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6 **It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light**
7 **on a new dimension of fossil track diversity**

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22

23 **Abstract**

24 The feet of ground-dwelling birds retain many features of their dinosaurian ancestry.
25 Experiments with living species offer insights into the complex interplay among anatomy,
26 kinematics, and substrate during the formation of Mesozoic footprints. However, a key aspect of
27 the track-making process, sub-surface foot movement, is hindered by substrate opacity. Here, we
28 use biplanar X-rays to image guineafowl walking through radiolucent substrates of different
29 consistency (solid, dry granular, firm to semi-liquid muds). Despite substantial kinematic
30 variation, the foot consistently moves in a looping pattern below ground. As the foot sinks and
31 then withdraws, the claws of the three main toes create entry and exit paths in different locations.
32 Sampling these paths at incremental horizons captures 2-D features just as fossil tracks do,
33 allowing depth-based zones to be characterized by the presence and relative position of digit
34 impressions. Examination of deep, penetrative tracks from the Early Jurassic confirms that
35 bipeds had an equivalent looping response to soft substrates ~200 million years ago. Our
36 integration of extant and extinct evidence demonstrates the influence of substrate properties on
37 sinking depth and sub-surface foot motion, both of which are significant sources of track
38 variation in the fossil record of dinosaurs.

39

40 **1. Introduction**

41 Fossil dinosaur tracks preserve unique evidence of locomotion in long-extinct species [1-
42 4]. Rather than being perfect molds of static feet, track morphologies arise through the dynamic
43 interplay of pedal anatomy, step kinematics, and substrate properties [5-10]. Ground-dwelling
44 birds have proven to be excellent models for experimentally studying these interactions [11-19].
45 The functionally three-toed feet of many species closely resemble those of bipedal, non-avian

46 dinosaurs [20-21], allowing the visible movements responsible for shallow tracks to be studied
47 directly.

48 With each step, a dinosaur deformed not only the exposed air-sediment boundary, but a
49 volume of substrate beneath [7,17,22-25]. Layered sediments, once lithified, can develop planes
50 of weakness at multiple potential track surfaces below the originally exposed horizon
51 [7,17,22,26-28]. In species with relatively narrow toes (theropods and small ornithopods),
52 compliant substrates can flow around and over the foot, leaving only furrow-like seams marking
53 its deep passage [14,27-32]. Such ‘penetrative tracks’ offer an excellent source of functional
54 information [14,33-36], capturing foot movements throughout the track volume. Yet tracks on
55 bedding planes sampled from within these depths can differ substantially [17,34,37-38], both
56 from each other and from the foot that made them.

57 Herein, we quantify the three-dimensional (3-D) foot movements of a chicken-like bird
58 (guineafowl) walking through a spectrum of deformable substrates. Following earlier studies of
59 burrowing [39-45] and stepping [17,46-48], we use X-ray imaging to see through opaque ground.
60 We emulate potential fossil track surfaces within each track volume by sampling guineafowl
61 movement data at depth intervals, thereby identifying common patterns among the highly
62 variable toe trajectories. Using this new perspective, we re-examine morphological variation
63 among the classic Early Jurassic tracks of the Connecticut Valley [37-38,49-57] and discern
64 previously unrecognized similarities with modern birds.

65

66 **2. Material and Methods**

67 *(a) Animals, substrates, and recording*

68 Biplanar X-ray data were collected from three adult Helmeted Guineafowl (*Numida*
69 *meleagris*). All live animal experiments were conducted in accordance with the Institutional
70 Animal Care and Use Committee of Brown University.

71 Dry and cohesive substrates were contained in a plastic trough filled to a depth of ~18 cm
72 to form a trackway, which was enclosed by a clear acrylic tunnel. In lieu of sand, we used poppy
73 seeds (*Papaver somniferum*) [17,58]. Artificial mud [10] was mixed from ~60 μ m glass bubbles,
74 ball clay, and water. Mud consistency was adjusted from very firm to semi-liquid by evaporating
75 or adding water. For comparison, birds also walked across a stiff, non-deformable trackway.

76 Walking guinea fowl were recorded at 250 fps by two X-ray and two standard light
77 cameras (Fig. 1a, b), along with images for camera calibration and X-ray undistortion. One bird
78 had ~2 mm disc-shaped lead markers fixed with cyanoacrylate beneath each claw (Fig. 1b).

79

80 *(b) Point tracking, animation, and depth sampling*

81 3-D toe coordinates for the marked individual were extracted in XMALab [59-60]. and
82 animated in Maya 2020 (Autodesk Inc., San Rafael, CA, USA). For the unmarked birds, point
83 rotoscoping [47] was done in Maya using virtual camera calibrations and undistorted video from
84 XMALab. 58 trials of birds walking on deformable substrates were analyzed, yielding 81
85 subsurface steps (Table 1). CT-based bone models were animated for several trials using a
86 combination of marker-based X-ray Reconstruction of Moving Morphology [61] and Scientific
87 Rotoscoping [59].

individual	tracking method	number of trials analyzed				number of complete steps analyzed			
		solid	dry granular	muds	total	solid	dry granular	muds	total
6	rotoscopy	6	2	16	24	10	4	22	36
7	marker-based	5	12	17	34	8	16	23	47
8	rotoscopy	5	11	0	16	8	16	0	24
		16	25	33	74	26	36	45	107

88

89 **Table 1.** Overview of analyzed guineafowl data.

90

91 The paths of the three main toes (II-IV) were visualized in Maya by connecting their claw
92 locations at each frame into motion trails (Fig. 1c). Substrate contact for digit III was identified
93 from standard video, thereby setting the initial height of the substrate surface. To sample sub-
94 surface motion trails in the vertical dimension (equivalent to bedding planes spanning the track
95 volume), we extracted the coordinates at which each claw passed down (entry) or up (exit)
96 through depth horizons set at 5 mm increments. At each increment, the 2-D horizontal position
97 of the claws were used to calculate three variables: ‘digit III offset,’ defined as the difference in
98 entry and exit of the middle toe, measured along the direction of travel; ‘digit II-IV width,’
99 measured as the distance between the side toes, for both entry and exit pairs; and, “digit
100 representation,” simply the presence or absence of each toe at each increment. Sample horizons
101 and variable graphs were plotted in R [62].

102

103 *(e) Fossil specimens*

104 All fossil specimens included in this study are housed in the Beneski Museum of Natural
105 History at Amherst College, Amherst, MA, USA and designated ACM-ICH.

106

107 For more information, see Supplemental information.

108

109 **2. Results**

110 *(a) Guineafowl sub-surface foot kinematics*

111 Across trials, guineafowl slowed down, sped up, and paused frequently. Such non-steady
112 locomotion provided a broad sampling of kinematic variation from the three individuals. Normal
113 striding steps were by far the most common, although a few trials included non-alternation.

114 Guineafowl sank to a wide range of depths (1.15 – 13.13 cm), penetrating deepest in semi-liquid
115 muds.

116 As characterized by the paths of the three main toes, sinking and withdrawal exhibited
117 consistent patterns. A lateral view of digit III, which forms the central axis of the tridactyl foot, is
118 exemplary. Unlike its V-shaped path above solid surfaces, digit III always followed a loop below
119 ground (Fig. 1d). Plotting digit III offset (Fig. 1e) reveals a consistent relationship between entry
120 and exit, despite step by step variation in angle of entry, specific loop shape, and maximum
121 depth. Digit III's arc-like withdrawal typically crossed from behind entry (negative) to in front of
122 entry (positive) prior to removal. As the foot sank, digits II and IV remained widely spread until
123 they reached their maximum depth. Upon withdrawal, the side toes collapsed towards digit III
124 throughout their arcing ascent (Fig. 1f, g). The combination of anterior-posterior looping and
125 transverse collapse indicates that the three main claws crossed through all horizons above their
126 maximum depth twice, but in different locations (Fig. 1h). Such dissimilar entry and exit paths
127 were found on all deformable substrates.

128

129 *(b) Depth zones and fossil tracks*

130 The common sub-surface motion pattern among guineafowl steps allows depth-based
 131 zones to be characterized by digit representation, digit III offset, and digit exit conformation,
 132 (Fig. 1h, Table 2). In Zone 1 (Fig. 1h, 0-1 cm), the adducted claws exit in front of their entry,
 133 often moving horizontally. In Zones 2 and 3, digit III offset is negative (Fig. 1h, 3-13 cm). All
 134 three toes are tightly converged when passing back up through Zone 2, but exit separately in
 135 Zone 3. The deepest zone can be further subdivided by the number of main toes represented: all
 136 three (3a), only two (3b), or just digit III (3a).

137 Using guineafowl sub-surface kinematics as a reference, we are now able to confirm the
 138 presence of comparable looping and depth zones in fossil penetrative tracks from Lower Jurassic
 139 strata of the Connecticut Valley (Fig. 2). Single slabs exposing penetrative tracks on both
 140 surfaces (Fig. 2b, c) support depth-based predictions of digit representation, anterior-posterior
 141 digit III offset, and digit exit conformation. Such patterns are particularly well-displayed when
 142 track volumes are split into multi-slabs. A five-slab specimen exposing track surfaces across
 143 Zones 2 and 3 preserves not only evidence of looping, but also allows specific details of digit III
 144 loop expansion and contraction to be distinguished (Fig. 2d).

145

Zone	digit representation	digit III offset	digit exit conformation
1	II - IV	exit in front	three converged
2	II - IV	exit behind	three converged
3a	II - IV	exit behind	three separate
3b	II + III or III + IV	exit behind	two separate
3c	III	exit behind	single

146

147 **Table 2.** Summary of depth zones.

148

149 **Discussion**

150 *(a) Impact on track diversity and interpretation*

151 Documentation of sub-surface looping in guineafowl walking through a wide variety of
152 substrates offers a new perspective on the tracks of extinct bipeds. If dinosaurs responded to
153 deformable ground similarly, we expected that the claws of the three main toes would have
154 likewise passed through most surfaces twice—once going down and once coming back up—in
155 different locations. Treatments of the Early Jurassic fauna of the Connecticut Valley [37-38,49-
156 51,56,63-64] do not recognize any evidence of withdrawal. Yet armed with an improved search
157 image, we have identified distinctly separate entry and exit features in hundreds of fossil
158 footprints (sampled in Fig 2). Once penetrative tracks are understood as slices through a
159 disturbed volume of sediment, their true nature becomes apparent. Such surfaces do not represent
160 anatomy per se, but rather the collapsed seams left behind by toes punching, slashing, scraping,
161 and ascending into and out of each potential track horizon on their looping paths.

162 A shared kinematic response to deformable substrates does not, however, mean that
163 movements were tightly stereotyped. X-ray imaging allows us to measure guineafowl inter-step
164 variation directly (Fig. 1e, g). In extinct dinosaur tracks, such kinematic variation must be
165 inferred from its morphological consequences. For example, Connecticut Valley tracks
166 assignable to Zone 2 reveal a wide range of loop-related disparity (Fig. 2e). Some preserve toe
167 withdrawal back up through the entry furrow of digit III (Zone 2, left), others near the confluence
168 of the digital furrows (Zone 2, middle), and yet others at the very rear of the track (Zone 2,
169 right). Workers have attributed such a diverse array of shapes to multiple taxonomic groups
170 (lizards, thin-toed birds, reptiles of uncertain affinity, and vertebrates of unknown class [38,50]).
171 Yet despite their distinctive forms and deviation from known dinosaurian pedal anatomies, we

172 propose that this diversity of penetrative tracks could all have been created by small theropods
173 and/or ornithopods.

174

175 *(b) Foot function in birds and other dinosaurs*

176 Evidence of sub-surface looping in ~200 million-year-old fossils supports the hypothesis
177 of functional continuity among tridactyl feet of birds and other bipedal dinosaurs when walking
178 through deformable substrates. Although sub-surface looping has been previously reported in
179 several dinosaur tracks [65-67], loops are ubiquitous and often of substantial magnitude in these
180 Early Jurassic penetrative specimens. Our kinematic perspective offers a fresh viewpoint on
181 depth-based track variation. Rather than being incomplete molds beneath the surface [38,68],
182 substrate-modulated foot motion is intimately accountable for these disparate tracks. Perhaps the
183 enduring success of the dinosaurian tridactyl foot design can be attributed, at least in part, to its
184 ability to provide a stable base when spread, yet collapse to facilitate extraction from deformable
185 substrates.

186

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198

199

200

201 **Figure Legends**

202 **Figure 1.** Sub-surface foot kinematics through a volume of substrate. Synchronized standard (a)
203 and X-ray (b) video frames of a guineafowl walking through a dry granular substrate. Toes and
204 markers are clearly revealed sub-surface (inset). c) Oblique view of digit claw marker motion
205 trails for one step through dry grains. d) Lateral view of a sample of digit III motion trails on
206 several deformable substrates (colored lines; thin = entry, bold = exit) and one solid substrate
207 (black line). Digit III offset (e) measured at 5 mm depth horizons (horizontal lines), are plotted
208 for 81 steps from all three individuals. f) Anterior view of claw motion trails showing the toes
209 widely spread when sinking (thin), and smoothly collapsing upon withdrawal (bold). g) Digit II-
210 IV width are plotted from 49 steps of two individuals (equal scales in d-g). h) Selected horizons
211 for the green step (d-g) showing changing locations of claw entry (filled circles) and exit (open
212 circles). The looping entry (thin) and exit (bold) path of digit III is indicated by a dashed line.
213 Division of this track volume into zones (gray bars). Vertical and horizontal scales in (d-g)
214 shown by axes in (e). Tick marks in (h) equal 1 cm. For foot animations, see supplemental video.

215

216

217 **Figure 2.** Exit features and depth zone attribution in Early Jurassic fossil tracks. a) Digit tip
218 impression identification on entry (small circles) and exit (large circle) on one surface of ACM-
219 ICH 37/24. b) A penetrated slab (ACM-ICH 39/8) from high in the volume reveals three
220 elongate Zone 1 tracks on its upper surface and furrowed, Zone 2 tracks on its lower surface
221 (mirrored). c) A penetrated slab (ACM-ICH 31/50) from low in the volume reveals a scrape-like,
222 Zone 3a track with separate exits on its upper surface; only digit III reached its lower, Zone 3c
223 surface (mirrored). d) A five-slab specimen (ACM-ICH 34/33) preserves the down and forward

224 penetration of the foot, followed by its looping withdrawal. Note changes in track morphology
225 with depth. Dashed line indicates the entry (thin) and exit (bold) paths of digit III. e) Tracings of
226 19 Early Jurassic track surfaces displaying inter- and intra-zone diversity (ACM-ICH specimen
227 numbers shown below). Exit features (black arrows) vary widely in location along the lengths of
228 the tracks (see Fig. S1 for specimen photos and entry/exit overlays). Scale bars equal 5 cm.

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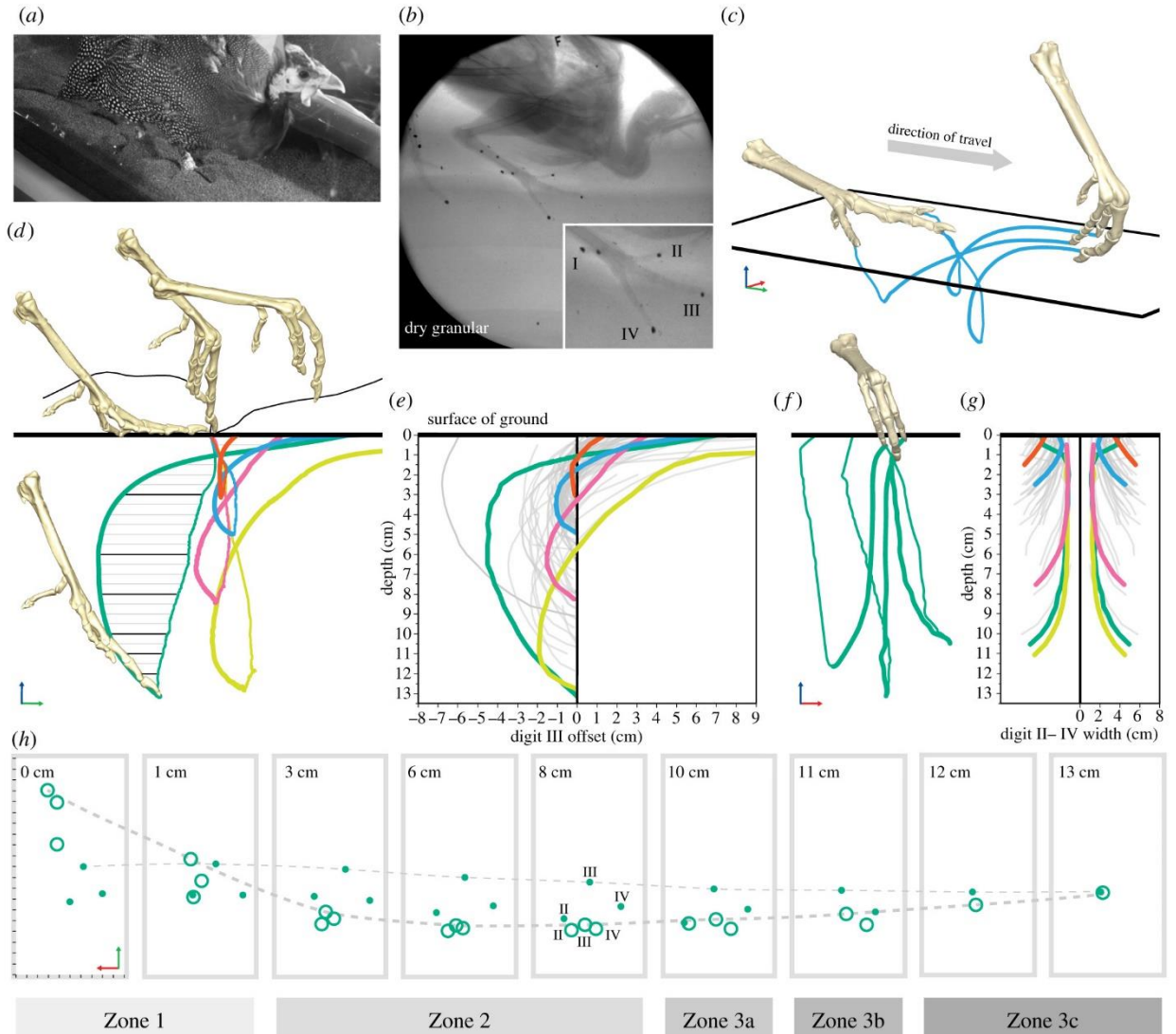
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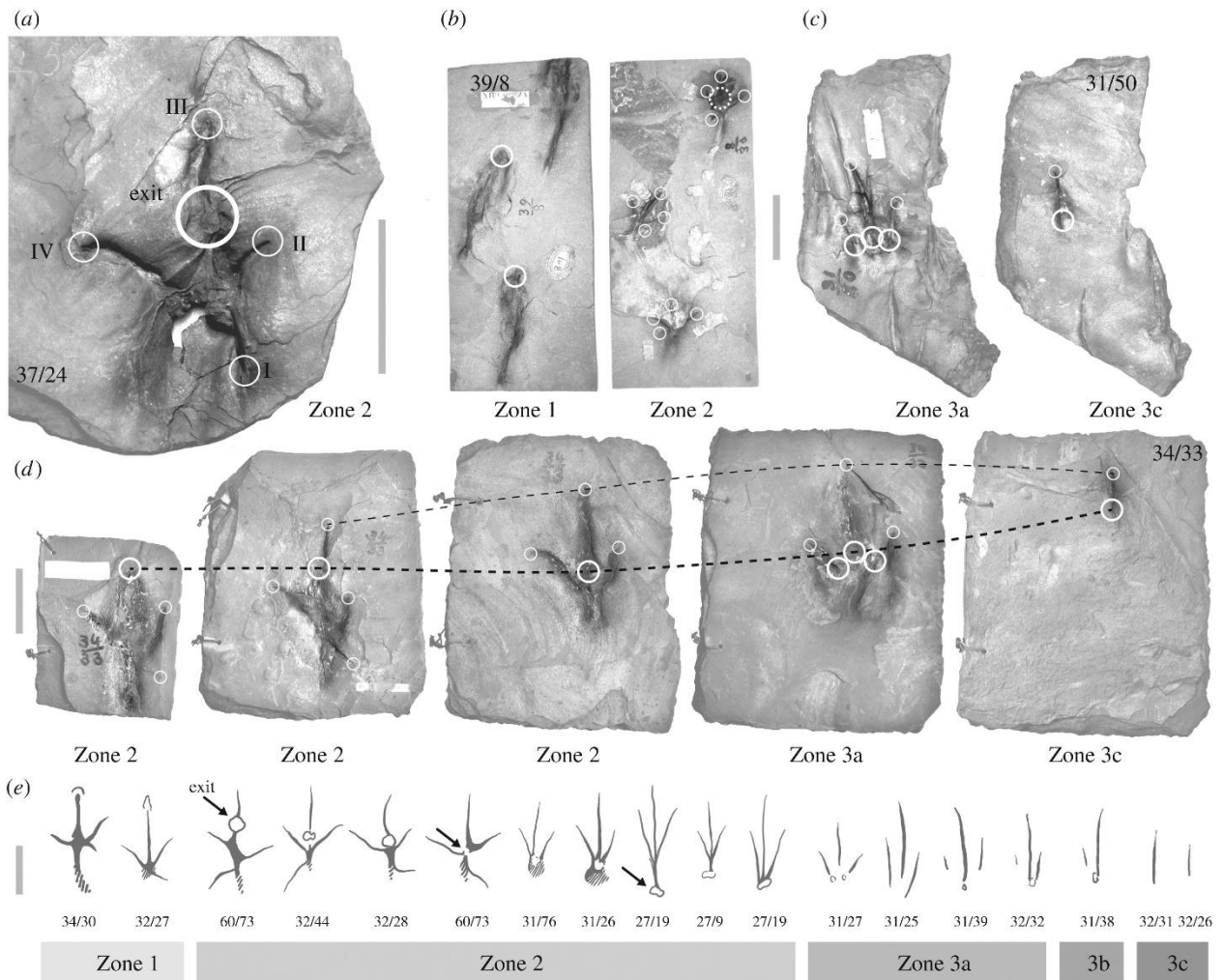
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400 *Figure 1. Sub-surface foot kinematics through a volume of substrate. Synchronized standard (a) and X-ray (b) video*
 401 *frames of a guineafowl walking through a dry granular substrate. Toes and markers are clearly revealed sub-surface*
 402 *(inset). (c) Oblique view of digit claw marker motion trails for one step through dry grains. (d) Lateral view of a sample*
 403 *of digit III motion trails on several deformable substrates (coloured lines; thin = entry, bold = exit) and one solid*
 404 *substrate (black line). Digit III offset (e) measured at 5 mm depth horizons (horizontal lines in (d)) and are plotted for*
 405 *81 steps from all three individuals. (f) Anterior view of claw motion trails showing the toes widely spread when sinking*
 406 *(thin), and smoothly collapsing upon withdrawal (bold). (g) Digit II–IV width are plotted from 49 steps of two*
 407 *individuals (equal scales in d–g). (h) Selected horizons for the green step (d–g) showing changing locations of claw*
 408 *entry (filled circles) and exit (open circles). The looping entry (thin) and exit (bold) path of digit III is indicated by a*
 409 *dashed line. Grey bars indicate zones for this track volume. Vertical and horizontal scales in (d–g) shown by axes in*
 410 *(e) and (g). Tick marks in (h) equal 1 cm. For foot animations, see electronic supplementary material, video.*

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Figure 2. Exit features and depth zone attribution in Early Jurassic fossil tracks. (a) Digit tip impression identification on entry (small circles) and exit (large circle) on one surface of ACM-ICH 37/24. (b) A penetrated slab (ACM-ICH 39/8) from high in the volume reveals three elongate Zone 1 tracks on its upper surface and furrowed, Zone 2 tracks on its lower surface (mirrored). (c) A penetrated slab (ACM-ICH 31/50) from low in the volume reveals a scrape-like, Zone 3a track with separate exits on its upper surface; only digit III reached its lower, Zone 3c surface (mirrored). (d) A five-slab specimen (ACM-ICH 34/33) preserves the down and forward penetration of the foot, followed by its looping withdrawal. Note changes in track morphology with depth. Dashed line indicates the entry (thin) and exit (bold) paths of digit III. (e) Tracings of 19 Early Jurassic track surfaces displaying inter- and intra-zone diversity (ACM-ICH specimen numbers shown below). Exit features (black arrows) vary widely in location along the lengths of the tracks (see electronic supplementary material, figure S1 for specimen photos and entry/exit overlays). Scale bars equal 5 cm.