

地球科学前沿



**SHORT PAPERS FOR THE 8TH INTERNATIONAL
CONGRESS ON THE JURASSIC SYSTEM**

Marine and non-marine Jurassic

Special Issue
2010 Vol.17

Vertebrate Assemblages from the Middle-Late Jurassic Yanliao Biota in Northeast China

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Introduction

In the last twenty years, many exceptional fossils have been recovered from the Early Cretaceous Jehol Biota (131-120 Ma) in western Liaoning, northern Hebei and southeastern Inner Mongolia, Northeast China, including early birds, feathered dinosaurs, mammals, pterosaurs, amphibians, fishes, insects and flowering plants (Zhou, 2006; Zhou and Wang, 2010). Relatively less known from almost the same region are many equally important Middle-Late Jurassic fossils belonging to the Yanliao Biota, including the oldest known feathered dinosaurs (Hu et al., 2009), swimming and flying mammals (Meng et al., 2006), pterosaurs with hair-like integuments, lizards, fishes, and abundant salamanders and insects. The recent fossil discoveries of the Yanliao Biota have extended the temporal distribution of feathered dinosaurs and helped to resolve the so-called “temporal paradox” that perplexed paleontologists studying the origin of birds. Despite its relatively lower vertebrate diversity, the Yanliao Biota is no less important evolutionarily than the more famous Jehol Biota. This short paper aims to provide a brief introduction to the vertebrate components of the Yanliao Biota as compared to that of the Jehol Biota, and to clarify the current debate on the age of the Yanliao Biota and the correlation of its fossil-bearing deposits.

Distribution and Age

Hong (1983) first used Yanliao to refer to an insect fauna from northern China, and it was later adopted by Ren et al. (1995) to refer to the Middle Jurassic fauna from mainly northern Hebei and western Liaoning. The Yanliao Biota is well known for including hundreds of insect species and many plants, conchostracans, ostracods and bivalves. It was, however, little known to vertebrate paleontologists due to the limited vertebrate fossil record. Important vertebrate fossils have now been reported from the Lanqi Formation at the Daohugou locality in Ningcheng, Inner Mongolia (sometimes referred to as the Daohugou Biota) and more recently from the Linglongta area in Jianchang, western Liaoning (Duan et al., 2009). In this paper, we regard the Daohugou Biota as equivalent to Yanliao Biota and adopt the latter as a more commonly accepted name for this Jurassic terrestrial biota.

Like the Jehol Biota, the Yanliao Biota is mainly distributed in western Liaoning, southeastern Inner

Mongolia and northern Hebei, but some elements of the biota have a broader distribution in Central Asia and East Asia. The Yanliao fossil-bearing horizons mainly include the Haifanggou Formation (or Jiulongshan Formation in Hebei) and the overlying Lanqi Formation (or Tiaojishan Formation in Hebei).

The age of the Yanliao Biota was traditionally considered to be Middle Jurassic (Ji and Yuan, 2008), but recent dating indicates that it actually ranges from Middle to Late Jurassic. A recent dating of the Lanqi Formation resulted in an age estimate of 166-153 Ma for this formation (Yang and Li, 2008; Ma and Zheng, 2009), consistent with an earlier estimate of 168-152 Ma (Liu et al., 2006). Furthermore, recent published dating (161 and 158 Ma) for the basal Lanqi Formation by Chang et al. (2009) even led to the proposal that the Lanqi Formation belonged completely to the Late Jurassic. This would imply that the major Yanliao fossil-bearing horizon (Lanqi Formation) is mostly Upper Jurassic, with only the earliest elements of the biota from the Haifanggou Formation (Ji and Yuan, 2008) being of Middle Jurassic age.

Composition of the Yanliao Vertebrate Assemblage

In the past, the only vertebrate fossils known from the Yanliao Biota were the reptile *Yabeinosaurus tenuis* (Young, 1958), the mammal *Liaotherium gracilis* (Zhou et al., 1991) and the acipenseriform fish *Liaosteus hongii* (Lu, 1994) from the Haifanggou Formation in Liaoning. In recent years more vertebrates, including fishes, amphibians, lizards, pterosaurs, dinosaurs and mammals, have been discovered and described from the Lanqi Formation at various localities in Inner Mongolia, western Liaoning and northern Hebei (Wang, 2004; Ji and Yuan, 2008; Zhang et al., 2008; Evans et al., 2009; Hu et al., 2009).

The vertebrates from both the Haifanggou and Lanqi formations include: *Liaosteus hongii* and an undescribed palaeonisciform fish (personal observation by F.J.); four genera and species of salamanders, *Chunerpeton tianyiensis*, *Jeholotriton paradoxus*, *Liaoxitriton daohugouensis* and *Pangerpeton sinensis*, and an unnamed juvenile anuran (Wang et al., 2010); “*Yabeinosaurus tenuis*” (Young, 1958) and two other unnamed lizards (Evans and Wang, 2009); five genera and species of pterosaurs, *Changchengopterus pani*, *Darwinopterus modularis*, *Jeholopterus ningchen-*

gensis, *Pterorhynchus wellnhoferi*, and *Wukongopterus lii* (Wang et al., 2009; Lü et al., 2010); four genera and species of theropod dinosaurs, *Anchiornis huxleyi* (Hu et al., 2009) *Epidendrosaurus ningchengensis* (= *Scansoriopteryx heilmanni*), *Epidexipteryx hui*, and *Pedopenna daohugouensis*; and four genera and species of mammals, *Castorocauda lutrasimilis*, *Liaotherium gracile*, *Pseudotribos robustus* (Ji and Yuan, 2008) and *Volaticotherium antiquum*.

Comparison and Discussion

The Yanliao Biota and the Jehol Biota represent the two most important late Mesozoic lagerstätten in Northeast China. They shared a similar paleogeographic distribution. The vertebrate assemblage from the Jehol Biota in western Liaoning, northern Hebei, and southeastern Inner Mongolia currently comprises, at generic level, approximately 31 birds, 30 dinosaurs, 16 pterosaurs, 13 mammals, five lizards, five choristoderes, two turtles, eight amphibians, and seven fishes as well as one agnathan, a total of 118 genera (Zhou and Wang, 2010). The Yanliao vertebrate assemblage currently comprises a much lower generic diversity with one fish, four salamanders, one lizard, five pterosaurs, four dinosaurs, and four mammals, as well as several unnamed taxa of fishes, frogs and lizards. Compared to the Jehol Biota, the Yanliao Biota lacks any record of teleost fishes, birds, choristoderes or turtles. Its relatively much lower vertebrate diversity can be at least partly explained by preservational and sampling bias. On the other hand, the great vertebrate diversity of the Jehol Biota also reflects the evolutionary radiation of major groups such as birds, dinosaurs, pterosaurs and mammals in the Early Cretaceous, a radiation that continued into the Late Cretaceous.

The Yanliao Biota and the Jehol Biota share some faunal components: the squamate *Yabeinosaurus* is reported from both biotas, though the identification of the older specimen is uncertain; the acipenseriform *Liaosteus* from the Yanliao Biota is referred to the same subfamily, Spherosteinae, as *Yanosteus* from the Jehol Biota (Jin, 1999); the pterosaurs *Jeholopterus* from the Yanliao Biota and *Dendrorhynchoides* from the Jehol Biota both belong to the family Anurognathidae (Wang et al., 2002); and two species of the salamander *Liaoxitriton* have been reported from the Yanliao and Jehol biotas, respectively (Wang, 2004). These similarities have led to the proposal that the Yanliao Biota represented a "Pre-Jehol Biota" (Zhang, 2002; Meng et al., 2006). However, there appears to be a clear interval between the Yanliao and Jehol biotas spanning the latest Jurassic and the earliest Cretaceous. The thick deposits laid down during this interval are generally referred to the Tuchengzi Formation (or Houcheng Formation in Hebei), previously considered Late Jurassic in age but currently dated as approximately 139-156 Ma (Zhou et al., 2009). Vertebrate fossils are rare and include palaeonisciform fishes and the ceratopsian dinosaurs *Chaoyangosaurus* and *Xuanhuaceratops* (Zhao et al., 2006). Despite the lasting controversy over

the continental Jurassic-Cretaceous boundary in China (Zhou et al., 2009), we consider that the J-K boundary probably lies within the Tuchengzi Formation.

Many of the Yanliao vertebrates bear some resemblance to those of other localities in Central and East Asia, and also Europe. The pterosaur *Jeholopterus* from Inner Mongolia belongs to the same rhamphorhynchoid family, Anurognathidae, as *Anurognathus* from Solnhofen, Germany (Upper Jurassic) and *Batrachognathus* from Karatau, Kazakhstan (Upper Jurassic). Among mammals, *Liaotherium* is related to *Amphilestes* from the Middle Jurassic of Europe (Ji and Yuan, 2008); *Castorocauda* is a member of the Docodonta, also known from the Middle-Upper Jurassic of Europe and Xinjiang; and *Pseudotribos* is related to *Shuotherium* from the Upper Jurassic of Sichuan, Southwest China (Wang et al., 2006). The Yanliao palaeonisciform fishes closely resemble *Pteroniscus* from Karatau, Kazakhstan, and *Jeholotriton* and *Pangerpeton* stem caudates as is the Karatau genus *Karaurus*.

Some paleobiogeographic barriers (e.g., Okhotsk Sea and Bering Sea) may have limited faunal exchange from the Middle Jurassic onward, but the fauna in Asia was probably never completely isolated from that of Europe in the Middle and Late Jurassic. By the Early Cretaceous, the disappearance of paleogeographic barriers had resulted in a more global distribution of vertebrate groups with the exception of freshwater fishes.

From the Middle Jurassic to Early Cretaceous, Northeast China underwent a period of tectonic activity with frequent volcanic eruptions. Ash beds are often interbedded with fossil-bearing fluvial or lacustrine deposits due to the Yanshan Orogeny and the destruction of the North China Craton. We consider that the evolutionary period between the Yanliao Biota and the Jehol Biota was punctuated by a long interval of dry climate, during the deposition of the Tuchengzi Formation. More fossil discoveries from this formation should help to clarify the transition between the two major terrestrial biotas of this region.

Acknowledgements: We thank Prof. Susan Evans (UCL) for discussion and help with the English. The research was supported by the Major Basic Research Projects (2006CB806400) of MST of China and the National Natural Science Foundation of China (40121202).

Key words: Yanliao Biota; Jurassic; Vertebrate assemblage; Northeast China

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