

Recent Progress in the Study of Pterosaurs from China

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Pterosaurs are the earliest vertebrates known to be able to fly in the sky. They existed from the Late Triassic to the end of the Cretaceous (about 220 to 65 million years ago), when the land was ruled by another kind of reptile—dinosaurs. Pterosaurs consist of the long-tailed Rhamphorhynchoidea and the short-tailed Pterodactyloidea. The former is a basal group and the latter is more derived.

Before the 1990s, there was sporadic pterosaur record in China. Young Chung-chien (C. C. Young), the doyen of Chinese vertebrate paleontology, reported the first Chinese pterosaur bones from Laiyang of Shandong Province in 1958. Later, a number of pterosaurs were described such as *Dsungaripterus weii*, *Noripterus complicitens* from Xinjiang, *Huanhepterus quingyangensis* from Gansu, *Angustinaripterus longicephalus* from Sichuan, and *Zhejiangopterus linhaiensis* from Zhejiang.

Moreover, since *Eosipterus yangi*, the first pterosaur was described from the Cretaceous Jehol Group, western Liaoning, in 1997, the number of pterosaur specimens has increased rapidly. Hundreds of articulated pterosaur specimens have been found and more than 20 new species established. Almost all of them are from the Jehol Biota, which occurs in the strata distributed in areas of western Liaoning, northern Hebei and southeastern Inner Mongolia. These new fossils shed new light on the origin, early evolution, and physiology of pterosaurs. Particularly, the discovery of the first pterosaur egg with an embryo in it and subsequent findings of two additional embryos suggest that the pterosaur was born more like a bird than a reptile. In recent years, paleontologists found new specimens of non-pterodactyloids, which are probably a missing link between Rhamphorhynchoidea and Pterodactyloidea. Here we briefly summarize recent progress

in the study of pterosaurs from China.

The smallest, swallow-sized arboreal pterosaur

Can you imagine a pterosaur as tiny as a swallow? It did exist about 120 million years ago. Despite representing an immature individual, *Nemicolopterus crypticus* (Wang *et al.*, 2008) is neither a hatching nor a newborn based on the ossification of the skeleton. With a wingspan of 25 cm, it is only slightly bigger than a newborn from the Solnhofen Limestone, which has a wingspan of 18 mm. This makes it the smallest pterosaur so far known in the world.



Holotype of *Nemicolopterus crypticus*, the smallest arboreal pterosaur yet in the world. This swallow-sized creature used to live in the forest and eat insects. On the left is the fossil skeleton and the right a reconstruction by ZHAO Chuang. Scale bar is 1 mm.

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This specimen was collected from the sedimentary rocks of the Jiufotang Formation, which were deposited 120 million years ago, from Jianchang County, Huludao City, Liaoning Province. This specimen is relatively complete and articulated. Its morphological features suggest that it is a basal dsungaripteroid and belongs to the sister-group of Ornithocheiroidea, a clade that includes all more derived pterodactyloids.

The largest pterosaur in the world, *Quetzalcoatlus*, has a wingspan of 12 m, nearly 50 times as large as *Nemicolopterus*. Amazingly, they have a relatively close relationship. Therefore we can imagine the great diversity of pterosaurs, at least in size and in the ecological niches they occupied.

A missing link between the two main pterosaur groups

Among the non-pterodactyloid pterosaurs in the Jehol Biota, two bear an elongated tail. One is *Pterorhynchus wellnhoferi*, known from a complete skeleton collected from the Daohugou Bed, Ningcheng of eastern Inner Mongolia, and its age remains controversial. The other is recently-described *Changchengopterus pani*, which is based on a partial skeleton lacking the skull. According to its original describers, the specimen was collected from the Tiaojishan Formation in Qinglong, Hebei, which is regarded the Middle Jurassic in age. Last year, we studied another long-tailed pterosaur from a new location.

A new long-tailed pterosaur, *Wukongopterus lii*, belonging to a new Family Wukongopteridae (Wang *et al.*, 2009), was described based on an almost complete skeleton representing an individual with an estimated wingspan of 73 cm. The specimen was discovered in the strata that possibly represent the Daohugou Bed at Linglongta, Jianchang, Liaoning Province. *Wukongopterus lii* is a non-pterodactyloid pterosaur given its elongated tail and digit V, but has some pterodactyloid features such as elongated cervical vertebrae and dentition. Some details in taphonomic aspect provide indirect evidence of an uropatagium (the membrane between the hindlimbs), supporting the hypothesis that at least all non-pterodactyloid pterosaurs show a membrane between the hindlimbs.

Although the number of non-pterodactyloid is small, *Wukongopterus lii* is the most particular one because of its relationship with other pterosaurs. Just like *Darwinopterus modularis* (Lü *et al.*, 2009), another long-tailed pterosaur published almost at the same time, it displays not only some primitive features but also advanced ones. It is reasonable to infer that this kind of long-tailed pterosaur is the missing link between the two main pterosaur groups. It seems that Wukongopterids, *e.g.*, *Wukongopterus* and *Darwinopterus*, have an interesting combination of characters, with feet and tails as found in primitive pterosaurs and, skulls and necks

as found in more advanced cousins. As a missing link this newly established family (Wang *et al.*, 2009) now helps us better understand the evolution of pterosaurs.



Holotype of *Wukongopterus lii*, a missing link between the two main pterosaur groups. It has an advanced head and neck but a primitive foot and tail. Scale bar is 5 cm.

A “hairy” pterosaur with membrane and web

The first clear evidence of what may be “hair” was reported by Wanderer in 1908, who described “needle-point pits” in a specimen of *Rhamphorhynchus* from the Solnhofen Limestone. Wanderer recognized these features as impression of the skin, and they were only later interpreted as “hair”. A famous hairy pterosaur is *Sordes* from the Upper Jurassic of Kazakhstan, which has “hair,” membrane, and some other soft tissues. *Jeholopterus ningchengensis* is another kind of pterosaur with clear soft tissues.

Jeholopterus was found at Daohugou, Ningcheng County, Inner Mongolia, and it was first reported in 2002 (Wang *et al.*, 2002). At that time, we only briefly described the soft tissues. In 2009, a detailed study on the membrane and other soft tissues was published (Kellner *et al.*, 2009). The main membrane between the trunk and forelimbs is divided into two parts: one is distal and comparatively more rigid and the other is proximal and more tensile. Moreover, the membrane is multilayered, with at least three layers, and the fibers of each layer are oriented differently. The configuration observed in *Jeholopterus* might have allowed subtle changes in the membrane tension during flight, resulting in better control of flight movements and organization of the wing membrane when the animal was at rest.

There is another well-developed integument over the body, and it is known as “hair.” The fibers of the “hair” are thicker than those of the membrane. Only one specimen preserved epidermis but without any “hair.” It is possible that “hair” was loosely attached to the body and could be readily lost after death, especially if the carcass was floating in the water for a while. However, the “hair” is still mysterious, and we need more advanced techniques to study this specimen.



Holotype of *Jeholopterus ningchengensis*: (a) fossil skeleton, (b) soft tissues and (c) reconstruction by LI Rongshan, with the well-preserved membrane and other soft tissues such as “hair” and web. Scale bar is 1 cm.

In summary, many pterosaurs were reported in the Early Cretaceous Jehol Group and earlier sediments from northeastern China. The Jehol Biota has become one of

the most important fossil lagerstätten in the world, and has attracted attention of many paleontologists from all over the world.

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