Preface

What I had to do,
I did the best I could

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With nearly 10,000 living species, birds are today's most diverse group of land animals and the heirs of a successful and fascinating story of vertebrate evolution. Ubiquitous and endowed with colorful plumages, exuberant behaviors, and an unrivaled grace for aerial propulsion, birds have always captured the interest of man. Since antiquity, philosophers, natural historians, and scientists have dedicated their efforts to studying the life of birds and understanding their place within our natural world. Still, with their feathered bodies, beaked heads, short bony tails, and other unusual features, the evolutionary origin of birds—and the search for their closest relatives—has been until recently a puzzling mystery of scientific inquiry. In the last few decades, however, our understanding of the origin and ancient divergences of these animals has advanced at an unparalleled speed. Not only has the ancestry of birds been greatly clarified but the anatomical and genealogical chasm between the first birds and the evolution of their living counterparts has been substantially filled. This book is an attempt to summarize the large volume of new evidence and provide a synthetic view of the Mesozoic saga of birds, an evolutionary odyssey narrated over 85 million years of our geologic past. This view, however, is not free of bias—my conclusions are the result of years of examining the pertinent fossil record and the interpretation of this evidence in light of specific methods for reconstructing genealogy.

Avian beginnings can be traced back to at least 150 million years ago, deep into the Mesozoic Era, a time when large dinosaurs dominated all terrestrial ecosystems, when climatic patterns were vastly different from those of today, and landmasses and oceans had a completely different configuration. But to understand the place birds have in the natural history of our planet, we need to dive far beyond, to the dawn of dinosaurs more than 230 million years before our present, for a vast amount of fossil evidence indicates that the ancestry of birds is deeply nested within these fascinating animals. Indeed, the fossils support the idea that birds evolved from ground-dwelling, predatory dinosaurs known as maniraptoran theropods. This and other hypotheses about avian origins, the development of feathers and the debate about the beginnings of flight are all related evolutionary events discussed in detail in the following pages. Because these events need to be explained through a genealogical lens, this book also presents methods and concepts used for establishing descent among organisms, setting up the *cladistic* way of thinking that will guide us throughout this book. Using these cladistic concepts, we can argue that because the ancestry of birds can be traced back to maniraptoran dinosaurs, it is logical to conclude that birds are living dinosaurs. And if birds encompass a group of dinosaurs, we could also logically reason that birds are reptiles, for all dinosaurs are classified as reptiles. Strange as it may seem, the reality (given the evidence at hand) is that birds are both avian dinosaurs and avian reptiles—they are a subset of dinosaurs and an even smaller subset of reptiles. Following these concepts, the traditional dinosaurs—from *T. rex* to *Triceratops* to *Brachiosaurus*—will be often referred to as large or nonavian dinosaurs.

The oldest preserved pages of the evolutionary history of birds are limited to a handful of fossils

of the famous *Archaeopteryx lithographica*. Few physical features set this 150-million-year-old bird—one with teeth, clawed wings, and a long skeletal tail—apart from its theropod dinosaur predecessors. In fact, new fossils and analyses have shown that many of the features commonly associated with birds—from feathers to wishbones to hollow bones—first evolved in theropod dinosaurs. Yet *Archaeopteryx* gives us paramount clues to the beginning of one of the most dramatic evolutionary events in the history of vertebrates—the development of powered flight in birds. With the Late Jurassic *Archaeopteryx* we begin to tell a story of transformation, reviewing the long history of anatomical changes that culminated in the unique aerodynamic design of modern birds. Following the sequence of early evolutionary divergences along a cladogram—a tree-like diagram of genealogical relationships—we discuss every later lineage of Mesozoic birds that played a significant role in the evolution of the group. We see how subsequent avian divergences are each a step further apart from their maniraptoran ancestors. Traveling across the cladogram beyond *Archaeopteryx*, we examine a diversity of other primitive, long-tailed birds. From here, we look at the rapid diversification of short-tailed birds. Undoubtedly, the abbreviation of the skeletal tail and the development of a number of critical aerodynamic features played a principal role in the fine-tuning of flight, an ability that birds mastered very early in their history and the recipe for their enormous success. Yet the details of this evolutionary transition are far from clear—the dawn of short-tailed birds is still shrouded in a cloud of mystery.

The 125-million-year-old *Confuciusornis sanctus* and its kin give us a picture of the earliest known short-tailed birds. These primitive-beaked birds thrived in the tropical environments that dominated eastern Asia during the Early Cretaceous—their fossils have been collected by the hundreds. The next divergence of our cladogram takes us to the most successful group of Mesozoic birds: the Enantiornithes. Like no other lineage of early birds, the history of discoveries of these fossils illustrates the remarkable burst of evidence unearthed in recent years—despite the fact that half of the known Mesozoic birds are Enantiornithes, the group itself was not recognized until two decades ago. A significant diversity of songbird-sized enantiornithines is recorded not much later than the start of the Cretaceous. The secret of such a successful and apparently rapid diversification may lie in their superior flying capabilities. Indeed, the skeletal plan of the earliest enantiornithines underwent a series of important transformations with respect to their short-tailed predecessors. It is likely that these skeletal innovations, combined with their small size, enabled them to fly nearly as well as their living relatives, and therefore to occupy a wide range of environments. The abundant fossil record of these birds, one that extends throughout the Cretaceous, provides important evidence for understanding the diversity of lifestyles, feeding behaviors, developmental strategies, and growth rates of early birds.

The next stop on our genealogical journey takes us to the earliest stages of the evolutionary radiation that culminated with the divergence of all modern birds. Here we explore the significance of the most archaic ornithuromorphs. Notorious among these primitive forebears of living birds is *Patagopteryx deferrariisi*, a Late Cretaceous animal that among other things offers clues to an early episode of flightlessness, a relatively common trend in the later evolutionary history of birds. Yet, the fossil record tells us that the diversification of ornithuromorphs is significantly more ancient, because a much older cast of these birds was unearthed from the same 125-million-year-old sediments that contain the most primitive short-tailed birds. Following the analysis of these primitive ornithuromorphs, our discussion visits other fossils that are closer to modern birds.

Remarkable among these are *Hesperornis regalis* and its allies, which with torpedo-like bodies, powerful hindlimbs, and atrophied wings, became superb foot-propelled divers of the Late Cretaceous seas.

If the Mesozoic Era witnessed a great deal of avian diversification, it was also a time of abundant extinction. Indeed, of the many lineages of birds that thrived during this long interval of our geologic past, all but one disappeared before the Mesozoic gave way to the current Cenozoic Era. Our journey through the evolutionary history of early birds ends with the humble beginnings of modern birds—the only avian lineage to survive the Mesozoic. We look at the possible closest relatives of our modern companions—toothed birds, but ones which were in many ways modern-looking. At the end of our story we also review the controversy around the earliest evolutionary divergence of modern birds, namely whether their origin is buried deep in the Cretaceous or if the first modern birds actually evolved at a significantly later time, not far from the closure of the Mesozoic.

History is often approached with two major purposes. On the one hand, we examine historical evidence as a way of easing our never-ending curiosity about what the past was like. On the other hand, we also look at history with hopes of finding clues for a better future, and as a source of information to solve our current problems. Our interest in the early history of birds is not an exception. We are naturally fascinated by birds that also had teeth, clawed wings, and long bony tails, a whole roster of unfamiliar animals that would take birding to a new dimension. We are also intrigued by the evolutionary mysteries that led to the development of the unique features of living birds and their mesmerizing aerodynamic capabilities. But by learning more about the ancient history of modern birds we also hope to reach a better understanding of the life of our familiar companions, because buried in such a history may also be clues about how to protect and manage the last descendants of a class of animals that once ruled the world.