



# INCREASES IN SAMPLING SUPPORT THE SOUTHERN GONDWANAN HYPOTHESIS FOR THE ORIGIN OF DINOSAURS

by JÚLIO C. A. MARSOLA<sup>1,2</sup> , GABRIEL S. FERREIRA<sup>1,3</sup> ,  
MAX C. LANGER<sup>1</sup> , DAVID J. BUTTON<sup>4</sup>  and RICHARD J. BUTLER<sup>2</sup> 

<sup>1</sup>Laboratório de Paleontologia, FFCLRP, Universidade de São Paulo, Ribeirão Preto-SP, 14040-901, Brazil; juliomarsola@gmail.com, gsferreirabio@gmail.com, mclanger@ffclrp.usp.br

<sup>2</sup>School of Geography, Earth & Environmental Sciences, University of Birmingham, Birmingham, B15 2TT, UK; r.butler.1@bham.ac.uk

<sup>3</sup>Fachbereich Geowissenschaften der Eberhard Karls Universität Tübingen, Hölderlinstraße 12, Tübingen, 72074, Germany

<sup>4</sup>Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5DB, UK; david.button44@gmail.com

Typescript received 26 June 2018; accepted in revised form 5 October 2018

**Abstract:** Dinosaurs were ubiquitous in terrestrial ecosystems through most of the Mesozoic and are still diversely represented in the modern fauna in the form of birds. Recent efforts to better understand the origins of the group have resulted in the discovery of many new species of early dinosaur and their closest relatives (dinosauromorphs). In addition, recent re-examinations of early dinosaur phylogeny have highlighted uncertainties regarding the interrelationships of the main dinosaur lineages (Sauropodomorpha, Theropoda and Ornithischia), and questioned the traditional hypothesis that the group originated in South Gondwana and gradually dispersed over Pangaea. Here, we use an historical approach to examine the impact of new fossil discoveries and changing phylogenetic hypotheses on biogeographical scenarios for

dinosaur origins over 20 years of research time, and analyse the results in the light of different fossil record sampling regimes. Our results consistently optimize South Gondwana as the ancestral area for Dinosauria, as well as for more inclusive clades including Dinosauromorpha, and show that this hypothesis is robust to increased taxonomic and geographic sampling and divergent phylogenetic results. Our results do not find any support for the recently proposed Laurasian origin of dinosaurs and suggest that a southern Gondwanan origin is by far the most plausible given our current knowledge of the diversity of early dinosaurs and non-dinosaurian dinosauromorphs.

**Key words:** Dinosauria, sampling, biogeography, BioGEOBEARS, Triassic, Gondwana.

DINOSAURS dominated Mesozoic terrestrial ecosystems for more than 140 million years, and remain highly diverse today, in the form of birds. As such, dinosaurs represent an outstanding example of evolutionary success among terrestrial tetrapods, which is reflected by the broad scientific interest in the group. Recently, there has been intense debate over the origins, early evolutionary radiation, and rise to ecological dominance of the group, stimulated by new discoveries of early dinosaurs and closely related taxa (Irmis *et al.* 2007; Nesbitt *et al.* 2009, 2010, 2013, 2017; Cabreira *et al.* 2011, 2016; Martínez *et al.* 2011), novel quantitative macroevolutionary analyses (Brusatte *et al.* 2008a, b; Sookias *et al.* 2012; Benton *et al.* 2014) and new geological data (Whiteside *et al.* 2015; Marsicano *et al.* 2016; Bernardi *et al.* 2018; Langer *et al.* 2018).

The discovery of many of the earliest known fossils of dinosaurs and their close relatives, non-dinosaurian

dinosauromorphs, in South America and other southern portions of the supercontinent Pangaea has led to the hypothesis that dinosaurs originated in this region (Nesbitt *et al.* 2009; Brusatte *et al.* 2010; Langer *et al.* 2010). However, a recent high-profile reassessment of the early dinosaur evolutionary tree (Baron *et al.* 2017a) not only challenged the long-standing classification of the three main dinosaur lineages (Seeley 1887; Gauthier 1986) but also questioned the southern Gondwanan origin of the clade. Based solely on the observed palaeogeographical distribution of some of the closest relatives of Dinosauria in their phylogenetic hypothesis (i.e. the Late Triassic *Saltopus elginensis* and the Middle–Late Triassic Silesauridae, which were recovered in a polytomy with Dinosauria), Baron *et al.* (2017a, b) proposed that dinosaurs may have originated in the northern part of Pangaea, referred to as Laurasia. However, this was suggested in the absence of any formal biogeographical analysis. Langer *et al.* (2017)

tested this hypothesis by running several quantitative biogeographical analyses to reconstruct ancestral areas, the results of which consistently recovered a southern Pangaeian (or Gondwanan) origin for dinosaurs. However, they only conducted these analyses for the Baron *et al.* (2017a) topology and did not consider alternative phylogenetic scenarios (Cabreira *et al.* 2016), or the long-term robustness of these results to new fossil discoveries.

In this paper we aim to: (1) further test hypotheses about the ancestral distribution of dinosaurs using a broader range of quantitative biogeographical models and alternative phylogenetic hypotheses; (2) test the stability of the biogeographical results over 20 years of additional scientific discoveries and new research that have dramatically changed our understanding of early dinosaur evolution; and (3) discuss how biased palaeogeographical sampling of the fossil record might impact our scenarios for dinosaur origins.

## MATERIAL AND METHOD

### *Source trees and time scaling*

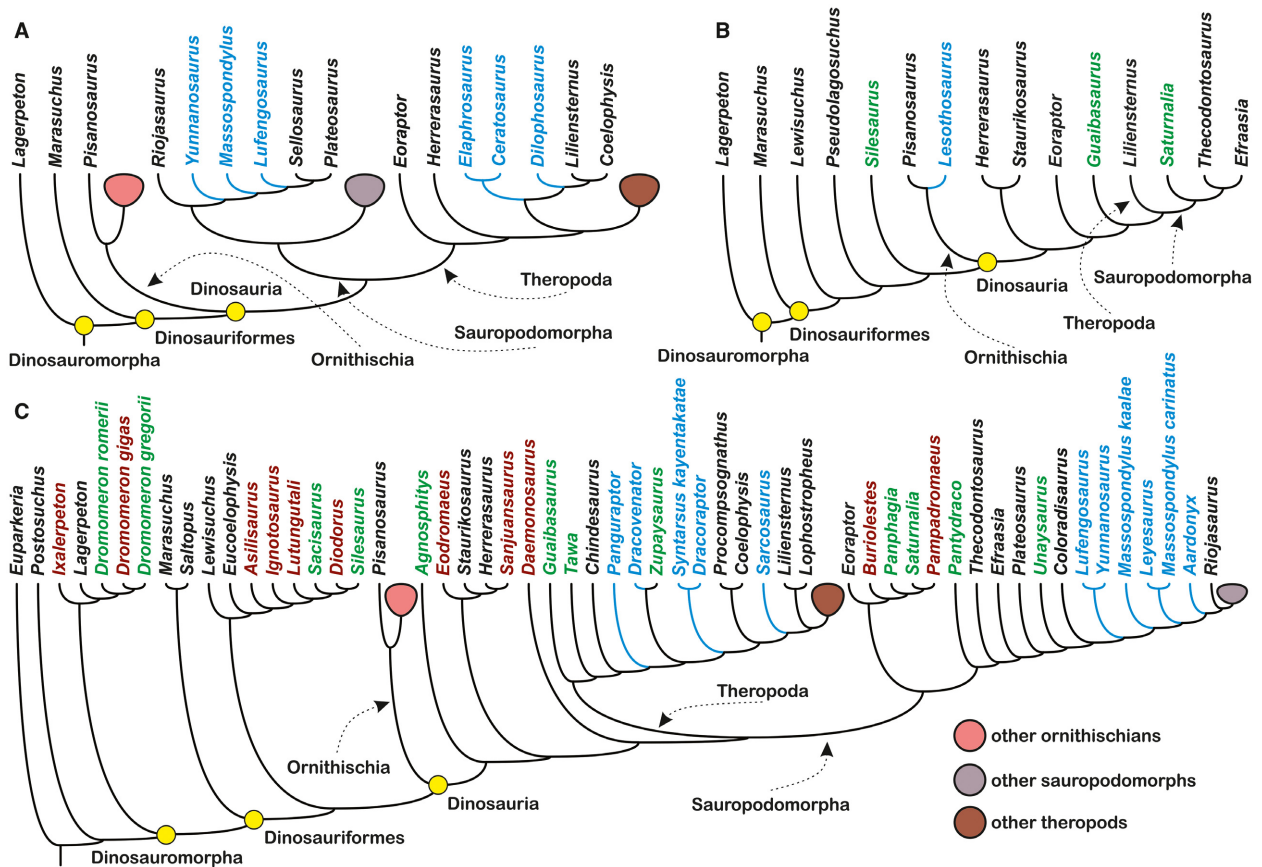
We sampled trees from six independent phylogenetic analyses from the last 20 years, each of which dealt with the major diversity of early dinosauriforms at the time they were published: (1) Sereno (1999); (2) Langer & Benton (2006); (3) Nesbitt *et al.* (2009); (4) Cabreira *et al.* (2016); (5) Baron *et al.* (2017a); and (6) Langer *et al.* (2017) (Fig. 1). For the Baron *et al.* (2017a) dataset, we created three alternative topologies to explore the impact of the uncertain relationships between *Saltopus*, Silesauridae and Dinosauria found by that study. The three topologies differ in the following arrangements: A, *Saltopus* sister to Silesauridae + Dinosauria; B, *Saltopus* sister to Silesauridae; and C, *Saltopus* sister to Dinosauria. We pruned Cretaceous taxa from the chosen topologies, as their biogeographical range is beyond the scope of our study. Supraspecific taxa were replaced by specific representatives of the same clade in order to generate a more explicit geographical distribution of terminal nodes. For example, in the topology of Sereno (1999) we replaced Diplodocidae with *Diplodocus*.

Since the biogeographical methods employed here require fully-solved, time-calibrated topologies, we resolved all polytomies in the sampled trees according to the following procedure. For hypotheses resulting from many most parsimonious trees (MPTs; Langer *et al.* 2017), we first obtained a majority-rule consensus tree (cut-off = 50). The remaining polytomies were manually resolved using a standardized procedure suggested by previous studies (Upchurch *et al.* 2015; Ferreira *et al.* 2018). First, wherever possible we resolved polytomies to

minimize biogeographical changes. For example, in a polytomy (A, B, C) where A and B share the same range, but C has a different range, we resolved A + B as sister-taxa to the exclusion of C. We further resolved polytomies based on relationships recovered in previous analyses. Finally, if polytomies remained, we chose the arrangement by randomly selecting one of the possible MPTs of that analysis. The dichotomous trees were then time-scaled using the R package *strap* (Bell & Lloyd, 2014), with branch lengths equally divided (Brusatte *et al.* 2008b) and a minimum branch length of 1 myr. Time ranges were based on the oldest and earliest dates of the stratigraphic stage (according to the International Chronostratigraphic Chart v. 2017/02; Cohen *et al.* 2013) in which a taxon occurs, the latter data being gathered from the literature. For example, the first and last appearances of all Carnian taxa were considered to be 237 and 227 Ma, respectively.

### *Biogeographical analyses*

In order to investigate the influence of phylogenetic uncertainty and sampling on ancestral distribution estimates for dinosaurs we conducted a series of stratified biogeographical analyses with the R package *BioGeoBEARS* (Matzke 2013) using the aforementioned phylogenetic trees. For each analysis, we ran two nested-models (M0 and M1; see below) of the likelihood-based models DEC (Dispersal-Extinction Cladogenesis; Ree 2005; Ree & Smith 2008) and DIVALIKE (Dispersal-Vicariance Analysis; Ronquist 1997). The DEC+J model was not explored because of its conceptual problems (Ree & Sanmartín 2018). Even though *BioGeoBEARS* enables us to fit a large number of additional models by changing the available parameters, for example the implemented likelihood version of BayArea (Landis *et al.* 2013), we opted to employ only the most commonly used biogeographical models, DEC and DIVA, to reduce the total number of analyses, since we are testing several sets of analyses based on different phylogenetic hypotheses. Each taxon was scored for four biogeographical provinces as defined by Langer *et al.* (2014): South Gondwana (S), Equatorial Belt (B), Euramerica (A), and Trans-Uralian domains (T). We set a maximum range size of two areas. Even though our analyses are temporally restricted to between the Middle Triassic and Middle Jurassic, a period during which no drastic palaeobiogeographical changes between the considered areas are supposed to have occurred, we conducted time-stratified analyses dividing the trees into two discrete periods: Middle Triassic to Norian (247.2–208.6 Ma) and Rhaetian to Middle Jurassic (208.5 Ma to the earliest tip of each tree). For each time stratum, a dispersal multiplier matrix was specified to model the



**FIG. 1.** Three phylogenetic topologies of early dinosaurs, showing the increased taxonomic and phylogenetic sampling of taxa since 1999. A, Sereno (1999). B, Langer & Benton (2006). C, Langer *et al.* (2017). Names in blue represent Jurassic taxa. Names in green represent taxa discovered from 1999 to 2009. Names in red represent taxa discovered from 2010 to 2017.

arrangement between the defined areas. To compare the effects of these assumptions, we followed the procedure of Poropat *et al.* (2016) and conducted analyses with ‘harsh’ and ‘relaxed’ versions of the ‘starting’ dispersal multiplier matrices (Marsola *et al.* 2018, appendix S1), and also set the parameter  $w$  to be free in one of the models (M1; for M0  $w$  is set to 1) in order to infer optimal dispersal multipliers during the analyses. It is important to consider that distinct models (e.g. DEC and DIVA) make specific assumptions about the biogeographical processes of range change. For that reason, the maximum-likelihood approach of BioGeoBEARS allowed us to test and choose the best fit model (Matzke 2014), using the likelihood-ratio test (LRT) and the weighted Akaike information criterion (AICc).

## RESULTS

With the sole exception of the ‘starting’ analysis of the Langer & Benton (2006) tree, for which a joint distribution of South Gondwana and Euramerica was estimated

for the Dinosauria node, the best fit models (for LRT and AICc test results see Marsola *et al.* 2018) obtained from all our analyses support a strictly southern Gondwanan origin for dinosaurs (Table 1). Changing the dispersal multiplier matrices did not yield distinct estimates. Similarly, our results yield high support for South Gondwana as the ancestral area for other ornithodiran clades leading to the Dinosauria node. Whereas all analyses of the Nesbitt *et al.* (2009) dataset and the ‘starting’ version of the Langer & Benton (2006) dataset support a joint distribution of South Gondwana and Euramerica as the ancestral area for Dinosauria, the clades Dinosauria and Dinosauriformes are supported as originating in South Gondwana in all other analyses, including those datasets that have the most extensive sampling of non-dinosaurian dinosauria (Cabreira *et al.* 2016; Baron *et al.* 2017a; Langer *et al.* 2017). South Gondwana is also inferred as the ancestral area for the Silesauridae + Dinosauria clade in all analyses in which this sister-group relationship is present (i.e. not in Sereno (1999) or iteration C of the Baron *et al.* (2017a) dataset) with the exception of the ‘harsh’ analysis of the Langer &

**TABLE 1.** Best fit models for each analysed tree.

Tree	Distance multiplier	Best model	Ancestral Area for Dinosauria
Sereno (1999)	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Langer & Benton (2006)	Starting	DEC M0	South Gondwana & Euramerica
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M1	South Gondwana
Nesbitt <i>et al.</i> (2009)	Starting	DEC M0	South Gondwana
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M0	South Gondwana
Cabreira <i>et al.</i> (2016)	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M0	South Gondwana
Baron <i>et al.</i> (2017a) A	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron <i>et al.</i> (2017a) B	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron <i>et al.</i> (2017a) C	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Langer <i>et al.</i> (2017)	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana

All results are available in Marsola *et al.* (2018, appendix S1).

Benton (2006) dataset. We note that the results for the Langer & Benton (2006) tree may not be reliable due to the low taxon sampling of the tree and the short branches surrounding Dinosauria.

Our results do not therefore support the hypothesis of a Laurasian origin for Dinosauria as proposed by Baron *et al.* (2017a), regardless of which of their three alternative topologies (Baron *et al.* (2017a): trees A, B and C) is employed. Although the problematic taxon *Saltopus elginensis* is known from Laurasia (Lossiemouth Sandstone Formation of Scotland, generally considered to be late Carnian in age, and almost certainly Late Triassic; Benton & Walker 2011), it is phylogenetically nested among South Gondwanan taxa in all alternative hypotheses and occurs stratigraphically 10–15 million years later than the main splitting events along the dinosauromorph lineage leading up to the origin of dinosaurs. Likewise, although Baron *et al.* (2017a) noted that the Laurasian *Agnosphitys cromhallensis* was positioned as sister to other silesaurids in their results, this taxon is known from the Rhaetian fissure fill deposits of southwest England, that is some 35–40 million years after the inferred origin of Silesauridae. All known Middle Triassic non-dinosaurian dinosauromorphs, as well as the only putative Middle

Triassic dinosaur (Nesbitt *et al.* 2013), are from South Gondwana and only from the Carnian onwards does their range expand into the northern hemisphere.

We conclude therefore, that the phylogenetic hypothesis proposed by Baron *et al.* (2017a) does not provide any significant support for a Laurasian origin of dinosaurs (Fig. 2). Instead, all our results strongly support those of Nesbitt *et al.* (2009) and Langer *et al.* (2017) (Figs 2, 3), in which southern Gondwana (‘southern Pangaea’ and ‘South America’, respectively, in their own terms) was also recovered as the ancestral area for dinosaurs. Furthermore, our analyses show that Ornithoscelida and Saurischia would also have originated in southern Gondwana in all possible versions of the Baron *et al.* (2017a) phylogenetic hypothesis.

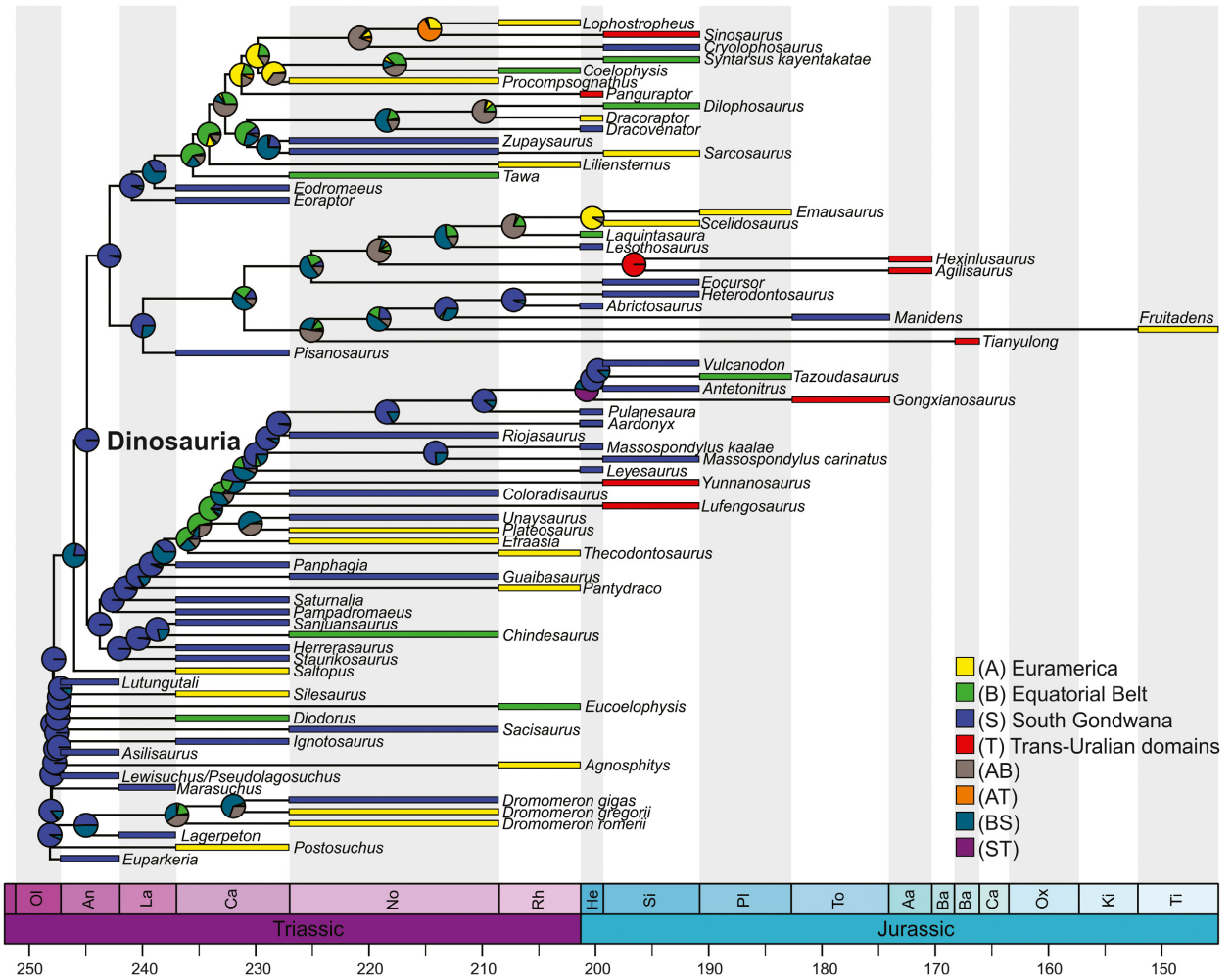
## DISCUSSION

### *Historical patterns*

Palaeontologists frequently use ancestral-area reconstruction approaches, such as those implemented by BioGeoBEARS, to infer ancestral ranges for clades and use these to make inferences about evolutionary histories (Upchurch *et al.* 2015; Poropat *et al.* 2016; Ferreira *et al.* 2018). However, they much more seldomly consider the robustness of those results to new fossil discoveries, which may include taxa from previously unsampled areas, and changes in phylogenetic hypotheses, which occur through the addition of more taxa and/or through changing topologies that result from new datasets or analytical approaches. For an ancestral range hypothesis to be considered well supported, it should be robust to such changes in the source data.

Here, we have provided a unique historical perspective on early dinosaur biogeography, by reconstructing ancestral areas for a series of alternative phylogenetic topologies taken from the last 20 years of research effort. Our key result, a South Gondwana origin for dinosaurs, has proved remarkably stable over two decades of new fossil discoveries and extensive phylogenetic research. Since the work of Sereno (1999), 23 new Triassic dinosaurs and non-dinosaurian dinosauromorphs have been discovered and/or added to phylogenetic studies. This includes new taxa from North America (Irmis *et al.* 2007; Nesbitt *et al.* 2009; Sues *et al.* 2011), Europe (Fraser *et al.* 2002; Dzik, 2003; Benton & Walker 2011) and North Africa (Kammerer *et al.* 2012). Yet, this greatly increased sampling has had few major impacts on models of early dinosaur biogeography, as the southern Gondwanan origin for the group is invariably supported as the best model throughout the research interval considered. We recommend using a similar historical perspective when estimating





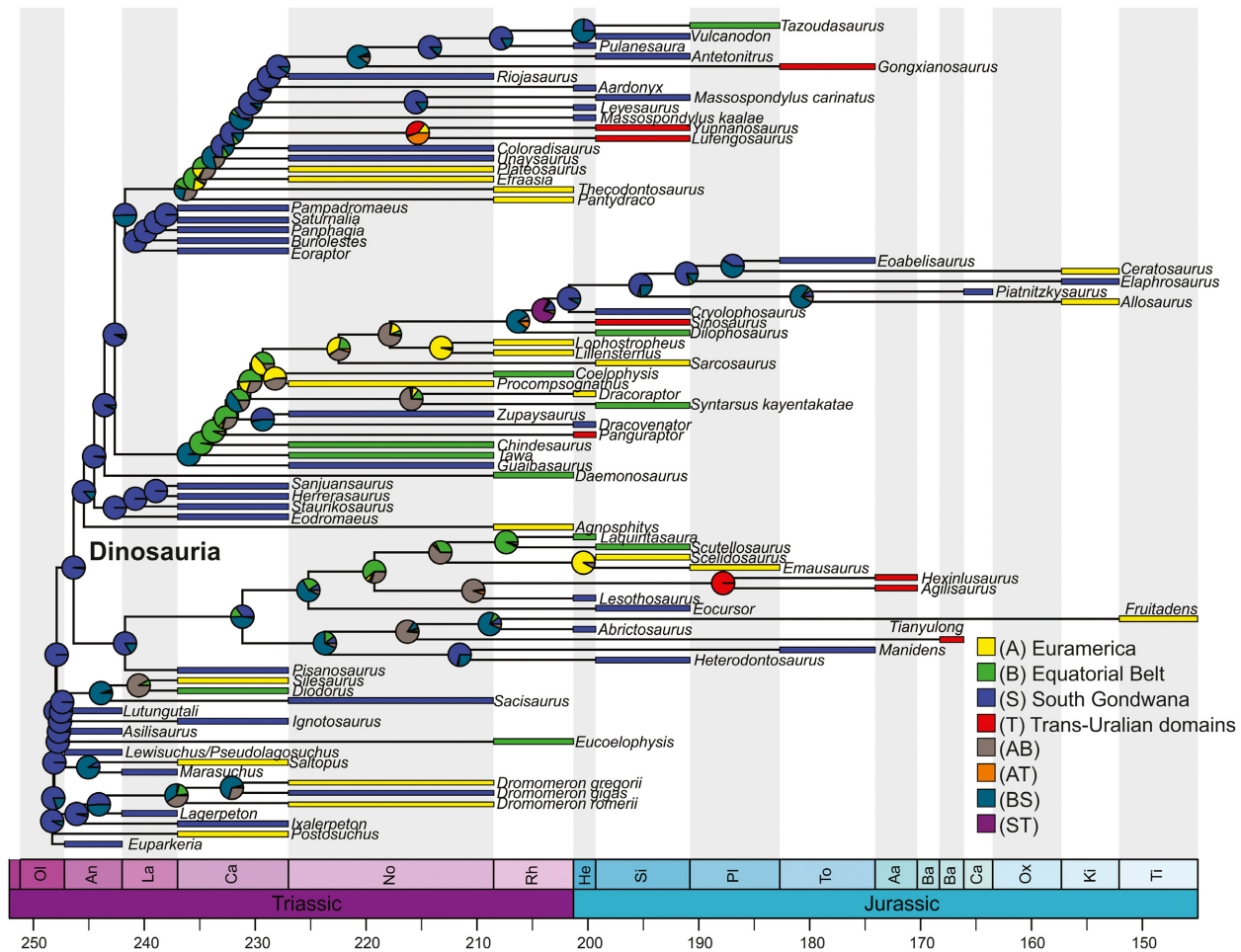
**FIG. 2.** Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the ‘starting’ version of Baron *et al.* (2017a, topology C) (DIVA M0). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

ancestral distributions of other clades, as a way of examining the support for biogeographical hypotheses.

Our results are also consistent despite highly divergent phylogenetic hypotheses for early dinosaurs. For example, Cabreira *et al.* (2016) recovered the majority of silesaurids within Dinosauria, as a paraphyletic array of early ornithischians. Baron *et al.* (2017a, b) proposed the unconventional clade Ornithoscelida, with Ornithischia as the sister-taxon of Theropoda, and herrerasaurids nested with sauropodomorphs within Saurischia, whereas Langer *et al.* (2017) reiterated support for a traditional Ornithischia–Saurischia dichotomy at the base of Dinosauria. However, our results show that none of these conflicting rearrangements of the three main dinosaurian lineages (Sauropodomorpha, Theropoda, Ornithischia) and Silesauridae challenge the long-standing biogeographical hypothesis of a southern Gondwanan origin for dinosaurs.

### Sampling biases

A biogeographical hypothesis, such as the southern Gondwanan origin of Dinosauria, may be well supported through research time and under alternative phylogenetic topologies, but could still be flawed if fossil record sampling is highly heterogeneous. For example, if dinosaurs actually originated in the late Middle to earliest Late Triassic in Laurasia, and dispersed quickly across the globe, they might still be reconstructed as ancestrally from South Gondwana if that region is the only one from which terrestrial vertebrate fossils have been sampled in that time interval. Reconstructions of ancestral areas for fossil taxa should therefore always be considered within an explicit consideration of how the fossil record has been sampled spatially, and temporally, but this is rarely the case. Here, we briefly discuss fossil record sampling through the inferred origin and initial radiation of dinosaurs (Middle



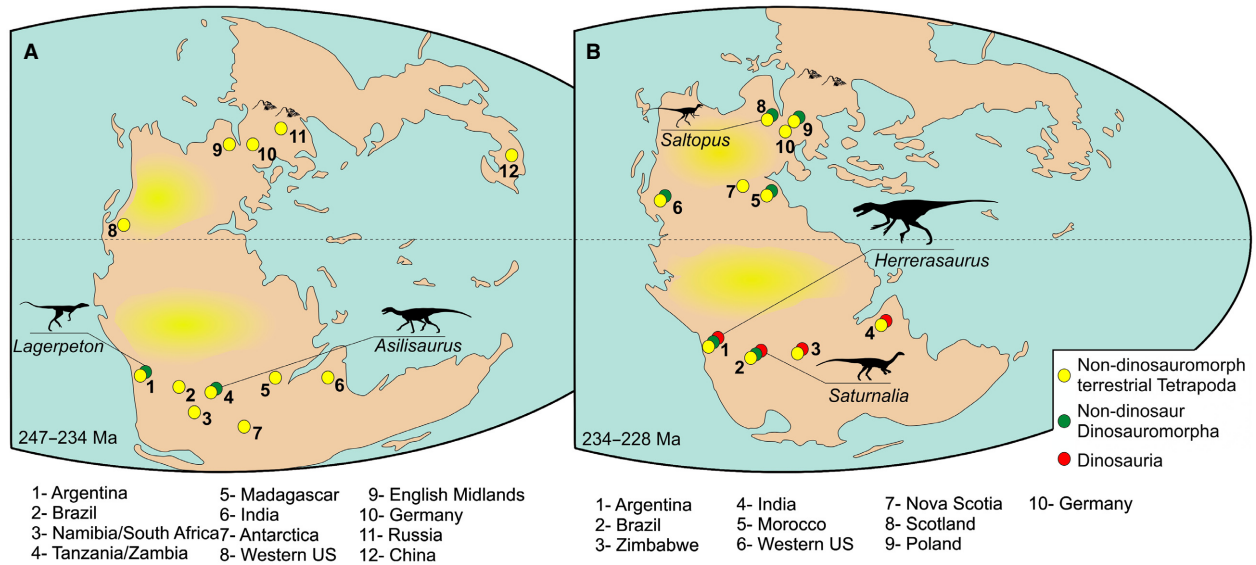
**FIG. 3.** Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the ‘starting’ version of Langer *et al.* (2017) (DIVA M1). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

Triassic to early Late Triassic: Anisian–Carnian), and the implications for the South Gondwana origins hypothesis.

The earliest dinosauriform body fossils, as well as the oldest putative dinosaur body fossil, are known from the Middle to earliest Late Triassic of South Gondwana, most notably from the Manda Beds of Tanzania (Nesbitt *et al.* 2010, 2013, 2017) and the Chañares Formation of Argentina (Serenó & Arcucci 1994*a, b*; Bittencourt *et al.* 2015; Ezcurra *et al.* 2017; Fig. 4). These represent two of the best-sampled stratigraphic units for terrestrial tetrapods in this interval, but Laurasian tetrapods of broadly comparable stratigraphic ages are known from various Laurasian localities, including the USA (Moenkopi Formation; Nesbitt 2005), the UK (Helsby Sandstone Formation; Coram *et al.* in press), Russia (Donguz and Bukobay horizons; Gower & Sennikov 2000), Germany (Erfurt Formation; Schoch & Sues 2015) and China (Ermaying Formation; Sookias *et al.* 2014). To date, none of these Laurasian deposits have yielded dinosauriform body fossils (Fig. 4).

Similarly, the earliest definitive dinosaur body fossils are from the early Late Triassic (late Carnian) of Argentina and Brazil (Alcober & Martínez 2010; Brusatte *et al.* 2010; Ezcurra 2010; Langer *et al.* 2010; Cabreira *et al.* 2011, 2016; Martínez *et al.* 2011; Müller *et al.* 2018; Pretto *et al.* 2018) (Fig. 4). Although the dating of many Laurasian rock sequences of putatively similar age is controversial, those in Germany (Butler *et al.* 2014), Poland (Dzik & Sulej 2007), North America (Sues & Olsen 2015) and the UK (Benton & Walker 1985) have failed thus far to yield definite dinosaur remains, although the silesaurid *Silesaurus* is known from Poland (Dzik 2003), and the problematic *Saltopus* from the UK (Benton & Walker 2011).

Putative dinosauriform footprint records have been reported from the Early–Middle Triassic of Laurasia (Brusatte *et al.* 2011). These include the ichnogenus *Prorotodactylus* from the Olenekian of Poland (Brusatte *et al.* 2011; Niedźwiedzki *et al.* 2013) and the ichnogenus *Rotodactylus* from the late Olenekian to Ladinian of Poland,



**FIG. 4.** Palaeogeographical distribution in continental deposits of non-dinosauromorph Tetrapoda, non-dinosaur Dinosauromorpha and Dinosauria during the Middle Triassic/early Carnian (A) and late Carnian (B).

Germany, France, the UK and the USA (Peabody 1948; Haubold 1999; Brusatte *et al.* 2011; Tresise & King 2012; Niedźwiedzki *et al.* 2013). If this interpretation of trackmaker affinities is correct, it represents a significant challenge to our current understanding of the biogeography of early dinosauromorphs (although not necessarily dinosaurs) suggesting that they were widespread over northern Pangaea in the late Early to Middle Triassic. However, trackmaker affinities for footprint ichnogenera are often difficult to constrain, and other workers have challenged the identification of *Prorotodactylus* and *Rotodactylus* as dinosauromorphs (Padian 2013), suggesting that they could instead represent basal archosauromorph or lepidosauromorph trackways.

In order to test the effects of the possible dinosauromorph affinities of the above-mentioned ichnogenera for dinosauromorph and dinosaur biogeography, we performed sensitivity analyses with *Prorotodactylus* added to the Baron *et al.* (2017a: tree C) and Langer *et al.* (2017) datasets (see Marsola *et al.* 2018). To do this, we considered two alternative possible scenarios where *Prorotodactylus* is sister-taxon to all other dinosauromorphs or is sister-taxon to all lagerpetids. Invariably, the results (Marsola *et al.* 2018, appendix S1) consistently continue to infer South Gondwana as the ancestral area for both Dinosauria and Dinosauriformes. On the other hand, a joint distribution of South Gondwana and Euramerica as the ancestral area for Dinosauromorpha is supported in most cases, although some analyses also suggest a joint distribution of Equatorial Belt and Euramerica.

It remains possible that, as suggested by Baron *et al.* (2017b), better future sampling of Middle to early Late

Triassic localities from Laurasia will overturn the South Gondwana hypothesis for dinosaur origins. However, compared to those from South Gondwana, these areas have been much more extensively sampled by palaeontologists for over 150 years and have so far failed to yield body fossils of Middle Triassic dinosauromorphs or early Late Triassic dinosaurs.

## CONCLUSIONS

The last two decades have witnessed a great increase in the taxonomic sampling of Triassic dinosaurs and non-dinosaurian dinosauromorphs. Unearthed from different parts of the world, these new discoveries have helped palaeontologists to better understand not only the morphology and diversity of early dinosaurs, but also to develop new models for their rise. Along with these new finds, new phylogenetic hypotheses for early dinosaurs have been proposed. These have challenged conventional understanding of the relationships of the main dinosaurian lineages (Cabreira *et al.* 2016; Baron *et al.* 2017a; Langer *et al.* 2017) and questioned the long-standing hypothesis of a southern Gondwanan origin for the clade (Baron *et al.* 2017a; Langer *et al.* 2017). In this study, we have shown that even in the most divergent phylogenetic hypotheses of early dinosaurs, a southern Gondwanan origin is strongly supported by quantitative biogeographical analyses. Additionally, we have demonstrated that South Gondwana is consistently supported as the ancestral area in a range of phylogenies from the last 20 years, and has therefore been robust to increases in taxonomic, geographical and phylogenetic

sampling. Although Middle–Late Triassic rock sequences worldwide have been sampled for decades, the oldest unequivocal dinosaur body fossil remains are still clustered in southern Gondwanan deposits. Given the present data, the South Gondwana hypothesis must therefore be considered the best-supported interpretation of the ancestral area for the rise of dinosaurs.

*Author contributions.* RJB conceived the study. JCAM collected data. JCAM, GSF, and DJB conducted analyses. JCAM, GSF and RJB wrote the paper. All authors revised and contributed comments to the final manuscript.

*Acknowledgements.* We thank Paul Upchurch for providing training in the use of BioGeoBEARS. This research was funded by the São Paulo Research Foundation (grants 2013/23114-1 and 2016/02473-1 to JCAM; 2014/25379-5 and 2016/03934-2 to GSF; 2014/03825-3 to MCL). RJB was supported by a Marie Curie Career Integration Grant (630123). The editor Roger Benson, Sally Thomas, and the referees Steve Brusatte and Martin Ezcurra are deeply thanked for their suggestions which greatly improved the final version of this manuscript.

## DATA ARCHIVING STATEMENT

R scripts and data for the biogeographical analyses for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6t5m946>

*Editor.* Roger Benson

## REFERENCES

- ALCOBER, O. and MARTÍNEZ, R. 2010. A new hererasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina. *ZooKeys*, **63**, 55–81.
- BARON, M. G., NORMAN, D. B. and BARRETT, P. M. 2017a. A new hypothesis of dinosaur relationships and early dinosaur evolution. *Nature*, **543**, 501–506.
- 2017b. Baron *et al.* reply. *Nature* **551**, E4–E5.
- BELL, M. A. and LLOYD, G. T. 2014. Strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology*, **58**, 379–389.
- BENTON, M. J. and WALKER, A. D. 1985. Palaeoecology, taphonomy, and dating of Permo-Triassic reptiles from Elgin. *Palaeontology*, **28**, 207–234.
- 2011. *Saltopus*, a dinosauriform from the Upper Triassic of Scotland. *Earth & Environmental Science Transactions of the Royal Society of Edinburgh*, **101**, 285–299.
- FORTH, J. and LANGER, M. C. 2014. Models for the rise of the dinosaurs. *Current Biology*, **24**, R87–R95.
- BERNARDI, M., GIANOLLA, P., PETTI, F. M., MIETTO, P. and BENTON, M. J. 2018. Dinosaur diversification linked with the Carnian Pluvial Episode. *Nature Communications*, **9**, 1–10.
- BITTENCOURT, J. S., ARCUCCI, A. B., MARSICANO, C. A. and LANGER, M. C. 2015. Osteology of the Middle Triassic archosaur *Lewisuchus admixtus* Romer (Chañares Formation, Argentina), its inclusivity, and relationships amongst early dinosauromorphs. *Journal of Systematic Palaeontology*, **13**, 189–219.
- BRUSATTE, S. L., BENTON, M. J., RUTA, M. and LLOYD, G. T. 2008a. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science*, **321**, 1485–1488.
- 2008b. The first 50 Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters* **23**, 733–736.
- NESBITT, S. J., IRMIS, R. B., BUTLER, R. J., BENTON, M. J. and NORELL, M. A. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews*, **101**, 68–100.
- NIEDZWIEDZKI, G. and BUTLER, R. J. 2011. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. *Proceedings of the Royal Society B*, **278**, 1107–1113.
- BUTLER, R. J., RAUHUT, O. W. M., STOCKER, M. R. and BRONOWICZ, R. 2014. Redescription of the phytosaurs *Paleorhinus* ('*Francosuchus*') *angustifrons* and *Ebrachosuchus neukami* from Germany, with implications for Late Triassic biochronology. *Zoological Journal of the Linnean Society*, **170**, 155–208.
- CABREIRA, S. F., SCHULTZ, C. L., BITTENCOURT, J. S., SOARES, M. B., FORTIER, D. C., SILVA, L. R. and LANGER, M. C. 2011. New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften*, **98**, 1035–1040.
- KELLNER, A. W. A., DIAS-DA-SILVA, S., SILVA, L. R., BRONZATI, M., MARSOLA, J. C. A., MÜLLER, R. T., BITTENCOURT, J. S., BATISTA, B. J., RAUGUST, T., CARRILHO, R., BRODT, A. and LANGER, M. C. 2016. A unique Late Triassic dinosauromorph assemblage reveals dinosaur ancestral anatomy and diet. *Current Biology*, **26**, 3090–3095.
- COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013. (updated) The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204.
- CORAM, R. A., RADLEY, J. D. and BENTON, M. J. in press. The Middle Triassic (Anisian) Otter Sandstone biota (Devon, UK): review, recent discoveries and ways ahead. *Proceedings of the Geologists' Association*. <https://doi.org/10.1016/j.pgeola.2017.06.007>
- DZIK, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology*, **23**, 556–574.
- and SULEJ, T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologia Polonica*, **64**, 3–27.
- EZCURRA, M. D. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. *Journal of Systematic Palaeontology*, **8**, 371–425.
- FIORELLI, L. E., MARTINELLI, A. G., ROCHER, S., VON BACZKO, M. B., EZPELETA, M., TABORDA,



- J. R. A., HECHENLEITNER, E. M., TROTTEYN, M. J. and DESOJO, J. B. 2017. Deep faunistic turnovers preceded the rise of dinosaurs in southwestern Pangaea. *Nature Ecology & Evolution*, **1**, 1477–1483.
- FERREIRA, G. S., BRONZATI, M., LANGER, M. C. and STERLI, J. 2018. Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira). *Royal Society Open Science*, **5**, 1–17.
- FRASER, N. C., PADIAN, K., WALKDEN, G. M. and DAVIS, A. L. M. 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. *Palaeontology*, **45**, 79–95.
- GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science*, **8**, 1–55.
- GOWER, D. J. and SENNIKOV, A. G. 2000. Early archosaurs from Russia. 140–159. In BENTON, M. J., SHISHKIN, M. A., UNWIN, D. M. and KUROCHKIN, E. N. (eds). *The age of dinosaurs in Russia and Mongolia*. Cambridge University Press, 740 pp.
- HAUBOLD, H. 1999. Tracks of the Dinosauromorpha from the Lower Triassic. *Zentralblatt für Geologie und Paläontologie*, **7**, 783–795.
- IRMIS, R. B., NESBITT, S. J., PADIAN, K., SMITH, N. D., TURNER, A. H., WOODY, D. and DOWNS, A. 2007. A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science*, **317**, 358–361.
- KAMMERER, C. F., NESBITT, S. J. and SHUBIN, N. H. 2012. The first silesaurid dinosauriform from the Late Triassic of Morocco. *Acta Palaeontologica Polonica*, **57**, 277–284.
- LANDIS, M. J., MATZKE, N. J., MOORE, B. R. and HUELSENBECK, J. P. 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, **62**, 789–804.
- LANGER, M. C. and BENTON, M. J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology*, **4**, 309–358.
- EZCURRA, M. D., BITTENCOURT, J. S. and NOVAS, F. E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews*, **85**, 55–110.
- RINCON, A. D., RAMEZANI, J., SOLORZANO, A. and RAUHUT, O. W. M. 2014. New dinosaur (Theropoda, stem-Averostra) from the earliest Jurassic of the La Quinta Formation, Venezuelan Andes. *Royal Society Open Science*, **1**, 1–15.
- EZCURRA, M. D., RAUHUT, O. W. M., BENTON, M. J., KNOLL, F., MCPHEE, B. W., NOVAS, F. E., POL, D. and BRUSATTE, S. L. 2017. Untangling the dinosaur family tree. *Nature*, **551**, E1–E3.
- RAMEZANI, J. and DA ROSA, Á. A. S. 2018. U-Pb age constraints on dinosaur rise from south Brazil. *Gondwana Research*, **57**, 133–140.
- MARSICANO, C. A., IRMIS, R. B., MANCUSO, A. C., MUNDIL, R. and CHEMALE, F. 2016. The precise temporal calibration of dinosaur origins. *Proceedings of the National Academy of Science*, **113**, 509–513.
- MARSOLA, J. C. A., FERREIRA, G. S., LANGER, M. C., BUTTON, D. J. and BUTLER, R. J. 2018. Data from: Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.6t5m946>
- MARTÍNEZ, R. N., SERENO, P. C., ALCOBER, O. A., COLOMBI, C. E., RENNE, P. R., MONTANEZ, I. P. and CURRIE, B. S. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science*, **331**, 206–210.
- MATZKE, N. J. 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, **5**, 242–248.
- 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, **63**, 951–970.
- MÜLLER, R. T., LANGER, M. C., BRONZATI, M., PACHECO, C. P., CABREIRA, S. F. and DIAS-DASILVA, S. 2018. Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a remarkably well-preserved dinosaur from the Upper Triassic of southern Brazil. *Zoological Journal of the Linnean Society*, zly009. <https://doi.org/10.1093/zoolinnean/zly009>
- NESBITT, S. J. 2005. A new archosaur from the upper Moenkopi Formation (Middle Triassic) of Arizona and its implications for rauisuchian phylogeny and diversification. *Neues Jahrbuch für Geologie und Paläontologie*, **6**, 332–346.
- SMITH, N. D., IRMIS, R. B., TURNER, A. H., DOWNS, A. and NORELL, M. A. 2009. A complete skeleton of a late Triassic saurischian and the early evolution of dinosaurs. *Science*, **326**, 1530–1533.
- SIDOR, C. A., IRMIS, R. B., ANGIELCZYK, K. D., SMITH, R. M. H. and TSUJI, L. A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, **464**, 95–98.
- BARRETT, P. M., WERNING, S., SIDOR, C. A. and CHARIG, A. J. 2013. The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. *Biology Letters*, **9**, 1–5.
- BUTLER, R. J., EZCURRA, M. D., BARRETT, P. M., STOCKER, M. R., ANGIELCZYK, K. D., SMITH, R. M. H., SIDOR, C. A., NIEDŹWIEDZKI, G., SENNIKOV, A. G., CHARIG, A. J. 2017. The earliest bird-line archosaurs and the assembly of the dinosaur body plan. *Nature*, **544**, 484–487.
- NIEDŹWIEDZKI, G., BRUSATTE, S. L. and BUTLER, R. J. 2013. *Prorotodactylus* and *Rotodactylus* tracks: an ichnological record of dinosauriforms from the Early–Middle Triassic of Poland. *Geological Society, London, Special Publications*, **379**, 319–351.
- PADIAN, K. 2013. The problem of dinosaur origins: integrating three approaches to the rise of Dinosauria. *Earth & Environmental Science Transactions of the Royal Society of Edinburgh*, **103**, 423–442.
- PEABODY, F. E. 1948. Reptile and amphibian trackways from the Moenkopi Formation of Arizona and Utah. *University of California Publications, Bulletin of the Department of Geological Sciences*, **27**, 295–468.
- POROPAT, S. F., MANNION, P. D., UPCHURCH, P., HOCKNULL, S. A., KEAR, B. P., KUNDRÁT, M., TISCHLER, T. R., SLOAN, T., SINAPIUS, G. H. K., ELLIOTT, J. A. and ELLIOTT, D. A. 2016. New

- Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Scientific Reports*, **6**, 1–12.
- PRETTO, F. A., LANGER, M. C. and SCHULTZ, C. L. 2018. A new dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Brazil provides insights on the evolution of sauropodomorph body plan. *Zoological Journal of the Linnean Society*, zly028. <https://doi.org/10.1093/zoolinlean/zly028>
- REE, R. H. 2005. Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. *Evolution*, **59**, 257–265.
- and SANMARTÍN, I. 2018. Conceptual and statistical problems with the DEC+J model for founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography*, **45**, 741–749.
- and SMITH, S. A. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4–14.
- RONQUIST, F. 1997. Dispersal-Vicariance Analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.
- SCHOCH, R. R. and SUES, H.-D. 2015. A Middle Triassic stem-turtle and the evolution of the turtle body plan. *Nature*, **523**, 584–587.
- SEELEY, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.
- SERENO, P. C. 1999. The evolution of dinosaurs. *Science*, **284**, 2137–2147.
- and ARCUCCI, A. B. 1994a. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology*, **13**, 385–399.
- — 1994b. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. 1994. *Journal of Vertebrate Paleontology*, **14**, 53–73.
- SOOKIAS, R. B., BUTLER, R. J. and BENSON, R. B. J. 2012. Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. *Proceedings of the Royal Society B*, **279**, 2180–2187.
- SULLIVAN, C., LIU, J. and BUTLER, R. J. 2014. Systematics of putative euparkeriids (Diapsida: Archosauriformes) from the Triassic of China. *PeerJ*, **2**, e658.
- SUES, H.-D. and OLSEN, P. E. 2015. Stratigraphic and temporal context and faunal diversity of Permian-Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. *Atlantic Geology*, **51**, 139–205.
- NESBITT, S. J., BERMAN, D. S. and HENRICI, A. C. 2011. A late-surviving basal theropod dinosaur from the latest Triassic of North America. *Proceedings of the Royal Society B*, **278**, 3459–3464.
- TRESISE, G. and KING, M. J. 2012. History of ichnology: the misconceived footprints of rhynchosaurs. *Ichnos*, **19**, 228–237.
- UPCHURCH, P., ANDRES, B., BUTLER, R. J. and BARRETT, P. M. 2015. An analysis of pterosaurian biogeography: implications for the evolutionary history and fossil record quality of the first flying vertebrates. *Historical Biology*, **27**, 697–717.
- WHITESIDE, J. H., LINDSTRÖM, S., IRMIS, R. B., GLASSPOOL, I. J., SCHALLER, M. F., DUNLAVEY, M., NESBITT, S. J., SMITH, N. D. and TURNER, A. H. 2015. Extreme ecosystem instability suppressed tropical dinosaur dominance for 30 million years. *Proceedings of the National Academy of Sciences*, **112**, 7909–7913.