MESOZOIC BIRDS

ABOVE THE HEADS OF DINOSAURS

EDITED BY LUIS M. CHIAPPE
AND LAWRENCE M. WITMER

Title page illustration: Archaeopteryx lithographica by Charles Knight (courtesy Los Angeles County Museum of Natural History).

University of California Press
Berkeley and Los Angeles, California

University of California Press, Ltd.
London, England

Library of Congress Cataloging-in-Publication Data

Mesozoic birds : above the heads of dinosaurs / edited by Luis M. Chiappe and Lawrence M. Witmer.
p. cm.
Includes bibliographical references and index.
ISBN 0-520-20094-2 (alk. paper)
1. Birds, Fossil. 2. Paleontology—Mesozoic. 3. Birds—Evolution. I. Chiappe, Luis M. II. Witmer, Lawrence M.

QE871 .M47 2002
568—dc21 2001044600

Printed in China

10 09 08 07 06 05 04 03 02
10 9 8 7 6 5 4 3 2 1

The paper used in this publication meets the minimum requirements of ANSI/NISO Z39.48-1992 (R 1997) (*Permanence of Paper*).♾

Preface

Less than two years after the 1859 publication of Charles Darwin's *Origin of Species,* the first skeletal specimen of *Archaeopteryx* was discovered—a nearly perfect evolutionary "missing link"—and since that time, the origin and early history of birds have been prime topics of debate among natural historians and evolutionary biologists (De Beer, 1954; Desmond, 1982; Elzanowski, Chapter 6 in this volume). Not much later, the paleontological exploration of the American West resulted in the discovery of multiple specimens of *Hesperornis, Ichthyornis,* and their kin (Marsh, 1880), toothed birds that, although much less primitive than *Archaeopteryx,* strongly influenced discussions about early avian evolution. For many decades, this handful of Mesozoic taxa was all we had. It was the only fossil evidence available for understanding this fascinating chapter of vertebrate history. In fact, it was not until the early 1980s that significant new data started to fill the extensive evolutionary gap separating the basal birds discovered in the previous century. The first evidence of a previously unknown radiation of Mesozoic birds, Enantiornithes, was announced by Cyril Walker in 1981 (Chiappe and Walker, Chapter 11 in this volume), and soon other taxa (e.g., the Mongolian *Gobipteryx*) were recognized as part of this radiation (Martin, 1983). In addition, the discovery in the 1980s of some fossil-rich Early Cretaceous lake beds in Spain (Sanz et al., Chapter 9 in this volume) and intensified collecting in previously underexplored sites in Spain (Chiappe and Lacasa-Ruiz, Chapter 10 in this volume) and China (Zhou and Hou, Chapter 7 in this volume; Sereno, Rao, and Li, Chapter 8 in this volume) led to many other discoveries not much younger than *Archaeopteryx.* The two-dimensional preservation of this Early Cretaceous avian diversity limited anatomical studies, but three-dimensional bird skeletons began to be found in other Mesozoic fossil sites (e.g., Molnar, 1986; Chiappe, 1991). At the same time, other Cretaceous discoveries (e.g., Kurochkin, 1985; Olson and Parris, 1987; Hope, Chapter 15 in this volume) afforded information about the closest relatives of the living lineages of birds (Neornithes). If the abundant discoveries of the 1980s made a significant contribution to our understanding of the early evolution of birds, the 1990s brought an embarrassment of riches. In just that decade alone, the number of species of Mesozoic birds probably tripled those discovered in all previous years (Chiappe, 1997). These fossils were unearthed all around the world (Chiappe, 1995; Feduccia, 1996; Chatterjee, 1997; Padian and Chiappe, 1998), although primarily in China, Mongolia, Argentina, Spain, Madagascar, and the United States.

A volume entitled *Mesozoic Birds* faces the sometimes sticky problem of just what constitutes a "bird." In our narrow time plane of the present day, birds are so markedly distinct from other vertebrates that our perception of what is or is not a bird is patently obvious. But the Mesozoic era witnessed the dawning of birds, or, in scientific parlance, the evolutionary transition to birds. As a result, the line between bird and not-bird is often a fuzzy one, and there are many taxa whose avian status is highly controversial. This volume deals with several of these controversial taxa: for example, *Protoavis* (Chapter 1), *Caudipteryx* (Chapters 1, 2, and 7), *Avimimus* (Chapter 3), *Mononykus* and its alvarezsaurid kin (Chapters 4 and 5). Decisions about where to draw the line could be made on the basis of particular features, such as feathers or a furcula (wishbone), but, as it turns out, virtually all the attributes that characterize modern birds were acquired sequentially in the Mesozoic.

Thus, the line between bird and not-bird is essentially arbitrary and must be defined. In this modern phylogenetic era, taxonomic definitions are based on relationships, and we have adopted for this volume the convention of regarding Aves (and the colloquial terms "birds" and "avian") as pertaining to the group comprising the most recent common ancestor of *Archaeopteryx* and neornithine ("modern") birds and all its descendants (Witmer, Chapter 1 in this

volume; Clark, Norell, and Makovicky, Chapter 2 in this volume; Sereno, Rao, and Li, Chapter 8 in this volume; see also Padian and Chiappe, 1998; Sereno, 1998, 1999). This convention, while not entirely satisfactory, conforms to traditional usage. Chapter 2, by Clark, Norell, and Makovicky, however, breaks with this convention and speaks cogently for another convention; as editors, we respect their position and have not forced them to conform.

Just as phylogenetic systematics (i.e., cladistics) has transformed taxonomy, it has also changed the way we approach just about every question in comparative biology. Fundamentally, cladistics is a means of discovering the genealogical relationships of organisms, and in their chapter Clark, Norell, and Makovicky provide a very useful guide to the objectives and methods of cladistics. A few of the chapters in *Mesozoic Birds* indeed have detailed phylogenetic analyses with character-taxon matrices (e.g., Chapter 2, by Clark, Norell, and Makovicky; Chapter 11, by Chiappe and Walker; Chapter 20, by Chiappe), but "phylogenetic thinking" pervades almost the whole volume. Most noteworthy perhaps is Gatesy's innovative phylogenetic treatment of the evolution of the avian locomotor system in Chapter 19. Likewise, Witmer in Chapter 1 discusses the role of cladistics in the debate on avian origins and the relationship of phylogenetics to theories on the origin of flight. At the same time, some chapters have relatively little overt phylogenetic focus, either because the authors were dealing with a diverse regional avifauna (e.g., Chapter 7, by Zhou and Hou) or because the authors are not cladists (e.g., Chapter 14, by Galton and Martin). Nevertheless, phylogenetics is the underpinning of the volume, and a simplified cladogram of Mesozoic birds is presented in Figure P.1.

The study of Mesozoic birds is diverse, and this volume has sought to characterize this diversity. *Mesozoic Birds* presents a collection of essays covering a wide range of topics bearing on the origin of birds, their Cretaceous morphological and osteohistological diversity, their genealogical history, and their functional transformations during 85 million years of Mesozoic avian evolution. We have divided the volume into four parts. Part I deals with larger and more conceptual issues, such as those surrounding avian origins (Chapter 1) and the broader phylogenetic relationships of birds (Chapter 2). Part II provides a treatment of some of the controversial taxa mentioned previously. We have separated these more contentious taxa out because, although some analyses have placed them within Aves, others have suggested placement outside birds. Part III presents the undisputed members of the Mesozoic aviary and is devoted to chapters dealing with the anatomy, systematics, and paleobiology of the various groups of Mesozoic birds. As workers struggle to keep pace with the seemingly endless new discoveries, a great deal of alpha-level description and systematic work is required, and this part of the volume presents these findings. Some of the chapters deal with a single clade or even a single species (e.g., Chapter 6, by Elzanowski, on *Archaeopteryx* and its kin; Chapter 8, by Sereno, Rao, and Li, on *Sinornis;* Chapter 10, by Chiappe and Lacasa-Ruiz, on *Noguerornis;* Chapter 12, by Forster et al., on *Vorona;* Chapter 13, by Chiappe, on *Patagopteryx;* and Chapter 14, by Galton and Martin, on *Enaliornis* and other Hesperornithiformes). However, other chapters have a more geographic flavor, dealing with the fossil birds from a particular region (e.g., Chapter 7, by Zhou and Hou, on the Chinese birds; Chapter 9, by Sanz et al., on the Spanish birds).

In all cases, our intent was to have the primary experts who had the actual fossils in their laboratories write the chapters, ensuring that the most up-to-date and authoritative treatments would be available. This principle of seeking primary workers also resulted in members of one taxon, Enantiornithes, being covered in five chapters (Chapter 7, by Zhou and Hou, on the Chinese birds; Chapter 8, by Sereno, Rao, and Li, on *Sinornis;* Chapter 9, by Sanz et al., on the Spanish birds; Chapter 10, by Chiappe and Lacasa-Ruis on *Noguerornis;* and a summary, phylogenetic chapter [Chapter 11] by Chiappe and Walker). We worked with these authors to minimize the amount of overlap, and, although some minimal redundancy was perhaps introduced, Enantiornithes is such a new and important clade—recognized only since 1981 yet having greater known species diversity than any other Mesozoic avian clade—that we felt that extensive coverage was merited.

Although virtually all the taxa discussed in *Mesozoic Birds* were previously described elsewhere, the original descriptions are often very brief parts of short papers in journals such as *Science* and *Nature.* We are very pleased to be able to present in this volume new, definitive descriptions and illustrations of a number of taxa, including the enigmatic *Avimimus* (Vickers-Rich, Chiappe, and Kurzanov), the alvarezsaurid *Shuvuuia* (Chiappe, Norell, and Clark), the enantiornithines *Sinornis* (Sereno, Rao, and Li) and *Eoalulavis* (Sanz et al.), the basal ornithuromorphs *Vorona* (Forster et al.) and *Patagopteryx* (Chiappe), and the hesperornithiform *Enaliornis* (Galton and Martin). Thus, although our intent was to assemble and synthesize available data, *Mesozoic Birds* exceeds this goal by offering descriptions, figures, and other data that cannot be found elsewhere.

Lamentably, our rule of using only primary experts resulted in the almost total absence from the volume of one major clade of Mesozoic birds (Ichthyornithiformes) and only partial coverage of another major clade (Hesperornithiformes); both are marine clades known best from the Late Cretaceous Niobrara Chalk of Kansas. Although we had an agreement from the main researcher on these two clades, it was not fulfilled. Rather than enlist a secondary author, we choose to refer the reader to Marsh's 1880 monograph, *Odontornithes: A Monograph on the Extinct Toothed*

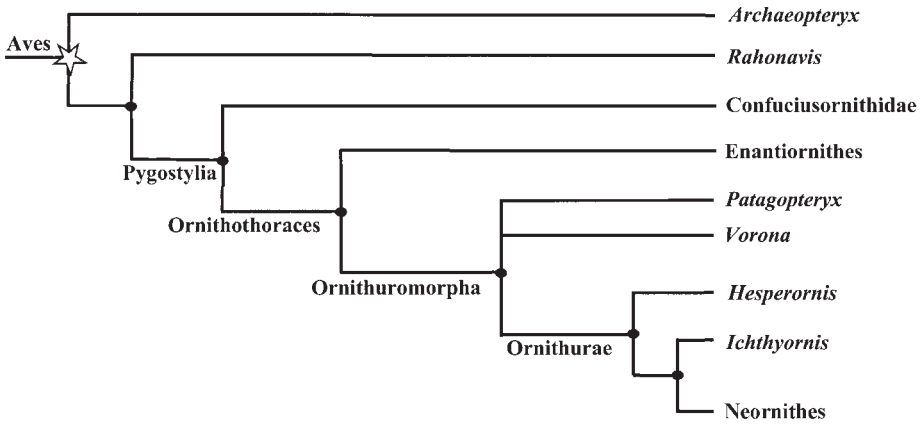

Figure P.1. Simplified cladogram of Mesozoic birds.

Birds of North America, which remains a useful source. Nevertheless, *Ichthyornis* and its kin are given passing treatment in Hope's chapter on Neornithes, and Chiappe (Chapter 20) includes *Ichthyornis* as a terminal taxon in his phylogenetic analysis. Chapter 14, by Galton and Martin, is largely devoted to the basal hesperornithiform *Enaliornis,* but they also discuss the anatomy and biogeography of other hesperornithiforms and provide a diagnosis of Hesperornithiformes; again, Chiappe includes this clade within his phylogenetic analysis presented in Chapter 20. For a detailed treatment of *Ichthyornis,* refer to Clarke (2002).

While we are on the subject of what might be perceived to be "missing" chapters, *Mesozoic Birds* lacks significant treatment of *Rahonavis,* the recently discovered Late Cretaceous bird from Madagascar (Forster et al., 1998). This discovery was so recent that a chapter for this volume was not feasible, and we regard the 1998 paper as sufficient for the time being (once again, Chapter 20, by Chiappe, includes *Rahonavis* in the phylogenetic analysis). But, truth be told, there are many such newly discovered Mesozoic birds that are absent from the pages of this volume and that, at this writing, remain unpublished. Discoveries are coming faster than scientists can write them up. With several new Mesozoic birds being discovered every year, the task of assembling exhaustive coverage of their early diversity became an impossible one. Although as editors we would prefer that the volume were "complete" (whatever that means), as avian paleontologists we are thrilled at the prospects that these new discoveries hold. We always knew that this volume would represent but a snapshot of this fast-moving field.

Part III concludes with two chapters on nonskeletal remains of Mesozoic birds, in particular an account of avian feathers by Kellner (Chapter 16) and a discussion of the footprint record by Lockley and Rainforth (Chapter 17). Part IV deals with issues surrounding the functional morphology, physiology, and evolution of birds. Chinsamy (Chapter 18) reviews the often contentious bone histology data for Mesozoic birds and its physiological implications. Gatesy (Chapter 19) provides an exciting new way of looking at locomotor evolution in birds that presents a true departure from previous studies. Finally, Chiappe (Chapter 20) presents a comprehensive phylogenetic analysis of basal birds and discusses its implications for avian evolution. Part IV would have been an appropriate place for a chapter on the origin of avian flight, and its absence may constitute, for some people, another "missing" chapter. In fact, Witmer's and Gatesy's chapters (Chapters 1 and 19, respectively) provide some discussion of the origin of flight, but, in general, our position is that so much has been written on the subject, with so little positive outcome, that another dedicated review was not warranted (see Chapter 1).

Mesozoic Birds has been a long and difficult project, but we believe the resulting volume is very satisfying. For the first time, most of the major primary workers on Mesozoic birds have been assembled to provide authoritative treatment of the subject from a variety of angles. The authors hail from ten different countries and all six inhabited continents—a truly international effort. The volume is more than a reference for the anatomy and systematics of Mesozoic birds—although we think that it performs that important task quite well. It also presents new ideas, new approaches, and new perspectives. As a result—although we always knew it would be valuable to those interested in birds and dinosaurs—we are confident that all vertebrate paleontologists and indeed most evolutionary biologists will find much of interest in its pages.

This volume would have not been possible without the help of a number of individuals and institutions. Special acknowledgment is given to Stacie Orell, a former volunteer at the American Museum of Natural History, who devoted many days to editing many of the manuscripts and bringing them to the required style and format. We are also grateful to many colleagues for acting as chapter reviewers and to two anonymous referees who painstakingly reviewed the whole volume and made numerous valuable suggestions.

The Frick and Chapman Funds of the American Museum of Natural History, the J. S. Guggenheim Foundation,

the Dinosaur Society, and the National Science Foundation (DEB-9407999; DEB-9873705) were the major sources of funding supporting Luis Chiappe's contributions to this volume. Lawrence Witmer was supported by the National Science Foundation (BSR-9112070; IBN-9601174), the Dinosaur Society, and grants from the Ohio University College of Osteopathic Medicine.

Finally, we are grateful to the staff of the University of California Press, especially Elizabeth Knoll and Doris Kretschmer, who over the years provided continuous support and assistance in seeing this project through to publication, and to George Olshevsky for his efforts in performing the daunting task of indexing the book.

Literature Cited

Chatterjee, S. 1997. The Rise of Birds. Johns Hopkins University Press, Baltimore, 312 pp.

Chiappe, L. M. 1991. Cretaceous avian remains from Patagonia shed new light on the early radiation of birds. Alcheringa 15(3–4):333–338.

———. 1995. The first 85 million years of avian evolution. Nature 378:349–355.

———. 1997. Aves; pp. 32–38 *in* P. Currie and K. Padian (eds.), The Encyclopedia of Dinosaurs. Academic Press, New York.

Clarke, J. A. 2002. The morphology and systematic position of *Ichthyornis* Marsh and the phylogenetic relationships of basal Ornithurae (dissertation). Yale University, New Haven, 532 pp.

De Beer, G. 1954. *Archaeopteryx lithographica:* A Study Based upon the British Museum Specimen. British Museum (Natural History), London, 68 pp.

Desmond, A. 1982. Archetypes and Ancestors. University of Chicago Press, Chicago, 287 pp.

Feduccia, A. 1996. The Origin and Evolution of Birds. Yale University Press, New Haven, 420 pp.

Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science 279:1915–1919.

Kurochkin, E. 1985. A true carinate bird from the Lower Cretaceous deposits in Mongolia and other evidence of early Cretaceous birds in Asia. Cretaceous Research 6:271–278.

Marsh, O. C. 1880. Odontornithes: a monograph on the extinct toothed birds of North America. Memoirs of the Peabody Museum of Natural History 1:1–201.

Martin, L. D. 1983. The origin and early radiation of birds; pp. 291–338 *in* A. H. Bush and G. A. Clark Jr. (eds.), Perspectives in Ornithology. Cambridge University Press, New York.

Molnar, R. 1986. An enantiornithine bird from the Lower Cretaceous of Queensland, Australia. Nature 322:736–738.

Olson, S. L., and D. C. Parris. 1987. The Cretaceous birds of New Jersey. Smithsonian Contributions to Science 63:1–22.

Padian, K., and L. M. Chiappe. 1998. The origin and early evolution of birds. Biological Reviews 73:1–42.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 210:41–83.

———. 1999. Definitions in phylogenetic taxonomy: critique and rationale. Systematic Biology 48:329–351.

Walker, C. A. 1981. New subclass of birds from the Cretaceous of South America. Nature 292:51–53.