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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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