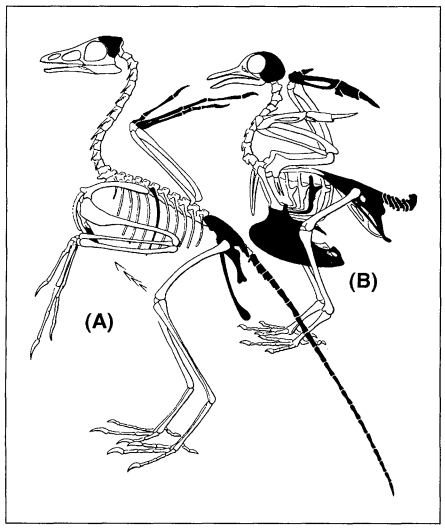
BOOK REVIEWS

Flying Feathers

The Origin and Evolution of Birds. ALAN FEDUCCIA. Yale University Press, New Haven, CT, 1996. xii, 420 pp., illus. $55 or £45. ISBN 0-300-06460-8.

Despite the uproar it has engendered in scientific journals and the general press, there is no avoiding the conclusion that Alan Feduccia's *The Origin and Evolution of Birds* is a landmark. It is certainly the most important single-authored volume on the subject since Gerhard Heilmann's 1926 opus, and probably will wind up being the most controversial, most reviewed paleontological work of the decade. Engaging a subject that, since Darwin's time, has generated an extraordinary amount of both heat and light, Feduccia's volume will do little to diminish the status of avian origins as the subject of perhaps the most high-profile debate in evolutionary biology. The controversy centers around Feduccia's position—heretical today but orthodox 25 years ago—that birds are not derived from dinosaurs. Feduccia sets the tone in the preface, writing of "perfidious traps . . . luring paleontologists to the theropod dinosaurian origin of birds." This is no even-handed textbook, but rather a personal and passionate vision of the debate.



"Comparison of the skeletons of *Archaeopteryx* (*A*) and a modern domestic pigeon (*B*). Comparable regions of the skeleton (braincase, hand, sternum, rib, pelvis, tail) are shaded black." [Reprinted from Colbert and Morales, *Evolution of the Vertebrates* (Wiley, 1991), in *The Origin and Evolution of Birds*]

The book is organized more thematically than systematically, beginning with the debates on avian ancestry and the origin of flight, then discussing the remarkable radiation of birds in the Cretaceous, and concluding with an exhaustive treatment of Tertiary birds and the origin of the modern avifauna. Although the first section has attracted the most attention, the last occupies more than half the volume and demonstrates that Feduccia has a firm command of the relevant literature (and many of the fossils). There are interesting analyses of a wide range of topics, such as the significance of "mosaics" like the Paleogene bird *Presbyornis*, the evolution of filter-feeding, and the recurrent development of flightlessness, although in most cases even a rudimentary phylogenetic framework would have greatly improved the discussions.

"*Apterornis* or *Aptornis* (10–13 kg; 22–29 lbs.), commonly known as the adzebill, was a large flightless gruiform bird of New Zealand, with a distinctive species on the North and South Islands." [From *The Origin and Evolution of Birds*; drawing by John P. O'Neill]

Feduccia also restates his case for the "explosive radiation" of the higher taxa of modern birds in the early Tertiary. This hypothesis has some interesting implications but is not entirely new. We have known for years that birds suffered a massive extinction at the end of the Cretaceous, with all of the "archaic" Mesozoic clades (Enantiornithes, Hesperornithiformes, Ichthyornithiformes, and others) succumbing and perhaps only a few neornithine lineages surviving to give rise to the modern groups. No amount of quibbling about how to allocate the scrappy late Cretaceous and early Paleocene neornithine fossils is likely to force a major revision of this scenario.

But if this book has a mission, it is to dismantle not only the notion of the dinosaurian affinities of birds but also the entire practice of phylogenetic systematics. For Feduccia, the two are inextricably linked. Indeed, cladistic analysis has firmly embedded birds within the nexus of Theropoda—in fact, repeatedly and by independent workers using somewhat different characters and taxa (a point neglected by Feduccia). Nevertheless, there is nothing inherent in the methodology that would preclude other outcomes. Although he regards cladistics as "the most rigorous method for the analysis of morphology," Feduccia has yet to perform this requisite broader analysis. His misgivings about cladistics center on issues associated with character weighting, convergence, the criterion of parsimony, and stratigraphic position. All of these are points of valid concern and have been widely discussed for 30 years. Instead of exploring and responding to this literature, Feduccia employs an alternative approach to phylogeny reconstruction.

Feduccia views the phylogenetic issue of the origin of birds and the functional issue of the origin of flight as basically the same. For him, any assessment of the relationships of birds methodologically is secondary to identifying the most likely scenario for the origin of flight; in other words, first reconstruct a hypothetical "proavis" and then search the animal kingdom for a match. This approach stands in opposition to a rich literature on the connection between functional and phylogenetic inference that regards the establishment of relationships (by whatever means) as logically prior to any functional inferences. It is not out of order to disagree with this literature, but Feduccia does not even discuss it, let alone offer a justification for his approach. He claims that "a dinosaurian origin of birds is inextricably linked with the cursorial, or ground-up origin, of avian flight, which is a biophysical impossibility." Therefore, he subscribes to the arboreal, or "trees-down," scenario, rejecting theropods as ancestors of birds and instead focusing on a variety of poorly known Triassic reptiles like *Longisquama*. Regardless of how one views the origin of avian flight (or whether any of the hypotheses are even testable), a major weakness of the pairing of theropods with ground-up and not-theropods with trees-down is that we have almost no knowledge of the behavioral repertoire of theropods. It is effective rhetoric to question how a large theropod could have gotten up a tree, but the theropods thought to be closest to birds are relatively small animals, and many paleontologists have re-

garded these forms as being at least partly arboreal.

Actually, *The Origin and Evolution of Birds* is replete with rhetorical devices likely to sway the uninitiated and frustrate the specialist. The "equation-of-whole-to-part" is used extensively. For example, Feduccia regards theropods (as a whole) as exhibiting "the worst possible anatomical architecture for flight evolution" because of their large size and particularly their reduced forelimbs; *Tyrannosaurus* is his exemplar. Amazingly, he makes no reference to "the part," that is, the subset of Theropoda named Maniraptora that reverses the general theropod trend and has secondarily elongate forelimbs closely resembling those of *Archaeopteryx*. In fact, the forelimb elongation of maniraptorans like *Deinonychus* is one of the many features that led to the current orthodoxy of considering birds to be maniraptorans.

Another rhetorical device is "maximize any difference," an egregious example being Feduccia's exploitation of the disparity in geological age between *Archaeopteryx* and "birdlike" theropods. To paleontologists who use cladistics "in an almost religious manner . . . it is inconsequential that birdlike dinosaurs occur some 75 million or more years after the origin of birds." Though the assertion about a time discordance is strictly true, there is reliable evidence—uncited by Feduccia—of true dromaeosaurids (the theropods closest to birds) extending back to within 35 million years (*Deinonychus*) and even 25 million years (*Utahraptor*) of *Archaeopteryx*, and there are dromaeosaur-like teeth that actually predate *Archaeopteryx* by some 20 million years. The point is that the time discordance is not as fatal as Feduccia indicates and may prove to be nonexistent.

Feduccia uses the same device in his anatomical comparisons of *Archaeopteryx* and birdlike theropods, in virtually all cases finding that the latter fall short. For example, although dromaeosaurids have a partially retroverted pubic bone—more birdlike than in other theropods—it is not retroverted enough, according to Feduccia. Similarly, although most theropods exhibit very birdlike feet, only *Archaeopteryx* and other birds have a reversed, grasping first toe. But the absence of fully retroverted pubic bones and perching feet in dromaeosaurids does not preclude a close relationship to birds. Some avian features are *restricted* to birds, because birds evolved their own suite of novelties. Dromaeosaurids are not birds and should not be expected to have all these novelties. Cladists emphasize similarity; Feduccia emphasizes difference. It is hard to imagine how the latter approach can clarify relationships.

What, then, are we to do with Feduccia's volume? We should read it, study it, even cherish it. It will remain the premiere document on the early evolution of birds for years to come. Although advocates of the theropod relationships of birds may find the book maddening, they should not ignore it but rather take it as a rallying cry. Feduccia calls some of the classic theropod-bird characters into question (for example, the wrist) and showcases other difficulties (for example, digital homologies). The research program advocating the theropod hypothesis has become complacent, wrapping the hypothesis in the warm blanket of parsimony, content that the sheer volume of characters will protect it from the cold. Breaking all the rules, Feduccia has attempted to strip off that blanket. Supporters of the theropod hypothesis (including myself) should rise to the challenge, answering Feduccia's objections, reanalyzing weak characters, and bringing out the unpublished evidence, much of which has been available for years. Dogma is a scary thing, and if *The Origin and Evolution of Birds* stimulates productive and vital discussion, history should judge it a resounding success.

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Browsings

A Century of Mathematical Meetings. Bettye Anne Case, Ed. American Mathematical Society, Providence, RI, 1996. xii, 332 pp., illus. $75; to AMS members, $45. ISBN 0-8218-0465-0. From a meeting, Cincinnati, OH, Jan. 1994.

Proceedings of the American Mathematical Society's 100th annual meeting, in which some 30 mathematicians present recollections of past meetings and colleagues, students, and institutions they have known.

Collected Papers of Sir James Lighthill. M. Yousuff Hussaini, Ed. Oxford University Press, New York, 1997. In four volumes, illustrated, variously paged. $395 or £299. ISBN 0-19-509222-8.

Ninety reprinted journal papers by a scientist, still active, who "ushered in a new era of fluid mechanics research."

Collecting the Natural World. Legal Requirements and Personal Liability for Collecting Plants, Animals, Rocks, Minerals and Fossils. Donald Wolberg and Patsy Reinard. Geoscience Press, Tucson, AZ, 1997. viii, 330 pp. Paper, $24. ISBN 0-945005-20-2.

A geologist and a lawyer collaborate to present a survey of U.S. federal and state laws pertaining to archaeological and natural-history exploration, with lists of relevant agencies and organizations, national parks and other sites, and endangered species.

Ecology. A Bridge Between Science and Society. Eugene P. Odum. Sinauer, Sunderland, MA, 1997. xiv, 330 pp., illus. Paper, $24.95. ISBN 0-87893-630-0. Revised edition of *Ecology and Our Endangered Life-Support Systems.*

An updating of a book "intended to be not only a textbook for beginning students, but also a citizen's guide to the principles of modern ecology as they relate to today's threats to our earth home."

In the Company of Mushrooms. A Biologist's Tale. Elio Schaechter. Harvard University Press, Cambridge, MA, 1997. xvi, 280 pp., illus., + plates. $24.95 or £16.50. ISBN 0-674-44554-6.

A microbiologist who "first got interested in wild mushrooms with eating in mind" shares his enthusiasm in a melding of natural history, collecting tips, mythology, and other mushroom lore.

The NASA Atlas of the Solar System. Ronald Greeley and Raymond Batson. Cambridge University Press, New York, 1996. 369 pp., illus. $150 or £90. ISBN 0-521-56127-2.

A 12-by-18-inch (~30-by-46-cm) collection of satellite photographs and other illustrations with a text aimed at the general reader, a glossary, a gazetteer, and other addenda.

T. ρεξ and the Crater of Doom. Walter Alvarez. Princeton University Press, Princeton, NJ, 1997. xii, 169 pp., illus. $24.95 or £18.95. 185 pp., illus., + plates. ISBN 0-691-01630-5.

One of the initial proposers of the impact theory of dinosaur extinction gives an informal personal account of the gathering of evidence and the debates thereupon.

This Gifted Age. Science and Technology at the Millennium. John H. Gibbons. AIP Press, Woodbury, NY, 1997. xviii, 346 pp., illus. $29.95. ISBN 1-56396-129-6. Masters of Modern Physics.

Writings and speeches, 1972–1995, by the former head of the Office of Technology Assessment and current science adviser to President Clinton.

X-Rays. The First Hundred Years. Alan Michette and Sława Pfauntsch, Eds. Wiley, New York, 1997. xiv, 262 pp., illus. $69.95 or £35. ISBN 0-471-96502-2. From a meeting, London, Nov. 1995.

Eleven papers, prepared for a celebration at King's College London, discussing the discovery of x-rays, their earliest medical uses, x-ray microscopy, microanalysis, and diffraction, synchrotron radiation, x-ray lithography, x-ray astronomy, and laser production of x-rays.