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Hatala, KG, Gatesy, SM and Falkingham, PL (2023) Arched footprints preserve the motions of fossil hominin feet. Nature Ecology and Evolution. ISSN 2397-334X

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2
3 **Title: Arched footprints preserve the motions of fossil hominin feet**

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12
13 **Abstract:**

14 The longitudinal arch of the human foot is viewed as a pivotal adaptation for bipedal
15 walking and running. Fossil footprints from Laetoli, Tanzania and Ileret, Kenya are believed to
16 provide direct evidence of longitudinally arched feet in hominins from the Pliocene and
17 Pleistocene, respectively. We studied the dynamics of track formation using biplanar X-ray, 3-D
18 animation, and discrete element particle simulation. Here we demonstrate that longitudinally
19 arched footprints are false indicators of foot anatomy; instead they are generated through a
20 specific pattern of foot kinematics that is characteristic of human walking. Analyses of fossil
21 hominin tracks from Laetoli show only partial evidence of this walking style, with a similar heel
22 strike but a different pattern of propulsion. The earliest known evidence for fully modern human-
23 like bipedal kinematics comes from the early Pleistocene Ileret tracks, which were presumably
24 made by members of the genus *Homo*. This result signals important differences in the foot

25 kinematics recorded at Laetoli and Ileret, and underscores an emerging picture of locomotor
26 diversity within the hominin clade.

27

28 **Main text:**

29 *Introduction*

30 Human bipedal locomotion is unique among living primates and has long been
31 considered a primary trait that defines the hominin clade¹. The longitudinal arch is often cited as
32 an important evolutionary innovation of the human foot that contributed to proficient bipedal
33 walking and adept endurance running in our fossil relatives²⁻⁴, and there exists tremendous
34 interest in the evolution of this distinctly human foot anatomy. However, skeletal fossils are
35 typically fragmentary and soft tissues rarely preserve, making it difficult to interpret arch
36 anatomy from hominin fossils. Fossil footprints provide an alternative, possibly more direct view
37 of intact feet of living individuals. The 1978 discovery of 3.66 Ma hominin tracks (i.e.,
38 footprints) at Laetoli, Tanzania appeared to provide the oldest fossil evidence of longitudinal
39 arches⁵. This interpretation has been supported repeatedly in the four decades since⁶⁻¹⁰.
40 Likewise, 1.5 Ma hominin tracks from Ileret, Kenya, are viewed as direct evidence of a
41 longitudinally arched foot in at least one Pleistocene taxon¹¹. Given the challenges of interpreting
42 arches from fossil feet^{12,13}, the Laetoli and Ileret tracks are considered the least equivocal
43 evidence for a deep history of longitudinally arched foot morphologies in hominin evolution.

44 Inferring longitudinally arched feet from longitudinally arched tracks (Fig. 1A-D)
45 appears straightforward, but the extent to which the topography of the deformed substrate
46 reflects foot arch morphology has never been demonstrated. Here we test this anatomical fidelity
47 hypothesis by using a ‘track ontogeny’ approach¹⁴⁻¹⁶ to elucidate the development of
48 longitudinally arched footprints. In biplanar X-ray experiments, we used 85 skin markers to

49 reconstruct the dynamic foot shape of four subjects walking across substrates spanning from a
50 solid to compliant wet mud. To directly compare 3-D arch morphologies of feet and their
51 resulting tracks, we developed a scale-free method for measuring their relative arch volumes
52 (RAV; Fig. 1E-G). We then input experimentally-derived and hypothetical animated foot models
53 to drive particle-based substrate simulations to assess spatiotemporal aspects of the sediment
54 deformation that leads to longitudinally arched tracks. Finally, we applied our findings to
55 reinterpret fossil hominin tracks through the unique perspective afforded by this lens.

56

57 *Results and Discussion*

58 When we measured each experimental subject's foot at mid-stance, their anatomical foot
59 RAVs were consistently much less than their unloaded resting foot RAVs across substrates.
60 Track RAVs showed a directional trend, becoming more arched in substrates where subjects'
61 feet sank deeper (Fig. 1H). Feet at mid-stance were notably less arched than all but their
62 shallowest tracks, in which the foot did not sink deep enough for the plantar surface beneath the
63 longitudinal arch to contact completely the substrate. In deeper experimental tracks – which
64 better resemble known fossil tracks from Laetoli and Ileret – track RAV was on average 1.85
65 times higher (range 1.3x to 2.1x) than foot RAV. Moreover, variation in foot RAV among our
66 subjects confirmed that even the least-arched individual consistently produced considerably
67 arched tracks in our softest, deepest, muds (Fig. 1H). In case this pattern that we observed among
68 our four biplanar X-ray subjects was influenced by sample size, we also examined the correlation
69 between track RAV and navicular height among a larger sample of footprints that were made by
70 habitually barefoot people as part of a previously published experiment¹⁷ (Supplementary Note
71 1; Extended Data Fig. 1). There we could statistically evaluate the correlation between track

72 RAV and navicular height. We found that this relationship was not statistically significant,
73 further demonstrating the disconnect between foot arch anatomy and track morphology.

74 The clear mismatch between the longitudinal arches of feet and tracks refutes the
75 prevalent assumption that foot arch morphology can be directly reconstructed from fossil
76 footprints⁵⁻¹¹. Beyond demonstrating this inferential flaw, we discovered that track longitudinal
77 arches originate and are shaped by the kinematics of the foot as it navigates a deforming
78 substrate. By using particle simulations to visualize track ontogeny, we found that the track's
79 longitudinal arch is shaped continuously throughout stance phase (Fig. 2A-D), with the proximal
80 part forming soon after heel strike. Soft substrates allow the heel to rise as the forefoot continues
81 to sink, leading track RAV to increase continuously throughout mid-stance. At 50% of stance
82 phase both the heel and forefoot are shallower than the maximum depths they reach earlier and
83 later in stance, respectively, as substrate beneath the midfoot appears to support it. Following
84 mid-stance, as the heel continues to rise and the forefoot pushes off, sediment travels backward
85 and upward, enhancing the longitudinal arch left behind. Rather than duplicating static pedal
86 anatomy, deep tracks more closely resemble the substrate volume swept by a cumulative
87 sequence of foot poses (Fig. 2A-B, Extended Data Fig. 2, Supplementary Note 2). Viewed
88 through the lens of how they form, a deep and highly arched track thereby records an important
89 biomechanical phenomenon.

90 When humans walk, the heel strikes the ground first, the forefoot pushes off at the end,
91 and a smooth transition occurs in between. This rotational motion pattern increases the effective
92 length of the lower limb, thereby reducing costs of inverted pendulum bipedalism and increasing
93 muscular efficacy for propulsive force generation^{18,19} (Fig. 3A-B). We visualized this heel-sole-
94 toe rollover in our experiments by calculating a sagittal pivot between those sole markers moving
95 upwards and those moving downwards. On soft substrates, this pivot starts proximally and then

96 translates distally from heel to toe, following a path akin to the center of plantar pressure on solid
97 ground (Fig. 3C). While we were unable to directly quantify forces or pressures in our
98 experiments, others have demonstrated the kinetic correlates of the kinematic patterns that we
99 observed¹⁸. As a consequence of these foot kinematics, regions of substrate descend and rise
100 depending on the presence and motion of the interacting foot (Fig. 3D). For an exaggerated
101 theoretical test, we also ran 3-D particle simulations in which a rigid, rectangular model was
102 animated with an anteriorly translating pivot following human-like motion (Fig. 3E). Even this
103 flat-bottomed block created longitudinally arched tracks. A longitudinally arched fossil track
104 therefore serves as evidence of similar bipedal foot kinematics in extinct hominins.

105 We measured longitudinal arch morphologies of Pliocene (Laetoli, Tanzania; 3.66 Ma),
106 Pleistocene (Ileret, Kenya; 1.5 Ma), and Holocene (Walvis Bay, Namibia, ~400-500 ybp)
107 hominin tracks^{5,11,20-23}. We compared these with our experimental human footprints made in
108 deep mud (made by eight subjects, total n = 53), and with footprints produced in prior
109 experiments by habitually unshod people¹⁷ (n = 36 tracks from 17 subjects) and by chimpanzees
110 walking bipedally¹⁰ (made by two subjects; n₁ = 22, n₂ = 21). Chimpanzee tracks are less
111 longitudinally-arched than those of humans and their track RAVs are highly variable irrespective
112 of depth (Fig. 4A). This track RAV inconsistency likely reflects that chimpanzees use heel
113 strikes but as part of their more variable bipedal foot kinematics^{24,25}. Even when chimpanzee
114 track RAVs approach values recorded in hominin tracks, their track arches differ substantially in
115 shape and are easily distinguished (Extended Data Fig. 3, Supplementary Note 3). By contrast,
116 the Namibia and unshod human experimental track RAVs vary with footprint depth in a pattern
117 congruous to that observed in our biplanar X-ray experiments. The Namibia tracks (made by two
118 individuals; n₁ = 13 and n₂ = 11) were produced across variable substrate conditions²², resulting
119 in relative track depths that span roughly the same range as our experimental tracks. That

120 Namibian and experimental human tracks follow similar trends offers confidence for mechanistic
121 inferences in samples from other bipedal fossil hominins.

122 We analyzed hominin tracks from three Laetoli trackways – G1 (n = 11), S1 (n = 2), and
123 A (n = 1). Laetoli G1 and S1 tracks are longitudinally arched, but their RAVs are notably smaller
124 and more variable than similarly deep tracks measured from human experiments or from younger
125 fossil sites (Fig. 4A). The S1 tracks are substantially larger²⁰ but their RAVs fall within the
126 distribution of G1, suggesting that they record similar foot kinematics. The only Laetoli A track
127 sufficiently cleared of matrix²³ (A3) is extremely flat, with a RAV far below our human data, and
128 much lower than all other fossil samples (Fig. 4A). Previous workers have proposed that the
129 deep heel impressions of the G1 tracks may reflect evidence of a bipedal gait that included a
130 human-like heel strike¹⁹. We can now confirm, based on track ontogeny, that the longitudinally
131 arched Laetoli G1 and S1 tracks preserve the earliest known evidence of a heel-sole-toe pattern
132 of foot kinematics in the hominin fossil record.

133 However, a key distinction between Laetoli and modern human tracks is their pitch. All
134 of the Laetoli G1 and S1 footprints have relatively deeper heel and shallower forefoot
135 impressions (positive pitch), whereas at similar depths human tracks tend to have minimal pitch,
136 or be deepest in the forefoot (negative pitch)^{8,22} (Fig. 4B). Based on track ontogeny, the Laetoli
137 asymmetry could result from kinematic differences in heel strike or push-off. Of these, we
138 believe a different manner of propulsion is both more plausible and more concordant with the
139 skeletal morphology of *Australopithecus afarensis*, the presumed creator of the Laetoli G1 and
140 S1 tracks^{7,20}. Specifically, calcaneal robusticity of *A. afarensis* appears well-suited for repetitive
141 stresses similar to those experienced during human bipedalism^{26,27}. The *A. afarensis* lateral
142 metatarsals and transverse arch configuration have been interpreted as potential evidence of
143 different propulsive mechanics than seen in modern humans^{28,29}. Likewise, tarsal morphology

144 may confer greater hallucial mobility, resulting in less stereotyped propulsive loading
145 postures^{30,31}, which could explain the variation observed in Laetoli RAV measurements (Fig.
146 4A). While isolated analyses of skeletal fossils have generated conflicting interpretations about
147 whether the *A. afarensis* foot functioned like a modern human's²⁶⁻³¹, our analysis of the arched
148 Laetoli footprints provides a unique kinematic synthesis. Brought into view through this new
149 lens is a pattern of foot function and bipedal locomotion that was human-like in some ways yet
150 still importantly different.

151 In contrast, 1.5 Ma tracks from Ileret, Kenya preserve the earliest evidence for a fully
152 human-like pattern of foot kinematics. Tracks from Ileret (total n = 4 from 3 trackways) have
153 RAVs where we would expect similarly deep modern human tracks to fall (Fig. 4A). These data
154 provide new evidence to support inferences of human-like foot kinematics in *Homo erectus*^{11,17}.
155 We emphasize, however, that our track ontogeny results simultaneously invalidate direct
156 association between arched footprint morphology and arched foot anatomy at Ileret¹¹. In contrast
157 with the Laetoli examples above, it appears that the Ileret tracks are fully consistent with not
158 only a heel-sole-toe rollover pattern, but also a pattern of forefoot propulsion closer to that
159 observed in modern humans. While Ileret tracks may be even more negatively pitched than our
160 experimental human sample (Fig. 4B), they are also slightly deeper. Prior studies of fossil and
161 modern human tracks have indicated that tracks become more negatively pitched with depth²².

162 The experimental evidence presented here demonstrates that the longitudinal arches of
163 footprints develop as a consequence of heel-sole-toe foot kinematics, irrespective of foot
164 anatomy. In modern humans, both longitudinally arched feet and flat feet are capable of
165 achieving the minimum threshold of foot stiffness required for a foot to move in this way³². That
166 threshold is perhaps achieved through the stiffness provided by the foot skeleton's transverse
167 arch²⁹, although it may be impossible to generate modern human-like propulsive forces without

168 other hard and/or soft tissue mechanisms for further stiffening the foot. For example, humans
169 exhibit substantial control of longitudinal arch stiffness via intrinsic foot muscles^{33–35}. Based on
170 skeletal fossils, it remains an open question when and how these foot stiffening mechanisms
171 evolved in hominins. The results of our track analyses suggest that important changes to foot
172 anatomy and function occurred at or before the emergence of the genus *Homo*, where a suite of
173 postcranial changes³⁶ could correspond to selective influences of locomotor behaviors such as
174 long-distance walking or endurance running⁴.

175 Ultimately, our results demonstrate that deciphering the mechanistic origins of fossil
176 hominin footprints can clarify and contextualize analyses of skeletal morphology and elucidate
177 the locomotor biomechanics of fossil hominins. In this case, the longitudinal arches of hominin
178 tracks offer invaluable and otherwise inaccessible information on hominin locomotion, yet not in
179 the manner that has long been assumed.

180

181 **Methods:**

182 Research activities involving human subjects complied with all relevant ethical
183 regulations, and followed protocols approved by the Institutional Review Boards of Brown
184 University and Chatham University.

185

186 *Biplanar X-ray experimental setup*

187 All biplanar X-ray experiments took place at the W.M. Keck Foundation XROMM
188 Facility at Brown University, and our methods for data collection have described previously¹⁶.
189 An elevated trackway measuring approximately 6 m long, 0.6 m wide, and 0.5 m tall was
190 constructed using wooden platforms at either end and a modified stone slab table in between.
191 Three rigid panels of closed-cell extruded polystyrene (EPS) were placed upon the stone slab

192 table (two panels 5 cm thick, one panel 2.5 cm thick). A diamond-shaped recess was cut into the
193 center of these foam panels, such that a 30 x 30 x 14.5 cm³ foam container could be securely
194 embedded at their center. Biplanar X-ray equipment was focused at the center of this trackway,
195 such that X-ray beams intersected the diamond-shaped recess. Two telescoping ceiling cranes
196 were attached to X-ray tubes that projected collimated X-rays that were received by two 40.64
197 cm diameter image intensifiers that were themselves attached to mobile bases. X-ray emitters
198 were placed 134 cm from image intensifiers, at an angle of roughly 90 degrees to each other and
199 pitched upwards 10 degrees relative to the ground plane. Video recordings were collected from
200 the image intensifiers by two Phantom v10 high-speed digital cameras (Vision Research, Wayne,
201 NJ, USA), at a resolution of 1760 x 1760 pixels². A third camera (Phantom v9.1) recorded
202 standard light video of each subject's right foot from a perspective perpendicular to the trackway
203 (Extended Data Fig. 4). All three cameras were synchronized to within 4 μs and recorded at 50
204 frames per second, with 2000 μs exposure times. The Phantom cameras' Extreme Dynamic
205 Range was set to between 300 and 500 μs, adjusting to improve visibility as needed for different
206 substrate conditions. Pulsed X-rays (2 ms pulse widths) were transmitted at voltages of 60-90 kV
207 and currents of 250-400 mA, with higher energies used for wetter/denser substrates. When using
208 higher energies for wetter/denser substrates, compensating filters consisting of plasticine blocks
209 were placed on the top halves of X-ray collimators to reduce exposure above the substrate
210 surface.

211 Four configurations of the trackway were used to conduct experiments on four different
212 substrates. In one setup, a rigid carbon fiber platform (70 x 30.5 x 2.7 cm³) was placed on top of
213 the diamond-shaped recess, and 2.5 cm thick EPS panels (~2.4 x 1.2 m²) were placed along the
214 remainder of the trackway such that its surface was flush and level. In the remaining three, a
215 square foam container (30 x 30 x 14.5 cm³, with 3 cm walls) was placed within the diamond-

216 shaped recess and filled with 11.5 cm of a deformable substrate¹⁶. Triangular foam wedges were
217 placed within the medial and lateral corners of the three containers (to reduce the amount of
218 substrate in order to improve the clarity of X-ray videos) reducing their widths to 22 cm
219 (maximum length was ~34 cm). The deformable substrates that filled the containers included a
220 24:5:9 volumetric ratio of 60 micron glass bubbles (Type K15, 3M Co., St. Paul, MN, USA),
221 modeling clay, and water, which was then mixed with a roughly equal volume of acrylic blast
222 media (Type V, 0.42-0.56 mm diameter, Kramer Industries, Piscataway, NJ, USA). The bottom-
223 most 6.5 cm of the foam containers were filled with this mixture plus EPS foam pellets 2-4 mm
224 in diameter (LACrafts, Commerce, CA, USA), which enhanced radiolucency while maintaining
225 relatively consistent bulk material properties. That combination was packed using a rubber
226 mallet to provide a 6.5 cm deep stable base. Three to four 3 mm diameter lead shot were placed
227 slightly below the surface of this stable base, in order to spatially register substrate volumes
228 during subsequent 3-D animation and analyses. Upon this base, the remaining 5 cm of the
229 deformable substrate varied across the three containers. In the first, called the “firm” condition,
230 the remaining 5 cm was filled with substrate and also packed using a rubber mallet. The
231 remainder of the trackway was covered with rigid, closed-cell EPS panels, as in the carbon fiber
232 condition. In the second variant, an additional 2.5 cm of the “firm” mud variant was added atop
233 the firm base. Additional water was added to the substrate, and this hydrated version was used to
234 fill the uppermost 2.5 cm of the foam container. This variant was called “hydrated 2.5 mud”¹⁶ or
235 “wet 2.5 mud” (Fig. 1H). When this substrate was in place, the remainder of the trackway was
236 made flush and level by covering it with 2.5 cm thick panels of soft, deformable upholstery
237 foam. In the third deformable substrate condition, the most superficial 5 cm of the foam
238 container was filled entirely with the hydrated substrate described immediately above. This was
239 termed “hydrated 5 mud”¹⁶ or “wet 5 mud” (Fig. 1H). When this was used, the rest of the

240 trackway was made flush and level by covering with 5 cm thick panels of soft, deformable
241 upholstery foam. For each of the three deformable substrate variants, a set of three or four 3 mm
242 diameter lead pellets were also placed on the substrate's surface, visible to both the biplanar X-
243 ray cameras and the 3-D scanner (see below) such that a 3-D model of the track produced in the
244 substrate could be accurately registered to the scene during 3-D animation.

245

246 *Biplanar X-ray experimental protocol*

247 Four adult subjects were recruited to participate in these experiments, and all provided
248 their informed consent following protocols approved by the Institutional Review Boards of
249 Brown University and Chatham University. A marker was used to draw an array of 85 dots
250 across each subject's right foot. Marker dots were placed at anatomical locations of interest (e.g.,
251 metatarsal heads, navicular tuberosity) but also at intermediate positions to provide roughly
252 uniform coverage across the plantar surface and onto the sides of the foot, as well as on the tops
253 of toes. A handheld structured light scanner (Creaform Go!SCAN 50, Creaform, Lévis, Québec,
254 Canada) was used to collect a 3-D scan of each subject's marked foot. Following 3-D scanning,
255 85 radiopaque beads (SureMark, Simi Valley, CA, USA) were placed at each of the marker dots
256 and secured using medical adhesive (SkinTacTM, Torbot, Cranston, RI, USA). Beads are
257 sufficiently small that subjects reported limited ability to sense their presence, particularly while
258 walking on deformable substrates, and they reported no discernible influences on their normal
259 foot function. Once beads were secured, subjects walked along the experimental trackway
260 several times until they felt comfortable moving across it.

261 Each subject completed a minimum of 13 trials. In the first, they stood still with their feet
262 slightly staggered (right in front of left) and their right foot within the biplanar X-ray view. A
263 single pair of X-ray images was captured of their marked foot. Subjects then completed at least

264 three trials walking across each of four substrate variants at a self-selected, comfortable walking
265 speed. If their foot missed the biplanar X-ray camera, they were asked to repeat the trial. After
266 walking through a deformable substrate, the track that a subject left behind was immediately 3-D
267 scanned. Most scans were captured with the handheld structured light scanner and processed
268 using Creaform VXElements software (Creaform, Lévis, Québec, Canada). However, for some
269 trials (nine), the software was still processing the previous track model and photogrammetry was
270 used instead so as to not delay the experiment. Photographs were taken using a Canon 5D Mark
271 III 22.3-Megapixel camera outfitted with a 50 mm prime lens (Canon, Melville, NY, USA) and
272 processed using Agisoft Metashape Professional (v.1.6.4, Agisoft LLC, St. Petersburg, Russia).
273 Both techniques produced 3-D models of tracks with sub-millimeter resolution. After a track had
274 been scanned, the surface beads were removed, the substrate was leveled using a trowel, and then
275 the surface beads were again placed on the surface of the substrate.

276 An additional four adult subjects completed trials with a slightly different protocol in a
277 subsequent year. This protocol was also approved by the Institutional Review Boards of Brown
278 University and Chatham University. Subjects in this later set of experiments also produced tracks
279 while walking at self-selected comfortable speeds through the same substrates, and so
280 measurements of RAV from their tracks are included to increase the sample of human
281 observations in Fig. 4.

282

283 *3-D animation of biplanar X-ray experiments*

284 Experimental data were animated following the procedures of Hatala et al.¹⁶, which were
285 themselves adapted from protocols for X-ray Reconstruction of Moving Morphology
286 (XROMM)³⁷. XMALab software (v.1.5.5)³⁸ was used to undistort and calibrate biplanar X-ray
287 videos, and then to compute the 3-D trajectories of the radiopaque beads on each subject's foot,

288 and on and within the substrate. These 3-D motion data were unfiltered, as they were not placed
289 on rigid bodies (both feet and substrates deformed dynamically) and filtering algorithms were
290 therefore more likely to introduce rather than reduce noise or error. Instead, XMA Lab's
291 polynomial fitting procedure was used to improve sub-pixel tracking accuracy, and this should
292 have the desired effect of minimizing potential noise/error in 3-D bead positions (B. Knörlein,
293 personal communication).

294 The 3-D scans of subjects' feet were exported in .obj format from VXElements software
295 and subsequently imported into Autodesk Maya 2020. The foot models were retopologized from
296 about 73,000-97,000 triangles to 5000 quads, in order to improve computation speeds without
297 sacrificing geometric detail. The radiopaque foot beads, and their 3-D trajectories, were imported
298 as virtual spheres using XROMM MayaTools (v.2.2.3)³⁹. The positions of beads on the 3-D foot
299 model were directly linked to the positions of imported spheres, and inter-connected to construct
300 a low-resolution proxy of the foot. The foot model was then linked to the low-resolution proxy
301 using Maya's wrap deformer tool, and this allowed the high-resolution 3-D foot model to
302 accurately move and deform in concert with the tracked 3-D trajectories of the radiopaque beads.
303 For trials on deformable substrates, the radiopaque substrate beads were also imported as virtual
304 spheres using XROMM MayaTools. The 3-D scans of tracks were imported in .obj format and
305 manually registered to the scene by matching the positions of surface beads on the track model to
306 their tracked 3-D positions.

307 Within Autodesk Maya, foot trajectories could be directly compared with track positions,
308 and used to formulate hypotheses for track arch creation. Within Maya, 3-D models of the foot's
309 volumetric sweep through the substrate were generated by using the "Create animation snapshot"
310 tool and combining the frame-by-frame foot poses into a composite mesh (Supplementary Note
311 2; Extended Data Fig. 2).

312 Marker displacement vectors (Fig. 3C) were visualized in Maya using custom Bifrost
313 Graph compounds. Within an animated sequence, the skin marker positions (acquired from the
314 vertices of the low-resolution foot mesh) from the current frame were subtracted from those of
315 the subsequent frame to calculate 3-D displacement vectors. Vectors were rendered as strands;
316 strand magnitudes were scaled up 20X to improve visibility and were colored based on their
317 vertical component (red up, blue down). The foot's sagittal pivot was identified in Maya by
318 averaging the coordinates of the subset of sole markers (57; toes excluded) that moved vertically
319 less than 0.2 mm between the current and subsequent frame. Thresholds of 0.1, 0.3, 0.4, and 0.5
320 mm showed nearly identical pivot placements and all shared the forward translation pattern.

321

322 *Particle simulation and track ontogeny*

323 To explore the mechanistic origins of track morphology via track ontogeny¹⁴⁻¹⁶, particle
324 simulations were conducted based on the discrete element method using LIGGGHTS⁴⁰
325 (Supplementary Video 1; Supplementary Video 2). A virtual tray measuring 21 x 35 x 8 cm³ was
326 created in Maya and registered to the same position as the volume of substrate that the foot
327 traversed during the biplanar X-ray experiment. The virtual tray was filled with ~800,000 virtual
328 particles, each measuring 2 mm in diameter. Particle properties (Young's modulus, Poisson ratio,
329 cohesion, and friction) were adjusted until macroscopic bulk behavior of the substrate was
330 similar to the substrate used in biplanar X-ray experiments.

331 Animations of 3-D foot motions were exported from Autodesk Maya and brought into the
332 virtual simulation environment of LIGGGHTS. The simulated feet deform to reproduce the
333 deforming external geometry of the foot, as reconstructed from the biplanar X-ray experimental
334 data (see also ¹⁶). Mesh and vertex positions were interpolated to increase temporal resolution of
335 the foot's motion to 1000 fps, in order to mitigate artificially rapid foot and substrate translations

336 and deformations that would occur if simulations were processed at the same 50 fps speed that
337 was used in experimental recording. Simulation data were visualized using OVITO (v.3.0.0)⁴¹.

338

339 *Quantifying foot and track arch volumes*

340 A new tool for quantitative, 3-D volumetric measurement of arch height from both feet
341 and tracks was also developed in Maya. Foot and/or track 3-D models were imported, and virtual
342 points were placed at the approximate positions of the first and fifth metatarsophalangeal joints,
343 and centrally beneath the heel (Fig. 1E). These points defined the inferior corners of a right
344 triangular prism, whose height was adjusted such that it extended above the track surface, or the
345 foot's plantar surface. A Boolean intersection was used to extract a 3-D model of the volume that
346 was enclosed by the prism and the track (Fig. 1F) or foot (Fig. 1G).

347 'Relative arch volume' (RAV) was calculated as 100 times the cube root of either
348 Boolean arch model's volume divided by the square root of the prism base's area.

$$349 \quad RAV = 100 * (\sqrt[3]{\text{arch volume}} \div \sqrt{\text{prism base area}})$$

350 Standardization by area permits the comparison of longitudinal arch volumes across
351 tracks that differ in absolute size. This is necessary for comparing similarly shaped tracks that
352 differ in length, such as those from Laetoli and those from modern humans. The longitudinal
353 arches of tracks that differ in width can also be compared, including those that differ in their
354 degrees of hallucial abduction (e.g., the chimpanzee tracks compared with hominin tracks in Fig.
355 4A).

356 To evaluate this measurement tool we also assessed interobserver variation. Two
357 observers (K.G.H. and P.L.F.) independently placed landmarks and measured RAVs from 37
358 track and four foot models. Paired t-tests (using R v.4.1.0)⁴² showed that across this sample,
359 measurements of RAV were not significantly different between the two observers ($t = -1.48$, $p =$

360 0.15; Extended Data Fig. 5). The average interobserver difference was 0.42, with a 95%
361 confidence interval of -1.00 to 0.15. In other words, the average difference between observers is
362 approximately 1% or less of the RAVs that we measured for human experimental tracks (Fig.
363 4A).

364

365 *Additional track arch variables*

366 The track arch axis was a line segment spanning from the heel landmark to the midpoint
367 between metatarsophalangeal landmarks (Fig. 1E). We aligned each track 3-D model such that
368 the surrounding, undisturbed substrate corresponded to the X-Y plane in 3-D space. Absolute
369 depth of each track was measured at the midpoint of its arch axis, and we defined ‘relative depth’
370 as the absolute depth of the midpoint of the track arch axis divided by the length of its arch axis.

371 ‘Pitch’ was defined as the minimum 3-D angle of the track arch axis with respect to
372 horizontal. A track with a positive pitch has the heel landmark deeper than the
373 metatarsophalangeal midpoint (nose up). A track with negative pitch has the metatarsophalangeal
374 midpoint deeper than the heel landmark (nose down). A horizontal track arch axis has a pitch of
375 0°.

376

377 *Modern and fossil track analyses*

378 Samples of Laetoli, Ileret, and Walvis Bay fossil tracks, and habitually barefoot human
379 and chimpanzee experimental tracks, were all measured using the same arch quantification tool
380 that was developed here in Autodesk Maya. Track models were imported to Maya in .obj format,
381 and subsequently measured using the procedures described above. Tracks were excluded from
382 fossil samples if erosional damage, over-printing, or taphonomic effects were evident in the 3-D
383 model and prevented arch measurement.

384 Our experimental results (Fig. 1H) and others²² have demonstrated that track arch
385 morphology is influenced by track depth. Fossil tracks and other experimental tracks were
386 included in comparative plots as long as their absolute depths (defined above) were within two
387 standard deviations of the mean absolute depth observed in deep mud tracks from our human
388 biplanar X-ray experiments (“wet 2.5” and “wet 5” conditions).

389 First-generation casts of the Laetoli G1 tracks (n = 11) housed at the National Museums
390 of Kenya were previously digitized by K.G.H. using photogrammetry¹⁰. Laetoli S1 (n = 2) and A
391 tracks (n = 1) were freely available via Morphosource (www.morphosource.org)^{20,23}. Ileret tracks
392 (n = 11 from 5 trackways; reduced to n = 4 from 3 trackways after filtering by depth) were also
393 digitized by K.G.H. using photogrammetry, with photographs taken immediately following their
394 excavation²¹. Models of Walvis Bay tracks were made freely available online by Professor
395 Matthew Bennett through NERC grant NE/HOO4211/1 (<http://footprints.bournemouth.ac.uk/>)
396 and are described in detail by Morse and colleagues²². From this site we focused on the tracks
397 from “Trail One” and “Trail Two”, as these sampled a broad range of substrate conditions
398 encompassing the range of track depths observed in our biplanar X-ray experiments (n₁ = 19 and
399 n₂ = 13; reduced to n₁ = 13 and n₂ = 11 after filtering by depth). Tracks produced by habitually
400 unshod humans were collected by K.G.H. in a previous study¹⁷. Briefly, these experiments
401 involved people making tracks while walking at a variety of speeds through hydrated mud, made
402 from the same sediments in which fossil tracks at Ileret are preserved. A subset of those tracks,
403 produced by people walking at comfortable, self-selected walking speeds, were included here for
404 comparison (n = 69 tracks from 24 subjects; reduced to n = 36 tracks from 17 subjects after
405 filtering by depth). Bipedal chimpanzee tracks were also collected by K.G.H. in a previous
406 study¹⁰ (n₁ = 24 and n₂ = 21; n₁ = 22, n₂ = 21 after filtering by depth).

407 Plots to compare experimental and fossil tracks were generated using R v.4.1.0⁴²,
408 including the dplyr and ggplot2 packages^{43,44}.

409

410 **Data and code availability:**

411 Source data and code used to generate the figures in this manuscript are publicly
412 available at the following address: <https://doi.org/10.6084/m9.figshare.20736697>. Raw data from
413 biplanar X-ray experiments are publicly available through the XMAPortal at the following link:
414 <https://xmaportal.org/webportal/larequest.php?request=CollectionView&StudyID=43&instit=BR>
415 [OWN&collectionID=20](https://xmaportal.org/webportal/larequest.php?request=CollectionView&StudyID=43&instit=BR).

416 Correspondence and requests for additional materials should be addressed to K.G.H.
417 (kevin.g.hatala@gmail.com).

418

419 **Acknowledgements:**

420 We thank David Baier, Beth Brainerd, Spencer Cheleden, Fritz Drury, Kay Fiske, Kia
421 Huffman, Ben Knörlein, David Laidlaw, Kyra Tani Little, Sabreen Megherhi, Johannes
422 Novotny, David North, Morgan Turner, and the students of CS137 for assistance directly related
423 to the design and implementation of this project, and we thank the anonymous volunteers who
424 participated in biplanar X-ray experiments. We are grateful to Armita Manafzadeh for feedback
425 at many stages of analysis. Discrete Element simulations were made possible through a PRACE
426 allocation of supercomputer resources (project 2021250007, Irene-Rome). This study received
427 funding support from the National Science Foundation (BCS-1825403 to K.G.H. and P.L.F.;
428 BCS-1824821 to S.M.G.) and from the Chatham University Research & Sabbatical Committee
429 (to K.G.H.).

430

431 **Author contributions:**

432 All authors participated in the conceptualization, planning, and administration of this
433 project. K.G.H. and S.M.G. carried out biplanar X-ray experiments with input from P.L.F. P.L.F.
434 carried out discrete element simulations with input from K.G.H. and S.M.G. All authors
435 participated in analyzing the data, and in writing and editing the manuscript.

436

437 **Competing interests:**

438 The authors declare no competing interests.

439

440 **Figure legends/captions:**

441 **Fig. 1. Arched hominin tracks in soft substrates do not faithfully record the feet that made**
442 **them.** Hominin tracks from Laetoli (A), Ileret (B), and our most- (C) and least-arched (D)
443 experimental subjects all appear longitudinally arched. (E) To quantify arch volumes, three
444 landmarks (aqua spheres) define a triangular prism. (F) The intersection between track model
445 (gray) and prism (yellow) yields a track arch model (red). (G) A comparable foot arch model
446 (blue) can be derived from anatomical landmarks. Relative arch volume (RAV) is calculated
447 from each arch model's volume and prism base area. (H) Foot (blue) and track (red) RAV for
448 four subjects' (four symbols) trials under five loading conditions (total n = 85). Compared to an
449 unloaded state, mid-stance foot RAV was significantly reduced when walking across all four
450 substrates. Track RAV varied with substrate deformability, from less than mid-stance foot RAV

451 on 'firm' ground to almost doubling mid-stance foot RAV in the deepest wet mud. Asterisks
452 indicate observations also shown in panels C, D, and G.

453

454 **Fig. 2. DEM simulations of arched track ontogeny.** Simulations for a relatively high-arched
455 (A) and low-arched (B) subject on wet 5 mud. Top views of simulated tracks and longitudinal
456 sections through 3-D animated foot models (black/gray outlines) and substrate (colored particles)
457 are shown at five instances during the stance phase of walking on wet 5 mud. Dashed lines show
458 the longitudinal section planes. (C and D) Dynamic RAVs for the feet (blue) and simulated
459 tracks (red) diverge in mid-late stance. Despite different foot arch anatomies, both subjects form
460 highly arched tracks.

461

462 **Fig. 3. Arched tracks arise from human foot kinematics.** (A) Data from rigid instruments,
463 such as pressure pads or force plates, document translation of the foot's center of pressure (CoP)
464 from heel to toe during a step. (B) CoP translation is thought to increase the effective length of
465 the limb pendulum (photo credit: K.G.H.). (C) Frame-frame displacements of 85 skin markers
466 reveal a similar anterior translation of the pivot between the descending (blue vectors) and
467 ascending (red vectors) portions of the foot through time. Vectors magnified 20X in all but the
468 first pose (2X). (D) Similar displacement coloration of simulated mud documents synchrony
469 between translation of the sole's pivot and ontogeny of the track's arch. (E) Applying an
470 advancing pivot kinematic pattern to a rigid flat-sided block (gray) in DEM-simulated mud
471 produces a longitudinally arched track.

472

473 **Fig. 4. Fossil RAV and implications for heel-toe kinematic pattern.** (A) Fossil human tracks
474 from Namibia (gray circles) and tracks from prior human experiments (open circles) closely

475 match the RAV-depth relationship observed in our experiments (black circles = original data;
476 black line and gray outline = logarithmic fit of experimental track RAV vs. relative depth, with
477 95% confidence interval around conditional mean; slope = 10.54, intercept = 69.21, F-statistic =
478 114.9, $p = 1.14 * 10^{-14}$, adjusted $R^2 = 0.69$). Relative depth (x-axis) is depth measured at the
479 midpoint of the track arch model's longitudinal axis, divided by the length of that axis. RAVs of
480 Ileret tracks (orange squares) fall within the range expected from similarly deep human tracks.
481 Laetoli G1 (dark blue triangles) and S1 tracks (light blue triangles) have lower RAV than
482 similarly deep human tracks, while Laetoli A (green triangles) is still lower than those.
483 Chimpanzee tracks (pink diamonds) are highly variable, but show lower RAV than human
484 tracks. **(B)** As human tracks get deeper, they are typically either minimally pitched or negatively
485 pitched. The Laetoli tracks diverge from this pattern and are positively pitched. One Ileret track
486 is very negatively pitched, a pattern that has been observed in other fossil and modern human
487 tracks in very deep mud²². Color and symbol scheme same as above.

488

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