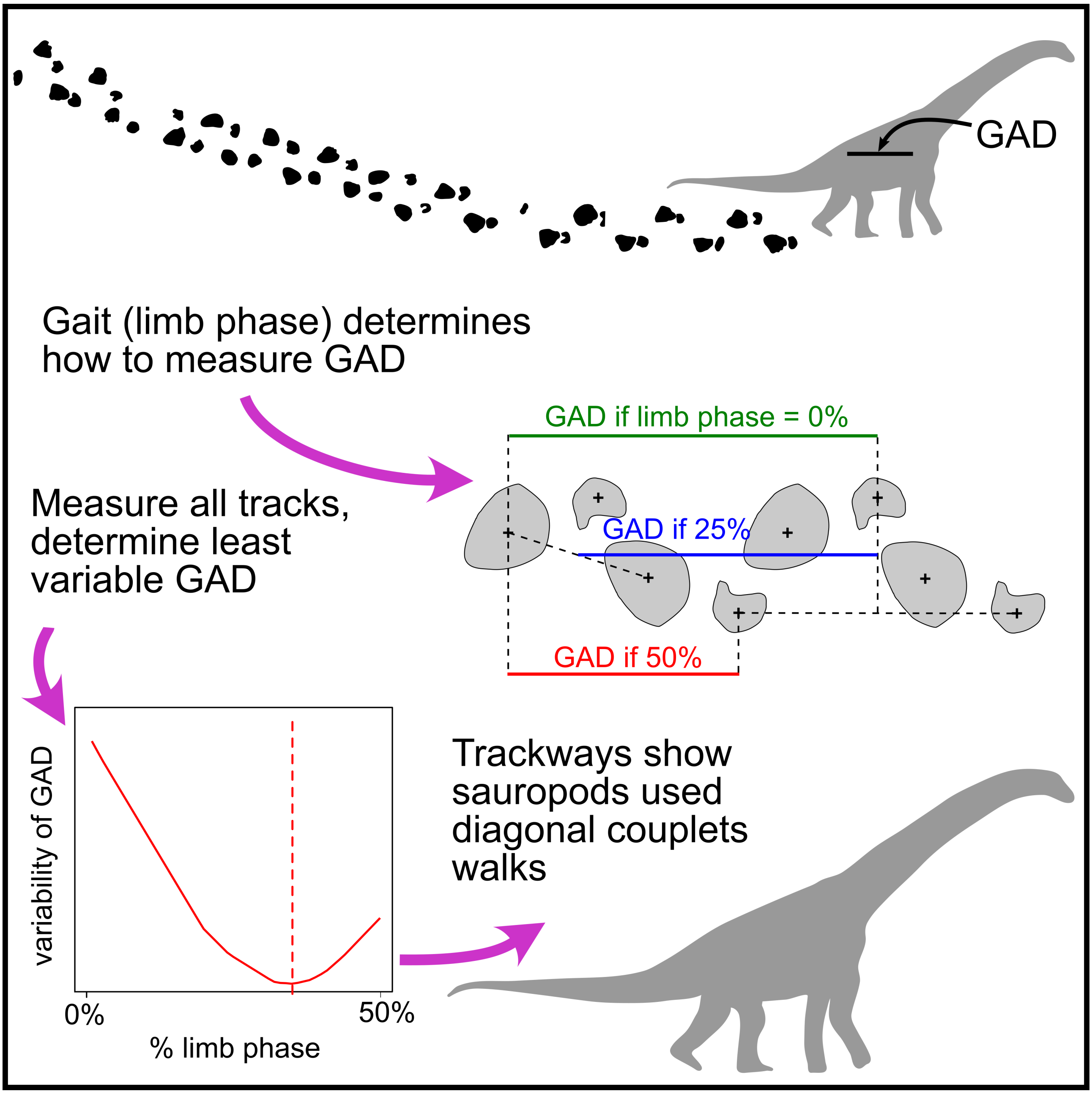

Gait (limb phase) determines how to measure GAD

Measure all tracks, determine least variable GAD

Trackways show sauropods used diagonal couplets walks

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

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SUMMARY

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

RESULTS

Ambiguity and within-trackway variation

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

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

1) measurement error or misidentification of tracks;

2) footfall positions not being precisely recorded by tracks (e.g., due to slipping, erosion, etc.);

3) individual behaviour;

4) variation in the timing and spacing of footfalls.

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

Our approaches may principally be applied to any trackmaker that employs a symmetrical gait, varies stride length, and does not use spine bending as a major means of locomotion. Importantly, these methods do not require *a priori* assumptions on trackmaker size or anatomy. In the following, we will restrict ourselves to discuss limb phases between 0% and 50%. While higher limb phases up to ~75% do exist, they are, among modern tetrapods, predominantly related to arboreality [13].

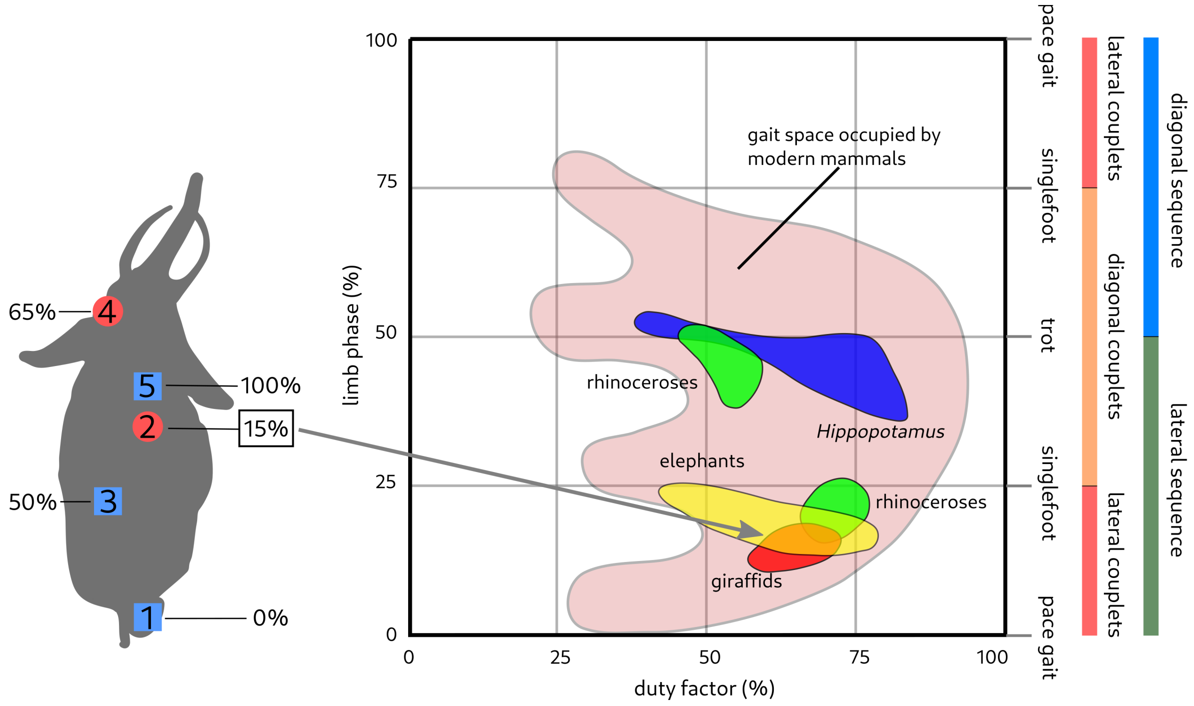

Figure 1. Classification of symmetrical quadrupedal gaits. Any gait can be described by two parameters: limb phase and duty factor. Duty factor is the percentage of the step cycle duration that a foot is in ground contact. Limb phase is defined as the percentage of the step cycle duration that the footfall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

Main approach

Our limb phase estimations are based on the hypothetical projection of the shoulder and hip joints onto the trackway, a measurement known as the apparent gleno-acetabular distance (GAD), which is an approximation of the trunk length of the trackmaker [14]. The way GAD is measured from a trackway depends on the limb phase employed (Fig. 2A–D). During a trot, the contralateral (opposite side) fore- and hind limbs swing in sync (limb phase ~50%). In a walking trot, the moment the animal shifts its weight from one contralateral limb pair to the other, all four feet will contact the ground, and the GAD can now be measured between the midpoints of these pes- and manus positions (Fig. 2B). With a pace gait, in contrast, the ipsilateral (same side) fore- and hind limbs swing in sync (limb phase ~0%), resulting in a larger GAD value than for the trot (Fig. 2D). Theoretically, the GAD measure that precisely reflects the employed limb phase does not change with speed, because the trunk length it reflects must remain constant (the animal is not lengthening nor shortening). GAD measures that assume different limb phases can be taken along a trackway once per half step cycle. The GAD measure that shows the least variation is assumed to be the most likely to reflect the actual limb phase.

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

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

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

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

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

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

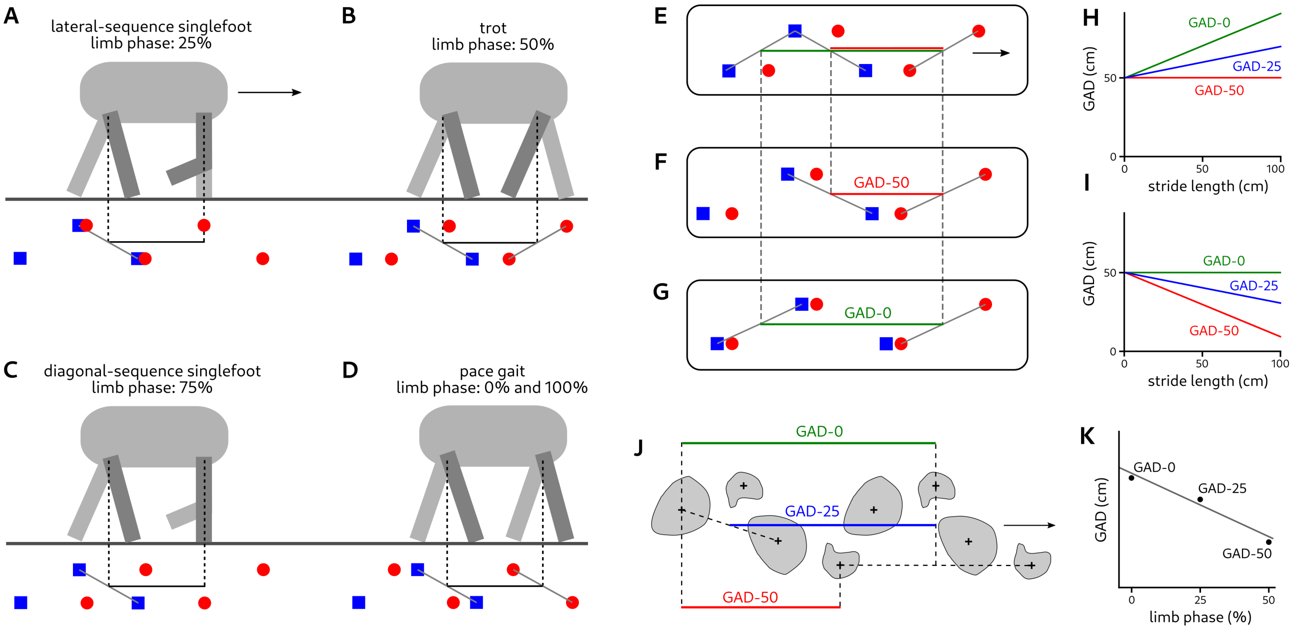

Figure 2. The influence of limb phase changes on trackway patterns. Squares indicate hind feet and circles forefeet footfalls; arrows indicate the direction of travel (left to right). A–D: Four discrete limb phases (25%, 50%, 75%, and 0/100%) and associated trackway patterns generated using Formula 1,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

Validation of results

We validated our approach on 15 trackways of various modern mammals of different body sizes and gaits, including three dogs, two horses, a camel, an elephant, a red fox, and a raccoon. For all trackways except for the red fox and the raccoon, the actually employed limb phase was extracted from video footage, allowing to determine the accuracy of our estimates. Several trackways were split into sections to determine how the methods perform on shorter trackways that exhibit less pronounced speed changes, resulting in a total of 32 trackways and trackway sections.

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	–	–

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

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

The presence of signal, and therefore the reliability of the estimate, may be assessed by plotting the GAD-0, GAD-25, and GAD-50 measures against stride length (Fig. 3C). We fit separate regression slopes to the point clouds of the three measures. A slope is expected to be horizontal if the GAD measure corresponds to the actually employed limb phase because trunk length does not change with speed (Fig. 2H–I). Significant differences in slopes are difficult to explain by other sources of variability that may overprint or skew the signal we aim to extract. However, the differences in slopes are significant ($p < 0.05$) only in 14 of the 32 mammal trackways and trackway sections.

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

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

Sauropod trackways

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

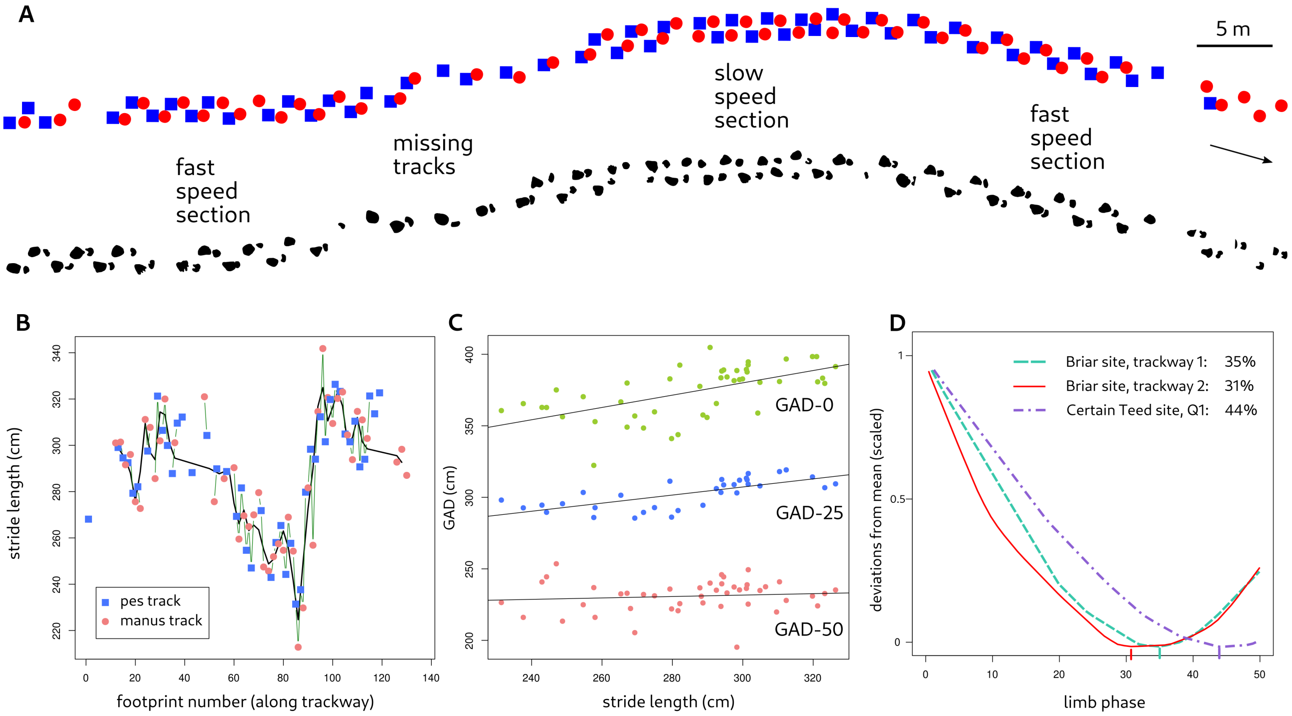

Figure 3. Results of the analysed sauropod trackways. A–C: The Certain Teed trackway (Q1) from the De Queen Formation of Arkansas, US [7]. A: Plotted track coordinates used for analysis (above) and site map of the trackway (below), where squares represent hind feet and dots forefeet. B: Differences in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

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

DISCUSSION

Generally high limb phases in wide-gauged sauropods are consistent with biomechanical considerations. Modern megaherbivores typically employ lateral-sequence walks somewhat below 25% unless running or moving very slowly (the short-legged common hippopotamus, which employs a trot, is a notable exception) [18]. However, these animals have very narrow gauges [1], unlike the wide-gauged sauropods analysed here. As gauge width increases, continuous diagonal supports become increasingly important [13]. In a pace gait, one side of the body is unsupported while the feet are swinging forwards. If the left and right feet are not placed precisely in front of each other, the centre of mass needs to constantly shift mediolaterally during walking in order to remain between the supporting limb pair. In a trot, in contrast, both body sides are always supported by at least one leg. We may assume that giant wide-gauged sauropods required diagonal supports throughout the step cycle to increase stability. Such continuous support of both body sides is only warranted at a limb phase of 25% or above, and, when at 25%, only at very slow gaits where one leg moves at a time (i.e., at duty factors >75%). The generally high limb phases reported here allow more efficient and/or faster walking while maintaining diagonal supports. At the same time, disadvantages of even higher limb phases approaching trots, including prevailing bipod rather than tripod supports [13] and more pronounced vertical accelerations [18], are avoided.

As direct records of animal activity, tracks provide information on extinct animals that cannot be derived from body fossils such as bones and teeth. While the importance of tracks as palaeobiological data sources cannot be overstated, their interpretation suffers from multiple levels of uncertainty, including time averaging of tracksites, trackmaker identification, and interpretation of track morphology and trackway patterns [20]. Limb phase, as a central parameter, is not only important in its own right, but may help to better constrain other uncertainties, such as duty factor and – because the apparent gleno-acetabular distance depends on limb phase – body size and shape of the trackmaker, which may eventually aid in identifying trackmaker taxa.

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AUTHOR CONTRIBUTIONS

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

DECLARATION OF INTEREST

The authors declare no competing interests.

STAR METHODS

RESOURCE AVAILABILITY

CONTACT FOR REAGENT AND RESOURCE SHARING

Lead Contact

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

Materials Availability

See Key Resources table for materials used in this study.

Data and Code Availability

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Modern mammals

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

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

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

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

Sauropods

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

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

Method details

Photogrammetry, data extraction, and analysis

All trackways of modern mammals, except for the camel, were digitised using photogrammetry [21]. Vertical photos were shot free-hand in sequence along the trackway from a height of approximately 2 m. High overlap (ca. 90%) between individual shots was aimed for in order to avoid little inaccuracies in image alignment, which along a long trackway would otherwise add up. A second photo sequence was shot in case the first set aligned imperfectly. At different points along the trackway, additional shots from different heights and camera orientations were shot of the same surface for calibration purposes. This process allowed for the accurate and time-efficient capture of large quantities of trackways. Photogrammetric models were then produced using Agisoft Metashape (agisoft.com). The horizontal plane was automatically fitted using the free software MeshLab (www.meshlab.net). Orthophotos and other graphical visualisations were produced with MeshLab; these outputs form the basis for our further analysis. See Lallensack et al. [22] for details on the photogrammetric procedure.

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

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

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

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Main approach

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

Additional approach 1

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

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

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

Additional approach 2

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

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

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

Validation

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

Changes in limb phase

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

Variation in limb phase that is not correlated with stride length is expected to increase noise, but will not skew overall results (although over- or underestimations due to such noise may occur by chance when few data points are available). More concerning are cases in which limb phase changes with stride length: a positive correlation between limb phase and stride length generally leads to an overestimation of the limb phase, while a negative correlation leads to an underestimation.

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

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

From the simulations, we derive the following observations:

1) positive correlation between stride length and limb phase leads to overestimation, and negative correlation to underestimation of the actually employed limb phase.
2) the slopes will be slightly curved upwards (if correlation is positive) or downwards (if correlation is negative) even when correlation is perfect.
3) The error (over or underestimation) increases with
    1) the Δlp/Δst ratio and
    2) the ratio between the minimum of the stride range and the GAD

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

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

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

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

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

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

Uncertain coupling values

The coupling value is the number of strides that separate pes- and manus tracks that belong to the same step cycle [15]. It can be high in long-bodied and short-legged animals or in such that make short steps (i.e., the manus may be several step cycles ahead of the pes as seen in a trackway).

While coupling values can be assumed *a priori* in most cases based on rough constrains on trackmaker anatomy, they may be ambiguous where trackmaker anatomy is very poorly constrained, especially in some long-bodied sprawling tetrapods. In such cases, coupling value may be determined by comparing the variability of GAD measurements that reflect the separate possibilities; the GAD measured between the pes and manus prints that are part of the same step-cycle should be expected to vary considerably less if speed changes (that are measurable as changes in stride length) occur. Evaluating this hypothesis on modern long-bodied sprawling tetrapods is, however, beyond the scope of the present study.

Additional resources

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

DATA AND SOFTWARE AVAILABILITY

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

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

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