Preface to the Second Edition

Endowed with colorful plumages and beautiful songs, birds in flight symbolize spirits released from the bondage of gravity. From the day that humans first looked up at the skies, birds have summoned a sense of wonder and mystery, enchanting our earthbound ancestors with their freedom and song. They fly where they please and when they please. The power of flight has opened up to birds a multilayered network of aerial highways and byways, enabling them to reach any place on our planet. They exhibit a wide variety of sizes, shapes, colors, and habits. Their awesome power of flight takes them to every continent, from pole to pole, and they fill every conceivable niche. Birds have enriched our life with their free spirit, beauty, and songs. They inform us about the rest of the natural world, control insect population, disperse seeds, and embody key values in human cultures. They have played a key role in many important developments of evolutionary theories. Given their stark beauty, graceful flight, exuberant activity, diurnal habits, dazzling feathers, and melodious songs, it is hardly surprising that birds feature strongly in every culture in painting, poetry, and music. Birds are the most successful terrestrial vertebrate, abundant in both numbers of species and populations. About 300 billion birds, with 10,000 species, now inhabit the Earth, as compared to 3,000 species of amphibians, 6,000 species of reptiles, and perhaps 4,500 species of mammals.

Birds are one of the oldest, most successful, and fascinating groups of flying vertebrates in our landscape. The story of bird evolution as revealed by the study of fossils is important not only to paleontologists but also to those engaged in other branches of science—geology, biology, ecology, evolution, and natural history—as well as the general public. Although living birds are one of the best-known groups of extant vertebrates, their origin, evolution, and early adaptive radiation are poorly documented in the fossil record. Until recently, most knowledge of the early history of birds and the evolution of their flight was based on handful of diverse Mesozoic taxa widely separated in time and restricted to marine environments. The rarity of bird fossils is generally attributed to the extreme fragility, lightness, pneumaticity, arboreal habits, and general smallness of their bones. However, there is a renaissance in the study of Mesozoic birds with the spectacular discoveries of amazing fossils from China during the past two decades. These new discoveries fill major gaps in the evolutionary history of birds and provide critical insights into the origin of feathers, evolution of flight, and their phylogenetic relationships.

The Mesozoic has often been referred to as the "Dark Ages of Birds" because only a limited number of fossils such as *Archaeopteryx* from the Late Jurassic of Germany and *Hesperornis* and *Ichthyornis* from the Late Cretaceous of Kansas filled the evolutionary gaps. *Archaeopteryx* was an icon in avian evolution, being regarded as the oldest and most primitive known bird. In recent decades the narrative of bird evolution has broadened considerably with the discovery of more fossils from around the world. Our story of bird evolution began 225 million years ago when *Protoavis* took to the air over tropical Texas forests at the very dawn of the age of dinosaurs and began to diverge in many forms and fashions. Soon after the discovery of *Protoavis*, remarkable fossils of Cretaceous birds were unearthed in China, Spain, Mongolia, Australia, Madagascar, Argentina, and Antarctica. The present edition represents a radical metamorphosis of the first edition of *The Rise of Birds*, published in 1997, amplified by the remarkable discovery of feathered dinosaurs and early

birds in China that led to dramatic breakthroughs in the origin and early evolution of birds and their flight. The discovery of a large number of new species of successive clades of Jurassic and Cretaceous birds and their immediate ancestors during the past two decades from the Tiaojishan Formation and Jehol Group of China supplies the missing evolutionary history from primitive basal birds to the forerunners of modern birds, along with their theropod ancestors. A coherent picture of the origin and early radiation of birds and their relationships began to emerge for the first time from these remarkable discoveries. The newly discovered feathered theropods from China show various transitional stages of flight—from wingless, tree-climbing coelurosaurs to parachuting, to gliding, to fully winged, actively flying birds. Some of the feathered dinosaurs had brilliant plumages that suggest that feathers might have initially evolved for sexual display and species recognition and later been co-opted for flight. A forest habitat and arboreal lifestyle might have played a critical role in the origin and early evolution of birds and their flight. Once flight was perfected, these birds may have begun to exploit other ecological niches, especially rivers, lakes, and seas, where food was abundant. They also reverted to being flightless, time and again.

This new view of the origin of birds and their flight is the centerpiece of this edition, which is based on the remarkable Chinese fossils. A modern synthesis of avian evolution is also presented using paleontology, biomechanics, and heterochrony. Both the remarkable feathered dinosaurs from China and new insights from developmental biology bring the evolutionary process alive and offer a more holistic picture of bird evolution. This book is thus in great measure a new work incorporating recent discoveries of avian fossils from different parts of the globe and their significance in the study of the origin and early evolution of birds and their flight in the framework of developmental mechanisms. The role of heterochrony in the evolution of birds is also new to this edition. Similarly, a computer simulation is used to trace the origin of flight.

To follow the various trends of bird evolution through geologic time was not an easy assignment, because so many evolutionary chapters were happening at once in the Early Cretaceous Jehol Group of China. Here I follow phylogeny as the guiding principle to tell the story of evolutionary events of birds, one by one, and of trying, somehow, to relate them to each other in the geologic time scale and paleobiogeography.

The overall picture of birds being descended from maniraptoran theropod dinosaurs is now firmly established, but the transition is often fuzzy and diffuse. Recent study suggests that *Archaeopteryx*, the most primitive and celebrated bird fossil on Earth that reigned for more than 150 years since its discovery, may not be a bird after all, but just another small feathered, bird-like theropod fluttering around during the Jurassic. The jury is still out regarding the status of *Archaeopteryx*. In this book I have treated *Archaeopteryx* as a basal bird. However, *Jeholornis* from the famous Jehol aviary of China can be a potential candidate for the status of Urvogel, the true primitive bird. Using both *Archaeopteryx* and *Jeholronis* as the basal members of avialans, I trace the origin and evolution of birds from their theropod ancestors along a cladogram through time, a genealogical tree, highlighting the anatomical changes and flight refinement in successive groups or clades, their classification and phylogenetic relationships.

Bird flight is inherently fascinating and appears to have been a fundamental factor in the early success of birds, but its origins remained murky for more than two centuries due to lack of a fossil record in the Mesozoic. With the discovery of remarkable feathered theropods and early birds in China, we have a better understanding of the origin and early evolution of avian flight and feathers. Combining both fossil evidence and aerodynamics, I offer an integrated view on the evolution of avian flight.

Other than flight, I also discuss fossil eggs and embryos of birds, the role of developmental constraints in their evolution, locomotion and footprints, and the evolutionary crisis at the end of the Cretaceous. I also include the explosive evolution of birds, their macroevolution and heterochrony, their feeding and cranial kinesis,

and their recent classification. Finally, I address the association of birds with humans during the Quaternary, and their fate in our hands with the environmental collapse.

I am a paleontologist, interested primarily in questions of biological evolution. Paleontology is fundamentally historical nature. When we look at birds, we see the shadow of dinosaurs in them, their antiquity and heritage. I wrote this book with several kinds of reader in mind: first, for anyone interested in nature and natural history who takes delight in observing birds and their acrobatic flight; second, for evolutionary biologists and others interested in the question of origins. In this book I present a readable and comprehensive narrative of the early history and radiation of birds that lived with dinosaurs for 160 million years. I also discuss the major radiation of birds after the end-Cretaceous extinction that led to the modern birds we see today. My goal in this book is to make available to a wide audience an account of our current scientific understanding of the origin and evolution birds and their flight. I have aimed this book primarily at bird lovers, both amateur and professional, interested in this subject as well as evolutionary biologists.

In the first edition of the book, I gratefully acknowledged my indebtedness to numerous individuals and institutions. I would like to add that I am grateful to my Chinese colleagues, especially Zhonghe Zhou, Xing Xu, Fucheng Zhang, Dong Zhiming, and Xiao-chun Wu, for their hospitality during my stay in China. They took me to the Liaoning fossil localities to understand the taphonomy and recurrent mass mortality events, allowed me to examine some of the spectacular feathered coelurosaurs and early birds, shared their ideas with me, and provided me with excellent photos and drawings. I feel lucky to know Xing Xu and Zhonghe Zhou, who uncovered and described the buried treasures in China and introduced them to the rest of the world. Their painstaking and brilliant work truly revolutionized Mesozoic vertebrate paleontology, especially the origin and evolution of early birds. They shared their knowledge freely with me. I acknowledge my heartfelt indebtedness to R. Jack Templin, the Canadian aeronautical engineer, for fruitful collaboration on animal flight during the past two decades that resulted in several major publications. Jack was my mentor for all these years and taught me basic aerodynamics. I thank John Talent, David Alexander, and James DeLaurier for reviewing various papers on bird flight that have been incorporated here. Larry Witmer, Luis Chiappe, and Julia Clarke were always generous to share their insights on avian evolution.

I thank my many professional colleagues who provided images of their fossils for this book. Michael W. Nickell and Patricia Koemmel carefully rendered the illustrations and made the book richer with their hard work and artistic acumen. Bill Mueller improved many illustrations, Aijuan Shi did the life restoration of *Jeholornis* on the cover, and Zhonghe Zhou, Xu Xing, and Luis Chiappe gave permission to reproduce several of their artworks. The book is the result of an ongoing and sometimes heated discussion among paleontologists in the origin of birds and their flight. The debate will continue as more and more fossils are discovered. I acknowledge all of the writers and philosophers whom I have quoted at the beginning of each chapter for their wisdom and inspiration.

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Preface to the First Edition

In the Hindu epic *Ramayana,* we find a poignant story of resurrection. The fiery sage Gautama curses his beautiful wife, Aholya, and turns her to stone with these words: "You shall remain thus for thousands of years. Only when Rama, the son of Dasharatha, passes this way will you be restored to life." Years pass. Gautama's hermitage has long been abandoned and decays with age, choked by creepers and swallowed by rainforest. Aholya waits alone in the ruins, a stone among crumbling stones. One day, after many millennia, a very young prince Rama comes across the old ashram and sees the petrified image of Aholya, waiting. In reverence, he touches her feet. Immediately, he sees tears where there once were no eyes, flesh where there had been rock. Aholya is alive once more, free from her terrible curse.

Paleontologists have long pursued petrified bones, much like the epic hero Rama. To them fossils are million-year-old Aholyas waiting to be discovered and resurrected. They put muscle and skin on these bones, color them with human passions, and give them life. They re-create the denizens of a lost world in proper chronological and evolutionary context. This book unfolds the story of *Protoavis texensis*—"first bird, from Texas." *Protoavis* predates *Archaeopteryx* by 75 million years, pushing the emergence of birds back to the Triassic period. Being the world's oldest bird, *Protoavis* provides a new view of avian origins. When I picked up two partial skeletons of *Protoavis* out of the Triassic red beds of Texas in the summer of 1983, I did not realize that they would generate so much controversy and excitement among scientists. Soon after, avian paleontology went through its own renaissance, as more Mesozoic birds were found during a span of fifteen years than had been discovered during the entire preceding century.

Dinosaurs are so popular that we often neglect their even more fascinating relatives that are still among us. Birds, the true living dinosaurs, deserve considerable respect as successful vertebrates that have evolved, adapted, and survived over a period of 225 million years. The rise of birds in the Pangean world, their flight refinement and global diversification during the continental breakup, their decline at the end of the Cretaceous period, and their explosive radiation during the Cenozoic era are some of the greatest events in the history of vertebrates. Yet their early history is obscure and just beginning to unfold. During the seventy years since the appearance of Gerhard Heilmann's monumental work *The Origin of Birds,* substantive progress has been made in the study of bird fossils and the understanding of the theropod-bird transition. No current book deals exclusively with Mesozoic birds, which compose the first two-thirds of avian history. *The Rise of Birds* is an effort to fill this void. In this book I have attempted a readable and comprehensive account of the early history of the radiation of birds in the shadow of dinosaurs; of their anatomy, function, and evolutionary trends; of the origin of flight; of fossil eggs and embryos, feathers and footprints; of the distribution of birds in the Mesozoic period; of classification and phylogenetic relationships; and of the evolutionary crisis at the end of the Cretaceous. I have also included the explosive evolution of birds during the Tertiary period and their association with humans during the Quaternary to complete my picture of the long odyssey of birds. This book is aimed at an audience beyond the confines of the paleontological community. I give detailed accounts of specific research topics that are currently highly contested or thought provoking.

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