TYPE Editorial
PUBLISHED 30 July 2025
DOI 10.3389/fevo.2025.1656851

OPEN ACCESS

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RECEIVED 30 June 2025
ACCEPTED 18 July 2025
PUBLISHED 30 July 2025

CITATION
Fröbisch J, Laurin M, MacDougall MJ, Modesto SP and Reisz RR (2025) Editorial: Origin and early evolution of amniotes. *Front. Ecol. Evol.* 13:1656851. doi: 10.3389/fevo.2025.1656851

Editorial: Origin and early evolution of amniotes

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KEYWORDS

Amniota, macroevolution, phylogeny, ecology, diversity, Paleozoic

Editorial on the Research Topic
Origin and early evolution of amniotes

Since the original recognition of the clade by Haeckel, 1866, the last few decades have seen a much-increased interest and research effort in investigating the origin and early evolution of amniotes (e.g., Gauthier et al., 1988; Laurin and Reisz, 1995; Sumida and Martin, 1997; Reisz, 1997; Ford and Benson, 2020; Brocklehurst and Benson, 2021; Simões et al., 2022). Especially the advent and development of new methodologies and approaches has allowed for new perspectives and insights into the origin, relationships, diversification patterns and paleobiology of this major clade of terrestrial vertebrates and several aspects of their evolutionary history remain hotly debated. This Research Topic comprises a total of 16 original articles, focusing on recent advances in methodology and their application to explore novel avenues and hypotheses surrounding the early diversification of amniotes.

Some of these articles apply descriptive anatomical approaches to further investigate phylogenetic, biostratigraphic, biogeographic, and evolutionary scenarios. For example, Cisneros et al. reassess the skeletal anatomy and phylogenetic relationships of South America's only pareisaurian reptile, *Provelosaurus americanus* from the middle Permian of Brazil. The study confirms the existence of a small clade of middle-late Permian dwarf pareiasaurs, as *Provelosaurus* groups with three other small upper Permian pareiasaurs from South Africa. *Provelosaurus* is evolutionarily precocious by co-occurring with dinocephalian therapsids, whereas the South African dwarf pareiasaurs are part of the late Permian climax amniote fauna.

Sidor et al. describe a new late Permian burnetiamorph therapsid, *Isengops luangwensis*, from Zambia. Typical for this group, this taxon is characterized by diagnostic cranial bosses and horns. A revised phylogenetic analysis conforms with previous analyses and recovers *Isengops* just outside Burnetiidae. Due to the wide range of cranial adornments in the clade and its species richness (13), especially given the small number of known specimens, the authors suggest that cranial ornamentation may have a macroevolutionary relationship with speciation rate, similar to what has been proposed for ceratopsian dinosaurs.

Rubidge et al. present a new specimen of the poorly-known South African dicynodont therapsid *Lanthanostegus mohoii*. The specimen provides novel information on the palate, occiput, and lower jaw of this taxon. Moreover, it represents the first record from the southwestern Karoo Basin, with the taxon being otherwise only known from a single locality in the Eastern Cape Province, emphasizing its biostratigraphic significance.

Reisz et al. describe in detail the cranial anatomy of the Permian caseid synapsid *Cotylorhynchus romeri*. Notable features include the slightly bulbous marginal dentition with three small denticles distally, and huge external naris, nearly as large as the orbit. Similarly, the lateral temporal fenestra is quite large, but the rest of the skull and jaws are fairly massive. The dentition (despite extensive palatal dentition) and the barrel-shaped body provide clear evidence of high fiber herbivory, emphasizing the importance of caseids, representing the first megaherbivores in vertebrate evolution.

Other articles apply computed tomography to study the anatomy and phylogeny of selected taxa. For example, MacDougall et al. revisit the anatomy of the recumbirostran 'microsaur' *Nannaroter* from the famous early Permian Richards Spur locality using CT data. This taxon is one of the smallest members of this clade, well ossified and likely representing a mature individual. CT data allows the authors to identify new, anatomical features in previously obscured regions, including parts of the palate, braincase, and lower jaw. An updated phylogenetic analysis confirms its position within Recumbirostra as sister to the much larger *Pelodosotis* and *Micraroter*.

Klembara et al. use X-ray microcomputed tomography scanning to study the internal skull anatomy of the Late Carboniferous diadectomorph *Limnoscelis dynatis*. They provide substantial new morphological information regarding the braincase and inner ear of this taxon, expanding the range of neuroanatomical conditions near the base of Amniota. The results of their parsimony and Bayesian analyses recover *Limnoscelis* as the most basal member of Diadectomorpha and the latter as sister group to Synapsida.

Based on neutron tomographic data, Rowe et al. describe for the first time an early Permian parareptile with multiple tooth rows. Based on fragmentary material from the early Permian Richards Spur locality in Oklahoma, the authors identify the new species *Delorhynchus multidentatus*. The multiple tooth rowed condition is present on the dentary, the upper jaw not being preserved. This discovery underscores the unusual taxic diversity of tetrapods at these cave infills.

Some additional studies of this Research Topic apply novel methodologies to reconstruct the paleobiology of their study organisms. For instance, Knaus et al. reassess the maximum metabolic rate (MMR) of Pennsylvanian to Triassic synapsids based on femoral length and the minimal cross-sectional area of the nutrient foramen. They conclude that Permo-Carboniferous synapsids already had a fairly high MMR, at least as high as that of varanids, and in the lower end of the range of mammalian MMR. However, based on previous studies that relied on other lines of evidence (e.g., Faure-Brac and Cubo, 2020), they conclude that endothermy appeared later, closer to the origin of Mammalia.

Romano et al. present both body mass estimates and a reconstruction of the late Permian Russian pareiasaur *Scutosaurus karpinskii*. Using a 3D photogrammetric skeletal model based on the largest known specimen of this taxon and by applying possible densities for living tissues, they produced three potential models (slim, average, and fat). They chose the average model as the most plausible and obtained a body mass estimate of 1160 kg. From this, they conclude that high fiber reptile herbivores weighing over a ton were already present in the late Paleozoic.

A particular focus of other articles of this Research Topic is on functional and behavioral aspects of early amniotes. For example, Benoit et al. report on an embedded tooth surrounded by a callus, representing the first record of a healed bite mark in the snout of an unidentified gorgonopsian from the middle Permian of South Africa. The authors propose two potential explanations, i.e. failed predation by another top predator or intraspecific social (face) biting, favoring the latter hypothesis, which would represent the first fossilized evidence of this behavior in non-mammalian therapsids.

Kammerer investigates potential relationships between the cranial sutural complexity and inferred ecology in the speciose as well as morphologically and ecologically diverse clade of anomodont synapsids. He focuses on the naso-frontal suture as it is usually well-preserved and visible in dorsal view, separating the snout from the remaining skull roof and reflecting potential biomechanical function. The results indicate a substantially increased complexity (interdigitation) in this suture in the fossorial cistecephalid dicynodonts, implying an important role of the head in locomotion in this otherwise as forelimb-diggers interpreted group.

Based on a new specimen of the Late Carboniferous reptile *Anthracodromeus longipes*, Mann et al. evaluate the locomotor ecology of this taxon, using morphometric analyses of the phalangeal proportions and ungual shape. The authors conclude that *Anthracodromeus* shows climbing adaptations, suggesting that the origin of scansoriality occurred earlier than previously suggested and shortly after the origin of amniotes.

Berman et al. undertake a thorough revision of the early Permian bolosaurid *Eudibamus cursoris* from the German Bromacker locality. The combination of new data from the holotype and a new partial but larger skeleton, allows the detailed study of the girdles and limbs to reconstruct the locomotory system. The authors propose the hypothesis of a parasagittal stride and a digitigrade stance, the oldest known example of this kind of evolutionary innovation. They further argue that *Eudibamus* was able to achieve relatively high running speeds during quadrupedal and bipedal locomotion, interpreted as escape mechanism from contemporary predators.

Finally, a selection of further articles focuses on the macroevolution and paleobiodiversity of early amniotes. Buchwitz et al. for instance study changes in posture and locomotion change in Permo-Carboniferous stegocephalians using ichnofossils and the presumed identity of the trackmakers. Their approach, which emphasizes taxa that have generally been assumed to belong to amniotes and their stem group, uses timetrees and ancestral value reconstructions to conclude that major size, posture and gait changes occurred around the Cotylosauria node, characterized by larger body size, a shorter, less flexible trunk, a less sprawling stance, longer strides and a higher maximal speed than those of older tetrapods.

Marchetti et al. evaluate the origin and early diversification of amniotes, specifically reptiles, based on the late Paleozoic tetrapod track record. For this purpose, they revise some critical ichnotaxa and discuss track-trackmaker correlations. A multivariate analysis of trackway parameters aims to infer evolutionary trends in the locomotory capabilities of alleged trackmakers. First occurrences of most clades based on the track record mostly match with the skeletal record, but the footprint record significantly enlarges the paleobiogeographic distributions of the respective groups.

Brocklehurst examines the alpha diversity of synapsid versus reptilian amniotes of the Pennsylvanian and Cisuralian following the recent descriptions of new taxa and systematic revisions of others. He discovers that diversity measures of these early amniotes are greatly influenced by the scale of analysis, and concludes that the conventional reconstruction of synapsid dominance during the Pennsylvanian and the Cisuralian is likely biased by data from mainly large synapsid amniotes collected from numerous red bed localities, whereas reptiles dominate at the Richard Spur lagerstätte, preserving overwhelmingly small faunal elements.

The current compilation of papers in this Research Topic reflects the concentrated but multifaceted research efforts of our community to unravel the early evolutionary history of this highly successful clade. This selection, as well as additional recent research (e.g., Benoit et al., 2021; Ponstein et al., 2024; Reisz et al., 2024; Jenkins et al., 2024, Jenkins et al., 2025), shows that the debate regarding the composition and relationships of early amniotes (e.g., microsaurs, diadectomorphs, parareptiles, varanopids) is still ongoing, aiming for a consensus that will form the basis for future macroevolutionary investigations.

Author contributions

JF: Conceptualization, Writing – original draft, Writing – review & editing. ML: Writing – original draft, Writing – review & editing. MM: Writing – review & editing, Writing – original draft. SM: Writing – review & editing, Writing – original draft. RR: Writing – review & editing, Writing – original draft.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. JF and MM were funded by the German Federal Ministry of Research, Technology and Space (BMFTR, formerly BMBF) for the BROMACKER Project 2020-2025, grant number 01UO2002A.

Acknowledgments

We would like to thank all authors for their submitted manuscripts and all reviewers for their contributions.

Conflict of interest

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The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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References

Benoit, J., Ford, D. P., Miyamae, J. A., and Ruf, I. (2021). Can maxillary canal morphology inform varanopid phylogenetic affinities? *Acta palaeont. Pol.* 66, 389–393. doi: 10.4202/app.00816.2020

Brocklehurst, N., and Benson, R. J. (2021). Multiple paths to morphological diversification during the origin of amniotes. *Nat. Ecol. Evol.* 5, 1243–1249. doi: 10.1038/s41559-021-01516-x

Faure-Brac, M. G., and Cubo, J. (2020). Were the synapsids primitively endotherms? A palaeohistological approach using phylogenetic eigenvector maps. *Phil. Trans. R. Soc B* 375, 20190138. doi: 10.1098/rstb.2019.0138

Ford, D. P., and Benson, R. B. (2020). The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. *Nat. Ecol. Evol.* 4, 57–65. doi: 10.1038/s41559-019-1047-3

Gauthier, J., Kluge, A., and Rowe, T. (1988). Amniote phylogeny and the importance of fossils. *Cladistics* 4, 105–209. doi: 10.1111/j.1096-0031.1988.tb00514.x

Haeckel, E. (1866). *Generelle morphologie der organismen* (Berlin: Georg Reimer).

Jenkins, X. A., Benson, R. B., Ford, D. P., Browning, C., Fernandez, V., Dollman, K., et al. (2024). Evolutionary assembly of crown reptile anatomy clarified by late Paleozoic relatives of Neodiapsida. *bioRxiv.* 2011–2025. doi: 10.1101/2024.11.25.625221

Jenkins, X. A., Sues, H.-D., Webb, S., Schepis, Z., Peecook, B. R., and Mann, A. (2025). The recumbirostran *Hapsidopareion lepton* from the early Permian (Cisuralian: Artinskian) of Oklahoma reassessed using HRμCT, and the placement of Recumbirostra on the amniote stem. *Pap. Palaeontol.* 11, e1610. doi: 10.1002/spp2.1610

Laurin, M., and Reisz, R. R. (1995). A reevaluation of early amniote phylogeny. *Zool. J. Linn. Soc* 113, 165–223. doi: 10.1111/j.1096-3642.1995.tb00932.x

Ponstein, J., MacDougall, M. J., and Fröbisch, J. (2024). A comprehensive phylogeny and revised taxonomy of Diadectomorpha with a discussion on the origin of tetrapod herbivory. *R. Soc Open Sci.* 11, 231566. doi: 10.1098/rsos.231566

Reisz, R. R. (1997). The origin and early evolutionary history of amniotes. *TREE* 12 , 218–222. doi: 10.1016/S0169-5347(97)01060-4

Reisz, R. R., Maho, T., and Modesto, S. P. (2024). Recumbirostran 'microsaurs' are not amniotes. *J. Syst. Palaeontol.* 22, 2296078. doi: 10.1080/14772019.2023.2296078

Simões, T. R., Kammerer, C. F., Caldwell, M. W., and Pierce, S. E. (2022). Successive climate crises in the deep past drove the early evolution and radiation of reptiles. *Sci. Adv.* 8, eabq1898. doi: 10.1126/sciadv.abq1898

Sumida, S. S., and Martin, K. L. M. (1997). *Amniote origins: completing the transition to land* (New York: Academic), 510.