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Editorial

An Introduction to Evolution and Palaeobiology of Flightless Birds

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Although flight is often considered as one of the most salient characteristics of birds, in the course of their evolution various avian lineages have lost the ability to fly. This has happened at different periods of the geological past, beginning in the Cretaceous with such forms as the terrestrial *Patagopteryx* and *Gargantuavis* and the marine Hesperornithiformes, and under very varied circumstances. In some cases, loss of flight is associated with strictly terrestrial habits in usually large forms, as in living and fossil "ratites" and in various extinct groups of giant ground birds (gastornithids, dromornithids, phorusrhacids, etc.). The case of birds deeply adapted to foraging in an aquatic environment, such as penguins and Hesperonthiformes, is a completely different instance of flightlessness. Loss of flight has often taken place in insular environments, where the lack of predators is supposed to have played a crucial part—the dodo is a case in point. However, it also occurred repeatedly on large land masses, as exemplified today by the ostrich and related birds.

This Special Issue explores various aspects of this multi-faceted evolutionary process, from phylogeny to palaeobiology. The nine papers in this collection deal with flightless birds belonging to widely different extinct and extant groups, from many parts of the world and from various time periods, from the Late Cretaceous to the Quaternary. The aim is not to provide a comprehensive review of the evolution and palaeobiology of the many groups that have lost the power of flight over the long time span extending back to the Cretaceous. Rather, the papers published here illustrate both the diversity of flightless birds and the multifarious approaches that can be used to study them, from stratigraphy and functional anatomy to phylogenetic analysis and bone histology.

The paper by Alyssa Bell and Luis Chiappe deals with the Hesperornithiformes, a group of Late Cretaceous diving birds that were among the first avians to become flightless. When first described in the 1870s, these "birds with teeth" attracted much attention, and Charles Darwin considered them as some of the best evidence in favour of his theory of evolution. Although they have been known for a century and a half, however, no recent global review of Hesperornithiforms was available. Bell and Chiappe's timely paper provides such a review, discussing their diversity, geographical and temporal distribution, and ecology. Even though they have been known for a long time, Hesperornithiformes remain a fascinating group of early birds, about which innovative approaches are revealing many new facts.

Federico Agnolin discusses the phylogenetic relationships of *Brontornis burmeisteri*, a giant bird from the Miocene of South America that has puzzled palaeornithologists since its original description in 1891. Although it has often been placed among the cursorial and carnivorous "terror birds" (Phorusrhacoidea), several of its osteological characters rather suggest a graviportal plant-eater. Agnolin's conclusion, based on modified datasets, is that it belongs to Galloanserae and is part of a still poorly known Tertiary radiation of large graviportal birds from South America.

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Klara Widrig and Daniel Field provide a comprehensive review of the fossil record and evolution of the Palaeognathae, a large avian group containing, besides the volant tinamous, a large number of flightless forms—including the living ostriches, rheas, emus and cassowaries, as well as many extinct taxa such as the moas and elephant birds. Despite remaining gaps in the fossil record, an evolutionary history emerges, starting with relatively small-sized ground-feeding birds which survived the end-Cretaceous extinction event and diversified considerably during the Paleogene, although the extant sub-clades do not become clearly recognizable until the Neogene. It is increasingly clear that flightlessness and large body size have appeared independently in several lineages.

Anusuya Chinsamy, Aurore Canoville and Delphine Angst present the results of histological studies carried out on a large sample of limb bones from various large flightless birds, including extant and extinct "ratites" as well as the Paleogene giant neognath *Gastornis*. Their results show that bone microanatomy can reflect locomotion type (graviportal versus cursorial), thus providing a useful tool for palaeobiological interpretations. In addition, somewhat unexpectedly, growth marks in the bones of various extant ratites indicate flexible growth patterns (in response to environmental conditions) that may represent the plesiomorphic condition in Palaeognathae and, more widely, Neornithes.

Peter Johnston and Kieren Mitchell's paper on sensory adaptation in flightless birds explores the intriguing topic of the sensory capacities of several extinct and extant forms, including moa, elephant birds, kiwi and the kakapo parrot. On the basis of various cranial skeletal features relating to vision, hearing and olfaction, they show how the different lifestyles of these birds have resulted in contrasting sensory strategies: for instance, the kiwi, the Upland Moa and the aepyornithids apparently were olfactory specialists, but the moa had a well-developed hearing sensitivity range lacking in the other taxa. This approach opens up interesting new directions for palaeobiological investigations and reconstructions.

Warren Handley and Trevor Worthy use morphometric methods to describe in detail the endocranial morphology of the dromornithids, or mihirungs, a group of extinct large flightless birds which flourished in Australia from the Eocene to the Pleistocene. This study has phylogenetic implications, since in terms of endocranial anatomy the mirhirungs appear to be closer to galliforms than to anseriforms, in agreement with a recent interpretation. From a functional point of view, this study supports the conclusion that they were diurnal herbivores with well-developed stereoscopic depth perception—the old myth of the dromornithids as "killer ducks" thus receives an additional blow from endocranial anatomy.

Anusuya Chinsamy and Trevor Worthy describe the bone histology of the Pleistocene dromornithid *Genyornis newtoni*, the last of the mihirungs. This study provides important new evidence about the still poorly known biology of this Australian giant bird. In particular, the growth pattern revealed by this study indicates that *Genyornis newtoni* took more than a single year to become sexually mature, and reached skeletal maturity after sexual maturity. In addition, it apparently retained a plesiomorphic flexible growth strategy, which enabled it to respond to changing environmental conditions.

Eric Buffetaut and Delphine Angst describe a large ostrich femur found in the 1920s in the Lower Pleistocene deposits of the Nihewan basin of northern China, which had hitherto been only very cursorily mentioned. It is referred to *Pachystruthio* and significantly enlarges the geographical distribution of this genus of giant ostriches which was previously known from Hungary, Crimea and Georgia. As shown by a review of the fossil ostriches from China, *Pachystruthio* is an element of the long and apparently complex history of this group of birds in eastern Asia, which extends from the Miocene to the Late Pleistocene.

Eric Buffetaut reviews the stratigraphic distribution of *Psammornis*, an enigmatic egg-based taxon from the Neogene and Quaternary of North Africa and possibly the Middle East. The genus was erected in 1911, on the basis of eggshell fragments indicating a very large bird, from a locality of uncertain geological age in Algeria. Since then, a number of eggshell finds from the Sahara and surrounding areas have been referred to *Psammornis*, but most of them are very poorly dated. Curiously enough, *Psammornis* localities with a reasonably good stratigraphic context, in Tunisia and Mauritania, have

often been overlooked, although they are of prime importance for unravelling the obscure history of what were probably giant ostriches.

It is expected that this collection of papers will both provide abundant new information about the evolution and biology of extant and extinct flightless birds and illustrate the wide spectrum of the approaches used to investigate them. Although these approaches have resulted in considerable progress in our understanding of these avian groups, an obvious lesson to be learnt from these contributions is that much remains to be discovered and investigated. Owing to both discoveries of new fossil specimens and the implementation of new, innovative techniques, our current picture of flightless birds is in many respects quite different from what it was a few decades ago. We hope these papers will reflect how fast this branch of ornithology is developing and hint at directions for future studies.

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