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Untangling the dinosaur family tree

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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 more commonly considered⁶⁻⁷. Here, we evaluate and reanalyse the morphological dataset underpinning the Baron *et al.* proposal⁵ 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 should not be taken face value, and that there is still great uncertainty around the basic structure of the dinosaur family tree.

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 those used to study early dinosaur phylogeny⁸⁻¹⁰. 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 most important concern is that the authors were able to personally study fewer than half of the taxa in their analysis; the others were scored based mostly 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 in any previous analysis and this represents one of the strongest aspects of the study. However, it would be interesting to explore the effect of including some early dinosaurs and close relatives (e.g. the newly described *Ixalerpeton* and *Buriolestes*, the early thyreophoran *Scutellosaurus*, the possible theropod *Daemonosaurus*, and a broader sample of averostran theropods). The lack of

these taxa may have a significant 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. Between us, 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, rescoring them if necessary based on first-hand observations, also 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 that of 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 a ornithischian-theropod clade as reported by Baron *et al.*⁵ and Templeton tests show no significant differences between the two hypothesis (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 many to have a complex distribution among early dinosaurs. Some are present not only in ornithoscelidans, but more broadly among early dinosaurs, including herrerasaurids and sauropodomorphs. Others are absent in many early-diverging ornithoscelidans and probably evolved independently in latter 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 biogeography 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 concerning 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 we did recover is weakly supported. It seems that the flood of new discoveries over the past decades⁹⁻¹³ 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 that careful consideration of primary homologies, construction of characters, and coding is 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 macroevolutionary 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. Yet, 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 1980s¹⁴⁻¹⁵, but rarely discussed since: that sauropodomorphs and ornithischians may form their own herbivorous group, exclusive of the ancestrally meat-eating theropods. Suboptimal trees showing this hypothesis of relationship are only four steps longer than the optimal MPTs (see Supplementary Information) and Templeton tests show no significant differences relative to the preferred 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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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 biogeography analyses. All authors discussed the data, wrote and approved the final manuscript (including the Supplementary Information).

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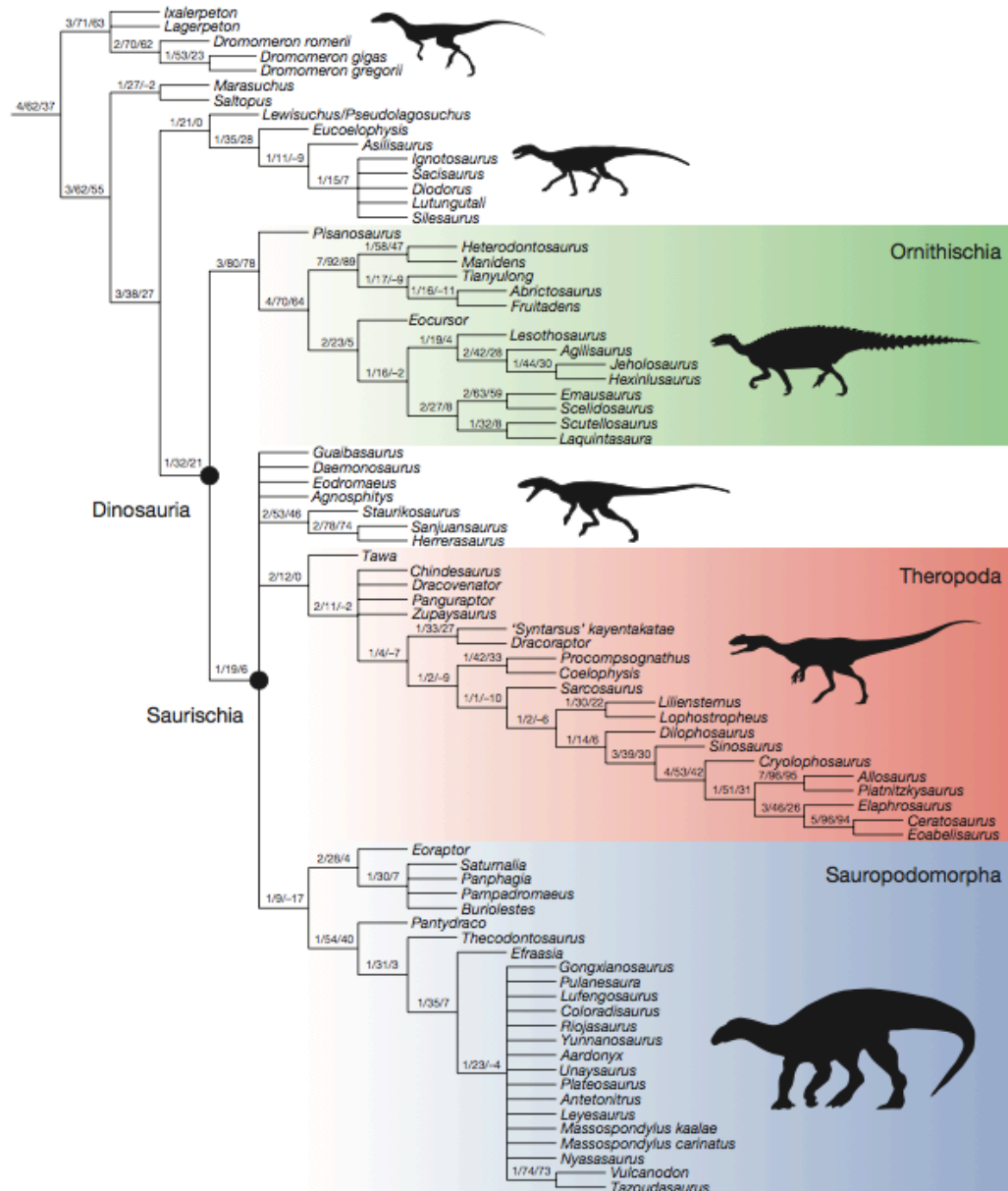


Figure 1 | Results of the analysis of the dataset following the re-scoring of previously published dataset. Strict consensus of the most parsimonious trees found in the analysis of the rescored dataset of Baron *et al.*⁵ with additional taxa, showing a monophyletic traditional Saurischia. Bremer support values (left) and bootstrap values (absolute (middle) and 3 ‘group present/contradicted’ (right)) are shown for each clade.