

Avian origins revisited

The recent discovery of the fossil dinosaur *Microraptor*, in which all four limbs are endowed with feathers that are shaped like flight-feathers with asymmetrical vanes (Xu *et al* 2003), and the analysis, a week earlier, of “wing-assisted incline running” by galliform birds (Dial 2003) are exciting contributions towards a more complete understanding of present and past organismal biodiversity. But this was not the reason why both articles received more than their share of media attention. Both articles asserted, as had many before, that they were providing evidence that would help solve a central part of the current controversy surrounding the evolutionary origin of birds.

Xu *et al* (2003) interpreted the bird-sized, 77 cm long *Microraptor gui* as a dinosaur with flight feathers along the forelimbs, hindlimbs, and tail that formed airfoils enabling *Microraptor* to glide from tree to tree. Based on these morphological data and functional inferences, Xu *et al* (2003) see *Microraptor* as representing an intermediate stage between a flightless, bipedal non-avian theropod dinosaur and an arboreal volant bird capable of flapping flight. Dial (2003), in contrast, observed living chukar partridges assisting their bipedal walk on inclined surfaces by flapping their wings. From these observations, he conjectured that flying birds might have evolved from a bipedal, cursorial dinosaur ancestor by passing through an intermediate organism that used wing-flapping to climb into trees. Xu *et al* (2003) and Dial (2003) both accept that dinosaurs are the ancestors of modern birds, but otherwise stand on opposite sides of the current controversy concerning the evolution of feathers, avian flight, and birds. Xu *et al* (2003) assume that birds and avian flight evolved from an arboreal ancestor that was able to glide; they support the “trees-down” version of avian evolution. Dial (2003), in contrast, assumes that birds and avian flight evolved from a cursorial ancestor that was able to lift off the ground by flapping its forelimbs; he supports the “ground-up” version of avian evolution.

At first view, the controversy concerning the origin and evolution of feathers, avian flight, and birds may be seen as a model for how science works: Competition between proponents of opposing hypotheses leads to a winning theory by majority vote of the scientific community. This image seems to be so compelling that news media started to cover the evolving scientific drama about a decade ago (for some recent examples, see Gorman 2003; Meek 2003; Wilford 2003). But is this image a realistic representation of how macroevolutionary questions are, or should, be addressed and solved? And why was the study by Tobalske *et al* (2003) not also highlighted by the media, even though it was published in the same issue of the journal *Nature* as the article by Xu *et al* (2003), and even though it analysed the relationships between a bird’s morphology, flight style, wing beat frequency, power output, and flight velocity? Could the reason be that the paper by Tobalske *et al* (2003) did not mention explicitly its relevance, ultimately, for a better understanding of the evolutionary origin of avian flight?

In the last 150 years, our understanding of the evolutionary history of birds has made enormous strides. When Darwin published his theory in 1859, birds were viewed as a clearly delimited vertebrate class that was as different from the other tetrapod classes as those are from fish-like vertebrates. Feathers and wing-like forelimbs set birds apart from all vertebrates to such a degree that it was far-fetched to conceive a reptilian ancestry for birds. Then, in 1861, the first fossil feather and, shortly thereafter, a fossil bird, *Archaeopteryx*, with feathers preserved *in situ*, were discovered from Jurassic deposits (e.g. Bühler and Bock 2002). This fossil was hailed as a “missing link” that had been predicted by Darwin’s theory, as it clearly comprised avian as well as reptilian characteristics. And almost immediately, two opposing theories emerged concerning the evolutionary origin of birds, namely an origin either from a cursorial dinosaurian ancestor or from a gliding arboreal reptilian ancestor (Bowler 1996). Subsequent discoveries of dinosaurian and reptilian fossils, as well as an expansion of studies of avian anatomy and biology, led to a first coherent evolutionary scenario (Heilmann 1927)

of avian origin based on a comprehensive review of data from disparate disciplines. The next major synthesis took place in Eichstätt, Germany, roughly six decades later (Hecht *et al* 1985). Since then, there has been a flood of new discoveries of fossil theropod dinosaurs and birds; of functional-morphological studies of the flight apparatus, respiratory system, and integument of birds; and of experimental-developmental and molecular studies of feathers (see, e.g. Feduccia 1996; Chatterjee 1997; Dingus and Rowe 1998; Shipman 1998; Maderson and Homberger 2000; Gauthier and Gall 2002; Zhou and Zhang 2002).

The task of synthesizing the enormous amount of the literature that is relevant to the question of avian evolution has become increasingly challenging, because it requires expertise in a broad range of biological, physical and chemical disciplines. This integrating task, however, is necessary, because it is part of the testing of macroevolutionary theories by checking the compatibility of their component hypotheses with one another and with the various observations and facts. Such a synthesis reduces the number of plausible hypotheses by culling those that are incompatible with facts and other tested hypotheses. Today, one may have the impression that this task has already been accomplished, as the controversy surrounding the evolutionary origin of feathers, avian flight, and birds is usually portrayed as involving only two theories – the “trees-down” and the “ground-up” theories. In reality, however, the controversy is much more complex – and interesting.

Macroevolutionary theories consist of numerous hypotheses, each of which deals with particular aspects of the morphology, biology, and environment of the organisms, whose evolutionary history is being reconstructed. So far, a large number of plausible hypotheses have been proposed to explain particular steps in the evolutionary history from a featherless tetrapod reptilian ancestor to extant bipedal, volant birds. These component hypotheses, however, need to be consistent with one another and with all the relevant observations and data. The remaining challenge, thus, is to create a biologically realistic evolutionary scenario that describes how mechanically and biologically coherent organisms may have interacted in particular ways with their presumed environment and may have changed gradually under the influence of a particular, realistic selective regime. In essence, this process of scenario building is an application of the known principles of Darwinian evolution.

Most of the currently available plausible hypotheses pertaining to the origin and evolution of birds have not yet been tested rigorously. But even more worrisome is the fact that many of the premisses that underlie these hypotheses have rarely been questioned. Two examples may suffice to illustrate this point. One of the premisses asserts that complex structures are statistically unlikely to have arisen more than once, and it underlies the idea that all vertebrates that possess feather-like integumentary appendages must have descended from a single ancestor. This premiss, however, has been shown to be unjustified in numerous cases, such as the presence of complex eyes in cephalopods and vertebrates, electroreceptive organs in sharks and the duck-billed platypus, batrachotoxins in South American poison-dart frogs and certain New Guinean birds, and, as the latest example, wings in stick insects (Whiting *et al* 2003). It appears that this premiss may have induced Xu *et al* (2003) and Prum (2003) to interpret the newly described four-winged dinosaur as an intermediate stage between an unfeathered four-legged ancestor and a bipedal two-winged bird, instead of considering the possibility that it may be a representative of a separate lineage that had evolved feathered wings and aerial locomotion independently from the lineage that eventually led to modern birds.

Another premiss assumes that structural similarities are expressions of homology and, hence, common ancestry. This premiss is heavily dependent on the previous premiss and, therefore, shares its limitations. Its general validity is further weakened by the fact that structural similarities among organisms are often a result of similar selective regimes. Actually, the existence of convergent, or homoplastic, structures in different organisms is perhaps the strongest piece of evidence supporting the theory of evolution through natural selection. Xu *et al* (2003) unwittingly exemplify this interpretation of similarity by using the asymmetrical wing feathers as evidence for the gliding capacity of *Microraptor*, based on the observation that only volant species among extant birds have asymmetrical wing feathers (Feduccia and Tordoff 1979). The premiss that similarity equates homology is still further weakened by the fact that certain structural similarities are the result of neither common ancestry nor similar selective regimes (Homberger 2001). For example, the presence of filamentous “hairlike” integumentary appendages forming the “beard”, or “brush”, of turkeys is evidence neither for common ancestry of mammals and birds, nor an indication of a similar role for

the beards in turkeys and goats. Even more importantly, the presence of filamentous integumentary appendages in birds should serve as a warning against interpreting filamentous structures in fossil dinosaurs simply as precursors of feathers. Another example of non-homologous, non-convergent structural similarities are many of the extreme feather types (e.g. curly, hairlike or excessively elongated feathers) that can be observed in unrelated domesticated birds, such as chickens, ducks, and parakeets (Bartels *et al* 1992). Consequently, the mere existence of branched, but otherwise variable integumentary appendages may not be as strong an evidence for common ancestry between dinosaurs and birds as has been claimed.

Even more problematic is the interpretation of similarities in behavioural traits, such as flight modes and locomotory patterns (e.g. Dial 2003), unless the underlying morphology has been analysed. Wing-assisted incline running has been known for other bird species, such as the Gymnogenes and Streaked Shearwaters, which are not closely related to one another or to galliform birds (Homberger 2002) and whose wing structures differ significantly from one another. Just because “wing-assisted incline running” looks like a plausible intermediate stage between running on a plane field and taking off from a tree branch does not necessarily make it a biologically realistic model for an ancestral stage from which avian flight might have evolved. Avian flight is highly variable and includes a variety of flight modes, such as gliding, soaring, flapping, flap-gliding, and flap-bounding, each of which being a function of body size, ecology, or past evolutionary history (Homberger 2002). This is the reason, why studies of the diversity of avian flight (e.g. Tobalske *et al* 2003) are relevant to the question of the evolution of avian flight, because they provide data that need to be considered when creating a biologically realistic scenario of the evolution of birds.

Hence, in order to clarify the evolutionary history of birds from unfeathered reptilian ancestors, it will be necessary not only to continue to gather new data and observations that can test earlier studies, but also to revisit some of the premisses that provide the theoretical framework guiding the interpretation of these data and observations. Currently, too little attention has been devoted to theoretical aspects of macroevolutionary questions. As long as this remains the case, the current controversy surrounding the evolutionary history of feathers, avian flight, and birds is likely to continue and remain unsolved.

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