Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history

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Recent model-based phylogenetic approaches have expanded upon the incorporation of extinct lineages and their respective temporal information for calibrating divergence date estimates. Here, model-based methods are explored to estimate divergence dates and ancestral ranges for titanosaurian sauropod dinosaurs, an extinct and globally distributed terrestrial clade that existed during the extensive Cretaceous supercontinental break-up. Our models estimate an Early Cretaceous (approx. 135 Ma) South American origin for Titanosauria. The estimated divergence dates are broadly congruent with Cretaceous geophysical models of supercontinental separation and subsequent continental isolation while obviating the invocation of continuous Late Cretaceous continental connections (e.g. ephemeral land bridges). Divergence dates for mid-Cretaceous African and South American sister lineages support semi-isolated subequatorial African faunas in concordance with the gradual northward separation between South America and Africa. Finally, Late Cretaceous Africa may have linked Laurasian lineages with their sister South American lineages, though the current Late Cretaceous African terrestrial fossil record remains meagre.

1. Introduction

The fossil record provides us a critical context for evolutionary biology; yet, it is notoriously incomplete and riddled with uncertainty. Model-based phylogenetic approaches offer us an explicit framework for addressing uncertainty as well as a likelihood model for morphological character evolution [1–4]. Recent studies [2–5] have incorporated morphological and temporal data (tip-dates) from both modern taxa and fossil specimens in order to co-estimate both phylogenetic relationships and divergence dates under an assumed ‘morphological clock’ that is analogous to a molecular clock. Here, this approach is applied to titanosaurian sauropod dinosaurs. Titanosaurs were a globally distributed clade of Cretaceous large-bodied terrestrial herbivores with a partially resolved phylogeny and an obscure origin near the Jurassic–Cretaceous boundary based on a deficit of unambiguous fossil specimens [6–11]. Model-based methods are implemented to take advantage of the worldwide distribution of titanosaurians for assessing the influence of Cretaceous supercontinental break-up and its reorganizational impact on the diversification of terrestrial biotas [12–18].

2. Methods

The dataset herein integrates several previous studies and includes autapomorphic characters for estimating terminal branch lengths (45 taxa, 262 variable and 230...
autapomorphic characters; see the electronic supplementary material, appendix; [1]). The reported stratigraphic range for each taxon was sampled using a uniform distribution prior (see appendix; [3,5]). Morphology models [1] differed in either equal or variable rates of character evolution within BEAST v. 2.1.3 [19] and MrBayes v. 3.2 [20]. The BEAST analyses implemented the relaxed clock model. MrBayes v. 3.2 cannot currently use birth–death rates to vary through time [21], under a lognormal birth–death–skyline–serial–sampling tree model, allowing birth likelihood-interpretations of both DIVA [24] and BAYAREA [25] the Bayes factor [22]. Palaeobiogeographic models DEC [23], the models ran for 20 million generations, sampling every 1000 generations, with a standard 25% burn-in. Models were compared using posterior probabilities (italics) located at respective nodes; blue nodal bar represents 95% highest posterior density (HPD) age estimates; pie charts indicate relative support for ancestral area reconstruction; branch tips represent the taxon 95% HPD age range (length) and area distribution (colour). (a) Select divergence dates (bold) and 4. Discussion

(a) Early Cretaceous (Berriasian–Barremian)
A titanosaurian origin is estimated at 134.88 million years ago (Ma; 95% highest posterior density: 143.88–127.12 Ma) and is compatible with the earliest unambiguous titanosaurian fossils that are known from the Barremian (130–125 Ma; [10,11]). Titanosauria is likely to have a Gondwanan origination in South America; however, the worldwide lack of an earliest Cretaceous (Berriasian–Barremian, approx. 145–125 Ma) titanosauriform fossil record renders our understanding of the models include the position of several unstable taxa, orderings within subclades and estimated topological parameters (see appendix). The topology is broadly congruent with recent titanosaurian phylogenies [29,30]. DEC + j is the slightly favoured palaeobiogeographic model (table 1), suggesting occasional dispersal episodes as a factor. Alternatively, the ‘+j’ models may reflect uneven spatial and temporal sampling as distributional ranges are likely incomplete; the majority of established titanosaurian taxa are known exclusively from Mid–Late Cretaceous South American deposits [31].

3. Results

The BEAST variable-rates model is strongly supported over other models (figure 1 and table 1) and differences among the
Jurassic–Cretaceous transition incomplete, though increased sampling efforts targeting this interval will certainly assist with better characterization of palaeobiogeographic patterns.

(b) Mid-Cretaceous (Aptian—Cenomanian)

 Recovered divergence dates for South American and African titanosaurian sister lineages follow the gradual northward ‘unzipping’ of these two continents and may have promoted the semi-isolation of subequatorial African faunas [32,33] prior to final separation (approx. 100 Ma; [34–38]). Subequatorial African titanosaurians are estimated to have diverged from their respective South American sister lineages earlier than the representative supra-equatorial African lineage, *Paralititan*. Within the aeolosaur lineage (here, taxa more closely related to *Aeolosaurus* than *Saltasaurus*), the predominately South American clade includes early-branching Malagasy and European lineages, suggesting a more widespread distribution than previously considered. *Rapetosaurus* (Madagascar) and *Iissusaurus* (India) lineages are estimated to have diverged from their respective South American sister lineages around 105 and 108 Ma, respectively, which generally corresponds to the isolation of Indo-Madagascar [15,37,39]. Overall, most Late Cretaceous titanosaurian lineages likely originated earlier within the mid-Cretaceous.

(c) Late Cretaceous (Turonian—Maastrichtian)

 Post-Cenomanian titanosaurian lineages support regionally isolated faunas [35,36] with a dispersal episode into North America from South America (*Alamosaurus* lineage). An ancestral supra-equatorial African stock may have bridged the recovered Eurasian clade with lineages from South America; however, Late Cretaceous African faunas remain poorly known [40,41]. Additional mid- and Late Cretaceous African fossils are required to rigorously evaluate and expand upon current palaeobiogeographic models (e.g. reticulated faunal associations). The estimated branch lengths obviate the invocation of ephemeral Late Cretaceous land bridges or other ad hoc explanations that have been proposed for other terrestrial taxa (e.g. theropod dinosaurs [42]).

## 5. Conclusion

 Stratigraphically calibrated topologies via ad hoc minimal distances or arbitrary branch lengths may lead to overestimates of continuous continental connectivity when it may not have existed [13,15,34]. Co-estimating divergence dates and phylogenetic relationships facilitates direct comparisons between phylogenetic branching patterns and geophysical models of landmass separation. The models herein suggest that titanosaurians had attained a near-global distribution prior to the isolation of the continents with limited dispersals rather than invoke poorly constrained and chronic Late Cretaceous global connections [34,35,42,43]. The study of palaeobiogeographic patterns may not be as straightforward as previously thought, but instead these patterns are likely to be more variable depending on the clad under examination [16–18,34,35,42,43]. In summary, our models estimate that the global distribution of titanosaurians, and the regionalization of their constituent subclades predominantly follow geophysical patterns of continental separation and isolation throughout the Cretaceous.

### Data accessibility

 Data available as electronic supplementary material.

### Authors’ contributions

 E.G. conceived the study, collected data, conducted analyses, and drafted the manuscript. P.M.O. coordinated the study, and helped draft the manuscript. Both authors are accountable and approve publication.

### Competing interests

 We have no competing interests.

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### Table 1. Model log-likelihood (ln) scores with Akaike information criterion (AIC) scores for BioGeoBEARS models.

<table>
<thead>
<tr>
<th>Model</th>
<th>ln</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>df.</th>
<th>D-statistic</th>
<th>p-value</th>
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<td>DEC</td>
<td>−89.6</td>
<td>183.2</td>
<td>—</td>
<td>2</td>
<td>—</td>
<td>—</td>
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<tr>
<td>DEC + j</td>
<td>−65.99</td>
<td>138</td>
<td>45.2</td>
<td>3</td>
<td>47.23</td>
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<td>—</td>
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<td>3</td>
<td>40.88</td>
<td>1.60 × 10⁻¹⁰</td>
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<td>—</td>
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<td>8.00 × 10⁻²⁰</td>
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### phylogenetic analyses

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<th>ln</th>
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References


26. Gaffney EV. 2007 break-up and early seafloor spreading between...

