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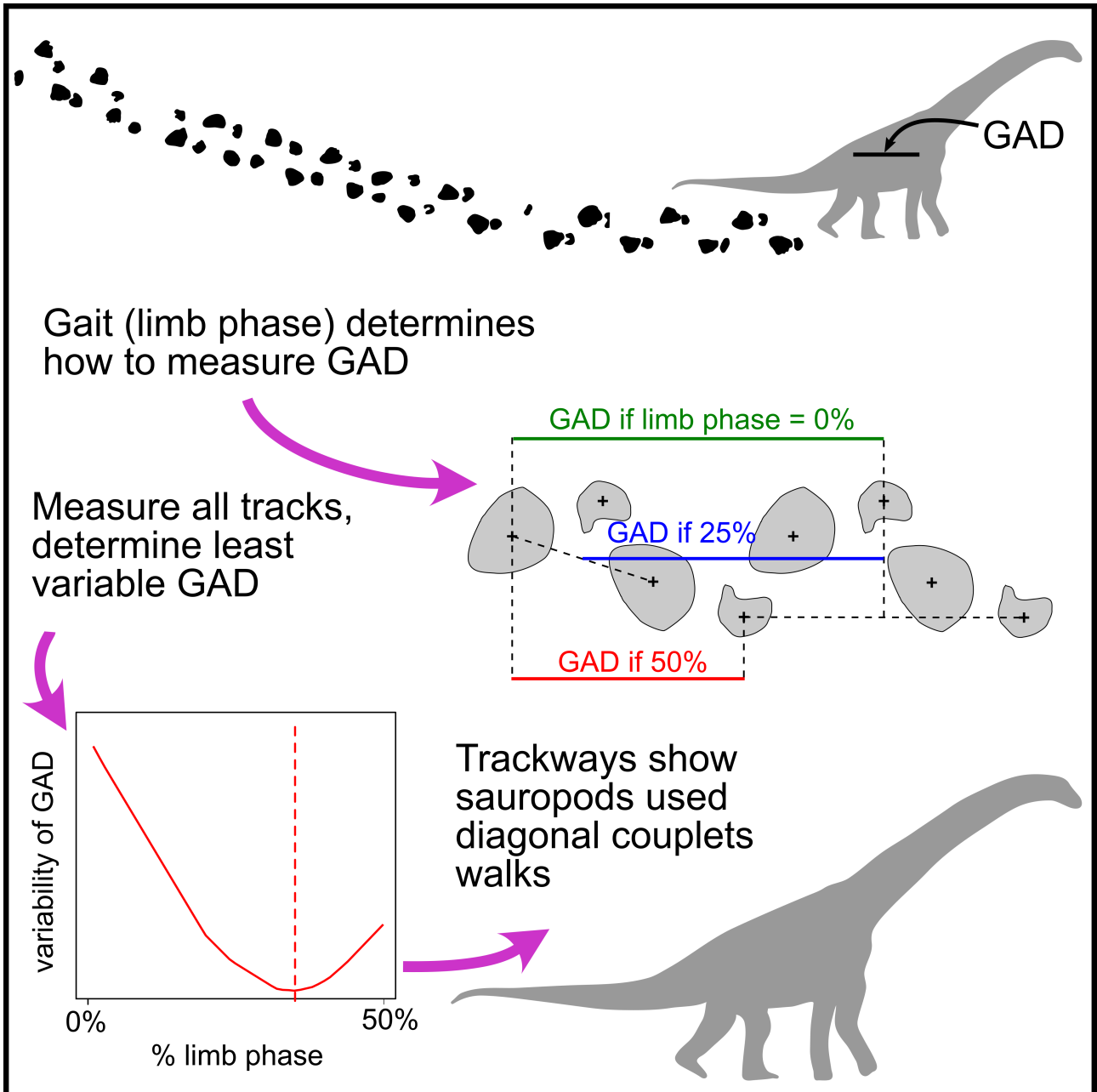
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2 A new method to calculate limb phase from trackways reveals gaits of
3 sauropod dinosaurs

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32 **SUMMARY**

33 Limb phase, the timing of the footfalls in quadrupedal locomotion that describes common
34 gaits such as the trot and the pace gait ^{1,2}, is widely believed to be difficult or even
35 impossible to estimate for extinct tetrapods ³⁻⁵. We here present a fundamentally new
36 approach that allows for estimating limb phase based on variation patterns in long
37 trackways. The approach is tested on trackways of modern mammals, where the
38 estimates generally correspond well with the actually employed limb phase. We then
39 estimate limb phases of giant wide-gauged sauropod dinosaurs based on three long
40 trackways from the Lower Cretaceous of Arkansas, US ^{6,7}. Gait selection at the largest
41 body sizes is of considerable interest given the lack of modern analogues. Contrary to
42 previous assumptions ^{8,9}, our estimates suggest lateral-sequence diagonal-couplets walks,
43 in which the footfalls of the diagonal limb pairs (e.g., right hind and left fore) are more
44 closely related in time than those of the same side of the body (e.g., right hind and right
45 fore). Such a gait selection allows for efficient walking while maintaining diagonal limb
46 supports throughout the step cycle, which is important for a giant, wide-gauged trackmaker
47 ¹⁰. Estimations of limb phase may help to constrain other gait parameters, body size and
48 shape, and, finally, potential trackmaker taxa.

49

50 **RESULTS**

51 **Ambiguity and within-trackway variation**

52 Many central aspects of the biology of extinct tetrapods remain inaccessible to science
53 because direct observation is not possible. One such aspect is an animal's gait,
54 specifically the relative timing of footfalls during quadrupedal locomotion, known as limb
55 phase ^{1,2}. Limb phase describes if a trot, a singlefoot, a pace gait, or any intermediate gait
56 is employed (Fig. 1, 2A–D). Previous attempts to interpret gaits from fossil trackways
57 remain speculative or inconclusive ^{3,4}. Stevens et al. ⁵ demonstrated that trackmakers that
58 only slightly differ in body length but employ different limb phases may produce identical
59 footfall patterns. Given this ambiguity, it seemed that limb phase could not be estimated
60 from trackways unless body size and shape of the trackmaker can be precisely
61 constrained ⁵ – a task which is notoriously difficult to achieve when the assumed
62 trackmaker taxon is extinct. One important source of information, however, remains almost
63 entirely unexplored: the within-trackway variation of the footfall pattern.

65 Variation in footfall positions as measured from a trackway can have multiple sources,
66 including:

- 67 1) measurement error or misidentification of tracks;
- 68 2) footfall positions not being precisely recorded by tracks (e.g., due to slipping, erosion,
69 etc.);

70

71 3) individual behaviour;

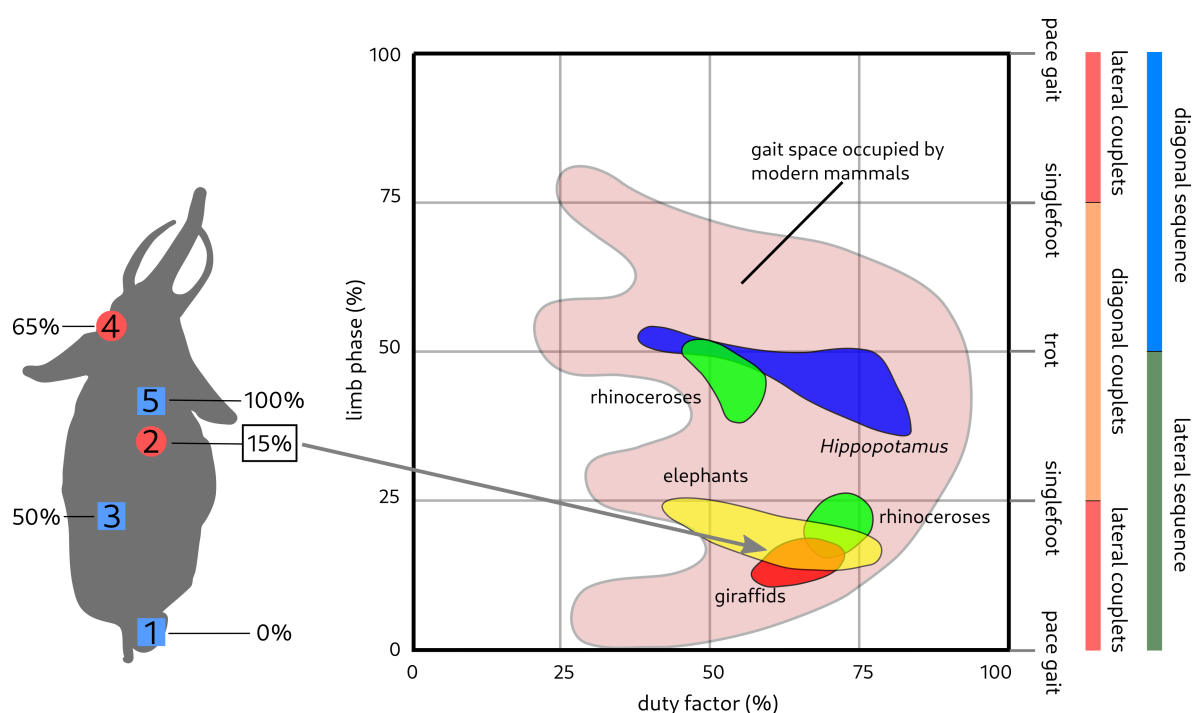
72 4) variation in the timing and spacing of footfalls.

73 It is this last source of variation which may allow for reconstructing limb phase. Such type
 74 4 variation will manifest if changes in stride length (measured between two subsequent
 75 footfalls of the same foot) do occur, which typically reflect changes in the speed of
 76 locomotion.

77

78 Our approaches may principally be applied to any trackmaker that employs a symmetrical
 79 gait, varies stride length, and does not use spine bending as a major means of locomotion.
 80 Importantly, these methods do not require *a priori* assumptions on trackmaker size or
 81 anatomy. In the following, we will restrict ourselves to discuss limb phases between 0%
 82 and 50%. While higher limb phases up to ~75% do exist, they are, among modern
 83 tetrapods, predominantly related to arboreality¹³.

84



85 **Figure 1. Classification of symmetrical quadrupedal gaits.** Any gait can be described by two parameters:
 86 limb phase and duty factor. Duty factor is the percentage of the step cycle duration that a foot is in ground
 87 contact. Limb phase is defined as the percentage of the step cycle duration that the footfall of a forefoot
 88 follows that of the hind foot on the same side of the body 2. Limb phase is here visualised in top view (left),
 89 where squares represent pes and circles manus footfalls, with numbers (1–5) indicating the sequence of the
 90 footfalls; the footfall relevant for determining the limb phase is framed. Redrawn and modified after
 91 Hildebrand 1,11 and Cartmill 13. Gait space occupation of selected modern megaherbivores shown after
 92 Hildebrand 1 and modified after Hutchinson et al. 12.

93 Main approach

94 Our limb phase estimations are based on the hypothetical projection of the shoulder and
 95 hip joints onto the trackway, a measurement known as the apparent gleno-acetabular
 96 distance (GAD), which is an approximation of the trunk length of the trackmaker¹⁴. The
 97 way GAD is measured from a trackway depends on the limb phase employed (Fig. 2A–D).
 98 During a trot, the contralateral (opposite side) fore- and hind limbs swing in sync (limb
 99 phase ~50%). In a walking trot, the moment the animal shifts its weight from one
 100 contralateral limb pair to the other, all four feet will contact the ground, and the GAD can
 101 now be measured between the midpoints of these pes- and manus positions (Fig. 2B).
 102 With a pace gait, in contrast, the ipsilateral (same side) fore- and hind limbs swing in sync
 103 (limb phase ~0%), resulting in a larger GAD value than for the trot (Fig. 2D). Theoretically,
 104 the GAD measure that precisely reflects the employed limb phase does not change with
 105 speed, because the trunk length it reflects must remain constant (the animal is not
 106 lengthening nor shortening). GAD measures that assume different limb phases can be
 107 taken along a trackway once per half step cycle. The GAD measure that shows the least
 108 variation is assumed to be the most likely to reflect the actual limb phase.

109 With the GAD computed, limb phase (LP) can be calculated based on trackway
 110 parameters with the formula

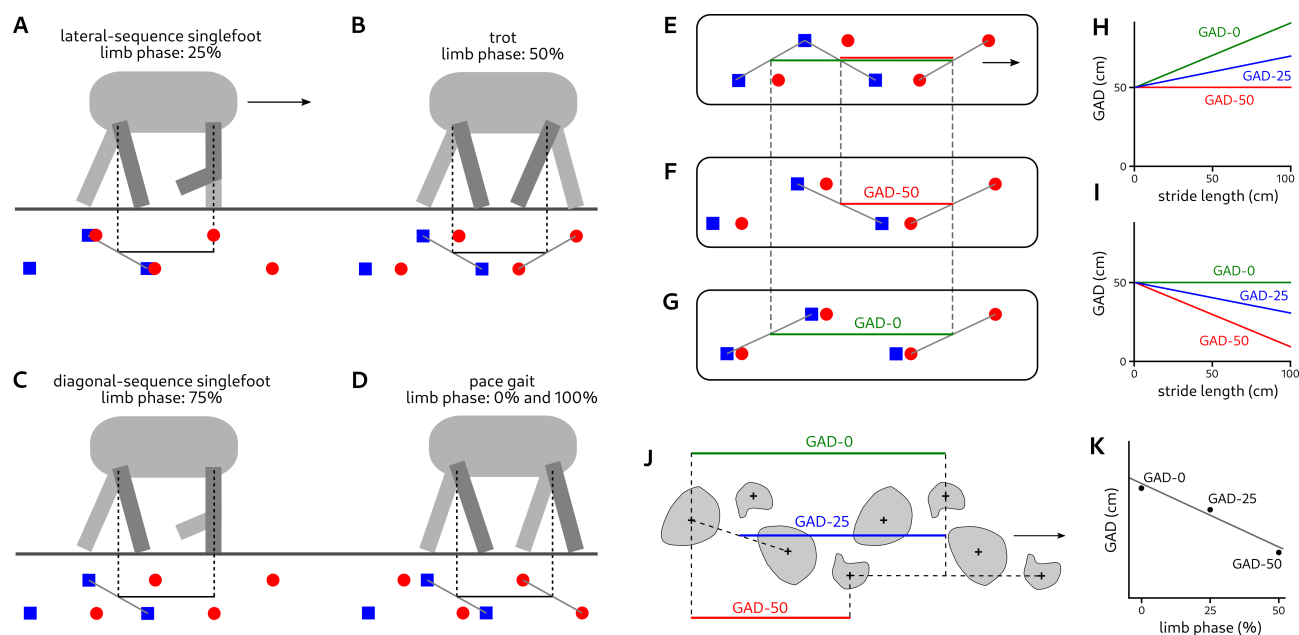
$$111 \text{ Formula I: } LP = 1 - \frac{GAD - PMD}{\text{Stride length}}$$

112 where PMD is the pes-manus distance parallel to the direction of travel.

113 GAD is traditionally measured between the midpoints of pes and manus track pairs (Fig.
 114 2A–D), and thus involves four tracks, or one complete step cycle^{15–17}. However, as speed
 115 changes do occur between half step cycles, such a definition would average out parts of
 116 the signal we are interested in. Consequently, we here define GAD based on only two
 117 tracks that represent one half step cycle (Fig. 2J). Direct measurements of GAD based on
 118 only two tracks are possible for those measures that assume a limb phase of 50% (GAD-
 119 50; trot) and 0% (GAD-0; pace gait). Because the relationship between limb phase and
 120 GAD is linear, GAD measures that assume intermediate limb phases can be calculated
 121 from these two measurements.

122 A GAD calculated from an assumed limb phase of 25% is the distance between the
 123 midpoint of a pes pair and the position of the swinging manus (Fig. 2A). The position of the
 124 manus at mid-swing needs to be inferred based on the preceding, subsequent, and
 125 contralateral manus tracks (Fig. 2J). Incorporating this more complex measure may reduce
 126 unwanted noise as more tracks are taken into account, but, at the same time, will skew
 127 variability because a larger number of tracks are involved (either 3 or 5) than is necessary
 128 for GAD-0 and GAD-50 (either 2 or 4). In order to avoid such skewing, we measure GAD-
 129 25 based on five tracks and regress all three GAD measures against limb phase (Fig. 2K).
 130 Deviations from linearity may be considered unwanted noise (Fig. 2K) and are
 131 consequently disregarded.

132 In our main approach, we calculate 51 GAD measures per half-step cycle that reflect limb
 133 phases from 0% to 50%, and check which of these measures varies least – which is then
 134 assumed to reflect the actually employed limb phase. Various measures of variability were
 135 tested; the sum of deviations from the mean provided the most accurate results.
 136 Alternative approaches have been tested and are discussed in the supplementary
 137 material.



138
 139 **Figure 2. The influence of limb phase changes on trackway patterns.** Squares indicate hind feet and
 140 circles forefeet footfalls; arrows indicate the direction of travel (left to right). A–D: Four discrete limb phases
 141 (25%, 50%, 75%, and 0/100%) and associated trackway patterns generated using Formula 1, with
 142 trackmaker size and speed remaining constant. E–I: The effect of speed changes on GAD (gleno-acetabular
 143 distance) measures. E: Trackway lacking any variability; it is unknown whether GAD should be measured
 144 according to a trot (GAD-50, 50% limb phase) or a pace gait (GAD-0, 0% limb phase). F–G: the same
 145 trackway as in E, but with stride length increased by 20%. If a trot was employed, GAD-50 remains constant
 146 while GAD-0 will increase (F). If a pace gait was employed, GAD-0 will remain constant while GAD-50
 147 decreases (G). H–I: Relationships between GAD-50, GAD-25, and GAD-0 and stride length, for a trackmaker
 148 with an actual GAD of 50 cm that employs a trot (H) and a pace gait (I). J: We here measure GAD-0 and
 149 GAD-50 based on two tracks, respectively, and GAD-25 (which assumes 25% limb phase) based on five
 150 tracks. K: Linear relationship between GAD measures (of the same step cycle) and limb phase.

151

152 Validation of results

153 We validated our approach on 15 trackways of various modern mammals of different body
 154 sizes and gaits, including three dogs, two horses, a camel, an elephant, a red fox, and a
 155 raccoon. For all trackways except for the red fox and the raccoon, the actually employed
 156 limb phase was extracted from video footage, allowing to determine the accuracy of our
 157 estimates. Several trackways were split into sections to determine how the methods

158 perform on shorter trackways that exhibit less pronounced speed changes, resulting in a
 159 total of 32 trackways and trackway sections.

160

Trackway	half- step cycles	% speed change	GAD vs stride (p- value)	estimated limb phase	actual limb phase (mean)	error (% limb phase)
Mammals						
Dog “Elli”, trot	21	25	<0.01	50	49	1
Dog “Elli”, walk	27	26	<0.01	24	18	6
Dog “Paul”, slow trot	13	11	0.59	50	50	0
Dog “Paul”, slow walk	27	14	0.02	7	15	8
Dog “Penny”, trot	13	15	0.07	42	48	6
Dog “Penny”, walk	34	36	<0.01	11	15	4
Horse “Calimero”, trot	29	20	0.13	50	50	0
Horse “Calimero”, walk	44	10	0.02	30	23	7
Horse “Phoenix”, trot	94	33	<0.01	50	50	0
Horse “Phoenix”, walk	61	17	<0.01	27	25	2
Red fox, trot	71	15	0.11	50	~50*	–
Raccoon, walk	51	32	<0.01	5	~14**	–
Camel, walk	20	44	<0.01	23	16	7
Elephant “Srisiam”, “walk”	62	23	<0.01	15	15	0
Elephant “Srisiam”, “run”	22	9	0.37	22	21	1
Sauropods						
Certain Teed Q1	36	31	<0.01	44	–	–
Briar site, trackway 1	31	23	0.11	35	–	–
Briar site, trackway 2	33	19	0.37	31	–	–

161

162

163 **Table 1. Results of our validation on recent mammals, and estimates obtained for the three sauropod**
 164 **trackways.** % speed change is calculated based on the range and mean of measured stride lengths. Actual
 165 limb phases marked with an * are not based on video footage but were estimated; ** from ¹⁴. See also Table
 166 S1.

167

168

169 Estimates of our main approach do generally correspond well with the actually employed
 170 limb phase. For the trackways plus shorter sections, the mean error is 4.96% and the
 171 median error 3% limb phase. When only the trackways are considered, the mean error is
 172 3.2% and the median error 2% limb phase.

173 The presence of signal, and therefore the reliability of the estimate, may be assessed by
 174 plotting the GAD-0, GAD-25, and GAD-50 measures against stride length (Fig. 3C). We fit
 175 separate regression slopes to the point clouds of the three measures. A slope is expected
 176 to be horizontal if the GAD measure corresponds to the actually employed limb phase
 177 because trunk length does not change with speed (Fig. 2H–I). Significant differences in
 178 slopes are difficult to explain by other sources of variability that may overprint or skew the

179 signal we aim to extract. However, the differences in slopes are significant ($p < 0.05$) only
180 in 14 of the 32 mammal trackways and trackway sections.

181 Within-trackway changes in limb phase will add additional noise to the data, but may lead
182 to significant overestimations of limb phase when the latter is positively correlated with
183 stride length, and underestimations when negatively correlated. In the analysed mammals,
184 however, such correlation is absent or weak in walking trackways that only show moderate
185 variation in stride length. We therefore do not expect such over- or underestimations to be
186 consistent in multiple trackways of the same trackmaker or in different sections of the
187 same trackway.

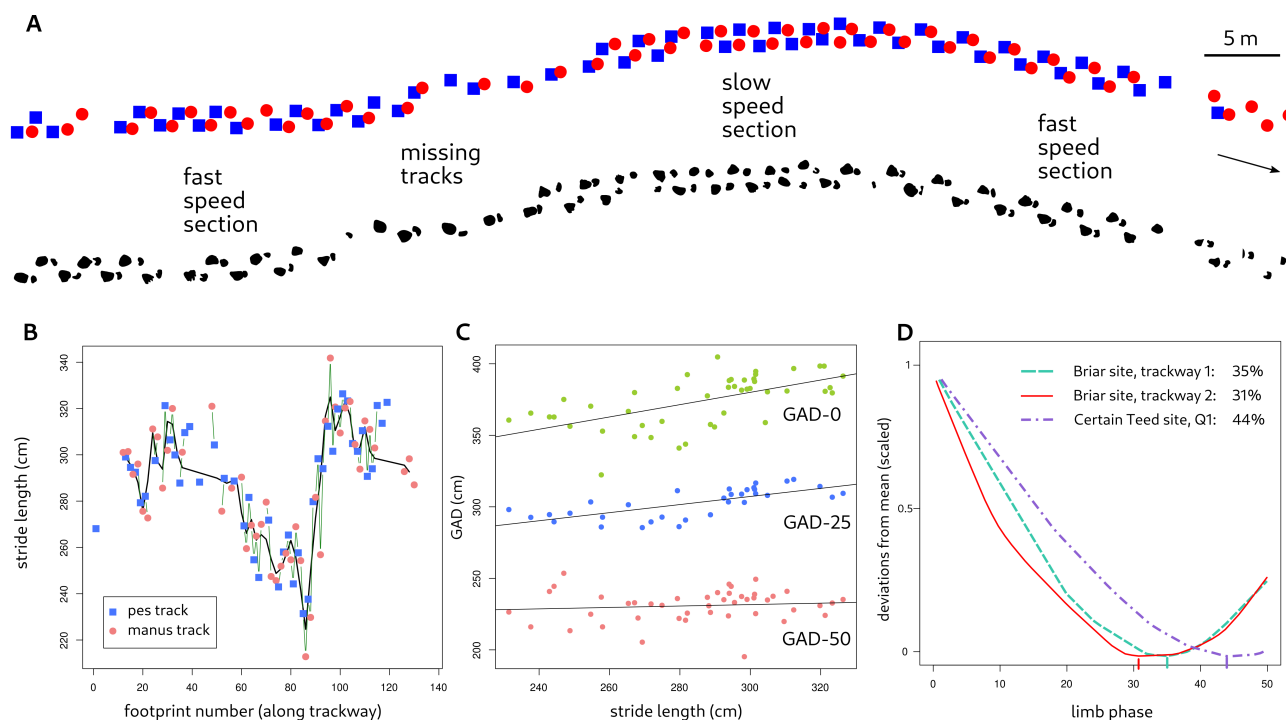
188 Based on above considerations, we conclude that 1) clear differences in regression slopes
189 (Fig. 3C) and 2) consistent estimates for multiple trackways of a sample and/or sections of
190 single trackways increase confidence in obtained estimates.

191

192 **Sauropod trackways**

193 We used our methods to estimate limb phase of three long trackways of sauropod
194 dinosaurs from the Lower Cretaceous De Queen Formation, Arkansas, US: Trackways 1
195 and 2 of the Briar site ⁶ and trackway Q1 of the nearby Certain Teed Gypsum mine site ⁷.
196 These trackmakers were of very large size (median pes length: 70–85 cm; maximum stride
197 lengths: 272–342 cm) and distinctly wide-gauged (i.e., the trackway is broad so that tracks
198 are well-separated from the trackway midline). The Certain Teed trackway shows the most
199 pronounced speed changes (Fig. 3A), with stride lengths ranging from ~230 cm to ~325
200 cm (Fig. 3B).

201



203 **Figure 3. Results of the analysed sauropod trackways.** A–C: The Certain Teed trackway (Q1) from the
 204 De Queen Formation of Arkansas, US ⁷. A: Plotted track coordinates used for analysis (above) and site map
 205 of the trackway (below), where squares represent hind feet and dots forefeet. B: Differences in stride length
 206 along the trackway, from which changes in locomotion speed are inferred. C: Plot of GADs against stride
 207 length, showing a significant difference between the slopes, indicating presence of signal. D: Results of our
 208 main approach for the three analysed sauropod trackways. The minima of the curves (marked) are
 209 interpreted as the most likely limb phases employed.

210

211 Gait selection at the largest body sizes is of particular interest given the lack of modern
 212 analogues. Previous studies suggested pace gaits (limb phase ~0%) or lateral-sequence
 213 singlefoot walks (limb phase ~25%) as likely options for sauropods ^{8–9,17}. Our results, in
 214 contrast, suggest significantly higher limb phases of 35%, 31%, and 44% for the two Briar
 215 trackways and the Certain Teed trackway, respectively, suggesting diagonal-couplets
 216 walks in lateral sequence (Fig. 3). The regression slopes of GAD-0 and GAD-50 against
 217 stride length are significantly different (p-value < 0.001) in the Certain Teed trackway (Fig.
 218 3C), indicating strong signal, while the other two trackways did not reach significance. The
 219 first half of the Certain Teed trackway gave a slightly lower estimate (38%) than the second
 220 half (44%), and it is possible that the limb phase estimated for whole trackway is a slight
 221 overestimation.

222

223 DISCUSSION

224 Generally high limb phases in wide-gauged sauropods are consistent with biomechanical
 225 considerations. Modern megaherbivores typically employ lateral-sequence walks
 226 somewhat below 25% unless running or moving very slowly (the short-legged common

227 hippopotamus, which employs a trot, is a notable exception)¹⁸. However, these animals
228 have very narrow gauges¹, unlike the wide-gauged sauropods analysed here. As gauge
229 width increases, continuous diagonal supports become increasingly important¹³. In a pace
230 gait, one side of the body is unsupported while the feet are swinging forwards. If the left
231 and right feet are not placed precisely in front of each other, the centre of mass needs to
232 constantly shift mediolaterally during walking in order to remain between the supporting
233 limb pair. In a trot, in contrast, both body sides are always supported by at least one leg.
234 We may assume that giant wide-gauged sauropods required diagonal supports throughout
235 the step cycle to increase stability. Such continuous support of both body sides is only
236 warranted at a limb phase of 25% or above, and, when at 25%, only at very slow gaits
237 where one leg moves at a time (i.e., at duty factors >75%). The generally high limb phases
238 reported here allow more efficient and/or faster walking while maintaining diagonal
239 supports. At the same time, disadvantages of even higher limb phases approaching trots,
240 including prevailing bipod rather than tripod supports¹³ and more pronounced vertical
241 accelerations¹⁸, are avoided.

242 As direct records of animal activity, tracks provide information on extinct animals that
243 cannot be derived from body fossils such as bones and teeth. While the importance of
244 tracks as palaeobiological data sources cannot be overstated, their interpretation suffers
245 from multiple levels of uncertainty, including time averaging of tracksites, trackmaker
246 identification, and interpretation of track morphology and trackway patterns²⁰. Limb phase,
247 as a central parameter, is not only important in its own right, but may help to better
248 constrain other uncertainties, such as duty factor and – because the apparent gleno-
249 acetabular distance depends on limb phase – body size and shape of the trackmaker,
250 which may eventually aid in identifying trackmaker taxa.

251

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261

262 AUTHOR CONTRIBUTIONS

263 J.N.L. conceptualised and performed analyses, collected data, and co-wrote the
264 manuscript. P.L.F. conceptualised analyses and co-wrote the manuscript.

265

266 **DECLARATION OF INTEREST**

267 The authors declare no competing interests.

268

269

270

271 **STAR METHODS**

272

273 **RESOURCE AVAILABILITY**

274 **CONTACT FOR REAGENT AND RESOURCE SHARING**

275 Lead Contact

276 Further information and requests for resources and reagents should be directed to and will
277 be fulfilled by the lead contact, Jens N. Lallensack (jens.lallensack@gmail.com).

278

279 Materials Availability

280 See Key Resources table for materials used in this study.

281

282 Data and Code Availability

283 Data and code used in this study is publicly available (see Key Resources table).

284

285 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

286 Modern mammals

287 We collected trackway data from a range of modern mammals with known gaits in order to
288 validate our approach. Of five individual animals (three dogs and two horses), we also
289 collected video footage while the tracks were made, which was then used to calculate the
290 precise limb phases employed.

291 Two of the dogs, “Elli” (a half-year old crossbreed) and “Penny” (adult crossbreed), were
292 repeatedly led on a leash over a paved surface of ca. 3 m in length. In separate crossings
293 of the surface, the dogs were asked to use different speeds, including slow and fast walks
294 and slow and fast trots. This approach did not produce any footprints; instead, the
295 positions of footfall patterns in 3D space was later determined based on video footage and
296 a photogrammetric model of the paved surface (see below). Crossings of the same dog
297 using the same gait were then combined to obtain longer trackways. Two trackways from a

298 third dog (“Paul”, an Airedale Terrier), including a slow walk and a trot, were produced in
299 snow. Again, this dog was led on a leash.

300 Trackways of the first horse (horse 1) were made in sand (two walks and two trots), with
301 the horse led on a rope. The second horse (horse 2) produced a very long trackway that
302 was made in snow while mounted; the horse was persuaded to increase its speed along
303 the way, covering the range from slow walk to fast trot. Trackway sections pertaining to
304 these gaits were then analysed separately.

305 Additional trackways produced by wild animals in snow were recorded in Höxter, Germany.
306 Although direct observation was not possible, the limb phases could be constrained based
307 on local knowledge of the trackmakers. Analysed trackways include red fox (*Vulpes*
308 *vulpes*; trot) and raccoon (*Procyon lotor*; lateral-sequence lateral-couplets walk). We
309 furthermore extracted trackway data based on video coverage of a camel employing a
310 lateral-sequence singlefoot walk that is freely available on the internet (see below for
311 methodology).

312

313 Sauropods

314 The sauropod trackways analysed herein stem from the Lower Cretaceous (Albian) De
315 Queen Formation, which is part of the Trinity Group and laterally equivalent to the Glen
316 Rose Formation of Texas. The sauropod trackways analysed herein stem from two
317 adjacent sites: the Briar site and the Certain Teed Gypsum mine site, both of which are
318 active quarries. We selected the three longest and most complete trackways for analysis,
319 including two trackways from the Briar site, originally reported by Pittman and Gillette in
320 1989 ⁶, and one trackway from the Certain Teed site that was reported by Platt and
321 colleagues in 2018 ⁷.

322 According to Pittman and Gillette ⁶, mapping of the Briar trackways (trackway 1 and 2) was
323 done using a portable grid of 3 x 5 m and the track outlines traced onto graph paper. As
324 these trackways were afterwards destroyed by quarrying operations. The Certain Teed
325 trackway (trackway Q1) was interpreted by one of us (JNL) from published LIDAR 3D data
326 ⁷. Interpretations were made more difficult by the presence of unrelated isolated prints in
327 some sections; we here follow the criteria discussed in ¹⁷ to identify footprints belonging to
328 the trackway.

329

330 **Method details**

331 Photogrammetry, data extraction, and analysis

332 All trackways of modern mammals, except for the camel, were digitised using
333 photogrammetry ²¹. Vertical photos were shot free-hand in sequence along the trackway
334 from a height of approximately 2 m. High overlap (ca. 90%) between individual shots was
335 aimed for in order to avoid little inaccuracies in image alignment, which along a long

336 trackway would otherwise add up. A second photo sequence was shot in case the first set
337 aligned imperfectly. At different points along the trackway, additional shots from different
338 heights and camera orientations were shot of the same surface for calibration purposes.
339 This process allowed for the accurate and time-efficient capture of large quantities of
340 trackways. Photogrammetric models were then produced using Agisoft Metashape
341 (agisoft.com). The horizontal plane was automatically fitted using the free software
342 MeshLab (www.meshlab.net). Orthophotos and other graphical visualisations were
343 produced with MeshLab; these outputs form the basis for our further analysis. See
344 Lallensack et al.²² for details on the photogrammetric procedure.

345 A different approach was employed to obtain footfall coordinates of two of the dogs (“Elli”
346 and “Penny”). The locomoting dogs were filmed simultaneously with two 4K video cameras
347 mounted on tripods, each covering the entire surface. After multiple crossings of the dogs
348 over this surface, an orthophoto of the surface was obtained using photogrammetry. The
349 paved surface was rich in features that were visible on both the videos and the orthophoto;
350 these were used to determine the footfall positions on the orthophoto.

351 Footfall data of the camel were collected from an openly available video
352 (https://www.youtube.com/watch?v=Uu2_AO6Ozlw) showing the walking animal in side-
353 view. Measurements of footfall positions were obtained using the free software Kinovea
354 (www.kinovea.org). The distances between each footfall along the trackway were then
355 summed up to obtain a one-dimensional trackway (the trackway width was arbitrarily set to
356 a fixed value).

357 Footfall data for the elephant were extracted from video frames that show the animal
358 walking repeatedly over a walkway. We here analysed trials 1–15 of a single elephant
359 individual (“Srisiam”), an sub-adult Asian Elephant (hip height: 1.32 m)^{23,24}. The data was
360 generously provided to the authors by John H. Hutchinson (Royal Veterinary College,
361 London).

362 Coordinates of the footfalls of all trackways except for the camel and the elephant were
363 extracted using Inkscape (see Lallensack et al. 2020 for details) and passed to a custom
364 set of scripts written in the free statistical computing environment R (www.r-project.org).
365 These scripts calculate a range of different trackway parameters, including slightly different
366 ways to compute the GAD (see below for details). These scripts (see Key Resources
367 table) furthermore calculate limb phases, perform statistical tests, and generate graphics.
368 We also explore the theoretical performance of the tested methods using a mathematical
369 model based on Formula 1.

370

371 **QUANTIFICATION AND STATISTICAL ANALYSIS**

372

373 Main approach

374 After calculating expected GADs for limb phases between 0 and 50% for all half-step
375 cycles of the trackway, we calculate variability for each of these discrete limb phases – the
376 limb phase with the lowest variability can be considered the most likely. We tested a
377 number of variability measures, including variance, median absolute deviation (MAD), and
378 the sum of deviations from the median or mean. This choice of method had a significant
379 impact on the accuracy of the results. The sum of deviations from the mean produced the
380 most accurate results on our mammal sample. In our implementation, we plot the
381 deviations from the mean against limb phase – the limb phase at which the deviations are
382 at a minimum is interpreted as the actually employed limb phase.

383

384 Additional approach 1

385 It is possible to calculate a limb phase based on only two half-step cycles. In our approach,
386 we plot GAD-0 and GAD-50 of both half-step cycles against their respective limb phase (0
387 and 50; resulting in four plotted points; Fig. S1A). The GAD-0 and GAD-50 measures
388 within a half-step cycle are then connected by a line, and the intersection between the two
389 lines is determined. This intersection point can be interpreted as the combination of GAD
390 and limb phase that both half-step cycles have in common – and is consequently the most
391 likely combination.

392 A single intersection, however, is a highly unreliable estimate as it is easily affected by
393 noise and/or absence of signal between the two half-step cycles. We therefore use all
394 possible pairs of half-step cycles in a trackway (so that the number of calculated limb
395 phases is higher than the number of half-step cycles when more than three half-step
396 cycles are available). We then plot a histogram and take the median of these calculated
397 limb phases, which is hypothesised to reflect the actually employed limb phase (Fig. S1B–
398 C).

399 To lessen the influence of noise, we implement a number of filtering and correction
400 procedures. First, we normalise all GAD measures to a range between 0 and 50, as
401 otherwise slope differences tend to decrease with trackmaker body size. We then remove
402 all half-step cycle pairs in which the slopes of the intersecting lines differ by less than 1.5°
403 (this value produced the best estimates in our mammal sample). Second, we remove
404 calculated limb phases if they fall way outside the target interval (i.e., $<-50\%$ and $>100\%$).
405 Third, we perform a leave-one-out permutation test to check if the removal of one half-step
406 cycle significantly affects the median of the overall limb phase calculated for a particular
407 trackway; if such is the case, the affected half-step cycle will be automatically removed,
408 and the limb phases and permutation test re-calculated. This step is required because a
409 single half-step cycle that gives an inaccurate signal will form pairs with all other half-step
410 cycles, and thus has a potentially large impact on the overall results.

411

412 Additional approach 2

413 This approach is not based on GADs but on differences between stride lengths, and may
414 detect if a trot (or, generally, limb phases >25%) or a pace gait (<25%) is significantly more
415 likely. This approach is based on the idea that the two strides associated with the limbs
416 that swing in sync (assuming either a trot or pace gait) are not separated by time, and
417 consequently will not differ due to small changes in speed. In contrast, the other limb pair,
418 which is out of sync, will record such speed changes – the later of the two strides tends to
419 be longer than the earlier if speed increases.

420 In our implementation, we compute the differences between contralateral strides (A and B
421 in Fig. S1D) as well as ipsilateral strides (A and C in Fig. S1D) along a trackway. We then
422 perform a chi-squared test to check for significant differences between these differences. If
423 the test is significant ($p < 0.05$), we may conclude that a trot is more likely than a pace gait if
424 the associated mean of the differences is smaller, or vice versa. When analysing multiple
425 trackways together, we scale the trackways to a common mean stride length, and then
426 perform a single test of the combined stride differences of all trackways.

427 While this approach did not reach significance for most mammal trackways (in which case
428 its result should be disregarded), it tended to be significant if trackways of separate
429 individuals that use similar limb phases are combined.

430

431 Validation

432 To test for the presence of signal, we use regressions of GAD against stride length to test
433 if a trackway contains relevant signal (Fig. 3C). For each half-step cycle, we pair GAD-0
434 and GAD-50 with the preceding pes stride (i.e., the stride that is completed when the
435 relevant footfalls for the two GAD-measurements do occur). If this stride is not available
436 (as is usually the case at the beginning of a trackway), we instead use the mean of the two
437 subsequent manus strides (left and right). We then plot both GAD-0 and GAD-50 against
438 stride length, and fit a linear regression for each of the two GADs. For visualisation
439 purposes, we also add GAD-25 to the plot. It has to be noted that the GAD-25 point cloud
440 tends to deviate less from the regression line because GAD-25 is measured based on five
441 footprints while GAD-0 and GAD-50 are measured based on only two footprints.

442

443 Changes in limb phase

444 Our methods assume that limb phase remains approximately constant throughout the
445 trackway, which is not necessarily the case. We here discuss the possible effects of within-
446 trackway changes of limb phase on our results.

447 Variation in limb phase that is not correlated with stride length is expected to increase
448 noise, but will not skew overall results (although over- or underestimations due to such
449 noise may occur by chance when few data points are available). More concerning are
450 cases in which limb phase changes with stride length: a positive correlation between limb

451 phase and stride length generally leads to an overestimation of the limb phase, while a
452 negative correlation leads to an underestimation.

453 Correlation between limb phase and stride length is most obvious when the change occurs
454 abruptly rather than gradual. Fig. S2A combines the walking trackway and trotting
455 trackway sections of the dog “Elli” (actual limb phases of 18% and 49%, respectively), and
456 performed our analysis as if both sections would represent a single trackway. The GAD vs
457 Stride plot shows the distinct gait transition, with stride lengths below 75 cm representing
458 the walks at low limb phases, and stride lengths above 75 cm representing trots. The
459 change in limb phase determines the slopes of the regression lines, and all three
460 regression lines are rising, indicating either changes in limb phase or body size, therefore
461 invalidating the signal. More difficult to detect, however, are cases where limb phase
462 changes are smaller and the correlation is continuous rather than abrupt.

463 The effects of perfect correlations between limb phase and stride length were explored
464 using simulated trackways generated based on formula 1 (Fig. S2B). We define Δl_p as the
465 total shift in limb phase that occurs (8% in Fig. S2B) and Δs_t as the range of stride lengths
466 that shows a correlation with limb phase (2 m in Fig. S2B).

467 From the simulations, we derive the following observations:

- 468 1) positive correlation between stride length and limb phase leads to overestimation,
469 and negative correlation to underestimation of the actually employed limb phase.
- 470 2) the slopes will be slightly curved upwards (if correlation is positive) or downwards (if
471 correlation is negative) even when correlation is perfect.
- 472 3) The error (over or underestimation) increases with
 - 473 1) the $\Delta l_p / \Delta s_t$ ratio and
 - 474 2) the ratio between the minimum of the stride range and the GAD

475 Limb phase remained relatively stable within the walks and trots of the dogs “Elli” and
476 “Paul”, while in the walks of the dog “Penny” limb phase varies from 9% to 28% (run
477 means range from 11–18%) (Table S2). The run means show a negative correlation (Fig.
478 S2C), but this correlation is much less evident when all values are plotted (Fig. S3D),
479 indicating that limb phase is not tightly controlled by stride length. The limb phase
480 estimated with our main approach is therefore only a slight underestimation (11% instead
481 of 15%); the estimate given by approach 2 is slightly lower (8%).

482 Elephants differ from other large mammals in lacking a discrete gait transition when
483 switching from walking to running^{12,23–24}. They do, however, increase their limb phase from
484 around 15% towards 25%¹²; such increases may possibly result in significant over-
485 estimations when limb phase is calculated from trackways using our methods. We here
486 analyse video footage of the elephant individual “Srisiam”. Footfall coordinates and limb
487 phases were extracted from the first 15 trials. Trials 001–008 and 014–015 represent
488 walks, while in trials 009–012 the elephant was agitated to run.

489 Limb phases of 14–16% were employed in the “walks” and limb phases of 20–22% were
490 employed in the “runs”. Stride length varied from around 190 to 240 cm in the “walks”, and
491 from around 290 to 310 cm in the “runs” (Fig. S2E). Combining all trials into a single
492 trackway, the limb phase was significantly overestimated (33% limb phase) (Fig. S2F).
493 However, limb phase does not change with speed when only the walks, or only the runs,
494 are considered: Our main approach suggests a limb phase of 15% for the “walks” and 22%
495 for the “runs”, closely matching the actual values (Fig. S2G–H).

496 Our methods may overestimate limb phase when the latter is positively correlated with
497 stride length, and underestimate it when this correlation is negative. A gradual shift in limb
498 phase was observed in one of the dogs (“Penny”) and in the elephant (“Srisiam”), but is
499 absent in the horses. In the dog “Penny”, the negative correlation between limb phase and
500 speed is only weak, resulting in an underestimation of the limb phase that is negligible. In
501 the elephant “Srisiam”, the overestimation is significant, but analysing the slow-speed and
502 high-speed sections separately produced very accurate estimates (errors of 0% and 1%
503 limb phase, respectively).

504 We conclude that, in modern mammals, correlations between limb phase and stride length
505 may occur but tend to manifest only when stride length increases substantially. Moderate
506 increases in stride length in the elephant “Srisiam” are not, or only weakly, correlated with
507 limb phase, but were substantial enough to produce accurate estimates. While this does
508 not rule out the possibility that such moderate stride length changes may occasionally
509 show problematic correlations with limb phase, these are expected to be inconsistent
510 within and between trackways.

511 Consequently, the risk of over- or underestimations due to changes in limb phase may be
512 reduced by 1) analysing multiple trackways of the same trackmaker taxon and 2) perform
513 separate analysis on separate sections of longer trackways (e.g., low-speed and high-
514 speed, or first half and second half). If the estimated limb phase is consistent for multiple
515 trackways and trackway sections, the possibility of a significant over- or underestimation
516 may be considered unlikely.

517

518 Uncertain coupling values

519 The coupling value is the number of strides that separate pes- and manus tracks that
520 belong to the same step cycle¹⁵. It can be high in long-bodied and short-legged animals or
521 in such that make short steps (i.e., the manus may be several step cycles ahead of the
522 pes as seen in a trackway).

523 While coupling values can be assumed *a priori* in most cases based on rough constrains
524 on trackmaker anatomy, they may be ambiguous where trackmaker anatomy is very poorly
525 constrained, especially in some long-bodied sprawling tetrapods. In such cases, coupling
526 value may be determined by comparing the variability of GAD measurements that reflect
527 the separate possibilities; the GAD measured between the pes and manus prints that are

528 part of the same step-cycle should be expected to vary considerably less if speed changes
529 (that are measurable as changes in stride length) occur. Evaluating this hypothesis on
530 modern long-bodied sprawling tetrapods is, however, beyond the scope of the present
531 study.

532

533 Additional resources

534 Animated step cycles of the sauropod Q1 that visualise our results are provided at
535 <https://doi.org/10.0.23.196/m9.figshare.18995255>.

536

537 DATA AND SOFTWARE AVAILABILITY

538 The data used in this paper are available at <https://doi.org/10.6084/m9.figshare.19078337>
539 and include footfall coordinates of all trackways (mammals and sauropods) as well as
540 individual results for all trackways.

541 R scripts used in this paper are available at <https://doi.org/10.6084/m9.figshare.19078337>.
542 Updated versions of the scripts will be hosted in our GitHub repository
543 (<https://github.com/JensLallensack/trackway-tools>).

544

545

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