

Article

Classical Hypotheses and New Tools in Dinosaur Ichnology: A Review of Footprints with Geometric Morphometrics, Machine Learning and Biomechanics

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Abstract

Dinosaur footprints are among the most abundant trace fossils, but they are not direct records of anatomy, behaviour or faunal composition. They preserve locomotion, substrate interaction and occurrence data only after those signals have been filtered by foot anatomy, movement, sediment properties and preservation. Classical dinosaur ichnology has relied on two-dimensional outlines, linear and angular measurements, qualitative ichnotaxonomy and influential hypotheses about trackmaker identity, speed, social behaviour and evolutionary timing. Here we review how these hypotheses are being reassessed with three-dimensional digitisation, geometric morphometrics, supervised and unsupervised machine learning, and biomechanical simulation. We first consider how different footprint representations, including interpretive outlines, landmarks, silhouettes, depth maps and three-dimensional models, shape the questions that track data can answer. We then assess analytical approaches ranging from multivariate statistics and landmark-based classifiers to convolutional neural networks and β -variational autoencoders. Against this methodological background, we revisit four linked problem domains: ornithomimid–theropod discrimination and the *Grallator*–*Anchisauripus*–*Eubrontes* plexus; speed and gait reconstruction; ecological and behavioural interpretations of track abundance, sauropod gauge and trackway arrangement; and macroevolutionary claims about body-size trends, functional morphotypes and avian-like pedal morphologies. Across these cases, newer methods rarely remove ambiguity. They more often show where classical interpretations are robust, where they depend on representation or prior labels, and where competing explanations remain hard to separate. We argue that footprint-based inference is strongest when tracks are treated as preservationally filtered products of anatomy, motion and substrate mechanics, and when they are integrated with skeletal data, experimental analogues and forward models in explicit, uncertainty-aware frameworks.



Academic Editor: Silverio Figueiredo

Received: 26 May 2026

Revised: 27 June 2026

Accepted: 1 July 2026

Published: 9 July 2026

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Keywords: dinosaur footprints; geometric morphometrics; machine learning; biomechanics

1. Introduction

Dinosaur footprints occupy an unusual place in the fossil record. They are often more abundant and spatially continuous than associated body fossils, and they preserve locomotor and substrate-interaction evidence that skeletons cannot record directly, although that evidence remains mediated by anatomy, kinematics and preservation [1–3]. Footprint and skeletal records are also commonly taphonomically decoupled. Conditions that favour

track formation and exposure need not favour burial and preservation of articulated skeletons. Tracks can therefore document dinosaur faunas in intervals or facies where body fossils are rare or taxonomically undersampled. This complementarity is clear in the Jurassic–Cretaceous boundary Tuchengzi Formation of northern China, where abundant dinosaur tracks supplement a sparse skeletal record, and in the Lower Cretaceous Jiaguan Formation of Sichuan and Chongqing, where extensive tracksites record diverse dinosaur and pterosaur activity in a region with uneven skeletal sampling [4–6]. Comparable cases occur elsewhere. On the Isle of Skye, Scotland, Middle Jurassic tracksites add sauropod, theropod, thyreophoran and possible ornithopod evidence to a fragmentary body-fossil record, indicating higher local dinosaur diversity than skeletons alone would suggest [7]. Footprints therefore do not duplicate skeletal evidence; they sample different preservational windows and can constrain diversity, habitat use and behaviour where osteological data are limited.

Footprint morphology is nevertheless the combined outcome of foot anatomy, limb kinematics and substrate mechanics [8,9]. The same pedal anatomy can leave markedly different impressions under different substrate and gait conditions, while distantly related taxa may converge on similar track forms in particular behavioural or environmental settings [8–11]. This superposition makes dinosaur tracks informative but difficult to interpret. Observed morphology is an integrated biological and taphonomic product, and separating those components requires explicit modelling rather than direct reading of the track surface.

For much of dinosaur ichnology, analytical practice was limited by available data and methods. Studies depended mainly on two-dimensional interpretive outlines, a small set of linear and angular measurements, and qualitative ichnotaxonomy supported by regional comparison [2,12]. Since the late twentieth century, multivariate statistics and geometric morphometrics have formalised these comparisons. Factor analysis and discriminant functions have tested separation between ornithopod and theropod tracks, whereas Procrustes alignment and principal component analysis have quantified shape variation, allometry and functional signal in tridactyl footprints [9,10,13,14]. These approaches sharpened inference, but they also exposed a persistent limitation: many track morphologies occupy continuous or overlapping regions of shape space rather than discrete, taxonomically clean clusters.

Several long-standing hypotheses have shaped dinosaur ichnology: that simple ratios and interdigital angles can separate ornithopod from theropod tracks; that the *Grallator*–*Anchisauripus*–*Eubrontes* plexus may represent an ontogenetic or allometric series; that trackway stride parameters can yield reliable speed estimates; that densely arranged or parallel trackways record behaviours such as predator-induced escape, migration or gregarious movement; and that slender, highly divaricate tridactyl tracks may indicate avian-like pedal morphologies before the oldest unambiguous avian body fossils [1,15–22]. These hypotheses were grounded in observable track morphology, trackway geometry or stratigraphic occurrence. Their weak point is the inferential gap between track shape and trackmaker biology. The gap is structural, not just a matter of sample size or measurement precision, because track morphology maps many combinations of anatomy, substrate and kinematics onto a smaller set of preserved shapes. Similar footprints can be produced by different feet under different conditions, and the same animal can produce different footprints as substrate or behaviour changes [8,9]. The central question is therefore how far the evidential basis of these classical interpretations can be tested using larger datasets, three-dimensional recording and model-based inference.

Three developments now make such re-evaluation possible. First, three-dimensional digitisation and standardised documentation protocols allow track surfaces to be captured, archived and re-analysed with explicit metadata, while automated outline extraction re-

duces, although it cannot remove, observer-dependent margin definition [3,23,24]. Second, geometric morphometrics and feature-based supervised classifiers have begun to quantify allometry, functional morphology and trackmaker discrimination across larger samples, including landmark datasets of more than 300 tridactyl footprints and machine learning models trained to distinguish ornithopod and theropod morphologies [9,25]. Third, image-based deep learning and unsupervised representation learning have expanded the analytical space: convolutional neural networks trained on 1372 silhouette outlines discriminate theropod from ornithischian tracks and expose cases where classification depends on outline interpretation, whereas β -variational autoencoders applied to 1974 silhouettes recover interpretable axes of shape variation without using prior taxonomic labels [26,27]. Track Recognition via Artificial Cognition (TRAC) extends this trajectory toward field-survey photographs and scalable semi-automated identification, but it remains at a preliminary data-curation stage rather than a validated ichnotaxonomic pipeline [28].

This review (Figure 1; Table 1) is organised around hypotheses rather than methods alone. After outlining changes in data acquisition and geometric representation, we survey analytical frameworks from multivariate statistics through supervised and unsupervised machine learning, and then discuss numerical simulation in locomotor and biomechanical inference. We next examine four linked problem domains: trackmaker identification and ichnotaxonomy; locomotion and biomechanics; behaviour and palaeoecology; and macroevolutionary questions concerning body-size trends, functional morphotypes and avian-like footprints. We also note that the new methods should not be treated as replacements for field observation, traditional measurement or ichnological expertise. Instead, we need to ask which long-standing interpretations remain well supported when tracks are analysed as indirect outcomes of anatomy, motion, substrate and preservation, with preservation quality, sample size and representation treated as first-order constraints.

Table 1. Classical hypotheses in dinosaur ichnology and their reassessment in this review. The table summarises the four problem domains considered here, linking classical interpretations to the newer analytical approaches, remaining uncertainties and representative studies discussed in the text.

Problem Domain	Classical Inference	Reassessment in This Review	Main Uncertainty	Key Examples
Trackmaker identification and ichnotaxonomy	Track outlines, digit proportions, divarication, pad/claw morphology and ichnotaxonomic comparison used to assign tracks to theropods, ornithopods or named ichnotaxa	Geometric morphometrics, supervised classifiers and CNNs show that many assignments are useful but probabilistic, especially where morphospaces overlap	Preservation quality, outline representation, prior labels, body size and functional convergence	[9,13,14,25,26,29]
Locomotion and biomechanics	Stride length, pace, trackway geometry and estimated hip height used to infer speed, gait and posture	Experimental trackways, 3D models, DEM simulation and musculoskeletal modelling test whether proposed motions and speeds are mechanically plausible	Hip-height uncertainty, substrate compliance, undertrack formation, depth-dependent deformation and foot motion through sediment	[15,30–35]
Behaviour and palaeoecology	Track abundance, repeated trackways, gauge, parallelism and trackway arrangement used to infer faunal composition, gregariousness or habitat use	Track abundance, gauge and parallel trackways are treated as useful evidence, but only after considering preservation, exposure, recognisability and time averaging	Preservational bias, repeated use of surfaces, temporal resolution, substrate-driven gauge variation and uncertainty in trackmaker identity	[5,36–40]
Macroevolution and timing	Track size, functional morphotypes and bird-like tridactyl morphologies used to infer body-size trends, functional transitions and possible early avian-like pedal morphology	Large comparative datasets and morphospace models can identify functional or avian-like shape signals, but these signals must be integrated with stratigraphy and skeletal evidence	Sampling bias, convergence, stratigraphic error, weak trackmaker linkage and the difference between avian-like morphology and avian affinity	[9,22,27,41]

Re-evaluating dinosaur footprints

Classical hypotheses, new tools, and cautious inference

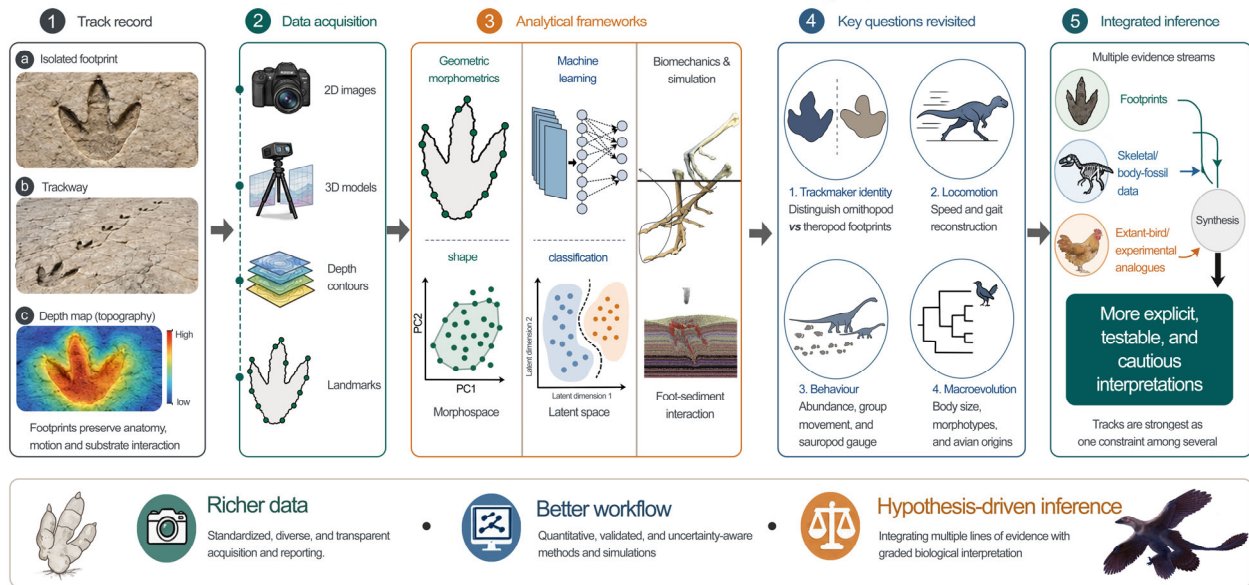


Figure 1. Integrated analytical and inference framework for dinosaur ichnology. The workflow links data acquisition, quantitative analysis, and biological synthesis. Data acquisition utilises 2D images and 3D models of isolated footprints and trackways to extract topography, depth contours, and landmarks. Analytical frameworks employ geometric morphometrics and machine learning to project these features into morphospaces and latent dimensions for shape classification. This structural pipeline addresses four core areas: trackmaker identity, locomotion, behaviour, and macroevolution. Track data are then integrated with skeletal fossils and extant analogues to support hypothesis-driven, uncertainty-aware biological interpretations. The “Biomechanics & simulation” and “Foot-sediment interaction” are adapted from Falkingham et al. [33] and Falkingham and Gatesy [11]. Bottom right *Microaptor* drawn by Ms. Yi Liu.

2. Data Acquisition and Representation

2.1. From Interpretive Drawings to Reproducible Digital Records

Early dinosaur-track studies relied on field sketches, tracings on transparent film, latex or silicone moulds, plaster casts and photographs. These methods remain valuable, especially for historically important sites that are inaccessible or degraded. They also provide the field context, repeated measurements and preservation observations against which newer analytical outputs have to be checked. For the questions addressed here, their limitation is that they often compress a three-dimensional, taphonomically complex structure into a two-dimensional interpretation without recording the criteria used to define the footprint margin. The effect is substantial: footprint length, width, digit divarication and apparent pad morphology can change with lighting, contour level, substrate deformation and the observer’s decision about where the anatomical track ends and extramorphological deformation begins.

Over the past two decades, close-range photogrammetry and laser scanning have changed the baseline expectation for ichnological documentation by allowing high-resolution three-dimensional surface models to be captured, scaled, oriented, archived and re-analysed [23,42]. Falkingham et al. [23] framed standardisation as a reproducibility problem: track data should remain useful to future researchers rather than survive only as selected figures or interpretive outlines. Three-dimensional capture does not solve taxonomic or behavioural interpretation on its own, but it preserves information that can later be examined using alternative contours, depth maps, relative-depth patterns or

numerical models [43]. This matters for machine learning because model performance depends on the repeatability, resolution and metadata quality of the input data as much as on algorithm choice. Terminological consistency is also important, because terms such as track, undertrack, true track and elite track have not always been used uniformly [44].

2.2. Landmark-Based Representations and Geometric Morphometrics

Despite the growth of three-dimensional documentation, much comparative work still reduces footprints to two-dimensional landmark configurations. In landmark-based geometric morphometrics, homologous or operationally repeatable points are placed on each footprint, aligned by Procrustes superimposition and analysed in multivariate shape space. The method retains spatial relationships among interpretable regions, such as digit tips, lateral digit margins and heel position, while removing variation due to position, orientation and scale. Lallensack et al. [9] used a literature-derived dataset of 303 tridactyl dinosaur footprints to quantify allometry, functional signal and differences between theropod and ornithischian morphologies. Their results showed that size and function strongly structure footprint shape, and that theropod–ornithischian separation is neither uniform across body sizes nor reducible to a single measurement. As body size increases, width-related features become more diagnostic than digit projection, so fixed metric thresholds lose power at the extremes of the size range [9].

Landmark datasets also inherit the assumptions used to define the original outline and the landmarks. Homology is often operational rather than strictly anatomical, particularly where pad boundaries are poorly preserved or the heel region grades into surrounding sediment. Literature-derived datasets combine drawings produced by different workers, under different conventions and preservation conditions. Lallensack et al. [9] acknowledged these problems and noted that published outline drawings can differ between researchers; large samples partly buffer non-systematic error, but they do not remove it. Landmark-based morphometrics is therefore a powerful comparative abstraction, not a direct measurement of original foot anatomy.

2.3. Silhouette Outlines and Image-Based Representations

A second strategy treats the footprint outline, rather than a predefined set of landmarks, as the analytical object. This approach is attractive because many diagnostic criteria used by ichnologists, including digit proportions, divarication, heel shape, claw expression and pad outline, are expressed along the external contour of the track. It also allows footprints to be represented as standardised binary images that can be used directly in convolutional neural networks without manually selecting measurements or landmarks. Lallensack et al. [26], for example, trained a deep convolutional neural network on 1372 silhouette outlines to discriminate theropod and ornithischian tracks, showing that image-based models can capture shape information missed by simple linear metrics.

The strength of silhouette-based representation is also its main weakness. A silhouette is a compressed interpretation of a three-dimensional structure, not a neutral record of the track. Published outlines may encode different decisions about whether collapsed track walls, displacement rims, claw traces or undertrack components belong to the “footprint”. Lallensack [24] addressed this problem with an R-based algorithm that derives repeatable outlines from 3D models by tracing the region of steepest slope along the footprint wall. The method reduces observer subjectivity and provides a reproducible basis for shape analysis, but it does not remove interpretive uncertainty. The steepest-slope contour may still include features unrelated to pedal anatomy, and faint anatomical details may be lost. It also presupposes a 3D model with sufficient resolution and relief; for weathered surfaces, undertracks or specimens with indistinct walls, the algorithm may produce outlines that

are repeatable but anatomically weak. Lallensack [24] therefore treated objective outlines as a basis for interpretation, not as a substitute for expert evaluation.

For machine learning, this distinction is critical. CNNs can learn subtle contour information, but classification performance remains bounded by the training set: outline conventions, preservation filters, taxonomic labels, image orientation, scale normalisation and publication history. Lallensack et al. [26] noted that silhouettes maximise sample size and remove much irrelevant visual noise, but at the cost of subjectivity and information loss relative to 3D models. Ha and Kim [45] likewise demonstrated the usefulness of CNN-based transfer learning for classifying large ornithopod ichnotaxa, while stressing that performance depends on the quality of footprint illustrations and that supervised models cannot recognise classes absent from the training labels. Image-based representations are therefore best read as model-assisted comparisons within existing labelled morphologies, not as direct taxonomic determinations.

2.4. Mesh-, Depth- and Volume-Based Representations

The most information-rich footprint representation is a full three-dimensional description of the surface and, where available, subsurface deformation. Photogrammetric or laser-scanned models can be analysed as meshes, height fields, contour stacks, slope maps, curvature plots or relative-depth maps. Unlike landmarks and silhouettes, these representations preserve information about depth, wall geometry, sediment displacement and the relationship between surface and transmitted structures. This matters because footprint morphology is produced partly by sediment failure and track-wall deformation, not only by the contact geometry of the foot. A surface outline integrates foot geometry, withdrawal kinematics and the elastic and plastic response of the substrate; considered alone, it may be a poor proxy for either anatomy or motion.

Three-dimensional representation becomes especially important when footprints are used to infer locomotor mechanics. Falkingham and Gatesy [32] combined X-ray reconstruction of moving morphology with discrete element simulation to show that track formation is dynamic: the exposed surface, subsurface deformation and final track morphology may differ substantially. Their work showed that a footprint has an ontogeny, forming through successive interactions between foot motion and sediment response rather than appearing as a static mould of the foot. Earlier experimental and fossil studies reached a similar point from observed tracks: emu tracks vary with walking pattern and substrate consistency [30], theropod traces can record foot movement through sediment [31], and undertracks can preserve deformation below the true track surface [46]. Falkingham et al. [33] extended this approach to fossil tracks by using digitisation and simulation to test alternative hypotheses of dinosaur foot motion against observed deformation patterns. These studies show why a full 3D structure is not just a richer illustration of the same evidence, but a different evidential object for testing biomechanical hypotheses.

Mesh- and volume-based representations remain underused in computational work because they are harder to standardise than outlines and require larger datasets, consistent metadata and more demanding architectures. Current dinosaur-track machine learning studies therefore still rely mainly on landmarks or 2D silhouettes, which are computationally efficient and can be compiled from the published literature. Lallensack et al. [26] noted that future networks trained directly on 3D models may reduce some information loss inherent in silhouettes, but this will require broader digitisation and larger curated 3D datasets. In the current data landscape, the practical issue is not to choose one representation as universally superior. Landmarks, silhouettes and meshes answer different questions: landmarks formalise comparable shape variables, silhouettes support scalable

image-based classification, and 3D models preserve the deformation context needed for biomechanical and taphonomic inference.

3. Analytical Frameworks

3.1. Multivariate Statistics and Geometric Morphometrics

The first generation of quantitative dinosaur-track studies formalised distinctions that had previously rested largely on expert visual comparison. Moratalla et al. [13] applied factor analysis and linear discriminant analysis to Lower Cretaceous tridactyl footprints to test whether linear and angular variables could discriminate ornithopod and theropod tracks in multivariate space. This work converted qualitative characters, including relative digit lengths, footprint width, digit divarication and mesaxony, into explicit variables that could be evaluated statistically. Later studies used related approaches to classify medium-sized tridactyl tracks and evaluate trackmaker hypotheses in local ichnofaunas, including Berriasian ornithopod-dominated assemblages from Spain [14].

The apparent objectivity of multivariate space depends on prior decisions: which measurements are chosen, how footprint margins are defined, which specimens are included and which labels are assumed to be correct. Linear discriminant analysis is especially vulnerable when groups overlap, sample sizes are modest or class proportions are uneven. These conditions are common in dinosaur-track data because substrate deformation, preservation quality and functional convergence often coincide with overlapping morphologies and uneven sampling. Early multivariate methods improved transparency, but they did not remove the dependence of classification on input definitions. They remain indispensable starting points, especially when preservation quality is high and sample sizes are large enough to show repeated patterns rather than isolated exceptions.

Geometric morphometrics shifted the problem by analysing overall landmark configurations rather than isolated ratios. Procrustes superimposition and principal component analysis allow shape variation to be examined independently of position, orientation and scale, while regression against centroid size can test allometric effects. Lallensack et al. [9] used a literature-derived sample of 303 tridactyl footprints from 134 publications to show that size and function strongly structure footprint shape: digit III projection and length-to-width ratio decrease with increasing size, whereas relative digit width increases, especially in ornithischian tracks. Their analysis also showed that theropod and ornithischian tracks occupy overlapping regions of morphospace, particularly where size and functional morphology converge. For the present review, this is a key result: geometric morphometrics did more than refine ichnotaxonomy; it showed that some classical taxonomic boundaries are probabilistic rather than discrete.

3.2. Feature-Based Supervised Classification

Feature-based supervised learning extends the same logic. Instead of assuming that a small set of ratios or discriminant axes is sufficient, algorithms such as logistic regression, support vector machines, random forests and multilayer perceptrons learn classification boundaries from labelled shape variables. Jones et al. [25] used the landmark dataset of Lallensack et al. [9], converting the 20 two-dimensional landmark coordinates into distances from the footprint centre before training several classifiers. Their best-performing method, a multilayer perceptron, achieved approximately 90% accuracy on the test set, with roughly balanced recall for ornithopods and theropods despite class imbalance.

The main contribution of this approach is not higher accuracy alone. It allows classical criteria to be checked against learned variable importance and misclassification patterns. Jones et al. [25] found that some landmarks selected by logistic forward regression occur in intuitively informative regions, such as the distal and posterior parts of the footprint, while

specimens misclassified by multiple models often show compromised shape or features typical of the alternative class. Supervised learning is therefore useful as a diagnostic tool for uncertainty: it identifies specimens whose morphology fits poorly within a binary theropod–ornithischian assignment and highlights regions of morphospace where classical criteria lose discriminating power.

The limitations are just as important. Supervised classifiers inherit their training labels, and those labels are ichnological interpretations. If training data contain misidentified tracks, preservationally biased samples or inconsistent outline conventions, the model will formalise those biases rather than correct them. Class imbalance is also persistent because theropod-like tridactyl tracks are more common in many compiled datasets than ornithischian tracks. Jones et al. [25] found that several models performed worse on the minority ornithopod class, whereas the multilayer perceptron handled the imbalance better. Feature-based supervised learning should therefore be treated as a way to quantify classification probability under specified assumptions, not as an independent authority on trackmaker identity.

3.3. Image-Based Deep Convolutional Networks

Deep convolutional neural networks shift the analytical unit from predefined measurements to rasterised images. In dinosaur ichnology, this has so far mainly meant binary silhouette outlines rather than raw field photographs or full three-dimensional models. Lallensack et al. [26] trained a modified VGG-style deep convolutional neural network on 1372 standardised tridactyl footprint silhouettes labelled as theropod or ornithischian. The model outperformed five human experts on an independent test set and was then applied to the contentious large tridactyl tracks from Lark Quarry.

This approach is useful for more than automation. CNNs can use distributed contour information, including digit curvature, heel geometry and relative digit proportions, without requiring these variables to be specified in advance. In the Lark Quarry analysis, Lallensack et al. [26] used Grad-CAM (Selvaraju et al. [47]) to visualise the image regions contributing to classification. For track LQ1-3, the highlighted regions indicated that digit III curvature and heel shape were important in producing a theropod-like score. Such visual explanations can test whether the network is attending to biologically plausible regions, but they do not validate the taxonomic attribution by themselves.

Substantial limitations remain. Silhouettes depend on prior outline interpretation, and classification can change when different researchers draw the same footprint differently or when different depth contours are extracted from the same 3D model. Lallensack et al. [26] used black-and-white silhouettes to maximise sample size and remove irrelevant visual noise, but acknowledged that the outlines retain subjectivity and simplify complex three-dimensional morphology. Ha and Kim [45] extended CNN-based classification to large ornithopod ichnotaxa using Xception transfer learning, but their study also illustrates a common constraint of supervised deep learning: model performance depends on illustration quality, and the model can classify only among labels present in the training data. CNNs should therefore be treated as comparative tools within a defined image-label space, not as independent authorities on trackmaker identity.

3.4. Unsupervised and Generative Models

Most machine learning applications in dinosaur ichnology have been supervised, meaning that the model learns from labels assigned by previous researchers. This is useful when labels are reliable, but problematic when labels encode contested interpretations. Unsupervised representation learning asks a different question: which axes of variation structure the data before taxonomic labels are imposed?

Hartmann et al. [27] applied a disentangled β -variational autoencoder to 1974 two-dimensional dinosaur footprint silhouettes spanning non-avian dinosaurs, fossil birds and extant ground-dwelling birds. The network was trained without taxonomic labels and identified eight interpretable axes of shape variation: overall load and shape, digit spread, digit attachment, heel load, digit and heel emphasis, loading position, heel position and left–right load. After training, expert labels were projected into the latent space, and distance-based comparisons showed 80–93% agreement with expert identifications for relatively unambiguous specimens.

This approach is especially relevant for contentious tracks because it reduces circularity, although it cannot eliminate it. Triassic–Early Jurassic “bird-like” tracks can be placed in a learned morphospace and compared quantitatively with fossil birds, modern birds and non-avian theropods without first assigning them to any one of those categories. Hartmann et al. [27] found that some problematic bird-like tracks group more closely with fossil and modern birds than with non-avian theropods. The interpretation must remain cautious: latent-space proximity demonstrates morphological similarity, not phylogenetic identity. A β -VAE cannot distinguish an early avian trackmaker from a non-avian dinosaur with convergently avian-like pedal morphology. Its value is to make this ambiguity explicit and measurable.

4. Trackmaker Identification and Ichnotaxonomy

4.1. Ornithopod Versus Theropod: From Diagnostic Characters to Probabilistic Assignment

The distinction between ornithopod and theropod tridactyl tracks has long been a central test case for dinosaur ichnology. Classical criteria are familiar: theropod tracks are usually described as narrower, more elongate and more asymmetric, with stronger digit III projection, sharper claw traces and lower interdigital divarication; ornithopod tracks are usually broader, more symmetrical and more blunt-toed, with shorter digit III projection and wider digit impressions. These distinctions are useful for idealised morphotypes, but they do not form stable diagnostic rules across the full range of track sizes, substrates and functional morphotypes. Moratalla et al. [13] formalised the problem by using multivariate analysis to discriminate Lower Cretaceous ornithopod and theropod tracks, while Castanera et al. [14] later applied related quantitative criteria to medium-sized Berriasian tridactyl tracks from Spain. These studies made the criteria testable; they also showed that separation depends on sampled morphospace, preservation quality and prior trackmaker assignments, which are rarely uniform across published ichnofaunas.

Larger datasets make the boundary less discrete. Lallensack et al. [9] analysed 303 tridactyl footprints and showed that theropod–ornithischian differences vary with size: at smaller sizes, interdigital angle and digit III projection are more informative, whereas at larger sizes digit widths and overall proportions become more important. This result weakens fixed-threshold ichnotaxonomy because the same measurement can have different discriminating value depending on size, functional morphology and preservation. Lallensack et al. [9] further showed that the two groups occupy overlapping regions of shape space rather than cleanly separable clusters, particularly in the mid-size range where functional convergence is most pronounced. This result supports the use of classical characters: well-preserved tracks with clear pads, consistent digit proportions and repeated trackway patterns can still support strong assignments, whereas isolated or poorly preserved tracks require wider uncertainty bounds.

Machine learning studies sharpen this conclusion rather than overturn it. Jones et al. [25] showed that feature-based classifiers trained on landmark-derived variables can reach approximately 90% accuracy, but that some models perform worse on the minority ornithischian class and that misclassified specimens often show compromised shapes or characters

typical of the alternative group. Lallensack et al. [26] trained a DCNN on 1372 silhouettes and found that it outperformed five human experts on a difficult test set, while also noting that the approach remains an early step limited by subjectivity and information loss in interpretive outlines. The appropriate conclusion is probabilistic: many tracks can be assigned confidently to a theropod-like or ornithischian-like region of morphospace, but some cannot be resolved from footprint shape alone. Downstream inferences that depend on binary trackmaker identity, such as predator–prey ratios, faunal composition or behavioural reconstruction, should propagate this uncertainty instead of treating assignments as error-free.

4.2. The *Grallator*–*Anchisauripus*–*Eubrontes* Plexus: Allometry, Taxonomy and Functional Convergence

The *Grallator*–*Anchisauripus*–*Eubrontes* plexus is a second test case because it links ichnotaxonomy directly to ontogeny and body-size inference. Olsen et al. [29] re-examined the type material of *Eubrontes giganteus*, *Anchisauripus sillimani* and *Grallator parallelus* from Early Jurassic strata of the Hartford and Deerfield basins. They concluded that the three ichnotaxa were most likely made by theropod dinosaurs, but also noted that their major proportional differences could reflect allometric growth among related species or even within a single trackmaker species. This observation underpins the view that the plexus may be a size-related series rather than three sharply separated biological taxa.

The broader comparative record complicates a simple growth-series interpretation. Lallensack et al. [9] showed that digit III projection and length-to-width ratio decrease with footprint size across tridactyl dinosaur tracks more generally, while relative digit width increases, especially in ornithischians. These trends resemble the proportional changes classically invoked for *Grallator*, *Anchisauripus* and *Eubrontes*, but their occurrence across broader taxonomic and functional contexts means they cannot demonstrate a single ontogenetic sequence on their own. Shared allometric trajectories may reflect ontogenetic growth within a lineage, yet similar patterns can arise from biomechanical scaling constraints and functional convergence toward graviportal morphologies at larger body sizes. Without independent skeletal or trackway evidence, these alternatives are difficult to separate.

The most defensible interpretation is mixed. The *Grallator*–*Anchisauripus*–*Eubrontes* plexus almost certainly contains a size-related component, and the type material remains central for Early Jurassic theropod ichnotaxonomy. Proportional continuity, however, is not the same as conspecific ontogeny. Without independent stratigraphic, trackway and skeletal constraints, the same pattern can be explained by overlapping taxa, related species with similar scaling trajectories or repeated functional convergence. The plexus is best treated as an unresolved partitioning problem among ontogenetic, taxonomic and functional sources of variation. Mixture models or latent-cluster analyses in landmark-size space could address this problem in principle, but they have not yet been applied specifically to the Newark material.

4.3. The Lark Quarry Tracks: When Classification Depends on Representation

The Lark Quarry tracksite in the Winton Formation of Queensland has become a model case for the limits of trackmaker identification. Thulborn and Wade [17] interpreted the assemblage as evidence of a “dinosaur stampede”, with a large theropod trackmaker triggering escape behaviour among smaller dinosaurs. Subsequent work challenged both parts of this interpretation: the identity of the large trackmaker and the behavioural inference drawn from the spatial arrangement of tracks. Romilio and Salisbury [20] reanalysed the large tracks using multivariate shape variables, noted morphological similarity to the ichnotaxon *Amblydactylus gethingi* and suggested an iguanodontian trackmaker. Romilio et al. [39] further questioned the stampede interpretation by re-examining the small tracks at Lark

Quarry. They showed that tracks previously separated as small theropod-type *Skartopus* and ornithopod-type *Wintonopus* can co-occur within individual trackways, and that some elongate digit traces reflect foot movement through sediment rather than discrete track-maker anatomy. In many cases, these traces may represent swimming or partially buoyant locomotion rather than running on exposed substrate [39].

Three-dimensional reanalysis made the problem clearer. Romilio and Salisbury [21] used 3D photogrammetric protocols and archival comparisons to show that several original outlines differed substantially from the preserved track morphology; some incorporated cracks or restoration-related modifications into footprint margins, and the best-preserved tracks showed blunt digit impressions consistent with an ornithopod interpretation. They also argued that overprinted traces and track succession make direct interaction between large and small trackmakers unlikely. Thulborn [48] contested parts of the ornithopod reinterpretation. For this review, the disagreement is informative because it did not arise simply from a lack of quantitative methods. It arose from different choices about which track features, outlines and preservation levels should be treated as anatomically informative.

Lallensack et al. [26] later used the Lark Quarry material as a test case for machine learning. Their CNN classified most large-track silhouettes as ornithischian-like, but one specimen, LQ1-3, received a stronger theropod-like score; Grad-CAM visualisation indicated that digit III curvature and heel shape contributed to that classification. More importantly, classification depended partly on representation. Outlines drawn by different researchers, or extracted from different contour levels of the same 3D structure, could yield different results. This is the central lesson of Lark Quarry: machine learning can make conflicting interpretations more explicit, but it cannot decide which surface, contour or outline best represents the original biological footprint. The case cautions against using track morphology alone to infer dramatic behaviours such as predator-induced stampedes. Lark Quarry is not only a dispute over whether one trackmaker was theropod or ornithopod; it shows how taxonomic and behavioural inference can become unstable when preservation, representation and prior interpretation are not separated.

5. Locomotion and Biomechanics

5.1. Speed Estimates: Useful Approximations with Limited Precision

Alexander's speed equation has shaped dinosaur-trackway interpretation because it gave researchers a simple way to convert stride length and estimated hip height into locomotor speed. In the original study, Alexander [15] derived an empirical relationship between dimensionless speed, stride length and hip height from living animals and applied it to dinosaur trackways, obtaining relatively low estimates of approximately 1.0–3.6 m/s. Because hip height cannot be measured directly from fossil trackways, Alexander approximated it as about four times footprint length. Later ichnological studies often adopted this approximation as a default parameter, with limited independent validation. The method was operationally powerful, but it embedded two major assumptions: that hip height can be inferred reliably from footprint length, and that relationships calibrated mainly from extant animals moving on firm substrates can be transferred to fossil trackways formed in compliant sediment.

Alexander-type equations are useful, but their uncertainty is often understated. Hip-height estimates vary with clade, size, limb posture and pedal anatomy. Footprint length can be distorted by substrate consistency, slipping, collapse of track walls, undertrack formation and erosion. Stride length is also not a pure kinematic variable; it can vary with acceleration, turning, substrate compliance and behavioural state. A single speed estimate therefore combines uncertainty in trackmaker identity, hip-height scaling, substrate mechanics and gait.

Prescott et al. [35] directly tested this problem using helmeted guineafowl moving over mud of different consistencies. Speeds measured from video ranged from 0.04 to 0.97 m/s, whereas speeds calculated from trackways using Alexander's equation ranged from 0.17 to 1.84 m/s. Calculated speeds were consistently higher than measured speeds, ranging from 1.17 to 4.74 times the measured values; even above approximately 0.3–0.4 m/s, calculated speeds remained about 1.2–2.5 times higher than measured speeds. The study also found that stride length varied within trackways even when speed was relatively constant, and that similar stride lengths could be produced at different actual speeds. These results do not invalidate all previous dinosaur speed estimates, but they change their evidential status. Trackway-derived speeds are best treated as approximate constraints on relative locomotor regime, not as precise measurements. They may help distinguish very slow movement from unusually rapid movement, but they should not be used alone to infer running, pursuit, escape or predator–prey interaction.

5.2. Depth Structure and Numerical Simulation

Speed estimates reduce trackways to stride geometry, whereas footprint formation is a three-dimensional deformation process. This distinction matters because the exposed surface is only one expression of a deeper sedimentary structure. Falkingham and Gatesy [32] used biplanar X-ray reconstruction of moving morphology (XROMM) to record the hindlimb motion of guineafowl walking through dry granular substrate, then incorporated the resulting three-dimensional kinematics into discrete element method (DEM) simulations. Their digital track models allowed deformation to be visualised at the surface and along virtual bedding planes, showing that track formation is a dynamic sequence of foot–substrate interactions rather than a static mould of pedal anatomy.

This framework is directly relevant to fossil dinosaur tracks because deep, penetrative tracks may record foot motion more extensively than shallow, foot-shaped impressions. Falkingham et al. [33] used deep Jurassic dinosaur tracks that had naturally split into layers to reconstruct hypotheses of foot motion and then tested those hypotheses with DEM simulations. Simulations whose predicted deformation patterns matched the observed cross-sectional morphology supported a proposed motion as consistent with the fossil evidence; simulations producing discordant morphologies rejected or refined the hypothesis. The implication is that track interpretation should move from direct reading to model comparison. A surface footprint may be ambiguous or distorted, but internal deformation can preserve evidence of entry angle, withdrawal path, digit motion and substrate response. Conversely, similar surface outlines may result from different combinations of kinematics and sediment properties.

5.3. Musculoskeletal Models and Integrated Biomechanical Constraints

Trackway evidence is strongest when combined with independent biomechanical constraints. Musculoskeletal modelling provides one such constraint because it tests which limb postures, joint motions and force regimes are mechanically plausible for a reconstructed animal. Bishop et al. [34] outlined a workflow for locomotor biomechanical analysis of extinct species, using *Coelophysis bauri* as a case study. Their workflow proceeds from digital capture of fossil bone morphology to jointed skeletal reconstruction, estimation of mass properties, soft-tissue and muscle reconstruction, computational musculoskeletal modelling and biomechanical simulation.

For ichnology, musculoskeletal modelling should constrain footprint interpretation rather than replace it. If a trackway-derived speed, gait or posture requires implausible joint excursions or force patterns for the reconstructed limb, the trackway inference should be reconsidered. Conversely, footprints document substrate interaction, pace and stride

parameters, and trackway patterns that record in situ locomotor behaviour under specific environmental conditions, information that skeletal models alone cannot provide. A stronger future framework would combine these sources hierarchically: skeletal models constrain feasible kinematics; substrate simulations generate possible track morphologies; empirical trackways provide observed constraints; and statistical or machine learning models estimate support for competing locomotor scenarios. This would move dinosaur locomotion studies away from single-point reconstructions toward explicit uncertainty propagation across anatomy, behaviour and preservation.

6. Behaviour and Palaeoecology

6.1. Track Abundances and the Problem of Ecological Inference

Track assemblages are tempting ecological datasets because they can contain hundreds or thousands of traces on a single bedding surface. In principle, such assemblages could inform questions about local abundance, habitat use, activity levels and community composition. In practice, observed track abundance is filtered through preservation, exposure and discovery. A track-bearing surface records animals that crossed a suitable substrate during a limited temporal window under conditions favourable for impression and burial. It enters the record only if that surface is later exhumed and discovered. It does not directly record standing population size.

This problem is especially relevant to theropod-dominated assemblages. Tridactyl theropod-like footprints are common in many Mesozoic tracksites, but high track frequency need not imply unusually high predator biomass. It may also reflect preservational and recognisability biases. Narrow tridactyl impressions are often easier to delimit and classify than broad, shallow or poorly bounded traces, especially where substrate deformation or erosion obscures footprint margins. Herbivorous dinosaurs, by contrast, may produce broad, shallow or poorly delimited traces that are harder to classify when preservation is poor. Lallensack et al. [9] showed that theropod and ornithischian tracks overlap in parts of shape space and that size and function strongly influence tridactyl footprint morphology, reinforcing the point that abundance estimates based on simple morphotype counts are not taxonomically neutral.

Small tracks expose the same bias at a different scale. *Minisauripus* is a useful example because it represents extremely small non-avian theropod tracks from East Asia. Kim et al. [38] reviewed more than 80 well-preserved *Minisauripus* tracks comprising at least 50 trackways from two localities in China and five in Korea, with foot lengths mostly in the 1.5–6.0 cm range, and interpreted them as evidence for diminutive theropod trackmakers. Xing et al. [40] later described a Lower Cretaceous *Minisauripus* assemblage from the Feitianshan Formation at Yangmozuo, Sichuan Province, where three trackways comprising ten pes impressions of 2.5–2.6 cm length were assigned to *Minisauripus*, and noted that all unequivocally identified *Minisauripus* tracks across known sites fall within approximately 1.0–6.1 cm. The point is not simply that small dinosaurs existed. It is that skeletal and ichnological records sample body-size distributions differently. Abundance patterns in track assemblages therefore require explicit correction for preservation probability, exposure area, sampling intensity and identification uncertainty before they can be used as ecological proxies.

6.2. Sauropod Gauge, Trackway Geometry and the Evidence for Gregarious Behaviour

Sauropod trackways have often been used to infer social behaviour, especially where multiple large trackways occur on the same surface with similar orientations. The underlying inference is straightforward: parallel trackways of similar-sized animals on the same surface may record coordinated group movement. The difficulty is temporal reso-

lution. Tracksites rarely preserve time finely enough to distinguish a cohesive herd from repeated passage along the same corridor. Parallelism, similar pace length and comparable footprint size are consistent with gregarious movement, but they do not by themselves demonstrate simultaneity.

Gauge adds another layer of inference. Wilson and Carrano [36] argued that wide-gauge sauropod trackways are linked to titanosauriform or titanosaur sauropods and reflect anatomical differences in limb posture and body breadth rather than arbitrary behavioural variation. Their study connected trackway geometry to skeletal morphology, making gauge a potential source of systematic and functional information rather than a purely descriptive variable. At the same time, gauge is not a simple taxonomic character. It can vary with turning, substrate consistency, preservation level and the exposed depth within a transmitted-track complex. Some effects are predictable: turning increases apparent gauge on the outer side of a curve, and deeper exposure within a transmitted-track complex tends to broaden apparent footprint and trackway dimensions. Other effects, such as substrate-driven postural adjustment, are harder to model without experimental data on the relevant taxa.

Castanera et al. [37] illustrated this problem with two Berriasian sauropod trackways from the Cameros Basin of Spain, in which gauge varied substantially along the same trackway. They linked these changes to turning behaviour in one case and to reduced speed, probably associated with substrate properties, in another. This does not negate the systematic value of gauge, especially where numerous well-preserved trackways show a consistent narrow- or wide-gauge pattern; it means that gauge should be interpreted together with behaviour, substrate and preservation level rather than as a fixed taxonomic character.

The behavioural inference is therefore probabilistic. Multiple parallel sauropod trackways of similar size, similar direction and comparable pace may increase the likelihood of group movement, especially if trackway spacing and sedimentological evidence suggest formation on the same exposed surface. That evidence still has to be weighed against alternatives: repeated use of shorelines or migration corridors, substrate-controlled pathway selection, or time-averaged accumulation on a persistent surface. Future work should treat trackway arrangement as spatial data rather than anecdotal evidence. Orientation, spacing, gauge, pace length, footprint size and cross-cutting relationships could be analysed jointly to test whether a surface contains statistically coherent trackway bundles or time-averaged traffic.

7. Macroevolution and Timing: Size Trends, Functional Transitions and Avian-like Footprints

7.1. Body-Size Trends and Functional Morphotypes Through the Mesozoic

Footprints provide an independent record of functional morphology because they preserve the geometry of the weight-bearing foot during substrate contact. Lallensack et al. [9] analysed 303 tridactyl dinosaur footprints from 134 publications and showed that footprint size and shape are strongly coupled across the Mesozoic. In both theropod and ornithischian tracks, digit III projection and length-to-width ratio decrease with increasing size, whereas digit width increases, especially in ornithischian tracks. These trends are consistent with a shift from narrow, high-projection, more cursorial morphologies toward broader, lower-projection, more graviportal morphologies as trackmaker size increases.

The macroevolutionary signal is asymmetric between the two main trackmaker groups. Lallensack et al. [9] found that ornithischian footprints increased in size from the Early Jurassic to the Late Cretaceous, whereas theropod footprints did not show a comparable secular increase. This pattern is broadly consistent with the diversification of large-bodied ornithischian herbivores and the increasing prevalence of broad, weight-bearing pedal

morphologies through the Jurassic and Cretaceous, but the ichnological evidence should not be read as a direct body-size curve. Track size reflects foot dimensions, substrate interaction and sampling. Track occurrences are also shaped by facies, exposure and publication bias. Some biases are directional: large, distinctive tracks are more likely to be collected, described and published, potentially inflating the apparent abundance of large-bodied morphotypes. Others, such as substrate-dependent impression depth, may cause large heavy-bodied trackmakers to be underrepresented on firm substrates where their weight does not produce discrete digit impressions. The result is best treated as a functional signal preserved in the footprint record, not as a substitute for skeletal body-mass estimates.

The broader implication is that footprint morphospace records functional convergence as well as phylogenetic history. Low digit III projection and broad digit impressions may occur in large ornithischians because of weight-bearing demands, but similar proportional trends can also appear in large theropod tracks. This overlap explains why trackmaker identification becomes harder at larger sizes and why ichnotaxonomic characters cannot be evaluated independently of body size and function. Footprints are useful for macroevolutionary questions precisely because they preserve locomotor consequences of size evolution, but they require models that separate taxonomic signal from allometry, function and substrate-mediated distortion.

7.2. Bird-like Tracks, Avian-like Pedal Morphology and the Timing Problem

Bird-like tridactyl tracks are among the most contentious trace-fossil evidence used in discussions of avian origins. The problem is inferential as much as chronological. Tracks can preserve avian-like pedal proportions, high digit divarication, narrow digits and reduced digit III projection, but these characters do not by themselves demonstrate an avian trackmaker. Similar morphologies may reflect true avian affinity, convergent pedal morphology in non-avian theropods, or even ornithischian trackmakers with superficially bird-like tridactyl footprints. This distinction matters because the oldest unambiguous avian body fossils are Middle–Late Jurassic, whereas several proposed bird-like footprints occur in older or approximately coeval strata [22].

The strongest current discussion centres on southern African material assigned to *Trisauropodiscus* [22,49]. Abrahams and Bordy [22] re-examined Late Triassic and Early Jurassic tridactyl tracks from Lesotho and surrounding regions and recognised two morphotypes, one of which shows bird-like features including small size, wide total digit divarication, slender digits, indistinct pad impressions and reduced digit III projection. They argued that these tracks show demonstrable bird-like affinities and predate basal bird body fossils by about 60 million years, while acknowledging that non-avian dinosaurian trackmakers with convergently bird-like feet remain a plausible alternative. The appropriate formulation is therefore not that these tracks record Triassic birds, but that they record avian-like pedal morphologies whose biological source remains unresolved.

Chinese *Anomoepus* records add a useful caution. Xing et al. [41] reported the first *Anomoepus* tracks from the Middle Jurassic of Henan Province, Central China, noting that the morphological similarity between small Jurassic *Anomoepus* tracks and avian theropod ichnogenera otherwise known only from the Cretaceous and Cenozoic reflects convergence rather than direct avian affinity. This supports the broader point that apparent similarities between Jurassic non-avian dinosaur tracks and avian morphotypes may reflect convergent pedal evolution rather than phylogenetic proximity, and that avian-like outline alone is insufficient for avian trackmaker attribution.

Unsupervised machine learning can describe this ambiguity quantitatively but cannot remove it. Hartmann et al. [27] used a β -variational autoencoder trained on 1974 dinosaur and bird footprint silhouettes without prior taxonomic labels. The model identified eight

axes of shape variation, and some problematic Triassic–Early Jurassic bird-like tracks occupied a region of shape space closer to fossil and modern birds than to typical non-avian theropod tracks. This result supports the observation that these tracks are genuinely bird-like in morphology. It does not show that their makers were birds. Latent-space proximity measures shape similarity, not descent. A non-avian dinosaur with convergently avian-like pedal anatomy or locomotor behaviour could occupy the same region of morphospace.

The most defensible conclusion is limited but important. Bird-like tracks extend the record of avian-like pedal morphologies beyond the secure body-fossil record, but they do not by themselves establish an older origin of birds. Their value lies in defining testable hypotheses: whether avian-like foot proportions evolved earlier than currently documented by skeletons, whether such morphologies evolved convergently in small non-avian dinosaurs, and whether substrate and locomotor effects can generate bird-like outlines from non-avian feet. Resolving these alternatives requires tighter stratigraphic control, larger comparative datasets including small ornithischian and theropod tracks, and explicit integration of trace fossils with skeletal anatomy rather than treating track morphology as a standalone phylogenetic signal.

8. Synthesis and Outlook

The cases reviewed here show that dinosaur footprints are most informative when treated neither as direct proxies for trackmaker anatomy nor as traces too ambiguous for macroevolutionary use. Their value lies between these extremes. Tracks preserve locomotor and substrate-interaction evidence unavailable from skeletons, and they can sample faunas in facies or intervals where body fossils are rare. At the same time, every footprint is a composite product of anatomy, motion, substrate and preservation. Newer methods have not removed this ambiguity; they help define where it matters.

The classical hypotheses reviewed here have fared differently. Some have been narrowed in scope, others have been rejected for specific cases while retaining partial validity, and one, the proposed Triassic avian footprint record from Argentina, has been withdrawn on stratigraphic grounds. Ornithopod and theropod tracks occupy partly distinguishable regions of morphospace, but the boundary is probabilistic and varies with size, function and preservation. The *Grallator*–*Anchisauripus*–*Eubrontes* plexus records size-related shape change, but proportional continuity alone cannot demonstrate a single ontogenetic series. Alexander-type equations remain useful for approximate locomotor regimes, but recent validation against birds on compliant substrates shows that they are poor precision instruments. Parallel trackways and gauge patterns may support hypotheses of group movement or systematic affinity, but they cannot by themselves establish simultaneity, taxonomy or social behaviour. Bird-like tracks can document avian-like pedal morphologies outside the secure skeletal record, but morphology alone cannot distinguish avian affinity from convergence.

The broader methodological lesson is that representation matters. A landmark dataset, a silhouette image, a 3D mesh and a depth-series model are not interchangeable versions of the same evidence. Each imposes a different abstraction and answers a different question. Landmark-based morphometrics is effective for quantifying comparable shape variables; silhouette-based CNNs are useful for scalable classification within defined label spaces; unsupervised latent models reveal structure in morphospace without prior taxonomic labels; DEM simulations and musculoskeletal models test whether proposed motions and anatomies are mechanically plausible. The practical question is which representation is appropriate for a given inferential problem, not which method is superior in general.

Future work should focus on integration rather than method accumulation. First, 3D track data, outlines, landmarks, metadata and code should be archived in forms that

allow reanalysis and alternative interpretations. Second, machine learning studies need explicit treatment of label uncertainty, class imbalance, preservation filters and geographic sampling bias. Third, experimental trackmaking studies and forward simulations should generate reference track morphologies under systematically varied foot anatomy, gait and substrate properties, establishing ground-truth datasets against which fossil interpretations can be calibrated. These synthetic or semi-synthetic datasets could then be combined with fossil data to train models that estimate ranges of plausible track-forming scenarios rather than single categorical labels.

A productive framework is hypothesis-driven and probabilistic. This framework keeps traditional field measurements and newer analytical tools in the same evidential chain. Tracks should be used as constraints in models that integrate skeletal anatomy, extant-animal biomechanics, sedimentology, stratigraphy and comparative morphometrics. This approach does not weaken ichnological inference; it makes it testable. Dinosaur footprints are structured, preservationally filtered records of animal–substrate interaction. Their value is clearest when the uncertainty embedded in that interaction is modelled rather than ignored.

Author Contributions: Conceptualization, A.P. and L.X.; methodology, A.P. and L.X.; software, A.P.; validation, A.P. and L.X.; formal analysis, A.P.; investigation, A.P. and L.X.; resources, L.X.; data curation, A.P.; writing—original draft preparation, A.P.; writing—review and editing, A.P. and L.X.; visualization, A.P.; supervision, L.X.; project administration, L.X.; funding acquisition, L.X. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (No. 42488201); the “Deep-time Digital Earth” Science and Technology Leading Talents Team Funds for the Central Universities for the Frontiers Science Center for Deep-time Digital Earth, China University of Geosciences (Beijing; grant 2652023001); the 111 project (B20011); and Fundamental Research Funds for Central Universities (265QZ201903).

Data Availability Statement: We declare that no new data were created in this study.

Acknowledgments: We thank Jian Wu and his team from the Dinosaur Odyssey Science Museum (DOM), Nanning, China, for their assistance in redrawing Figure 1. We also express our gratitude to Xinnan Yang from the China University of Geosciences, Beijing, for compiling the machine learning data.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Farlow, J.O. *A Guide to Lower Cretaceous Dinosaur Footprints and Tracksites of the Paluxy River Valley, Somervell County, Texas*; Geological Society of America, South-Central Section Field Trip Guidebook; GeoScienceWorld: McLean, VA, USA, 1987.
2. Lockley, M.G.; Hunt, A.P. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*; Columbia University Press: New York, NY, USA, 1995. [[CrossRef](#)]
3. Marchetti, L.; Belvedere, M.; Voigt, S.; Klein, H.; Castanera, D.; Díaz-Martínez, I.; Marty, D.; Xing, L.; Feola, S.; Melchor, R.N.; et al. Defining the morphological quality of fossil footprints: Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Sci. Rev.* **2019**, *193*, 109–145. [[CrossRef](#)]
4. Xing, L.; Zhang, J.; Lockley, M.G.; McCrea, R.T.; Klein, H.; Alcalá, L.; Buckley, L.G.; Burns, M.E.; Kümmell, S.B.; He, Q. Hints of the Early Jehol Biota: Important dinosaur footprint assemblages from the Jurassic–Cretaceous boundary Tuchengzi Formation in Beijing, China. *PLoS ONE* **2015**, *10*, e0122715. [[CrossRef](#)] [[PubMed](#)]
5. Xing, L.; Lockley, M.G.; Marty, D.; Zhang, J.; Wang, Y.; Klein, H.; McCrea, R.T.; Buckley, L.G.; Belvedere, M.; Mateus, O.; et al. An ornithopod-dominated tracksite from the Lower Cretaceous Jiaguan Formation (Barremian–Albian) of Qijiang, South-Central China: New discoveries, ichnotaxonomy, preservation and palaeoecology. *PLoS ONE* **2015**, *10*, e0141059. [[CrossRef](#)] [[PubMed](#)]
6. Xing, L.; Lockley, M.G.; Zhang, J.; Klein, H.; Persons, W.S., IV; Dai, H.; Romilio, A.; Matsukawa, M.; Wang, F. The longest theropod trackway from East Asia, and a diverse sauropod-, theropod-, and ornithopod-track assemblage from the Lower Cretaceous Jiaguan Formation, southwest China. *Cretac. Res.* **2015**, *56*, 345–362. [[CrossRef](#)]

7. dePolo, P.E.; Brusatte, S.L.; Challands, T.J.; Foffa, D.; Wilkinson, M.; Clark, N.D.L.; Hoad, J.; da Costa Pereira, P.V.L.G.; Ross, D.A.; Wade, T.J. Novel track morphotypes from new tracksites indicate increased Middle Jurassic dinosaur diversity on the Isle of Skye, Scotland. *PLoS ONE* **2020**, *15*, e0229640. [[CrossRef](#)] [[PubMed](#)]
8. Falkingham, P.L. Interpreting ecology and behaviour from the vertebrate fossil track record. *J. Zool.* **2014**, *292*, 222–228. [[CrossRef](#)]
9. Lallensack, J.N.; Engler, T.; Barthel, H.J. Shape variability in tridactyl dinosaur footprints: The significance of size and function. *Palaeontology* **2020**, *63*, 203–228. [[CrossRef](#)]
10. Lallensack, J.N.; van Heteren, A.H.; Wings, O. Geometric morphometric analysis of intratrackway variability: A case study on theropod and ornithopod dinosaur trackways from Münchehagen (Lower Cretaceous, Germany). *PeerJ* **2016**, *4*, e2059. [[CrossRef](#)] [[PubMed](#)]
11. Falkingham, P.L.; Gatesy, S.M. Formation, preservation, and interpretation of dinosaur tracks. *J. Geol. Soc.* **2020**, *177*, 853–864.
12. Thulborn, R.A. *Dinosaur Tracks*; Chapman & Hall: London, UK, 1990.
13. Moratalla, J.J.; Sanz, J.L.; Jiménez, S. Multivariate analysis on Lower Cretaceous dinosaur footprints: Discrimination between ornithopods and theropods. *Geobios* **1988**, *21*, 395–408. [[CrossRef](#)]
14. Castanera, D.; Pascual, C.; Razzolini, N.L.; Vila, B.; Barco, J.L.; Canudo, J.I. Discriminating between medium-sized tridactyl trackmakers: Tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PLoS ONE* **2013**, *8*, e81830. [[CrossRef](#)] [[PubMed](#)]
15. Alexander, R.M.N. Estimates of speeds of dinosaurs. *Nature* **1976**, *261*, 129–130. [[CrossRef](#)]
16. Olsen, P.E. Fossil great lakes of the Newark Supergroup in New Jersey. In *Field Studies in New Jersey Geology and Guide to Field Trips*; Manspeizer, W., Ed.; New York State Geological Association: New York, NY, USA, 1980; pp. 352–398.
17. Thulborn, R.A.; Wade, M. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Mem. Qld. Mus.* **1984**, *21*, 413–517.
18. Farlow, J.O. Estimates of dinosaur speeds from a new trackway site in Texas. *Nature* **1981**, *294*, 747–748. [[CrossRef](#)]
19. Farlow, J.O. *Noah's Ravens: Interpreting the Makers of Tridactyl Dinosaur Footprints*; Indiana University Press: Bloomington, IN, USA, 2018.
20. Romilio, A.; Salisbury, S.W. A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: A case for mistaken identity. *Cretac. Res.* **2011**, *32*, 135–142. [[CrossRef](#)]
21. Romilio, A.; Salisbury, S.W. Large dinosaurian tracks from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, Lark Quarry, central-western Queensland, Australia: 3D photogrammetric analysis renders the “stampede trigger” scenario unlikely. *Cretac. Res.* **2014**, *51*, 186–207. [[CrossRef](#)]
22. Abrahams, M.; Bordy, E.M. The oldest fossil bird-like footprints from the upper Triassic of southern Africa. *PLoS ONE* **2023**, *18*, e0293021. [[CrossRef](#)] [[PubMed](#)]
23. Falkingham, P.L.; Bates, K.T.; Avanzini, M.; Bennett, M.; Bordy, E.M.; Breithaupt, B.H.; Castanera, D.; Citton, P.; Díaz-Martínez, I.; Farlow, J.O.; et al. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology* **2018**, *61*, 469–480. [[CrossRef](#)]
24. Lallensack, J.N. Automatic generation of objective footprint outlines. *PeerJ* **2019**, *7*, e7203. [[CrossRef](#)] [[PubMed](#)]
25. Jones, M.; Lallensack, J.N.; Jarman, I.; Falkingham, P.; Siekmann, I. Classification of dinosaur footprints using machine learning. *J. Vertebr. Paleontol.* **2024**, *44*, e2493157. [[CrossRef](#)]
26. Lallensack, J.N.; Romilio, A.; Falkingham, P.L. A machine learning approach for the discrimination of theropod and ornithischian dinosaur tracks. *J. R. Soc. Interface* **2022**, *19*, 20220588. [[CrossRef](#)] [[PubMed](#)]
27. Hartmann, G.; Blakesley, T.; dePolo, P.E.; Brusatte, S.L. Identifying variation in dinosaur footprints and classifying problematic specimens via unbiased unsupervised machine learning. *Proc. Natl. Acad. Sci. USA* **2026**, *123*, e2527222122. [[CrossRef](#)] [[PubMed](#)]
28. Murphey, P.C.; Romilio, A.; Matthews, N.A.; Lockley, M.G.; Breithaupt, B.H.; Houck, K.J.; Chin, K.; Milner, A.; Díaz-Martínez, I.; Xing, L.; et al. Track Recognition via Artificial Cognition (TRAC): Preliminary report on the application of machine learning to identify dinosaur tracks. In *Vertebrate Paleoichnology: A Tribute to Martin Lockley*; Taylor, L.H., Reynolds, R.G., Lucas, S.G., Eds.; New Mexico Museum of Natural History and Science Bulletin 95; The New Mexico Museum of Natural History and Science: Albuquerque, NM, USA, 2024; pp. 349–356.
29. Olsen, P.E.; Smith, J.B.; McDonald, N.G. Type material of the type species of the classic theropod footprint genera Eubrontes, Anchisauripus, and Grallator (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U.S.A.). *J. Vertebr. Paleontol.* **1998**, *18*, 586–601. [[CrossRef](#)]
30. Milàn, J. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks, reflecting differences in walking pattern and substrate consistency: Ichnotaxonomic implications. *Palaeontology* **2006**, *49*, 405–420. [[CrossRef](#)]
31. Milàn, J.; Avanzini, M.; Clemmensen, L.B.; García-Ramos, J.C.; Piñuela, L. Theropod foot movement recorded from Late Triassic, Early Jurassic and Late Jurassic fossil footprints. *New Mex. Mus. Nat. Hist. Sci. Bull.* **2006**, *37*, 352–364.

32. Falkingham, P.L.; Gatesy, S.M. The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 18279–18284. [[CrossRef](#)] [[PubMed](#)]
33. Falkingham, P.L.; Turner, M.L.; Gatesy, S.M. Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. *Palaeontology* **2020**, *63*, 865–880. [[CrossRef](#)]
34. Bishop, P.J.; Cuff, A.R.; Hutchinson, J.R. How to build a dinosaur: Musculoskeletal modeling and simulation of locomotor biomechanics in extinct animals. *Paleobiology* **2021**, *47*, 1–38. [[CrossRef](#)]
35. Prescott, T.L.; Griffin, B.W.; Demuth, O.E.; Gatesy, S.M.; Lallensack, J.N.; Falkingham, P.L. Speed from fossil trackways: Calculations not validated by extant birds on compliant substrates. *Biol. Lett.* **2025**, *21*, 20250191. [[CrossRef](#)] [[PubMed](#)]
36. Wilson, J.A.; Carrano, M.T. Titanosaurs and the origin of “wide-gauge” trackways: A biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **1999**, *25*, 252–267. [[CrossRef](#)]
37. Castanera, D.; Pascual, C.; Canudo, J.I.; Hernández, N.; Barco, J.L. Ethological variations in gauge in sauropod trackways from the Berriasian of Spain. *Lethaia* **2012**, *45*, 476–489. [[CrossRef](#)]
38. Kim, K.S.; Lockley, M.G.; Kim, J.Y.; Seo, S.J. The smallest dinosaur tracks in the world: Occurrences and significance of Minisauripus from East Asia. *Ichnos* **2012**, *19*, 66–74. [[CrossRef](#)]
39. Romilio, A.; Tucker, R.T.; Salisbury, S.W. Reevaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): No longer a stampede? *J. Vertebr. Paleontol.* **2013**, *33*, 102–120. [[CrossRef](#)]
40. Xing, L.; Lockley, M.G.; Yang, G.; Cao, J.; Benton, M.J.; Xu, X.; Zhang, J.; Klein, H.; Persons, W.S., IV; Kim, J.Y.; et al. A new Minisauripus site from the Lower Cretaceous of China: Tracks of small adults or juveniles? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2016**, *452*, 28–39. [[CrossRef](#)]
41. Xing, L.; Abbassi, N.; Lockley, M.G.; Klein, H.; Jia, S.; McCrea, R.T.; Persons, W.S., IV. The first record of Anomoepus tracks from the Middle Jurassic of Henan Province, Central China. *Hist. Biol.* **2017**, *29*, 223–229. [[CrossRef](#)]
42. Matthews, N.A.; Noble, T.A.; Breithaupt, B.H. Close-range photogrammetry for 3D ichnology: The basics of photogrammetric ichnology. In *Dinosaur Tracks: The Next Steps*; Falkingham, P.L., Marty, D., Richter, A., Eds.; Indiana University Press: Bloomington, IN, USA, 2016; pp. 29–55.
43. Mujal, E.; Marchetti, L.; Schoch, R.R.; Fortuny, J. Upper Paleozoic to Lower Mesozoic tetrapod ichnology revisited: Photogrammetry and relative depth pattern inferences on functional prevalence of autopodia. *Front. Earth Sci.* **2020**, *8*, 248. [[CrossRef](#)]
44. Lallensack, J.N.; Leonardi, G.; Falkingham, P.L. Glossary of fossil tetrapod tracks. *Palaeontol. Electron.* **2025**, *28*, a8. [[CrossRef](#)] [[PubMed](#)]
45. Ha, Y.; Kim, S.-S. Classification of large ornithopod dinosaur footprints using Xception transfer learning. *PLoS ONE* **2023**, *18*, e0293020. [[CrossRef](#)] [[PubMed](#)]
46. Graversen, O.; Milàn, J.; Loope, D.B. Dinosaur tectonics: A structural analysis of theropod undertracks with a reconstruction of theropod walking dynamics. *J. Geol.* **2007**, *115*, 641–654. [[CrossRef](#)] [[PubMed](#)]
47. Selvaraju, R.R.; Cogswell, M.; Das, A.; Vedantam, R.; Parikh, D.; Batra, D. Grad-CAM: Visual explanations from deep networks via gradient-based localization. *Int. J. Comput. Vis.* **2020**, *128*, 336–359. [[CrossRef](#)]
48. Thulborn, R.A. Lark Quarry revisited: A critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa Australas. J. Palaeontol.* **2013**, *37*, 312–330. [[CrossRef](#)]
49. Ellenberger, P. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stormberg d’Afrique du Sud. *Palaeovertebrata Mémoire Extraordin.* **1974**, *6*, 1–141. [[CrossRef](#)]

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