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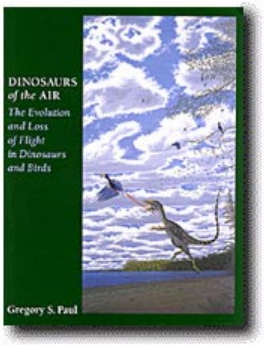
Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds[1]

Mesozoic Birds: Above the Heads of Dinosaurs[2]

reviewed by Kevin Middleton

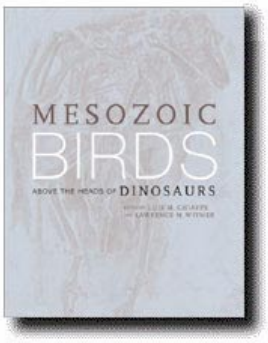
[1]by Gregory S. Paul
Johns Hopkins University Press, Baltimore, 2002, 472 pp.
ISBN: 0-8018-6763-0 $54.00 (cloth)

[2]edited by Luis M. Chiappe and Lawrence M. Witmer
University of California Press, Berkeley and Los Angeles, 2002, 536 pp.
ISBN: 0-520-20094-2. $95.00 (cloth)



When Ostrom (1973, 1974, 1975, 1976) and Bakker and Galton (1974) revived interest in an evolutionary relationship between theropod dinosaurs and birds, *Archaeopteryx, Ichthyornis,* and *Hesperornis* were the only well-known species of Mesozoic birds. During the past fifteen years fossil evidence of the diversity of Mesozoic birds and their non-avian theropod relatives has grown tremendously. Whereas only a few fossil avian taxa were available to Gauthier (1986) in his landmark cladistic analysis of the systematic position of birds, a tremendous number of avian species are now known from the Mesozoic, and new taxa are being described at a remarkable pace.

Recent years have seen a proliferation of books on the increasingly broad topic of the origin and early evolution of birds. Coupled with this interest in avian relationships is the frequently contentious issue of the origin of avian flight. Two new books take radically different approaches in their treatments of these topics.



In *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds* (The Johns Hopkins University Press, 2002) Gregory Paul likens himself to a modern day Gerhard Heilmann. In 1926, Heilmann, an illustrator like Paul, wrote *The Origin of Birds.* After presenting a great deal of comparative anatomical data suggesting a link between birds and theropod dinosaurs, Heilmann infamously concluded that the two could not be closely related. At the time, clavicles had not been discovered among non-avian theropods, and,

under a strict interpretation of Dollo's Law, Heilmann hypothesized that birds evolved from a group of basal archosaurs, the "thecodonts" (Gauthier, 1986). Whereas Heilmann failed because of an incomplete fossil record - theropod clavicles were not discovered until 1936 - Paul's effort to present a synthetic book on the origin of birds and of avian flight fails for rather different reasons.

Paul's book follows in the footsteps of recent quasi-technical books on birds and their dinosaurian ancestors. This lineage of nominally scientific books began in 1986 with the publication of *Dinosaur Heresies: New Theories Unlocking the Mystery of the Dinosaurs and Their Extinction* by Robert T. Bakker, which quickly became the bible of self-proclaimed "dinosaurologists," of whom Paul is one. Bakker's book was followed shortly by Paul's first book, *Predatory Dinosaurs of the World: A Complete Illustrated Guide* (1988), which carried Bakker's analyses several steps further. After the tremendous recent growth in the number of Mesozoic bird fossils, several authors have written books in which they attempt to integrate the new fossil avian and non-avian theropod discoveries of the last fifteen years to develop a coherent picture of the origin and evolution of birds and avian flight. These books include Alan Feduccia's *The Origin and Evolution of Birds* (1996), *The Rise of Birds: 225 Million Years of Evolution* by Sankar Chatterjee (1997), and *Taking Wing: Archaeopteryx and the Evolution of Bird Flight,* written by Pat Shipman (1998).

These books have been applauded for their attempts to bring paleontology and evolution to the general public in an accessible manner. However, they also have been soundly criticized in the paleontological community for their speculative and unfounded assertions as well as their frequent summary dismissal or outright omission of sources or contrasting views. Both of these faults contribute to an overall lack of scientific rigor. While the aims of each book have been quite different, their collective failures are startlingly similar.

Unfortunately, Paul's new book offers more of the same and can be regarded as just another entry in this increasingly crowded bookshelf. Criticisms that have previously been leveled against the books by Bakker, Paul, Feduccia, Chatterjee, and Shipman are equally applicable to Dinosaurs of the Air.

One of the principal criticisms of these books has been that they rely on confident assertion rather than scientific data to support their hypotheses. Of Bakker's *Dinosaur Heresies,* Ostrom (1987, p. 58) wrote, "In marshaling evidence to support his claim, most of which is presented in an unjustifiably authoritative style, Bakker oversimplifies the history and present state of dinosaur studies." Data and conjecture are rarely delineated in *Dinosaurs of the Air.*

For example, Paul states that "flight, even the flapping version, is a comparatively simple operation" (p. 131). He then erroneously compares flapping flight in birds to the flight of fixed-wing aircraft. He presents his analysis of avian flight as if it is well supported by scientific evidence, although, even after more than 50 years of research, the mechanisms of avian flight - anatomical, biomechanical, aerodynamic - are still not well understood. Furthermore, Paul virtually ignores fifteen years of research on the kinematics, neuromuscular control, and aerodynamics of avian flight. It is egregious to present such a scenario as though it is based upon actual data rather than just his own intuition. When reviewing Feduccia's *The Origin and Evolution of Birds,* Brush (1997, p. 450) cautioned, "The reader must temper the words knowing that the use of assumptions about evolutionary processes or adaptational scenarios can be misleading when trying to understand historical events or relationships." Readers of *Dinosaurs of the Air* would do well to follow this advice.

Frequently Paul summarily dismisses contrasting viewpoints. For example, he writes that "... Ruben and co-workers' analysis is without sufficient basis and must be rejected" (p. 202). Padian (1989, p. 283) noted a similar pattern in Paul's first book, *Predatory Dinosaurs of the World,* and commented that "Paul takes a confident, assertive tone, but often fails to credit or discuss the ideas of others with more than a curt dismissal, notably when they controvert his own."

Early in *Dinosaurs of the Air,* Paul states that "a computer generated cladistic analysis of bird origins is premature at this time" (p. 21). His attitude reveals a misunderstanding of the goal of cladistic analysis: to generate *hypotheses* of relationships between organisms. To say that not enough complete specimens are known to even try a cladistic analysis is to defeat the purpose and render any evolutionary hypotheses useless. I agree with Clark et al. (in *Mesozoic Birds;* p. 33), who state that "the importance of phylogenetic hypotheses to the study of evolution cannot be overstated." Any discussion of evolution must be predicated upon an hypothesis of relationships. Presently the tool requiring the fewest number of untestable hypotheses is cladistic analysis. Because a cladogram, by definition, has the fewest ad hoc hypotheses of change, any other methodology will have less explanatory power.

In a sense, Paul's line of argument throughout the book is backward. He begins the book with an overview of non-avian and avian theropod skeletal anatomy. From this base, he discusses forelimb function and "The Beginnings of Flight," moves on to "The Early Evolution of Flight," and concludes with "Who is Related to Whom and Why?" By putting function and evolution before phylogeny, in the end he is left searching for the most likely organism in which flight would have evolved, as he imagines it to have evolved. He goes so far as to say, "The methodology I use here presumes that the presence of a birdlike character in a group that is clearly unrelated to birds is not of phylogenetic importance" (p. 171).

The end result and perhaps most damning fault is that *Dinosaurs of the Air* and the other books mentioned herein simply lack scientific rigor. They are not reviewed by peers and thus are not subject to the same scrutiny. I will not contend that peer review is a cure-all for poor science or faulty reasoning, but some of the more fatuous statements made by these authors certainly would not pass unnoticed. The failure of these books was recognized by Crompton and Gatesy (1989, p. 113), who observed, in reference to *Predatory Dinosaurs of the World,* "This is not to say that there is no place for such individual views, but they need to be balanced in some way so that readers who are not familiar with the field will recognize that not all paleontologists would agree." They added that "Paul fails to give the curious reader a view of how the science of paleontology works; instead, anything goes" (p. 113).

One could reasonably ask: Why are these books published? And do they have any scientific value whatsoever? The first question is more easily answered; simply, dinosaurs sell books (or scientific magazines, but that topic is better left to another editorial). The second, evaluating the scientific merit of these books, is more troublesome. The hypotheses proposed by Gregory Paul and authors of books I have mentioned here could very well have appeared in the scientific literature had the authors been interested in pursuing that route. Indeed, parts of all of the books mentions here, except for Shipman's *Taking Wing,* had appeared in scientific journals. In this way, the books are part review and part speculation, aimed at a nonprofessional audience. It is with the speculative portion that I take issue, for significant portions of the books are simply opinion disguised as science.

Paul et al. some day may be shown to be correct, but their present methods are a distortion of evidence-based, hypothesis-driven science. I would welcome a well-reasoned analysis of the origin of birds and evolution of flight, rather than the uneven, sparsely documented presentations that have been offered so far. The authors expect to be taken seriously by the paleontological community, but the approach used precludes such acceptance.

In conclusion, I agree with Benton's (1990, p. 350) assessment that *Predatory Dinosaurs of the World* "will do great good in promoting paleobiology to a wide readership, but it may do great harm to the professional study of dinosaurs." While the goals may be admirable, the methods employed by Paul in both *Predatory Dinosaurs of the World* and *Dinosaurs of the Air* misrepresent the science of paleontology and the study of evolution and ultimately discredit the science as a whole.

In contrast, *Mesozoic Birds: Above the Heads of Dinosaurs* (University of California Press, 2002), edited by Luis M. Chiappe and Lawrence M. Witmer, is a multi-author work with two purposes: first, to survey the present state of Mesozoic avian paleontology; and, second, to provide full descriptions of specimens previously only preliminarily discussed in the literature.

The first two chapters, under the heading "The Archosaurian Heritage of Birds," are outstanding and should be required reading for those interested in avian evolution. In Chapter 1, Witmer provides a refreshingly evenhanded review of the debate on bird origins, both past problems and emergent questions. With the admonition that "bombast is a poor substitute for evidence" (p. 4), Witmer examines the published data on the questions of (1) the importance of the evolutionary relationship of birds among Reptilia (to allow inferences both about their ancestors and descendants); (2) the validity of *Archaeopteryx* as a central taxon in the debate about avian origins (warranted); and, (3) the importance of *Protoavis* in the debate (minimal).

The most significant portion of Witmer's chapter examines the relationship between the origin of birds and the evolution of avian flight. These two issues have, in too many analyses, become synonymous. Witmer argues that, while the origin of birds is a genealogical question, the origin of flight is an evolutionary question; the latter relies on the hypotheses of the former. Soberly, Witmer says that "it is conceivable that the origin of flight – as a matter of scientific discourse – is out of reach." While experimental data (e.g., Dial, 2003) may provide novel hypotheses for the origin of flight, reconstructing a complex behavior that evolved at least 145 million years ago may ultimately prove impossible.

In the second chapter, Clark et al. present a phylogenetic analysis of theropod relationships. Although the lengthy process of book publishing

means that new taxa often are omitted, the authors did include recently described taxa such as Microraptor as well as several taxa whose phylogenetic relationships have been uncertain (e.g., Caudipteryx and alvarezsaurids). However, the most important aspect of this chapter may be that the authors additionally present a clear and concise explanation of the central principles of cladistic analysis.

Part II contains three chapters covering historically controversial taxa. With the goal of fostering renewed research, Vickers-Rich et al. present a pictorial atlas of *Avimimus portentosus,* an enigmatic theropod that has been hypothesized to be a flightless bird. Two chapters address members of the clade Alvarezsauridae. Chiappe et al. discuss the skeletal material of alvarezsaurids, which now are known from Asia, North America, and South America. The authors note that the phylogenetic relationships of alvarezsaurids among other theropods are complicated by their highly apomorphic skeletons.

Novas and Pol (Chapter 5) present a phylogenetic analysis which places alvarezsaurids well outside Avialae as a distinct clade of coelurosaurs. Their results agree broadly with those of Clark et al. (Chapter 2), but disagree with Chiappe (Chapter 20, see below), who found that Alvarezsauridae was the sister group of *Archaeopteryx*. The disparity in these conclusions may result from differences in taxa that were included in the different analyses. Novas and Pol as well as Clark et al. focused their analyses more broadly on non-avian theropods, while Chiappe mainly was concerned with the interrelationships among birds and their close relatives. The results found by Novas and Pol and by Clark et al. may not have even been possible in Chiappe's analysis.

The third section of the book is comprised of systematic overviews of various clades (*Archaeopteryx*, Chinese birds, Euenantiornithes, Mesozoic Neornithes), longer anatomical descriptions (*Vorona, Sinornis, Noguerornis, Eoalulavis, Patagopteryx, Enaliornis*), and review chapters on Mesozoic feathers and avian tracks. Because phylogenetic and subsequent functional hypotheses will be refined as new specimens are described, the full descriptions are perhaps the most lasting contribution of this volume. Many of these descriptions, particularly those of *Sinornis* and *Vorona*, have been much anticipated by researchers. Furthermore, those of *Eoalulavis* and *Patagopteryx* are important for the critical positions that these taxa occupy in phylogenetic analyses.

In addition to Lockley's and Rainforth's chapter reviewing avian tracks from the Mesozoic, Kellner reviews avian feather diversity. Although admirably detailing the range of feathers known from the Mesozoic, Kellner's chapter on feathers is particularly lacking. He omits all of the known non-avian theropod taxa that are known to have feathers or feather-like integumentary structures - e.g., *Beipiaosaurus, Caudipteryx, Protarchaeopteryx, Sinornithosaurus,* and *Sinosauropteryx* - instead focusing on isolated feathers.

The final section of the book concerns "Functional Morphology and Evolution." In "Bone Microstructure of Early Birds" Chinsamy reviews past work on bone microstructure and discusses present areas of research. Whereas early paleohistology was mainly concerned with potential phylogenetic information to be garnered, recent work has been used to shed light on paleophysiology and growth rates of Mesozoic birds. New data are presented on the bone histology of *Cimolopteryx, Gobipteryx,* and an unnamed Cretaceous taxon.

In "Locomotor Evolution on the Line to Modern Birds", Gatesy draws on studies of anatomy in fossil and extant archosaurs as well as kinematic and muscle activity pattern data for extant archosaurs (alligators and birds) to trace the evolution of theropod locomotion. Gatesy uses optimization to assign character states to internal nodes of the cladogram and, by only choosing certain nodes at which to reconstruct ancestors, is able to assign states to nodes that may be ambiguous lower on the cladogram. The book concludes with a cladistic analysis of Mesozoic birds by Chiappe. Unfortunately, the pace of new discoveries makes this chapter somewhat dated, as many new taxa are omitted from the analysis. These include both basal (e.g., *Sapeornis* and *Jeholornis*) and derived forms (e.g., *Yanornis* and *Yixianornis*) (Zhou and Zhang, 2002a, 2002b, 2001).

Mesozoic Birds is a significant and important book that will be particularly useful to paleontologists and ornithologists alike. Despite the publisher's claims, it is not for the nonspecialist, as technical terms and anatomical minutiae are not likely to be easily digested by the lay reader. Delays associated with publication raise two issues. First, the anatomical descriptions may have benefited from more rapid publication in scientific journals. Second, phylogenetic analyses may not belong in a book like *Mesozoic Birds* because the analyses are likely to be outdated as soon as they are published. However, these problems are relatively minor and do not detract significantly from what is, overall, an excellent volume.

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