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# The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence

**Abstract** The study of the origin and early evolution of birds has never produced as much excitement and public attention as in the past decade. Well preserved and abundant new fossils of birds and dinosaurs have provided unprecedented new evidence on the dinosaurian origin of birds, the arboreal origin of avian flight, and the origin of feathers prior to flapping flight. The Mesozoic avian assemblage mainly comprises two major lineages: the prevalent extinct group Enantiornithes, and the Ornithurae, which gave rise to all modern birds, as well as several more basal taxa. Cretaceous birds radiated into various paleoecological niches that included fish- and seed-eating. Significant size and morphological differences and variation in flight capabilities, ranging from gliding to powerful flight among early birds, highlight the diversification of birds in the Early Cretaceous. There is little evidence, however, to support a Mesozoic origin of modern avian groups. Controversy and debate, nevertheless, surround many of these findings, and more details are needed to give a better appreciation of the significance of these new discoveries.

and Rao 1992; Hou et al. 1995, 1996, 2004; Martin and Zhou 1997; Chiappe et al. 1999; Zhang and Zhou 2000; Zhou and Zhang 2002a, 2002b). Many of the exceptionally preserved bird-like theropod dinosaurs from Mongolia, Argentina, North America, and China, in particular the Early Cretaceous feathered-dinosaurs from Liaoning, have fueled discussions on the origin of birds and fired the imagination of the public (Chen et al. 1998; Novas and Puerta 1997; Ji et al. 1998; Norell and Makovicky 1999; Clark et al. 2001; Norell et al. 2002; Xu et al. 2003; Zhou et al. 2003). Reexamination of fossils such as *Archaeopteryx* (Elzanowski 2001; Chatterjee 2003; Alonso et al. 2004) and *Longisquama* (Jones et al. 2000b) has resulted in new perspectives and controversies concerning the early evolution of birds. Studies on the phylogeny (Padian and Chiappe 1998a, 1998b; Chiappe and Witmer 2002), histology (Ricqlès et al. 2001; Chinsamy 2002), development (Burke and Feduccia 1997; Kundrát et al. 2002; Feduccia and Nowicki 2002), functional morphology (Gatesy and Dial 1996; Yalden 1997; Hopson 2001;

## Introduction

The past decade has witnessed a boom in the study of Mesozoic birds, largely as a consequence of abundant finds of diverse early bird fossils from Cretaceous deposits worldwide (Sanz et al. 1996; Forster et al. 1996, 1998; Padian and Chiappe 1998a, 1998b; Feduccia 1999a; Norell and Clarke 2001; Chiappe and Dyke 2002). Of these, the Early Cretaceous deposits of Liaoning, northeast China (Fig. 1) have been the most productive (Sereno

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**Fig. 1** Famous bird and feathered dinosaur locality Sihetun village in Beipiao, Liaoning, northeast China

Burgers and Chiappe 1999; Jones et al. 2000a; Zhou and Farlow 2001), and tracks (Lim et al. 2000; Melchor et al. 2002) of birds and their ancestors have also aided our understanding of early avian evolution. Molecular studies of modern avian taxa have led to new proposals concerning the origin and diversification of the major groups of extant birds (Ericson et al. 2001; Van Tuinen and Hedges 2001).

As a result of the increasing number of discoveries and studies of Mesozoic birds and their putative ancestors, Mesozoic birds have become a much more popular topic at the meetings of the Society of Avian Paleontology and Evolution (SAPE) and a number of symposium proceedings and books have been published focusing on the origin of birds and of bird flight (Feduccia 1996, 1999a; Chatterjee 1997; Dingus and Rowe 1997; Paul 2002; Chiappe and Witmer 2002).

Despite overwhelming evidence supporting the dinosaurian origin of birds, there are still many unanswered questions, e.g., those concerning the origin of bird flight (Zhou and Hou 1998; Xu et al. 2000, 2003; Prum 2003; Stokstad 2000, 2003; Witmer 2002; Dial et al. 2003). In addition, relatively little is known about the origin and the immediate ancestor of all extant avian groups. The aim of this review is, therefore, to provide a summary of the new discoveries of Mesozoic birds and feathered dinosaurs over the past decade, and the implications that these have for the origin and evolution of early birds, their diversification, and the development of feathers and flight.

## New discoveries of Mesozoic birds: their habit and diet specializations

More fossils of Mesozoic birds have been discovered in the past two decades than had been discovered in total from the 1860s to the 1970s. Most of the recent discoveries of early birds are from continental Early Cretaceous deposits, with a few from the Late Cretaceous. Interestingly, with the new discoveries, the Early Cretaceous, which previously had the poorest avian record from the Mesozoic, has now become the best-known Mesozoic period in terms of both the number of specimens found and the amount of information on the diversification of early birds. Our understanding of avian evolution in the Mesozoic has been greatly enriched by these new finds (Feduccia 1996, 1999a; Chiappe and Witmer 2002; Chiappe and Dyke 2002; Zhou et al. 2003). The exceptional preservation of many completely articulated avian fossils with stomach contents, including seeds, gastroliths, and fish remains, provides new information concerning the diet and habits of early birds (Zhou and Zhang 2002a, 2003b; Zhou et al. 2002; Hou et al. 2004).

Enantiornithine birds were first recognized in 1981 as a group of specialized and extinct birds from the Late Cretaceous of Argentina (Walker 1981). Later, many Early Cretaceous forms were referred to the Enantiornithes on the basis of a suite of uniquely shared synapomorphies such as metacarpal III distinctly extending past metacarpal II distally and a V-shaped furcula (Martin 1995). Until now, no enantiornithine has been reported from the Cenozoic: thus it is likely that this group of early birds became extinct at the end of the Mesozoic together with non-avian dinosaurs. Enantiornithines coexisted with another derived avian group, Ornithurae, which includes all living birds, as well as their basal relatives, which all possessed a flight apparatus nearly identical to those of modern flying birds (Zhou and Zhang 2001a). Synapomorphies of the Ornithurae include, among many others, an elongated sternum with a keel extending along its full length and a coracoid with a well-developed procoracoidal process and a round fossa for articulation with the scapula. In addition, several more basal avian taxa have been recognized from the Early Cretaceous that share plesiomorphic resemblances to the oldest known bird, *Archaeopteryx* (Martin 1991; Wellnhofer 1992). These basal forms include *Confuciusornis*, *Sapeornis*, *Rahonavis*, and *Jeholornis*. Enantiornithes remains the most important group of early birds in terms of the number of taxa, ecological diversification, and their nearly global distribution during the Cretaceous (Chiappe and Walker 2002).

## Enantiornithine birds

All known enantiornithines appear to be perching forms, as indicated by their large and curved pedal claws and toe proportions adapted to an arboreal life. These forms include such well-preserved taxa as *Sinornis* (Sereno and Rao 1992), *Cathayornis* Zhou, Jin & Zhang 1992, and *Boluochia* (Zhou 1995a), as well as several recently described forms such as *Eoenantiornis* (Hou et al. 1999a), *Liaoxiornis* (Hou and Chen 1999), *Protopteryx* (Zhang and Zhou 2000), *Longipteryx* (Zhang et al. 2001), and Longirostravis (Hou et al. 2004).

Detailed description and phylogenetic discussion of several Early Cretaceous birds from Spain has led to the recognition of additional enantiornithine synapomorphies, confirming previous suggestions that they belonged to this clade (Fig. 2). These forms include the Spanish birds *Concornis* (Sanz and Buscalioni 1992; Sanz et al. 1995), *Iberomesornis* (Sanz and Bonaparte 1992; Sereno 2000), and *Neuquenornis* (Chiappe and Lacasa-Ruiz 2002). More Late Cretaceous enantiornithines have been reported from areas outside South America. For example, a new species was reported from marine deposits in Alabama, USA (Chiappe et al. 2002a). Description of a new skull of the Late Cretaceous enantiornithine *Gobipteryx minuta* from Mongolia not only provides more information about the palatal structure of Mesozoic birds but also shows that *Nanantius valifanovi* is probably a junior synonym of *Gobipteryx minuta* (Chiappe et al. 2001).

Among the recently discovered Early Cretaceous enantiornithines from China, *Protopteryx* (Zhang and Zhou 2000) from Hebei Province is probably the most noteworthy as it is considered to be the most primitive known member of the Enantiornithes. The fossil-bearing deposit yielding its remains is usually referred to the Dabeigou

**Fig. 2** Phylogenetic relation-
ship of major groups of birds
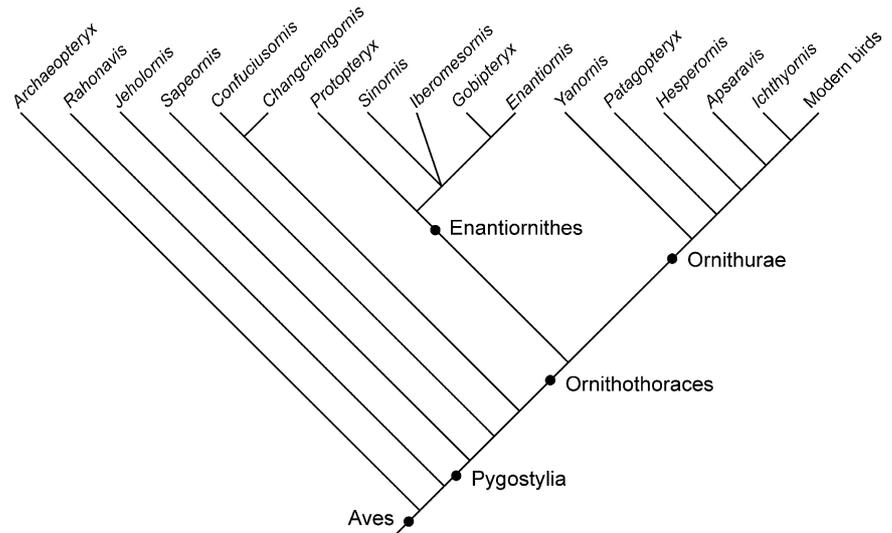


Formation, which is generally believed to be equivalent or slightly older in age to than the Yixian Formation in neighboring Liaoning Province. It has an alular digit of equal length to that in such primitive forms as *Archaeopteryx*, *Jeholornis*, and *Confuciusornis*. However, in contrast to these basal forms, *Protopteryx* has a preserved alula associated with the alular digit, suggesting that it already possessed sophisticated flight skills that were absent in more basal birds. Since several other enantiornithine birds (e.g., *Eoalulavis* and *Eoenantiornis*: Sanz et al. 1996; Hou et al. 1999a) also possess an alula, it is most likely that this advanced flight feature appeared at the origin of the Enantiornithes.

The recently discovered *Longipteryx* (Zhang et al. 2001) is probably the most important taxon in terms of the ecological differentiation of the Enantiornithes. Like *Sinornis*, *Cathayornis*, *Eocathayornis* (Zhou 2002), and *Boluochia* (Zhou 1995a), this fossil was collected from the Jiufotang Formation, which overlies the Yixian Formation in Liaoning Province. It has features of the foot and toe, such as the trochleae of the metatarsals being almost on the same level, which indicate a strong perching capability. However, this bird is distinguishable from all other known enantiornithines in having a wing remarkably longer than the hindlimb, a ratio of wing (humerus + ulna + carpometacarpus) to leg (femur + tibiotarsus + tarsometatarsus) length of more than 1.5, a tibiotarsus shorter than the humerus and ulna, and a skull with an elongated snout and densely distributed teeth. *Longipteryx* was recognized as a new ecological type different from all known members of the Enantiornithes (Zhang et al. 2001). It was apparently adapted for feeding on fishes, perhaps perching in nearby trees while waiting in ambush. In this respect, *Longipteryx* resembles coraciiform birds such as the kingfisher in having powerful wings, well-developed perching capability and relatively short hindlimbs (Zhang et al. 2001). *Longipteryx* also shows that enantiornithines had experienced a rapid increase in ecological diversity by the Early Cretaceous.

*Longirostravis* is the latest reported enantiornithine from the Yixian Formation in China. It is unique among enantiornithines for having an extremely slender and pointed snout. It was suggested that the long slender bill of *Longirostravis* could be explained as a tool for probing in the mud (Hou et al. 2004). Also, the teeth in the rostralmost portion of the skull probably facilitated securing the prey. Such a new discovery indicates that, by the Early Cretaceous, enantiornithines had diversified significantly in diet.

Other recently described enantiornithines from China include *Eoenantiornis* from the Yixian Formation, in which the alula was also preserved, which retained some transitional features between *Protopteryx* and more advanced enantiornithines. *Eocathayornis*, from the same locality as *Cathayornis* (Jiufotang Formation), shows more primitive traits than *Cathayornis* in such features as the sternum (Zhou 2002).

All known Early Cretaceous enantiornithines are relatively small in size in comparison with contemporaneous ornithurines and other basal forms. A nestling bird from the Lower Cretaceous of Spain (Sanz et al. 1997) provides evidence of the presence of a diapsid skull. Another well-known taxon, *Liaoxiornis* (a juvenile), has preserved a relatively long tail with a pygostyle. Several new specimens referable to this taxon possess enantiornithine synapomorphies. Since the holotype of *Liaoxiornis* is clearly a juvenile, it cannot be regarded as the smallest known Mesozoic bird taxon (Hou and Chen 1999).

## Ornithurine birds and their implications for the origin of modern avian groups

Ornithurine birds are less well known than enantiornithines in the Early Cretaceous, although our knowledge of the evolution of ornithurines in the Late Cretaceous, and of their explosive radiation in the Cenozoic, is much more comprehensive. Ornithurine birds are the only group of Mesozoic birds to have survived the K/T extinction

(Feduccia 1999a; Hope 2002). Thus, studies on Mesozoic ornithurines not only help us to understand the early radiation of birds, but also illuminate the origin of living avian groups.

Little was known about Early Cretaceous ornithurines until the late 1970s and 1980s when two incomplete birds, *Ambiortus* (Kurochkin 1985, 1999) and *Gansus* (Hou and Liu 1984), were reported from Mongolia and China, respectively. However, due to their fragmentary preservation, it was hard to infer their phylogenetic relationships to other early birds and living avian groups. Better-preserved taxa such as *Chaoyangia*, *Songlingornis* and *Liaoningornis* were reported from the Early Cretaceous of China in the 1990s, providing evidence of the early ornithurine radiation. It should be noted that although *Otogornis* was referred to the ornithurine clade Ambiortiformes (Kurochkin 1999), it is now generally believed to be an enantiornithine, as it possesses typical enantiornithine features in the scapula–coracoid articulation and the humerus (Zhou and Hou 2002; Chiappe and Walker 2002).

Only recently have nearly complete skeletons of ornithurine birds been found. These come from the Early Cretaceous deposits of Liaoning and add substantially to our understanding of the early evolution of ornithurine birds with regard to flight capability, habit, dietary differentiation, and relationships to modern birds. The ornithurines *Yixianornis* and *Yanornis* (Zhou and Zhang 2001a; Zhou et al. 2002) are represented by nearly complete articulated skeletons, the latter being represented by several complete individuals. Both taxa exhibit a well-developed flight apparatus, suggesting strong flying capabilities virtually identical to those of modern birds. The most significant features are a longitudinally elongated sternum with a long and deep keel, a strut-like coracoid with a well-developed and large procoracoid process, a completely fused carpometacarpus, and a short pygostyle, as in living birds.

Despite the appearance of significantly advanced flight features in *Yixianornis* and *Yanornis*, they also retain several primitive traits that exclude them from a close relationship with any of the more advanced groups within the Neornithes. For instance, they still retain reduced teeth in the jaws, there are still two claws on the wing, and the pubic foot is unreduced, as in more primitive forms. The combination of advanced flight features with some primitive features in the pelvis and skull highlights the mosaic pattern of character evolution in early birds.

*Apsaravis* from the Late Cretaceous of Mongolia (Norell and Clarke 2001) is taxonomically placed between *Ichthyornis* and more basal forms. It represents the most basal bird with an extensor process on the hand, thus showing a stronger flight capability than Early Cretaceous ornithurines. *Apsaravis* displays several features that were previously known only in the Enantiornithes, indicating a complex pattern of character evolution. The presence of several autapomorphies in *Apsaravis* excludes it from the direct ancestry of extant avian groups. Another Late

Cretaceous ornithurine, *Limenavis*, from Patagonia, was recognized as even more advanced than *Ichthyornis*, lying just outside the avian crown clade (Clarke and Chiappe 2001).

Paleontological studies show that modern avian groups probably first appeared in the Paleocene or Eocene and experienced an explosive radiation in the early Cenozoic (Feduccia 1995, 1999a, 2003). Molecular studies have, however, favored a much earlier origin of modern avian groups, nearly 50 million years earlier than that inferred from the fossil record (Hedges et al. 1996; Cooper and Penny 1997; Kumar and Hedges 1998; Cracraft 2001; Ericson et al. 2001; Van Tuinen and Hedges 2001). Although ornithurine birds possessed modern sophisticated flight skills by the Early Cretaceous, and had occupied paleoecological niches (mostly near-shore environments) that were seldom visited by other Mesozoic birds, none of the Cretaceous ornithurines can be regarded as crown group birds. Material used to propose the existence of a Cretaceous parrot (Stidham 1998, 1999; Dyke and Mayr 1999) is considered inadequate. A Cretaceous loon has been reported from the Antarctic (Chatterjee 2002), but has not yet been commonly accepted. Therefore, recent ornithurine discoveries lend further support to the Cenozoic origin of the modern bird groups.

*Yixianornis* and *Yanornis* have jaws with densely packed teeth, suggesting that they were probably piscivorous. Fish remains in the stomach of a specimen referable to *Yanornis*, including vertebrae, opercular elements, and ribs, support this hypothesis (Zhou et al. 2002). The pedal digits of both *Yixianornis* and *Yanornis* are relatively long with moderately curved claws, and their toe proportions also show a shore-wading adaptation, in contrast with the typical arboreal foot of enantiornithines and other basal birds. The first known Chinese Mesozoic bird, *Gansus*, is also an ornithurine. It is approximately the same size as *Yanornis*, but its foot is even more specialized for use in water or near a water environment (Hou and Liu 1984).

Many bird tracks have recently been reported from Mesozoic deposits, mainly Cretaceous lacustrine and costal plain deposits (Lockley and Rainforth 2002). For instance, footprints of a presumably web-toed bird were reported from the Early Cretaceous of Korea (Lim et al. 2000), which was paleogeographically close to Liaoning, northeast China.

The infamous composite fossil '*Archaeoraptor*' is now recognized as comprising the counterpart tail of the holotype of the dromaeosaurid dinosaur *Microraptor* and a nearly complete skeleton of *Yanornis* (Xu et al. 2000; Zhou et al. 2003). Thus, the 'better half' of '*Archaeoraptor*' is in fact a fish-eating bird rather than the body of a long-tailed bird (Zhou et al. 2002). As will be explained below, all known long-tailed birds have a relatively advanced wing, albeit not necessarily as advanced as in an ornithurine birds.

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## More basal birds

Even with the recent increase in Mesozoic bird finds, *Archaeopteryx* remains the oldest and most primitive bird, and Enantiornithes and Ornithurae remain the two most important monophyletic avian groups in the Mesozoic, comprising the majority of known early avians (Fig. 2). In addition, there are several basal avians that are phylogenetically intermediate between *Archaeopteryx* and the Enantiornithes + Ornithurae. These basal forms include Confuciusornithids, *Rahonavis* (see below under 'Controversial birds'), *Sapeornis* and *Jeholornis*.

*Confuciusornis* is the oldest bird known to possess a horny beak (Hou et al. 1995; Chiappe et al. 1999). It was first reported from the Yixian Formation, which is dated at 125 Ma. More recently, *Confuciusornis* specimens were collected from the Jiufotang Formation (Swisher et al. 2002). The age of the Jiufotang Formation is 120 million years (He et al. 2004). These discoveries indicate that confuciusornithids probably lived for approximately 15 Ma in the Early Cretaceous. Several species of *Confuciusornis* have been described (Hou 1997).

Detailed descriptions of *Confuciusornis* have revealed anatomical features that were previously unknown in Cretaceous birds, e.g., a diapsid skull, suggesting some primitive characters in common with *Archaeopteryx* (Peters and Ji 1998; Martin et al. 1998; Hou et al. 1999b). *Confuciusornis* has a fully opposable foot, as in *Archaeopteryx*, and its claw and toe proportions indicate perching capabilities (Zhou and Farlow 2001).

*Changchengornis* was a new genus referred to the Confuciusornithidae (Ji et al. 1999). This fossil is from the same horizon as *Confuciusornis*, but it is relatively smaller in size. It is distinguished from *Confuciusornis* on the basis of a shorter and taller lower jaw, a deltopectoral crest that is unperforated, and a relatively long hallux. Whether or not the small size of this genus is due to its juvenile status remains to be confirmed.

*Sapeornis* is a recently described bird from the Jiufotang Formation (Zhou and Zhang 2002b, 2003b). Its extremely elongated forelimbs and large body size distinguishes it from all other known Mesozoic birds. It represents the largest bird known from the Early Cretaceous; it is slightly larger than *Archaeopteryx*. Phylogenetically, *Sapeornis* occupies a more basal position than *Confuciusornis*. However, it resembles *Confuciusornis* in possessing a large fenestra at the proximal end of the humerus, in contrast to other Mesozoic birds. The skull is generally similar to that of *Archaeopteryx* and most enantiornithines. There are four teeth in the premaxilla, as in *Archaeopteryx* and most enantiornithine birds, but teeth are absent from the lower jaw. The furcula of *Sapeornis* is distinctive in having a hypocleidum (apophysis furculae), as in enantiornithines, while the clavicles are robust, as in *Archaeopteryx* and *Confuciusornis*. *Sapeornis* also has a hand with a phalangeal formula of '2–3-2', which is more advanced than that of *Archaeopteryx*, *Jeholornis* and *Confuciusornis*. Thus, *Sapeornis* has a combination of derived and primitive features: a short, robust non-strut-like coracoid and a fibula reaching the distal end of the tarsal joint, as in *Archaeopteryx*, and a pygostyle, reduced manual digits, and well-fused carpometacarpus, as in more advanced birds. This represents further evidence for a mosaic pattern in the early evolution of birds. It is also noteworthy that gastroliths were found in one specimen of *Sapeornis*, suggesting an herbivorous diet (Zhou and Zhang 2003b).

Among recently described basal birds, *Jeholornis* is undoubtedly the most important (Zhou and Zhang 2002a, 2003a). It not only exhibits a complete skeletal tail comparable to that of *Archaeopteryx*, *Rahonavis* and dromaeosaurs, but also has well-preserved seeds in the stomach, indicating that it is a seed-eating bird. *Jeholornis* is probably only slightly more derived than *Archaeopteryx* and *Rahonavis*. It has a fused carpometacarpus, a scapula with a dorso-laterally exposed glenoid facet, a better-developed sternum (with a pair of lateral processes) and a more elongate coracoid, suggesting powerful flight capability. In contrast, the tail includes up to 27 caudal vertebrae (Zhou and Zhang 2003a), which is more than in *Archaeopteryx* (up to 23 caudals). The elongated prezygopophyses and chevrons of the caudal vertebrae bear a close resemblance to those of dromaeosaurs, confirming a close link between birds and this lineage of non-avian theropod dinosaurs.

The seeds in the stomach of the holotype of *Jeholornis* are about 1 cm in diameter. None of the referred specimens of *Jeholornis* have preserved gut contents. At present it cannot be determined whether the seeds belong to angiosperms or gymnosperms.

With the new discoveries of numerous Mesozoic birds, we now have a much better picture of the earliest stage of avian evolution, although *Archaeopteryx* is still isolated in the Jurassic as the oldest and most primitive bird. By the Early Cretaceous, however, there were already significant changes in bird morphology, ecology and diet.

## Controversial birds

As discussed above, one of the more contentious issues raised by the study of the feathered dinosaurs and their close relatives is that some of them (e.g., oviraptorosaurids and dromaeosaurids) have been proposed to be flightless birds. However, there are other controversial Mesozoic birds that have drawn even more attention with debates focusing on whether they are birds, non-avian dinosaurs, or composites of more than one taxon.

*Protoavis texensis* was described as a Late Triassic bird (Chatterjee 1991, 1999). This attracted a lot attention because if it were correctly identified as a bird, then it would be 75 million years older than *Archaeopteryx*. Many workers, however, have argued that it is a chimera belonging to two different species. For this reason, it has neither been widely accepted nor seriously considered as a Triassic bird (Witmer 2001). Although some workers have accepted *Protoavis* as a bird, and argued that it would disapprove the theropod relationships of birds

(Bock 1997), Witmer (2002), who has examined the material and is one of the few workers to have seriously considered Chatterjee's proposal, argued that the avian status of *P. texensis* is probably not as clear as generally portrayed by Chatterjee, and further recommended minimization of the role that *Protoavis* plays in the discussion of avian ancestry. On the other hand, Witmer (2002) argued that *Protoavis* represents a temporal range extension for Coelurosauria, which helps to provide some circumstantial support for the dinosaurian origin of birds.

A recent report of possible Triassic avian footprints merits attention, as the tracks show a clearly preserved hallux, which is currently known only in birds (Melchor et al. 2002). At present, the best we can say about Triassic birds is that more material is needed to confirm their existence.

*Mononykus* represents another controversial Mesozoic animal characterized by a very reduced hand. It was first reported as a bird from the Late Cretaceous of Mongolia (Perle et al. 1993). Later, related taxa (e.g., *Shuvuuia* and *Patagonykus*) were reported and referred to the family Alvarezsauridae (Chiappe et al. 1998, 2002b). The avian status of *Mononykus* was questioned immediately after its publication, due largely to its ambiguous avian features such a keeled sternum, which was proposed to be a digging adaptation developed independently of that of birds (Wellnhofer 1994; Zhou 1995b; Feduccia 1996; Martin 1997). These earlier questions regarding its avian status have, however, been criticized as being based on phylogenetically unsound methods (Chiappe et al. 1995, 1997; Chiappe and Dyke 2002). Ironically, several more detailed phylogenetic analyses also questioned the avian relationships of *Mononykus* and its alvarezsaurid relatives (Sereno 1999, 2001; Norell et al. 2001; Novas and Pol 2002). Interestingly none of these cladistic analyses agree on the position of Alvarezsauridae except in placing this group outside Aves. For example, Sereno (1999, 2001) proposed a sister-taxon relationship between alvarezsaurids and ornithomimids, as first proposed by Martin (1997), while other authors have proposed a sister-taxon relationships between alvarezsaurids and birds (Chiappe 2001) or alvarezsaurids and birds plus some other theropod lineages (Norell et al. 2001; Novas and Pol 2002). Consequently, it has been almost universally accepted that *Mononykus* and its alvarezsaurid relatives are not birds.

*Rahonavis* is a Late Cretaceous long-tailed bird from Madagascar (Forster et al. 1998). Some suspicion has surrounded the association of its preserved skeletal elements: Feduccia (1999a) suggested that they represented a composite of an avian wing and pectoral girdle with a theropod pelvis, hindlimb, and tail. Chiappe and Dyke (2002) argued that although the fossil was mostly disarticulated, the single specimen has no duplicated elements and was found on a surface of less than 0.14 m$^2$, suggesting that all described bones belong to a single individual. In addition to taphonomic arguments, Forster et al. (1998) also provided other evidence supporting the association of these skeletal remains: they conducted separate cladistic analyses, one scoring the whole specimen and the other excluding the forelimb and shoulder girdle, but recorded the same phylogenetic result in both cases.

The controversy surrounding *Rahonavis* is probably partly related to another bird, *Vorona*, which was reported from the same quarry in Madagascar (Forster et al. 1996). The holotype of *Vorona* was represented only by hindlimbs; however, *Vorona* is clearly a much more advanced bird, probably an enantiornithine (Feduccia 1999a), and it is distinctively different from *Rahonavis*.

The recent discovery of *Jeholornis*, another long-tailed bird with a combination of advanced forelimb and pectoral characters and some striking dromaeosaurid features, also shows the complex mosaic pattern of character changes in early avian evolution. Consequently, there is currently no evidence to suggest that *Rahonavis* is a composite. Therefore there is no reason not to regard it as another long-tailed bird. Like *Jeholornis*, *Rahonavis* also possesses several features that bear resemblances to non-avian theropod dinosaurs and are more primitive than in *Archaeopteryx*. For instance, the sickle-like second pedal claw and the elongated chevron of the tail in *Rahonavis* provide strong evidence supporting a close relationship between birds and theropod dinosaurs.

## The origin of birds: is the debate already over?

The study of bird origin is over 150 years old. The dinosaurian origin of birds had gained broad support since the resemblance between birds and theropods was first recognized by Huxley (1868) and other paleontologists. This theory held sway until the publication of the classic book '*The origin of birds*' by Heilmann (1926). Heilmann showed that despite the similarity between birds and theropods, dinosaurs were probably too specialized (e.g., he suggested that the reduced clavicles of dinosaurs could not have evolved into the furcula in birds) to be the direct ancestors of birds. Instead he proposed that birds and dinosaurs probably evolved from a common ancestor in a group called Thecodontia. Heilmann's proposal was so authoritative and influential that the thecodont origin of birds became the prevalent theory for nearly half a century.

The resurrection of the dinosaurian–bird hypothesis by John Ostrom in the 1970s (Ostrom 1976a), with the support of cladistic analysis since the 1980s (Gauthier 1986; Sereno 1999; Norell et al. 2001; Clark et al. 2002), has resulted in a general consensus among many paleontologists on the validity of the dinosaurian–bird hypothesis. The discovery of many new and better preserved theropods in the past two decades, particularly those with feather impressions from the Lower Cretaceous of Liaoning, have provided some of the most compelling evidence supporting the hypothesis (Xu et al. 2003; Zhou et al. 2003). For many paleontologists the evidence supporting a dinosaurian origin of birds is much stronger than we could have hoped for only a few years ago. Many paleontologists are tempted to declare the end of the de-

**Table 1** List of some most remarkable 'bird' features in theropod dinosaurs

| | |
|---|---|
| Furcula (wishbone) | Oviraptorosaurids, dromaeosaurids |
| Retroverted pubis | Dromaeosaurids, troodontids |
| Sternal keel | Alvarezsaurids |
| Third manual digit comprising two small phalanges | Oviraptorosaurids |
| Branched feathers | Oviraptorosaurids, dromaeosaurids, and other coelurosaurids |
| Asymmetric feathers | Dromaeosaurids |
| Alula | Dromaeosaurids |
| Nesting behavior | Oviraptorosaurids |

bate on the origin of birds (Prum 2002), stating that birds are dinosaurs just as humans are mammals. On the other hand, there is still disagreement. For instance, Alan Feduccia, who is one of the strongest opponents of the dinosaurian origin of birds, added a new chapter to his book (Feduccia 1999a) entitled '*T. rex* was no four-ton roadrunner and other revelations'. It is clear that the debate is not over (Feduccia 2002; Galis et al. 2003).

## Newest evidence

The discoveries of feathered dinosaurs have provided some of the most significant evidence supporting the dinosaurian origin of birds. Since 1996, a total of eight species of feathered dinosaurs have been reported from the lacustrine Early Cretaceous deposits of Liaoning Province. They are *Sinosauropteryx prima* (Chen et al. 1998), *Protarchaeopteryx robusta* (Ji et al. 1998), *Caudipteryx zoui* (Ji et al. 1998), *Caudipteryx dongi* (Zhou and Wang 2000), *Beipiaosaurus inexpectus* (Xu et al. 1999a), *Sinornithosaurus millenii* (Xu et al. 1999b), *Microraptor zhaoianus* (Xu et al. 2000), and *Microraptor gui* (Xu et al. 2003). It is notable that integumentary structures in these dinosaurs can be roughly classified into two categories: one mostly fiber-like and unbranched, and the other including unambiguous true feather structures. Integumentary structures of *Sinosauropteryx* and *Beipiaosaurus* clearly belong to the first category. The preservation of feathers in *Microraptor zhaoianus* is not good enough to show unambiguous branching features, therefore it is also temporarily listed in the first category. The second category currently includes *Protarchaeopteryx*, *Caudipteryx*, and *Microraptor gui*. *Sinornithosaurus* has been reported with two types of primitive branching structure (Xu et al. 2001) although the branching evidence is not as convincing as in *Caudipteryx*. Another specimen possibly referable to *Sinornithosaurus* preserved true branched feathers (Norell et al. 2002), and can be listed in the second category.

As *Caudipteryx* is now generally considered to be a member of Oviraptorosauria (Sereno 1999; Zhou et al. 2000; Clark et al. 2002) (see below under 'Feathered dinosaurs or newly recognized flightless birds?'), both *Microraptor* and *Sinornithosaurus* are dromaeosaurids, and the phylogenetic position of *Protarchaeopteryx* is not known but is thought to lie among coelurosaurids, it can be concluded that at least two groups of coelurosaurs have preserved feathers with the diagnostic features of shafts and barbs. These modern feathers are distributed in both the forelimb and tail region (and also in the hindlimb in *Microraptor gui*). In addition, the attachments of the forelimb feathers in these dinosaurs are consistent with those of modern birds (Xu et al. 2003).

Although lacking the high-profile public attention concerning feathers in dinosaurs, skeletal evidence supporting a dinosaurian origin of birds also increased in this period. For example, the furcula used to be a diagnostic feature of birds, and the reduction of this structure in dinosaurs was one of the major reasons for Heilmann (1926)'s rejection of the dinosaurian origin hypothesis. However, this structure has now been shown to be present in many oviraptorosaurids (e.g., *Caudipteryx*, *Heyuannia*, and other oviraptorids) (Clark et al. 1999, 2001; Zhou et al. 2000; Lü 2002; Lü et al. 2002), dromaeosaurids (*Velociraptor*, *Bambiraptor*, *Sinornithosaurus*, *Microraptor*) (Norell et al. 1997, 2000; Burnham et al. 2000; Xu et al. 1999b, 2003), and other dinosaurs. Other skeletal features that were previously known only in birds have also been recently reported in non-avian dinosaurs, including uncinate processes on the ribs in dromaeosaurids (Clark et al. 1999; Xu et al. 2003), oviraptorosaurids (*Caudipteryx* and oviraptorids) (Zhou and Wang 2000; Zhou et al. 2000; Lü 2002), and therizinosaurs, non-serrated teeth with a constricted waist in troodontids (Norell et al. 2000), scapula with a laterally exposed glenoid facet in dromaeosaurids, such as *Sinornithosaurus* (Xu and Wu 2001), and other theropods (Novas and Puerta 1997), retroverted pubis in dromaeosaurids (Norell et al. 1997) and the troodontid *Sinovenator* (Xu et al. 2002), and a pygostyle in oviraptorosaurids (Barsbold et al. 2000). All these new skeletal discoveries have shown a close link between birds and theropod dinosaurs (see Table 1). Although the distribution of such advanced avian features in these theropod groups are generally held to be compelling evidence supporting the dinosaurian origin hypothesis of birds by most paleontologists, some other workers regard them as evidence that these theropod taxa were flightless birds (see below under 'Feathered dinosaurs or newly recognized flightless birds?').

## Temporal paradox?

One of the most commonly raised arguments against the dinosaurian origin of birds is that there is a temporal paradox. To put it simply, Feduccia (2002) stated 'Many examples exist, but the point is that the group of ther-

opods thought to be avian ancestors is strictly a Cretaceous radiation', while the oldest bird *Archaeopteryx* is from the Late Jurassic. Although most of the bird-related theropod dinosaurs are known from the Late Cretaceous, there are some earlier records. For instance, a non-avian maniraptoran fossil was reported from the Late Jurassic Morrison Formation in the USA (Jensen and Padian 1989) and dromaeosaurs from the Jurassic in Europe (P. Barrett, personal communication).

Some recent Chinese fossil discoveries seem to have significantly reduced the temporal paradox, indicating that the fossil record could be misleading. For example, Early Cretaceous dromaeosaurids (*Sinornithosaurus* and *Microraptor*) and troodontids (*Sinovenator*) are known from Liaoning. The age of these fossils has been dated to be 125–128 million years old, albeit still much younger than *Archaeopteryx* (Swisher et al. 2002; Zhou et al. 2003).

*Epidendrosaurus*, an arboreal maniraptoran dinosaur, was reported from Daohugou, in east Nei Mongol, northeast China (Zhang et al. 2002). The age of the deposit at this locality is controversial, with estimates ranging from Middle Jurassic to Early Cretaceous (Zhang 2002; Wang and Zhou 2004); however, this fossil is associated with a more primitive biota than the famous Early Cretaceous Jehol Biota. Although the exact age of this fossil is still unknown, it does provide evidence that it is likely we will find older fossils of bird-like theropods.

## Homology of the hands between birds and dinosaurs

The issue of the homology of the manual digits between birds and dinosaurs is probably the most controversial in the debate on the origin of birds. Paleontological evidence indicates that the three digits in the hand of birds and maniraptoran theropods are 'I-II-III' of the ancestral five digits; conversely, embryological studies have provided strong evidence showing that the three manual digits of modern birds represents 'II-III-IV' (Burke and Feduccia 1997; Feduccia 1999b; Feduccia and Nowicki 2002; Kundrát et al. 2002). Evidence from both the fossils and embryology appears difficult to refute, and this would appear the biggest obstacle to the dinosaurian origin of birds (Hinchliffe 1997; Feduccia 2002; Galis et al. 2003).

Wagner and Gauthier (1999) proposed a 'frame shift' theory as a compromise to explain these contradictory observations. They accepted that comparative embryological evidence correctly identifies the homology of the primordial condensations in birds as CII, CIII, and CIV; however, they further argued that subsequent anatomical differentiation reflects a frame shift in the developmental identities of the avian digits anlagen in later ontogeny such that CII becomes digit I, CIII becomes digit II, and CIV becomes digit III (Wagner and Gauthier 1999). Therefore, in their opinion, the 'I-II-III' digits of theropod dinosaurs are in fact the same as the avian 'II-III-IV' digits because they are from the same primordial condensations (CII, CIII, and CIV). To enhance their argu-

ment, Wagner and Gauthier (1999) also provided an evolutionary scenario, suggesting that there existed two opposing evolutionary constraints during the evolution from theropod lineage towards birds: one is the functional necessity to retain the inner three fingers (I, II, and III) and the second is a developmental constraint favoring the loss of the I and V condensations first. Therefore, in their opinion, a frame shift occurred as a result of these two opposing constraints.

Although some researches have provided indirect support for the 'frame shift' hypothesis (Dahn and Fallon 2000; Drossopoulou et al. 2000), Feduccia (2002) has correctly pointed out that there is no demonstrable evidence for a single homeotic frame shift in any known amniote, in the manus or pes, nor is there any evidence for a change in theropod digital numbering throughout their evolution. If a frame shift never happened, is there a possibility that the 'I-II-III' model for birds and maniraptoran theropods is still correct?

It is probably fair to say that the homology of the hands of birds and dinosaurs will remain a hotly debated issue for years to come. However, let us view this problem in a different way. If we simply compare the hands of *Archaeopteryx* and some maniraptoran theropods, such as *Microraptor*, they are almost the same in every detail, including the phalangeal formula. If we accept the 'II-III-IV' for modern birds, and assume the same for *Archaeopteryx*, then why not accept the same conclusion for *Microraptor*? In other words, if embryological evidence can be applied to *Archaeopteryx* and other early birds, then the same logic applies for maniraptoran theropods. Therefore, the debate on the issue of the digital homology may be an unsolved mystery; it does not provide truly negative evidence against the dinosaurian origin of birds.

## Feathered dinosaurs or newly recognized flightless birds?

The hypothesis of the dinosaurian origin of birds has been very successful due to the discovery of new fossil evidence, of which the recognition of feathered dinosaurs is undoubtedly the most significant. However, the most recent challenge to this evidence has come from the argument that these feathered dinosaurs might have been flightless birds. For example, since the 1980s, Gregory Paul has consistently argued that some theropods, such as dromaeosaurids, troodontids, and oviraptorosaurids, are secondarily flightless descendants of a persistent lineage of 'protobirds' (Paul 2002). Several other workers have also proposed that oviraptorosaurids (Elzanowski 1999; Feduccia 1999a, 2002; Maryańska et al. 2002; Lü 2002; Lü et al. 2002), and at least some dromaeosaurids, were flightless birds (Feduccia 2002; L.D. Martin, personal communication).

These ideas have the advantage of explaining why some advanced avian features, such as uncinate process of the ribs, more caudally retroverted pubes in dromaeosaurids, and a pygostyle, appeared in some feathered

**Fig. 3** Life reconstruction of *Caudipteryx*, a feathered oviraptorosaurid theropod (by Anderson Yang)

theropods but not in the most basal birds. The long-tailed bird *Jeholornis* has a tail comprising more caudal vertebrae and a more dromaeosaurid-like tail than *Archaeopteryx*; in this respect it appears to have provide ambiguous evidence for the dinosaurian origin of birds because it could be viewed either as evidence of birds' descent from dromaeosaurids or evidence that some birds could secondarily develop a more dinosaur-like tail. The late Cretaceous long-tailed bird *Rahonavis* also has some features more primitive than in *Archaeopteryx* in the tail and foot regions (Forster et al. 1998).

While Witmer (2002) believed that these ideas lie outside of the mainstream of current thought and present some problems for testing by phylogenetic analysis, he suggests that they merit the scrutiny that they have never adequately received. In fact, some serious phylogenetic analyses have already been conducted (Maryańska et al. 2002), suggesting that *Caudipteryx* and other taxa that belong to Oviraptorosauria are flightless birds (Fig. 3).

In my view, despite the body of evidence supporting the dinosaurian origin of birds, it is probably too early to declare that 'it is time to abandon debate on the theropod origin of birds' (Prum 2002). Abandoning debate may succeed in concealing problems rather than finding solutions to important scientific questions.

## Disputes over the origin of avian flight

The issue of the origin of birds is fundamental to discussions on the origin of bird flight. Recent progress in the study of bird origin has certainly had an impact on the study of the origin of avian flight.

## Decoupling of the origin of flight from the origin of birds

In the past decades there has been a general dichotomy in the discussion of the origin of avian flight, i.e., the arboreal hypothesis or 'trees-down' theory of flight which was tightly linked with the thecodont origin of birds (Bock 1985, 1986; Feduccia 1999a) and the terrestrial hypothesis or 'ground-up' theory of flight that was coupled with the dinosaurian ancestry of birds (Ostrom 1976b, 1986; Padian and Chiappe 1998a, 1998b; Padian 2001a, 2001b).

Chiappe (1997) argued that non-avian theropods such as *Velociraptor*, *Compsognathus*, and *Tyrannosaurus* were clearly terrestrial cursors, thus the ancestral mode of life of birds was that of a cursorial biped, and inferences about the habits of *Archaeopteryx* should be made within this framework and not the inverse. Padian and Chiappe (1998a) further commented that the cursorial hypothesis of birds is strengthened by the fact that the immediate theropod ancestors of birds were terrestrial.

On the other side of the debate, the scholars who disapprove of the dinosaurian origin of birds almost unanimously support the arboreal hypothesis of the origin of avian flight. To many of these workers, the arboreal hypothesis is obviously superior to the terrestrial hypothesis; hence the large-sized, terrestrial dinosaurs could not be ancestors of birds. As Feduccia (1999a) has summarized, birds and avian flight originated in the trees, taking advantage of gravity, and the ancestors of birds must be represented by small, arboreal archosaurs.

Witmer (2002) argued that functional hypothesis and scenarios would be best tested within the context of a strict hypothesis of phylogenetic relationships. Although I agree that the latter is important for understanding functional scenarios, I disagree that functional hypothesis should be confined to this context, though phylogeny is an important tool. Phylogeny is based on homology; however, functional biology is also based on analogy. A simple coupling of phylogeny and functional reconstruction is difficult to support.

This tight linking of the issue of the origin of birds and flight has been seriously challenged since the late 1990s. Various workers have tried to decouple the dinosaurian ancestry of birds and the 'ground-up' hypothesis of avian flight.

The description of the dromaeosaurid theropod, *Microraptor zhaoianus* provides the first good evidence of an arboreal dinosaur (Xu et al. 2000). A second arboreal theropod (*Epidendrosaurus*) was recently reported as having even stronger perching capabilities than the oldest known bird *Archaeopteryx* (Zhang et al. 2002). The reported four-winged dinosaur, *Microraptor gui* (Xu et al. 2003), represents the latest arboreal theropod; the large and curved claws and the toe proportions of the foot of this dromaeosaurid show evidence of strong arboreal capability, although it remains unclear how the hindlimb feathers would be folded during this action.

According to Witmer (2002), there is currently no good reason to rigidly couple models for the origin of flight with particular phylogenetic clades. Among the supporters of the dinosaurian–bird hypothesis, he is one of the few who is serious about the question 'Is the arboreal hypothesis truly inconsistent with theropod relationship?' (Witmer 2002). In other words, is there any way to bridge the gap between the theory of the dinosaurian origin of birds and the arboreal hypothesis of the origin of flight?

In addition to the evidence provided by Chatterjee (1997), and recent discoveries of arboreal theropods (Xu et al. 2000, 2003; Zhang et al. 2002), Paul (2002) also showed several features in dromaeosaurids indicating that they might have been arboreal.

## Habit of the most basal birds

In my opinion, one question is critical to the study of the origin of flight in birds, i.e., 'Were the ancestors of birds and the earliest birds arboreal?' In the past, many workers have explored this issue, with a focus on the habits of the oldest known bird *Archaeopteryx*.

As the most primitive bird, *Archaeopteryx* is undoubtedly one of the key fossils to help us understand the beginnings of flight in birds; in fact its locomotory habit has been controversial. Various analyses, and their resultant restorations, depict it as an arboreal trunk-climber (Feduccia 1993), a terrestrial runner (Chiappe 1995, 1997; Padian and Chiappe 1998a, 1998b), or a combination of between arboreal and terrestrial features (Hopson 2001).

Padian and Chiappe (1998b) argued that *Archae-opteryx* and its maniraptoran relatives have no obviously arboreal adaptations, such as feet fully adapted for perching, and anatomical and aerodynamic analyses of fossils and living birds show that birds evolved from small, predatory dinosaurs that lived on the ground. Contrary to Padian and Chiappe's opinion, interpretations of the climbing ability of *Archaeopteryx* based on its foot claw morphology (Feduccia 1993; Yalden 1997) have, in fact, provided strong evidence supporting its arboreal habit in addition to hindlimb proportions that are also similar to most arboreal birds. Other basal birds such as *Jeholornis* and *Sapeornis* also have arboreal features in the pedal claws. The pedal claws of *Confuciusornis* are medio-laterally compressed, as in *Archaeopteryx* and extant arboreal birds (Zhou and Farlow 2001). Nevertheless, such evidence has been challenged by the assertion that similar, highly recurved claws may be found in some small theropod dinosaurs that were almost certainly terrestrial (Chiappe 1997).

If the claw evidence is not convincing, luckily a second line of evidence is available. Fisher (1946) noticed that perching birds, as a rule, have reduced proximal phalanges and elongate distal phalanges. However, Fisher's observation had attracted little attention in reconstructing the life habit of fossil birds.

Clark et al. (1998) used comparisons between the second and third phalanges of pedal digit III to distinguish ground birds from arboreal ones, and applied this rule to the study of pterosaurs; a similar comparison has now been used to describe the habits of fossil birds. Zhou and Hou (1998) explored the comparison between the first and second phalanges of digit II and the first and fourth phalanges of digit IV and found them useful in distinguishing ground birds from arboreal birds. Principal components analysis of the pedal phalangeal proportions has been used to compare and contrast the habits of *Archaeopteryx* and *Confuciusornis* (Hopson 2001; Zhou and Farlow 2001). For instance, *Archaeopteryx* does not show typical arboreal phalangeal proportions, and it does not show ground phalangeal proportions either (Zhou and Farlow 2001). These basal birds appear to have possessed a foot (at least in terms of the evidence from the phalangeal proportions) suitable neither for a specialized terrestrial life nor a specialized perching life. Interestingly these authors independently concluded that these basal birds had the capability to live in trees using their extremely specialized grasping hands and relatively unspecialized feet. Zhou and Farlow (2001) also noted that *Archaeopteryx* has a less well-developed perching foot than *Confuciusornis*.

The basal phalanges of the hand are relatively shorter than the distal phalanges in the hands of *Archaeopteryx*, *Jeholornis*, and *Confuciusornis*, which probably indicate that the hands of these early birds were used in grasping tree trunks or branches. Thus, there existed an evolutionary transition from a less arboreal foot with a climbing hand to a perching foot with a reduced hand. Therefore, a typical perching foot was perfected gradually in the early evolution of birds. This may explain why *Archaeopteryx* lacks the phalangeal proportions of typical modern arboreal birds. In other words, the phalangeal proportions of the foot of *Archaeopteryx* represent a transitional stage between the ancestor of birds and more advanced perching forms.

The juvenile hoatzin of South America retains two wing claws for climbing. The lifestyle of a juvenile hoatzin may, to a degree, mirror the habit of early birds. The long and stiffened skeletal tail of the early birds such as *Archaeopteryx* and *Jeholornis* provide some evidence supporting the arboreal habit of these forms.

It should be noted that the hallux is reversed in all known basal birds but it has not been confirmed in any dinosaurs. Therefore, the character of the opposable hallux of the foot is still one of the few characters unique to birds. No evidence indicates that this character was developed for any adaptation other than an arboreal life style.

## Arboreal dinosaurs?

If the habits of all known basal birds including *Archaeopteryx*, *Jeholornis*, *Sapeornis*, and *Confuciusornis* are already too specialized to allow inferences regarding the habit of their ancestor, then within the currently popular dinosaurian ancestry context we will have to

**Fig. 4** Skeletal reconstruction of *Jeholornis*, a seed-eating bird with a complete skeletal tail. Scale bar equals 5 cm
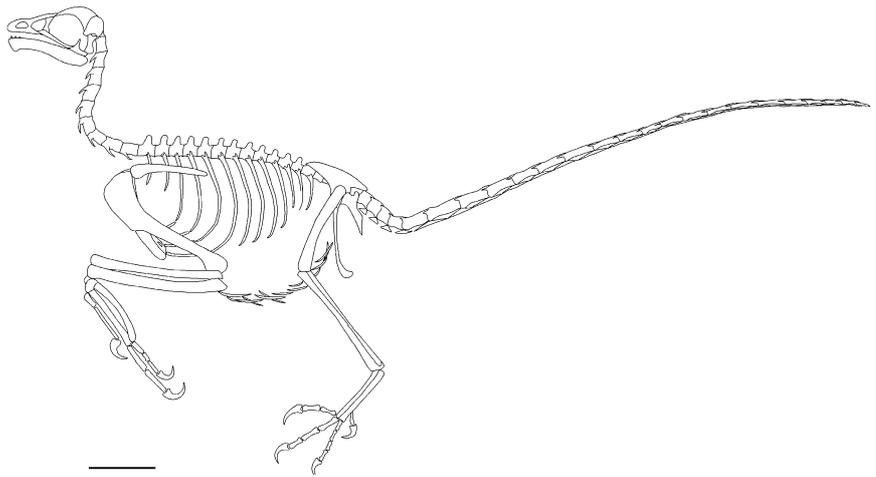
concur with Witmer's (2002) comment that 'The question ultimately comes down to the actual theropod ancestor of birds: what it looked like and how it lived its life'.

Traditionally, dromaeosaurids have been depicted as being fast runners and dangerous predators, as popularized in the film *Jurassic Park*. The evidence usually cited by Ostrom (1976a) includes the long and stiffened tail and the strongly curved claws. However, a stiffened tail in dromaeosaurids and some early birds such as *Jeholornis* (Fig. 4) can also be explained as a structure used in climbing. Following the recognition of several arboreal theropods, and the arboreal nature of most basal birds, the large, curved and sharp pedal claws of small sized dromaeosaurids are probably better explained as arboreal, rather than predatory, adaptations.

The elongated penultimate phalanges of the manus of many theropods such as *Deinonychus* may also indicate a climbing habit. Hence, small dromaeosaurids like *Bambiraptor* (Burnham et al. 2000) might have been able to climb, although the foot has fewer arboreal features in comparison to those of *Microraptor* and *Epidendrosaurus* (Zhang et al. 2002).

Chatterjee (1997) was the first to propose the existence of arboreal theropods, which led him to support the arboreal origin of birds from dinosaurian ancestors. Unfortunately little attention has been paid to his analysis, probably because of the lack of modern analogues and because of the then predominant dogma that dinosaurs were terrestrial.

The discovery of the smallest adult dinosaur *Microraptor zhaoianus* (Xu et al. 2000) provided some concrete evidence for Chatterjee's hypothesis. The small body size, the lower position of the first metatarsal, the partially posteriorly directed hallux, the sharp and strongly curved pedal unguals, and elongated penultimate phalanges of *Microraptor zhaoianus* indicate the presence of arboreal dinosaurs (Xu et al. 2000).

*Epidendrosaurus* represents another recently recognized arboreal maniraptoran dinosaur, which lies phylogenetically close to birds in the phylogenetic tree (Zhang et al. 2002). Preserved are an extremely long tail and a relatively elongated forelimb (compared to the hindlimb). The most significant anatomical feature of this creature is in the foot, which shows unambiguous arboreal adaptation. Metatarsal I is articulated with metatarsal II at such a low position that the trochleae of metatarsals I-IV are almost on the same level, which is similar to those of perching birds, including the Early Cretaceous flying birds *Sinornis* (Sereno and Rao 1992), *Boluochia* (Zhou 1995a), and *Longipteryx* (Zhang and Zhou 2000). Further evidence for the arboreal capability of *Epidendrosaurus* can be found in the toe proportions (Zhang et al. 2002). The penultimate phalanges are longer than their neighboring proximal phalanges (Zhou and Hou 1998; Clark et al. 1998; Hopson 2001; Zhou and Farlow 2001).

A newly reported dromaeosaurid, *Microraptor gui*, provides the latest evidence supporting the presence of arboreal theropod dinosaurs (Xu et al. 2003). Long feathers attached to the short metatarsus and the especially large and curved pedal claws clearly preclude it from being a terrestrial animal (Prum 2003). This new fossil also appears to provide evidence for a four-winged stage in the evolution of avian flight (Beebe 1915; Xu et al. 2003). However, no firm conclusions may be drawn because we do not know whether or not hindlimb feathers were common in theropod dinosaurs or whether they were simply a specialization of *Microraptor gui*. Padian (2003) has commented 'Birds from *Archaeopteryx* onward have not used the hind limbs as airfoils and do not involve them in the flight stroke. So the leg feathering in *Microraptor* has nothing demonstrably to do with the evolution of the kind of flight that more derived birds use'.

## New arguments for the cursorial origin of avian flight

While there is increasing fossil evidence supporting the arboreal hypothesis, there are some new and interesting arguments for the cursorial origin of avian flight. For instance, Padian and Chiappe (1998a, 1998b) argued that, because the immediate theropod ancestor of birds were

bipedal, their arms were free to evolve flapping flight, which cannot be said for other reptiles of their time. They further argued that most small animals, and even some goats and kangaroos, can climb trees, but that does not make them tree dwellers. Padian (2001a) insisted that claw shape is not a good indicator of habits because some large-sized non-avian theropods also have similar features. It is notable that one of his assumptions is that these large-sized, non-avian theropods could not climb.

In support of the terrestrial origin of bird flight, Burgers and Chiappe (1999) provided a theoretical model to argue that *Archaeopteryx* and non-avian maniraptoriforms could use their wings to produce a primary thrust during the take-off process from the ground. This thrust, according to these authors, together with the propulsion generated by the hindlimb, could provide a sufficient minimum flying speed for *Archaeopteryx*.

Padian (2001a) also reemphasized the implications of phylogenetic analysis for functional analysis in the case of the origin of bird flight. He argued that the cross-test of hypotheses of the evolution of several functions and adaptations related to the origin of bird flight with independently derived phylogenetic analysis, indicating that consilience does not support ideas that the close ancestors of birds were arboreal or evolved flight from the trees.

These new arguments for the cursorial origin of the flight of birds are almost all based on the assumption that bird-related theropods are cursorial animals. This view is not supported by direct analysis of evidence from the fossil record.

Ostrom (1986), who has been the primary supporter of the 'ground-up' hypothesis in recent decades, admitted that the logic of the arboreal scenario is difficult to refute. Such misgivings, in the light of recent finds of arboreal dinosaurs, may have prompted him to question the terrestrial hypothesis for the origin of avian flight.

Witmer's (2002) conclusion that we simply have too few data on the functional capabilities of any of the principal taxa and that the knowledge of the origin of flight is out of reach, is obviously too pessimistic. I believe that Padian's (2003) opinion, that the issue of whether birds evolved flight in the trees or on the ground is effectively dead because it is not testable, is probably too pessimistic because any phylogenetic hypothesis of extinct animals is also not testable in a strict philosophical sense by this token. It appears that no matter what kind of bird ancestor we accept, most of the fossil evidence points to an arboreal scenario for the origin of avian flight.

Finally, it should be noted that a new hypothesis, namely 'wing- assisted incline running' (WAIR), has provided an interesting explanation for the origin and evolution of avian flight (Dial 2003). It argues that the incipient wings of feathered theropod dinosaurs probably played a role similar to that of modern birds which employ wing-assisted incline running, rather than flying, to reach elevated refuges such as cliffs, trees, and boulders. This hypothesis appears to combine aspects of the arboreal and cursorial scenarios.

## *Microraptor gui* and the origin of feathers

Feathers have long been held as being unique to birds. This notion has now been seriously challenged by the discovery of feathered dinosaurs from Liaoning Province. A summary of the discoveries of feathers in dinosaurs, as well as their implications for the origin and early evolution of feathers, have been provided by Zhou and Zhang (2001b) and other workers (Prum and Dyck 2001; Prum and Brush 2002). Here I will focus only on some newly discovered fossils, in particular, a new species of *Microraptor*, *M. gui*, with preserved branched feathers on both its forelimbs and hindlimbs (Prum 2003; Stokstad 2003; Xu et al. 2003).

*Microraptor gui* differs from *M. zhaoianus* in preserving perfectly distributed feathers over the whole body. True branched feathers are clearly preserved on the forelimb, hindlimb, and tail. This discovery might indicate that modern feathers are present and common in coelurosaurids, including dromaeosaurids (e.g., *Sinornithosaurus*, *Microraptor*), oviraptorosaurids (*Caudipteryx*) (Fig. 5D), and the poorly known coelurosaur *Protarchaeopteryx*. Preserved in these feathers are both a shaft and barbs. Probably the most interesting feature is the asymmetry of the feathers in *Microraptor gui* in both the forelimb and hindlimb (Fig. 5C), and the appearance of the alula: this is surprising, as both asymmetrical feathers and an alula have been known previously only in volant birds. Although the presence of such advanced avian features in *Microraptor gui* might suggest that it could already fly, as in some primitive birds, there is currently no detailed anatomical analysis to support this hypothesis. If *Microraptor gui* could not fly, then it may be suggested that asymmetrical feathers and an alula were developed initially for some more primeval stage of flight (see above under 'Feathered dinosaurs or newly recognized flightless birds?').

Recognition of the evolutionary stages of feathers in known feathered dinosaurs is destined to produce more controversy than the original discovery of feathers in these animals. The fiber-like, non-branched integumental structures in basal coelurosaurs such as *Sinosauropteryx* (Fig. 5A) have been regarded as representing the first stage of feather evolution (Xu et al. 2001; Prum and Dyck 2001; Prum and Brush 2002). This hypothesis has the advantage of being consistent with phylogenetic results, which show that birds evolved from basal coelurosaurs through the intermediate stages of more advanced coelurosaur groups such as dromaeosaurids and oviraptorosaurids. However, it has to be admitted that there is still little evidence from the fossils that allows us to be positive about any conclusion on the intermediate stages of feather evolution. Some workers have proposed that the filaments are collagenous fibers (Feduccia 1999a, 2002; Lingham-Soliar 2003).

It is noteworthy that fiber-like structures similar to the protofeathers of basal coelurosaurs have been reported in some pterosaurs (Fig. 5B), in which they are generally called 'hairs' (Bakhurina and Unwin 1995; Wang et al.

**Fig. 5** Integuments in theropods and pterosaurs. **A** unbranched feathers from the tail region of *Sinosauropteryx* sp. (IVPP V12415); **B** integuments from the tail region of a rhamphorhynchoid pterosaur *Jeholopterus ningchengensis* (IVPP V12705) **C** branched and asymmetric feathers attached to the foot of *Microraptor gui* (IVPP V13477); **D** branched and symmetric feathers attached to the forelimb of *Caudipteryx dongi* (IVPP V12344). Not to scale
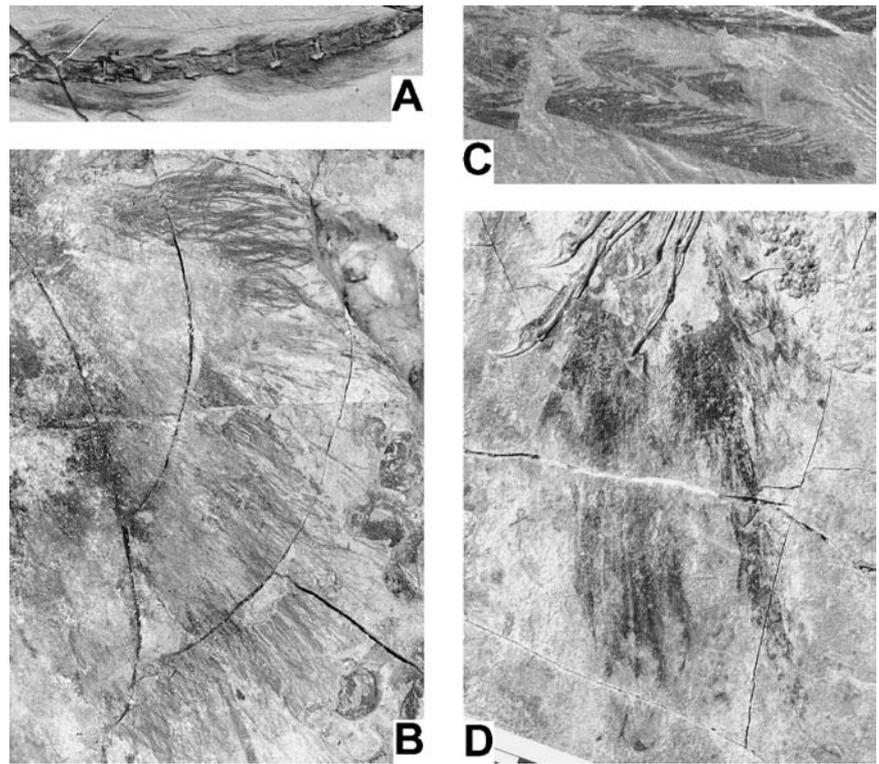


2002). There is no evidence either supporting or disproving the homology of pterosaur's 'hairs' with 'protofeathers' in dinosaurs. If the first stages of feather evolution were indeed present in pterosaurs, then the next question we are going to ask is 'are there feathered pterosaurs?' Although this proposal may not reduce the importance of feathered dinosaurs for the dinosaurian origin of birds, it would indeed push the history of feathers to more basal archosaurs. The homology of fiber-like integuments in the ornithischian dinosaur *Psittacosaurus* is also an open question (Mayr et al. 2002), and potentially may have important implications for the discussion of the homology of various integumentary structures in dinosaurs.

## Concluding remarks

The past decade has witnessed one of the most exciting periods in the study of the origin and early evolution of birds. Many extremely interesting birds have been described from the Cretaceous, and our understanding of the early evolution and diversification of birds has been improved in an unprecedented way, yet there is still no fossil evidence indicating the origin of modern groups in the Mesozoic. The evolution of birds from theropod dinosaurs has never been so much in the limelight and so popular as today, largely thanks to the discoveries of feathered dinosaurs from the Early Cretaceous of China. Traditional views on the origin and early evolution of flight and feathers have also been challenged, and the arboreal origin of avian flight is attracting a wider range of supporters, including some of those who also believe in the dinosaurian origin of birds. Many of the features, such as feathers, wishbones, uncinate processes, and pygostyle, which are traditionally associated with birds, are now found to have appeared first in much more remote avian ancestors, and the mosaic pattern of character evolution has been recognized as more complex in early avian evolution than thought previously.

It must be emphasized that the significance of this wealth of new evidence on Mesozoic birds and dinosaurs will come to be better appreciated in the years to come. The present conflicts between evidence from fossils, embryology, and molecular biology highlights problems that merit more attention. Scientific breakthroughs usually result from analysis of problems and debate rather than the celebration of achievements that have already been made. Hence, debate should be encouraged rather than discouraged.

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