

Preface

The scope of this book ranges widely, from biomolecular aspects of avian biology to details of the anatomy of dinosaurs. However, it is not just a simple compilation of current material. Its purpose is to help bridge a gap that has developed between those who study birds as fossils and those who study the living animals. The size of that gap has much to do with two controversies related to the evolution of birds that remained unresolved for much of the 20th century. One involved the origin of birds, from dinosaurs or not, and the other involved the inability of ornithologists to reach a general agreement on the relationships among the living groups of birds. The first was resolved at the very end of the 20th century, in favor of an origin of birds from ancestors among theropod dinosaurs, and although the second remains unresolved, it is being pursued by a host of optimistic scientists using novel techniques. These include new methods of interpreting morphological characters (cladistics) and sophisticated analyses of genetic material. Each chapter of this book puts current understanding in context with directions that research may take over the next few years.

Most of the organisms discussed are true birds in the sense that they include the most recent common ancestor of *Archaeopteryx* and all of its descendants among the Neornithes (Gauthier & de Quieroz, 2001). The remainder are those dinosaurs considered to be the closest relatives of that ancestor. The emphasis of the discussions is on evolutionary aspects of function and ecology rather than the technical description of individual fossils, many of which are discussed in *Mesozoic Birds* (Chiappe & Witmer, 2002) and other recent works.

Shortly after Charles Darwin offered natural selection as the driving force behind the evolutionary process, the origin of birds and the path of

their subsequent development seemed remarkably clear. The 140 million year-old *Archaeopteryx* bridged the gap between birds and their reptilian ancestors among the dinosaurs (Huxley, 1868), and within a few years toothed birds, such as *Ichthyornis* and *Hesperornis* (Marsh, 1888), seemed to confirm that birds enjoyed a simple and straightforward evolutionary story from primitive, reptilian forms to modern varieties. It was one of the great triumphs of early evolutionary theory – the living birds that we are all so familiar with are descended from ‘reptile-like’ forms including the toothed and long-tailed *Archaeopteryx*. Nothing in biology is ever that simple.

In 1926, the Dane, Gerhaard Heilmann, shattered the complacency of Victorian biologists with carefully constructed arguments that birds could not be related to dinosaurs. Among other things, dinosaurs lacked the distinctively avian furcula or wishbone. His arguments held sway through much of the 20th century but could not stand up to sophisticated advances in interpretive methodology and the discovery of dinosaurs with wishbones and other features shared with birds (Gauthier & Gall, 2001; Chiappe & Witmer, 2002). The intensity of this controversy was one of the factors that led to the isolation of students who studied fossil birds from those who studied the living animals. Gradually most ornithologists became so focused on experimental ecology and energetics that they no longer had the background to appreciate the subtle anatomical differences between *Archaeopteryx* and nonavian dinosaurs, such as *Velociraptor* and *Troodon* (Makovicky & Zanno: Chapter 1, O'Connor *et al.*: Chapter 3).

In spite of resolution of the fundamental issue – that birds are a living lineage of dinosaurs – the

immediate source of the living groups of birds (Neornithes) remains a controversial subject among both ornithologists and paleontologists (Lindow: Chapter 14). The absence of undoubtedly modern birds, except for Anseriformes, in the Mesozoic fossil record contradicts many of the biomolecular studies that show very early divergence dates (Brown & van Tuinen: Chapter 12). Many hope for greater success from analyses of the actual genome (Organ & Edwards: Chapter 13). Biomolecular techniques appear to be well founded in theory, but at a practical level they have yet to produce a generally accepted phylogeny for the living groups of birds. They have produced a variety of results from the much-maligned "tapestry" of Sibley & Ahlquist (1990) (Houde, 1987; Sarich *et al.*, 1989; Lanyon, 1992; Harshman, 1994) to the more technologically sophisticated analyses of Fain & Houde (2004) or Hackett *et al.* (2008). They all vary greatly from morphology-based hypotheses such as that of Livezey & Zusi (2007). Without an agreed-upon phylogeny, the evolutionary story of the whole group is moot (Livezey: Chapter 5).

In comparison to the fundamental problem of avian phylogeny, recent puzzles posed by the discovery of fossils of avian and nonavian animals bearing feathers, seem almost trivial. The presence of feathers no longer defines birds; feathers are now known from a variety of flightless animals and seem most likely to have arisen as insulation (O'Connor *et al.*: Chapter 3). *Anchiornis* (Xu *et al.*, 2008; Hu *et al.*, 2009), *Confuciusornis* (Hou *et al.* 1995), and the entire lineage of Cretaceous Enantiornithes (Walker, 1981) can tell us much about the advantages of being somewhat bird-like even if the actual relationship of those fossil forms to modern lineages is tenuous, and the implications for the eventual success of the Neornithes are slight.

Flight appears to have been a fundamental factor in the early success of birds but its origins are not likely to be revealed by the fossil record. For many years, two competing theories dominated discussion of the origin of flight. Either birds learned to fly by jumping from trees or by

flapping their wings while running across the ground. Recently, the tendency of flightless nestlings to flap their wings while running uphill has been developed into the theory of "Wing-assisted Inclined Running" (Tobalske *et al.*: Chapter 10). On the other hand, recently discovered fossils imply that a variety of small, feathered animals could be found in the canopies of Mesozoic trees. Not all had effective wings but wings are not the only organs required for flight. An endocast of the brain of *Archaeopteryx* suggests that it could already have been capable of processing the large amounts of data accumulated by a flying animal. Subsequent changes in the shape of the brain can be tracked into modern times (Walsh & Milner: Chapter 11).

The first section of the book reviews the early ancestry of birds and the conditions under which they, and their nearest relatives, diversified in the Cretaceous. It is intended to provide ornithologists with an overview of the fossil record and describes the history of some highly specialized groups such as extinct giants and seabirds from the Tertiary (Alvarenga *et al.*: Chapter 7, Bourdon: Chapter 8). Other middle chapters focus on adaptations contributing to the success of living forms such as penguins (Ksepka & Ando: Chapter 6) or other seabirds (Kaiser: Chapter 15), and are intended to provide paleontologists with a basic introduction to groups whose specialized lifestyles are reflected in their skeletal anatomy. It is the adaptations of these and other living species that are being tested by the alienation of habitats for human use and the effects of global warming (Thomas: Chapter 16).

We hope that by bringing together such a wide range of areas in one volume, the reader will find an entrée into less familiar topics and appreciate the potential value of linkages among seemingly unrelated approaches to the study of avian evolution.

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