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REVIEW ARTICLE

Difficulties with the origin of dinosaurs: a short comment on the current debate

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Abstract: The origin and early evolutionary history of the dinosaurs is a topic that has recently gone through a period of renewed interest and academic debate. For 130 years, one way of classifying the various dinosaur subgroups persisted as the accepted model, with increasing levels of research in the past quarter-century also providing evidence for the hypothesis that dinosaur origination occurred in the Southern Hemisphere, particularly in South America. It is, after all, from within the Late Triassic strata of countries like Argentina and Brazil that we get some of the very best early dinosaur specimens; many of these specimens are the earliest known representatives of some of the major dinosaur subgroups, such as the theropods and sauropodomorphs. However, some recent analyses have brought about a shift in terms of what is currently accepted and what is now disputed regarding the origin of dinosaurs – the Southern Hemisphere origination hypothesis was questioned (although this was based upon observations and not with quantitative analysis techniques), as has the shape of the dinosaur tree. Responses to the new hypothesis were numerous and robust, and new analyses further supported a Southern Hemisphere point of origin. Whilst the interrelationships between the major dinosaur clades remains to be fully resolved, the current data does seem to comprehensively answer the question of where the dinosaurs first originated. However, it is arguable whether or not the current data that is being used in such palaeobiogeographical analyses is sufficient to provide a meaningful answer to the question of where specifically the dinosaur clade first appeared. This short communication urges a degree of caution about the current consensus and what steps may need to be taken to ensure that more meaningful results are produced in the future.

Keywords: palaeobiogeography; dinosaur evolution; dinosaur anatomy; Triassic Period; Ornithoscelida

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INTRODUCTION

In 2017 a largescale study of early dinosaurs and their closest kin posed the first serious challenge in modern times to the traditional model of early dinosaur evolution and interrelationships (Baron *et al.*, 2017a), a theory which had since the late 19th century been accepted and supported almost universally (Seeley, 1887-1888; Sereno, 2005; Langer & Benton, 2006; Brusatte *et al.*, 2010a; Nesbitt, 2011). In place of the traditional dinosaur family tree that positioned the long-necked sauropodomorphs and the carnivorous theropods together into a group called the Saurischia - or 'lizard-hipped' dinosaurs - a new grouping put theropods and ornithischian ('bird-hipped' dinosaurs) together for the first time (Figure 1). This newly proposed clade was named Ornithoscelida (Baron *et al.*, 2017a). The new proposal came after a series of phylogenetic analyses of a new early dinosaur dataset, which was constructed to try and broaden species sampling and choice of anatomical characters used in assessing dinosaur interrelationships. In the results the tree topology within Dinosauria was rearranged and, based upon this new tree structure, the authors went on to suggest that the point of origination of the whole dinosaur clade may not have been the Southern Hemisphere, as was the current consensus (e.g., Langer & Benton, 2006; Brusatte *et al.* 2010a; Martinez *et al.*, 2011; Sereno *et al.*, 2013). The results of this large new analysis proved to be controversial, and a flurry of responses and comments followed (Baron *et al.*, 2017b; Brusatte, 2017; Langer *et al.*, 2017; Parry *et al.*, 2017; Baron & Barrett, 2017; Baron & Williams, 2018; Marsola *et al.*, 2019; Müller & Dias-da-Silva, 2019).

Almost immediately, new teams challenged the choice of anatomical characters in the early dinosaur dataset and set about reworking and rescoring certain dinosaur species based upon different interpretations of their anatomy, the meaning of certain anatomical characters and character states (e.g., Langer *et al.* 2017). One such study found that the traditional model, the newly proposed model and a third alternative model of dinosaur relationships were not significantly different from one another (see figure 1) and that, based upon the available data, each hypothesis was a distinct possibility. This was perhaps surprising, given how prevalent the historic ideas had been, and how little confidence it seemed could be had about such fundamental questions about early dinosaur evolutionary history. However, one aspect of this first follow-up study was unequivocal in its findings – the Southern Hemisphere was, after analysis of a modified version of the original dataset, demonstrated to be the point of ancestral origin for the dinosaurs. The earlier suggestion (Baron *et al.*, 2017a) that taxa in the Northern Hemisphere may have played a more significant role in early dinosaur evolution was flatly rejected on the strength of the current data. Subsequent studies that utilised more sophisticated phylogenetic techniques (Lee *et al.*, 2017) and wider sampling of datasets (Marsola *et al.*, 2019) further tested the biogeographic implications of the original study and a Southern Hemisphere, or 'Gondwanan', origin for dinosaurs was confirmed. Based upon these analyses, the idea that the Northern Hemisphere could have played a role in early dinosaur evolution was quickly dismissed.

Around the same time as the large early dinosaur dataset of Baron *et al.* (2017a) was being constructed, analysed and challenged, other teams of researchers were starting to publish a large quantity of data on new early dinosaurs and close dinosaur relatives from the Late Triassic strata of South America

(Cabreira *et al.*, 2016; Müller *et al.*, 2018; Pacheco *et al.*, 2019; Pretto *et al.*, 2019). Many of these studies utilised a different anatomical dataset and followed more traditional approaches to taxon sampling and anatomical character selection. The results of the analyses that were presented alongside descriptions of new dinosaur species closely mirrored the traditional hypothesis of dinosaur interrelationships, with a few minor differences in the positions of one or two taxa (Figure 1). These studies, while not finding support for the new model proposed by Baron *et al.* (2017a), did not incorporate the new anatomical characters, character scores or sampling methods from the studies by Baron *et al.* (2017a, b) and others (e.g., Agnolin & Rozadilla, 2017; Baron & Williams, 2018) and so the value of direct comparisons between results is, for now, limited by a lack of overlap. Likewise, in other follow up studies, such as that by Baron & Barrett (2017), Baron & Williams (2018), and Müller & Dias-da-Silva (2019), the data that has been recently presented on the newly discovered South American taxa was also not incorporated. This lack of current overlap between datasets and taxon sampling has had a detrimental overall effect on our understanding of early dinosaur evolution and has offered very little by way of a solution to the any of issues still outstanding. The author recognises his own failing in this respect and would further seek to draw attention the fact that the original ‘challenge’ to a Southern Hemisphere point of origination was speculative, rather than robustly supported by data. However, it is this author’s view that there are still areas that need to be properly explored, and new data that needs to be incorporated into working datasets before an alternative hypothesis about the point of origination of the dinosaurs can be completely rejected. Further, it is suggested that developments in data compilation and analysis can be better utilised through a more collaborative approach, rather than a continued series of reply and rebuttals.

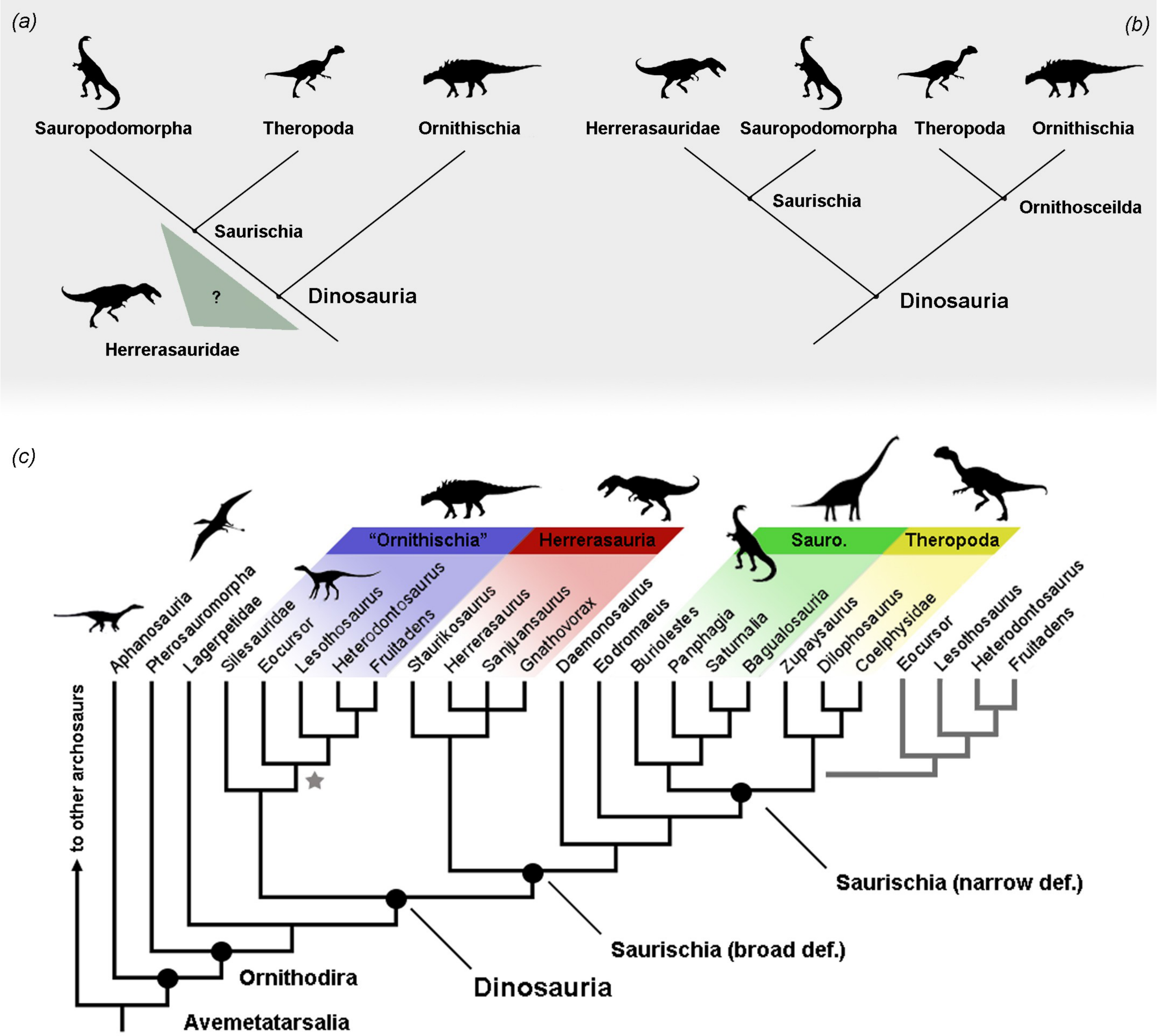

Figure 1. Dinosaur family trees. Each tree (a-c) has been recovered in recent phylogenetic analyses of early dinosaurs. (a), the ‘traditional model’ of dinosaur interrelationships, with Ornithischia and Saurischia as sister-taxa; (b), the ‘Ornithoscelida’ model; (c), consensus tree made from a combination of results from recent analyses (black), with superimposition (grey) of Ornithischia into an alternate position, as suggested in other studies. Both the broad definition of Saurischia and narrower definition are marked. Key: Sauro. = Sauropodomorpha.

DISCUSSION

First, to try and resolve the issue relating the topology within the dinosaur lineage, the datasets produced in each of the various analyses discussed above should be combined and an effort made to consistently score all species using a standardised set of definitions for anatomical characters and character states. Much of the current disagreement about the interrelationships between major dinosaur subgroups may be resolved and one of the three distinct hypotheses that are currently considered to be possible may emerge as being statistically significantly more likely than any other. Second, and most importantly, it is only through the full incorporation of data from newly discovered species both within and without Dinosauria, that more confidence could be placed in our understanding of the geographic setting of the common ancestor of all dinosaurs.

Particularly in terms of the biogeographic analyses used to determine the origin of dinosaurs, there are a number of potential setbacks and limitations that arise from the available data. The first and most striking issue that needs to be addressed is the potential sampling bias that has led to most datasets of early dinosaurs becoming very South American taxon heavy. Whilst it is certainly true that Triassic formations in South America have recently yielded a plethora of exquisite specimens, while other fossil bearing localities have yet to, it is not logically consistent to conclude that this is sufficient evidence that dinosaurs originated in Triassic South America. Absence of evidence for Late Triassic dinosaurs in other localities does not equate to evidence of their absence. While increased sampling twinned with consistent absence does increase the probability of a ‘true absence’ being the case, it can be argued that current sampling is not sufficient to be confident of true absence. In fact, we do know from fossil evidence that the same potential diversity of dinosaur taxa existed in parts of the globe outside of the Southern Hemisphere in the Late Triassic (Nesbitt *et al.*, 2007, 2013, 2017; Brusatte *et al.*, 2010b; Niedźwiedzki *et al.*, 2015). Herrerasaurs, theropods and even a possible neotheropod have been reported from the Norian (mid-Late Triassic) of Poland (Niedźwiedzki *et al.*, 2015), a similar diversity of forms is known from Late Triassic North America (Nesbitt *et al.*, 2007; Baron & Williams, 2018), and perhaps most significantly of all, early Middle Triassic footprints found in the Holy Cross Mountains of Poland have been suggested to possibly belong to early diverging members of the dinosaurian lineage (Brusatte *et al.*, 2010b); their discovery was said to ‘push back’ the dinosaurs’ origin in time (though nothing was said about ‘pushing it up’ geographically). However, the fossil record in the Northern Hemisphere is, generally, not yet of a high enough quality to allow for identification of specimens to a generic or specific level, as is the case for South America. This has led to most of the earliest occurring Late Triassic Northern Hemisphere dinosaurs being excluded from datasets, which largely score only for named genera and species. As a result, this important data from Northern Hemisphere localities has not yet contributed to analyses of dinosaur origination. In contrast, South American specimens have the advantage of being complete enough to be diagnosable to generic and specific levels. Hence, lists of the earlier Late Triassic dinosaurs are dominated by such specimens, because it is only in South America that the record is good enough to warrant generic and specific naming. This does not preclude the distinct possibility that an equal or greater number of genera and species were present in other, northern regions around the same time as the best Late Triassic South American faunas existed, but that these are simply not yet captured in the fossil record. The exclusion of such data could potentially be a problem even for the most sophisticated and powerful of palaeobiogeographic analyses. In the analysis of Lee *et al.* (2019), for example, which utilised a new method combining anatomical, tectonic, and stratigraphic data in investigating the dinosaurs’ ancestral origin, was limited by the data being input into the analysis software. The study, to which this author was a contributor, was hampered to a degree in that it did not include the full range of early non-South American Triassic dinosaur specimens. Future iterations of this same type of analysis should make every effort to address this. Even fragmentary dinosaur specimens that are only diagnosable to the level of Order could, in a dynamic biogeographical analysis such as that of Lee *et al.* (2019), fundamentally alter the outcome.

Another substantial omission of most studies of this kind are pterosaurs. Pterosauromorpha is a clade of flying Mesozoic reptiles that are very closely related to the dinosaurs, forming with them the clade Ornithodira (e.g., Nesbitt *et al.*, 2017). All of the earliest undisputed pterosaur specimens that we currently have are known from Northern Hemisphere localities (Barrett *et al.*, 2008). Just as with fragmentary Triassic dinosaurs, the general exclusion of such specimens from biogeographic analyses means that substantial and informative datapoints are lost and a potentially false signal is being generated. With an exclusively Northern Hemisphere record, the pterosaurs might hint that early ornithodirans, which eventually gave rise to the dinosaurs, started off their evolutionary history in northern localities. It is true that the pterosaurs could fly, and therefore arguably cover a broader geographic range, but this argument could not account for the total absence of definitive pterosaurs in Southern Hemisphere localities, and in particular their absence in the extremely well-sampled early Late Triassic strata in Argentina and Brazil. Silesaurids, a clade of animals even more closely related to the dinosaurs, are also found in both the Northern and Southern Hemispheres (Dzik, 2003; Ferigolo & Langer, 2006). Again, this data might present a counterpoint to the arguments about a Southern Hemisphere origination of dinosaurs, though more silesaurids have been included in recent analyses, with some even suggesting that they may in fact be dinosaurs (e.g., Ferigolo & Langer, 2006). Indeed, if silesaurids are dinosaurs, related to or within Ornithischia, as suggested by Ferigolo & Langer (2006) and supported in some recent phylogenetic analyses (e.g., Cabreira *et al.*, 2016; Pacheco *et al.*, 2019), then we do have evidence for the presence of dinosaurs in the Carnian (early Late Triassic) formations in Europe (Dzik, 2003). Further down the tree, aphanosaurs, sister-group to ornithodirans, also appear to have a global distribution, with species known from southern Africa, South America, India and Russia (Sennikov, 1988; Nesbitt *et al.*, 2017). Ideally, an effective dataset would include all these taxa, and all other Triassic dinosaur specimens, regardless of their level of completeness, along with information about their geographic setting and age.

As a final point, it is worth remembering that during the Late Triassic, every continent was united into a single landmass, Pangea, and our current concepts of geographical delineation into Northern Hemisphere (i.e., North America, Europe, Asia) and Southern Hemisphere (i.e., Australia, South America, Africa and Antarctica) had little meaning. Specimens of each of the main dinosaur subgroups can be found on every continent in all three periods within the Mesozoic Era suggesting that the common ancestors of these groups covered all corners of Pangea before it split toward the end of the Triassic and

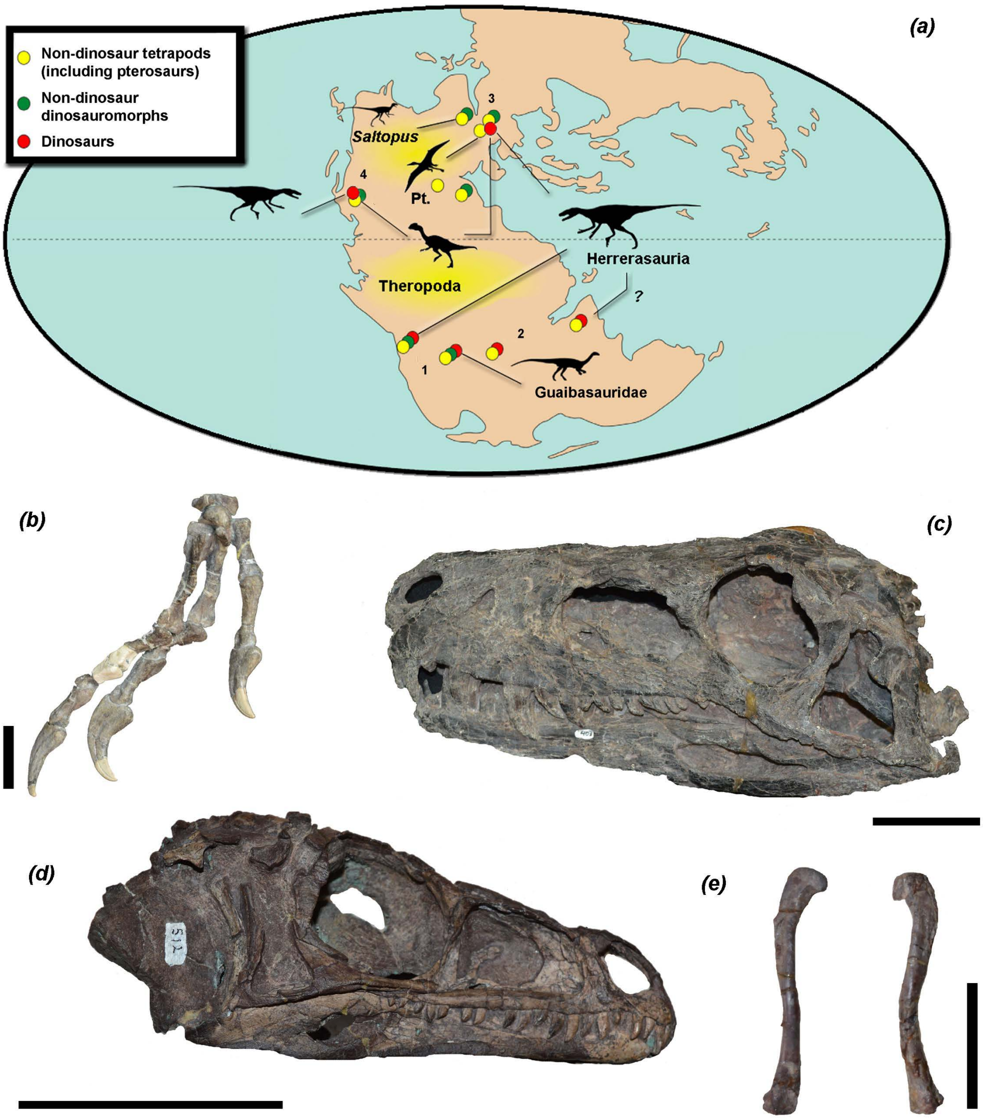

Figure 2. Triassic dinosaurs of Pangaea. (a), map of Earth showing dinosaur (and close dinosaur relative) distribution across Pangaea during the early-middle Late Triassic - Herrerasauria is represented in Europe, North America and possibly India (?), in addition to South America. Theropoda is also represented in both North America and Europe; (b) manus of early dinosaurian *Herrerasaurus*, scale bar = 3cm; (c), skull of *Herrerasaurus*, scale bar = 7cm; (d), skull of early sauropodomorph *Eoraptor*, scale bar = 7cm; (e), pair of femora from an early close dinosaur relative *Marasuchus*, scale bar = 4cm. Key: areas of rough modern-day equivalence, 1 = South America; 2 = southern Africa; 3 = Europe; 4 = North America; Pt = Pterosauromorpha. Adapted from Marsola *et al.* (2019) with additional data included.

Early Jurassic, and may have travelled freely across the supercontinent of Pangea from any point of origin (Figure 2). Whilst informative, we should always keep in mind the fact that the record we have for South American Triassic faunas is not going to be the whole story.

While it is not disputed what the results of recent analyses have clearly found in terms of a dinosaur origin point, it is right to say that the fossil record is ultimately a very poor reflection of the real biodiversity of any given time and place. What is more, our understanding of it is continually changing with new finds. It should always be kept in mind that new discoveries and re-evaluation of a previously named species have the potential to change or even reverse our understanding of an entire group's evolutionary history and geographic point of origin, and it is therefore suggested that a more open-minded approach be maintained as this field of research progresses further.

CONCLUSIONS

The current debate around early dinosaur evolution and the clade's origin in time and space is one of the liveliest topics in palaeontological research. Clear differences still exist between the various competing hypotheses and disagreements persist among researchers. However, as new discoveries and new analyses add more information to the collective pile, a sensible approach might be to agree to focus efforts on achieving a common goal. Collaborative (as opposed to competitive) research may be the best way to find solutions to the outstanding issues and settle the debate of dinosaur origination. By producing an agreed large working dataset of early dinosaurs and close dinosaur relatives, which includes indeterminate dinosaurs, pterosaurs and other taxa, as well as data on locality and age, a much clearer picture of the first stages in the history of the dinosaurs might emerge.

BIBLIOGRAPHY

Agnolín, F. L., Rozadilla, S. 2017. Phylogenetic reassessment of *Pisanosaurus mertii* Casamiquela, 1967, a basal dinosauriform from the Late Triassic of Argentina. Journal of Systematic Palaeontology 16 (10):853-879. https://doi.org/10.1080/14772019.2017.1352623

Baron, M. G., Barrett, P. M. 2017. A dinosaur missing-link? *Chilesaurus* and the early evolution of ornithischian dinosaurs. Biology Letters 13 (8): 20170220. https://doi.org/10.1098/rsbl.2017.0220

Baron, M. G., Williams, M. E. 2018. A re-evaluation of the enigmatic dinosauriform *Caseosaurus crosbyensis* from the Late Triassic of Texas, USA and its implications for early dinosaur evolution. Acta Palaeontologica Polonica 63 (1): 129-145. https://doi.org/10.4202/app.00372.2017

Baron, M. G., Norman, D. B., Barrett, P. M. 2017a. A new hypothesis of dinosaur relationships and early dinosaur evolution. Nature 543, 501-506. https://doi.org/10.1038/nature21700

Baron, M. G., Norman, D. B., Barrett, P. M. 2017b. Untangling the dinosaur family tree: a rebuttal. Nature 551:E4-E5. https://doi.org/10.1038/nature24012

Barret, P. M., Butler, R. J., Edwards, N. P., Milner, A. R. 2008. Pterosaur distribution in time and space: an atlas. Flugsaurier: Pterosaur papers in honour of Peter Wellnhofer. 2008. Hone, D. W. E., and Buffetaut, E. (eds). Zitteliana B, 28. p.61-107.

Brusatte, S. L. 2017. Evolution: Uprooting the Dinosaur Family Tree. Current Biology 27(10): R390-R392. https://doi.org/10.1016/j.cub.2017.04.001

Brusatte, S. L, Nesbitt, S. J., Irmis, R. B., Butler, R. J., Benton, M. J., Norell, M. A. 2010a. The origin and early radiation of dinosaurs. Earth-Science Reviews 101(1):68-100. https://doi.org/10.1016/j.earscirev.2010.04.001

Brusatte, S. L., Niedźwiedzki, G., Butler, R. J. 2010b. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. Proceedings of the Royal Society B. 278 (1708): 1107-1113. https://doi.org/10.1098/rspb.2010.1746

Cabreira, S. F, Kellner, A. W. A., Dias-da-Silva, S., da Silva, L. R, Bronzati, M., Marsola, J. C. A., Müller, R. T., de Souza Bittencourt, J., Batista, B. J., Raugust, T., Carrilho, R., Brodt, A., Langer, M. C. 2016. A unique Late Triassic dinosauromorph assemblage reveals dinosaur ancestral anatomy and diet. Current Biology 26 (22): 3090-3095. https://doi.org/10.1016/j.cub.2016.09.040

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology 23 (3): 556-574. https://doi.org/10.1671/A1097

Ferigolo, J., Langer, M. C. 2006. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone. Historical Biology 19 (1): 1-11. https://doi.org/10.1080/08912960600845767

Langer, M. C., Benton, M. J. 2006. Early dinosaurs: a phylogenetic study. Journal of Systematic Palaeontology 4:309-358. https://doi.org/10.1017/S1477201906001970

Langer, M. C., Ezcurra, M. D., Rauhut, O. W. M., Benton, M. J., Knoll, F., McPhee, B. W., Novas, F. E., Pol, D., Brusatte, S. L. 2017. Untangling the dinosaur family tree. Nature 551 (7678): E1-E3. https://doi.org/10.1038/nature24011

Lee, M. S. Y., Baron, M. G., Norman, D. B., Barrett, P. M. 2019. Dynamic biogeographic models and dinosaur origins. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 109 (1-2): 325-332. https://doi.org/10.1017/S1755691018000920

Marsola, J. C. A., Ferreira, G. S., Langer, M. C., Button, D. J., Butler, R. J. 2019. Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. Palaeontology 62: 473-482. https://doi.org/10.1111/pala.12411

Martinez, R. N., Sereno, P. C., Alcober, O. A., Colombi, C. E., Renne, P. R., Montañez, I. P., Currie, B.S. 2011. A basal dinosaur from the dawn of the dinosaur era in Southwestern Pangaea. Science 331 (6014):206-210. https://doi.org/10.1126/science.1198467

Müller, R. T., Dias-da-Silva, S. 2019. Taxon sample and character coding deeply impact unstable branches in phylogenetic trees of dinosaurs, Historical Biology, 31:8, 1089-1092. https://doi.org/10.1080/08912963.2017.1418341

Müller, R. T, Langer, M. C., Dias-da-Silva, S. 2018. An exceptionally preserved association of complete dinosaur skeletons reveals the oldest long-necked sauropodomorphs. Biology Letters 14 (11): 20180633. https://doi.org/10.1098/rsbl.2018.0633

Nesbitt, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. Bulletin of the American Museum of Natural History 352:1-292. https://doi.org/10.1206/352.1

Nesbitt, S. J., Irmis, R. B., Parker, S. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. Journal of Systematic Palaeontology 5(2): 209-243. https://doi.org/10.1017/S1477201907002040

Nesbitt, S. J, Barrett, P. M., Werning, S., Sidor, C. A., Charig, A. J. 2013. The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. Biology Letters 9 (1): 20120949. https://doi.org/10.1098/rsbl.2012.0949

Nesbitt, S. J., 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 (7651): 484-487. https://doi.org/10.1038/nature22037

Niedźwiedzki, G., Brusatte, S. L., Sulej, T., Butler, R. J. 2015. Basal dinosauriform and theropod dinosaurs from the mid–late Norian (Late Triassic) of Poland: implications for Triassic dinosaur evolution and distribution. Palaeontology 57(6): 1121-1142. https://doi.org/10.1111/pala.12107

Pacheco, C., Müller, R. T., Langer, M. C., Pretto, F. A., Kerber, L., Dias da Silva, S. D. 2019. *Gnathovorax cabreirai*: a new early dinosaur and the origin and initial radiation of predatory dinosaurs. PeerJ 7:e7963. https://doi.org/10.7717/peerj.7963

Parry, L. A., Baron, M. G., Vinter, J. 2017. Multiple optimality criteria support Ornithoscelida. Royal Society Open Science 2017(4):170833. https://doi.org/10.1098/rsos.170833

Pretto, F. A., Langer, M. C., Schultz, C. L. 2019. 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 185(2): 388-416. https://doi.org/10.1093/zoolinnean/zly028

Seeley, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43:165-171. https://doi.org/10.1098/rspl.1887.0117

Sereno, P. C. 2005. The logical basis of phylogenetic taxonomy. Systematic Biology 54:595-619. https://doi.org/10.1080/106351591007453

Sereno, P. C., Martínez R. N., Alcober, O. A. 2013. Osteology of Eoraptor lunensis (Dinosauria, Sauropodomorpha). Basal sauropodomorphs and the vertebrate fossil record of the Ischigualasto Formation (Late Triassic: Carnian-Norian) of Argentina. Journal of Vertebrate Paleontology Memoir 12: 83-179. https://doi.org/10.1080/02724634.2013.820113

Sennikov, A. G. 1988. Novyye rauizukhidy iz triasa yevropeyskoy chasti SSSR. Paleontol. Zhurn 1990 (2): 124-128.