

## A taxonomic and phylogenetic review of the anhanguerid pterosaur group Coloborhynchinae and the new clade Tropeognathinae

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*Acta Palaeontologica Polonica* 65 (4), 2020: 743-761 doi:<https://doi.org/10.4202/app.00751.2020>

Anhanguerids are a particular group of pterodactyloid pterosaurs, characterized mainly by their rostral sagittal crests, well laterally expanded jaw tips and enlarged anterior teeth. Due to the fragmentary nature of most known specimens, including holotypes, the taxonomy of the group has proved particularly difficult and controversial.

Coloborhynchinae is a recently proposed clade within the Anhangueridae, and was defined as the most inclusive clade containing *Coloborhynchus clavirostris* but not *Anhanguera* or *Ludodactylus*. Coloborhynchinae was originally thought to include *Coloborhynchus*, *Uktenadactylus*, and *Siroccopteryx*. Here we present a reassessment of the taxonomy and phylogeny of all proposed members of the Coloborhynchinae and *Coloborhynchus* complex, with new anatomical comparisons and a novel phylogenetic analysis. Several features allow us to establish that coloborhynchines were much more diverse than previously thought, englobing four genera and seven species: *Aerodraco sedgwickii* gen. et comb. nov., *Coloborhynchus clavirostris*, *Nicorhynchus capito* gen. et comb. nov., *Nicorhynchus fluviferus* gen. et comb. nov., *Uktenadactylus rodriguesae* sp. nov., and *Uktenadactylus wadleighi*. *Nicorhynchus* and *Uktenadactylus* are considered sister taxa, being distinct on the basis of several rostral characters. Although with a homoplastic flat rostrum surface, *Siroccopteryx* was recovered out of the Coloborhynchinae, as sister taxon of *Tropeognathus*, due to similarities on the palatal ridge (which is broad and deep, and starting at the same level) and the relatively stout teeth compared to other anhanguerids. *Tropeognathus* and *Siroccopteryx* are further related to the Australian taxa *Ferrodraco* and *Mythunga*, which are all grouped in a new clade: the Tropeognathinae. Our analysis suggests that morphological evolution within anhanguerids was quite more complex than previously thought, with coloborhynchines representing the oldest recorded lineage of Anhangueridae, which achieved a worldwide distribution at least from the Aptian to the Cenomanian.

**Key words:** Pterosauria, Pterodactyloidea, morphology, taxonomy, phylogeny, Cretaceous, USA, United Kingdom.

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