ORIGIN OF FLIGHT

Could 'four-winged' dinosaurs fly?

Arising from: X. Xu *et al.* *Nature* 421, 335–340 (2003); F. Zhang & Z. Zhou *Nature* 431, 925 (2004)

Our understanding of the origin of birds, feathers and flight has been greatly advanced by new discoveries of feathered non-avian dinosaurs, but functional analyses have not kept pace with taxonomic descriptions. Zhang and Zhou describe feathers on the tibiotarsus of a new basal enantiornithine bird from the Early Cretaceous of China[1]. They infer, as did Xu and colleagues from similar feathers on the small non-avian theropod *Microraptor* found in similar deposits[2], that these leg feathers had aerodynamic properties and so might have been used in some kind of flight.

Claims that these were 'four-winged' dinosaurs that took to the air require investigations using independent lines of evidence, which was done by neither team of authors. There is no evidence to confirm the existence of a four-winged stage that involved feathers on the hindlimbs and that could have been an intermediate between feathered, ground-dwelling theropods and aerial birds.

First, the long leg feathers in question are said to preserve either asymmetrical vanes[2] or little asymmetry but curved shafts[1], from which the authors infer that these feathers had a residual aerodynamic function[1]. Neither feature indicates a function in lift or thrust (and therefore in flight). It has been suggested[3] that both features are functionally correlated to flight, but the connection is not causal. Asymmetrical feathers resist torsion, and both features slightly reduce drag, which would be useful to a running animal with long feathers but would make no difference at realistic running speeds. Small non-avian theropods were good runners, but there is no evidence as yet that they flew.

Second, no evidence[1,2] of how the feathers were attached to the hindlimb has been documented, so there is no indication that the feathers could have supported an aerodynamic load.

Third, Xu *et al.*[2] offer no support for their statement that the hindlimbs (and therefore the inferred 'hindwing') of *Microraptor* extended laterally like those of bats, but unlike those of any bird or other theropod dinosaur. Furthermore, no explanation is given of how the leg could have been raised and extended into the lateral plane without dislocating the hip joints. Their remarkable assertion that the tibia of *Microraptor* is 'bowed' is also unsupported, and this is more likely to be the result of being crushed and of crossing other preserved bones. Even a revised posture of the hindlimbs does not mitigate the case for 'four-winged gliding' — it would also have to be subjected to functional tests.

Fourth, the proposed function of leg feathers in flight is unknown in birds of today, and the necessary structural modifications are not present in these extinct animals or in their relatives; therefore, the inferences drawn by the authors have no support from either the extinct or extant phylogenetic brackets[4]. Because leg feathers first appeared in non-flying theropods[2], some of considerable size, their original function was not in flight, and no flight-related explanation for their presence in basal birds is necessary[5]. Long leg feathers are found in owls and grouse, and in nearly all raptors[6]: as with the feathers in these extinct forms, these are long, vaned and nearly symmetrical, but they have no demonstrated role in flight.

Fifth, the analogy that the authors draw[1] between the use of webbed feet in kittiwakes as airbrakes and the extension of the hindlimbs in rapidly descending vultures[1] is inappropriate: the first example induces drag, and the second relocates the centre of mass as the bird increases the angle of attack of the wings. Neither function uses or requires leg feathers, or produces lift. To be useful in flight, the advantage to lift must outweigh the disadvantage of drag.

Sixth, the authors should have calculated the mass, wing area, centre of mass and the centre of lift that would have been necessary to test whether the reconstruction of *Microraptor* was likely to be able to glide[2]. Such basic calculations must precede any assertion about gliding ability.

Most important, none of the evidence reported by the authors[1,2] should have been advanced as support for an 'arboreal' origin of bird flight. It is recognized that the arboreal versus cursorial dichotomy of models for the origin of bird flight is not capable of resolution and should have been abandoned long ago[7,8]. Rather, the origin of the flight stroke is the central problem in the origin of flight, and so far nothing has been brought to light to indicate that *Microraptor* has any bearing on this question. Functional inferences should be based on functional studies, not just on analogies[9]. Ideas about arboreality should hinge on more than toe and claw proportions, and ideas about gliding on more than the profile of leg feathers.

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1. Zhang, F. & Zhou, Z. *Nature* **431,** 925 (2004).
2. Xu, X. *et al.* *Nature* **421,** 335–340 (2003).
3. Feduccia, A. & Tordoff, H. B. *Science* **203,** 1021–1022 (1979).
4. Witmer, L. D. in *Functional Morphology in Vertebrate Paleontology* (ed. Thomason, J. J.) 19–33 (Cambridge Univ. Press, 1995).
5. Gould, S. J. & Vrba, E. S. *Paleobiology* **8,** 4–15 (1982).
6. Perrins, C. M. *The Illustrated Encyclopedia of Birds* (Prentice Hall, New York, 1990).
7. Padian, K. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. A. & Gall, L. F.) 255–272 (Yale Univ. Press, New Haven, 2001).
8. Dial, K. P. *Science* **299,** 402–404 (2003).
9. Padian, K. *Am. Zool.* **41,** 598–607 (2001).

doi:10.1038/nature04354

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Xu et al. *reply*

Replying to: K. Padian & K. P. Dial *Nature* 438, doi:10.1038/nature04354 (2005)

We agree that a strict biomechanical analysis is needed to reconstruct *Microraptor*'s locomotory mode, but we disagree with several of Padian and Dial's arguments[1]. In addition to the six *Microraptor* specimens we described[2], other similarly preserved specimens[3] have been discovered that also had long, asymmetrical pennaceous feathers attached to the hindlimbs[2]. These feathers show features that are functionally correlated with flight[4]. A large, feathery surface on the legs would increase, rather than decrease[1], drag during running, as evidenced by the reduced or lost filamentous integumentary structures on the lower legs of cursorial birds and mammals.

We have proposed a possible flight posture for *Microraptor*[5], in which the hindlimbs stretch posteriorly, avoiding dislocation of the femur from the hip joint and maintaining consistency with the parasagittal posture of hindlimbs among dinosaurs: the hindlimb and tail feathers together form an aerofoil that provides a lift-surface, and the front wings supply the other lift-surface and generate thrust. We drew no functional inference from the bowed tibia[2,5].

Padian and Dial have overlooked a fundamental difference between the long leg feathers of *Microraptor* and those of some living birds. The former are asymmetrical and have an arrangement similar to the flight feathers in the wings of flying birds[2], whereas the latter are bunched pennaceous feathers without aerodynamic modification. These functionally different structures are unsuitable for analysis by the extinct or extant phylogenetic bracket method.

The flight apparatus of *Microraptor*, such as the elongate, robust winged arms capable of flapping flight, is almost identical to that of *Archaeopteryx*. Some flight-related features, such as the large sternum and the relatively long flight feathers (compared with the forelimbs) are more developed in *Microraptor*. Assertions that *Microraptor* was non-flying on the basis of its non-avian status are unfounded without biomechanical analysis.

It is unwise to rely on the highly modified features of extant animals to deduce the behaviour of an ancient relative, without considering the basal taxon's morphology. For example, there was a stage in their evolution when whales had hindlimbs with large feet that functioned as flippers in the aquatic environment, before they became smaller and were eventually lost[6]: without discovery of these basal forms, the extinct or extant phylogenetic bracket method would have predicted a different evolutionary pathway.

The systematic position of *Microraptor* as a close relative of birds and its possession of nearly all the flight features of basal birds make it ideal for studying the origin of flight, including the origin of the flight stroke. We disagree with Padian and Dial[1] that the arboreal versus cursorial debate is dead: either hypothesis could be accepted or rejected based on whether protoavians take advantage of gravity when taking off, which could be tested against a biomechanical analysis. *Microraptor*, which provides negative evidence for the cursorial hypothesis[2], could have taken to the air[7] according to our recent biochemical analysis. Moreover, a new maniraptoran of the avian lineage has long metatarsalian feathers, indicating that hindwings may have been a common adaptation during the dinosaur–bird transition[8]. This unusual morphology should not be ignored in the study of the origin of flight, particularly as it bears distinct aerodynamic features and occurs phylogenetically close to the origin of birds.

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1. Padian, K. & Dial, K. P. *Nature* **438,** doi:10.1038/nature04354 (2005).
2. Xu, X. *et al. Nature* **421,** 335–340 (2003).
3. Ji, Q. *et al.* in *The Mesozoic Jehol Biota in Western Liaoning, China* 1–373 (Geology Press, Beijing, 2004).
4. Feduccia, A. & Tordoff, H. B. *Science* **203,** 1021–1022 (1979).
5. Xu, X., Zhou, Z., Zhang, F., Wang, X. & Kuang, X. *J. Vert. Paleontol.* **24** (suppl.), 133A (2004).
6. Thewissen, J. G. M., Hussain, S. T. & Arif, M. *Science* **263,** 210–212 (1994).
7. Dyke, G. J., Nudds, R. M., Rayner, J. M., Norell, M. & Xu, X. *Proc. R. Soc. Lond. B* (submitted).
8. Xu, X. & Zhang, F.-C. *Naturwissenschaften* doi:10.007/s00114-004-0604-y (2005).

doi:10.1038/nature04355

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Zhang & Zhou reply

Replying to: K. Padian & K. P. Dial *Nature* 438, doi:10.1038/nature04354 (2005)

Padian and Dial[1] challenge our view that the evolution of flight involved a four-winged stage. This disagreement stems from our different views on the origin of bird flight and from the methodology we use to analyse functional morphology in the non-avian theropod *Microraptor*[2] and in an enantiornithine bird[3] from the Early Cretaceous period in China.

Although the wing produced the main force for lift and thrust in the new enantiornithine bird, the curved shaft and asymmetric vanes of the leg feathers indicate that they could still produce some lift and thrust, as well as reducing drag. The arboreality of this bird is indicated by the curvature of the pedal claws and toe proportions[4]. It is not self-evident that small non-avian theropods were good runners: indeed, some of them may actually have been arboreal[5,6].

Contrary to Padian and Dial's assertions[1], attachments of leg feathers to the external side of the leg bones (tibia or metatarsals) have now been documented not only in *Microraptor gui* but also in *Archaeopteryx*[7], *Confuciusornis*[8] and several enantiornithine birds[3,8], which would have enabled them to be extended into the lateral plane to produce some lift.

Padian and Dial argue that there is no evidence for a four-winged stage in flight origin. Leg feathers first appeared in non-flying theropods, which may have conferred some aerodynamic advantage, judging by their asymmetry and by the presence of an alula in the forelimb. So the original function of leg feathers might have been for gliding. We agree with Padian and Dial that these feathers were probably not used for active flight in *Microraptor* or in early birds. Although long leg feathers are found (but not to assist flight) in many living birds, these do not show the asymmetry or curved shaft indicative of aerodynamic properties.

The absence of aerodynamic function in leg feathers in modern birds does not mean that it did not exist in their ancestors. Reduction of drag is probably one of the main functions of the leg feathers in *Microraptor* and early birds, and modern birds such as kittiwakes use the leg feathers on their extended hindlimbs as well as their webbed feet for this purpose.

Although we believe that leg feathers had some aerodynamic function in *Microraptor* and that this was weaker in early birds, they were probably not the main flight apparatus. However, their role in the origin of bird flight should not be ignored — functional inferences should be based mainly on functional studies, not on phylogenetic brackets[9].

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1. Padian, K. & Dial, K. P. *Nature* **438,** doi:10.1038/nature04354 (2005).
2. Xu, X. *et al. Nature* **421,** 335–340 (2003).
3. Zhang, F. & Zhou, Z. *Nature* **431,** 925 (2004).
4. Zhou, Z. & Farlow, J. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 237–254 (Yale Univ., New Haven, 2001).
5. Xu, X., Zhou, Z. & Wang, X. *Nature* **408,** 705–708 (2000).
6. Zhang, F., Zhou, Z., Xu, X. & Wang, X. *Naturwissenschaften* **89,** 394–398 (2002).
7. Christiansen, P. & Bonde, N. *C. R. Palevol.* **3,** 99–118 (2004).
8. Zhou, Z. & Zhang, F. *Vertebrata PalAsiatica* (in the press).
9. Zhou, Z. *Naturwissenschaften* **91,** 455–471 (2004).

doi:10.1038/nature04356