

Untangling the dinosaur family tree

ARISING FROM M. G. Baron, D. B. Norman & P. M. Barrett *Nature* **543**, 501–506 (2017); doi:10.1038/nature21700

For over a century, the standard classification scheme has split dinosaurs into two fundamental groups¹: ‘lizard-hipped’ saurischians (including meat-eating theropods and long-necked sauropodomorphs) and ‘bird-hipped’ ornithischians (including a variety of herbivorous species)^{2–4}. In a recent paper, Baron *et al.*⁵ challenged this paradigm with a new phylogenetic analysis that places theropods and ornithischians together in a group called Ornithoscelida, to the exclusion of sauropodomorphs, and used their phylogeny to argue that dinosaurs may have originated in northern Pangaea, not in the southern part of the supercontinent, as has more commonly been considered^{6,7}. Here we evaluate and reanalyse the morphological dataset underpinning the proposal by Baron *et al.*⁵ and provide quantitative biogeographic analyses, which challenge the key results of their study by recovering a classical monophyletic Saurischia and a Gondwanan origin for dinosaurs. This shows that the Ornithoscelida hypothesis is not the final word, and that there is still great uncertainty around the basic structure of the dinosaur family tree. There is a Reply to this Comment by Baron, M. G. *et al.* *Nature* **551**, <http://doi.org/10.1038/nature24012> (2017).

The size and scope of the Baron *et al.*⁵ dataset (457 anatomical features scored for 74 early dinosaurs and close relatives) are important advances on previous studies of early dinosaur phylogeny^{8–10}. It combines previously published and new morphological characters, setting a standard for the field, which we applaud. With that said, however, the results of the new study⁵ differ so radically from all previous cladistic analyses, and decades of pre-cladistic research, that they deserve close scrutiny. Our main concern is that the authors were able to personally study fewer than half of the taxa in their analysis; the others were scored mostly based on published literature, which is problematic, because many characters relate to fine anatomical details, requiring first-hand study to be reliably documented. The taxon sample of Baron *et al.*⁵ is larger than any previous analysis and this represents one of the strongest aspects of the study. However, the lack of some important taxa (for example, the early thyreophoran *Scutellosaurus*, the possible theropod *Daemonosaurus*, the newly described *Ixalerpeton* and *Buriolestes*, and a broader sample of averostran theropods) may have a substantial effect on character optimizations near the base of the dinosaur tree, and thus on the interrelationships of early dinosaurs.

Our international consortium of early dinosaur evolution specialists has come together to critically assess the Baron *et al.*⁵ dataset. We have personally studied nearly all included taxa, and some of us were the original authors of most of the characters incorporated in the dataset. Our aim was straightforward: check the scorings for each taxon in the analysis, rescore them if necessary based on first-hand observations and adding a small number of taxa (see Supplementary Information). We did not add or rewrite characters, as this would go beyond our intention to provide a quality control check on taxon scoring. Although we note that character definition and delimitation are critical, these would be better addressed in a longer, more detailed study.

Our rescored dataset produced a strict consensus tree (Fig. 1), showing the traditional arrangement of the three major dinosaur groups: sauropodomorphs and theropods united as Saurischia, with Ornithischia on a separate branch. This tree is less resolved than the one described in Baron *et al.*⁵, and the same basic arrangement is found when we analyse only those taxa included in the original study. Relationships are, however, not particularly well supported: it would take two (full dataset) or three (original taxon sample) additional steps to enforce an ornithischian–theropod clade as reported by Baron *et al.*⁵

and Templeton tests show no significant differences between the two hypotheses (see Supplementary Information).

Character scoring changes explain our different results. They also alter the optimisation of the 21 putative ornithoscelidan synapomorphies proposed by Baron *et al.*⁵ (see Supplementary Information), revealing that many have a complex distribution among early dinosaurs. Some are not only present in ornithoscelidans, but can also be found more broadly among early dinosaurs, including herrerasaurids and sauropodomorphs. Others are absent in many early diverging ornithoscelidans and probably evolved independently in later ornithischians and theropods. Several of the characters used by Baron *et al.*⁵ have uninformative distributions, are poorly defined and/or completely or partially duplicate one another (see Supplementary Information). This may have resulted from a largely uncritical assembling of characters from previous analyses with different aims, without integrating or modifying their descriptions and states.

Baron *et al.*⁵ also argued, without a quantitative analysis, that the placement of *Saltopus* and Northern Hemisphere silesaurids as close outgroups to Dinosauria suggests a northern Pangaeian origin for the clade. Instead, our numerical estimate of ancestral states (using three different evolutionary models and with an over 90% log-likelihood in two of them) and two biogeographic analytical tools (statistical dispersal–vicariance analysis and implementation of the dispersal–extinction–cladogenesis model) predict that dinosaurs originated in southern Pangaea for all three possible solutions provided by Baron *et al.*⁵ regarding the positions of *Saltopus*, Silesauridae and Dinosauria (see Supplementary Information).

Our reanalysis highlights three central issues:

(1) There is currently great uncertainty about early dinosaur relationships and the basic structure of the dinosaur family tree. We did not recover the Ornithoscelida of Baron *et al.*⁵, but the more traditional saurischian–ornithischian dichotomy that we did recover is weakly supported. It seems that the flood of new discoveries over the past decades^{9–13} has revealed unexpected complexity. Homoplasy was rampant in early dinosaurian evolution, and the earliest members of the major subgroups were very similar in body size and morphology, which makes unravelling their relationships remarkably difficult.

(2) Dataset construction is key. Morphological phylogenetic analyses hinge on taxon and character sampling and scoring, so careful consideration of the primary homologies, and careful construction and coding of characters are very important. Our critical revision of the scorings of Baron *et al.*⁵ indicates that the original version of that dataset is not reliable for testing the phylogenetic relationships of early dinosaurs.

(3) It is important to use appropriate computational analytical tools before making macro-evolutionary claims. Such methods can provide a range of results, depending on models of evolution and tree reconstruction, and allow hypotheses to be explicitly tested against one another.

In conclusion, the data we present here lead us to be sceptical of the new phylogeny proposed by Baron *et al.*⁵ We are excited about the Ornithoscelida hypothesis, which will certainly reinvigorate the study of dinosaur origins. However, we do not currently find strong evidence to discard the traditional Ornithischia–Saurischia division, and we must also entertain a third possibility that was articulated in the 1980s^{14,15}, but rarely discussed since: that sauropodomorphs and ornithischians may form their own herbivorous group, separate from the ancestrally meat-eating theropods. Suboptimal trees show

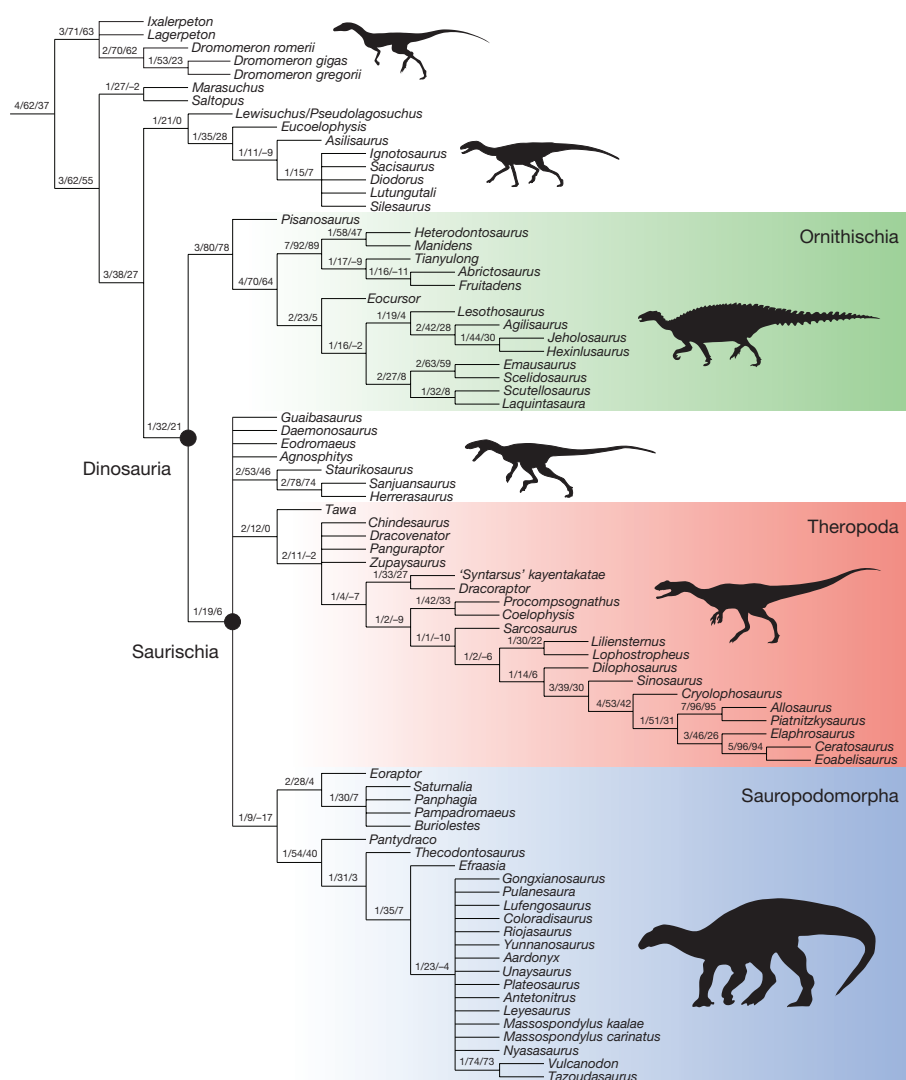


Figure 1 | Results of the reanalysis of a revised dataset on early dinosaur relationships. Strict consensus of the most parsimonious trees found in the analysis of the rescored dataset of Baron *et al.*⁵ with additional taxa,

showing a monophyletic traditional Saurischia. Bremer support values (left) and bootstrap values (absolute (middle) and 'group present/contradicted' (right)) are shown for each clade.

that this hypothesis of relationship is only four steps longer than the optimal most parsimonious trees (see Supplementary Information) and Templeton tests show no significant differences between the Ornithoscelida and Saurischia–Ornithischia topologies. This shows that these, and other, hypotheses of early dinosaur relationships must continuously be tested as new fossils are found. But at this point, a more critical evaluation of characters—how they are defined and scored, whether they are independent from one another, how different authors have used them—is the best tool for untangling the roots of the dinosaur family tree.

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Data Availability All data are available in the Supplementary Information.

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BRIEF COMMUNICATIONS ARISING

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Supplementary Information accompanies this Comment.

Author Contributions M.C.L., M.D.E., O.W.M.R., M.J.B., B.W.M., F.E.N. and S.L.B. designed the project. M.C.L., M.D.E., O.W.M.R., M.J.B., F.K., B.W.M., F.E.N. and D.P. rescored the data matrix. M.D.E. and D.P. conducted the phylogenetic analyses. M.J.B., B.W.M. and D.P. conducted the biogeographic analyses. All authors discussed the data, wrote and approved the final manuscript (including the Supplementary Information).

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Baron *et al.* reply

REPLYING TO M. C. Langer *et al.* *Nature* **551**, <http://doi.org/10.1038/nature24011> (2017)

The principal aims of our Article¹ were to establish a new taxon–character dataset that future works can build on, and to examine the implications of the trees generated with this dataset¹. In the accompanying Comment², Langer *et al.* provide the first re-examination of our new hypothesis on early dinosaur relationships and we welcome their critical appraisal. Following scrutiny of the character data underpinning our phylogeny¹, Langer *et al.*² identify numerous disagreements in terms of character scoring and suggest changing approximately 2,500 scorings, around 10% of the character data. This extensive re-scoring results in recovery of the ‘traditional’ topology, although with less resolution and very weak support; their result is statistically indistinguishable from the possibility that our topology provides a better explanation of the data. This weak support, despite these extensive changes, suggests that the ‘traditional’ tree struggles

to account for many character distributions. Moreover, we disagree with many of the re-scorings suggested by Langer *et al.*². For example, their re-scored *Pisanosaurus* includes character scores that are impossible to observe, such as ratios between skull length and body length, and skull length and femur length; the only known specimen of *Pisanosaurus* does not preserve a complete skull, axial column or femur. For this reason, the conclusions of Langer *et al.*² should not be accepted as correct without in-depth assessment of their revised matrix. Re-scoring of *Pisanosaurus* alone, based upon our personal observations of the material, results not only in the recovery of Ornithoscelida, but also in the identification of this enigmatic taxon as a sailesaurid (Fig. 1). Such a novel position for *Pisanosaurus* has been hinted at in previous works^{3,4}, but has not yet been recovered in any form of phylogenetic analysis. This finding might also account for a result

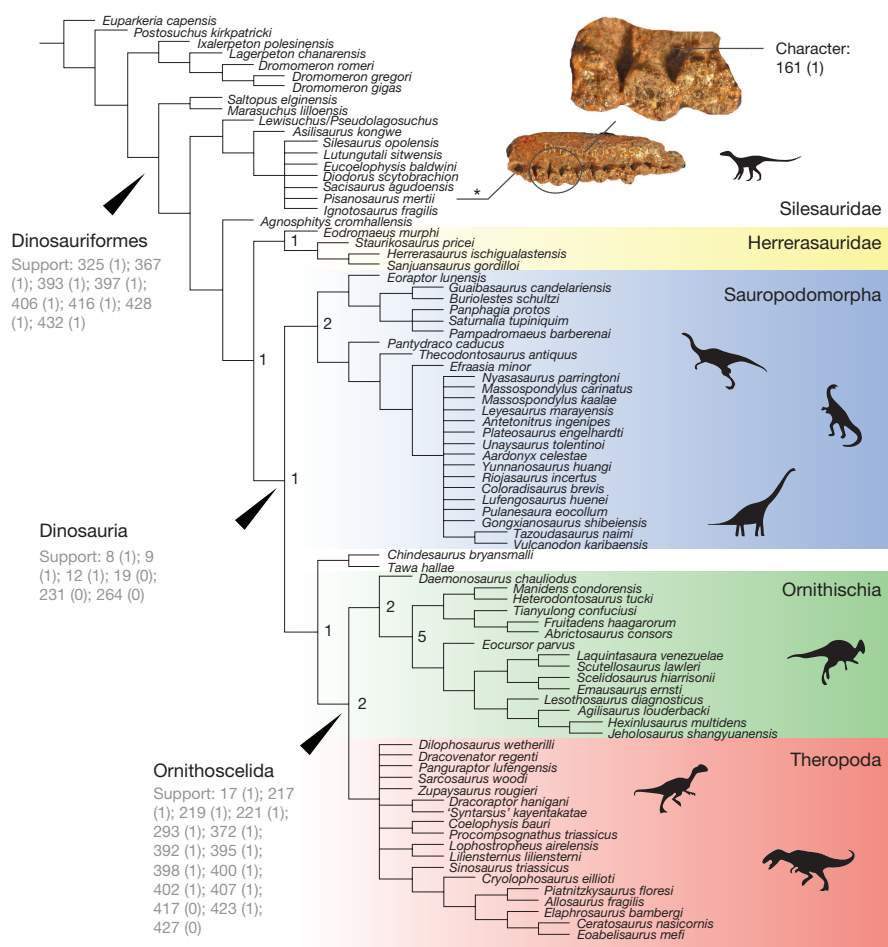


Figure 1 | Results of the phylogenetic analysis of the dataset following the re-scoring of *Pisanosaurus mertii*. Strict consensus tree of the 427 most parsimonious trees (length = 1,923) found in the re-analysis of the early dinosaur dataset following the re-scoring of Langer *et al.*² and our own re-scoring of *Pisanosaurus mertii* alone (indicated by an asterisk). Analyses were carried out using the new technology search function in TNT¹⁰, following the original protocol¹ and using tree bisection reconnection (TBR) branch swapping; by applying a second round of TBR

branch swapping, following the protocol of Langer *et al.*², we recover a polytomy within Dinosauria and note that a monophyletic Saurischia is not recovered. Although this is not conclusive evidence in favour of either hypothesis, we stress that this result follows corrections to only a single taxon in the revised matrix provided by Langer *et al.*². This suggests that their result hinges on the scorings of one or two key early taxa. It also suggests that additional changes, where justified, may further support the results of our original study.

obtained in other studies where ornithischians were recovered as the sister-taxon of silesaurids^{5,6}; it is also interesting to note that the silesaurid–ornithischian clade recovered by Cabreira *et al.*⁵ is recovered in neither our original analysis¹, nor Langer *et al.*². We also disagree with the re-scoring of various other taxa proposed by Langer *et al.*² and corrections to many of these would further support our original hypothesis.

We applaud Langer *et al.*² for presenting their rigorous analysis of early dinosaur palaeobiogeography, which uses both our new tree and their expanded version of our dataset. This work was beyond the scope of our original study and we limited our comments on palaeobiogeography to a single sentence of speculation in the discussion: it is pleasing to see our new tree being used for broader macro-evolutionary studies. We concur with the results presented by Langer *et al.*², but note that Northern Hemisphere taxa are underrepresented in these trees due to a paucity of material and localities, although fragmentary evidence indicates the presence of silesaurids, herrerasaurids and other early dinosaur taxa in these faunas⁷. Our intention was to indicate that we should not rely on the southern Pangaeian record alone when attempting to reconstruct dinosaur evolutionary history^{5,6,8}, and to suggest that northern Pangaea might prove important in unravelling the early evolutionary history of avemetatarsalians, as has also been suggested by other recent discoveries⁹.

Data Availability All data are available from the corresponding author upon reasonable request.

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