How Many Dinosaurs Are Birds?

Romancing the Birds and Dinosaurs: Forays in Postmodern Paleontology. Alan Feduccia. Brown Walker Press, 2020. 314 pp., illus., $34.95. (ISBN: 9781599426068 paper).

E very school child knows that birds are dinosaurs. Numerous magazine articles and popular books on the topic are available. If they report the history of the subject, they say that Thomas Huxley, known as Charles Darwin’s bulldog in Victorian England, was the first to propose the idea that birds evolved from dinosaurs (Huxley, 1868, 1870) or, at least, that birds and dinosaurs have a common ancestor (Naish 2012). The more specific idea that birds evolved from small theropod dinosaurs was proposed in 1969 in John Ostrom’s monograph about the bipedal raptor Deinonychus (Ostrom 1969). Ostrom wrote that the skeleton of Deinonychus, like that of Archaeopteryx (the oldest known bird at the time), had fused collarbones, long arms, and wrist bones that permitted the forelimb to fold like a bird’s wing. He suggested that Archaeopteryx was ground dwelling and could not fly; he also thought that dinosaurs might have been warm-blooded like modern birds.

Those ideas are still held by some of today’s prominent dinosaur paleontologists, and they are presented in displays in many museums. Other paleontologists have switched their view to one in which avian flight arose in an arboreal context, especially after the arboreal gliding four-winged microraptors were described as theropods (Xu et al. 2003). Whether or not dinosaurs were warm-blooded is still a matter of controversy (Benson 2018). Even so, as new discoveries of fossils from China, Mongolia, and elsewhere have been pouring in, their data have been incorporated into ever-larger matrices for analysis. The results are consistently interpreted as further confirmation of Ostrom’s hypothesis, that birds evolved from small theropod dinosaurs. The laterally flexing wrist and modern-type feathers evolved in theropods for reasons unrelated to birds or flight (Padian and Chiappe 1998, Clarke 2013).

Even more specifically, the prevailing hypothesis today is that the closest relatives (sister group) of birds are among the maniraptoran theropod dinosaurs. Theropoda is a large group of bipedal dinosaurs, most of which had three forward-facing toes and three fingers. They ranged in size from diminutive to gigantic, like the famous Tyrannosaurus rex. Members of the theropod group Maniraptora have a half-moon shaped (semilunate) bone in the wrist and a wing-like forelimb.

Recently, three groups of maniraptorans were named the Pennaraporta (Foth et al. 2014). They have the same type of wing feathers (penneous) and V-shaped collar bones as modern birds. Opinions differ about which maniraptoran group is closest to birds, but the overall framework of the hypothesis that birds are maniraptoran theropods (the BMT hypothesis) is hailed as one of the great achievements of vertebrate paleontology (Xu et al. 2014). The maniraptorans have specialized skeletal features that are found only in birds, and independent supporting data exist. According to the BMT hypothesis, in the Jurassic Period (between 201 and 145 million years ago), some bipedal theropods with reduced forelimbs reelongated them into wings.

In spite of all this confidence that the problem of the origin of birds has been solved, strong grounds exist for regarding the issue as unsettled, and that is exactly the subject of Alan Feduccia’s new book. He thinks not only that Archaeopteryx could fly but also that birds and avian flight evolved long before Archaeopteryx. Indeed, in his view, birds were already distributed worldwide at the time of Archaeopteryx. The book is a detailed, up-to-date, and accessible report of the evidence that Feduccia finds contrary to the BMT hypothesis. Each of the 23 short essays is followed by suggestions for further reading.

Feduccia’s biggest issue is the neoflightless problem. He argues that some unknown number of flying and flightless birds are being misclassified as dinosaurs. In combination with the data-analysis problem, the BMT issue should not be considered settled at all. In addition, there are the reduced-forelimb problem, the protofeather problem, the digit problem, the behavior problem, the confirmation-bias problem, and so forth. Feduccia charges that BMT advocates are not fully addressing these problems (table 1).

Feduccia’s skepticism has been growing for decades. His original research is what showed that Archaeopteryx could climb (Feduccia 1993) and fly (Feduccia and Tordoff 1979, Olson and Feduccia 1979) and that the digits of the hands of birds are the second, third, and fourth of the tetrapod five-fingered plan (Feduccia and Nowicki 2002). Romancing the Birds and Dinosaurs is his fourth major book. In The Age of Birds (Feduccia 1980), he tentatively followed Heilmann (1926), who argued that, overall, a pretheropod origin of birds seemed more likely than a dinosuarian one. He emphasized that avian feathers are highly aerodynamic and unlikely to have been originally adapted for any function other than flight. In his next book, The Origin and Evolution of Birds (Feduccia 1996, 1999), he added a critique of the way that cladistic methods of data analysis were being used to estimate phylogenetic trees from morphological data. The analyses are unable to detect the parallelism and convergence that are such common features of the evolutionary history of lineages, especially
Table 1. Problems with the prevailing view that birds evolved from maniraptoran theropod dinosaurs.

| Birds are maniraptoran theropod dinosaurs (BMT) | Main problems raised by Alan Feduccia |
|-----------------------------------------------|--------------------------------------|
| The flight architecture of birds evolved in a nonflight context | Neoflightless problem: Some flying and flightless birds are being misclassified as theropods. |
| Standard phylogenetic analyses applied to fossils support the main framework of the BMT. They can be used to estimate basic similarities (homologies) after the analysis. | Data analysis problem: Standard phylogenetic analyses are unable to detect complex evolutionary processes like convergence. Flightless birds converge on the body plan of theropods. To estimate basic similarities (homologies), anatomical studies are needed before the phylogenetic analysis. |
| The reduced forelimbs of early theropods evolved into wings. | Reduced forelimb problem: Complex characters, once lost, are unlikely to reevolve. Dollo's Principle. |
| The integumentary filaments (protofeathers) in the Maniraptora are homologous with feathers. | Protofeather problem: "Protofeathers" may be degraded collagen fibers. |
| The difference in the manual digits (II-III-IV in birds, I-II-III in theropods) can be accounted for by a digital frame shift. | Digit problem: The frame shift is a verificationist explanation, designed to fit the BMT. |
| Studies that infer the nesting behavior of theropods support the BMT. | Behavior problem: Studies that infer bird-like behavior in dinosaurs are about misidentified birds. |
| Scansoriopterygids are assumed to be theropods. | Confirmation problem: Scansoriopterygids have no distinctive theropod characters. An assumption that they are theropods is a form of confirmation bias. |

those related to flightlessness. In his third book of this series, *Riddle of the Feathered Dragons*, Feduccia (2012) agreed with Lingham-Soliar (2003a, 2003b) that the "protofeathers" of theropods were probably degraded collagen fibers. Many of the unambiguously feathered recent fossils from China that had been identified as theropods were probably misidentified flightless birds. The BMT phylogeny was being turned topsy turvy by the parsimony criterion used in cladistic data analyses. It seeks the smallest number of character changes and minimizes convergent evolution among taxa.

Feduccia supports the neoflightless hypothesis of Gregory Paul (Paul 1988, 2002) that some fossils identified as theropods were actually flying and flightless birds, more advanced toward modern birds than *Archaeopteryx*. Like Feduccia, Paul has been skeptical about the reliability of analyses that presume to identify basic structural similarities (homologies) after an analysis. An example with modern birds is with the large flightless ratites. The ostrich, rheas, cassowary, elephant bird, and moa are now known from molecular analyses to have converged on the same body plan. They became large and flightless independently (Mitchell et al. 2014). Similarly, early birds that became flightless would have converged on bipedal theropods in their body plan. Paul’s current view is that bipedal theropods evolved into long-armed climbers, which evolved into sprawling flying birds. Then some, like *Deinonychus*, became large and flightless, but they still retained characters that were better adapted for flight than those of *Archaeopteryx*. Even so, Paul thinks that his version of the neoflightless hypothesis is compatible with the BMT (figure 1; Paul 2016).

The case for neoflightless status is best for the bird-like Pennaraptora (figure 2). If the hypothesis is true, this error accounts for all kinds of improbable inferences that are now part of the BMT. One no longer ends up having to invent exaptations (characters that evolved for functions other than their current use). A well-studied example of a flightless bird that shows up in most phylogenetic analyses as an oviraptorid theropod is *Caudipteryx*. *Caudipteryx* has an avian hand with a digital formula more advanced toward modern birds than that of *Archaeopteryx*. Maryanska and colleagues (2002) found all oviraptorosaurs to be flightless birds.

Another aspect of Feduccia’s skepticism is that Ostrom’s model requires that birds and avian flight evolve in bipedal theropods with greatly shortened forelimbs. Even Huxley’s original concept was that bipedal dinosaurs evolved first into ostrich-like flightless birds, which then acquired the ability for powered flight. The legacy of Huxley’s error seems to be the failure of BMT advocates to recognize flightless birds among the theropods. It is contrary to Dollo’s principle, by which a complex character like a forelimb, once reduced, is unlikely to reevolve. Feduccia’s alternative scenario is that birds may have evolved from climbing quadrupedal dinoauromorphs or even earlier archosaurs. No evidence exists that any flightless bird lineage ever regained flight.

Feduccia also thinks that dinosaur paleontologists are dismissing some of the sound principles of evolutionary reasoning, morphological interpretation, and homology determination that emerged from the Modern Synthesis, when Darwin’s ideas about natural selection were put together with Mendelian genetics—hence his subtitle’s reference to the term postmodern paleontology. He dedicates *Romancing the Birds and Dinosaurs* to Ernst Mayr, and the book has the same format: a set of short essays building up to one long argument, that Mayr used when explaining Darwinian thought. He emphasizes that applications of phylogenetic methods of data analysis to morphological data, though useful, can be misleading if they fail to detect
larger while retaining juvenile characters (paedomorphosis). They converge on the basic theropod body plan. Another advantage of Feduccia’s objections to the BMT is that they eliminate the need for improbable changes in the function of highly sophisticated aerodynamic structures (exaptations), now thought to have evolved in a nonflight context. Feduccia’s concept also accounts for the digital mismatch in the hand whereby birds appear to retain digits II, III, and IV, whereas theropods appear to retain digits I, II, and III. He does not need to postulate implausible mutations or alterations in the conserved process of limb-bud development, and he does not need to postulate an Ostrom-like ground-based origin of flight.

Feduccia claims that BMT advocates fail to recognize contradictory evidence. Their intention, which is to interpret all future discoveries in terms of the BMT (Smith et al. 2015), is a clear example of confirmation bias. A recent example from China is their treatment of the recently discovered mid-Jurassic (174–164 million years ago) scansoriopterygids, which appear to be more primitive than Archaeopteryx.

None of the four species that have been identified so far has any salient

convergence, mosaic evolution, and the retention of ancestral juvenile characters. All three of these processes occur regularly in vertebrate evolution and are known to confound analyses.

After a major study of salamanders, Wiens and colleagues (2003) concluded that their phylogenetic analysis was misleading and that “ontogeny discombobulates phylogeny.” Flightless birds often become

https://academic.oup.com/bioscience

Figure 1. Two proposals about the origin of birds. In the prevailing view (left side), anatomical studies support the hypothesis that the origin of birds was among maniraptoran theropod dinosaurs. Independent studies are interpreted as lending support for this BMT hypothesis. In Gregory Paul’s and Alan Feduccia’s views, anatomical studies indicate that at least some maniraptorans are misclassified flying and flightless birds. Paul thinks this neoflightless hypothesis can be integrated with the prevailing view. Feduccia argues that other independent information supports his view that the origin of birds is unknown.

Figure 2. According to the hypothesis that birds are maniraptoran theropod dinosaurs (left side), their lineage is nested within the pennaraptorans, maniraptorans, and theropod dinosaurs. The pennaraptorans have modern-type vaned feathers and a V-shaped fused collarbone. The maniraptorans have an enlarged breast bone (sternum) and a fused semilunate wrist bone that facilitates folding of the forelimb. These characters are presumed to have evolved in theropods, for unknown functions, before the origin of birds. Alan Feduccia thinks that at least the pennaraptorans are flying and flightless birds, not dinosaurs (right side). He argues that birds are more likely to have evolved from predinosaurian early archosaurs than from bipedal dinosaurs with foreshortened forelimbs.
Special Book Article

dinosaur or theropod features (Czerkas and Yuan 2002, Czerkas and Feduccia 2014). These animals have bird-like bones in the wrist, unusual feathers, and a reversed first toe like birds but also have membranous wings, boxy skulls, and a nontheropod type femur. They were just assumed to be theropods and added to the bird and dinosaur matrices.

So far, no molecular data are available from as deep in history as the origin of birds. All we have is morphology, and we do not know its limits for revealing genealogy. But, contrary to Prum (2002), a challenge to a hypothesis need not propose an alternative. Surely, admitting that the hypothesis that birds are maniraptoran theropods has serious problems would be better than to defend it so strongly. Romancing the Birds and Dinosaurs offers an accessible and challenging entry into this complex subject.

References cited

Benson RBJ. 2018. Dinosaur macroevolution and macroecology. Annual Review of Ecology, Evolution and Systematics 49: 379–408.

Clarke J. 2013. Flight before feathers. Science 340: 690–692.

Czerkas SA, Yuan C. 2002. An arboreal maniraptoran from northeast China. Pages 63–95 in Czerkas SJ, ed. Feathered Dinosaurs and the Origin of Flight. Dinosaur Museum Journal, vol. 1. Dinosaur Museum, Blanding, Utah.

Czerkas SA, Feduccia A. 2014. Jurassic archosaur is a non-dinosaurian bird. Journal of Ornithology 155: 841–851.

Feduccia A, Tordoff HB. 1979. Feathers of Archaeopteryx: Asymmetric vanes indicate aerodynamic function. Science 203: 1021–1022.

Feduccia A. 1980. The Age of Birds. Harvard University Press.

Feduccia A. 1993. Evidence from claw geometry indicating arboreal habits of Archaeopteryx. Science 259: 790–793.

Feduccia A. 1996, 1999. The Origin and Evolution of Birds. Yale University Press.

Feduccia A, Nowicki J. 2002. The hand of birds revealed by early ostrich embryos. Naturwissenschaften 89: 391–393.

Feduccia A. 2012. Riddle of the Feathered Dragons. Yale University Press.

Foth C, Tischlinger H, Rauhut OWM. 2014. New specimen of Archaeopteryx provides insights into the evolution of pennaceous feathers. Nature 511: 79–82.

Heilmann G. 1926. The Origin of Birds. Witherby.

Huxley TH. 1868. On the animals which are most nearly intermediate between birds and reptiles. Annals and Magazine of Natural History 2: 66–75.

Huxley TH. 1870. Further, evidence of the affinity between the dinosaurian reptiles and birds. Quarterly Journal of the Geological Society of London 26: 12–31.

Lingham-Soliar T. 2003a. Evolution of birds: Ichthyosaur integumental fibers conform to dromaeosaur protofeathers. Naturwissenschaften 90: 563–567.

Lingham-Soliar T. 2003b. The dinosaurian origin of feathers: Perspectives from dolphin (Cetacea) collagen fibers. Naturwissenschaften 90: 563–567.

Maryanska T, Osmolska H, Olson SL. 2002. Avialan status for Oviraptorosauria. Acta Palaeontologica Polonica 47: 97–116.

Mitchell KJ, Llamas B, Soubrier J, Rawlence NJ, Worthy TH, Wood J, Lee S-MY, Cooper A. 2014. Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite origins. Science 346: 1253293.

Naish D. 2012. Birds. Pages 379–423 in Brett-Surman MK, Holtz TR Jr, Farlow JO. The Complete Dinosaur, 2nd ed. Indiana University Press.

Olson SL, Feduccia A. 1979. Flight capability and the pectoral girdle of Archaeopteryx. Nature 278: 247–248.

Ostrom JH. 1969. Osteology of Deinonychus antirrhopus, an Unusual Theropod from the Lower Cretaceous of Montana. Peabody Museum of Natural History, Yale University. Bulletin of the Peabody Museum of Natural History no. 30.

Padan K, Chiappe LM. 1998. The origin and early evolution of birds. Biological Reviews 73: 1–42.

Paul GS. 1988. Predatory Dinosaurs of the World. Simon and Schuster.

Paul GS. 2002. Dinosaurs of the Air. Johns Hopkins University Press.

Paul GS. 2016. The Princeton Field Guide to Dinosaurs, 2nd ed. Princeton University Press.

Prum R. 2002. Why ornithologists should care about the theropod origin of birds. Auk 119: 1–17.

Smith NA et al. 2015. Rhetoric versus reality: A commentary on “Bird Origins Anew” by A. Feduccia. Auk 132: 467–480.

Wiens JJ, Chippendale PT, Hillis DM. 2003. When are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. Systematic Biology 52: 501–514.

Xu X, Zhou Z, Wang X, Kuang S, Zhang F, Du X. 2003. Four-winged dinosaurs from China. Nature 421: 335–340.

Xu X, Zhou Z, Dudley R, Mackem S, Choung C-M, Erickson GM, Varricchio DJ. 2014. An integrative approach to understanding bird origins. Science 346: 1253293.

FRANCES C. JAMES

Frances C. James (james@bio.fsu.edu) is a professor emerita at the Department of Biological Science at Florida State University

doi:10.1093/biosci/biab060