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Mesozoic birds of China: an introduction and review *

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Abstract Over the last decade, more Mesozoic birds have been discovered from the Early Cretaceous of Liaoning Province in northeast China than from any other region on earth. Chinese Mesozoic birds represent the earliest significant avian diversification yet known after the oldest known bird *Archaeopteryx* appeared in the fossil record about 20 million years earlier. They not only include a long-tailed form reminiscent of dinosaurian ancestry but also comprise many other special or derived forms, such as the oldest-known beaked bird, the largest Early Cretaceous bird, the most primitive enantiornithine bird and the best preserved ornithurine bird, with a flight apparatus nearly identical to that of modern birds. Remarkable evolutionary, morphological and ecological differentiation, such as in flight, size and diet, are well documented by the Chinese fossils. The long-tailed, basal bird *Jeholornis* bears a remarkable resemblance to dromaeosaur dinosaurs, thus providing important clues in support of the dinosaurian origin of birds. Chinese Early Cretaceous birds, as well as arboreal dinosaurs of the same age in China, also provide compelling evidence for the arboreal hypothesis of the origin of avian flight. The 'Dinosaur-trees-down' hypothesis, which combines the dinosaurian origin of birds and the arboreal hypothesis of avian flight, is thus well collaborated. Because feathers were present in various dinosaurs, the association of endothermy with feathers becomes purely speculative; endothermy probably did not develop in birds until the Early Cretaceous [*Acta Zoologica Sinica* 50 (6): 913-920, 2004].
Key words Mesozoic, Fossil, Bird, Origin, China

中国中生代的鸟类：介绍及综述 *

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摘 要 最近十来年，中国辽宁发现的早白垩世的鸟类化石超过了世界上其它任何一个地区。中国的中生代鸟类化石代表了始祖鸟化石之后鸟类历史上第一次显著的分异。它们不仅包括了带有明显恐龙祖先特征的长尾的鸟类，而且还包括了许多进步或特化的种类，如早白垩世最大的鸟类，最原始的反鸟类，以及保存最好的、飞行结构和现生鸟类几乎一样的今鸟类。这些早期鸟类在诸如飞行、大小和食性等所反映的演化、形态和生态学特征等方面出现了重大的分异。具有长尾骨骼的原始基干鸟类热河鸟和驰龙类具有的相似性，进一步支持了鸟类起源于恐龙的学说。中国发现的早白垩世的鸟类以及树栖的恐龙化石还为鸟类飞行的树栖起源假说提供了十分重要的证据。"恐龙下树"的假说结合了鸟类起源于恐龙的学说和鸟类飞行的树栖起源学说，因此也得到了化石证据的支持。由于多种恐龙带有羽毛，因此羽毛不一定代表了恒温。恒温的鸟类可能到了早白垩世的进步鸟类中才开始出现［动物学报 50 (6): 913-920, 2004］。
关键词 中生代 化石 鸟类 起源 中国

1 Introduction: historical and geological background

Archaeopteryx has long been held as the oldest and most primitive bird ever since its discovery in late Jurassic sediments in 1861 (Wellnhofer, 1992); yet since then the fossil history of birds has only become relatively well documented from the Late Cretaceous on (Martin, 1991). Little, accordingly, has been known about birds in the intervening period until the last two decades of the 20th century when Early Cretaceous avian fossils began to be discovered in Mongolia (Kurochkin, 1985), Spain (Sanz et al., 1995, 1996) and China (Zhou, 2002; Zhou and Zhang,

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2002a, b). Since then, the discoveries of Early Cretaceous birds in western Liaoning Province in northeast China have not only improved our understanding of the early evolution of birds significantly but also made China the most important area for the study of early birds today.

Although the results of finding Mesozoic birds in China did not explode upon the world until the early 1990s, the discovery of the fossil sites dates back to 1982. Three stages of discovery can be recognized. From 1982 to 1993, fossils were found in the Jiufotang Formation, mainly in Gansu Province in northwest China (Hou and Liu, 1984), in Inner Mongolia in northern China (Hou, 1994) and at Chaoyang County in western Liaoning Province, northeast China (Sereno and Rao, 1992; Zhou et al., 1992; Hou and Zhang, 1993; Zhou, 1995; Martin and Zhou, 1997). The fossils include mainly enantiornithines (e.g., *Sinornis*, *Cathayornis* and *Otogornis*) and a few incomplete ornithurines (*Gansus*, *Chaoyangia* and *Songlingornis*).

Then, from 1994 to 1999, hundreds of fossils were found in the Yixian Formation, which underlies the Jiufotang Formation, at Beipiao (Hou et al., 1995, 1996, 1999a, b; Zhou and Hou, 1998; Chiappe et al., 1999) and Lingyuan (Hou and Chen, 1999) in western Liaoning Province, as well as in neighboring northern Hebei Province (Zhang and Zhou, 2000). The fossils include the abundant *Confuciusornis*, a few primitive enantiornithines (*Protopteryx*, *Eoenantiornis* and *Liaoxiornis*), and one primitive ornithurine *Liaoningornis*. Since 2000, many more new taxa of birds have been described from the Jiufotang Formation following discoveries at several new localities near Chaoyang City and in Yixian County of Jinzhou City in Liaoning Province (Zhang and Zhou, 2001; Zhou and Zhang, 2001b, 2002a,b). The fossils include some completely articulated ornithurine birds (*Yixianornis* and *Yanornis*), the largest Early Cretaceous bird *Sapeornis*, and the long-tailed *Jeholornis* and enantiornithines *Longipteryx* as well as *Confuciusornis*.

Without exception, all Mesozoic birds in China have been found in lacustrine Cretaceous sediments, primarily the Yixian Formation and the overlying Jiufotang Formation. Both $^{40}Ar/^{39}Ar$ and U-Pb zircon dating of the Yixian Formation suggests an age of about 125 million years before present (Swisher et al., 1999, 2002; Wang et al., 2001), with the Jiufotang Formation slightly younger, around 120 million years before present (Eberth et al., 1993; He et al., 2004).

The exceptional abundance and diversity of early avian populations in western Liaoning can probably be attributed to frequent volcanic activity and the development of many partly isolated inter-mountain lakes during the Early Cretaceous (Chen, 1988). Mass mortality caused by volcanic eruptions resulted in the preservation of not only hundreds of individuals of *Confuciusornis* but also many juvenile individuals of early birds. Feathers were preserved either attached to complete skeletons or separated. In some unusual cases, nearly complete plumage was preserved without any skeletal elements.

All known Mesozoic bird fossils in China belong to the Jehol Biota, which is endemic to East Asia. Although this biota includes some relics that survived from the Late Jurassic or earlier, it mostly comprises taxa typical of Early Cretaceous times and indicates that East Asia was then a center of diversification for various dinosaurian lineages. Abundant vertebrates, invertebrates and plant fossils are equally well-preserved and -known. Probably the most significant among them are the many feathered dinosaurs, *Sinosauropteryx*, *Protarchaeopteryx*, *Caudipteryx*, *Beipiaosaurus*, *Sinornithosaurus* and *Microraptor* (Chen et al., 1998; Ji et al., 1998; Xu et al., 1999a,b, 2000, 2003; Zhou and Wang, 2000; Zhou et al., 2000), the early mammals *Zhangheotherium*, *Jeholodens*, *Eomaia*, *Repenomamus*, *Sinobaatar*, *Sinodelphys* (Hu et al., 1997; Ji et al., 1999, 2002; Wang et al., 2001; Hu and Wang, 2002; Luo et al., 2003), and putative angiosperms such as *Archaefructus* (Sun et al., 1998, 2002) and the non-controversial angiosperm *Sinocarpus* (Leng and Friis, 2003). Other important vertebrate groups include fishes (acipenseriforms, bowfins and teleosts), amphibians (frogs and salamanders) (Wang et al., 2001; Gao and Shubin, 2001), turtles *Manchurochelys* (Li and Liu, 1999), aquatic reptiles (e.g., *Monjurosuchus* and *Haphalosaurus*) (Gao et al., 2000), lizards (*Yabeinosaurus*), pterosaurs (pterodactyloids and anurognathids) (Wang et al., 2002), as well as other dinosaurs that did not have feathers (psittacosaurids, iguanodontids, oviraptorids, troodontids, ankylosaurids and sauropods) (Wang and Xu, 2001; Xu et al., 2001, 2002a,b). The invertebrates include insects, spiders, crustaceans (Ostracoda, Notostraca, Conchostraca, Decapoda, Peracarida), and bivalves and gastropods. The flora is dominated by conifers but also contains bryophytes, lycopods, sphenopsids, ferns, Bennettitales, Czekanowskiales, Ginkgoales, Gnetales and putative angiosperms (Zhang et al., 2001). It is notable that among the over one thousand species of insects, many are nectar-feeders with long tubular mouth-parts (Ren, 1998).

2 Implications for the early evolution and diversification of birds

The Mesozoic avian fossils of China represent some of the most basal birds known in avian evolution, notably *Jeholornis*, *Sapeornis* and *Confuciusornis* (Fig.1). These birds form the sister groups of nearly all major groups of extinct and extant birds, including Enantiornithes and Ornithurae (Martin, 1991). Among them, *Jeholornis* is most similar to *Archaeopteryx* in terms of primitiveness. It retained an unreduced skeletal tail and was toothed, though the teeth were reduced and its flight structures are obviously much improved (Zhou and Zhang, 2002b). *Sapeornis* has a tail reduced to a pygostyle, yet it still retained a short and robust coracoid nearly identical to that of *Archaeopteryx*; interestingly, it is the largest bird known from the Early Cretaceous and it is also larger than *Archaeopteryx* (Zhou and Zhang, 2002a). Its extremely elongated forelimbs suggest that it may have been able to soar in flight. *Confuciusornis* represents the oldest known bird with a horny beak. Like *Sapeornis*, *Confuciusornis* has a pygostyle, but its strut-like coracoid indicates more powerful capability in flight. Sets of long (male) and short (female) tail feathers also suggest sexual dimorphism; and the unusual accumulation of massed individuals at a site indicates that *Confuciusornis* gathered socially in flocks.

The majority of early Chinese birds belong to the prevalent Mesozoic avian group, Enantiornithes, which became extinct by the end of that era. These birds were all toothed, arboreal, and usually small, and, with a well-fused carpometacarpus and reduced manual digits, were evidently capable of powerful flapping flight (Zhou, 2002). On the other hand, they lack a deep keel on the sternum and their coracoids lack a well-developed procoracoid; therefore the triosseal canal characteristic of modern birds was probably missing. Among them, *Protopteryx* is the most primitive, with unique tail feathers showing features transitional between scales and modern feathers (Zhang and Zhou, 2000); yet it also possessed the advanced flight structure, the alula, which is absent in *Archaeopteryx* and *Confuciusornis*. *Eoenantiornis* also had the alula (Hou et al., 1999b). Another enantiornithine *Longipteryx* is specialized with relatively long wings and short hindlimbs indicative of a perch-and-pounce life style similar to that of a kingfisher, i.e. perching in trees near water and catching fish from soaring sweeps over the surface of lakes (Zhang and Zhou, 2001).

Another major group of birds in the Early Cretaceous deposits of China is the Ornithurae, to which all extant birds belong, as well as their extinct kin that first appeared then. All Chinese fossil ornithurines were toothed, like other Mesozoic birds. Among them, *Liaoningornis* from the Yixian Formation is the smallest and most primitive; it is also obviously arboreal (Hou et al., 1996). Other forms such as *Yixianornis* and *Yanornis* are from the Jiufotang Formation and are similar to *Confuciusornis* in size, much larger than contemporaneous enantiornithines (Zhou and Zhang, 2001b). Unlike *Confuciusornis* and enantiornithines, which are mainly perching forms, the ornithurines lived mostly near the water, perhaps as waders, as indicated by long pedal toes and toe proportions. They probably fed on fish and other aquatic animals. Although they possessed flight structures barely distinguishable from those of modern birds (well-fused carpometacarpus, well-developed procoracoid, and deep keel on the sternum), they also retained some primitive traits such as teeth, a pubic symphysis, gastralia and wing claws as in *Archaeopteryx*, *Jeholornis*, *Sapeornis* and the enantiornithines. Thus, they could not have been the immediate ancestors of modern birds. From known evidence, modern orders of birds did not arise until at least the Mid Cretaceous, no earlier than 110 million years before present.

The Early Cretaceous birds of China provide the best material yet for studying the early evolution of birds, between Late Jurassic (*Archaeopteryx*) and Late Cretaceous times. The Chinese deposits reveal and record in detail, for the first time, a remarkable diversification of birds in the Early Cretaceous. While many primitive basal forms continued to survive then, a group of birds of modern appearance, the ornithurines, began to evolve in a direction that finally led to modern birds. Early Cretaceous birds show not only remarkable evolutionary, morphological and ecological differentiation, but also significant variation in size. Moreover, although relatively little is known about the feeding habits of these birds, differentiation in dietary habits had obviously developed. Thus stomachs of the long-tailed *Jeholornis* preserved seeds, convincing evidence of granivory, while those of some ornithurine birds such as *Yanornis* preserved fish, consistent with the life style reconstructed above.

3 Implications for the origin of birds

Since its discovery, *Archaeopteryx* has been regarded as one of the foremost links between birds and reptiles. Further, as the oldest bird, it has also become the focal source for perceptions of the ancestral bird. Since the 1970s, John Ostrom has rejuvenated the dinosaurian hypothesis of the origin of birds based on a detailed comparison of *Archaeo- pteryx* with theropod dinosaurs (Ostrom, 1976).

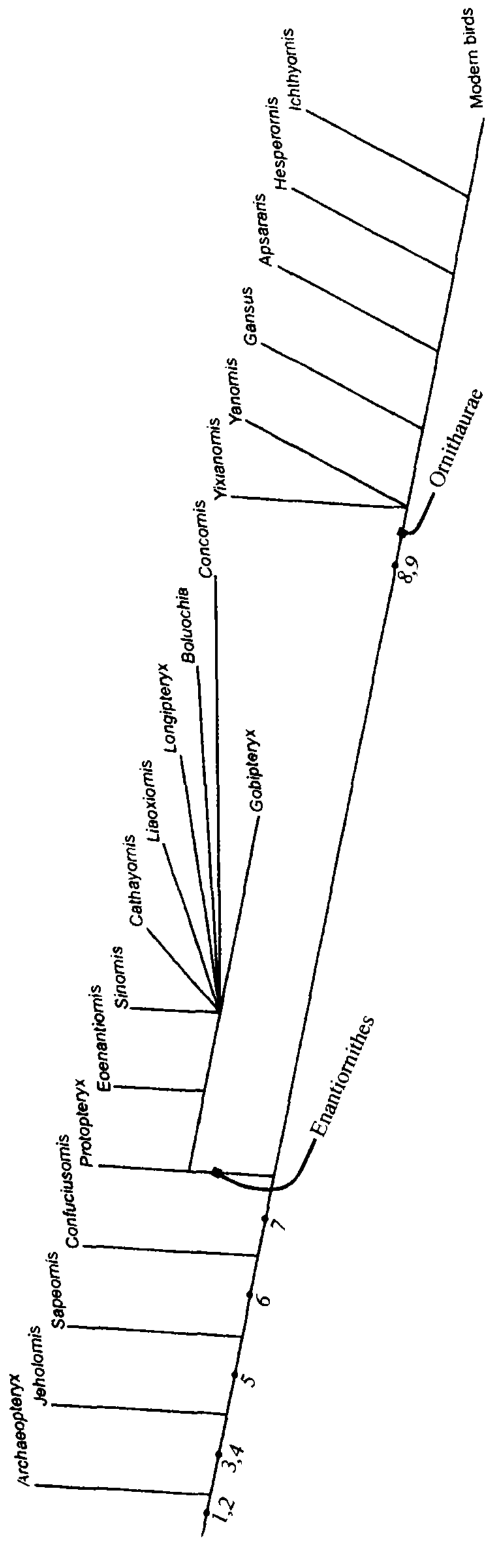

Fig. 1 Cladogram showing the phylogenetic relationship of the major Mesozoic birds of China

Numerals 1 – 9 represent the appearance of important morphological features in the early evolution of birds. 1: Asymmetry of flight feathers. 2: Reversed hallux. 3: Carpometacarpus. 4: Lateral trabeculae of the sternum. 5: Pygostyle. 6: Horny beak. 7: Alula. 8: Elongated and well-keeled sternum. 9: Well-developed procoracoid and triosseal canal.

Jeholornis from the late Early Cretaceous of China (Zhou and Zhang, 2002b) is now the second bird known with a complete long skeletal tail. Perhaps more importantly, its caudal vertebrae, like those in *Archaeopteryx*, have long elongated chevrons and prezagopophyses similar to those of dromaeosaurid dinosaurs, further evidence linking birds with this particular group of theropods. Another similarity shared with some theropods is a relatively large sickle-shaped claw on the second pedal digit. Fan-shaped tail feathers in *Jeholornis* also bear a remarkable resemblance to those of theropods such as *Caudipteryx* and the dromaeosaurids.

It may be significant that nearly all of the known theropods thought to be closely related to birds (specifically, the maniraptorans) have been collected from deposits younger than the age of the oldest bird, *Archaeopteryx*. Phylogenetically, this does not negate the dinosaurian origin hypothesis of birds. Rather, for critics of this hypothesis, it poses a problem: could the bird-like dinosaurs have developed their many bird-like traits secondarily, or, in other words, are the similarities shared with birds the result of parallel evolution?

It is equally noteworthy that up to ten years ago, before the discoveries of feathered dinosaurs from the Liaoning Province in China, the most bird-like dinosaurs (= the closest relatives of birds) that were used for phylogenetic comparisons with birds came from the Late Cretaceous, such as *Deinonychus*, *Dromaeosaurus* and *Velociraptor*. The Chinese fossils have now pushed back their record to the Early Cretaceous. Yet Early Cretaceous times post-date the oldest known bird by about 20 million years, and are still too young for the origin of birds. Significantly, the recently described maniraptoran *Epidendrosaurus*, which was believed to be very close to the transition between dinosaurs and birds, comes from an older deposit bordering western Liaoning: the Daohugou Formation in Inner Mongolia (Zhang et al., 2002). The age of the Daohugou Formation is still controversial, ranging from Middle Jurassic to Early Cretaceous according to different workers. If this is confirmed, then it fills another big temporal gap that has perplexed paleontologists about the origin of birds.

Although *Jeholornis* is obviously a more advanced bird than *Archaeopteryx*, its tail comprises more caudal vertebrae and more elongated skeletal chevrons, which in turn appear more like those of the dromaeosaurids. This suggests that *Archaeopteryx* may be no more than a side branch on the avian evolutionary tree. On the other hand, it can also be argued that the longer and more dinosaur-like tail of *Jeholornis* is a secondary adaptation. In other words, if the feathered dinosaurs such as dromaeosaurids are secondarily flightless, *Jeholornis* might be viewed as a transition between *Archaeopteryx* and the secondarily flightless Cretaceous birds (Martin, pers. comm.). Despite this inspiring and tantalizing thought, we have to admit that a complete and compelling phylogenetic analysis has still to be presented for the view that feathered dromaeosaurids and oviraptorids are indeed more derived than the most primitive birds such as *Archaeopteryx* and *Jeholornis*. In the interim, we continue to regard *Jeholornis* as a bird that retained some very primitive traits from dinosaurian ancestors.

4 Implications for the origin of flight in birds

Controversy over the origin of the flight has never been as heated as it has over the origin of birds themselves; yet the two are tightly connected. The competing 'Ground-up' and 'Trees-down' hypotheses for the origin of avian flight are often linked automatically with dinosaurian and non-dinosaurian origins respectively (Ostrom, 1986; Feduccia, 1999). Yet recently, a third and growing view accepts the dinosaurian origin of birds together with the arboreal hypothesis for the origin of flight. This we coin as the 'Dinosaur-trees-down' hypothesis. The 'Dinosaur-trees-down' hypothesis encapsulates our view because we believe that (1) a majority of evidence supports the dinosaurian origin of birds, and (2) as we show below, all current fossil evidence from both early birds and dinosaurs supports the arboreal hypothesis for the origin of flight.

We believe that the habit and life style of the most primitive birds and their closest ancestors is central to the issue of the origin of the flight. The recent record of arboreal dinosaurs from the Early Cretaceous of Liaoning provides the best evidence yet for testing our hypothesis. But how can we reconstruct the habits of extinct forms? The curvature of the pedal claws has been shown to be a simple but effective means of distinguishing between ground-living and tree-living birds (Feduccia, 1993). The shape of the cross-section of the claws can also be useful here (Yalden, 1997), and also the proportions of pedal digits, i. e., distal toes are relatively longer in arboreal forms and *vice versa* (Hopson, 2001; Zhou and Farlow, 2001).

Microraptor is a small dromaeosaurid dinosaur with foot features that indicate an arboreal habit (Xu et al., 2000). Such traits include slender and recurved pedal claws, a distally positioned digit I, and elongated penultimate phalanges, all comparable to those of arboreal birds (Xu et al., 2000). Probably just as significantly, *Sinornithosaurus*, another dromaeosaurid from the Early Cretaceous of China, has feet covered by elongated feathers, strongly suggesting that it was also arboreal. *Epidendrosaurus* from the Late Mesozoic of Inner Mongolia, the oldest known maniraptoran and occupying a position very close to the transition from dinosaurs to birds, seems to have been arboreal too (Zhang et al., 2002). Evidence for this is to be found not only in toe proportions (the penultimate phalanges are longer than the phalanges immediately proximal to them), but also in the surprisingly distal position of the first pedal digit. The first pedal digit is relatively long and is positioned so far distally that the distal ends of the four metatarsal bones are nearly on the same level; it is a construction very similar to that in advanced arboreal birds.

The most primitive bird *Archaeopteryx* has the pedal claw curved like that of a trunk-climbing bird (Feduccia, 1993). *Confuciusornis* is similar, not just in the curvature of the claws but also in cross-section shape (Zhou and Farlow, 2001), indicating that both birds possessed climbing capability. The toe proportions of *Archaeopteryx* and *Confuciusornis* indicate that both could perch; yet that capability is still not as good as in typical perching birds (Zhou and Farlow, 2001). Pedal toe proportions in *Jeholornis* are similar to those in most other basal birds, and are more-or-less transitional between those of a dinosaurian ancestor and more advanced perching birds such *Sinornis* (Sereno and Rao, 1992) and *Boluochia* (Zhou, 1995).

It should be pointed out that the foot is not the only apparatus involved in climbing and the arboreal life of early birds and feathered maniraptoran dinosaurs. The manual toe proportions of these animals are similar to those in the foot of arboreal birds, with elongated penultimate phalanges. We interpret such structures as adaptations for grasping tree branches. As the perching capability of the foot improved, so the climbing or grasping role of the forelimb declined (claws reduced, loss of phalanges and shortening of distal phalanges). Such trends are well documented in the fossil forms from the Early Cretaceous of China.

Evidently then, all the most basal birds were arboreal; and their closest dinosaurian relatives were arboreal too. From all this evidence, we find the arboreal hypothesis the most likely explanation for the origin of flight in birds. Further, one of the major differences between birds and dinosaurs is the reversed hallux in birds, which we interpret as an adaptation for improved arboreal life, again consistent with the arboreal hypothesis scenario.

During the evolution of birds and flapping flight, feathers evolved in their own way. The initial unbranched feathers in basal coelurosaurs were probably only for display or thermoregulation; but in arboreal maniraptoran dinosaurs, primitive feathers were probably used to help in balance and/or steering while climbing or jumping, or helped to reduce the rate of descent while falling or jumping to the ground. But only birds evolved asymmetric flight feathers for flapping flight; and from there more derived feathered structures, such as the alula, developed in later, more advanced birds such as the enantiornithines.

So the 'Ground-up' hypothesis for the origin of flight of birds is not supported by any substantial fossil evidence; on the contrary, the 'Dinosaur-trees-down' hypothesis is not only consistent with the phylogenetic background for the origin of birds, but also with all reconstructions of the arboreal habit of early birds, as well as their putative ancestors.

5 Feathers and endothermy

The issue of the origin of feathers has been dealt with by us in a separate paper in the Proceedings of this Congress, so here we will only focus on one topic, the relationship between feathers and endothermy. All modern birds are hot-blooded; but what about fossil birds? Feathers have been considered a unique characteristic of endothermic birds. The discovery of feathered dinosaurs, however, has not only changed our view on the origin of birds and the life of dinosaurs, but also of the role of feathers in avian evolution. The basal coelurosaurid *Sinosauropteryx* has proto-feathers, but their function remains speculative; they could have functioned either for thermoregulation or display. As this dinosaur was a bipedal cursorial animal, its protofeathers were not yet linked with flight. It is also notable that the crest in feathered dinosaurs, including *Sinosauropteryx* and dromaeosaurids, seems to provide evidence for the display hypothesis for the origin of feathers.

It is generally accepted that dinosaurs are more similar to birds than extant reptiles in terms of growth rates (Zhang et al., 1999; Erickson et al., 2001; Padian et al., 2001), an assessment consistent with the currently popular view that birds are the crow group of the Dinosauria. But how, exactly, are dinosaurs close to extant birds in physiology? Are they still ectotherms or not? Erickson et al. (2001) found that all dinosaurs grew at rates more rapid than those of extant reptiles; but as a whole the rates were not intermediate between, nor equivalent to, those in birds and mammals. Erickson et al. (2001) also noticed that non-avian dinosaurs never attained the extremely rapid rates found in extant altricial birds; even the largest sauropods would have grown at rates half those of a scaled-up altricial bird. Small dinosaurs, moreover, tended to have slow growth rates. Erickson et al. (2001) estimated that small non-avian dinosaurs have growth rates typically 2 – 7 times slower than those of precocial birds of similar size.

It is notable that the recently discovered Chinese dromaeosaurids (e.g. *Microraptor*), which are close relatives of birds, are very small; they probably had much slower growth rates than large dinosaurs. The adaptation towards small size during the transition from dinosaurs to birds does not seem to be advantageous for the evolution of endothermy. As Padian et al. (2001) have correctly pointed out, reduction in body size was almost certainly associated with a reduction in the time needed to reach adult size. The relative elongation of forelimbs and feathers, coincident with a phyletic reduction in adult size, would have been advantageous for the inception of flight by decreasing wing loading and improving the power-to-weight ratio. Reduction in size continued on into the early evolution of birds. All early enantiornithines are smaller than such basal forms as *Archaeopteryx*, *Sapeornis* and *Jeholornis*.

There is currently no compelling evidence that any dinosaurs were hot-blooded. The association of feathers with endothermy is purely speculative, not only for dinosaurs but probably also for some early birds. Bone histology studies show that enantiornithines lacked vascular canals and had clear lines of arrested growth (LAGs), which are distinct from those of *Confuciusornis* and modern birds. These features are commonly found in extant ectothermic reptiles such as crocodiles. Basal birds probably did not possess the physiological organization of modern birds, and they could have been ectodermic. The late Cretaceous ornithurine birds *Hesperornis* and *Ichthyornis* have higher vascularity and lack LAGs, showing greater similarity to extant birds. Based on these data, Padian et al. (2001) suggested that modern birds gained a fully endothermic metabolism gradually. Zhang et al. (1999) compared the bone histology of *Confuciusornis* with that of an extant crocodile *Alligator* and modern birds. They concluded that *Confuciusornis* was more like extant birds than enantiornithines, and further suggested that it could be endothermic. Because *Confuciusornis* is phylogenetically more basal than the enantiornithines, its endothermy probably evolved independently.

Early Cretaceous ornithurine birds such as *Yixianornis* and *Yanornis* from China possess flight structures almost indistinguishable from those of modern birds (Zhou and Zhang, 2001b). Phylogenetically they are also much closer to extant birds than the enantiornithines and other basal forms such as *Confuciusornis*. Even though they retained some primitive traits that preclude them from being the direct ancestor of modern birds, the early ornithurines represented the highest evolutionary level attained by birds in the Early Cretaceous. In contrast to the enantiornithines, which were generally small in the Early Cretaceous, the ornithurines were all of considerable size, indicating that they had faster growth rates. It is this group that probably first possessed true endothermy among early birds.

Although some of the features thought to be unique to birds, such as feathers, are now known to have appeared earlier in dinosaurian ancestors, there are still many fundamental traits in modern birds that did not arise until later stages in avian evolution. Thus the horny beak is first known to have appeared in the Early Cretaceous *Confuciusornis*, a pygostyle first appeared in such basal birds as *Sapeornis*, an alula first appeared in the Early Cretaceous *Protopteryx*, and well-developed procoracoids, triosseal canals and sternal keels first appeared in the Early Cretaceous ornithurines. The Early Cretaceous is undoubtedly a critical stage for the evolution of birds, and we believe that like many other features, avian endothermy first appeared then.

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