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Dinosaur Evolution: Feathers Up for Selection

A new specimen of the early bird *Archaeopteryx* shows remarkable plumage preservation, including pennaceous leg feathers. But whether birds went through a four-winged stage, and in what exact functional context feathers evolved remains a matter of debate.

Zhonghe Zhou

After nearly one and half century of study and debate on whether extant birds are descendants of dinosaurs, paleontologists now generally agree that all birds are derived from a group of small-sized theropods (a suborder of bipedal saurischian or ‘lizard-hipped’ dinosaurs). In the past two decades, paleontology has also made remarkable progress in understanding of the origin and early evolution of bird feathers. Since the first report of proto-feathers from the theropod dinosaur *Sinosauropteryx* [1], diverse types of feathers in dinosaurs, including theropods and ornithischians, (one of the two basic divisions of dinosaurs, the ‘bird-hipped’ dinosaurs) have been reported mainly from the Early Cretaceous (about 120 million years ago) but also Middle-Late Jurassic (about 160 million years ago) deposits in northeastern China that have tremendously improved our understanding of the evolutionary transition from dinosaur to bird [1–4]. More recently, evidence of the color of fossil feathers in the form of preserved melanosomes has been found in various dinosaurs and early birds, providing evidence of their appearance and inferred behaviors [5–7]. This further allowed new investigations into the details of feather morphology and their functional explanations in these new taxa as well as rekindled studies on previously known birds, such as the well-known *Archaeopteryx lithographica* [8–10]. Many of our traditional views on the origin and early evolution of bird feathers have since been revolutionized; we now know that feathers are not restricted to birds, but are also found in some non-avian dinosaurs; also, they probably did not originally evolve for flight, but rather in some other functional context such as insulation, display, camouflage etc. There is also support for hypotheses that flapping flight in modern birds most likely evolved through a four-winged stage in dinosaurs. Clearly, feathers are key to understanding the evolutionary forces and events that led to the emergence of flying birds. Now, Foth and colleagues [11] report a new specimen of the iconic early bird *Archaeopteryx* that shows unique preservation of feathers.

Archaeopteryx lithographica, arguably the most studied species in vertebrate paleontology, has long been held as the earliest and most primitive bird, ever since its first skeleton was reported in 1861. Undoubtedly, *Archaeopteryx* has played a key role in the discussion of the origin of birds, feathers, and avian flight. However, with the remarkable discoveries of feathered dinosaurs (*e.g.*, *Anchiornis* and *Xiaotingia*), particularly from the Jurassic lake deposits in northeastern China, even the iconic status of *Archaeopteryx* as the oldest known bird has been challenged [4]. Furthermore, until now, information on the plumage of *Archaeopteryx* (largely limited to the London and Berlin specimens) remained incomplete compared to the exceptional preservation of the plumage in several feathered dinosaurs and early birds from China. The complete articulated 10th

Figure 1. The 11th *Archaeopteryx*.
The 11th skeletal specimen of *Archaeopteryx* under ultraviolet light. Photograph courtesy of Oliver Rauhut.

skeleton of *Archaeopteryx* (Thermopolis specimen) added little information on early feather evolution, although its excellent preservation of skeletal morphology confirmed the role of this taxon as a missing link between dinosaurs and birds [12].

Foth and colleagues [11] now report the 11th skeletal specimen of *Archaeopteryx* (Figure 1). Despite the crushed nature of its skull, the new specimen has the rest of the skeleton intact and most notably preserves feathers not only on the wings and tail, but also on the body including the distal parts of the legs, suggesting that the entire body of *Archaeopteryx* was covered in pennaceous feathers (quill-like feathers with a long central shaft with vanes on either side). The leg feathers are particularly well preserved, with long, symmetrical feathers along the thigh and shank and short feathers on the foot. Thus, this new specimen of *Archaeopteryx* is the most important yet with regards to understanding the early evolution of feathers.

Foth and colleagues [11] have conducted a comprehensive analysis of the phylogenetic distribution of pennaceous feathers on the tail, leg and arms of advanced maniraptorans (a clade of theropods containing birds and some of the most closely related non-avian dinosaurs), and concluded that the distribution of pennaceous feathers is highly variable even before the advent of flight, indicating that different functional aspects were involved in the early evolution of these structures [11]. This has obviously been true since the discovery of *Sinosauropteryx*, but this new study may also indicate that not only primitive proto-feathers, i.e., filamentous plumages, but also more advanced pennaceous feathers probably first evolved in a functional context other than flight, such as balancing, brooding, insulation or display. This further suggests that the aerodynamic function, which evolved independently in some feathered dinosaurs and most birds, is most likely an exaptation.

Reconstructing the behaviour of an extinct animal is always a challenge and a matter of debate. The flight capability of *Archaeopteryx* is no exception. The new specimen with its excellent plumage preservation sheds new light on flight in the oldest bird. Foth and colleagues [11] showed that the wing morphology of *Archaeopteryx* conforms to that of modern birds, with dorsal coverts preserved above the primary feathers measuring approximately half the length of the primaries, contrary to a recent interpretation that the feather pattern in this taxon was primitive [10]. They also show that the rachides (shafts) of the wing feathers were comparable in strength to those of modern birds, again contrary to a previous estimate that also suggested an absence of powered flight capabilities [9]. The new specimen also for the first time preserves the complete distal end of the tail in *Archaeopteryx* [11], showing the lateral rectrices (tail feathers) were asymmetrical, supporting previous studies that the tail had aerodynamic function and could have increased the total lift of the animal.

Despite the new information on its plumage, caution should be used when estimating the exact flight capability of *Archaeopteryx*. The skeletal components of the wing (relative to leg) and the wing feathers themselves appear short compared with more advanced birds. *Archaeopteryx* retained a long bony 'dinosaurian' tail, but lacked a bony, keeled sternum and features of the pectoral girdle important in more advanced birds, e.g., strut-like coracoid, triosseal canal and a laterally compressible furcula (wish bone) that are central to full powered flight. Thus, it is probably safe to conclude that *Archaeopteryx* was not a good flier compared to modern birds.

One of the most controversial issues in the study of feather evolution is probably the function of the pennaceous leg feathers in some feathered dinosaurs and early birds. Did the leg feathers form a so called hindlimb wing that worked in conjunction with the forelimb wing in a four-winged gliding mode of flight? If so, how did the two pairs of wings function exactly? Foth and colleagues [11] argue that leg feathers were generally not aerodynamic in *Archaeopteryx* and other dinosaurs with pennaceous leg feathers (e.g., *Anchiornis*) based on their distribution and attachment to the leg bones, as well as their symmetrical shape. Instead, these authors propose that their leg feathers were used for display, breeding or some other function, similar to the pennaceous leg feathers in modern birds of prey, such as falcons and eagles. The complex color or iridescent patterns documented in the hindlimb feathers of some feathered dinosaurs lends further support for a primarily display function [11].

However, contrary to Foth and colleagues [11], it is probably premature to reject a four-winged stage during the origin of avian flight. The leg feathers of *Archaeopteryx* are relatively short, yet they are weakly curved like the flight feathers and are not so short that an aerodynamic function can be excluded. There is still no evidence showing unequivocally that leg feathers lacked aerodynamic function in the direct ancestor of birds. In fact, *Microraptor* probably represents only one of many extinct feathered dinosaurs that maintained an ancestral aerodynamic role in the leg feathers [2]. A recent study on the leg feathers of a primitive bird, *Sapeornis*, suggested a distal-to-proximal pattern of reduction during leg feather evolution [13]. It is possible that an aerodynamic function of pennaceous feathers could have evolved several times in various theropod lineages; however, it is also more likely that flight and aerodynamic functions of the pennaceous feathers could have been lost many times in theropod (including birds) evolution — during evolution, the loss of features is far more common than the evolution of novel features.

Finally, it remains a challenge for paleontologists to answer questions regarding the exact functional context in which feathers of various types (e.g., filamentous feathers, pennaceous feathers) and positions (e.g., leg feathers, tail feathers) evolved in their early stages. Existing evidence from feathered dinosaurs and early birds seems to confirm that feathers generally did not evolve for flight, but for other functions. However, it is difficult to identify a single fitness advantage that fully explains the origin or proliferation of feathers. In most cases, it was probably a combination of more than one selective force that produced the diversity of feather plumages during the transition from dinosaurs to birds. For instance, in the case of *Jeholornis*, the only long-tailed bird known from the Early Cretaceous, the unique 'two tail' plumage — the presence of a fan-shaped tract of feathers over the proximal tail vertebrae like that of modern birds in addition to the distal frond like that of feathered dinosaurs such as *Microraptor* — was explained as the evolutionary result of complex interactions between natural and sexual selection with the tail serving both aerodynamic and ornamental purposes, which also provided a plausible functional explanation for the elongation of the bony tail in *Jeholornis* relative to *Archaeopteryx* [14].

As suggested by Foth and colleagues [11], it is obviously true that feather distributions during the origin and evolution of birds were more complex than previously recognized, as this is the nature of the fossil record. And it is also true that the diversity of feather types and their distribution in early birds and their ancestors must be the evolutionary product of complex interactions between various selective forces, which we are still struggling to understand.

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Vision: Two Plus Four Equals Six

Using two UV-sensitive visual pigments and the UV-filtering properties of four mycosporine-like amino acids, mantis shrimp create six spectrally distinct UV receptors. This is yet another example of the unique ways in which mantis shrimp have adapted to extract information from their visual world.

Ellis R. Loew

The eyes of mantis shrimps are truly wondrous organs. One only has to see them waving around on their stalks with the various pseudopupils 'looking' at you from clearly identifiable structural regions to appreciate their complexity (Figure 1). These eyes have evolved often unique mechanisms to extract all manner of information from the environment produced by interactions of photons with the medium and targets within it. To accomplish this,