

REVIEW

Feathered dinosaurs from China and the evolution of major avian characters

Xing XU

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

Abstract

Recent discoveries of feathered dinosaurs from Early Cretaceous deposits in Liaoning, China, have not only lent strongest support for the dinosaurian hypothesis of bird origins, but have also provided much-needed information about the origins of feathers and avian flight. Preliminary analysis of character evolution suggests that the major avian osteological characters were acquired during the early evolution of maniraptoran dinosaurs. The available evidence also suggests that the first feathers with a filamentous morphology probably evolved in basal coelurosaurs and pennaceous feathers (including those with aerodynamic features) were developed in non-avian maniraptorans, indicating that feathers evolved before the origin of birds and their flight. An evolutionary model is proposed here to describe the major stages of feather evolution, a process characterized by a combination of both transformational and innovative modifications. This model is different from some recent developmental models, which suggest that feathers are evolutionary novelties without a homologous relationship to reptilian scales. Although non-avian theropods are traditionally regarded as distinctly cursorial animals, recent discoveries suggest that the closest relatives of birds might be arboreal theropods. Many bird features, such as the furcula and pennaceous feathers, evolved in a terrestrial context, whereas others, such as some pedal modifications, may have evolved in an arboreal context. Consequently, arboreality may have also contributed to the origin of avian flight.

Key words: birds, feathered dinosaurs, feathers, flight.

INTRODUCTION

Over the last 30 years, there have been significant advances in the long-debated and intriguing study of the evolutionary origins of birds (Witmer 1991). Although there are various objections based on different perspectives, such as homology, physiology, chronology, methodology, and even fossil provenance, the theropod ancestry of birds has gained widespread acceptance (Witmer 2002), especially in light of the feathered non-avian coelurosaurs discovered in Liaoning, China.

Correspondence: Xing Xu, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China. Email: xu.xing@pa.ivpp.ac.cn

ADVANCES IN SUPPORT OF THE THEROPOD ANCESTRY OF BIRDS

Since Ostrom's pioneering work revived the theropod ancestor hypothesis of bird origins (Ostrom 1969, 1974, 1976), significant advancements have been made in reconstructing the theropod-bird transition. The adoption of cladistic methodology, in particular, helped to establish a strictly hierarchical map of dinosaur genealogy and strongly supports the hypothesis that birds are direct descendents of theropods and, more specifically, coelurosaurs (Fig. 1; Gauthier 1986; Sereno 1999; Holtz 2000; Norell *et al.* 2001; Xu 2002).

Osteological transformation

Information from both non-avian theropods and primitive birds suggests a sequential and hierarchical acquisi-

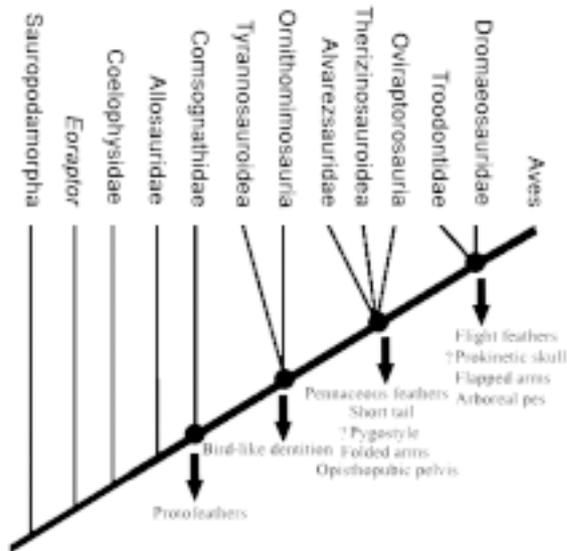


Figure 1 Evolution of major avian characters. The cladogram is based on several recently published coelurosaurian phylogenetic hypotheses (Holtz 2000; Sereno 1999; Norell *et al.* 2001; Xu 2002).

tion of major bird characters (Fig. 1), although homoplasies are strongly featured in this process. Worthy of mention are several non-avian and avian dinosaurs recently discovered from western Liaoning, China: *Sinornithosaurus* is a basal dromaeosaur that has numerous avian-like features, including flapping arms and a basal-avian-like pelvis (Xu *et al.* 1999b); *Microraptor* is a basal dromaeosaur of *Archaeopteryx*-size that has a large sternum composed of two fused plates, an *Archaeopteryx*-like shoulder girdle, and forelimbs that are long and robust when compared with the hind limbs (Xu *et al.* 2000, 2003; Hwang *et al.* 2002); *Mei* is a basal troodontid of *Archaeopteryx*-size, with numerous cranial and postcranial avian features, such as a prokinetic skull, and a basal-avian-like shoulder girdle and pelvis (Xu & Norell 2004); and *Jeholornis* is a long-tailed basal bird that has more powerful wings than *Archaeopteryx* has, but has also retained several features of the dromaeosaurid dinosaurs (Zhou & Zhang 2002). Examination of character distributions along maniraptoran lineages reveals that the major structural bird-like modifications were acquired in the early stages of maniraptoran evolution. For example, bird-like dentition, and pelvic and shoulder girdles evolved in the early stages of coelurosaurians, maniraptorans, and eumaniraptorans, respectively (Xu 2002). The small size of these non-avian coelurosaurians deserves special note. A consistent trend of decreasing body size is present along the proposed evolutionary line to birds (although it is interesting that most

coelurosaurian sub-lineages show an evolutionary trend of increasing body size, which possibly led to the primitive conditions for many characters in the large-bodied, derived members of these sub-lineages). Consequently, it is believed that miniaturization not only played a key role in the origin of bird flight, but was also critical in shaping some other major avian characters, such as cranial kinesis (Xu & Norell 2004) and possibly feathers.

Origin of feathers

Feathers are the most complicated integumentary derivatives of vertebrates, and the most characteristic feature of living birds. Although the diverse morphology of modern feathers most likely developed gradually from simpler integumentary structures, little was known about how the earliest feathers evolved and diversified until recently.

Morphologically, although nearly all feathers feature a rachis and barbs, modern feathers have a great variety of forms. Functionally, feathers are the most diverse integumentary appendage in living vertebrates. Furthermore, modern feathers have unique biochemical and developmental features, suggesting that feathers represent evolutionary novelties (Prum & Brush 2002). Due to these unique features, piecing together the origin and early evolution of these highly specialized structures is difficult. As such, a diversity of hypotheses, some being largely speculative, have been proposed.

Theoretically, the evolutionary origin of certain structures should be put into a phylogenetic framework of bearers. Structure origin and evolution should be traced on an independently developed phylogenetic tree. Tracing feather origin and evolution is no exception. Given that the theropod ancestry of birds is supported by considerable osteological and other lines of evidence, feather precursors or homologues should also be present in the dinosaurian ancestors of birds, as predicted decades ago by the proponents of the theropod hypothesis of bird origin (Bakker & Galton 1974).

Although soft tissues were very rarely fossilized, many recently recovered dinosaur fossil remains from the Early Cretaceous of Liaoning, China preserve horny claw sheaths, various integumentary structures, and even internal organs. In particular, the discovery of filamentous protofeathers and even true feathers in numerous non-avian theropod specimens from Liaoning provides direct evidence for the dinosaurian history and evolution of feathers.

Since the discovery of *Sinosauropteryx*, the first non-avian dinosaur discovered with protofeathers (Ji & Ji 1996; Chen *et al.* 1998; Currie & Chen 2001), dozens of non-avian theropod specimens with preserved integumentary struc-

tures have been recovered from the Early Cretaceous Jehol Group of western Liaoning, China. These specimens are from several non-avian theropod groups, which, cladistically, are positioned from the very basal portion of the coelurosaurian tree to the portion nearing the Aves node, and they represent several different stages in coelurosaurian evolution (Xu 2003). The integumentary structures on Liaoning coelurosaurs are morphologically diverse. Single filaments, compound structures (composed of either multiple filaments joined in a basal tuft, or multiple filaments joined at the base either in series along a central filament or at the distal portion of a central filament), plumulaceous feathers, and pennaceous feathers with symmetrical and asymmetrical vanes have all been observed. Studies of the fine details of the filamentous structures of some Liaoning specimens also reveal that there are longitudinal grooves and ridges along the filaments: a feature also seen in modern feathers, but absent in mammalian hair (the other extant filamentous integumentary appendage).

The feather morphologies of Liaoning coelurosaurs display an evolutionary trend of increasing complexity and, closer to the base of the Aves clade, a distinctive body-distribution pattern. However, some contradictory information is present. For example, the absence of pennaceous feathers on the known specimens of *Beipiaosaurus* and *Sinornithosaurus* is contradictory to their phylogenetic positions (Xu *et al.* 1999a, 1999b), although this absence may be the result of factors such as preservation, ontogeny, or molting.

Some feather morphologies in non-avian theropods are comparable to those of modern feathers, but others are not commonly observed in living birds. The single filament structure is not known in living birds, although in several species of living birds, some highly specialized integumentary structures are superficially similar to the single filament seen in non-avian theropods. The integumentary structures composed of multiple filaments joined in a basal tuft are similar to the natal down in living birds. The integumentary structures composed of a series of filaments joined at their bases along a central filament are similar to modern down feathers in some ways, but they lack barbules. The integumentary structures composed of a series of filaments joined at their bases at the distal portion of a central filament are superficially similar to the filoplume. The pennaceous feathers along the limbs and tails are almost identical to the remiges and rectrices, respectively, of modern birds. Of interest is a surprising character distribution pattern that feathers with modern traits, including feathers with aerodynamic features, are all present in non-avian theropods. Therefore, the hypothesis that feathers originated as uniquely avian structures is shown to be

inappropriate.

Both paleontological and developmental studies support the following evolutionary scenario for the origin and early evolution of feathers (Fig. 2): (i) first, feathers were single filaments; (ii) next, branching structures developed; (iii) then, the rachis evolved; (iv) fourth, pennaceous feathers came into being; and (v) last, aerodynamic morphologies (curved shaft and asymmetrical vanes) appeared. This scenario appears to indicate that downy feathers, contour feathers, and flight feathers in modern birds are successively more derived, but this is not necessarily the case. It is likely that the simple protofeathers or primitive feathers disappeared early in feather evolution and that less complex feathers in modern birds are secondary and thus have nothing to do with the primitive condition in feather evolution. The early evolution of feathers might have featured some sort of degeneration: after various morphologies evolved, some might have quickly disappeared (such as single filaments), some were restricted to limited stages of the ontogeny (such as natal downs), and others were restricted to a more limited distribution on the body (such as the pennaceous feathers with asymmetrical vanes). In other cases, some morphologies might have become dominant on the modern avian body. For example, the pennaceous feathers on the limbs and tails of non-avian dinosaurs have a much more extensive distribution on the bodies of more derived birds. In this case, the homologues of remiges and rectrices might have evolved into the contour feathers, instead of vice versa.

Recent developmental evidence suggests that feathers are not homologous with the scales of living reptiles (Prum & Brush 2002). In addition, a recent developmental model that was independently derived from developmental data suggests that the evolution of feathers is a totally innovative and hierarchical process. The model proposes that feather evolution began with the emergence of the feather follicle, a unique structure that has nothing to do with reptilian scales, and then a series of developmental and morphological novelties, with a constant addition of structural complexity, evolved (Prum 1999; Prum & Brush 2002). Although the distribution of various feather morphologies on the coelurosaurian phylogeny is largely congruent with this model, it is also at odds with the model in several cases. In particular, the morphology of several interesting integumentary structures of some living birds (such as the bristles of wild turkey beards) and of some close relatives of theropod dinosaurs (the hair-like structures in pterosaurs and the filamentous integumentary structures in the ornithischian dinosaur *Psittacosaurus*) are thought to be not homologous to modern feathers, but they display some distinct feather-like features. Thus, it is possible that feath-

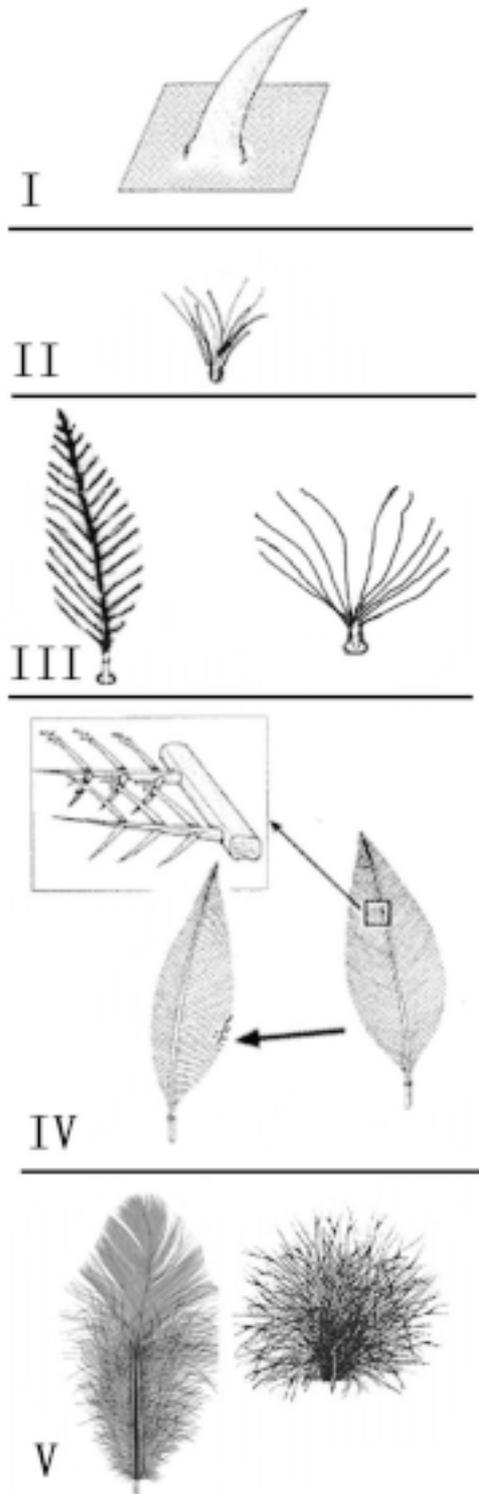


Figure 2 An evolutionary model for the origin and early evolution of feathers.

ers have scale-like homologues at some level.

A new evolutionary model is proposed here to describe the major stages of feather evolution (Fig. 2). During stage I, tubular filaments and feather-type beta-keratin emerged. The *Psittacosaurus* tail filaments and probably the pterosaur hair-like structures may be a testament to this stage. Stage II is characterized by the distal branching of the filamentous structure. The distal branching structure can easily be derived from splits along the distal end of the tubular filament. A modern example might be the bristles of wild turkey beards, and its historical existence might be documented by the filaments in some non-avian coelurosaurs such as *Sinosauropteryx*, *Beipiaosaurus*, *Dilong*, and *Sinornithosaurus* (Xu 2002; Xu *et al.* 2004a). Stage III is probably the most critical stage of feather evolution. In this stage, the main structure, the feather follicle, appeared and the rachises and planar forms developed. The evolution of these three features is the most critical stage in feather evolution, especially of the follicle, a structure from which all of the later feather morphologies are produced. Stage III is supported by the following developmental evidence: feather follicles developed later than barb ridges, the follicle has a unique role in formation of the rachis, and the helical growth of barb ridges within the follicle is correlated with the formation of the planar form. In this stage, a number of non-avian dinosaurs evolved certain feather morphologies with obvious rachises and attached barbs (such as those in *Sinornithosaurus*, *Caudipteryx* and *Protarchaeopteryx*). Stage IV is represented by the large stiff pennaceous feathers on the limbs and tails of *Microaptor*, *Caudipteryx* and *Protarchaeopteryx* (Ji *et al.* 1998; Xu *et al.* 2000, 2003), and it is in this stage that the barbules evolved. Although the stiff pennaceous feathers of *Microraptor* are different from those of *Caudipteryx* and *Protarchaeopteryx* with respect to several features related to aerodynamic functions, they all belong to the same category because they evolved form-stiffening barbules on the feathers. Stage V is represented by the evolution of feather tracts (pennaceous feathers are found in regions other than the limbs and tail) and by various specialized or degenerated pennaceous feathers.

This new model is similar to Prum's model (Prum 1999) but the two models differ with respect to several major points. First, the new model features a combination of transformation and innovation, whereas Prum's model suggests that feathers are completely evolutionary novelties. Second, the new model suggests that some distinctive feather features, such as tubular filaments and branching, evolved before the appearance of the feather follicle. However, the new model confirms that the follicle is a critical innovation in feather evolution. Third, the new model emphasizes that

the rachis and planar form are the two most distinctive features of feathers and suggests that these two features are hallmarks of feather evolution. Finally, among the various feathers of modern birds, the flight feather homologue may have evolved before the other types of feathers. Needless to say, these two models should be tested against future fossil discoveries and development observations.

In summary, our understanding of the origin and early evolution of feathers has advanced significantly thanks to paleontological and developmental studies. However, the much-needed information necessary to reconstruct a complete scenario for feather evolution has yet to present itself, particularly information about the morphology and distribution of integumentary structures in primitive theropods.

Origin of flight

Study of the origin of avian flight has been advanced along two aspects: the evolution of flight apparatus and the evolutionary path for flight. The origin of avian flight is characterized by a series of morphological changes. Various studies show that the major modifications necessary for avian flight occurred in the course of maniraptoran evolution before the origin of birds. Ostrom and others (Ostrom 1969) demonstrated that maniraptorans could fold their arms like birds. Novas and others (Novas & Puerta 1997; Norell & Makovicky 1999) provided evidence showing that some maniraptorans could move their arms in an avian-like manner. Gatesy and coworkers (Gatesy & Dial 1996; Gatesy 2001) suggested that various avian locomotion-related changes to the vertebral column and hind-limbs occurred before the origin of birds. Xu and others (Xu 2002; Xu *et al.* 2003) showed that functional wings with true flight feathers evolved in non-avian maniraptorans. These combined works strongly indicate that flight apparatus was already well developed before the origin of Aves.

In comparison, the evolutionary path for flight is hotly debated. A tree-down hypothesis has long been thought to be implausible within the current phylogenetic framework (nevertheless, Chatterjee [1997] has recently produced a detailed model with mechanical analyses and an account of the climbing adaptations of dromaeosaurids). The assumed incompatibility between the arboreal hypothesis and current phylogenetic hypotheses is mainly caused by (i) the traditional view that all theropods are distinctly cursorial animals; (ii) the use of modern analogues without consideration of their evolutionary history; and (iii) poor preservation of forms from the time of the theropod-bird transition. Based on the assumption that a modified structure indicates a derived function within an evolutionary framework, Xu (2002) showed that the major structural modifications for an arboreal lifestyle occur at the nodes of

Eumaniraptora, Aves, and Ornithothoraces. Xu *et al.* (2003) noted that, based on soft tissue information, basal dromaeosaurids are not well adapted for a cursorial lifestyle. They further proposed that basal dromaeosaurids are probably four-winged animals and that basal eumaniraptorans evolved large and highly specialized pennaceous leg feathers for aerodynamic purposes. These leg feathers were later reduced and lost in birds, as birds depend completely on their fore-wings for flight. Most recently they proposed a primitive flight posture for basal dromaeosaurs (Xu *et al.* 2004b): while taking off, the hind-limbs of basal dromaeosaurids were capable of stretching posteriorly and also deflecting slightly so that the hind-limbs were placed in a subparallel position with respect to the tail. In this posture, the leg and tail feathers created surface for lift. Such a posture could easily be derived from the parasagittal posture of dinosaurs, and the posture is consistent with the osteological features of the pelvis and hind-limbs of eumaniraptorans. Xu and colleagues further proposed that primitive eumaniraptorans developed two lift-generating airfoils: the front-wings (which also serve to generate thrust) and the hind-wings (formed by both hind-limbs and the tail). During early avian evolution, the front-wings became the main airfoil, while the hind-wings lost their role in producing lift. *Microaptor gui* represents an early stage in the evolution of flight, with two large lift-generating surfaces, whereas *Archaeopteryx* has reduced leg feathers but a comparatively large feathered tail.

Other lines of evidence

The theropod hypothesis of avian origins has also been supported by other lines of evidence. For example, bird-like brooding and sleeping behavior has been documented in a few groups of non-avian maniraptoran dinosaurs (Norell *et al.* 1995; Xu & Norell 2004), a bird-like growth strategy is present in dinosaurs (Padian *et al.* 2001), and the microstructure of the eggshells and bones of dinosaurs is also similar to that of birds (Chinsamy & Hillenius 2004).

EXISTING PROBLEMS IN RECONSTRUCTING THE THEROPOD-BIRD TRANSITION

Most problems in reconstructing the theropod-bird transition result from ambiguous information from relevant fossils. One concern is that fragmentary specimens (Chatterjee 1997; Xu *et al.* 2001) may be critical to recovering the evolutionary process but, being incomplete specimens, research could easily be misinterpreted (for example, *Protoavis* and other fragmentary Jurassic specimens, possibly coelurosaurian, may or may not indicate an early divergence time for major coelurosaurian

groups). This is particularly true when it comes to the study of feather evolution.

Although a general framework of feather evolution has been established, detailed information is still scarce because of limited or poorly preserved samples. For example, although there is evidence suggesting that primitive non-avian theropods had scale-like integumentary structures (Martin & Czerkas 2000), little is known about the distribution of these scale-like integumentary structures on the body and whether these animals had any other types of integumentary structures. Considering the diverse integumentary structures in modern amniotes, it is entirely possible that multiple types of integumentary structures were present in non-avian theropods. Hundreds of specimens of non-avian theropods and basal birds have been found with preserved integumentary information, but some critical information is missing. For example, it is difficult to determine the evolution of feather tracts because the distribution pattern for different types of protofeathers or feathers is not well known. Further, although there is evidence suggesting that branching structures are present in the filamentous integumentary structures of basal coelurosaurians, we do not know exactly when the follicles, a critical feature in feather development, evolved.

There are also several other important questions: Did tubular filaments evolve before follicles? Is the accepted feather distribution pattern biased by preservation? Is it because of preservation that body contour feathers are not substantially preserved? Are there ontogenetic or molting factors influencing our reconstructed patterns? If so, how much influence is being exerted? Are barbules present in some protofeathers? Did specialized scales homologous with feathers ever exist on non-avian theropods? Finally, are feathers evolutionary novelties without any intermediate precursors? Some of these questions can be addressed by detailed research on known specimens using methods such as scanning electron microscopy and preservation experiments. Other answers will depend on the discovery of further well-preserved or better-preserved specimens. Understanding the origin and early evolution of feathers is also dependent on research in other areas of expertise. For example, there is an indication that pennaceous feathers developed comparatively later ontogenetically in non-avian theropods relative to modern birds. However, to confirm this inference, the developmental strategy of non-avian theropods needs to be addressed first. In addition, there is current evidence that favors the hypothesis that the initial function of feathers was related to insulation (Chen *et al.* 1998), but no compelling evidence suggests that coelurosaurians were distinctly different from more primitive non-insulated theropods physiologically or

ecologically. One possible piece of evidence suggesting a physiological change is miniaturization at the base of the Coelurosauria. It appears that miniaturization characterizes basal coelurosaurians. If this holds true, the development of substantial feathered coverings is likely to be solicited to insulate the small bodies of basal coelurosaurians.

Some ambiguous information is not related to preservation, but pertains to the researchers' preferences in interpreting data, such as the debate on the arboreality of basal birds (Xu 2002). In other cases, the fossil itself may not be informative enough (such as Triassic bird-like footprints that are indirectly contrary to the theropod hypothesis). The other problem is related to the poor representation of early coelurosaurs in the fossil record. Although the argument of stratigraphic disjunction against the theropod ancestry of birds is not valid, reconstruction of the theropod-bird transition is hindered by a lack of information from early members of various coelurosaurian lineages. Reconstruction of the theropod-bird transition is particularly difficult because of the significantly uneven distribution of bird-like characters in different coelurosaurian groups. The best examples are the debated phylogenetic positions of the oviraptorosaurs and alvarezsaur (Chiappe *et al.* 1996; Sereno 1999, 2001; Maryanska *et al.* 2002; Xu 2002; Xu *et al.* 2002).

FUTURE PROSPECTS IN RESEARCHING THE ORIGIN OF BIRDS

A robust phylogeny is the basis for reconstructing the theropod-bird transition, and it is still the most significant research for future prospects. A reliable phylogenetic analysis that evaluates the effect of homoplasies, such as the flight-related characters of the possibly secondarily flightless taxa that appeared soon after the origin of birds (Paul 2001), is needed. Accurate morphological information from well-preserved specimens or from earlier, more basal members of major maniraptoran lineages is critical to phylogenetic reconstruction.

The paleoecology of coelurosaurs is an important but poorly understood issue, and anatomical and other lines of evidence can be used for a reconstruction. Further, a thorough functional analysis of major modifications in the evolution of coelurosaurs, including a detailed analysis of flight-related characters and of possible arboreal features, could more clearly illuminate the origin of flight and the evolution of the flight stroke. It should be noted that an accurate reconstruction should be based on the more basal members of each coelurosaur lineage. Another important issue is the study of individual and ontogenetic variations. In particular, the latter information can be put within the

phylogenetic framework and can thus be used to infer the developmental mechanism for this important evolutionary transition.

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