

The complicated and surprisingly early origin of the pterodactyloid bauplan

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The origin of the pterodactyloid bauplan from that of non-monofenestratan ('rhamphorhynchoid') pterosaurs involved extensive anatomical changes and had profound consequences for the evolutionary history of Pterodactyloidea, a clade that dominated the aerial realm throughout the Cretaceous. This important evolutionary transformation, about which almost nothing was known for almost two centuries, is now rapidly coming into focus thanks to a plethora of new pterosaur fossils from the Middle and Upper Jurassic of South America, Europe and China. So far, however, these finds have largely been considered in isolation from each other and few have been thoroughly evaluated. Phylogenetic analysis, combined with improved stratigraphic data for all potentially relevant taxa including putative non-pterodactyloid monofenestratans (NPMs) and the oldest known pterodactyloids (e.g. *Liaodactylus*) was used to generate a new map of the anatomical transformations and temporal history of the non-monofenestratan–pterodactyloid transition. Evolution of the pterodactyloid skull construction predates the Middle Jurassic, but remains almost completely undocumented by fossils. *Liaodactylus* reveals that innovation in pterodactyloid skull anatomy and the appearance of derived features was well underway prior to the Upper Jurassic. *Douzhanopterus*, a derived NPM, demonstrates that elongation of the metacarpus and reduction of the tail and fifth toe (classic pterodactyloid synapomorphies) also predates the Upper Jurassic, but disjunction in the degree of their development across taxa is not consistent with simple explanations such as 'adaptation for flight'. Overall, late Early to early Late Jurassic pterosaurs were much more diverse and had a far more complex evolutionary history than heretofore recognised.