Paleornithology of China: A general review

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Abstract Study of fossil birds in China was first conducted by western scholars in last century, and extensive study of Cenozoic birds by Chinese scholars since the 1970s. However, it is the finding of Mesozoic birds, mostly from northeast China since the 1990s, that has become the focus and highlight of paleornithology of China. Enantiornithine birds from the Late Jurassic-Early Cretaceous of China provide the most complete record of the early evolution of this extinct group. The co-existence of the most primitive ornithurine bird Liaoningornis with the oldest known Confuciusornis indicates an earlier and more significant diversification of birds than previously recognized. Evidence from the Chinese Mesozoic birds seems to support the arboreal hypothesis of the origin of avian flight. Despite the controversy, the recent discovery of various feathered dinosaurs in China may provide the most compelling evidence for the hypothesis of the dinosaurian origin of birds.

Keywords: Mesozoic brids, origin of brids, origin of avian flight.

RECENT findings and studies of Chinese Mesozoic birds have resulted in a great deal of information on the early evolution of birds[1]. The documentation of the *Confuciusornis* Fauna indicates that the ancestor of birds had probably appeared much earlier than previously thought. *Liaoningornis* represents the oldest known member of the branch Ornithurae that gave rise to modern birds. The Chinese materials support the arboreal hypothesis of the origin of avian flight. *Sinosauropteryx* is a small-sized theropod, the nature of whose "fiber"-shaped structure is still debatable. *Protarchaeopteryx* and *Caudipteryx* are generally believed to be feathered dinosaurs; if this proves to be true, it will provide the most important and direct evidence for the hypothesis of dinosaurian origin of birds. However, the controversy is unlikely to be solved as both *Protarchaeopteryx* and *Caudipteryx* have already been alternatively suggested by some as flightless birds. This paper is aimed at providing a general review of the study of paleornithology of China. Emphasis will be laid on the major aspects and significance of the Mesozoic birds which highlight the recent findings in Liaoning, northeastern China.

1 Historical review

Studies of Chinese fossil birds can be traced back to as early as 1895 when Eastman published a paper on the ostrich fossils from northern China. Western scholars such as Anderson, Schlosser, Boulin and Lowe also investigated the Cenozoic deposits in northern China and reported the occurrence of fossil birds from the 1920s to the 1930s. Among them, Schlosser (1924) described ten Pliocene species of birds from Inner Mongolia, Boulin (1928) reported nine different Pleistocene species of birds also from Inner Mongolia, and Lowe (1931) described an ostrich and seven other fossil birds from China. Wetmore (1934) also published a paper on some primitive gruiformes from the Eocene of Inner Mongolia.

C.C. Young was the first Chinese paleontologist to publish a paper on fossil birds. In 1932, he reported an *Aquila heliaca* from an area near the Peking Man Site in Zhoukoudian. Since then several studies on ostrich eggs have also been reported by him. Since the 1970s, studies on the Cenozoic birds in China have gained momentum, including the study on the Pleistocene birds from Zhoukoudian, and the Miocene birds from Shanwang in Shandong Province, Sihong in Jiangsu Province and Lufeng in Yunnan Province. Eocene birds have been found from many sites in Xinjiang Uygur Autonomous Region, Henan, Hubei, Anhui and Shaanxi provinces. In 1984, Hou and Liu reported the first Mesozoic bird from China, *Cansus*. Although the material of this Early Cretaceous bird from Gansu Province, northwestern China includes only a partial hindlimb, it was then one of the most complete Early Cretaceous fossil birds in the world.

Since early 1990s, the findings of Early Cretaceous birds such as *Sinornis*, *Cathayornis*, *Chaoyangia*, *Otogornis* and *Boluochia* marked a new era in the study of Mesozoic birds in China. These fossils

are from the lacustrine deposits associated with plants, fish and many other animal fossils. All but *Otogornis were collected from the Jiufotang Formation in Chaoyang, Liaoning Province in northeastern China.* The number of individuals of the Chinese Early Cretaceous birds probably already exceeds that of their contemporaries from the rest of the world.

The subsequent discoveries of *Confuciusornis* and *Liaoningornis* from the Late Jurassic-Early Cretaceous Yixian Formation in Beipiao, Liaoning Province have provided evidence of the oldest bird with a horny beak and the oldest ornithurine bird, and thus greatly enriched our understanding of the early evolution and diversification of birds.

Shortly after the discovery of *Confuciusornis* and *Liaoningornis*, three interesting fossils have been found from essentially the same locality in Liaoning Province. *Sinosauropteryx* is a compsognathid theropod with hotly debated "fiber-"vs. "feather"-like structures. *Protarchaeopteryx* and *Caudipteryx* though have undisputed feathers, and yet are believed by many workers to be feathered dinosaurs. However, some critics strongly suggest they are flightless birds. These materials have recently become the most controversial but important evidence for the study of origin of birds and their flight.

2 Early Cretaceous enantiornithine and ornithurine birds

Archaeopteryx was first found in 1861, and so far only seven skeletal specimens have ever been reported. As the oldest known bird, *Archaeopteryx* has long been cited as the sole most important fossil evidence in discussing the origin of birds and their flight. Our knowledge of the Late Cretaceous birds had been basically limited to the well-known Hesperornithiformes and Ichthyornithiformes until the discovery of Enantiornithes, which was initially known from Argentina in 1981. However, record of the Early Cretaceous birds has been very poor until very recently. *Ambiortus* from Mongolia and *Gansus* from China probably represent the best Early Cretaceous birds until the 1980s, and yet neither of them is nearly complete.

The discovery of abundant Early Cretaceous birds from China has brought in several significant changes in the study of Mesozoic birds[2]. More fossil birds in terms of both number and types have probably now been known from the Early Cretaceous than ever before from either the Late Jurassic or the Late Cretaceous. Significance of the findings may include: (ⅰ) Enantiornithes, the dominant Mesozoic terrestrial birds, probably originated from Eurasia instead of South America. The enantiornithines known from China and Spain are more primitive than the rest of their relatives in other continents. Recently an undescribed specimen from the locality of *Confuciusornis* is recognized as the oldest and most primitive enantiornithine; (ⅱ) *Chaoyangia* is probably the most complete ornithurine bird in the Early Cretaceous. It shows remarkable distinctions from the contemporaneous enantiornithines such as *Cathayornis* and *Sinornis*. *Chaoyangia* is very similar to modern birds in many flight related apparatus. It has uncinate processes and a long and large keeled sternum typical of modern birds, indicating that it could have sustained powerful flight and highly efficient one way flow-through breathing lung. *Chaoyangia* was probably endothermic with the presence of efficient breathing system and overwhelming structural similarities to modern birds. On the other hand, *Chaoyangia* also retained teeth and a long pubic foot, showing the mosaic evolution of characters in the early birds; and (ⅲ) Chinese fossils show bifurcation in the early evolution of birds. Majority of the Chinese Early Cretaceous birds are members of Enantiornithes, all of which have developed a dorsal process from the ischium. This character is also found in *Archaeopteryx* and *Confuciusornis*, but not in ornithurine birds or outgroups of birds. This seems to confirm the monophyly of Sauriurae, which includes *Archaeopteryx*, *Confuciusornis* and Enantiornithes. Sauriurae was dominant in the Mesozoic and became extinct by the end of Mesozoic together with dinosaurs, while Ornithurae, though less represented in the Mesozoic, survived into the Cenozoic and gave rise to all modern birds.

3 *Confuciusornis* and *Liaoningornis*

Both *Confuciusornis* and *Liaoningornis* are from the Yixian Formation, the age of which is still controversial but definitely older than the Jiufotang Formation where most of the Chinese Early Cretaceous birds came from. *Confuciusornis* is nearly as big as *Archaeopteryx* and has retained the "2-3-4" phalangeal format in the wing[3]. Wing claws are large. The fifth metatarsus is present. A large postorbital is present and is in contact with the squamosal and the jugal respectively, forming an unreduced ancestral

diapsid temporal region in the skull as probably in *Archaeopteryx*. The gastralia is present. The sternum is short, flat without a keel, as in *Archaeopteryx*. The scapula and coracoid are still fused, a character more primitive than in *Archaeopteryx*. On the other hand, *Confuciusornis* is distinctive from all other Late Jurassic-Early Cretaceous birds in having the oldest known horny beak. Teeth are lost. The mosaic pattern of evolution in the skull of *Confuciusornis* is best illustrated by the presence of a very derived jaw and a primitive temporal region.

It is also worth noting that hundreds of well-preseved specimens of *Confuciusornis* were collected from nearly the same locality. This may also indicate the presence of certain kind of social behavior. Preliminary study also shows sexual dimorphism with male individuals possessing a pair of long tail feathers.

Liaoningornis, the oldest known ornithurine bird, is most clearly distinguishable from *Confuciusornis* by its much smaller size and several derived characters[4]. It has a sternum with long keel. The tarsometatarsus seems to be fused at both ends, while the tarsometatarsus of Sauriurae is usually fused only at the proximal end. Other ornithurine birds such as *Chaoyangia* also have a distally fused tarsometatarsus, which is probably related to the presence of the vertical take-off ability in these birds.

4 New evidence for arboreal hypothesis of avian flight

Two hypotheses on the origin of flight of brids, namely the arboreal and the terrestrial hypotheses, have competed with each other for over a century, and there is no evidence showing that the debate will be over soon. Although the debate on the origin of avian flight has involved many different lines of evidence, the early fossil birds remain the focus for both sides of the argument. The habit of *Archaeopteryx* has been frequently debated and remains controversial among workers of early birds[5,6]. The recent studies of the Chinese Mesozoic birds have revived the discussion of the origin of avian flight.

Like *Archaeopteryx*, *Confuciusornis* has retained large and curved pedal claws, its tarsometatarsus is short and only about half as long as the tibiotarsus. These features are consistent with those of arboreal birds. *Confuciusornis* has retained three large and curved wing claws. Early Cretaceous birds such as *Cathayornis* and *Sinornis* retained only two in the first two digits, resembling young boatzin in which the calws are used for climbing.

Pedal proportions can distinguish arboreal birds from ground types. Arboreal birds usually have relatively long distal phalanges in contrast to relatively long proximal phalanges in ground birds. *Archaeopteryx* is more similar to arboreal birds in this aspect, and the pedal phalanges of *Confuciusornis* are almost the same as in typical arboreal birds. In addition, the tail feathers supported by a long pygostyle in *Confuciusornis* might be helpful in climbing trees.

Both *Archaeopteryx* and *Confuciusornis* also share a short, flat and keel-less sternum. It is doubtful that the supracoracoideus muscle was present in these earliest birds as it is mainly attached to the keel in modern birds. The supracoracoideus muscle is essential in the taking-off of modern birds from the level ground. Therefore we suggest that the ability to take off directly from the ground had probably not occurred in these two genera. Instead, it probably evolved later in more derived birds such as *Cathayornis* and *Chaoyangia*, which are also smaller in size.

In short, the fossil evidence seems inconsistent with the terrestrial hypothesis, which would assume that the most primitive birds were highly terrestrial, and the flight of birds started out from the ground up. Therefore, the fact that both *Archaeopteryx* and *Confuciusornis* were arboreal and unable to take off directly from the ground supports the arboreal hypothesis of the origin of avian flight.

5 Comments on *Sinosauropteryx*, *Caudipteryx* and *Protarchaeopteryx*

Sinosauropteryx is a small theropod that is most closely related to *Compsognathus* from the Late Jurassic of Germany where *Archaeopteryx* was discovered. A distinctive character of this theropod is that is has preserved some "fiber-" or "filament"-like structures along the dorsal and ventral midline of the body[7]. These structures have been regarded by some workers as the proto-feathers, hence one of the most important evidence for the dinosaurian origin of birds, although it has now been generally agreed that these structures lack any character of feathers of modern birds such as rachis and branching.

The current debate on these "fiber"-like structures centers on the nature of themselves (fig. 1).

Some workers believe that they are not homologous with the feathers at all, they are internal collagenous connective tissue fibers underneath the skin instead. Their lines of evidence include: (i) the "fiber-like" structure of *Sinosauropteryx* is similar to internal collagenous connective tissue fibers of some sea lizards; and (ii) they are preserved underneath the skin line in more than one specimens of *Sinosauropteryx* (Ruben, Martin, pers. comm.). We believe that it is probably premature to draw any conclusion about the nature of the "fiber-like" structure in *Sinosauropteryx* at present. Future study of the chemical feature of the strcutures as well as further evidence on its relationship with the skin may finally settle the disputes over the "fiber"-like structure in *Sinosauropteryx*.

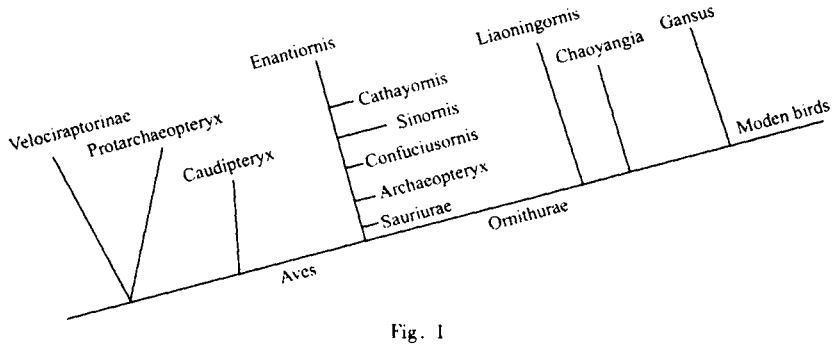

Fig. 1

Caudipteryx and *Protarchaeopteryx* were also found from the Yixian Formation as *Sinosauropteryx* and *Confuciusornis*. These two genera are generally believed to be feathered theropods that are phylogenetically very close to birds[8].

Undoubtedly, both *Caudipteryx* and *Protarchaeopteryx* have feathers, and are larger than *Archaeopteryx* and *Confuciusornis*. And they are also more primitive than the oldest known birds in some aspects such as the presence of serration of teeth in *Protarchaeopteryx*, and unfused metatarsals and short forelimb in both genera. However, some workers believe that they might be flightless birds (Martin, Ruben, pers. comm.). They argued that *Caudipteryx* has no serration in teeth, the tooth typical of those of toothed birds, the bony tail is shorter than in *Archaeopteryx*, and the tail in *Protarchaeopteryx* is probably short too. The short forelimb in both *Caudipteryx* and *Protarchaeopteryx* could have been the result of secondary loss of flight.

As the study of the *Caudipteryx* and *Protarchaeopteryx* is still under way, more details of their morphology remain to be understood. They could be real feathered dinosaurs or the descendents of certain primitive ancestor of birds. Even though we may reach some agreement on their identity in the future, the controversy will probably remain. The real question is when we can call an animal a bird or just a feathered dinosaur.

Acknowledgement We thank Miao Desui and Chang Meemann for reading the manuscript and providing valuable suggestions. This work was supported by the National Natural Science Foundation of China, the Natinoal Geographic Society of the United States and the Special Fund for Paleontology from the Chinese Academy of Sciences.

References

1 Hou, L., *Mesozoic Birds of China*, Taiwan Phoenix Valley Bird Garden, Nantou, Taiwan, 1997, 1—208.
2 Zhou, Z., The discovery of Early Cretaceous birds in China, *Courier Forschungsinstitut Senkenberg*, 1995, 181: 9.
3 Hou, L, Zhou, Z, Martin, L.D., Feduccia, L., A beaked bird form the Jurassic of China, *Nature*, 1995, 377: 616.
4 Hou, L., Martin, L.D., Zhou, Z. *et al*., Early adaptive radiation of birds: evidence from fossils from northeastern China, *Science*, 1996, 274: 1164.
5 Ostrom, J., *Archaeopteryx* and the origin of flight, *Quarterly Review of Biology*, 1974, 49: 27.
6 Feduccia, A., *The Origin and Evolution of Birds*, New Haven: Yale University Press, 1996.
7 Chen, P., Dong, Z., Zhen, S., An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China, *Nature*, 1998, 391: 147.
8 Ji, Q, Currie, P., Norell, M. A., Ji, S., Two feathered dinosaurs form northeastern China, *Nature*, 1998, 393: 753.

(*Received April* 6, 1999)