

## **An early origin and diversification of macrophagous metriorhynchid crocodylomorphs, with evidence for multiple instances of parallel evolution**

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Metriorhynchids were a widely distributed group of marine crocodylomorphs that thrived during the Middle Jurassic–Early Cretaceous. Within this group there is a subclade, Geosaurini, that evolved craniodental characteristics indicative of macrophagy (feeding on large-bodied prey items). When this subclade evolved and began to diversify into the myriad of morphologically distinct lineages is still unclear. Previous phylogenetic analyses suggest this clade evolved during the Late Jurassic, and rapidly diversified into numerous different ecomorphotypes. It was hypothesized that this was in response to the absence of small and medium-sized pliosaurs after the Middle-Late Jurassic Boundary. However, re-examination of poorly preserved fossils from the Callovian of England and France casts doubt on this. Based on our comparative study of these fossils, and new phylogenetic analyses, we conclude that Geosaurini had evolved and diversified by the mid Callovian. Although comparatively rare in the Middle Jurassic, at least four morphofunctionally distinct lineages of macrophages had evolved. Moreover, based on maximum likelihood modelling analyses, numerous macrophagy-linked characters (e.g. contiguous tooth serrations, low tooth count) evolved independently in these different lineages. Thus, the characteristics that previously suggested a Late Jurassic origin of Geosaurini was due to long-branch attraction and incomplete sampling. That these different macrophagous lineages evolved distinct morphofunctional complexes and began niche partitioning early in their evolution, suggests that their diversification was driven by foraging specialisation. We hypothesise that this may be a common driver of rapid diversification in marine tetrapod evolution.