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## A Review of "Living Dinosaurs: The Evolutionary History of Modern Birds"

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# LIVING DINOSAURS: THE EVOLUTIONARY HISTORY OF MODERN BIRDS, by Gareth Dyke and Gary Kaiser (editors), 2011. John Wiley & Sons, Ltd., West Sussex, U.K., xv + 422 pp. US\$134.95, hardcover, ISBN: 978-0-470-65666-2.

At this point in the early part of the 21st century, most people have at least heard of the concept that modern birds are 'dinosaurs' or are in some way related to the former megastars of the Mesozoic. In fact, casual discussions in most local schools would demonstrate this point all too well, as I witnessed firsthand during a visit to East Elementary School in Athens, Ohio. Nonetheless, this concept has not always found a safe haven in modern society, falling in and out of vogue on an approximately 50 year cycle. Huxley (1868) first articulated the anatomical basis for hypothesizing the relationship between birds and nonavian theropod dinosaurs. Although not without critics or alternative hypotheses, this concept remained at least a viable consideration until Heilmann (1926) published his comprehensive treatment on the topic-a treatment that ultimately relegated any morphological similarity between birds and dinosaurs to mere convergence. It wasn't until John Ostrom's work on dromaeosaurs in the late 1960s and early to mid-1970s (e.g., 1969, 1976) that the bird-theropod hypothesis was formally resurrected, rising like the proverbial phoenix from the flames. This concept has now withstood the rigor of contemporary comparative biology (e.g., Gauthier, 1986; and summaries in Gauthier and Gall, 2001; Chiappe and Witmer, 2004), with more recent semipopular treatments (e.g., Chiappe, 2007) doing a very good job of targeting a broad audience while still consolidating the wealth of new scientific information on the topic. Although the paleontology community has fully embraced the historical perspective that fossils necessarily bring to this debate, less well integrated in this particular community is the range of neontology-derived inferences related to the evolution of modern birds. Ongoing recent efforts (e.g., the Hieronymus et al. symposium at the 2012 Society of Vertebrate Paleontology meeting) are attempting to better integrate Recent and deep-time data sets and methodologies for addressing organismal evolution. In the same vein, Living Dinosaurs editors Gareth Dyke and Gary Kaiser have assembled a diverse assemblage of researchers with expertise ranging from morphological phylogenetics and geochemistry to experimental functional morphology and genomic evolution, all of whom weigh in to articulate contemporary viewpoints on the evolution of modern birds (Neornithes).

The first part of the volume sets the stage for understanding the deep history of birds, encompassing both historic (phylogenetic) and abiotic perspectives. Makovicky and Zanno (Chapter 1) provide the contemporary phylogenetic perspective of birds as theropod dinosaurs. This sets the appropriate tone for the volume and highlights recent advances in our understanding of a number of anatomical, physiological, and behavior inferences that blur the 'traditional' bird-theropod dichotomy. Ward and Berner (Chapter 2) follow with an overview of atmospheric gas concentration dynamics, particularly that of  $O_2$ , and its potential role in shaping the extinction and diversification profiles of terrestrial vertebrates during the Mesozoic. This offers a paleoenvironmental backdrop for the origin of dinosaurs, with a provocative title that uses the interrogative 'Why'-not once, but twice! O'Connor et al. (Chapter 3, and no relation to me) contribute the first datarich chapter, characterizing the major lineages of basal (i.e., nonneornithine) birds during the Mesozoic. Its success stems from

the inclusion of both extremely good photography of exemplar specimens and a novel phylogenetic analysis complete with data matrix and character list.

The second part of the volume focuses on the fossil record of Neornithes, and its impact for capturing the ebb and flow of modern bird diversification. Brad Livezey (Chapter 4) starts the section with a sojourn through the past 40 years of avian phylogenetics, providing an extremely critical commentary on the interplay (or lack thereof) between those utilizing molecular data and those grounded in the phenotype. This contribution is extremely well considered and written, and fully captures the intellectual essence and rigor of the late Curator of Birds at Carnegie Museum of Natural History. Although written in the context of birds, this effort clearly transcends this particular group of animals and is well worth the time it takes to read, digest, and internalize it. Dyke and Gardiner (Chapter 5) follow with a modeling treatment of predicting divergences for major neornithine clades, but do so using our knowledge of the actual fossil record rather than the more common molecular approaches used for this purpose today. Ksepka and Ando (Chapter 6) provide another gem for the volume, taking us on a detailed survey of the evolution of penguins, past, present, and future. Alvarenga et al. (Chapter 7) undertake a phylogenetic treatment of the emblematic Cenozoic predatory birds, the phorusrhacids (terror birds), and give a detailed taxonomic and stratigraphic listing, in addition to character definitions and a data matrix. Another now extinct, but ever impressive neornithine group, the large-bodied, soaring, pseudotoothed birds (Odontopterygiformes) receives a similar examination by Bourdon (Chapter 8). Closing this section of the volume, Barker (Chapter 9) tackles the question of passerine diversification, including considerations of the when and the where-and importantly, whether or not they are more diverse than expected relative to other clades.

The next six chapters form Part 3 of the volume and represent the most diverse, yet perhaps least conceptually cohesive, section, entitled "The Evolution of Key Avian Attributes." Brett Tobalske and colleagues (Chapter 10) bring us up to speed on the current understanding of the component parts of different types of flight. This effort attempts to integrate skeletal and muscular morphology, muscle activity (electromyography [EMG]), wing kinematics, and flow-field analyses. Walsh and Milner (Chapter 11) provide a nice review of avian neuroanatomy and selected senses (e.g., vision, balance), with a closing discussion on the utility of fossil specimens for inferring neurosensory evolution in birds. Brown and van Tuinen (Chapter 12) then take us for a ride into the realm of the genome, providing an insightful discussion on different molecular modeling approaches for estimating divergences, including an overview of the different software packages available for phylochronology. Organ and Edwards (Chapter 13) bring 'comparative biology' to the table in this volume and consider genomic evolution in birds as they discuss variation in everything from total genome and intron sizes to chromosome number, all examined in the phylogenetic context of the nuclear-gene-based Hackett at al. (2008) topology. Lindow (Chapter 14) reviews the main viewpoints regarding neornithine divergence estimates and discusses the impact of the Cretaceous-Paleogene extinction and selective lineage survival through this event. The evolution of marine and aquatic birds closes this section. Co-editor Gary Kaiser (Chapter 15) reviews a number of anatomical, functional, and behavioral characteristics (ones that represent convergences related to life in aquatic or subaquatic milieux) that no doubt confounded early efforts for understanding the phylogenetic relationships among these groups. The lone contribution to Part 4 of the volume consists of a treatment of avian diversity set within the context of modern day extinction by Thomas (Chapter 16). This discussion takes on topics ranging from relative extinction risk (i.e., not all species or clades are equally susceptible to extinction) to the impact of climate change on avian biology and diversity.

My only minor criticism is that the volume is a bit uneven in terms of 'depth of approach' from one chapter to another. For example, contrast the blazing (and detailed!), but altogether spoton commentary provided by the late Brad Livezey (Chapter 4) on the status of modern bird phylogenetics with the broad-brush approach at linking dynamic atmospheric gases with the maintenance and diversification of dinosaurs (and by extension, birds?) by Ward and Berner (Chapter 2). Admittedly, the volume includes contributions by a wide range of experts on topics ranging from phorusrhacid (terror bird) morphology and phylogenetics to a consideration of different clock models for estimating evolutionary rate heterogeneity underlying the neornithine diversification. Given this range, it is difficult to envision that this volume would or should target a singular demographic-professional or avocational, undergraduate or graduate-and that in fact is what makes it appealing. Nearly all of the contributions have extensive bibliographies, with some also including comprehensive listings of the fossils for a particular clade (e.g., penguins by Ksepka and Ando) and/or data matrices. As such, this resource provides a very good overview on a plethora of topics related to the evolution of modern birds-and does so in what should allow easy access for any reader to jump into the deep end of the pool should they feel compelled to do so. Most importantly for the paleontology/morphology community, the component parts of this volume dealing with inferences derived from molecular sequence (Brown and Van Tuinen) and/or genomic (Organ and Edwards) data offer a window into the world of the 'other' (i.e., the molecular evolutionary biology community). It is a lingering historical legacy that many students of paleontology have limited fluency, not to mention even a basic understanding, of both approaches and the requisite theoretical background of how our neontologist colleagues attempt to characterize organismal diversity and evolution. Clearly this not only impacts basic communication and conversation, but it seriously limits rigorous scientific discourse on any variety of topics. These chapters should serve as a gateway for many. And before changing your focus from morphologybased to molecular phylogenetics, thoroughly read the carefully

crafted chapter on modern phylogenetics by Brad Livezey. This is of course contextualized for birds, but elements of this commentary are useful for considering phylogenetics for virtually any group of organisms at this point in the 21st century.

In closing, the one lingering question remaining for this reviewer relates to how soon something like this will need to be updated, given both the rate of discovery and description of fossil birds from places like China and Madagascar, and the ever changing world of comparative biology, a dynamic subdiscipline that continually promotes the development of novel analytical approaches for characterizing organismal evolution (e.g., quantifying rates of clade diversification, modeling character evolution, etc.) on a seemingly triennial basis. Who knows what the next decade will bring? Who knows what questions we will even be asking? But I am certain that the never-waning interest in bird biology and evolution will be retained by both professional and avocational natural historians—not to mention by elementary school kids the world over.

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