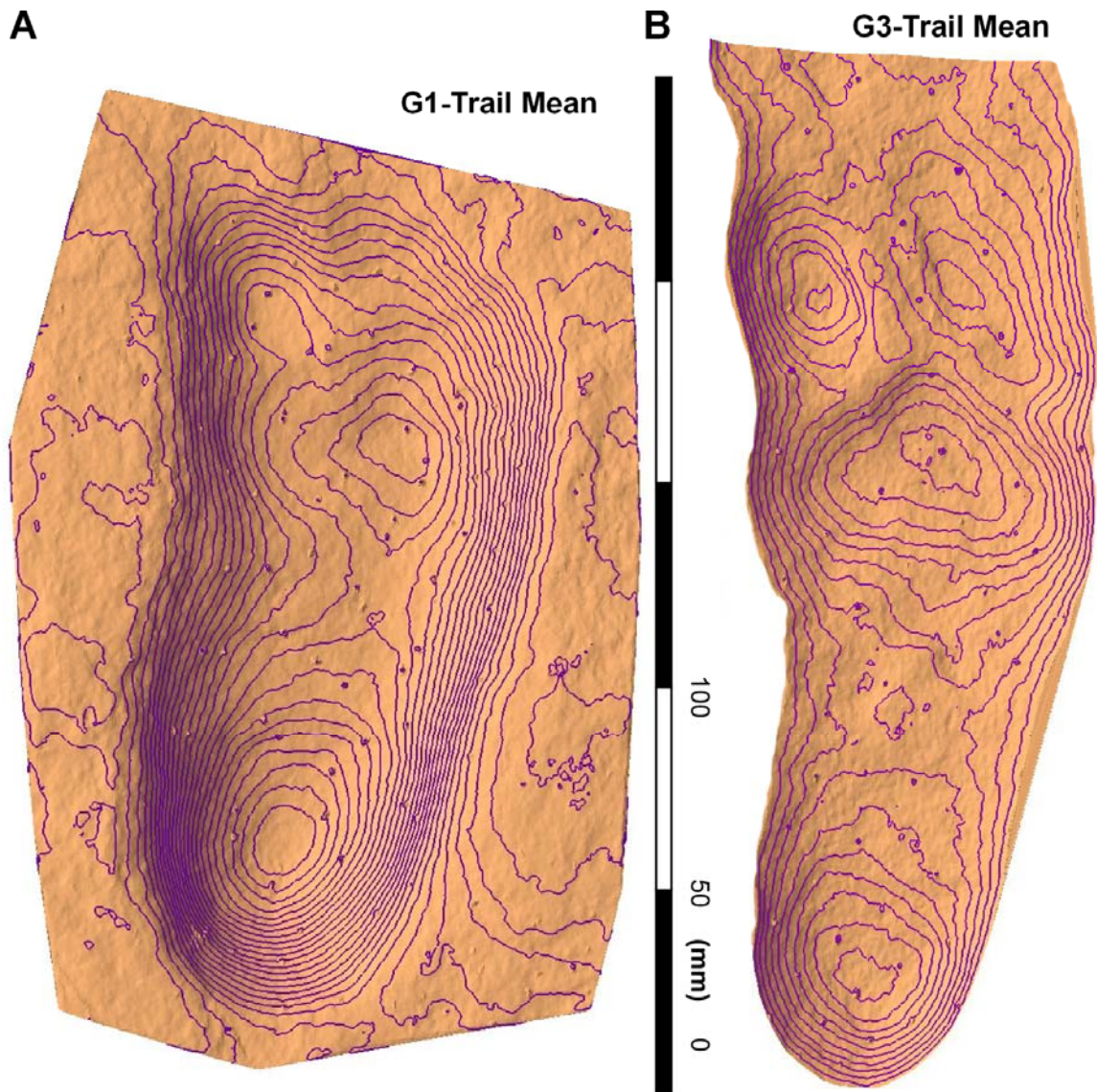
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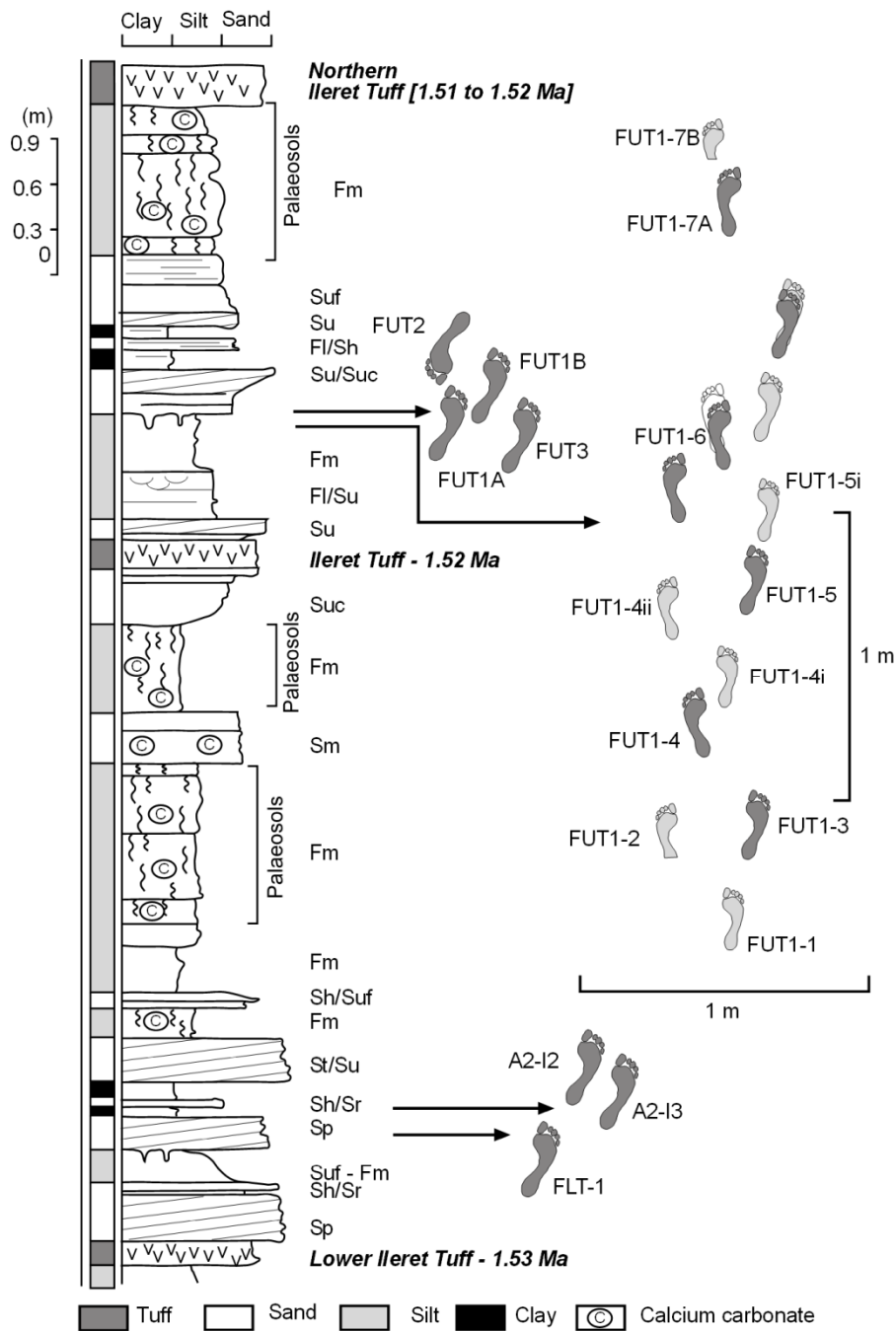
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Figure 1: Optical laser colour rendered scan of part of the Laetoli trail. This was captured by the senior author using a Vi900 Konica-Minolta scanner from a first generation cast held at the National Museum of Kenya in 2008.



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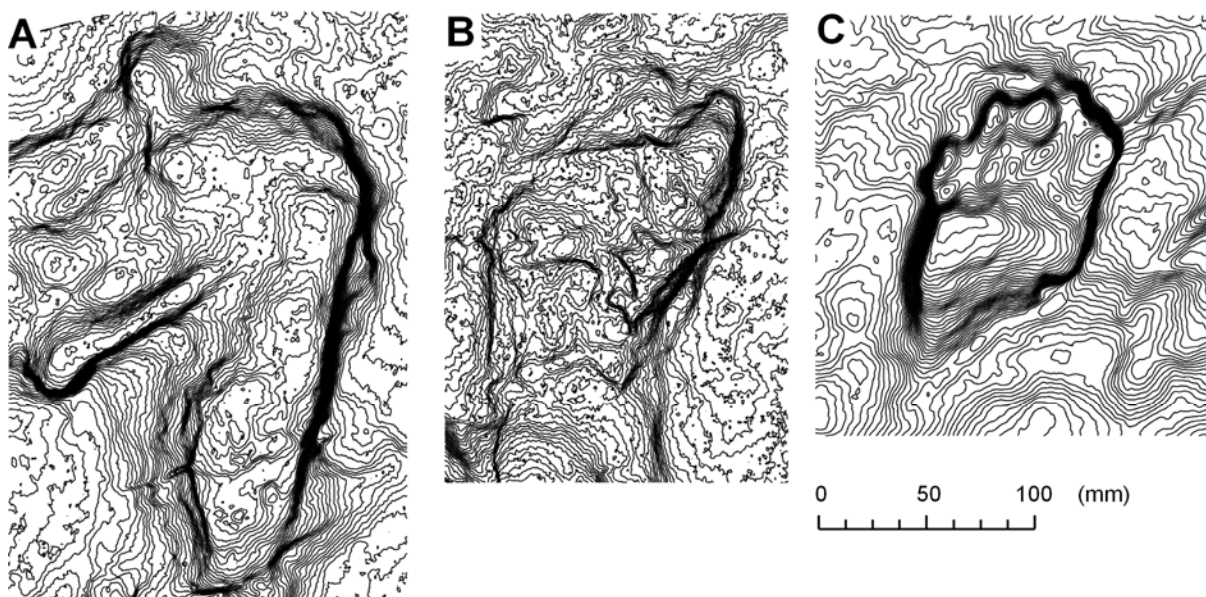
528 Figure 2: Mean tracks for the G1 and G3 trackways with superimposed contours at 1 mm vertical
 529 intervals. The data was captured by the senior author using a Vi900 Konica-Minolta scanner from
 530 a first generation cast held at the National Museum of Kenya in 2008 and processed in DigTrace
 531 and ArcGIS Version 10 (<http://www.esri.com/software/arcgis>). The G1 mean is based on eleven
 532 individual tracks: G1-23, G1-25, G1-26, G1-27, G1-31, G1-33, G1-34, G1-35, G1-36, G1-37, G1-
 533 39. The G3 mean is based on: G2-18, G2-26, G2-27, G2-28 and G2-29.



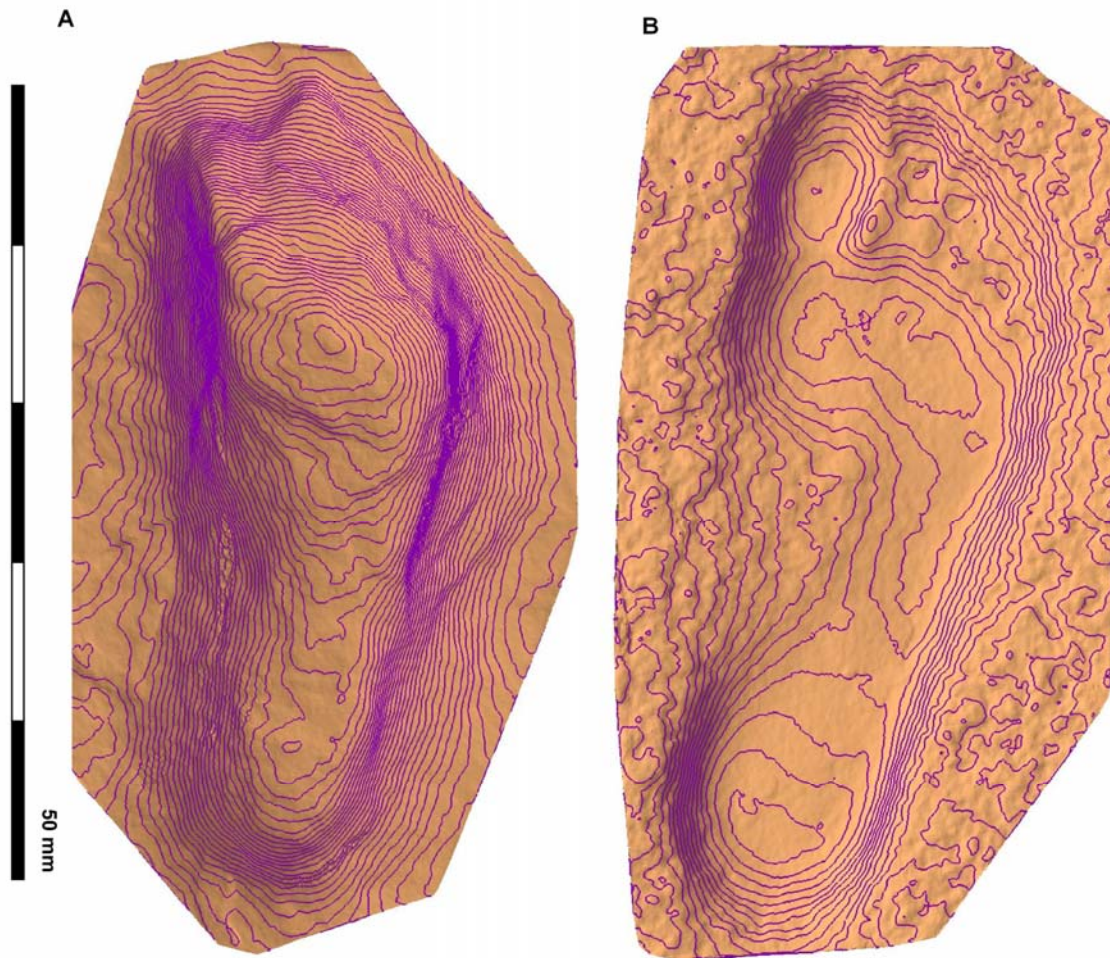
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Figure 3: Summary

figures for the Ileret tracks showing the stratigraphy and the excavated tracks as of 2011. Modified from Bennett et al. (2009) and Dingwall et al. (2013). The facies codes are after Maill (2016): Fm = massive silt, FI = laminated silts, Sm = massive sands, Sp = planar cross-bedded sands, Sh= horizontally stratified sands; Su= scours and shallow cross-bedded sands, Sr = rippled sands, St = trough cross-bedded sands, Suf = upward fining sands, Suc = upward coarsening sands.

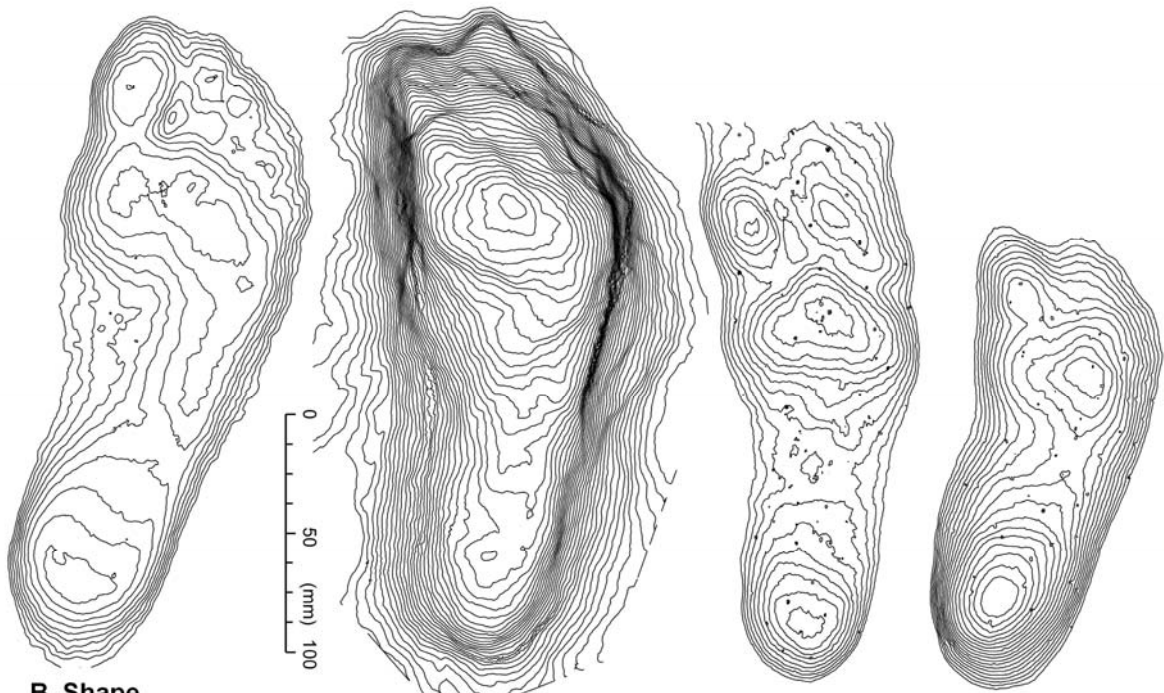


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 541 Figure 4: Selected tracks from Ileret: (A) FUT1-3, (B) FUT1-2, (C) FUI8. In all cases the contour
 542 interval is 1 mm. The data was captured by the senior author in the field using a Vi900 Konica-
 543 Minolta scanner in 2007/2008 and processed in DigTrace and ArcGIS Version 10
 544 (<http://www.esri.com/software/arcgis>).

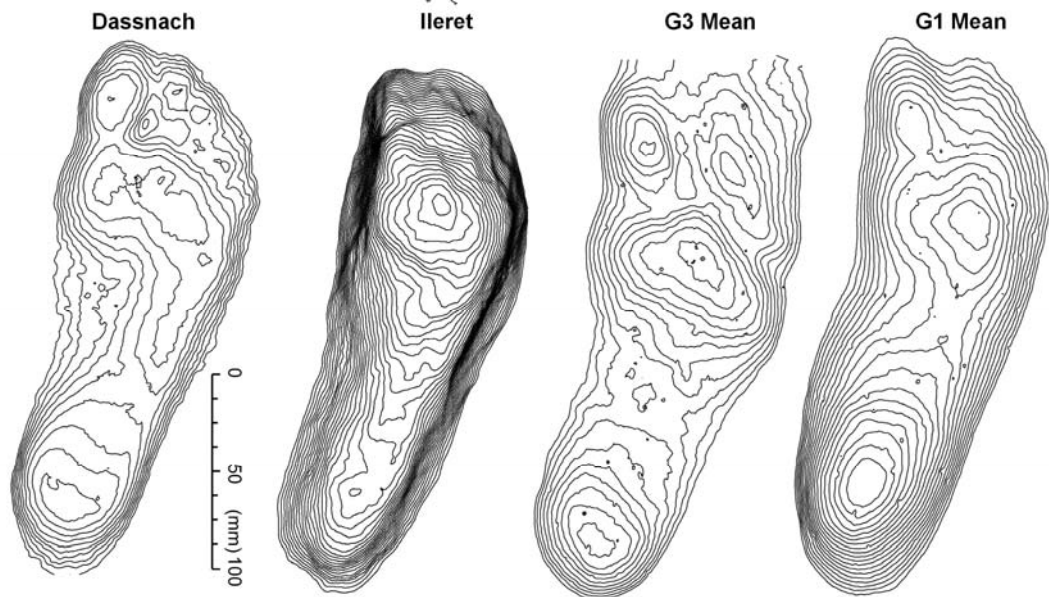


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 546 Figure 5: Mean tracks for the upper trail at Ileret (FwJj14E; A) and for the Daasanach modern
 547 mean (B; N=33) with superimposed contours at 1 mm intervals. The Ileret mean is based on
 548 FUT1-1, FUT1-3, FUT1-5, FUT1-6 and FUT1-7A. This may include tracks from two individuals
 549 according to Dingwall et al. (2013). The data was captured by the senior author using a Vi900
 550 Konica-Minolta scanner in the field in 2007/2008 and processed in DigTrace and ArcGIS Version
 551 10 (<http://www.esri.com/software/arcgis>).

A. Size + shape

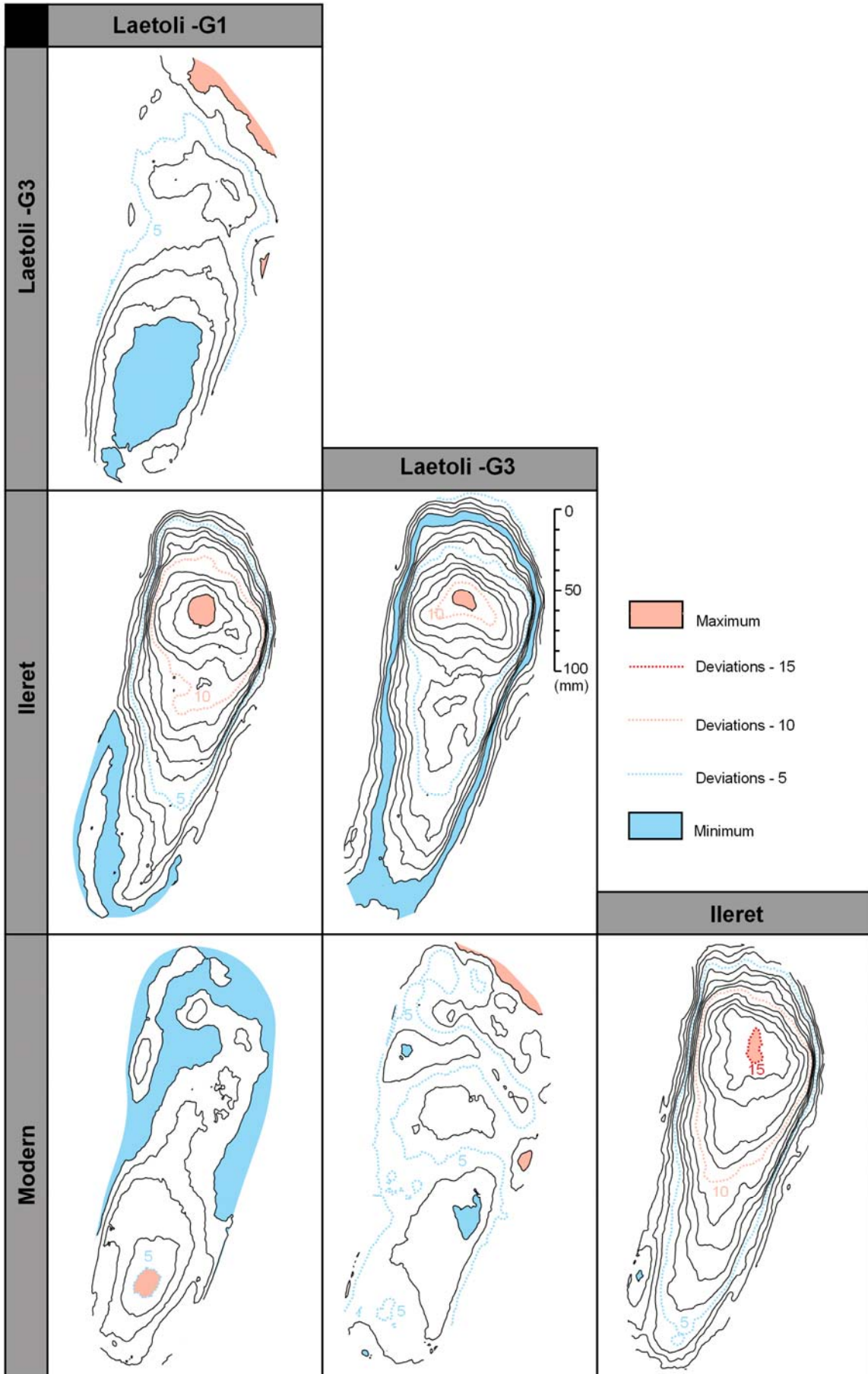


B. Shape

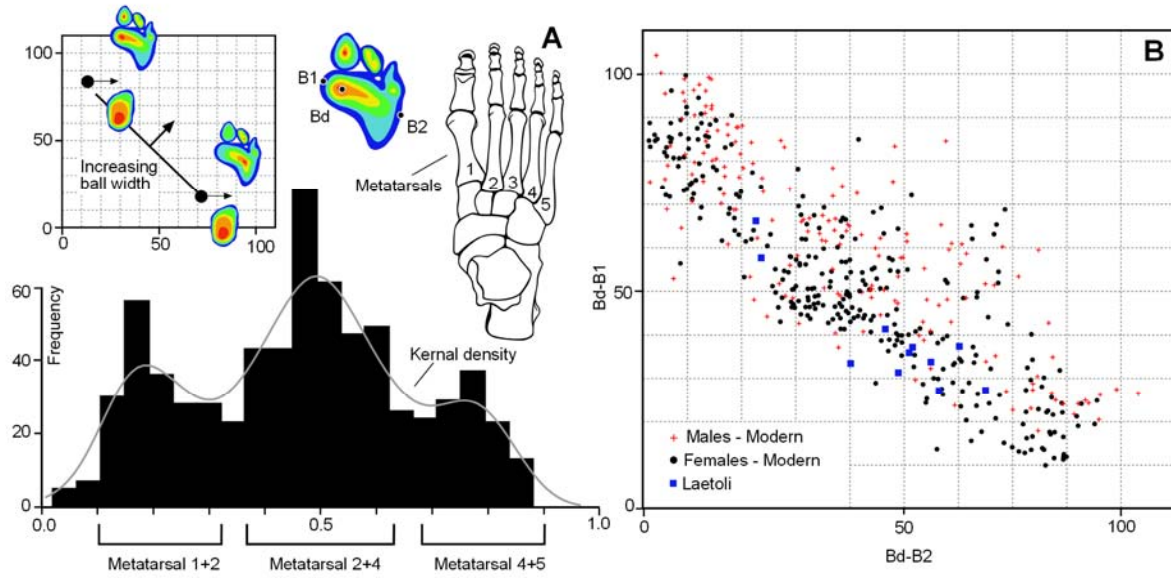


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Figure 6: Mean track for the various track populations available across the Australopith to Homo transition. A. Tracks reproduced at relative size. B. Tracks registered against the Daasanach mean in DigTrace using an affine transformation thereby removing the influence of size.



557 Figure 7: Comparison represented here by standard deviation of all the different track means.



558 Figure 8: Simple landmark based experiment to explore the degree of medial transfer. A.
559 Histogram of 695 tracks of made by both shod and unshod modern humans. B. Scatter plot of 470
560 modern tracks (habitually shod) plus data from the G1 Laetoli trackway.
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