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 birds², 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 lost⁶: 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 Dial¹ 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 hypothesis², could have taken to the air⁷ 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 transition⁸. 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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ORIGIN OF FLIGHT

Zhang & Zhou reply

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

Padian and Dial¹ 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 bird³ 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 proportions⁴. 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 assertions¹, attachments of leg feathers to the external side of the leg bones (tibia or metatarsals) have now been documented not only in *Microraptor* but

also in *Archaeopteryx*⁷, *Confuciusornis*⁸ and several enantiornithine birds^{3,9}, 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 brackets⁹.

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