

Mesozoic birds of China—a synoptic review

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Abstract A synoptic review of the discoveries and studies of Chinese Mesozoic birds is provided in this paper. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of several bird-bearing deposits in the Jehol Group has established a geochronological framework for the study of the early avian radiation. Chinese Mesozoic birds had lasted for at least 11 Ma during about 131 Ma and 120 Ma (Barremian to Aptian) of the middle and late Early Cretaceous, respectively. In order to further evaluate the change of the avian diversity in the Jehol Biota, six new orders and families are erected based on known genera and species, which brings the total number of orders of Chinese Mesozoic birds to 15 and highlights a remarkable radiation ever since the first appearance of birds in the Late Jurassic. Chinese Early Cretaceous birds had experienced a significant differentiation in morphology, flight, diet and habitat. Further examination of the foot of *Jeholornis* suggests this bird might not have possessed a fully reversed hallux. However, the attachment of metatarsal I to the medial side of metatarsal II does not preclude trunk climbing, a pre-adaptation for well developed perching life of early birds. Arboreality had proved to be a key adaptation in the origin and early evolution of bird flight, and the adaptation to lakeshore environment had played an equally important role in the origin of ornithurine birds and their near-modern flight skill. Many Chinese Early Cretaceous birds had preserved the direct evidence of their diet, showing that the most primitive birds were probably mainly insectivorous and that specialized herbivorous or carnivorous (e.g., piscivorous) dietary adaptation had appeared only in later advanced forms. The only known Early Cretaceous bird embryo fossil has shown that precocial birds had occurred prior to altricial birds in avian history, and the size of the embryo and other analysis indicate it probably had a short incubation period. Leg feathers probably have a wide range of distribution in early birds, further suggesting that leg feathers had played a key role in the beginning stage of the flight of birds. Finally, the Early Cretaceous avian radiation can be

better understood against the background of their unique ecosystem. The advantage of birds in the competitions with other vertebrate groups such as pterosaurs had probably not only resulted in the rapid differentiation and radiation of birds but also the worldwide spreading of pterosaurs and other vertebrates from East Asia in the Early Cretaceous.

Keywords China, Early Cretaceous, birds

1 Introduction

The position of *Archaeopteryx* as the earliest and the only bird known from the Late Jurassic has hardly been challenged since its first discovery in 1861 while the Early Cretaceous remains a very critical stage in the study of the early evolution of birds. Thanks to the extremely abundant discoveries of the diverse Early Cretaceous birds, particularly from Liaoning Province, northeast China in the last two decades, our knowledge of the early evolution of avian morphology, diet, habit, development, systematics and radiation has been significantly improved (Zhou, 2004b).

Since the discovery of the first Chinese Mesozoic bird, *Gansus*, was reported from the Lower Cretaceous of Gansu, northwest China in 1984 (Hou and Liu, 1984), over two-dozen species of fossil birds, represented by hundreds of individuals, have been reported from the same age. Except a few species, most of them have been discovered from western Liaoning Province in northeast China (Fig. 1). These birds are exclusively known from the lacustrine shale deposits. Many of them comprise completely articulated skeleton with well-preserved feather imprints, and some even preserved stomach contents (gizzard stones, fish bones or seeds). In addition to many adult specimens, juveniles and embryonic fossils are also preserved, containing much information previously unknown on the development of early birds (Hou and Chen, 1999; Zhou and Zhang, 2004). Such exceptional preservation of early birds, largely due to frequent volcanic eruptions, provides a rare chance for us to reconstruct their flight and life styles.



Fig. 1 Major Lower Cretaceous fossil bird sites in Liaoning Province

Chinese Early Cretaceous birds coexisted with abundant mammals, dinosaurs, pterosaurs, lizards, turtles, aquatic reptiles, frogs, salamanders, fishes, insects and other invertebrates, angiosperms and other plants. Our knowledge of the Jehol Biota has also been significantly enriched in recent years, which enables us to have a better understanding of the interactions between birds and other coexistent members of the Jehol Biota (Chang et al., 2003; Zhou et al., 2003; Zhou, 2004a; Zhou, 2006). It also becomes increasingly important to study the evolution of early birds from an ecological perspective in order to further investigate the evolutionary mechanism of the biota and its environment. Recent progress in the study of the stratigraphy, particularly the $^{40}\text{Ar}/^{39}\text{Ar}$ dating of various horizons of the bird-bearing sediments, has established a preliminary age frame for studying the evolution of birds and the Jehol Biota (Swisher et al., 1999, 2002; Liu et al., 2003; He et al., 2004). By combining the information from new fossils and geochronological results, we are now able to conduct a more precise comparison with their equivalents from other major continents in the Early Cretaceous, to further distinguish endemic and cosmopolitan taxa in the biota in order to study the potential origin and diversification centers of major biological groups in the Cretaceous.

Despite the astonishing discoveries of Early Cretaceous birds, there is yet no convincing evidence of Late Cretaceous birds in China. *Yandangornis longicaudus* was described as a long tailed bird from the Upper Cretaceous of Zhejiang Province in southeast China (Cai and Zhao, 1999). Unfortunately, this fossil was only preliminarily described, showing no diagnosis of birds. As a result, it remains a mystery whether it is a bird or bird-like dinosaur.

In this paper we provide a synoptic review of the recent discoveries and studies of these birds and their geological background, and discuss their major significance in various aspects of avian paleontology, such as the early evolution of flight, feathers, development, diet and habitat differentiation, and avian radiation in the unique Jehol ecosystem.

2 Stratigraphic and geochronological background

The stratigraphic correlations of the late Mesozoic lacustrine deposits in northern China has been a long-standing debatable issue. Equally controversial is the age of these deposits. Such controversies are mainly stemmed from the fact that the tectonic activities were very strong during this time, sediments were often preserved in many isolated small intermontaneous basins, and there were not sufficient and reliable isotope dating results.

Recent discoveries of early birds, feathered dinosaurs, early mammals, angiosperms and other interesting fossils from the Jehol Biota have prompted the involvement of more geologists with geochemical and geophysical expertise in the study of the stratigraphy and geological background of the biota. Recent stratigraphic and isotope dating work has clarified some long-standing confusions over the correlation of deposits in various sedimentary basins, and enabled us to understand the evolution of Chinese Early Cretaceous birds in a more precise geochronological framework (Swisher et al., 1999, 2002; Liu et al., 2003; He et al., 2004; Zhou, 2006). Geomagnetic work in this region has also contributed to the comparisons with global events in the Early Cretaceous (Zhu et al., 2003).

The Lower Cretaceous bird-bearing deposits in western Liaoning Province and other areas in northern China such as Hebei Province, Nei Mongol (Inner Mongolia) and Gansu Province are generally comparable, and can be referred to the Jehol Group in a broad sense although different stratigraphic formations have been named in different regions. For instance, in Liaoning, the bird-bearing deposits comprise the Yixian Formation and the overlying Jiufotang Formation. In Hebei, the bird-bearing deposits comprise, from bottom to top, the Dabeigou Formation, Dadianzi Formation and Xiguayuan Formation, respectively (Liu et al., 2003). The Dabeigou Formation is now regarded as the lowest horizon of the Jehol Group and is only restricted to Hebei. The Dadianzi and Xiguayuan formations are regarded as comparable to the lower and upper part of the Yixian Formation in Liaoning, respectively. Birds in Nei Mongol are known from the Yijinhuoluo Formation, which is comparable to the Jiufotang Formation in Liaoning. In Gansu Province, the bird-bearing deposits, called the Xiagou Formation, is generally regarded as comparable to the Jiufotang Formation or slightly younger.

Isotope dating of these bird-bearing deposits has a relatively long history. However, these results are often disputed probably due to two major reasons: first, the relationship between the dated volcanic rock and the fossil-bearing sediments is less certain; and second, the previously used K–Ar and Rb–Sr dates on biotite and whole rock are regarded as less reliable than those based on the $^{40}\text{Ar}/^{39}\text{Ar}$ methods that are currently employed.

The first reliable date on the bird-bearing deposits of the Yixian Formation was obtained in 1999. Swisher et al. (1999)

used replicate Ar-ion-laser total-fusion analyses of single sanidine feldspar crystals and CO₂-laser incremental-heating of a bulk sanidine separate to obtain a result of (124.6 ± 0.3) Ma of the Jianshangou Bed of the lower Yixian Formation. A refined result of 125.0 ± 0.19 Ma was obtained from the same horizon slightly later (Swisher et al., 2002). Because the dated crystals were derived from the interbedded tephra in the fossil-bearing sediments, this age is therefore believed to represent the most direct age for the fossil-bearing sediments. This result is generally consistent with a U-Pb date on zircon from the tuffs from the same locality of the lower Yixian Formation, which produced an age of 125.2 Ma (Wang et al., 2001). Because a precise dating of the bird-bearing deposits of the middle and upper parts of the Yixian Formation has not been published, the exact temporal duration of the Yixian Formation still remains to be determined.

The age of the Jiufotang Formation of the upper Jehol Group was recently determined as (120.3 ± 0.7) Ma, based on ⁴⁰Ar/³⁹Ar dating on the sanidine crystals from tuffs interbedded within the fossil-bearing deposits. This also represents the first direct age determination for the bird-bearing deposits of the Jiufotang Formation (He et al., 2004).

The Dabeigou Formation in Hebei Province had been correlated with the lower Yixian Formation by some workers (Wang et al., 2000). However, recent biostratigraphic and geochronological work has confirmed that the former is actually lower than the latter, and should represent the most basal horizon of the Jehol Group. Liu et al. (2003) obtained the first direct age of the Dabeigou Formation based on the dating of the two tuffaceous sandstones by SHRIMP U-Pb dating, producing a mean age of (133.9 ± 2.5) Ma and (130.1 ± 2.5) Ma, respectively. Recently, this has been confirmed by ⁴⁰Ar/³⁹Ar dating of the K-feldspar from tuffs interbedded in the bird-bearing shales of the Dabeigou Formation, which gives a weighted mean age of (130.8 ± 0.5) Ma (He et al. pers. comm.).

Till now, there is only one avian genus and species, *Protopteryx*, known from the Dabeigou Formation. The rest of the Chinese Early Cretaceous birds have all been collected from the Yixian or Jiufotang formations in Liaoning or equivalent deposits in other regions of northern China. These birds had a temporal range of at least 11 Ma from 131 Ma to 120 Ma. The lower Yixian Formation (125 Ma) and the Jiufotang Formation (120 Ma) represent two major radiations of birds in the Jehol Biota (Zhou, 2006).

3 Taxonomy and avian diversity

In the past decade, the speed of discovery of Early Cretaceous birds has exceeded that of their description. Many newly known taxa have only been preliminarily reported, without an account of their detailed anatomy or broad implications. Taxonomic confusions such as the appearance of many junior synonyms have been caused by hasty descriptions or lack of communications among competing teams. Further, although over twenty species have been erected from the Early

Cretaceous of China, their high rank classifications (e.g., on the order or family level) have not been well determined, which has hindered the discussion of the changes of the diversity of birds in the Early Cretaceous, particularly when compared with other major animal groups. To meet this need, six new orders and families are erected herein on the basis of known taxa from the Lower Cretaceous of Liaoning and Hebei provinces. These new orders and families are currently each represented by only one genus and species.

Class Aves Linnaeus, 1758

Subclass indet.

Order Jeholornithiformes ord. nov.

Family Jeholornithidae fam. nov.

Included genus *Jeholornis prima* Zhou et Zhang, 2002.

Diagnosis Teeth absent on premaxilla. Lachrymal with two vertical and elongated pneumatic fossae. Mandibles robust with well-ossified symphysis. Metacarpal III strongly bow-shaped. First phalanx of minor manual digit twice as long as the second. 20–22 caudal vertebrae behind the transition point. Lateral trabecula of the sternum with a rounded fenestra distally. Ratio of forelimb (humerus + ulna + carpometacarpus) to hindlimb (femur + tibiotarsus + tarsometatarsus) about 1.2.

Distribution Chaoyang City, Liaoning Province; Yixian and Jiufotang formations, Early Cretaceous.

Remarks Two junior synonyms of *Jeholornis prima* were proposed in the past based on different specimens of *Jeholornis*. One is *Shenzhouraptor* (Ji et al., 2002b), published in the same month (July 2002) as *Jeholornis*, but the *Chinese Geological Science Bulletin* that published the name is a monthly journal, therefore *Jeholornis*, which was published in the weekly journal *Nature* (25 July 2002), according to international nomenclature rule, clearly has the priority. Another junior name of *Jeholornis* (Ji et al., 2002c) is *Jixiangornis orientalis*, which was published much later than *Jeholornis*, but like *Shenzhouraptor*, it possesses no obvious difference from *Jeholornis prima*. Therefore both *Shenzhouraptor* and *Jixiangornis* are regarded as junior synonyms of *Jeholornis prima*.

Class Aves Linnaeus, 1758

Subclass indet.

Order Sapeornithiformes ord. nov.

Family Sapeornithidae fam. nov.

Included genus *Sapeornis chaoyangensis* Zhou et Zhang, 2002.

Diagnosis Teeth absent on mandibles. Furcula robust with a short hypocleidum. Forelimb (humerus + ulna + carpometacarpus) about one and half the length of the hindlimb (femur + tibiotarsus + tarsometatarsus). Proximal end of the humerus with an elliptical fenestra, and a large deltoid crest with the dorso-distal portion tapering into a distinctive acute angle. Major and minor manual digits straight and tightly attached without intermetacarpal space. Minor manual digit comprises two slender phalanges. Femur only slightly shorter than the tibiotarsus.

Distribution Chaoyang City, Liaoning Province; Jiufotang Formation; Late Early Cretaceous.

Class Aves Linnaeus, 1758

Subclass Enantiornithes Walker, 1981

Order Boluochiformes ord. nov.

Family Boluochidae fam. nov.

Included genus *Boluochia zhengi* Zhou, 1995.

Diagnosis Teeth absent on premaxilla. Tip of premaxilla hook shaped. Metatarsals II–IV nearly of equal length. Trochleae for metatarsals II–IV nearly on the same level. Trochlea for metatarsal II wider than those of metatarsals III and IV. Intercondylar groove narrow at the distal tibiotarsus. Medial condyle of tibiotarsus nearly as wide as lateral condyle, and cranial margin of the medial condyle flat in distal view.

Distribution Chaoyang City, Liaoning Province; Jiufotang Formation; Late Early Cretaceous.

Class Aves Linnaeus, 1758

Subclass Enantiornithes Walker, 1981

Order Protopterygiformes ord. nov.

Family Protopterygidae fam. nov.

Included genus *Protopteryx fengningensis* Zhang and Zhou, 2000.

Diagnosis “Y”-shaped furcula with an interclavicular angle of about 45°. Clavicular ramus thin and pointed dorsally. First phalanx of alular digit curved and extending to distal end of Metacarpal II. Trochlea for pedal digit II much wider than that for III and IV. Second pedal digit more robust than other digits.

Distribution Fengning County, Hebei Province; Dabeigou Formation; Early Cretaceous.

Class Aves Linnaeus, 1758

Subclass Enantiornithes Walker, 1981

Order Longirostravisiformes ord. nov.

Family Longirostravisidae fam. nov.

Included genus *Longirostravis hani* Hou et al., 2004.

Diagnosis Both upper and lower jaws very elongated and slender with pointed rostral end. Dentition restricted to cranial tip of rostrum and mandible. Cranial two premaxillary teeth more than twice as long as the caudal two teeth, with caudally curved tip of crown. Lateral trabeculae of sternum with a caudally notched distal extremity, with three branches. Deltoid crest of humerus short and less than one third the length of the humerus. Proximal one third of the tibiotarsus medially-inclined as compared to the distal two thirds of the tibia. Tibiotarsus only slightly longer than femur.

Distribution Yixian, Jinzhou City, Liaoning Province; Yixian Formation; Early Cretaceous.

Class Aves Linnaeus, 1758

Subclass Ornithurae Haeckel, 1866

Order Yixianornithiformes ord. nov.

Family Yixianornithidae fam. nov.

Included genus *Yixianornis grabaui* Zhou et Zhang, 2001.

Diagnosis Ratio of skull length to width about 1.5. Postcranial long bones slender. Head of humerus protruding and elliptical. Metacarpal II less than 1/3 the width of metacarpal III. Pubic symphysis about 1/5 the length of pubis. Ratio of femur to tibiotarsus 1.6. Ratio of pedal digit III to tarsometatarsus length about 1.3.

Distribution Yixian, Liaoning Province; Jiufotang Formation; Late Early Cretaceous.

Among the six new orders and families erected in this paper, two cannot be referred to any subclass, three are referred to the subclass of Enantiornithes, and one referred to the subclass of Ornithurae. Each of them is now only represented by one genus and species. However, their morphology shows sufficient distinctiveness from other known early birds.

Several known avian genus and species from the Jehol Biota are presently not referred to any known or newly established orders and families. Potentially, some new order and families can be erected when more comprehensive anatomical work is done and more detailed comparisons are made in the future. On the other hand, Liaoxiornithiformes is now only based on one juvenile specimen, and thus it remains a debatable issue whether this taxon is valid at all.

The Chinese Early Cretaceous avian assemblage now comprises 15 orders and as many families (Table 1). Compared to only one family (Archaeopterygidae) in the Late Jurassic (Elzanowski, 2002), such a taxonomic diversity undoubtedly documents the first major avian radiation in its evolutionary history. Chinese Early Cretaceous birds are mainly from three formations or equivalent deposits, namely, the Dabeigou, Yixian and Jiufotang formations, respectively. Only one order (Protopterygiformes) is known from the Dabeigou Formation. Five orders have been described from the Yixian Formation, including Confuciusornithiformes (Hou et al., 1995a), Eoenantiornithiformes (Hou et al., 1999), Liaoxiornithiformes (Hou and Chen, 1999), Longirostravisiformes, and Liaoningornithiformes (Hou, 1997b). A recently discovered specimen from the Yixian Formation can be tentatively referred to Jeholornithiformes (pers. observ.). As a result, six orders have been discovered from the Yixian Formation, two of them (Jeholornithiformes and Confuciusornithiformes) extended their occurrence to the Jiufotang Formation. A total of 10 orders have been described from the Jiufotang Formation. In addition to the two orders sharing with the Yixian Formation, eight orders are now exclusively known from the Yixian Formation. They are Sapeornithiformes, Cathayornithiformes (Zhou et al., 1992), Boluochiformes, Longipterygithiformes (Zhang et al., 2000), Chaoyangornithiformes (Hou, 1997a), Yanornithiformes (Zhou and Zhang, 2001), Yixianornithiformes and Gansuornithiformes (Hou and Liu, 1984).

The number of avian orders had increased from the Dabeigou Formation, through the Yixian Formation to the Jiufotang Formation. The number of ornithurine orders had also increased from one in the Yixian Formation to four in the

Table 1 List of Chinese Early Cretaceous birds and their distribution and horizon information

Order	Family	Genus	Species	Distribution and horizon
Jeholornithiformes	Jeholornithidae	<i>Jeholornis</i>	<i>J. prima</i>	Chaoyang; Jiufotang and Yixian formations
Sapeornithiformes	Sapeornithidae	<i>Sapeornis</i>	<i>S. chaoyangensis</i>	Chaoyang; Jiufotang Formation
Confuciusornithiformes	Confuciusornithidae	Confuciusornis	<i>C. sanctus</i>	Beipiao and Chaoyang; Yixian and Jiufotang formations
			<i>C. dui</i>	Beipiao; Yixian Formation
			<i>C. suni</i>	Beipiao; Yixian Formation
			<i>Changchengornis</i>	Beipiao; Yixian Formation
			<i>Jinzhounornis</i>	Jinzhou; Yixian Formation
Proopterygiformes	Proopterygidae	<i>Proopteryx</i>	<i>J. yixianensis</i>	Beipiao; Yixian Formation
			<i>J. zhangjiyingia</i>	Beipiao; Yixian Formation
			<i>P. fengningensis</i>	Fengning, Hebei; Dabeigou Formation
			<i>J. luanhera</i>	Fengning; Yixian Formation
Eoenantiornithiformes	Eoenantiornithidae	<i>Vescornis</i>	<i>V. hebeiensis</i>	Fengning; Yixian Formation
Longipterygiformes	Longipterygithidae	<i>Eoenantiornis</i>	<i>E. buhleri</i>	Beipiao; Yixian Formation
Cathayornithiformes	Cathayornithidae	<i>Longipteryx</i>	<i>L. chaoyangensis</i>	Chaoyang; Jiufotang Formation
		<i>Eocathayornis</i>	<i>E. walkeri</i>	Chaoyang; Jiufotang Formation
		<i>Cathayornis</i>	<i>C. yandica</i>	Chaoyang; Jiufotang Formation
		<i>Sinornis</i>	<i>S. santensis</i>	Chaoyang; Jiufotang Formation
Boluochiformes	Boluochidae	<i>Boluochia</i>	<i>B. zhengi</i>	Chaoyang; Jiufotang Formation
Liaoxiornithiformes	Liaoxiornithidae	<i>Liaoxiornis</i>	<i>L. delicatus</i>	Lingyuan; Yixian Formation
Longirostravisiformes	Longirostravisidae	<i>Longirostravis</i>	<i>L. hani</i>	Yixian; Yixian Formation
		<i>Otogornis</i>	<i>O. genghisi</i>	Otog, Nei Mongol; Jiufotang Formation
Liaoningornithiformes	Liaoningornithidae	<i>Liaoningornis</i>	<i>L. longidigitris</i>	Beipiao; Yixian Formation
Chaoyangornithiformes	Chaoyangornithidae	<i>Chaoyangia</i>	<i>C. beishanensis</i>	Chaoyang; Jiufotang Formation
		<i>Songlingornis</i>	<i>S. linghensis</i>	Chaoyang; Jiufotang Formation
Yanornithiformes	Yanornithidae	<i>Yanornis</i>	<i>Y. martini</i>	Chaoyang; Jiufotang Formation
Yixianornithiformes	Yixianornithidae	<i>Yixianornis</i>	<i>Y. grabaui</i>	Yixian; Jiufotang Formation
Gansuornithiformes	Gansuornithidae	<i>Gansus</i>	<i>G. yumenensis</i>	Yumen, Gansu; Jiufotang Formation

Jiufotang Formation while the number of enantiornithine orders increased from one in the Dabeigou Formation, to three in both the Yixian and Jiufotang formations.

It is notable that both the enantiornithines and ornithurines are represented by different orders in each of the three bird-bearing formations, reflecting that rapid turnover of the faunal composition in the Jehol Biota.

4 Flight capability

Despite the significant differentiation of the flight capability and style, the Chinese Early Cretaceous birds had, with no exception, possessed more powerful flight than the Late Jurassic *Archaeopteryx*, as most notably shown in the pectoral girdle, sternum and wing. For instance, they all have a relatively long wing compared to the leg, and a well-fused proximal carpometacarpus with a well-developed carpal trochlea.

Jeholornis represents the most basal and the sole known bird with a long skeletal tail from the Early Cretaceous of China (Zhou and Zhang, 2002a). Further, its tail comprises more caudal vertebrae (up to 27) than *Archaeopteryx* (up to 23) with more elongated chevron and zygapophyses, arguably another feature linking birds and non-avian theropods. The wing retains an ancestral 2–3–4 phalangeal formula as in *Archaeopteryx* and their closest dinosaur relatives. However, several of the derived flight-related features clearly show that it had a stronger flight capability than *Archaeopteryx*. For instance, the coracoid is much more elongated; scapula has a

dorso–laterally facing glenoid facet; the ossified sternum has a pair of lateral trabeculae with fenestra; the carpometacarpus is better fused proximally, with a prominent carpal trochlea; Metacarpal II is bow-shaped and the major digit is shorter and more robust (Zhou and Zhang, 2003a).

Another basal bird *Sapeornis* retains a short coracoid much similar to that of *Archaeopteryx*; however, it also possessed many derived flight-related features, suggesting a more powerful flight (Zhou and Zhang, 2002b). It is interesting to note that no sternum has been found in any known specimens (either sub-adults or adults), similar to the case in *Archaeopteryx* (Wellnhofer and Tischlinger, 2004), which probably indicates that the sternum was ossified in very late stage of development. *Sapeornis* has a distinctly long wing compared to the leg; the ratio of humerus + ulna + metacarpal II to femur + tibiotarsus + metatarsal III is about 1.52, which is larger than any other known early birds (Zhou and Zhang, 2003b), and may suggest that it had a soaring flight.

Confuciusornis is another bird from the Jehol Biota that is more basal than enantiornithines and ornithurines (Hou et al., 1995a, b; Chiappe et al., 1999). As in *Jeholornis*, it has a flat sternum lacking a prominent keel, and the wing also retains an unreduced phalangeal formula. As in *Sapeornis*, *Confuciusornis* possessed a pygostyle, instead of a long skeletal tail such as in *Archaeopteryx* and *Jeholornis*.

Like *Archaeopteryx*, too, *Jeholornis*, *Sapeornis* and *Confuciusornis* probably still had limited flight capability. None of these birds had preserved an alula, a derived feather feature indicative of sophisticated flight. Their sternum (if preserved) is relatively short and flat, lacking a prominent

keel, the major bone for the attachment of the supracoracoid muscle that is responsible for the lifting of the wing during flapping flight of modern birds. Their coracoid lacks a well-developed procoracoid, probably indicating the absence of a triosseal canal, hence the absence of typical modern flapping flight (Zhou and Farlow, 2001). Therefore, it remains unclear whether or not these birds could take off directly from the ground like modern flying birds.

Enantiornithine birds are the most diverse group in the Jehol Biota. Compared with the more basal birds mentioned above, these birds all have a pygostyle, a strut-like coracoid, a sternum with a concave dorsal surface and a primitive keel, a compressible furcula with a long hypocleidum contacting the sternum, a compact wing with an alula, and a more elongated synsacrum. These relatively small sized birds had obviously possessed powerful and skilled flight. On the other hand, the coracoid of these birds lacks a well-developed procoracoid; the sternal keel is low and ridge-shaped, restricted to the posterior half of the sternum, and the major manual digit is not significantly expanded laterally, indicating that their flight is still poor compared to the contemporaneous ornithurine birds. It is also notable that enantiornithines had also shown a differentiation of flight styles. Although most of them have a wing slightly longer than the leg as in *Archaeopteryx* and *Confuciusornis*, *Longipteryx* represents a specialized type, characterized by a remarkably elongated wing, which is probably related to its unique combination of arboreal habit and piscivorous diet that requires a relatively strong wing for soaring over the lake surface (Zhang et al., 2001).

Early Cretaceous ornithurines reached the climax in flight evolution among early birds (Zhou and Zhang, 2001). They had possessed a suite of advanced flight-related characters that distinguish them from other contemporaneous birds. Most notable among them are the antero-posteriorly elongated sternum with a deep keel extending along the full length of the sternum, a coracoid with a well-developed procoracoid process indicative of the presence of triosseal canal (Fig. 2), a pygostyle much shorter than those of enantiornithines and

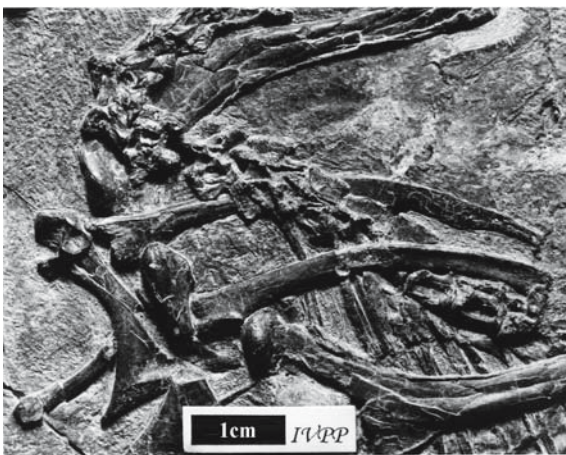


Fig. 2 Scapula and coracoid of *Yixianornis* (IVPP V 12631)

other basal birds, and the major digit of the wing significantly expanded laterally. In addition, these birds also display more fusions among bones, such as a completely fused tarsometatarsus, a carpometacarpus fused at both proximal and distal ends, and a synsacrum with more sacral vertebrae etc. These Early Cretaceous birds undoubtedly had possessed a powerful and skillful flight nearly identical to that of modern birds.

In summary, Early Cretaceous birds had shown a wide range of variations in flight capabilities and styles, further confirming that this is a critical time for the evolution of avian flight, which had obviously contributed to the earliest and successful radiation in avian history.

5 Size variation and change

Chinese Early Cretaceous birds had also displayed a wide spectrum of size variations, ranging from the largest exceeding the smallest dinosaurs (Xu et al., 2000; Zhou and Zhang, 2002b) to the smallest nearly of the size of a passerine bird. The size variations of early birds were probably influenced by both the phylogeny and the flight. On the other hand, they also reflect the adaptation for different ecological niches where body size could have a major impact on their feeding strategies.

The most basal birds are generally large, which probably represents an inherited feature from *Archaeopteryx*. Both *Jeholornis* and *Sapeornis* are of approximately the same size of *Archaeopteryx*, although the former two have a much longer wing. *Confuciusornis* is slightly smaller, representing the first example of size reduction in early avian evolution associated with a slight improvement of the flight capability.

The Early Cretaceous enantiornithines are comparatively small, representing a remarkable size decrease from more basal birds. The trend towards a smaller body size in enantiornithines must be regarded as an advanced feature derived from their larger-sized ancestors, and can probably be explained as a strategy for obtaining sustained flight capability when the flight apparatus was not significantly modified from their ancestral forms. The small size of Early Cretaceous enantiornithines could also be critical for the success of this dominant Mesozoic avian group to live in a relatively dense forest environment and feed on insects. The enantiornithine *Liaoxiornis* was reported as the smallest Mesozoic bird (Hou and Chen, 1999). Although the holotype was obviously a juvenile individual, several of the referred specimens, which are adult or subadult individuals, appear to show that the adults are still very small compared to other contemporaneous Mesozoic birds.

Ornithurine birds started out small, but became larger shortly later. For instance, the most basal ornithurine *Liaoningornis* from the lower Yixian Formation is about the size of an enantiornithine from the same age (Hou, 1997b). Several newly discovered yet undescribed basal ornithurines from the Yixian Formation are also comparatively small

compared to later more derived forms (pers. observ.). Ornithurines from the Jiufotang Formation are much larger than the Early Cretaceous enantiornithines although they are slightly smaller than more basal birds such as *Archaeopteryx*, *Jeholornis*, *Sapeornis* and *Confuciusornis*. Because there is a general trend for ornithurines to occupy the near lakeshore environment and feed on fishes, it appears that the size increase in early birds was probably an adaptation for more efficient fish-eating capability while competing with pterosaurs for the same food resources (Zhou and Zhang, 2001; Zhou et al., 2002; Want et al., 2005; Zhou, in press). On the other hand, the size increase in ornithurines is constrained by the phylogeny and flight capability; and it is not coincidental that the first size increase in bird evolution had occurred in the most derived avian group in the Early Cretaceous. By contrast, enantiornithines had not become much larger until the Late Cretaceous.

To sum up, during the early avian evolution, birds had first experienced a general size reduction. And their first size increase had occurred in ornithurines when the flight apparatus were already indistinguishable from those of modern birds. The strategic change from a size reduction towards size increase best reflects the improvement of flight capability during the Early Cretaceous.

6 Arboreality and habitat differentiation

Like *Archaeopteryx*, most Chinese Early Cretaceous birds are arboreal. These birds usually preserved completely articulated foot showing a great degree of variation in the structures that are presumably related to their climbing or perching capability, which enable us to reconstruct the process of a gradual perfection of a perching foot in the early avian evolution. The most basal birds such as *Archaeopteryx*, *Jeholornis*, *Sapeornis* and *Confuciusornis* all possessed a foot with large and strongly curved unguals. Besides, they also retained a grasping hand with large and curved unguals. Like their immediate dinosaurian ancestors, these birds probably used their wings to assist their climbing to an arboreal life (Zhou, 2004b).

It is notable that the character of a reversed hallux used to be a key innovation distinguishing birds from their dinosaurian ancestry. However, recent discoveries of more *Jeholornis* specimens appear to show that this basal bird might still retain an incomplete reversed hallux or simply lack a reversed hallux (Fig. 3). Other Early Cretaceous birds all possessed a well-developed reversed hallux. The lack of a well-developed reversed hallux is obviously a primitive feature from their dinosaurian ancestors. On the other hand, it should

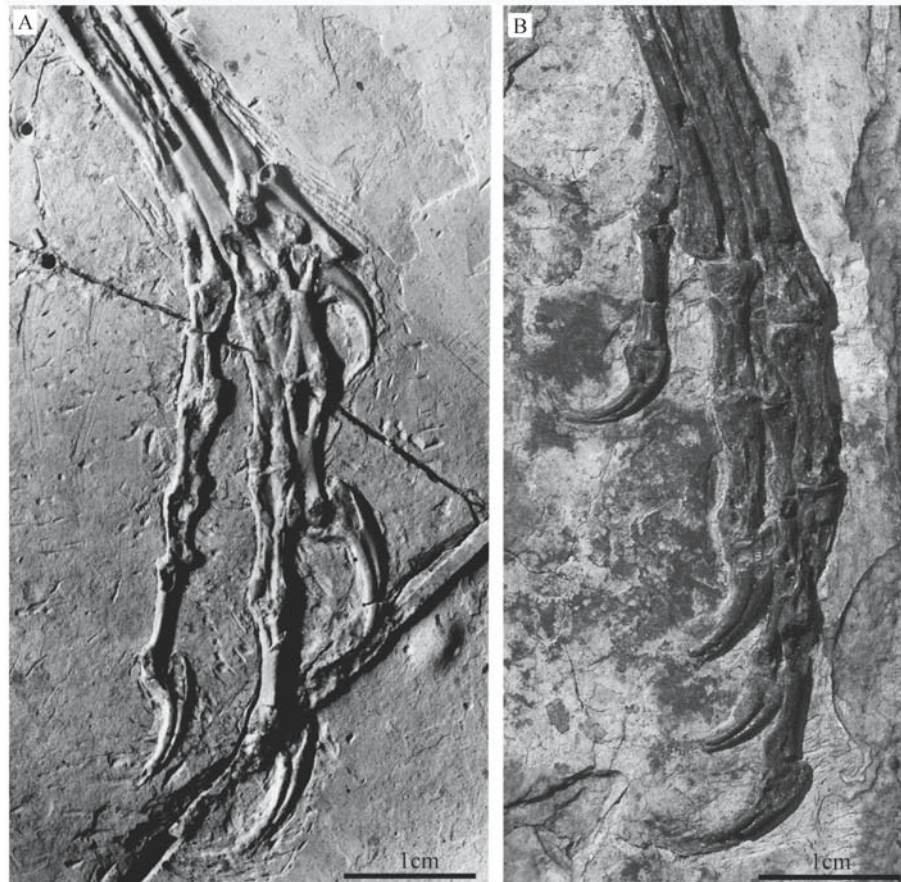


Fig. 3 Foot of *Jeholornis*, showing the non-reversed hallux, A. IVPP V 13350, right side; B. IVPP V 13353, left side

be noticed that the earliest birds were probably mainly trunk climbers; therefore a less well-developed reversed hallux might be more useful for such an adaptation. In addition, these birds could also use their wings to assist climbing.

More advanced birds had possessed a better perching foot. For instance, the small sized enantiornithines already possessed a nearly perfect perching capability as indicated by the low position of the articulation of the reversed hallux to metatarsal II and the typical arboreal toe proportions (Hopson, 2001; Zhou and Farlow, 2001). On the other hand, the role of the wing in the arboreal life had become significantly reduced. Morphologically, the wing is shorter than those in more basal birds, and the unguals are also much reduced, and the toe proportion no longer permits any efficient grasping function as in more basal birds or their dinosaurian ancestry.

The significance of tree adaptation in the origin and early evolution of avian flight can probably be well compared with the role of a similar adaptation for the origin of primates in the early Eocene. Early primates probably ate insects as early birds. The primates distinguish themselves from other mammals by having a grasping hand with a flexible wrist to hold branches and secure quality food, a good eyesight to keep from running into things as they move rapidly through trees, and an expanded brain with the capability of complex process in order to adapt to a living in a complicated forest space. The appearance of a hand with grasping function finally evolved into a hand to use tools in humans. Equally, tree living had resulted in the reversed hallux typical of birds, a large eye and expanded brain, which had contributed to the explosive development of birds in the Cenozoic (Feduccia, 2003).

While most Early Cretaceous birds inhabited the forest, more advanced ornithurine birds had mainly lived in a near lakeshore habitat. Accordingly, these birds have a more slender and elongated legs and pedal digits with smaller and less curved unguals. It is notable that the earliest ornithurines such as *Liaoningornis* still retained an arboreal habit (Hou et al., 1996), highlighting a transition of ornithurines from arboreal to terrestrial evolution in the Early Cretaceous.

7 Diet differentiation

Accompanying the earliest major avian radiation as documented by the taxonomic diversity, and variations in morphology, flight and size, Chinese Early Cretaceous birds have also displayed a wide range of diet adaptations. A brief summary of their diet differentiation may help to understand the mechanism of the success of this radiation.

Our understanding of the diet of fossil birds is often speculative or controversial due to rare preservation of stomach contents in the fossil record. Thanks to the exceptional preservation of fossils in the Jehol Group, many of the Chinese birds have preserved direct evidence for reconstructing their diet. For instance, *Jeholornis* preserved several dozen seeds in its stomach, representing the earliest known bird with a specialized seed-eating diet (Zhou and Zhang, 2002a). The

inference of the diet of *Jeholornis* was also supported by its specialized and robust upper and lower jaws, which had only retained a small number of small teeth on the lower jaw.

Sapeornis preserved gizzard stones, which indicate an herbivorous diet (Zhou and Zhang, 2003b). Unlike *Jeholornis*, it has a toothless lower jaw, but retains teeth in the upper jaw. The largest birds from the Jehol Biota were obviously adapted for an herbivorous diet, which were probably related to their arboreal adaptation and the relatively poor flight capability.

The ornithurine *Yanornis* represents another Early Cretaceous bird that has preserved direct evidence of its diet. The preservation of fish remains (opercula, ribs and vertebrae etc.) in the stomach of one referred specimen confirmed a piscivorous diet as previously suggested based on its skull morphology (Zhou and Zhang, 2001; Zhou et al., 2002). *Yanornis* also represents the earliest record of a definite fish-eating bird. The discovery of gizzard stones in another referred specimen of *Yanornis* (Fig. 4) has led to the hypothesis that there existed seasonal diet switching in early birds (Zhou et al., 2004). It is notable that fragmentary plant imprints have been well preserved in association with the gizzard stones, further showing the grinding of the plants in the stomach (Fig. 5). Such a discovery of dual diet choices also calls caution in inferring the diet of a fossil bird even when direct evidence is present. A comprehensive study of the morphology and other evidence is necessary to correctly reconstruct the diet of a fossil bird.

None of the enantiornithine birds from the Early Cretaceous of China has preserved direct evidence of their diet. Our conclusion of their diet is currently inferred from their morphology and the environment they presumably inhabited. Since most of these small sized birds are equipped with well-developed conical teeth and arboreal in habit, it is likely they were mainly insectivorous or omnivorous. There are, however, at least two exceptions. Although the enantiornithine *Longipteryx* is arboreal, it has a particularly elongated wing, an elongated rostrum with pointed teeth, which is explained to have a piscivorous dietary adaptation while perching in near-shore trees similar to a kingfisher (Zhang et al., 2001). Another recently described enantiornithine *Longirostravis* has an elongated and pointed rostrum and the teeth are restricted to the rostralmost end of the upper and lower jaws, and probably represent a new trophic type, probing in soft substrates (Hou et al., 2004).

In sum, although little is known about the diet of the earliest bird *Archaeopteryx*, Early Cretaceous birds had obviously diversified in their feeding strategies, including insectivorous, herbivorous and piscivorous forms coexisting in the same ecosystem. Piscivorous feeding had obviously independently occurred in enantiornithines and ornithurines despite the competition of many large piscivorous pterosaurs.

8 Development

A bird embryo was recently briefly described from the Yixian Formation (Zhou and Zhang, 2004), which represents the

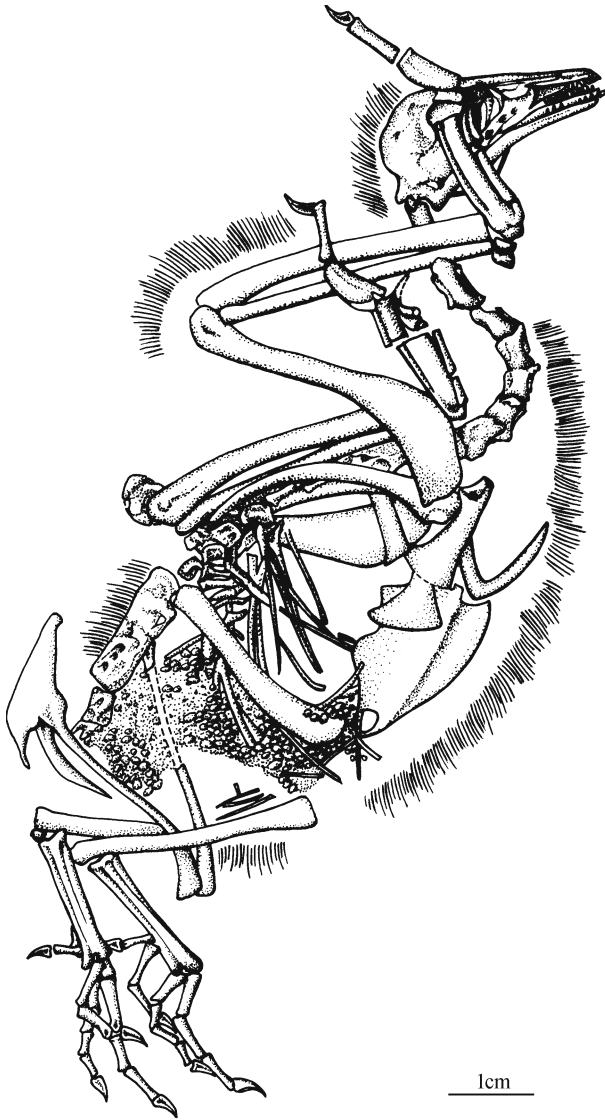


Fig. 4 Line drawing of *Yanornis* specimen with gizzard stones (IVPP V 13358)



Fig. 5 Plant fragment impressions in the stomach of *Yanornis* with gizzard stones (IVPP V 13358)

earliest known and probably best preserved avian embryo in fossil records, providing strong evidence in support of the hypothesis that precocial embryonic development is an ancestral mode and altricial mode is a derived one.

The embryo, of the size of an average chicken's egg, belongs to an unnamed enantiornithine bird, and contains a nearly completely articulated and relatively well-ossified skeleton with imprints of well-grown feather anlagen (Fig. 6). The skeleton is tucked and reaches both the blunt and sharp ends of the tight confines presumably formed by the eggshell. The jaws lie below the wing as a result of the rotating of the skull. In the development of living birds, the distal elements of the wing ossify later than proximal elements, and the ossification of digits occurred in the late stage of the embryological development (Starck, 1996, 1998). The distal elements of the wing such as the unguals in the Liaoning embryo are well ossified, further confirming that it was in the final stage of the embryologic development. Moreover, the posture of the skeleton is obviously more consistent with a late stage embryo rather than a hatchling, in which case the head would have raised beyond the vicinity of the feet. Therefore, all available evidence indicates that the Liaoning embryo was at a terminal embryologic stage when the chick was about to hatch out.



Fig. 6 Photo of the embryo of an enantiornithine bird (IVPP V 14238)

The skull is preserved in lateral view, and strongly curved relative to the rest of the body, forming an inverse U-shape with the cranial portion of the vertebral column. We estimate 8–9 cervicals, and approximately 12 thoracics. The thoracic ribs are well ossified. There are approximately 7–8 unfused sacrals and 15–16 unfused caudals. The 9 distal caudals are relatively elongated with elongated chevrons, and form a straight caudal series, which presumably would fuse into a long pygostyle in the adult.

The scapula has a pointed acromion and a straight and slender shaft. The coracoid is strut-like, with a convex lateral

margin as in enantiornithines. The furcula is partially exposed, and appears “V”-shaped, but with no hypocleidum preserved. The sternum is absent, presumably attributable to an unossification for the sternum only ossifies well after hatching. In fact, all known specimens of young adult *Archaeopteryx* and *Sapeornis* lack an ossified sternum.

The ulna and radius are slightly longer than the humerus, in contrast to the most basal birds such as *Archaeopteryx* and *Jeholornis*. The carpometacarpus is present because a large semilunate carpal appears to be partially fused with metacarpals II and III. Metacarpal III extends well past metacarpal II distally as in other enantiornithines. The manus is significantly shorter than the ulna, and the alular digit is reduced, as in more advanced enantiornithines.

The ilium has an expanded pre-acetabular wing and a short and slender post-acetabular wing as in other enantiornithines and many other basal birds. Both the ischium and the pubis are caudally directed. Well-developed proximodorsal processes are present on the short ischia as in all enantiornithines as well as some more basal birds such as *Jeholornis*, *Sapeornis* and *Confuciusornis*. The pubis is slender and curved, lacking the distal portion.

Both hindlimbs are nearly completely preserved; they are tightly folded in tight contact with the skull, wing and other postcranial bones. Metatarsals II, III and IV are unfused. Metatarsal I is small and distally positioned. Metatarsal IV is markedly slender compared to metatarsals II and III as in enantiornithines. Distally, metatarsal II has a wider trochanter than other metatarsals. The pedal digits are preserved as impressions. The unguals are long and strongly curved.

One of the important features of postnatal growth in birds is the dichotomy between precocial and altricial developmental modes. Altricial birds are usually naked and helpless when they hatch out, whereas precocial birds are covered with fuzzy natal down and can move and feed themselves independently. It has also been noted that precocial birds hatch with relatively large brains that grow slowly to adult size (Starck, 1993). The presence of well-developed flight and tail feathers, coupled with the large brain, in the Liaoning embryo may indicate it as a precocial or even a superprecocial bird, which would soon develop the flight ability after hatching (Zhou and Zhang, 2004). Superprecocial and precocial birds are generally less specialized in feeding adaptation. The flourishing plants, abundant seeds, invertebrates and fishes in the Jehol Biota provide sufficient accessible food resources to meet the immediate nutritional needs of precocial chicks, enabling them to survive without first acquiring adult skills and strength.

There is no evidence indicative of the incubation period in fossil birds. It varies in living birds from 10 days to 80 days, and is determined by many factors such as the egg size, adult body weight, different species and environments. For instance, short incubation periods are advantageous when the rate of water loss is high. The incubation period is directly related to egg size, but is independent of the developmental mode. Considering its small egg, presumed small body size of

the adult bird, and the arid climate of the region during the Early Cretaceous, we propose that the Liaoning embryo probably had a short incubation period.

9 Feathers

The Jehol Group is famous for preserving completely articulated skeletons of birds, dinosaurs, pterosaurs and mammals as well as soft tissues such as feathers and other integuments, and stomach contents largely due to the frequent volcanic eruptions that had resulted in the catastrophic death and rapid burial of the organisms by both tuffs and normal lake shale deposits (Wang et al., 1999a, b; Zhou et al., 2003; Wang and Zhou, 2003c). As a result, feathers of birds were often well preserved although their studies have lagged behind the studies of their skeletons. Generally, the preservation of feathers as well as the skeletons in the Yixian Formation is better than in the Jiufotang Formation probably due to relatively less frequent volcanic activities and more fluvial interferences in the lake sedimentation in the Jiufotang Formation.

Flight feathers in the Chinese Early Cretaceous birds are often well preserved, showing no significant difference from those of living birds. Asymmetric flight feathers further confirmed the flight capability as inferred from the skeleton. *Confuciusornis* is represented by more specimens than any other Mesozoic bird; it has also preserved more feather information than other early birds. It is interesting to note that the primaries are significantly elongated compared to short secondaries (Fig. 7).

Alula has been observed in a number of enantiornithines including the most primitive enantiornithine *Protopteryx* (Zhang and Zhou, 2000); however, it has not been reported in any of the more basal birds such as *Archaeopteryx*, *Jeholornis*, *Sapeornis* and *Confuciusornis*. Such an observation is consistent with the conclusion of their primitive flight capability as inferred from the skeleton. It remains a puzzle why an alula exists in the dromaeosaurid dinosaur *Microraptor gui* (Xu et al., 2003) but is lacking in these most basal birds.

Leg feathers have first been reported in *Microraptor gui* (Xu et al., 2003), but are now confirmed in several early birds including *Archaeopteryx* (Christiansen and Bonde, 2004), *Confuciusornis* (Fig. 8) and *Longipteryx* and an unnamed enantiornithine (Zhang and Zhou, 2004). It is notable that the leg feathers in these birds are much shorter than those of *Microraptor*. Functional explanations of these leg feathers are still controversial (Padian, 2003), but it appears that leg feathers are common in early birds, and more discoveries might help to understand their role in the origin and early evolution of avian flight.

Relatively little attention has been paid to the study of the tail feathers in early birds. *Archaeopteryx* and *Jeholornis* are the only two birds with a long skeletal tail associated with tail feathers. It is interesting to compare their tail feathers with some feathered dinosaurs. *Jeholornis* appears to have



Fig. 7 Wing of *Confuciusornis* (IVPP V 13156), showing the elongated primaries compared to short secondaries



Fig. 8 Leg feathers of *Confuciusornis* (IVPP V 10895)

the long tail feathers associated mainly with the distal caudal vertebrae (Zhou and Zhang, 2003a), forming a fan-shaped outline as in *Caudipteryx* (Ji et al., 1998; Zhou et al., 2000) and *Microraptor gui* (Xu et al., 2003). However, *Archaeopteryx* has the tail feathers in association with all the caudal vertebrae, forming a spindle-shaped outline. A recently described fossil from the Lower Cretaceous of Hebei in northeastern China, *Jinfengopteryx* (Ji et al., 2005), which was misidentified as a bird but probably represents a troodontid, preserved tail feathers in a much similar way as in *Archaeopteryx*.

No tail feathers have been reported in known specimens of *Sapeornis*, the most basal bird with a pygostyle. Many *Confuciusornis* preserved a pair of long central tail feathers that contain barbs only at the distal end (Chiappe et al., 1999), yet the proximal and middle portion of the vanes is undifferentiated. A pair of similar long central tail feathers were also reported in *Protopteryx*, and regarded as a transitional type between reptilian scale and typical avian feather (Zhang and Zhou, 2000).

It has been pointed out that except the long central tail feathers the tail feathers are generally short in early birds compared with those of extant birds (Zhang and Zhou, 2004). Since tail feathers play a key role in the balance of the bird during flight, it was proposed that leg feathers in early birds were probably partly used as an auxiliary tool for their balance during the flight (Zhang and Zhou, 2004).

10 Role of Chinese birds in the Early Cretaceous ecosystem

The discoveries of Chinese Early Cretaceous birds are accompanied by extremely abundant fishes (Jin et al., 1995; Jin, 1999), amphibians (Wang and Gao, 2003), turtles (Liu, 2003a), lizards (Ji, 1998; Liu, 2003b), dinosaurs (Chen et al., 1997; Xu, 2003; Xu and Norell, 2004; Xu et al., 2004), pterosaurs (Wang and Zhou, 2003a, b; 2004; Wang et al., 2005), aquatic reptiles (Gao et al., 1999, 2000; Liu and Wang, 2003; Liu, 2004), mammals (Wang et al., 2001; Ji et al., 2002a; Luo et al., 2003; Hu et al., 2005), plants (Sun et al., 2001, 2002; Friis et al., 2003; Zhou and Zheng, 2003; Leng and Friis, 2003; Leng et al., 2003), insects (Ren, 1998; Zhang, 2004; Zhang and Rasnitsyn, 2004) and other invertebrates, which enable us to discuss the role of birds in the Jehol ecosystem and further understand the success of the early radiation of birds.

As most birds inhabited the forest environment, therefore it would be necessary to know what other animals were occupying the same habitat. Insects were probably the most abundant and diverse animals in the forest. Presumably most arboreal enantiornithine birds were insectivorous; and they might be omnivorous and feed on plants or small lizards as well. The large sized birds such as *Jeholornis* and *Sapeornis* are both herbivorous forms and the former was specialized for seed eating, exemplifying the co-evolution between birds and plants. Together with insects and other herbivorous

vertebrates such as pterosaurs and dinosaurs, these birds could have played an important role in the dispersal of plants due to their strong mobility.

Birds are not the only kings in the forest. They had encountered competitions from many other vertebrates such as dinosaurs, pterosaurs, lizards and mammals. Many of these vertebrates were carnivorous and birds could be their preys. These potential predators of birds were mostly arboreal or scansorial (Xu et al., 2000; Ji et al., 2002a; Luo et al., 2003). Although Mesozoic mammals are generally small, some of them were already large enough to eat some small dinosaurs (Hu et al., 2005).

The competition between birds and pterosaurs was not restricted to the forest, and their strongest competition probably occurred near the lake. Many pterosaurs and birds (e.g., *Yanornis*) are carnivorous and specialized for eating fishes or other aquatic animals. Carnivorous birds show no advantage in size, but they obviously had possessed more sophisticated and skillful flight. Wang et al. (2005) has revealed the prevalence of the birds over pterosaurs in the Jehol Biota and discussed the competition between these two flying vertebrate groups, and explained the dominant distribution in coastal regions of pterosaurs as a strategy to avoid competition with birds in inland environments. There existed a wide range of faunal exchanges between Europe and East Asia in the middle to late Early Cretaceous, and East Asia was probably the center for the origin and diversification of a variety of pterosaur groups, which finally had a worldwide distribution.

In sum, the success of the avian radiation in the Jehol ecosystem is closely related to the flourishing forest and the extensive distribution of lakes abundant with fishes and aquatic reptiles such as the choristodere *Hyphalosaurus* (Gao et al., 1999), which is now represented by hundreds of fossils. Birds had probably mainly fed on insects, plants, fishes and other aquatic animals that were equally abundant at the same time. Despite the competitions from dinosaurs, pterosaurs, lizards and mammals, birds had taken advantage of their superb flight capability to achieve an unprecedented success. Birds had probably dispersed from East Asia to a cosmopolitan distribution in the Early Cretaceous due to both the population pressure and the competition from other competitors such as pterosaurs. On the other hand, the competition among various vertebrate groups including birds, pterosaurs, dinosaurs and mammals had probably played a key role in the intercontinental dispersal of all these groups. One interesting question remains unanswered as to what role birds or pterosaurs had contributed to the dispersal of plants such as angiosperms in the Early Cretaceous.

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