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Accounting for sampling heterogeneity suggests a low paleolatitude origin for dinosaurs

Highlights

- Dinosaurs likely originated in low-latitude Gondwana
- The archosaur radiation also began in the paleotropics
- Mesozoic terrestrial vertebrates are under-sampled at low paleolatitudes
- Spatiotemporal sampling biases obscure biogeographic patterns in deep time

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In brief

Heath et al. investigate the paleobiogeographic origins of dinosaurs using historical biogeographic estimation, while accounting for sampling heterogeneity and phylogenetic uncertainty. Their models support a low-latitude Gondwanan origin, highlighting how biogeographic patterns in deep-time are obscured by spatiotemporal sampling biases.

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Accounting for sampling heterogeneity suggests a low paleolatitude origin for dinosaurs

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SUMMARY

Dinosaurs dominated Mesozoic terrestrial ecosystems for ∼160 million years, but their biogeographic origin remains poorly understood. The earliest unequivocal dinosaur fossils appear in the Carnian (∼230 Ma) of southern South America and Africa, leading most authors to propose southwestern Gondwana as the likely center of origin. However, the high taxonomic and morphological diversity of these earliest assemblages suggests a more ancient evolutionary history that is currently unsampled. Phylogenetic uncertainty at the base of Dinosauria, combined with the subsequent appearance of dinosaurs throughout Laurasia in their early evolutionary history, further complicates this picture. Here, we estimate the distribution of early dinosaurs and their archosaurian relatives under a phylogenetic maximum likelihood framework, testing alternative topological arrangements and incorporating potential abiotic barriers to dispersal into our biogeographic models. For the first time, we include spatiotemporal sampling heterogeneity in these models, which frequently supports a low-latitude Gondwanan origin for dinosaurs. These results are best supported when silesaurids are constrained as early-diverging ornithischians, which is likely because this topology accounts for the otherwise substantial ornithischian ghost lineage, explaining the group's absence from the fossil record prior to the Early Jurassic. Our results suggest that the archosaur radiation also took place within low-latitude Gondwana following the end-Permian extinction before lineages dispersed across Pangaea into ecologically and climatically distinct provinces during the Late Triassic. Mesozoic terrestrial vertebrates are under-sampled at low paleolatitudes, and our findings suggest that heterogeneous sampling has hitherto obscured the true paleobiogeographic origin of dinosaurs and their kin.

INTRODUCTION

The evolutionary radiation of the dinosaurs is a keystone event in the history of terrestrial ecosystems, but their paleobiogeographic origin remains a topic of fierce debate.[1–5] The oldest unequivocal dinosaurs are from the late Carnian Santa Maria and Ischigualasto formations of Brazil and Argentina, respectively, as well as the Pebbly Arkose Formation of Zimbabwe (?late Carnian) and the Maleri Formation of India (?late Norian-earliest Rhaetian; Figure 1).[6–16] Laurasian representatives, however, first appear in the Norian Dockum Group and Chinle Formation of the USA.[17–19] Consequently, most authors have suggested that dinosaurs originated in southern South America, potentially dispersing into Laurasia in the Norian, after the Carnian Pluvial Event (CPE; 234–232 Ma) led to the dissipation of low-paleolatitude climatic barriers.[4,5,16,20–24]

Recent debate on early dinosaur relationships, however, has cast doubt on a mid-latitude Gondwanan origin. Traditionally, dinosaurs have been divided into Ornithischia and Saurischia, with the latter subdivided into Sauropodomorpha and Theropoda, forming the three primary dinosaur clades.[25] However, Baron et al.[3] found evidence to support a sister group relationship between theropods and ornithischians and suggested a Laurasian origin for dinosaurs based on the placement of *Saltopus* and northern Pangaean silesaurids as close outgroups to Dinosauria.[26,27] Subsequent assessments of early dinosaur phylogeny identified that Silesauridae may form a paraphyletic array of stem ornithischians.[28,29] Because silesaurids are known from the Middle Triassic, this would constrain the origin of dinosaurs to before the Carnian while also explaining the substantial Triassic ornithischian ghost lineage.[15] This scenario is supported by the putatively Anisian or Ladinian age of the controversial dinosauriform *Nyasasaurus* of the Manda Beds of Tanzania, often suggested to represent the first true dinosaur.[15,27,30]

Potential paleobiogeographic scenarios for the origin of dinosaurs are complicated further when considering that the absence of unequivocal Carnian dinosaur body fossils from outside southern Gondwana may be an artefact of heterogeneous sampling of the fossil record, but this has never been tested.[2] Carnian-age terrestrial deposits yielding vertebrate skeletal fossils are especially scarce in Laurasian regions and essentially non-existent at low latitudes across Gondwana.[31,32]

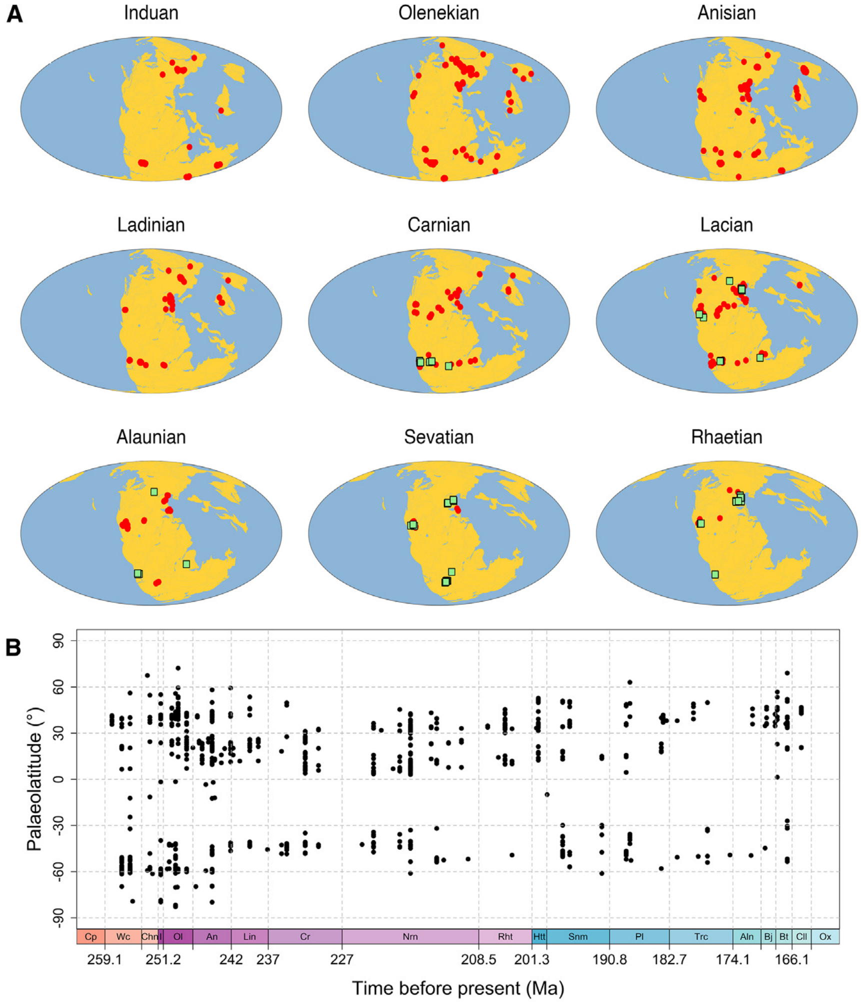

Figure 1. Triassic-Jurassic terrestrial tetrapod occurrence distribution

(A) Distribution of terrestrial tetrapod occurrences (red circles) across Pangaea during the Triassic (251.9–201.3 Ma). Dinosaurs (green squares) can be first seen in Gondwana during the Carnian before appearing in Laurasia during the Norian.

(B) Paleolatitudinal distribution of terrestrial tetrapod occurrences from the Late Permian-Middle Jurassic (259.1–163.5 Ma).

Additionally, the high morphological and taxonomic diversity of Carnian dinosaur fossils suggests that a more ancient evolutionary history might currently be obscured by these sampling biases.[6,10,33,34]

Here, we estimate the distribution of the earliest dinosaurs and their archosaurian relatives using historical biogeographic estimation methods.[35] We construct three archosauromorph supertrees, each designed to reflect one of the leading hypotheses of early dinosaur evolution (Figure S1). Our supertrees are designed to encompass the entire early archosauromorph radiation (dinosaur tips ~39%), which we calibrate against geological time using both the cal3 method[36] and the fossilized birth-death (FBD) model.[37,38] We use these time-calibrated supertrees, which sample four times the number of taxa used in previous studies, in a series of paleobiogeographic analyses. We incorporate into these models information on potential climatic and geographic barriers to dispersal that may have been present on Pangaea during the Triassic and Jurassic and, for the first time, include information on spatiotemporal sampling heterogeneity to account for biases in the fossil record. Our results support a novel low-latitude western Gondwanan (LLWG) origin for dinosaurs, which has substantial ramifications for our understanding of their origins, as well as implications for the ongoing debate on early dinosaur phylogeny.

RESULTS

Area of origin of Dinosauria

Ancestral distribution estimates for dinosaurs were derived using archosauromorph supertrees constructed to reflect the three leading hypotheses of early dinosaur evolution, while also incorporating uncertainties regarding climatic and geographic barriers to dispersal. To evaluate how these barriers might influence dispersal patterns, we performed analyses under four different constraint regimes: "intermediate" (default constraints based on initial assumptions), "relaxed" (allowing greater potential dispersal across barriers), "strict" (enforcing stronger barriers to dispersal), and "unconstrained" (with no barriers to dispersal or information on the spatial arrangements of areas). These analyses were conducted using two biogeographic presence-absence matrices: a "standard" format typical of previous studies, where taxa are assigned to regions based on fossil presence, and a modified format designed to account for uneven spatiotemporal sampling in the fossil record. Additionally, two tree-calibration methods were employed to address uncertainties associated with different node-dating approaches, resulting in sets of BioGeoBEARS analyses with and without sampling bias adjustments (see STAR Methods for details).

The historically proposed range of mid-latitude western Gondwana (MLWG) is recovered as the area of origin for dinosaurs (Tables 1 and 2) in all 18 of our standard constrained analyses, whereas this result is only recovered in five instances when incorporating sampling bias into the models. Instead, a novel area of origin that includes the low-latitude zone of Gondwana is found in 13 cases out of 18 when considering sampling heterogeneity (Tables 1 and 2). Of these 13 low-latitude Gondwanan distributions, LLWG is recovered as the sole ancestral area for Dinosauria on eight occasions, whereas low-latitude eastern Gondwana (LLEG) is recovered on one single occasion. A range encompassing LLWG plus LLEG is recovered on two occasions, as is a range encompassing MLWG and LLWG. Support for each

Table 1. BioGeoBEARS results for cal3 trees

Topology	Matrix version	Ambiguities	Best model	MLWG	LLWG	MLWG + LLWG	LLWG + LLEG
Traditional	intermediate	TRUE	DIVALIKE,* DEC**	–	–	0.32*, 0.37**	–
		FALSE	DEC	0.89	–	–	–
	strict	TRUE	DIVALIKE	–	–	–	0.43
		FALSE	DEC	0.94	–	–	–
	relaxed	TRUE	DIVALIKE	–	–	0.39	–
		FALSE	DEC	0.88	–	–	–
Ornithoscelida	intermediate	TRUE	DEC*, DIVALIKE**	0.76*, 0.84**	–	–	–
		FALSE	DEC	0.97	–	–	–
	strict	TRUE	DEC	–	–	–	0.40
		FALSE	DEC	0.98	–	–	–
	relaxed	TRUE	DIVALIKE*, DEC**	0.96,* 0.79**	–	–	–
		FALSE	DEC*, DIVALIKE**	0.96,* 0.99**	–	–	–
Silesaurids as ornithischians	intermediate	TRUE	DIVALIKE	–	0.77	–	–
		FALSE	DEC	0.67	–	–	–
	strict	TRUE	DEC	–	0.43	–	–
		FALSE	DEC	0.78	–	–	–
	relaxed	TRUE	DIVALIKE	–	0.73	–	–
		FALSE	DEC	0.64	–	–	–

BioGeoBEARS results, showing estimated ancestral area for the dinosaur node on cal3-calibrated trees based on the three leading hypotheses of early dinosaur evolution, each dispersal matrix, and showing whether ambiguities = TRUE (taking into account spatiotemporal sampling bias) or FALSE (a standard BioGeoBEARS analysis). The strict matrix imposes a stronger penalty on dispersal across climatic and geographic barriers compared with the intermediate matrix, whereas the relaxed matrix applies a milder penalty than the intermediate matrix (Figure S3). MLWG, mid-latitude western Gondwana; LLWG, low-latitude western Gondwana; LLEG, low-latitude eastern Gondwana. Numbers in the columns are the marginal probabilities (*p*) of each state. Asterisks (*) and (**) indicate models that could not be distinguished using corrected Akaike Information Criterion (AICc); the corresponding marginal probabilities are denoted by the same symbols in each cell. See also Tables S5, S6 and S8.

range, when taking into account sampling heterogeneity, varies greatly between each analysis. An ancestral range for Dinosauria encompassing the low-latitude regions of Gondwana is supported by a marginal probability (*p*) greater than 0.5 in 6 out of 18 constrained models (Tables 1 and 2), where a probability greater than 0.5 suggests that the model is more likely than not to correctly represent the ancestral distribution. The probability for a range restricted to MLWG alone exceeds 0.5 on five occasions (all within the Ornithoscelida topology) and lies below 0.05 for this range on 11 out of 18 occasions (Table S8).

Topological impacts on ancestral area estimation

When we account for sampling bias, the node for Dinosauria in the cal3-calibrated "traditional" topology shows support for a mixed distribution spanning MLWG and LLWG (Table 1). This suggests that the ancestral distribution for Dinosauria is uncertain between these regions, rather than indicating a broad initial range. Although the strength of this support is low (DIVALIKE: $p = 0.32$, DEC: $p = 0.37$), all other ranges are less well supported (Figure 2). LLWG is also recovered as the ancestral range of Dinosauria in the FBD-calibrated traditional topology (Table 2) but with higher support (DEC: $p = 0.67$). When analyzing the cal3-calibrated Ornithoscelida topology and accounting for sampling bias, MLWG is recovered as the most likely ancestral area for Dinosauria (DEC: $p = 0.76$ or DIVALIKE: $p = 0.84$) (Table 1). This result is also found when analyzing the FBD-calibrated version of this topology but with greater support (DEC: $p = 0.98$) (Table 2). When silesaurids are constrained as early-diverging ornithischians, LLWG is strongly supported as the ancestral area in both the cal3- (DEC: $p = 0.77$; Table 1) and FBD-calibrated (DEC: $p = 0.86$; Table 2) supertrees. Our results are not sensitive to the placement of controversial taxa such as *Nyasasaurus* and *Agnosphytis* (see Table S5).

Impact of dispersal multiplier choice on ancestral area estimation

Across all dispersal multiplier matrices using the cal3-calibrated "silesaurids as ornithischians" topology, an ancestral distribution of LLWG for dinosaurs (Table 1) is consistently recovered, whereas MLWG is recovered in the cal3 Ornithoscelida topology on all but one occasion. A distribution spanning LLWG and MLWG is found in both the intermediate (DEC: $p = 0.32$) and relaxed (DIVALIKE: $p = 0.39$) versions of the traditional topology. Using this topology, in conjunction with the strict dispersal multipliers, the ancestral range of Dinosauria has a combined distribution of LLWG and LLEG, with slightly higher support (DIVALIKE: $p = 0.43$) than in the intermediate and relaxed analyses. An ancestral range spanning LLWG and LLEG is also found when imposing strict dispersal constraints on the Ornithoscelida topology (DEC: $p = 0.40$).

Results based on the FBD-calibrated trees are slightly different to the cal3 analyses, which show more consistent results across the different dispersal multiplier matrices used. When analyzing the silesaurids as ornithischians topology using all three dispersal matrices, a distribution of LLWG as a single area is recovered as the ancestral area for Dinosauria (Table 2).

Table 2. BioGeoBEARS results for FBD trees

Topology	Matrix version	Ambiguities	Best model	MLWG	LLWG	LLEG
Traditional	intermediate	TRUE	DEC	–	0.67	–
		FALSE	DEC	0.87	–	–
	strict	TRUE	DIVALIKE	–	–	0.37
		FALSE	DEC	0.91	–	–
	relaxed	TRUE	DEC	–	0.64	–
		FALSE	DIVALIKE*, DEC**	0.96*, 0.96**	–	–
Ornithoscelida	intermediate	TRUE	DIVALIKE	0.98	–	–
		FALSE	DIVALIKE	>0.99	–	–
	strict	TRUE	DEC	0.79	–	–
		FALSE	DEC	0.96	–	–
	relaxed	TRUE	DIVALIKE	0.98	–	–
		FALSE	DIVALIKE	>0.99	–	–
Silesaurids as ornithischians	intermediate	TRUE	DEC	–	0.86	–
		FALSE	DEC	0.66	–	–
	strict	TRUE	DEC	–	0.47	–
		FALSE	DEC	0.83		–
	relaxed	TRUE	DIVALIKE*, DEC**	–	0.92*, 0.69**	–
		FALSE	DIVALIKE	0.69	–	–

BioGeoBEARS results, showing estimated ancestral area for the dinosaur node on FBD-calibrated trees based on the three leading hypotheses of early dinosaur evolution, each dispersal matrix, and showing whether ambiguities = TRUE (taking into account spatiotemporal sampling bias) or FALSE (a standard BioGeoBEARS analysis). The strict matrix imposes a stronger penalty on dispersal across climatic and geographic barriers compared with the intermediate matrix, whereas the relaxed matrix applies a milder penalty than the intermediate matrix (Figure S3). MLWG, mid-latitude western Gondwana; LLWG, low-latitude western Gondwana; LLEG, low-latitude eastern Gondwana. Numbers in the columns are the marginal probabilities (*p*) of each state. Asterisks (*) and (**) indicate models that could not be distinguished using AICc; the corresponding marginal probabilities are denoted by the same symbols in each cell. See also Tables S5 and S8.

Similarly, when analyzing the Ornithoscelida topology, dinosaurs are found to have originated in MLWG under all dispersal constraints. In the traditional topology, LLWG is found as the ancestral area for Dinosauria when using the intermediate and relaxed matrices, whereas a slightly different result is obtained when using the strict matrix, which recovers an ancestral distribution of LLEG (DIVALIKE: $p = 0.37$).

Unconstrained analyses

Unconstrained models, which contain no information on potential barriers to dispersal or the spatial arrangements of areas, strongly support a combined distribution of LLWG, MLWG, and WPG across all of the three cal3-calibrated topologies (Table S4). Results from the FBD-calibrated unconstrained analyses are different to those of the cal3-calibrated trees, showing an ancestral range for dinosaurs of MLWG in all three occasions, indicating that choice of calibration method does have an effect on the outcome of biogeographic analyses, particularly when the spatial arrangements of the areas are not considered.

Paleobiogeographic results for Archosauria

Our paleobiogeographic analyses also yield insights into the potential ancestral distributions of other groups within Archosauria (Figures 2 and 3). When considering sampling heterogeneity, our results show that the Pseudosuchia-Avemetatarsalia divergence also probably took place in LLWG (see Table S7 for a summary of ancestral area estimation at key nodes). In our standard analyses that do not account for sampling heterogeneity, the area estimation for this node is more poorly resolved (Figures 2 and 3). The most likely area of origin for Pterosauromorpha varies slightly depending on which topology is used, with no one range combination being particularly well supported above any other. However, the most common result is an ancestral range of LLWG. This is best supported in the FBD-calibrated Ornithoscelida topology (DIVALIKE: $p = 0.61$) and the cal3-calibrated Ornithoscelida topology (DIVALIKE: $p = 0.28$). Silesaurids are found to have originated in LLWG across all topologies and calibration methods.

DISCUSSION

Influence of topology on ancestral area estimation

Previous studies have suggested that phylogenetic topology does not have an impact on the outcome of ancestral area estimation in dinosaurs.[4,5] Although the inclusion of controversial taxa of biogeographic significance in our phylogenies has minimal impact on our results (Table S4), our results show that paleobiogeographic estimations in early dinosaurs can be sensitive to input topology. Evidence for this can be seen most clearly in the Ornithoscelida topology, wherein the ancestral node for Dinosauria is recovered as MLWG, even when accounting for sampling heterogeneity, in all but one occasion. This probably reflects the MLWG distribution of Herrerasauridae and its position as the sister group to Ornithischia in this supertree (topology based on the Bayesian analyses of Griffin et al.,[16] see STAR Methods). Herrerasaurids

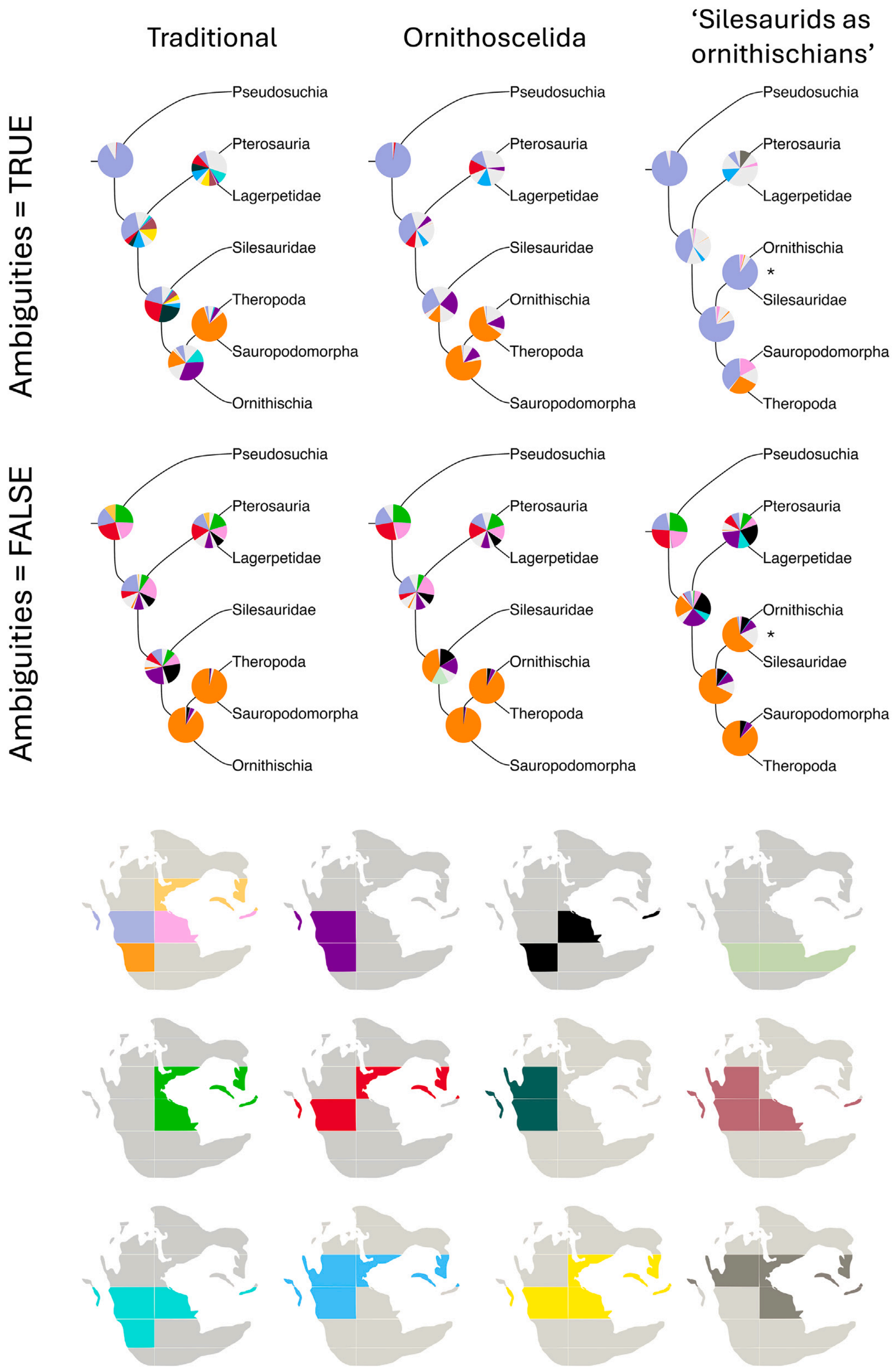

Figure 2. BioGeoBEARS pie plots for cal3 trees

BioGeoBEARS ancestral area estimation on cal3 trees based on the three leading hypotheses of early dinosaur evolution using intermediate dispersal matrices. Ambiguities: TRUE are analyses that take into account spatiotemporal sampling bias, whilst ambiguities: FALSE are standard BioGeoBEARS

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are among the earliest known dinosaurs, with some studies placing them as basal saurischians, the sister group to Sauropodomorpha, or even as the sister group to Dinosauria.[3,15,39,40] Their age, uncertain phylogenetic placement, and distribution in southern South America mean that the results of paleobiogeographic analyses could be heavily influenced by the chosen taxonomic position of Herrerasauridae. The placement of this clade as the sister group to Ornithischia ultimately leads to increased support for MLWG as the ancestral distribution of ornithschians, as well as the Ornithoscelida node. This is further supported by the MLWG distribution of Carnian-early Norian sauropodomorphs, which ultimately increases support for MLWG as the ancestral range for the Dinosauria node. Paleobiogeographic estimations based on Ornithoscelida supertrees, with Herrerasauridae constrained as the sister group to Sauropodomorpha[3] or Dinosauria,[39,41] confirm this interpretation, with both topologies showing reduced support for MLWG as the area of origin for Dinosauria (although this is still the best-supported ancestral area; Figure S4). Another factor that has likely influenced this result is that several Laurasian silesaurid taxa (*Soumyasaurus*, *Technosaurus*, and *Kwanasaurus*[42–44]) are not included in the Ornithoscelida dataset and could not be individually integrated into the supertree as their placement is not supported anywhere within this topology. On the other hand, the traditional and silesaurids as ornithischians topologies both enabled the inclusion of these taxa and show increased support for an ancestral distribution for Dinosauria within the low-latitude zone of Gondwana.

The lowest support for a MLWG origin of Dinosauria is seen when silesaurids are constrained as stem ornithischians, which results in the highest support for an LLWG origin. Again, this likely reflects the inclusion in this topology of several early branching silesaurids known from the Norian of Laurasia.[26,43–49] Several members of Silesauridae also constitute some of the oldest-known dinosauromorphs, with representatives such as *Asilisaurus*, *Lutungutali*, *Lewisuchus*, and *Gamatavus* of potentially Ladinian age.[15] Crucially, if silesaurids are not ornithischians, then the earliest ornithischians, and consequently a large portion of the earliest dinosaurs, are essentially absent from the fossil record. This would raise the possibility that the earliest unequivocal South American dinosaurs actually represent the descendants of an older lineage of dinosaurs that dispersed to southwest Gondwana from undersampled areas of the globe. The more limited support for LLWG as the inferred ancestral range of dinosaurs in the traditional and Ornithoscelida trees may stem from this missing phylogenetic information, with the silesaurids as ornithischians topology being a more robust and biogeographically plausible scenario for the earliest stages of dinosaur evolution. It is evident that ongoing discoveries contributing to the changing landscape of early dinosaur phylogeny, particularly within the Silesauridae, will be key to uncovering the secrets of dinosaur origins.

Sampling heterogeneity strongly influences the outcome of paleobiogeographic estimation

For the first time, we have shown that accounting for sampling bias in the fossil record uncovers a low-latitude Gondwanan origin for dinosaurs as well as for the wider archosaur radiation. To our knowledge, no previous quantitative paleobiogeographic study has identified the low-latitude regions of Gondwana as a potential area of origin of dinosaurs (although see Bernardi et al.[50]). For most of the Mesozoic, the southern low paleolatitudinal zone (0°–30° S) is largely barren of terrestrial vertebrate fossils.[31,32] One explanation for this absence is that this region may simply lack suitable sedimentary rocks for preserving Mesozoic terrestrial vertebrate fossils, possibly because the arid conditions of the southern Gondwanan desert belt provided an unsuitable environment for skeletal fossilization to occur.[50] However, the abundance of terrestrial tetrapod occurrences within the proposed northern low-paleolatitude desert belt, coupled with the observation that the number of occurrences does not appear to increase within the southern desert belt during the period of increased global precipitation following the CPE, contradicts this notion.[16,22] Instead, these absences may potentially be explained by anthropogenic biases. Today, this region constitutes the northern parts of Africa and South America. Paleontological expeditions to these regions may be less common as a result of the harsh environment of the Sahara and inaccessibility of many areas of the Amazon. It is also well documented that socioeconomic factors and the legacy of colonialism, coupled with political instability, have likely hindered research efforts in these regions.[51–53] The way in which terrestrial tetrapod occurrences are globally distributed, combined with our understanding of their phylogenetic relationships, suggests that these animals must have dispersed repeatedly through the southern low-paleolatitude zone during the Triassic and Jurassic. Therefore, we reason that fossilized remains of these animals in all likelihood do lie within this region but that challenges stemming from anthropogenic and socioeconomic factors may be impeding crucial fossil discoveries in these areas today. The application of approaches such as ecological niche modeling and occupancy modeling could help address these questions by determining whether regions were climatically suitable for early dinosaurs and whether observed absences are likely genuine.[31,32,54–57] Future studies may also benefit from exploring techniques that are able to jointly estimate phylogeny and biogeography, which may offer a promising complementary approach for integrating taxa with ambiguous phylogenetic placement into biogeographic estimations.[58]

The paleobiogeography of the archosaur radiation

Our analysis underscores how integrating the diversity of archosaur taxa provides a richer picture of the biogeographic context within which dinosaurs emerged, highlighting the critical role that low-latitude Gondwana may have played in the early stages of archosaur evolution and divergence. By including key archosaur clades such as pseudosuchians, pterosaurs, and lagerpetids,

analyses. Pies at the nodes show the marginal probabilities (p) of each biogeographical state at that node. Colors on pies relate to ancestral ranges shown in the paleogeographic maps below the phylogenies. Any state with $p < 0.1$ is presented in grey to simplify the figures. Areas are defined in Figure S2. * Note that this node represents the most inclusive clade including ornithischians and silesaurids, not the time of divergence between the two groups. See also Figure S4 and Table S7.

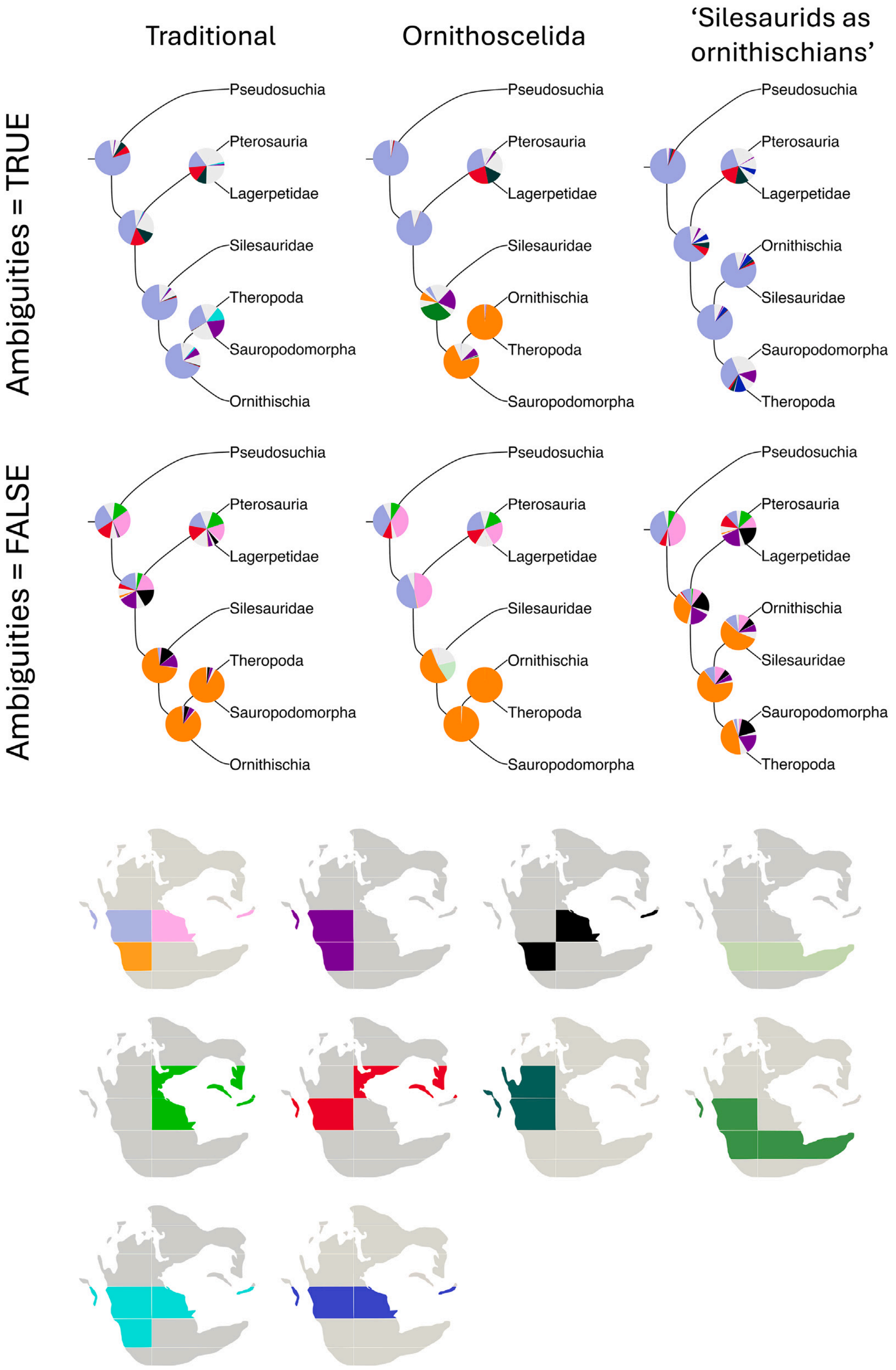

Figure 3. BioGeoBEARS pie plots for FBD trees

BioGeoBEARS ancestral area estimation on fossilised birth-death (FBD) trees based on the three leading hypotheses of early dinosaur evolution using intermediate dispersal matrices. Ambiguities: TRUE are analyses that take into account spatiotemporal sampling bias, whilst ambiguities: FALSE are standard

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we have constructed a more comprehensive biogeographic framework for dinosaur evolution. The inclusion of these groups, particularly those well-represented in Laurasian deposits, bolsters the robustness of our models, offering increased support for a dinosaur origin within the low-latitude Gondwanan zone. This intermediate region, situated between southern Gondwana and Laurasia, emerges as a natural convergence point in our models, reflecting areas where these broader archosaur distributions intersect. Notably, the exclusive presence of pterosaurs in Laurasia during the Late Triassic—alongside recent evidence that pterosaurs may be the sister group to lagerpetids—suggests a divergence between these two clades somewhere between their respective endemic regions in mid-latitude Laurasia and mid-latitude Gondwana.[28] When incorporating information on sampling heterogeneity into our analyses, the ancestral node for Pterosauromorpha is most often recovered with a LLWG distribution. Like dinosaurs, pterosauromorphs have not been identified to have originated in this region in previous paleobiogeographic studies.[59] However, it should be noted that support for any estimated ancestral range for pterosaurs is often poor across analyses, suggesting a complex biogeographic and evolutionary history that is currently obscured by inadequate sampling of the fossil record.

We have also shown that pseudosuchians might have originated at low paleolatitudes in Gondwana. Together with the results for Avemetatarsalia, this may suggest that the establishment of the major archosaur clades occurred within the interior of Pangaea following the end-Permian mass extinction, before various lineages dispersed across the supercontinent into ecologically and climatically distinct biogeographic provinces during the Late Triassic. The most recent study that presented a quantitative analysis of the paleobiogeographic history of early archosauriforms found that the ancestral area for the archosaur radiation was a distribution made up of Europe and Greenland, Asia, east Africa, and Brazil, with low support.[59] This biologically unlikely biogeographic signal likely stems from the spatiotemporally and heterogeneously distributed fossil record for Early-Middle Triassic archosauriforms, with representatives of Archosauria appearing to show a near-global distribution when they first begin to appear in the fossil record following the P/T mass extinction.[60,61] We have shown here that, when accounting for this sampling bias, a low-paleolatitude origin for the group is much more strongly supported. These findings support the view that the earliest stages of the archosaur radiation are currently obscured by poor sampling in the region in which they potentially originated (i.e., the paleotropics). This hypothesis receives support from the observation that there is an abundance of Early Triassic archosauriform trackways located throughout the paleotropical zone of Laurasia, whereas body fossils in this region are scarce.[62] Based on this evidence, we suggest that the earliest archosaurs must have been present within the paleotropical belt soon after their origin but that the environmental conditions of this region during the Early-Middle Triassic may not have favored the preservation of terrestrial vertebrate skeletal fossils. This bias has likely been exacerbated further in the southern paleotropical zone by socioeconomic factors and the history of colonialism, as well as the harsh environmental conditions present in this region today.[60,62,63]

The area of origin for Dinosauria

If dinosaurs did originate in the low latitudes of Gondwana, this could suggest a reduced role for the southern arid desert belt in constraining the distribution of the earliest dinosaurs. The majority of Triassic terrestrial tetrapod occurrences are situated in the low latitudes of Laurasia (Figure 1), which may have been occupied by a similar arid belt.[16,22] This could be interpreted as evidence that at least some terrestrial vertebrates had adapted to the conditions that are thought to have confined avemetatarsalians to the southern portions of Gondwana during their early evolutionary history.[16,22]

Recent studies have shown that dinosaurs probably occupied a wide range of climatic niches, even during the earliest stages of their evolution in the Late Triassic.[31,55] Chiarenza et al.[64] identified that early dinosauromorphs may have initially thrived in arid, high-temperature environments, with early endothermic adaptations in theropods and ornithischians likely supporting dispersal into cooler, varied climates, whereas sauropodomorphs retained a preference for warmer temperatures. Our results align with these findings, suggesting that early dinosaurs were well adapted to the hot, arid conditions characteristic of low-latitude Gondwana, where they likely originated. The subsequent diversification of dinosaurs into broader climatic niches as they evolved throughout the Late Triassic and Early Jurassic likely facilitated their dispersal and ecological success across various paleoclimatic zones, where discovery of their remains has been facilitated by improved fossilization rates and/or through increased sampling efforts related to socioeconomic factors.

Although our models indicate that low-paleolatitude desert belts might not have constrained the distribution of the earliest dinosaurs to southwestern Gondwana, they do align with various alternative scenarios that could elucidate why dinosaur body fossils are not known in the Northern Hemisphere until the early Norian. One possibility is that the earliest dinosaurs (that are currently unsampled) may have been tolerant of the arid climate in the low paleolatitudes of Gondwana, but later southern Gondwanan lineages could have been less tolerant of these conditions. Previous studies have argued that the increased global humidity that followed the CPE facilitated the decline of ecologically dominant Laurasian herbivores, such as rhynchosaurs and dicynodonts, providing early dinosaurs with opportunities to diversify in the Northern Hemisphere.[50,65–67] Alternatively, it has been suggested that the CPE lasted only 1–2 million years, was just one of several humid episodes that occurred during the Late Triassic, and that each of these episodes might have been divided into several distinct pulses of increased humidity and aridity, followed by a return to arid conditions in the late Carnian.[68] The continued oscillation of climatic conditions from humid to arid throughout the Norian may then have driven the

BioGeoBEARS analyses. Pies at the nodes show the marginal probabilities (p) of each biogeographical state at that node. Colors on pies relate to ancestral ranges shown in the paleogeographic maps below the phylogenies. Any state with $p < 0.1$ is presented in grey to simplify the figures. Areas are defined in Figure S2. * Note that this node represents the most inclusive clade including ornithischians and silesaurids, not the time of divergence between the two groups. See also Table S7.

ecological reshuffling of the major herbivore clades across Pangaea, ultimately facilitating the rise to dominance of sauropodomorphs throughout Laurasia.[67,68] It has also been proposed that the increased humidity brought about by the CPE may have actually hindered dinosaur diversification, with a return to more arid conditions in the late Carnian being a key factor driving the dispersal of mid-latitude Gondwanan dinosaurs into the Northern Hemisphere.[68] Thus, our results do not necessarily conflict with previous claims that the CPE was a major contributing factor in the global diversification of dinosaurs in the Norian but do potentially dispute the role of arid desert belts in constraining the distribution of the first dinosaurs, particularly in the earliest lineages that are currently unsampled in the fossil record. Volcanic winters brought on by the episodic activity of the Central Atlantic Magmatic Province have been proposed as another potential climatic agent to have influenced early dinosaur diversification.[69] These cycles of cooling and warming may have initially constrained early dinosaurs to low paleolatitudes but ultimately favored their evolution into climatically adaptable species, eventually outcompeting more temperature-sensitive stenothermal groups, including many pseudosuchian and synapsid lineages.

Large dinosaur-like footprints from Europe have been highlighted as evidence that this clade had already begun to diversify in the Northern Hemisphere during the late Carnian, though the attribution of these trackways to dinosaurs has been disputed.[50,70] Recent radiometric, biostratigraphic, and geomorphological evidence also supports the view that dinosaurs might have been present in Laurasia earlier than currently realized. Fissure fill deposits in the UK, which house a diverse terrestrial fauna, including the early-diverging sauropodomorph *Thecodontosaurus*,[71,72] have traditionally been considered Rhaetian in age but might actually date back to the middle Carnian.[73] If correct, this would indicate that dinosaurs were already present in Laurasia at approximately the same time as their earliest Gondwanan counterparts are found in the Santa Maria and Ischigualasto formations, further complicating potential paleobiogeographic scenarios.

In summary, our findings show that dinosaurs—and, potentially, archosaurs as a wider group—likely radiated in the low-latitude region of Gondwana, a result that has not been recovered in previous paleobiogeographic estimations. Past studies may have failed to detect this signal because of sampling inconsistencies resulting from a spatiotemporally heterogeneous fossil record, an issue that has long plagued the field of paleontology. Our results also show that support for a LLWG origin of dinosaurs is greatest when silesaurids are constrained as early diverging ornithischians, likely because this topology closes the substantial Triassic ornithischian ghost lineage present in the other leading topologies analyzed here. If this phylogenetic hypothesis is incorrect, it would mean that a significant portion of early dinosaur evolution remains undetected in the fossil record, with this missing information potentially lying within the heavily undersampled low-latitude zone of Triassic Gondwana. The underlying factors causing these absences in the terrestrial tetrapod fossil record require further investigation, and it is critical that future studies consider these substantial spatiotemporal sampling biases when conducting paleobiogeographic analyses across the tree of life.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joel Heath (joel.heath.21@ucl.ac.uk).

Materials availability

This study did not generate new unique materials.

Data and code availability

- All fossil occurrence data, phylogenetic trees, and paleogeographic maps used in this study have been deposited at Zenodo and are publicly available as of the date of publication at https://doi.org/10.5281/zenodo.14245516.
- All original code has been deposited at Zenodo and is publicly available at https://doi.org/10.5281/zenodo.14245516 as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

P.D.M. conceived the project idea. All authors contributed to the design of the project. J.A.H. collated the data, performed all analyses, and produced all figures, with input from P.D.M., P.U., and N.C.; N.C. wrote the R code to produce node pie plots; J.A.H. wrote the manuscript with contributions from all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- METHOD DETAILS
  - ○ Supertree construction
  - ○ Time scaling the supertrees
  - ○ Palaeobiogeographic analyses
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Biogeographic model fitting

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Dinosaur fossil occurrences, palaeogeographic maps, phylogenetic trees, and BioGeoBEARS files used in this study	https://zenodo.org/records/14245516	Supplementary_data
Paleobiology Database	https://paleobiodb.org	Accessed August 2024
Software and algorithms		
Mesquite	https://www.mesquiteproject.org/	Version 3.70
R computing environment	https://www.r-project.org/	Version 4.2.1
MrBayes: Bayesian Inference of Phylogeny	https://nbisweden.github.io/MrBayes/	Version 3.2.7
R package ape	https://cran.r-project.org/web/packages/ape/index.html	Version 5.8
R package paleotree	https://cran.r-project.org/web/packages/paleotree/index.html	Version 3.4.7
R package phytools	https://cran.r-project.org/web/packages/phytools/index.html	Version 2.3.15
R package BioGeoBEARS	https://github.com/nmatzke/BioGeoBEARS	Version 1.1.3
R package cladoRcpp	https://cran.r-project.org/web/packages/cladoRcpp/index.html	Version 0.15.1
R package palaeoverse	https://palaeoverse.palaeoverse.org/index.html	Version 1.4.0
GPlates	https://www.gplates.org/	Version 2.4.0
R package rgplates	https://cran.r-project.org/web/packages/rgplates/index.html	Version 0.4.1
R package ggplot2	https://ggplot2.tidyverse.org/	Version 3.5.1
R package sf	https://cran.r-project.org/web/packages/sf/index.html	Version 1.0.18
R package strap	https://cran.r-project.org/web/packages/strap/index.html	Version 1.6.1

METHOD DETAILS

Supertree construction

Using Mesquite version 3.70,[74] we built informal supertrees based on the three leading hypotheses of early dinosaur evolution. The three supertree topologies are: (1) the 'traditional' hypothesis of Saurischia as the sister taxon of Ornithischia[4]; (2) the Ornithoscelida hypothesis, in which Theropoda and Ornithischia form sister taxa, to the exclusion of Sauropodomorpha[3]; and (3) the 'silesaurids as ornithischians' hypothesis, where Silesauridae is constrained as a paraphyletic array of early diverging ornithischians (Figure S1).[28] We based these topologies on the Bayesian trees presented in Griffin et al.[16] for hypotheses 1 and 2. For hypothesis 3, we altered a version of the hypothesis 1 supertree to constrain silesaurids as ornithischians following the topology of Müller and Garcia.[75] For the 'traditional' topology of hypothesis 1, Silesauridae was modified to follow the ingroup relationships presented by Martz and Small,[44] but was left as the sister group to Dinosauria. For hypothesis 2, silesaurids were also left as the sister group to Dinosauria, but with the ingroup relationships recovered by Griffin et al.[16] We modified the sauropodomorph branches of each tree to match the topology of Beccari et al.,[76] with Sauropodiformes further adjusted to follow the topology of Pol et al.[77] For Neotheropoda, each supertree employed the topology of Spiekman et al.[78], whereas Averostra followed Rauhut and Pol.[79] For Ornithischia, the topology was based on Hui et al.,[80] with Heterodontosauridae based on Madzia et al.[81] In all three topologies we also updated the position of *Scleromochlus* to an early-branching lagerpetid as has been recovered in the most recent phylogenetic analyses on this taxon.[82,83]

Although previous studies that have assessed the palaeobiogeographic origin of the dinosaurs have often incorporated phylogenetic uncertainty, they have usually been limited to the use of small datasets in their analyses, resulting in the absence of key taxa from the wider archosauromorph tree, namely from within Pseudosuchia, Lagerpetidae, and Pterosauria (Table S2).[4,5,16,20,24] Additionally, the exact taxa sampled in different phylogenetic studies can often vary significantly, resulting in a lack of overlap in taxonomic sampling between datasets. For example, the Muller et al.[75] dataset contains key Laurasian silesaurids such as

Soumyasaurus, *Technosaurus*, and *Kwanasaurus*, but these taxa are not contained in any iteration of the Langer et al.[4] or Baron et al.[3] datasets. Inconsistencies such as these ultimately result in biogeographic studies failing to use trees composed of the widest possible range of currently accepted species. Insufficient sampling of a clade can have a severe effect on the results of biogeographic inference.[84] To account for these issues, we added Triassic and Early–Middle Jurassic dinosaurian taxa to each of our three starting supertrees, based on their position in the most recent phylogenetic studies to include them (see Table S1, for details). We then added archosauromorphs as a wider group to each supertree, based on the topology of Bestwick et al.[85] (and references therein).

Because the present study is primarily focused on deciphering the origin and dispersal of early dinosaurs and their archosaurian relatives (Triassic to Middle Jurassic), we pruned all Late Jurassic and Cretaceous taxa from the archosauromorph supertrees. We resolved polytomies at random in R version 4.2.1,[86] using the function multi2di from the ape package.[87] The total number of operational taxonomic units (OTUs) in each supertree topology is 433 (hypothesis 1), 430 (hypothesis 2), and 434 (hypothesis 3). Differences in the number of OTUs among the supertrees reflect the incompatibility of hypothesis 2 with the placement of *Kwanasaurus*, *Technosaurus*, and *Soumyasaurus*, while the placement of the recently discovered *Amansaurus* is only compatible with hypothesis 3. To our knowledge these are the largest supertrees to have been used to perform ancestral area estimation in early dinosaurs and their relatives, with our final dataset being around four times larger than any to be used previously (Table S3).[4,5,16,20,75] We also constructed several alternative versions of these topologies to test the sensitivity of our biogeographic analyses to topological uncertainty, e.g., placing Herrerasauridae as the sister taxon to Sauropodomorpha[3] or Dinosauria[39,41] in the Ornithoscelida tree. We additionally tested the effect of including controversial but potentially biogeographically significant taxa such as *Nyasasaurus* and *Agnosphitys* (see Table S5 for all sensitivity tests).

Time scaling the supertrees

We sourced stratigraphic ages (first appearance datum [FAD] and last appearance datum [LAD]) for each operational taxonomic unit (OTU) from the Paleobiology Database (PBDB; https://paleobiodb.org) and the recent literature, and updated these to match values from the latest version of the International Chronostratigraphic Chart from the International Commission on Stratigraphy (https://stratigraphy.org/ [88]). Specifically, FAD and LAD for Triassic dinosaur taxa were updated using stratigraphic information contained in Langer and Godoy[89] and Novas et al.[15] (and references therein). In order to evaluate the effect of different time-scaling methods on the results of our palaeobiogeographic estimations, each supertree was time-calibrated using two different approaches, both of which have been shown to be effective when dating trees primarily consisting of fossil taxa.[90–92]

Firstly, we used the cal3 method developed by Bapst,[36] which works by stochastically drawing divergence times from a distribution based on the prior calculation of three different rate parameters: speciation rate, extinction rate, and sampling rate. The majority of dinosaur fossil ages in our tree represent single point occurrences found somewhere within the range of their FAD and LAD and thus represent uncertainty between these limits. The cal3 method accounts for this uncertainty by using these rate parameters to generate probabilistic distributions of divergence times that reflect the range of possible dates for evolutionary events, including the entire timespan during which fossil taxa existed. We obtained these parameters from estimates for dinosaurs in Lloyd et al.[93] (sampling rate of 0.018 per lineage million years (Lmy), and an extinction rate of 0.935 Lmy, which is also used as a proxy for the speciation rate.[94,95] We applied these rate parameters to the bin_cal3TimePaleoPhy function of the palaeotree package, which accounts for uncertainty when producing time-scaled trees in which only discrete interval data are available for tip ages. The cal3 method is a stochastic approach, meaning that a single tree alone produced by this method may not be reliable for interpreting the timing of divergence events and testing evolutionary hypotheses. Therefore, we replicated the time-scaling analyses 1000 times, with the mean age of all nodes across each tree used to time scale a final 'average' tree using the R script provided by Groh et al.,[92] with tip ages set as the midpoint of FAD and LAD values for each taxon.

We also time calibrated each supertree using the Fossilised Birth-Death (FBD) model[37,38] in MrBayes version 3.2.7.[96] The FBD model is a Bayesian tip-dating technique that incorporates a birth-death process to account for the likelihood of fossilisation and sampling. This method simulates the presence of fossilised species within a phylogenetic tree to infer divergence times, and is advantageous because it does not rely on node ages being drawn from random probability densities. We generated an empty character matrix (where all taxa are coded for a single missing character) using the createMrBayesTipDatingNexus function from the paleotree package.[82] This approach allows for the estimation of node ages and branch lengths based on a fixed phylogenetic topology without character data. Instead, the MCMC algorithm is informed by fossil tip ages and the FBD prior itself.[38] This method is particularly suitable for analyses using large supertrees that lack consistently scored character matrices, as it permits the integration of fossil data without requiring additional character information.[94] We followed the protocol of Dunne et al.[55] using the provided R script. FBD analyses in MrBayes disregard topological constraints when the root node is fully resolved. To overcome this drawback, we followed the protocol of Herrera-Flores et al.,[97] introducing *Sophineta cracoviensis* and *Paliguana whitei* as two outgroup stem lepidosauromorph taxa into a polytomy at the root. Each supertree was used as a topological constraint with a uniform prior on tip ages with FAD and LAD. We used a uniform root prior to constrain the root to a range of 254.7–269.3 Ma, which reflects the minimum and maximum calibration dates for the lepidosauromorph-archosauromorph divergence estimated by Ezcurra et al.[98] For each topology, we used two runs with four chains of 100,000,000 generations and a burn-in of 25%. We considered MCMC runs to have converged once the Potential Scale Reduction Factor approached 1.0, the average standard deviation of split frequencies was below 0.01, and all Effective Sample Size (ESS) values exceeded 200. After 100,000,000 generations, the traditional topology still showed some ESS scores below 200, and so we increased the generations using this dataset to 150,000,000 which resolved the issue. The resulting trees were then summarised using the obtainDatedPosteriorTreesMrB function in paleotree, producing a single maximum clade credibility (MCC) tree (per topology) for use in palaeobiogeographic analyses. The two stem lepidosauromorph taxa were then pruned from the calibrated trees. We found that MCC trees produced using this method often contained zero length (or close to zero length) branches which cannot be used in BioGeoBEARS analyses. FBD analyses in MrBayes also frequently produced MCC trees containing 'singleton' nodes. This occurs where intervening nodes may be present along a branch, which can result in the tree being misinterpreted by BioGeoBEARS as non-binary (a tree can only be considered binary if all nodes have two descendants). To resolve these issues, we increased all branches in MCC trees by 0.001, and removed singleton nodes using the phytools[99] function collapse.singles.

Because of time and computational limitations, all supertrees constructed for taxonomic sensitivity analyses were calibrated using only the computationally more efficient cal3 method.

Palaeobiogeographic analyses

We used the R packages BioGeoBEARS[35] and cladoRcpp[100] to infer the biogeographical history of early dinosaurs in a phylogenetic maximum likelihood framework. BioGeoBEARS implements six different models of range evolution at ancestral nodes within the tree. The simplest model is DEC (Dispersal, Extinction, Cladogenesis), which allows for narrow (within one area) and subset (within a subset of the ancestral range) sympatric speciation. This model also allows narrow vicariance events, where a daughter lineage inherits just one of the available areas present at its ancestral node, with the other daughter lineage inheriting all remaining ancestral areas. Alternative models of range evolution within BioGeoBEARS include DIVALIKE and BAYAREALIKE. DIVALIKE is a likelihood adaptation of the DIVA model[101]; it is similar to the DEC model, but allows any form of vicariance to occur during cladogenesis and prohibits subset-sympatric speciation. The BAYAREALIKE model is a likelihood interpretation of the BayArea program of Landis et al.[102] This model does not allow vicariance or subset-sympatric speciation to occur, but enables both widespread (across multiple areas) and narrow sympatry.

We did not use models with a +J parameter, where +J denotes "jump" or founder-event speciation, as these are not well-suited to studying early dinosaur palaeobiogeography. The +J models build upon DEC, DIVALIKE, and BAYAREALIKE by adding a parameter for sudden, long-distance dispersal to non-adjacent areas—a mechanism more typical of island biogeography.[103] In contrast, the contiguous landmass of Triassic Pangaea likely supported speciation in early dinosaurs through gradual range expansions, vicariance due to climatic or ecological barriers, and sympatric speciation within diverse habitats. These modes of speciation are effectively captured by the DEC, DIVALIKE, and BAYAREALIKE models, which model gradual dispersal across connected regions. By omitting the +J parameter, we also align our approach with prior studies on early dinosaur biogeography, enabling a direct comparison of results.[4,5,16,20,75]

Fitting paleobiogeographical models in BioGeoBEARS typically requires a phylogenetic tree and a geographic range file containing information on the spatial distribution of each OTU (i.e. a palaeogeographically unconstrained analysis [see]). However, such analyses do not take into account the spatial arrangements or connectedness of the geographic areas analysed, which can result in the recovery of biologically implausible biogeographic scenarios. Moreover, the limitations on dispersal between different areas are likely to have varied through time because of changes in palaeogeography and palaeoclimate throughout the Triassic and Jurassic. Including such information in analyses is thus likely to improve the accuracy of biogeographic estimations.[104,105] Therefore, we also performed a series of 'constrained' analyses, which required the following additional files: (1) an 'ancestral areas allowed matrix', which restricts dispersal between two areas to only occur via intermediate areas, and disallows biologically implausible ranges made up of disconnected areas; (2) a time periods file, which divides the analysis into stratigraphically distinct intervals; (3) and a dispersal multiplier matrix, which reduces the probability of dispersal occurring between more distant areas or areas separated by geographic/climatic barriers; and 4) a modified geographic range file, which accounts for 'missing' occurrence data in under-sampled areas. We describe each input below, starting with the geographic range file used for both unconstrained and constrained analyses. All of these files can be found in Data S1.

Geographic range file

For our geographic range file, we chose 11 palaeobiogeographic regions defined by 30° latitudinal bins north and south of the palaeoequator, which were further divided into east and west longitudinally, and are designed to capture the presence of proposed latitudinal climatic barriers, as well as geographic barriers resulting from the breakup of Pangaea in the Jurassic.[16] These palaeobiogeographic regions are an extension of those used by Marsola et al.[5] and Griffin et al.,[16] which were in turn based on the four palaeobiogeographic provinces of Pangaea first defined by Langer[106] (South Gondwana, Equatorial Belt, Euramerica, and Trans-Uralian domains). Our choice of areas thus also enables the direct comparison of our results to those of these previous studies. The 11 areas defined herein are as follows: western polar Gondwana, eastern polar Gondwana, mid-latitude western Gondwana, mid-latitude eastern Gondwana, low-latitude western Gondwana, low-latitude eastern Gondwana, low-latitude western Laurasia, low-latitude eastern Laurasia, mid-latitude western Laurasia, mid-latitude eastern Laurasia, and eastern polar Laurasia (Figure S2). We excluded western polar Laurasia because this area was primarily made up of ocean during the majority of the Triassic and Early Jurassic.[107] In order to assign each taxon to one or more of these areas, we converted coordinates from the PBDB into palaeocoordinates using the function palaeorotate from the R package palaeoverse[108] using the "grid" method and the GPlates[109] "MERDITH2021" rotation model.[110] Of the 434 OTUs, six taxa were assigned to two areas, and the remaining 428 taxa were assigned to a single area. Taxa considered present in an area were scored as a '1', whereas taxa considered absent from an area were scored as a '0'. The geographic range file is named 'geog_range_1' and can be found in Data S3.

A potential drawback of our choice of areas may stem from the fact that some are substantially smaller than others. It could be argued that this would result in a bias in the number of fossil-bearing collections that may be contained within each area. However, the typical modes of vertebrate preservation and discovery mean that the majority of terrestrial tetrapod occurrences are concentrated in clusters within very tightly constrained sites, and thus have a chance of appearing in large numbers within very small regions. Moreover, the largest of our areas (low-latitude western Gondwana, ∼17600000 km^2 in the Ladinian, 0 occurrences; size estimated using GPlates v2.4.0[109]) is also the most under-sampled, whilst much smaller areas, such as low-latitude eastern Laurasia (∼11100000 km^2 in the Anisian, 237 occurrences; size estimated using GPlates v2.4.0[109]) are some of the best sampled areas. There is also an argument that taxa would traverse smaller areas at an increased rate relative to larger areas. However, even if dispersal occurs at only 0.1 km per year, taxa could traverse any of these areas (irrespective of their size) "instantaneously" on a geological timescale, and such subtleties would easily be swamped by the issue of the level of resolution of the ages for Triassic formations, which at the very best are of the order of a few hundred thousand years either side of the estimated date. Thus, these issues are unlikely to have a substantial impact on our biogeographic analyses and assessment of sampling bias in the terrestrial tetrapod fossil record (see 'accounting for sampling heterogeneity' below).

Dispersal multiplier matrices

We first designed a set of 'Intermediate' dispersal matrices, where adjacent areas that were not separated by barriers to dispersal (e.g. palaeolatitudinal climatic barriers, or oceanic barriers formed as Pangaea begun to break up in the Jurassic [see 'Time periods file' below]) were assigned a dispersal multiplier of 1 and non-adjacent areas a dispersal multiplier of 0.5, 0.25, or 0.1, corresponding to the number of intermediate areas separating the areas in question (i.e. 0.5 for one area, 0.25 for two areas, 0.1 for three areas). This approach mirrors one of the most recent attempts to estimate palaeobiogeographic dispersal patterns in Triassic avemetatarsalians,[16] and thus enables comparison of the latter's findings with the results of our study. Areas separated by potential abiotic barriers were given a dispersal multiplier of 0.5. Because of uncertainties pertaining to the existence of climatic and geographic barriers to dispersal in the Triassic and Jurassic, we constructed three different sets of dispersal matrices to use alongside our unconstrained analyses (see Figure S3), following the protocol of Poropat et al.[104] (see also Marsola et al.,[5] Xu et al.,[111] and Mannion et al.[112]: (1) 'Intermediate', with dispersal multipliers as outlined above; (2) 'Strict', with dispersal multipliers of 0.25 between areas separated by barriers, representing a scenario in which barriers to dispersal are stronger; and (3) 'Relaxed', with areas separated by barriers given dispersal multipliers of 0.75, representing a scenario in which barriers to dispersal are weaker. Each set of dispersal multiplier matrices can be found in Data S3.

Time periods file

We ran time-stratified analyses, with a time periods file (Data S3) comprising five time bins, in order to represent changes in palaeogeography that might have formed or removed barriers to dispersal at some point during the Triassic and Early Jurassic: (1) 251.9–234 Ma; (2) 234–217.49 Ma; (3) 217.49–201.3 Ma; (4) 201.3–190.8 Ma; (5) 190.8 – age of youngest taxa in tree (variable depending on calibration method). To model palaeogeographic changes occurring during these time intervals that may have influenced dispersal between our biogeographic regions, we constructed a different set of dispersal matrices for each time period. Recent evidence has suggested that low-latitude palaeoclimatic barriers may have played a key role in inhibiting dinosaur dispersal at different stages throughout the Triassic and Jurassic.[16,21–23] Although tectonic barriers (typically areas of ocean) resulting from the breakup of Pangaea have been incorporated into previous biogeographic reconstructions, climatic barriers have rarely been considered in these analyses.[4,5,20,24] Therefore, starting from time bin 1, we restricted dispersal that required taxa to cross low palaeolatitudinal zones (for example, from mid palaeolatitudinal areas to low palaeolatitudinal areas, and vice versa), based on the proposal that arid desert belts might have acted as effective barriers to dispersal in dinosaurs and their relatives.[16,22] We removed these restrictions during time bin 2, at which point these barriers are thought to have temporarily dissipated.[16] Dispersal across low palaeolatitudinal zones during time bin 2 was thus unrestricted. We reintroduced these barriers to dispersal during time bins 3, 4, and 5, based on Griffin et al.,[16] who identified that these arid belts might have returned by the middle Norian. From time bin 4 onwards, we restricted dispersal between North America and Europe when the opening of the Viking Corridor is thought to have formed a marine barrier between these areas.[113] We also considered Europe and Africa to be disconnected in this time bin based on the palaeogeographic maps of Scotese.[107] For time bin 5, we considered a marine barrier between North and South America to have been present, following the opening of the Hispanic Corridor during the Pliensbachian.[114]

Ancestral areas allowed matrix

Traditionally, an areas allowed file has been used in BioGeoBEARS analyses to model the disappearance and emergence of oceanic islands during different time periods.[35] However, such a file can also be modified to limit dispersal between areas to only occur if they are adjacent to one another, even if they exist in all time periods analysed. This approach was most recently used by Griffin et al.[16] when modelling dispersal patterns in early dinosaurs in relation to the dissipation and re-emergence of low-palaeolatitude climatic barriers during the Late Triassic. We also took this approach, modifying our own areas allowed file (which from here on we term the 'ancestral areas allowed file', [Data S3]) forcing dispersal between nonadjacent areas to occur only through intermediate 'stepping stone' areas. Inclusion of this file in our analyses allowed us to exclude biologically improbable range combinations, such as a taxon possessing a range comprising the polar regions of Pangaea, without having ever occupied intermediate zones within the interior of the supercontinent. This also significantly reduces the computational power and time required to perform a single constrained BioGeoBEARS analysis. With 11 areas and a maximum of three areas occupied at a node at any given time, the number of possible states is 232. However, when enforcing a stepping stone model, the maximum number of states is significantly reduced to 52 more biogeographically plausible states, drastically increasing the efficiency of our analyses.

Accounting for sampling heterogeneity

Because the potential for sedimentary rocks to preserve fossilised material varies across different geographic regions, the fossil record only provides information on a small fraction of the geographic ranges occupied by a clade, ultimately concealing the true biogeographic history of the group.[115] Although certain biogeographic patterns may still be detectable despite these biases,[116] the patchy nature of the fossil record continues to introduce significant challenges, which are often considered in reconstructions of past diversity patterns but rarely in palaeobiogeographic analyses.[84,117,118] We incorporated information on potential spatiotemporal sampling bias in the fossil record into our BioGeoBEARS analyses by constructing a second geographic range file (geog_range_2 [Data S3]). In this file, taxa that are absent from an area and time bin in which there are no terrestrial tetrapod body fossil occurrences, (including indeterminate occurrences) are scored as '?' (i.e. 'missing data') rather than '0' (i.e. absent). This method has recently been used to effectively infer the palaeobiogeographic history of Late Jurassic–Cretaceous sauropod dinosaurs, as well as in extant and fossil cycads,[112,119] but has so far not been used when assessing the past distribution of Triassic dinosaurs and their archosaurian relatives. In order to determine whether to score a taxon as 'missing data' or absent from a given area, we downloaded late Permian–Middle Jurassic tetrapod occurrences from the PBDB, including generically indeterminate remains, which were then filtered to exclude non-terrestrial taxa. FAD and LAD for Triassic dinosaurs were again checked and updated using the relevant literature.[15,89] We then produced palaeogeographic maps showing the distribution of these occurrences within our biogeographic areas and their respective geological stages (Data S2). Because of its increased length relative to other geological stages, we divided the Norian into the Lacian (227 – 217.49 Ma), Alaunian (217.49 – 214.03 Ma), and Sevatian (214.03 – 208.5 Ma), based on stratigraphic ranges defined by Ogg et al.[120] Any area lacking terrestrial tetrapod occurrences within a given time bin was considered to be undersampled. For example, if an area shows no terrestrial tetrapod occurrences during the Carnian, but does during the Ladinian, then supertree taxa that are absent from that area in the Carnian are scored as missing data ('?') rather than a genuine absence ('0'). In contrast, supertree taxa that are absent from that area during the Ladinian would be scored as genuinely absent ('0'), given that there is evidence for a skeletal fossil record in the area during that particular temporal window. Although terrestrial tetrapod diversity is thought to have been highest in the mid-latitude regions of Triassic Pangaea, dinosaurs have recently been shown to have been capable of inhabiting a wide range of climatic niches even during the earliest stages of their evolution.[32,55,69] Thus, we chose to include the high and low palaeolatitudinal regions of Pangaea when scoring taxa as 'missing' from an area in our second geography file. To incorporate these ambiguities into BioGeoBEARS, we added "*useAmbiguities = TRUE*" to our BioGeoBEARS analysis scripts.

It is important to note that this method addresses sampling bias in a single way—by assuming that regions lacking any terrestrial tetrapod fossils represent areas where dinosaur occurrence data are 'missing.' However, it does not adjust for regions that are likely under-sampled despite known fossil occurrences. For instance, a region with only one tetrapod fossil is treated as equally well-sampled as a region with 500 occurrences. In reality, dinosaur occurrences are also likely underrepresented in the sparsely sampled area. One potential improvement could involve assigning an ambiguity to a taxon absent from a region located between areas with known fossils of the same taxon. This refinement could not be implemented in our study, as Triassic dinosaur species are rarely documented from more than one locality. However, we encourage future studies to explore such methodological improvements to better address these limitations.

QUANTIFICATION AND STATISTICAL ANALYSIS

Biogeographic model fitting

We fitted the three time-stratified BioGeoBEARS models (DEC, DIVALIKE and BAYAREALIKE) to each of the three supertree topologies ('traditional', Ornithoscelida, and 'silesaurids as ornithischians', as well as to the sensitivity-testing versions of these topologies), for the unconstrained analyses and for the three different constrained analyses (Intermediate, Strict and Relaxed), and with sampling uncertainty excluded or included (FALSE, TRUE). In total we fitted 48 models (Table S4). In all constrained analyses (i.e. all models except those with unconstrained dispersal), the maximum number of areas a taxon/node could occupy was three (i.e. the maximum number of areas any one terminal taxon occupied, plus one; this is the recommended setting in BioGeoBEARS[103]). With 11 areas and a maximum of three areas allowed at a given node, and the constraints imposed from the inclusion of our ancestral areas allowed file, the total number of possible combinations of biogeographic ranges/states was 52. We compared model fit using sample size-corrected Akaike Information Criterion (AICc) using a difference in AICc of 2 units to distinguish between the best-fitting model and alternative models. Instances where models had differences in AICc values of less than 2 units were considered indistinguishable, and we recorded all equivalent models to reflect this uncertainty.[35,121,122] Marginal probabilities for each state were extracted from the best-fitting model and used to determine the most likely biogeographic distribution at the dinosaur node, as well as other key archosaur nodes within the supertrees.