Dinosaurs take to the air

Richard O. Prum

Flying birds evolved from a group of bipedal dinosaurs. The latest fossil discoveries from China indicate that the dinosaurian ancestors of birds had four wings — and that these animals glided rather than flapped.

Three questions lie at the heart of the debate about the evolution of birds: the origin of the group itself, the origin of feathers and the origin of flight. Progress in reconstructing the evolutionary history of dinosaurs has established a well-corroborated answer to the first question[1]. Birds are a lineage of dinosaurs, and are most closely related to dromaeosaurs and troodontids, both of which belong to a group of bipedal, carnivorous dinosaurs called theropods. Since 1997, new fossils and insights from developmental biology have also supported a coherent solution to the second question[2]. Feathers evolved in theropod dinosaurs before the origin of birds or flight through a series of developmental novelties. Now (page 335 of this issue), Xu *et al.*[3] report spectacular 124–128-million-year-old fossils from Liaoning, China, that promise to revolutionize discussion of the last question — how did avian flight evolve?

For more than a century, debate on the origin of bird flight has centred on two different hypotheses[4]. According to arboreal theories, flight arose in tree-dwelling creatures through an intermediate gliding stage, an idea that has been supported by the observation that flight is energetically more efficient at higher speeds (when more lift is generated)[5]. Further, the flight stroke in continuous, level flight is simpler than in take-off from the ground. According to the competing, cursorial theories, flight evolved in ground-living animals via a powered running stage. This view is supported by the evidence that birds evolved from a lineage of terrestrial, bipedal theropods, and that many components of the avian flight apparatus evolved originally in a terrestrial context[4]. Moreover, aerodynamic models[6] of the flight stroke of *Archaeopteryx*, the earliest bird accepted as such, indicate that its wings could have provided thrust as well as lift, and aided the legs in achieving enough ground speed for a running take-off.

In a colourful and prescient paper of 1915, however, William Beebe[7] proposed that avian flight evolved through a gliding, four-winged — tetrapteryx — stage with wing feathers on both the arms and the legs. Now Xu and colleagues[3] describe a small dromaeosaur, *Microraptor gui*, that sports four wings of fully modern, asymmetrical feathers on its forelimbs and legs, and looks as if it could have glided straight out of the pages of Beebe's notebooks. Although the specimens of *Microraptor* are younger than those of *Archaeopteryx*, *Microraptor* is a basal member — an early evolutionary branch — of the closest relatives of *Archaeopteryx* and other birds (Fig. 1). In support of the arboreal theory, Xu *et al.* propose that the most recent common ancestor of birds and dromaeosaurs was a four-winged creature that lived in and glided among trees.

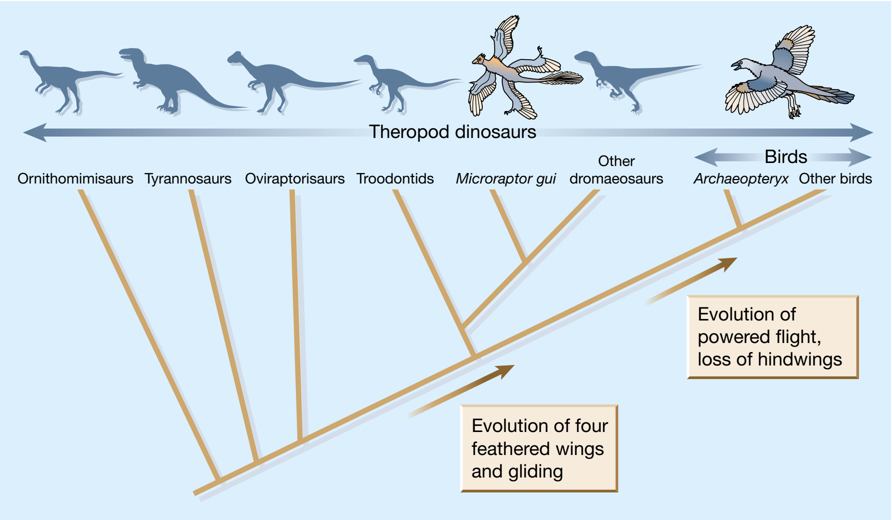

Figure 1 **The origin of birds within the theropod dinosaurs[1]. Xu *et al.*[3] describe a four-winged dromaeosaur, *Microraptor gui*, which they hypothesize glided from tree to tree. They further propose that gliding evolved initially in the four-winged ancestor of the birds, dromaeosaurs, and troodontids. Subsequently, the hindwings were lost with the origin of powered, flapping flight in the ancestor of *Archaeopteryx* and other birds.**

The evidence of an aerodynamic function for *Microraptor*'s forelimb and leg feathers is excellent. Asymmetrical feather vanes have long been recognized as indicating aerodynamic function in flight or gliding. Furthermore, the feathers of both the forewings and the hindwings increase in asymmetry towards the end of the limb in a striking match with the primary and secondary feathers of a modern bird wing. The discovery of dromaeosaur hindwings was presaged last year by the description of 13-cm-long modern, vaned feathers on the tibia of an even larger, unnamed dromaeosaur from Liaoning[8], but that specimen lacked enough detail to describe the entire structure. The long tail of *Microraptor* also features a terminal tuft of feathers like that found on other basal dromaeosaurs[8] and on another theropod, the oviraptoran *Caudipteryx*[9].

The discovery of a logical functional intermediate provides striking support for the arboreal–gliding hypothesis of the origin of bird flight. However, substantial questions remain. In particular, how did *Microraptor* actually use its four wings? Perhaps because flapping hindwings are so unlikely, Xu *et al.* conclude that *Microraptor* merely glided, and did not have a powered flight stroke. Palaeontologists and functional morphologists will be eager to study the shoulder and wing anatomy to judge whether *Microraptor* could sustain powered flight. More information is also required on how the animal could have rotated its legs to deploy its hindwings.

Xu *et al.* maintain that all four wings were present in the earliest ancestors of birds and dromaeosaurs, and that with the evolution of powered flight the hindwings were lost in the avian lineage before the advent of *Archaeopteryx*. It is also possible, however, that the hindwings are a unique feature of dromaeosaurs. Palaeontologists will want to re-examine specimens of *Archaeopteryx* for any evidence of a vestigial hindwing (Beebe found none). Regardless of the upshot of those enquiries, there is no doubt that the forewings of *Microraptor*, *Archaeopteryx* and other birds are homologous and had an aerodynamic function.

Xu *et al.* also argue that the extensively feathered legs of *Microraptor* would have been incompatible with life on the ground. The feathers extend all the way down the leg, much further than they do in Beebe's mythical tetrapteryx. Dragging your wing feathers in the dirt would doubtless be aerodynamically disadvantageous, but it will require detailed reconstructions of *Microraptor*'s hindlimbs with feathers attached to rule out the possibility that it could have walked and run.

Finally, although Xu and colleagues report that *Microraptor* has the anatomical features of a dromaeosaur, firm conclusions about the evolution of bird flight will require new systematic analyses incorporating this and other newly discovered theropod species from Liaoning to confirm their phylogenetic position. Sceptics will argue in any case that *Microraptor* and dromaeosaurs are more closely related to modern birds than is *Archaeopteryx* — but then they will also have to address the problem of why a bird that could flap its wings perfectly well would evolve a second pair of wings.

Birds are traditionally considered to be animals with a difference: that is, to be a distinct vertebrate class despite their origins within the reptiles. But advances in palaeontology, phylogenetics and evolutionary biology have erased the anatomical gap between birds and their dinosaur ancestors[10]. Now that dromaeosaurs have taken to the air, in the form of *Microraptor*, there remain no major traits that are unique to birds — with the possible exception of powered flight. Although some may be irked at this lost distinction, the benefits will be a fuller, more integrated understanding of avian biology. This new evidence of an arboreal, gliding stage in the evolution of bird flight complements the evidence of terrestrial evolution in the theropod dinosaurs. Terrestrial theropod dinosaurs had evolved for millions of years before the ancestors of *Microraptor* and the birds took to the trees or to the air. Moving beyond the arboreal versus cursorial debate over the origins of bird flight[4], the task ahead is to understand which components of the avian flight apparatus evolved in a terrestrial and which in an arboreal context. ■

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Global change

Monsoon linkages

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An excellent sediment record from the Arabian Sea traces recent patterns in the activity of the Asian monsoon. It reveals both variability in monsoon strength and links with climatic events elsewhere.

The monsoon is the main determinant of environmental conditions over much of Asia, and so affects the most densely populated region on Earth. Differential heating of the north Indian Ocean and the northwest Pacific, and of the Asian landmass, cause the seasonal reversal of monsoon winds. In summer, these winds blow northwards over the northern Indian Ocean, carrying huge amounts of moisture over the neighbouring land. The ensuing heavy rainfall can have devastating consequences for human life and livelihood. Conversely, agriculture in Asia depends on monsoon rains; and the seasonal upwelling of nutrient-laden subsurface waters, driven by monsoon winds, is essential to the success of coastal fisheries.

Understanding monsoon history and past dynamics is necessary for improving our knowledge of the monsoon system and how it may respond to changing global conditions. On page 354 of this issue[1], Gupta *et al.* take us a step further down that road. They present a fine-scale palaeoceanographic record, from a marine sediment core from the Arabian Sea, that traces the operation of the Asian monsoon 11,000 years back in time — that is, over the Holocene, the epoch that spans the interval from the end of the last glacial period until the present day.

The record is derived from fluctuations in the abundance of a planktonic organism, a foraminifer, that is known to thrive particularly well in waters that provide an ample supply of food. The link with monsoon intensity is through coastal upwelling, induced by monsoon winds, that stimulates marine biological productivity off Oman, including the growth of this foraminiferal species. Gupta and colleagues' record is particularly valuable because the core comes from a depositional environment in which sediments have accumulated swiftly, so limiting the extent to which burrowing organisms have mixed the sediment column. This record, then, is a very precise one, and the variations in foraminiferal abundance indicate that the Holocene was punctuated by a quasi-periodic recurrence of increased monsoon activity on timescales of 1,000 years.

This picture is supported by oxygen isotope analyses[2] — a part indicator of water temperature — of the same species in a sediment core from the Somali continental margin to the south. The isotope record documents rapid changes in the summer temperature of surface water during the early Holocene, 11,000–6,500 years ago. In turn, both records fit in nicely with isotope analysis[3] of a stalagmite, from Hoti Cave in northern Oman, that likewise indicates much variability in monsoon intensity over that interval.

The work of Gupta *et al.*[1] also takes the record of monsoon variability further into the mid- and late Holocene. They detect continued swings in monsoon intensity, including a notable shift from strong to weak activity during the transition from the Medieval Warm Period (AD 800–1300) to the Little Ice Age (AD 1300–1870). This is confirmed by faunal and organic molecular data from the region[4,5]: monsoon variation, including an increase in strength during the past century or so, is evidently a robust feature of its climatic history.

To add to the excitement, Gupta and colleagues' record shows some resemblance to that seen in the distribution of haematite in Holocene sediments from the North Atlantic. Haematite is believed to be a key indicator of sand debris that was frozen into icebergs and carried across the North Atlantic, and therefore of the rhythmic recurrence of cold spells in the region. A link between cold episodes in the Atlantic and a weakened Asian monsoon has already been documented for the last glacial period, when cold spells — the so-called Dansgaard/Oeschger and Heinrich events — periodically produced arctic conditions in the North Atlantic region[6–8]. The Dansgaard/Oeschger and Heinrich events caused far more dramatic environmental changes than any of the climatic cycles in the Holocene, so their influence on climatic regimes well beyond the Atlantic region is not surprising. Remarkably, however, the findings of Gupta *et al.* indicate that this linkage continued into and throughout the current warm period of the past 11,000 years, even though the climatic anomalies have been far smaller.

The monsoon system does not operate in isolation, of course. It is only one of many participants in the global dance of climate oscillators and dipoles (see Box 1), and many of these climatic regimes have evidently undergone rapid swings during the Holocene[9–11]. Following the initial appearance of ice-core palaeoclimate records from Greenland, a belief that climate has been highly stable during the Holocene briefly fluttered through the scientific community.