Dispatches

Evolution: Taking Wing with Weak Feathers

Scientists long thought they knew what the wings of early birds looked like. But new reconstructions of *Archaeopteryx* and its kin suggest quite different feather arrangements on their wings with profound implications for the evolution of flight.

Xing Xu

Archaeopteryx is an icon of evolution. With feathers, toothed jaws and a long bony tail, *Archaeopteryx* represents a truly transitional form [1]. However, a close look at the various specimens of *Archaeopteryx* reveals some surprisingly modern features, such as the asymmetric form of the flight feathers, in this 150-million-year-old bird. In fact, the flight feathers of *Archaeopteryx* were traditionally considered very similar to those of modern birds in shape, arrangement, and distribution on the body, implying that the feathery wing has remained essentially the same in structure since the appearance of the earliest known birds [1–3]. However, several recent studies [4–7], including one by Nicholas Longrich and colleagues in this issue of *Current Biology* [8], demonstrate that the flight feathers of *Archaeopteryx* and its kin are different from modern ones in all these respects, and distinctly transitional.

Early Wings

Birds (the Avialae) are a group of feathered animals with a unique body-plan adapted to flight. As the earliest known bird, *Archaeopteryx* has many flight-related features, including flight feathers, long and robust arms, and modified shoulder girdles allowing the arms to move laterally. Interestingly, all of these features, even flight feathers, are now seen in theropod dinosaurs, and in particular, in the birds' closest relatives, the Deinonychosauria [6].

Living birds share a common basic wing configuration: a row of long flight feathers form the main part of the wing, and several rows of much shorter feathers (coverts) provide limited additional support [9]. *Archaeopteryx* has been widely accepted to have had feathery wings with this modern configuration [1–3], which is somewhat surprising given the otherwise transitional status of this taxon. Nevertheless, the traditional reconstruction has generally been considered reliable because it is based on exceptionally-preserved feather impressions [10], although the seemingly modern nature of the wing plumage once prompted a suggestion that the feather impressions were in fact nineteenth-century forgeries [11]. This suggestion was never supported by substantive evidence, but the fact remains that reconstructions of an essentially modern feathery wing in *Archaeopteryx* seem out of step with the transitional evolutionary position of this ancient bird.

Having closely examined two *Archaeopteryx* specimens, Longrich and colleagues [8] believe that *Archaeopteryx* does have a transitional feathery wing (Figure 1). Instead of being mostly single-layered like modern wings, the wings of *Archaeopteryx* wings are multi-layered, the additional layers being formed by elongated coverts. Interestingly, this unusual wing configuration is also present in *Anchiornis*, a recently-reported Jurassic *Archaeopteryx*-like dinosaur [7]. Longrich and colleagues [8] suggest that the multi-layered configuration represents a primitive stage in wing evolution.

Longrich and colleagues' hypothesis casts new light on the results of an earlier study [4] that examined the flight feathers of *Archaeopteryx* from the perspective of functional morphology. This study found the shafts of the flight feathers of *Archaeopteryx* to be proportionally too slender to have the strength needed for flight, assuming that the traditional wing reconstruction was roughly correct [4]. Under Longrich and colleagues' interpretation, the presence of multiple feather layers compensates for the weakness of the individual feathers, allowing *Archaeopteryx* to have a strong wing even without strong flight feathers. So, quantity makes up for lack of quality.

Interestingly, *Archaeopteryx* not only evolved an unusual feather arrangement, but also had more than two wings for flight. The discovery of the four-winged dinosaur *Microraptor* [6] inspired Nicholas Longrich to re-examine *Archaeopteryx* fossils in another study, which led to the suggestion that *Archaeopteryx* also had wings on the hind legs, a feature not known in modern birds [5]. The slender-shafted flight feathers of *Archaeopteryx*, as well as the large, wing-forming leg feathers and now the multi-layered configuration of the arm wings, all demonstrate that the flight plumage of *Archaeopteryx* was significantly different from that of modern birds [4–8].

Early Flight

Inferring the flight capability of a transitional fossil species is a challenging task. Some studies, e.g. [12], have suggested that *Archaeopteryx* was indeed able to fly, based on such morphological features as the presence of flight feathers with asymmetrical vanes. However, other studies [4,13] have questioned the flight capability of *Archaeopteryx* based on different lines of evidence. Much of this debate reflects the fact that different researchers use different features to infer flight capability. Given the complex pattern of morphological evolution seen across the dinosaur-bird transition [14], the diversity of opinion is not surprising. Longrich and colleagues' study [8] shows how new observations can sometimes alter the significance of old ones, helping to integrate them into a more coherent understanding of the early evolution of flight.

The relatively weak-looking flight feathers of basal birds [4], then, do not necessarily suggest that flight capability was poor, let alone entirely absent. Early birds and their close relatives could assemble an effective flying wing using multiple rows of relatively weak feathers, as demonstrated by Longrich's analysis of specimens of *Archaeopteryx* and *Anchiornis* [8]. However, Longrich and colleagues [8] also note that the multi-layered wing lacks a distally slotted configuration, a feature that reduces induced drag during flight [15] and is particularly important at slow speeds. This suggests that high-speed flight was a preferred mode of flight in *Archaeopteryx* and its relatives. A strength of this inference is that it is based on a comprehensive analysis of the relevant available data rather than a single feature.

The early history of flight is highly complex. As Longrich and colleagues [8] point out, flight capability is likely to have evolved independently on multiple occasions among *Archaeopteryx* and its kin. For example, flight feathers with asymmetrical vanes seem to have evolved independently at least twice near the dinosaur-bird transition, once near the base of the Avialae and once in the deinonychosaurs [8]. *Archaeopteryx* and its kin also have wings of varying shapes. The arm wings of *Microraptor* seem to be proportionally narrower than those of *Archaeopteryx* and *Anchiornis*, and the leg wings of *Archaeopteryx* and its kin are highly variable in morphology [5–7,10]. These data suggest that early flight was probably not uniform, and that any simple scenario for the early evolution of flight will likely be inadequate.

Our understanding of how feathered dinosaurs close to the origin of birds built their wings, and of how they got into the air, has improved greatly in recent decades. However, there are many issues yet to be addressed. First of all, a better understanding of the range of feather morphologies present in taxa near the dinosaur–bird transition is particularly important. The flight feathers of the earliest known birds and their close relatives are, in general, similar to those of modern birds [16,17]. However, there are also various differences between early and modern flight feathers in development, morphology, fine-scale arrangement, and large-scale distribution on the body [4,5,8,18]. It will be necessary in the course of future research to undertake more extensive and detailed investigations of these differences, and to search for additional ones. An obvious priority will be to study the arrangement of the flight feathers in other transitional forms such as *Xiaotingia* and *Microraptor*, as well as in more basal taxa such as *Caudipteryx* [8].

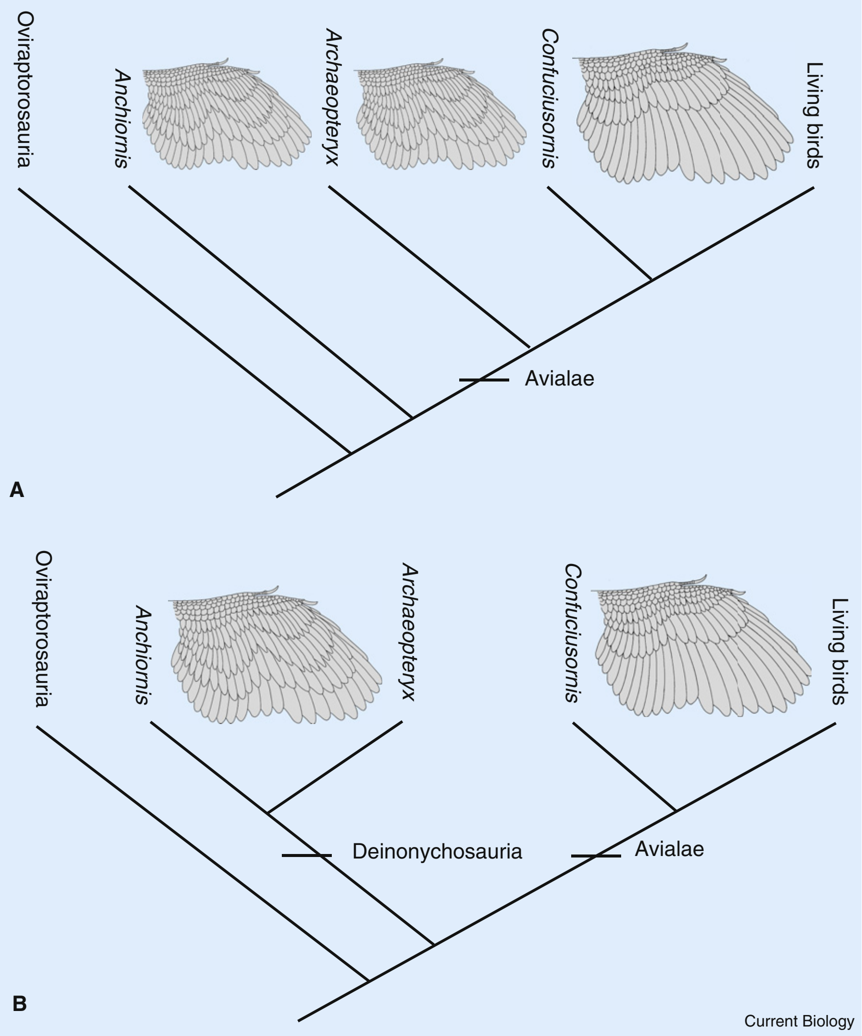

Figure 1. Different scenarios for the evolution of bird wings.
The multi-layered wings of *Archaeopteryx* and *Anchiornis* could represent a transitional stage in the evolution of modern wings (A) or a dead-end experiment in early flight evolution (B).

Any credible evolutionary scenario must be built within a firm phylogenetic framework. In this case, an accurate theropod phylogeny will provide the basis for reconstructing the dinosaur-bird transition, and the systematic position of *Archaeopteryx* plays a key role in interpreting the evolutionary history of avian wings [14]. If *Archaeopteryx* is an early representative of the bird lineage, as suggested by most phylogenetic studies [19,20], the unusual wings of this taxon are best explained as an intermediate stage in wing evolution (Figure 1A). However, if *Archaeopteryx* and *Anchiornis* lie in Deinonychosauria, a side-branch in bird evolution, as suggested by a recent phylogenetic study [14], their multi-layered wings are likely to be unique to the Deinonychosauria [8] or an even more exclusive group and are more likely to represent an evolutionary dead end (Figure 1B). The wings of *Archaeopteryx* and its kin are very complex and highly variable, and this was probably also true of the early evolution of flight.

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Institute of Vertebrate Paleontology and
Paleonanthropology, Key Laboratory of
Evolutionary Systematics of Vertebrates,
Chinese Academy of Sciences,
142 Xiwai Street, Beijing, 100044, China.
E-mail: xuxing@ivpp.ac.cn

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Neuroscience: A More Dynamic View of the Social Brain

Information relevant for social interactions is thought to be processed in specific neural circuits. Recent studies shed new light on how that social information is encoded and processed by different brain areas.

J. Sallet[1], R.B. Mars[1,2], and M.F.S. Rushworth[1,2]

Human and non-human primates are social animals and living in complex social environments has an impact on brain structure and function [1–3]. Social information is thought to be processed by a specific set of neural circuits often referred to as the ‘social brain’ [4–6]. How social information is encoded and the nature of the computations performed by different brain areas is nevertheless still debated. Papers in this issue of *Current Biology* by Watson and Platt [7] and Santiesteban *et al.* [8], focusing on the orbitofrontal cortex (OFC) and the temporo-parietal junction (TPJ), respectively (Figure 1), begin to unpick some of these issues. These two studies nicely complement recent observations on the roles of the OFC and TPJ from other laboratories [9,10]. Altogether, the results suggest that the context in which a social decision is taken strongly affects how the information is processed, suggesting a quite dynamic view of how social information is encoded and used by the social brain.

In their study, Watson and Platt [7] presented macaque monkeys with a simple decision-making task in which they could sacrifice juice to watch social images — pictures of other animals of various social statuses or pictures of female macaque perinea that male macaques appear to find intrinsically interesting. They found that neural activity in the OFC is modulated by both social and reward information, but most of the OFC neurons that show such modulated activity are *either* sensitive to reward *or* to social information [7]. This is one of the first tests of OFC single neuron activity in the social domain, but the result is broadly in line with previous reports that only a small proportion of OFC neurons multiplex values across reward dimensions [11].

It is interesting to compare the results of the Watson and Platt study [7] with those from the one other recent investigation of single neuron activity in OFC during social cognition. Azzi *et al.* [9] taught monkeys a simple oculomotor task in which their choices could lead to rewards either for just themselves or for a second animal too. The authors argue that the receipt of a reward by the second macaque apparently diminishes the value of rewards received by the first macaque. They found that lateral OFC neurons also reflect this apparent diminution of the reward value for the experimental animal when rewards are simultaneously given to another macaque. In other words, Azzi *et al.* [9] report the consequences of integrating both social and reward information in the firing rates of individual OFC neurons.

These two studies, by Watson and Platt [7] and by Azzi *et al.* [9], can be seen to be complementary if one remembers that, in order to be able to learn the links that exist between choices and their outcomes, it is crucial to compute not only the scalar values of choice outcomes but also the identities of choice outcomes [12,13]. In other words, it is not just important whether an outcome is rewarding, but it is important to know what type of reward it is. One of the other key results reported by Watson and Platt [7] is the observation of a strong modulation of OFC activity by social categories (images with a dominant animal, a subordinate animal or with sexual content) — just what would be needed if the monkey is to learn about the precise category of outcome that is to be expected from a choice.

But while it is essential to understand the identity of the outcome that is expected from a choice, it is also important to be able to compare the values of different outcomes on a single