

The Red Queen versus the Court Jester: do biotic or extrinsic factors shape the reptilian tree of life?

[Dr Graeme T. Lloyd](#) (SEE), [Dr Katie E. Davis](#) (University of York), [Prof Paul Wignall](#) (SEE)

Contact email: g.t.lloyd@leeds.ac.uk

Living reptiles – the group that includes turtles, lizards, snakes, crocodiles, and birds – represent a highly successful radiation of terrestrial vertebrates containing roughly four times as many species as their sister clade, the mammals. Explaining this numerical superiority is complex, especially as reptiles are often thought of as being more constrained by abiotic (“Court Jester”) factors, such as climate, than their mammalian counterparts (Mannion et al. 2015). On the other hand, reptiles are also considered more resistant to mass extinctions (Longrich et al. 2012), which are typically abiotically driven, e.g., by bolide impacts or volcanism. However, biotic (“Red Queen”) factors such as competition are also likely to play a role in shaping living species diversity and are becoming more testable thanks to advances in methodology.

This project will begin by assembling the largest ever tree of life (phylogeny) for reptiles. This will be achieved through synthetic approaches (“supertrees” and “metatrees”), in which the supervisors are world experts (e.g., Hill and Davis 2014; Lloyd et al. 2016). You will develop and expand a pre-existing database of reptilian phylogenies (found at graemetlloyd.com/matr.html). The final tree will cover a variety of extinct and extant clades, including: birds, crocodiles, dinosaurs, ichthyosaurs, lizards, plesiosaurs, pterosaurs, snakes, and turtles. Alongside this a database of traits will also be assembled, covering: geologic age, geographic range, body size, diet, and habitat. Again, this will be advanced by existing databases, such as the Paleobiology Database (paleobiodb.org), HerpNet (herpnet.org), and ORNIS (ornisnet.org). Finally, time series of abiotic factors will also be assembled (including sea-level curves and temperature proxies).

Collectively this data will allow a comprehensive study of whether reptilian biodiversity has been more strongly shaped by biotic or abiotic factors. Reptiles have switched habitat many times, for example by invading the marine realm (ichthyosaurs, penguins, turtles) or developing powered flight (birds, pterosaurs), but it is not clear if this has a positive or negative effect on diversification. This can be directly tested using software such as BAMM (or fossil BAMM, Mitchell et al. in press), as was done by Davis et al. (2018). Competition between clades can be tested using character displacement (Davies et al. 2012) and how mass extinctions prune the tree of life can be tested with phylogenetic clustering (Soul and Friedman 2017). Additionally, differing time series of palaeobiodiversity will be compared with longer term drivers, such as climate, sea-level, and palaeogeography using generalised linear models and phylogenetic biogeographic connectedness (Button et al. 2017; Cleary et al. 2018; Dunne et al. 2018).

The student will primarily use the statistical programming language “R”, in which full training will be given. Any code or data produced will be shared openly through portals such as Dryad, github, and the Paleobiology Database.

Objectives:

1. To generate the largest phylogenetic hypothesis (tree) of its kind, linking together extinct and extant reptilian species into a single, comprehensive tree of life.
2. To establish if and how extrinsic factors, such as climate and geography have determined reptilian evolution over the past 300 million years.
3. To establish if and how biotic factors, such as competition and key innovations (marine invasions, flight) have shaped the reptilian tree of life.

Potential for high impact outcome:

A phylogenetic hypothesis for all reptilian species, extinct and extant, will form a major resource for future macroevolutionary research and can be expected to attract a high number of citations.

Other publication outputs can be expected to appear in broad interest scientific, biological, or palaeobiological venues (see references for examples).

Training:

Over the course of the project you will pick up a wide range of practical skills, including: databases, phylogenetics, and programming (in the R language). These will be taught directly by the supervisory team although attendance of courses will also be encouraged. It is expected that by the end of the PhD the student will have developed a broad set of transferrable skills enabling multiple employment opportunities, whether in academia or industry.

Student profile:

The project will suit a student who has a first degree in either geology or biology (a Masters is desirable but not essential). Proficiency with computational and numerical skills will be helpful, but is not essential as these can be taught by the supervisory team. Strong organisational skills are also important.

References:

- Button, D. J., Lloyd, G. T., Ezcurra, M. D. and Butler, R. J., 2017. Mass extinctions drove increased global faunal cosmopolitanism on the supercontinent Pangaea. *Nature Communications*, **8**, 733.
- Cleary, T. J., Benson, R. B. J., Evans, S. E. and Barrett, P. M., 2018. Lepidosaurian diversity in the Mesozoic–Palaeogene: the potential roles of sampling biases and environmental drivers. *Royal Society Open Science*, **5**, 171830.
- Davies, T. J., Cooper, N., Diniz-Filho, J. A. F., Thomas, G. H. and Meiri, S., 2012. Using phylogenetic trees to test for character displacement: a model and an example from a desert mammal community. *Ecology*, **93**, 544-551.
- Davis, K. E., De Grave, S., Delmer, C. and Wills, M. A., 2018. Freshwater transitions and symbioses shaped the evolution and extant diversity of caridean shrimps. *Communications Biology*, **1**, 16.
- Dunne, E. M., Close, R. A., Button, D. J., Brocklehurst, N., Cashmore, D. D., Lloyd, G. T. and Butler, R. J., 2018. Diversity change during the rise of tetrapods and the impact of the 'Carboniferous Rainforest Collapse'. *Proceedings of the Royal Society B*, **285**, 20172730.
- Hill, J. E. and Davis, K. E., 2014. The Supertree Toolkit 2: a new and improved software package with a Graphical User Interface for supertree construction. *Biodiversity Data Journal*, **2**, e1053.
- Lloyd, G. T., Bapst, D. W., Friedman, M. and Davis, K. E., 2016. Probabilistic divergence time estimation without branch lengths: dating the origins of dinosaurs, avian flight, and crown birds. *Biology Letters*, **12**, 20160609.
- Longrich, N. R., Bhullar, B.-A. S. and Gauthier, J. A., 2012. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *PNAS*, **109**, 21396-21401.
- Mannion, P. D., Benson, R. B. J., Carrano, M. T., Tennant, J. P., Judd, J. and Butler, R. J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Communications*, **6**, 8438.
- Mitchell, J. S., Etienne, R. S. and Rabosky, D. L., in press. Inferring diversification rate variation from phylogenies with fossils. *Systematic Biology*.
- Soul, L. C. and Friedman, M., 2017. Bias in phylogenetic measurements of extinction and a case study of end-Permian tetrapods. *Palaeontology*, **60**, 169-185.