

# 孔子鸟与鸟类的早期演化<sup>1)</sup>

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## 摘 要

大量孔子鸟标本的出现,使得我们能够识别这一早期鸟类的一些前所未有的形态特征。依据这些特征,并结合近年来中国发现的其他中生代鸟类资料,我们可以进一步探讨早期鸟类研究中存在的某些问题,诸如鸟类飞行的起源等。

孔子鸟头骨的最典型特征是进步的角质喙的出现和原始眶后骨的完全保留。孔子鸟的眶后骨和颧骨相连接,这一特征尚未见于其他鸟类。由于始祖鸟也已缺失了眶后骨,因此眶后骨在孔子鸟中的存在,进一步证实了始祖鸟在早期鸟类演化中的旁支地位,同时也表明,鸟类真正的祖先比我们以往所了解的更加原始。

孔子鸟保留了三个指爪。第三指爪(中间一个)常较退化,这和飞羽附着第三指有关。发育的趾爪及指爪,显示孔子鸟适应攀援树木的生活。基本愈合的尾椎和尚不完善的飞行器官,不仅支持这一假设,而且可能还表明,孔子鸟尚不能从地面起飞。孔子鸟尚未发育小翼羽,这也更加证实了其飞行的原始性。

孔子鸟的某些个体,保存一对长的尾羽,这可能代表雄性的特征。另一些个体的头部还保留装饰性羽毛。数百件个体的集中发现或许还表明,孔子鸟具备了某些现生鸟类集群性的行为方式。

个体大小的变化在早期鸟类飞行能力演化中的作用十分显著。早白垩世的反鸟类的成员都明显小于始祖鸟和孔子鸟,加之拥有具龙骨突的胸骨和长的鸟喙骨,推测已能够直接从地面起飞。新鸟亚纲的成员(如辽宁鸟),个体的减小过程早在早白垩世以前已经完成。至早白垩世,伴随飞行功能的增强,新鸟亚纲的成员(如朝阳鸟),已开始能够承受个体的增大。而蜥鸟亚纲的成员,可能直到晚白垩世才又开始出现较大的个体。

蜥鸟亚纲的早期成员,如始祖鸟和孔子鸟,相对于新鸟亚纲的代表(如辽宁鸟),保留了更多鸟类祖先的特征,如较大的个体和原始的飞行结构。这些鸟类攀援树木的能力,反映了在进化的这一阶段鸟类尚未脱离借助树木作滑翔和原始飞行。早期鸟类最终能从地面起飞,一方面依赖飞行器官的完善,另一方面则依靠个体的减小。这一分析支持鸟类的树栖起源学说。

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甘肃鸟是已知最早完全脱离树栖生活的鸟类。甘肃鸟适应水域生活的能力,可能比以往所知道的更强。

**关键词** 中生代, 孔子鸟, 鸟类演化

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## CONFUCIUSORNIS AND THE EARLY EVOLUTION OF BIRDS

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### 1 Introduction

When *Confuciusornis* was first published (Hou *et al.*, 1995), only three incomplete specimens were known. Hundreds of excellently preserved specimens, however, have been collected since then, mostly from the same locality in Liaoning Province, northeast China. Even though many of these specimens have been well curated and prepared in the Chinese research institutions, probably more have been smuggled out of China. Much of the locality and stratigraphic information about these specimens was inevitably lost during this process. All of *Confuciusornis* specimens are from the lacustrine Yixian Formation, which is generally believed to be from the Late Jurassic to Early Cretaceous (Wang and Diao, 1984; Hou *et al.*, 1995; Jin, 1996). Among the other vertebrates associated with *Confuciusornis* from the same horizon in Liaoning Province are *Liaoningornis*, the oldest known ornithurine bird (Hou *et al.*, 1996; Hou, 1997), the oldest known enantiornithine bird (Hou *et al.*, MS), *Zhangheotherium*, a symmetrodont mammal (Li *et al.*, 1995; Hu *et al.*, 1997), *Eosipterus*, a pterosaur (Ji and Ji, 1997), a frog (Yuan Wang, pers. comm.), *Peipiaosteus*, a sturgeon (Zhou, 1992) and many other fossil reptiles and fishes (Jin *et al.*, 1995). The finding of *Confuciusornis* is important because it is not only the oldest known beaked bird but also the most primitive bird after *Archaeopteryx* (see Wellnhofer, 1993). *Confuciusornis* is only slightly younger than *Archaeopteryx* but older than the Early Cretaceous birds such as *Cathayornis* Zhou *et al.* 1992 (also see Zhou, 1995b), *Sinornis* Sereno and Rao 1992, *Chaoyangia* Hou and Zhang 1993, *Boluochia* Zhou 1995, *Otogornis* (Dong 1993; Hou, 1994) and *Gansus* Hou and Liu

1984. What is even more important is that *Liaoningornis*, the oldest known ornithurine bird, and the oldest known enantiornithine bird (IVPP V11537) appeared at the same time, indicating the presence of a striking diversification of birds during the time from the Late Jurassic to Early Cretaceous (Hou *et al.*, 1995).

In this paper, we will provide a brief description and discussion of some of the newly recognized important features of *Confuciusornis*, based mainly on the materials collected by the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) over the past five years.

## 2 Comments on some features of *Confuciusornis*

### 2.1 The mosaic of derived and primitive features in the skull

The initial recognition of *Confuciusornis* as the oldest beaked bird (Hou *et al.*, 1995) was based mainly on indirect evidence: absence of teeth and presence of nutrient foramen and pits. A recently found specimen of *Confuciusornis* (IVPP V11553) provides more direct evidence for the presence of a horny beak. In this specimen, in front of the premaxilla and dentary the impression of the bill is clearly preserved and pointed anteriorly. The upper bill also appears to be slightly curved dorsally. Additional evidence shows that *Confuciusornis* is an extinct sauriurine bird, and is probably not even close to the common ancestor of modern birds. Therefore, the appearance of a horny bill in *Confuciusornis* only represents the oldest known attempt by ancient birds to achieve a more efficient feeding apparatus after the loss of teeth, and the avian horny bill has independently evolved more than once in the evolutionary history of birds. It further shows the high frequency of parallelism occurring in the early evolution of birds (Martin and Zhou, 1997). It is interesting that the flowering plants have been reportedly found from the same horizon as *Confuciusornis*. Whether they might be ecologically associated remains to be investigated in the future.

The postorbital was not initially recognized in the holotype of *Confuciusornis*, even though further examination and preparation clearly shows its presence in the type specimen. The postorbital is basically a tri-radiate or "Y"-shaped bone. It makes a wide and close contact with a bump on the jugal bar. The dorso-anterior branch of the postorbital is in contact with the frontal and tapers anteriorly. The posterior branch of the postorbital contacts the squamosal. The postorbital is probably absent in *Archaeopteryx*. It is either lost or fused in *Cathayornis* and modern birds. A postorbital reportedly present in the Early Cretaceous enantiornithine bird from Spain (Sanz *et al.*, 1997) is, however, dubious due to its poor preservation. An alternative explanation is that it is part of the broken postorbital process of the frontal. If this bone is indeed the postorbital, then a remarkable difference exists between it and that of *Confuciusornis*, which is that the postorbital of the Spanish bird is greatly reduced

and has completely lost its contact with the jugal bar and with the squamosal. The presence of a complete postorbital in contact with the jugal bar in *Confuciusornis* also indicates that the real ancestor of birds is probably much more primitive than we expected. *Archaeopteryx* is thus further confirmed to be a side branch in early avian evolution.

*Confuciusornis* has a large orbit, indicating that it already had a bird's large eye. It has a small antorbital fenestra, anteriorly bordered by the nasal process of the maxillary and part of the nasal. *Confuciusornis* has a primitive quadrate that lacks an orbital process and the deep bowl-shaped socket on the lateral side. In modern birds the socket is for the articulation of a process on the medial side of the quadratojugal, forming a pushing system of the upper jaw that is unique to birds.

The lower jaw of *Confuciusornis* has a large fenestra. The dentary is forked into two branches posteriorly with the ventral one nearly extending to the end of the lower jaw. There also exists a small circular caudal mandibular fenestra. The splenial is not much different from that of a chicken, but quite different from the triangle-shaped splenial in *Archaeopteryx*.

## 2.2 A primitive wing that could climb

There is no doubt that *Confuciusornis* has the most primitive avian wing after *Archaeopteryx*. The ulna is shorter than the humerus. The carpometacarpus is not completely fused. The semilunate bone is exclusively fused with the third metacarpal (Note: we accept the numbering of 2, 3, 4 for the avian wing digits; also see Burke and Feduccia, 1997) as is typical of birds. The second digit is long and unreduced. Complete claws are retained. The phalangeal format is 2-3-4 as in *Archaeopteryx*. In addition to the fusion of the semilunate bone with the third metacarpal, another obvious bird feature in *Confuciusornis* is the relative enlargement of the third metacarpal and the third digit. This can be seen in *Archaeopteryx* and is clearly modified for the attachment of the secondary flight feathers (Zhou and Martin, in press).

The bastard wing (alula) has been found in an Early Cretaceous bird from Spain (Sanz *et al.*, 1996). And it has also recently been recognized in the oldest known enantiornithine bird (Hou *et al.*, MS) which represents the oldest record of this structure in birds. The bastard wing has never been recognized in any *Confuciusornis* specimens even though hundreds of well preserved specimens with feather impressions have already been discovered. We believe that the bastard wing has not been developed in *Confuciusornis* or *Archaeopteryx*. This is probably because that the second wing digit in these birds is still unreduced. In both the oldest known enantiornithine bird (Hou *et al.*, MS) and the Spanish bird *Eoalulavis*, the second digit is reduced and the claw is small.

*Confuciusornis* has retained large claws on the second and the fourth wing digits. The claw on the third digit is usually reduced and small. This is supposedly related to the feather attachment role of the third digit. In most specimens, the claw on the second digit is extremely large and curved. *Confuciusornis* is generally believed to have been able to climb trees as was *Archaeopteryx* (Hou *et al.*, 1996). In modern birds wing claws are retained only in some nestling (such as hoatzin), and help the young birds climb trees. Adult tree climbers usually have either strong and stiff tail feathers (some climbers have an elongated pygostyle) or have enlarged first pedal claws. *Confuciusornis* has a long pygostyle. We suspect that the large wing claw is probably related to the use of the wing in climbing.

### 2.3 The typical sauriurine pelvis

*Confuciusornis* has a typical sauriurine pelvis. The ilium is expanded anteriorly but reduced posteriorly. The most significant feature is probably the strut-like dorsal process on the proximal ischium. This process is short and situated more proximally in *Archaeopteryx* than in other sauriurine birds. Such a process is present in all enantiornithine birds. In *Confuciusornis*, it is long and nearly in contact with the posterior ilium. In ornithurine birds, none has shown the development of such a process on the ischium. In *Chaoyangia*, the ischium is only slightly expanded in the middle. The ischium is fused with the ilium in modern birds. Since none of the possible ancestor of birds has developed a strut-like dorsal process on the ischium, it may represent an evolutionary novelty in sauriurine birds designed to strengthen the pelvis.

The ischium of *Confuciusornis* is more primitive than any other birds except for *Archaeopteryx* in that it remains robust. The pubis is retroverted as is confirmed by hundreds of specimens. The pubis is about twice as long as the ischium. The distal end of the pubis are symphysed.

### 2.4 The early evolution of the social behavior

Previously, we have suggested the fact that hundreds of specimens have been found from a small area in such a short time probably indicates the presence of social behavior (Hou *et al.*, 1996). We can never estimate the actual number of birds living together in the past, but the abundance of fossil birds discovered in Liaoning Province can scarcely be duplicated even in Cenozoic localities. The cause of such an unusual death assemblage is hard to determine without further evidence.

Probably the most significant feature revealed by findings after our initial description of *Confuciusornis* is that some of the specimens preserve a very distinctive pair of long tail feathers, while others do not. We suppose that those with the long tail feathers are male individuals, and those without are probably females. We have also noticed the preservation of crest-like structures on the head of some

*Confuciusornis* specimens (pers. observ). These distinctive features may indicate the presence of the similar behavior as seen in some modern birds.

### 3 Early diversification and the origin of avian flight

#### 3.1 Body size—more than a single character

The importance of the change of the body size has usually been ignored. However, body size is probably one of the most important characters in the study of vertebrate evolution (Peter, 1983). This is particularly true in the study of avian evolution.

In the earliest stage of the avian evolution, size change plays a very important role in the process of initial avian flight. This is best represented by the Late Jurassic–Early Cretaceous fossil evidence found from Liaoning, China. The dichotomy between Sauriurae and Ornithurae in Mesozoic birds has been well documented. Ornithurine birds are significantly more advanced than the contemporaneous sauriurine birds, which has been previously argued mainly on the presence of a modern elongated sternum with a keel that extends along the full length of the sternum. The Early Cretaceous ornithurine birds such as *Chaoyangia* and *Ambiortus* (Kurochkin, 1985) already possess modern type coracoids and furcula. Another significant difference between early ornithurine birds and the oldest sauriurine birds is that the former are much smaller in size. *Liaoningornis* is found from the same horizon as *Confuciusornis* and it is only about half the size of *Confuciusornis* which is nearly as big as *Archaeopteryx*. We may conclude that in order to prolong flight, ornithurine birds have improved their flight apparatus simultaneously with a reduction of body size.

The enantiornithine birds in the Early Cretaceous reduced their body size as well but slightly later in time. The Chinese Early Cretaceous enantiornithine *Cathayornis*, *Sinornis*, *Boluochia*, *Otogornis* as well as all the Early Cretaceous Spanish birds (Sanz *et al.*, 1988, 1997; Sanz et Buscalion, 1992) are very close to each other in size and are much smaller than *Archaeopteryx* and *Confuciusornis*. It is noteworthy that the new Late Jurassic–Early Cretaceous Chinese bird (IVPP V11537) may represent the most primitive type of Enantiornithes (Hou *et al.*, MS) and is between *Archaeopteryx* and Early Cretaceous enantiornithine birds in body size.

The Early Cretaceous ornithurine bird *Chaoyangia* is slightly larger than the Late Jurassic–Early Cretaceous *Liaoningornis*, probably indicating that by the Early Cretaceous ornithurine birds could afford a slight increase in body size. On the other hand, the late Early Cretaceous enantiornithine *Nanantius* from Australia is still small (Molnar, 1986), enantiornithine birds probably could not afford to increase their size until the Late Cretaceous. By the Late Cretaceous, members of both Sauriurae and Ornithurae were much bigger than their Early Cretaceous ancestors (Walker, 1981;

Martin, 1991).

An important implication of the reduction in body size in ornithurine birds is that they not only prolonged flight but also enhanced the ability to take off from the ground. Endothermy was probably acquired by early ornithurine birds as is supported by their possession of modifications for powerful flight and presence of uncinata process that indicates an advanced modern breathing system. There must have been a balance between reduction in body size and the preservation of body temperature.

### 3.2 From trees down or ground up? — a few new arguments

The arguments on the origin of the avian flight have been as controversial as the origin of birds (Feduccia, 1996). Previous arguments mainly stemmed from the study of *Archaeopteryx* or from pure theoretical speculations (Bock, 1985; Ostrom, 1974, 1976; Feduccia, 1993). A survey of the recent findings of the Late Jurassic–Early Cretaceous birds from the northeast China may provide some new insight into this long-standing question.

The recognition of a dichotomy in early avian evolution further strengthens the side branch position of *Archaeopteryx* (Martin, 1983, 1991; Hou *et al.*, 1996). Furthermore, the appearance of members of both Sauriurae and Ornithurae during the Late Jurassic to Early Cretaceous shows that their common ancestor should be both older and more primitive. Nevertheless, the sauriurine birds, especially *Archaeopteryx* and *Confuciusornis* can probably provide characters that we may expect to see in the ancestor of birds. Ornithurine birds, on the other hand, may be less similar to the primitive ancestor.

Both *Confuciusornis* and *Archaeopteryx* could fly. However, long, sustained flight was probably still impossible. Besides body size and a primitive wing design, these birds lack a sternal keel and a laterally compressible furcula. The claws suggest a climbing, arboreal life. The large and curved wing claws are completely retained, and they are supposed to be used as an auxiliary tool during the climbing. In *Confuciusornis*, the posterior caudal vertebrae of *Confuciusornis* have fused into a pygostyle, and it is still relatively longer than that in modern birds. The second wing claw is usually very long and curved. All these seem to confirm the climbing life of *Confuciusornis*.

One of the biggest challenge the early birds had to face is how to take off from the ground. Considering the body size and the flight capability of *Archaeopteryx* and *Confuciusornis*, there appears to be no evidence suggesting that they might be able to take off from the ground. Climbing is probably still a necessity rather than a luxury. This might explain why the wing claws are retained and unreduced. Compared with *Archaeopteryx* and *Confuciusornis*, the Early Cretaceous enantiornithine bird *Cathayornis* and *Sinornis* lost the fourth wing claw, and the other two claws were

greatly reduced, strongly indicating a loss of climbing function for the wing at this stage of sauriurine evolution. These Early Cretaceous birds are all relatively small and have a sternum with a keel and long coracoids. We believe they are capable of taking off from the ground. As we mentioned earlier in this paper, ornithurine birds had probably evolved a lot more from their common ancestor than the sauriurine birds. Therefore their supposed capability of taking off from the ground is better explained as an improvement on the more primitive situation in which *Archaeopteryx* and *Confuciusornis* are more or less still in the learning stage of flying with the assistance of trees.

The oldest known ornithurine birds are already very small. And they have developed an elongated sternum with cranio-lateral processes and a keel extending along its full length. *Liaoningornis* has a tarsometatarsus that is fused at both of its proximal and distal ends. *Chaoyangia* also shows distal fusion. We have no doubt that these ornithurine birds could take off from the ground.

The pedal claws of both *Archaeopteryx* and *Confuciusornis* are sharp and curved. This is also true of *Liaoningornis* and the oldest known enantiornithine bird (Hou *et al.*, MS), both of which are found from the same horizon as *Confuciusornis*. All the Early Cretaceous enantiornithine birds show this character. The shape of the pedal claws in these early birds indicates that all of them spend most of the time on the tree. This again conforms with the arboreal theory of avian flight. The Early Cretaceous ornithurine bird *Chaoyangia* has relatively short pedal claws, which may show that this bird spends a lot of time on the ground. Another Chinese Early Cretaceous ornithurine bird, *Gansus*, has totally given up the tree life. All of these birds could probably take off from the ground easily by then, but this must be viewed as secondary rather than an avian characteristic initially associated with the putative ancestor of birds.

### 3.3 From trees to water, a new expansion

The early diversification of birds is also best represented by the materials found in China. *Confuciusornis*, the oldest known enantiornithine bird (Hou *et al.*, MS) and *Liaoningornis* are three very different birds from the Late Jurassic to Early Cretaceous Yixian Formation in Liaoning, northeast China. In the Early Cretaceous, *Cathayornis*, *Sinornis*, *Boluochia* and *Otogornis* are all enantiornithine birds (Hou *et al.*, 1995); *Chaoyangia* and *Gansus* are ornithurine birds. The size diversification of these early birds has already been briefly summarized earlier in this paper, and from the fossil evidence found from the Late Jurassic to Early Cretaceous of China we accept the concept of arboreal origin of avian flight. And as mentioned above, the majority of the early birds spend most of the time on the trees. Living away from trees was probably still rare during the Late Jurassic to Early Cretaceous. And *Gansus* is probably the



oldest evidence of a bird that had completely left the trees.

*Gansus* is an Early Cretaceous bird from Gansu Province, northwest China. It is probably as old as or slightly younger than *Sinornis* and *Cathayornis*. *Gansus* also has a well fused tarsometatarsus, showing that it may have been more derived than such early ornithurine birds as *Liaoningornis* and *Chaoyangia*. This bird was previously purported to be a shore bird or wading bird (Hou and Liu, 1984). With mainly a complete foot preserved, the most distinctive feature of this bird is that it has short pedal claws and relatively long phalanges. Another significant feature of this bird is the presence of a peculiar tubercle on the claws. This claw tubercle has seldom received any attention in any avian literature. And it has previously been cited as evidence of land adaptation by its original authors. However, our recent efforts to find the similar structures in modern birds resulted in a totally different conclusion. Even though seen only in a few of modern groups, this structure is found associated with diving (e.g. Alcidae) or wading birds (e.g. Recurvirostridae, Scolopacidae etc.). Thus, the presence of this structure in *Gansus* actually provides another piece of evidence for its aquatic adaptation.

*Gansus* shares with Alcidae not only similar claw tubercles but also many of the other details in the foot. As the function of this tubercle is still unclear to us, it is probably still too early even to speculate about its possible connection to any particular aquatic adaptation. But it seems clear that *Gansus* had probably specialized to the aquatic life more than previously thought.

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