

# PENNARAPTORAN THEROPOD DINOSAURS PAST PROGRESS AND NEW FRONTIERS

Edited by

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## PREFACE

The origin of birds and flight was a major event in the history of life. A wealth of spectacular fossils of early birds and their closest relatives has demonstrated that birds are maniraptoran theropod dinosaurs, with Pennaraptora being the most relevant theropod group to the “dinosaur-bird” transition. Pennaraptora comprises birds themselves as well as the pennaceous feathered dromaeosaurids, troodontids, scansoriopterygids, and oviraptorosaurians. Fossils and neontological insights show that many salient avian traits originated deep within theropod evolutionary history, accumulating over a significant temporal and phylogenetic interval and often appearing in a complex mosaic across phylogeny. This includes endothermic physiology, unique reproductive strategies, as well as flight itself. Hallmark features necessary for flight appeared among pennaraptoran dinosaurs including a laterally oriented, long, and robust forelimb; a refined “flight ready” brain; and large, vaned flight feathers. Proxies for modern flight capability, modelling work and functional morphology support flight and near-flight capabilities among paravian pennaraptorans, with powered flight probably evolving independently multiple times. However, in order to deepen our understanding of avian and flight origins as well as other important pennaraptoran evolutionary events, more progress is needed in achieving better systematic consensus both within and between clades.

In this context, the inaugural discussion-focused International Pennaraptoran Dinosaur Symposium (IPDS) was held at the University of Hong Kong between March 29 and April 1, 2018, with the goal of making substantial advances in our understanding of pennaraptoran palaeobiology and evolution. The conference documented past progress, worked toward consensus on key unresolved issues, and broke new ground in the field. This volume curates the main outcomes of the IPDS symposium including priority areas identified for future research. The volume

involved 49 experts from more than 10 countries whose views cover much of the current discussion on this topic. The volume is made up of 14 chapters organized in three sections:

**SECTION ONE: SYSTEMATICS, FOSSIL RECORD, AND BIOGEOGRAPHY:** This section surveys the pennaraptoran fossil record and underscores parts where further attention is likely to make headway in answering pressing questions in the field. The current state of pennaraptoran systematics is presented, providing the context needed to understand the group’s evolution. Areas of uncertainty and controversy are highlighted and suggested improvements proposed. This section includes a chapter dedicated to improving how rogue taxa/wildcards are identified in phylogenetic analyses, which is of interest to the broader palaeontological community. Section one also uses an updated coelurosaurian phylogeny to present the first quantitative palaeobiogeographic analysis of the Coelurosauria. This allowed identification of key tectonic drivers of evolution, providing a stronger basis for investigating evolutionary drivers among pennaraptorans as well as non-pennaraptoran theropods, other dinosaur groups, and Mesozoic vertebrates more generally.

**SECTION TWO: ANATOMICAL FRONTIERS:** This section focuses on recent discoveries in pennaraptoran anatomy, particularly of the hand and head. It explores the implications this knowledge has and will have on our understanding of pennaraptoran palaeobiology and evolution. These discoveries involve a wide range of adopted approaches including geometric morphometrics, mechanical advantage calculations, and evo-devo approaches as well as the phylogenetic context provided in section one. The world of fossil pennaraptorans has become technicolored in recent years thanks to the advent of melanosome-based paleocolor reconstruction. As an important reappraisal of this work, an actuo-paleontological experiment is presented that quantitatively tests the premise of this method for the first time.

**SECTION THREE: EARLY FLIGHT STUDY: METHODS, STATUS, AND FRONTIERS:** This section begins by detailing the methods currently available for studying early theropod flight and discusses the priorities to address in future methodological development work. As an example, a methodological frontier is explored by marrying recent advances in soft-tissue imaging with quantitative methods of early flight study to create a new framework on which to build. Section three also covers recent efforts to identify the small pennaraptorans that first took to the skies, what their flight capabilities were and how their flight might have been acquired. A new broader context is proposed for flight behavior in a conceptual chapter about its functional landscape. Wing-assisted incline running (WAIR), a behavior seen in modern birds, is part of this functional landscape and a proposed stage of early flight development. To stimulate further exploration of this functional landscape, chapter 14 argues that this behavior is a later innovation instead on the basis of experimental data collected from modern ostriches.

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Michael Pittman and Xing Xu  
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