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Timing of the earliest known feathered dinosaurs and transitional pterosaurs older than the Jehol Biota

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ABSTRACT

The Early Cretaceous Jehol Biota in China has produced numerous well preserved fossils of feathered theropods and early birds. Recent discoveries of feathered dinosaurs, as well as transitional pterosaurs and a sexually mature individual of *Darwinopterus* preserved together with an egg from the Daohugou Biota of an earlier age than the Jehol Biota, in northeastern China, have greatly enriched our knowledge of the transition from dinosaurs to birds and primitive to derived pterosaurs. The age estimate of fossils or host strata, however, has proven to be contentious and varies widely from the Middle Jurassic to the Early Cretaceous. Here, we report a SHRIMP U–Pb zircon date unambiguously associated with the fossil horizons, and thus, for the first time, provide an age calibration for the earliest appearance of feathered dinosaurs and transitional pterosaurs. Date results indicate that the feathered dinosaurs of China were present more than 161 Ma ago, unquestionably older than *Archaeopteryx* in Germany, and are the earliest known feathered dinosaurs in the world. Furthermore, feathers appeared in ornithischians before 159 Ma rather than late in the Early Cretaceous. The known transitional pterosaurs first emerged before 161 Ma. The Daohugou Biota, containing mammals, primitive pterosaurs, insects and plants, in addition to the feathered dinosaurs, was living in Inner Mongolia ,western Liaoning and northern Hebei in northeastern China during the Middle Jurassic.

1. Introduction

The Early Cretaceous Jehol Biota (Grabau, 1928; Gu, 1962; Chen, 1988) of northeastern China has revealed a plethora of extraordinarily well preserved fossils of feathered theropods and early birds over the past 10 years (Chen et al., 1998; Ji et al., 1998; Xu et al., 1999a,b, 2001, 2002, 2003, 2004, 2010; Zhou et al., 2003). However, the Daohugou Biota (Zhang, 2002), which is older than the Jehol Biota and estimated to be of Jurassic age, was discovered in recent years at Ningcheng, Inner Mongolia, and in northeastern China, and has yielded spectacular fossil mammals (Ji et al., 2006; Meng et al., 2006; Luo et al., 2007a, 2007b, 2011), pterosaurs (Ji and Yuan, 2002; Lü et al., 2009, 2011), and insects (Ren et al., 2009), in addition to feathered dinosaurs (Hu et al., 2009; Xu and Zhang, 2005; Xu et al., 2009; Zheng et al., 2009; Zhang et al., 2000), which have greatly expanded our knowledge of the diversity and palaeobiology of a time before the Jehol Biota and contributed to our understanding of the origin of the Jehol Biota.

Though the feathered dinosaur species (Zheng et al., 2009; Hu et al., 2009; Xu and Zhang, 2005; Xu et al., 2009, 2011) and transitional pterosaurs (Lü et al., 2009, 2011) were discovered more recently in China, their age and that of the Daohugou Biota has been contentious. Some authors concluded that it belongs to the Early Cretaceous (He H., 2004a, 2004b, 2005; Wang et al., 2005b; Xu et al., 2009; Zheng et al., 2009) and others describe it as Jurassic (Zhang J, 2002; Zhang H, 2008a, 2008b, 2009; Liu et al., 2004; Liu and Liu, 2005; Liu et al., 2006; Duan et al., 2009; Hu et al., 2009; Lü et al., 2009; Chen et al., 2004). The timing of their earliest emergence and evolution remains to be confirmed. Feathered theropods from the Jehol Biota previously date to 125 Ma (Swisher et al., 1999,2002) and were deemed to be younger than *Archaeopteryx lithographica* at 150 Ma from Solnhofen, Germany (Wellnhofer, 1992). In terms of evolutionary biology, feathered dinosaurs and associated birds older than 150 Ma or of Jurassic age should exist if in fact birds evolved from theropods. More recently, ornithischians (*Tianyulong confuciusi*) with feathers of "the early Cretaceous " were reported at Yaolugou, Jianchang, western Liaoning, China (Zheng et al., 2009), which challenges the evolution of dinosaur feathers and implies that hairlike structures may be common for either the early dinosaurs or their descendents, or both. In addition, another new, feathered theropod, *Anchiornis huxleyi* (Hu et al., 2009), was also reported in 2009 from the same locality. Based on its well preserved morphology, it is thought to be closely related to basal birds. The two above-mentioned important discoveries expand our knowledge of the

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origin and evolution of feathers, but an accurate timing of the emergence of feathered theropods and ornithischians remains unclear. More recently, Xu et al.(2011) reported an Archaeopteryx-like therpod (*Xiaotingia zhengi*) from China, and concluded that Archaeopteryx was an animal very closely related to the featured therpod and not a bird. These current dates will help palaeontologists to understand when the ancestors of modern birds or closely related cousins appeared.

Over the years, both primitive and derived species of pterosaurs, separated by a large time gap that had never been filled before, were frequently discovered in China and abroad (Wang et al., 2002, 2005a, b; 2009; Wang and Zhou, 2006). Transitional pterosaur specimens, however, were not found in these expeditions. One transitional form (*Darwinopterus*) from the same locality and horizon yielding *A. huxleyi* was reported (Lü et al., 2009), which fills a gap in pterosaur evolution. In addition, a sexually mature individual of *Darwinopterus*, preserved together with an egg, was reported from the same horizon as *Darwinopterus* and *A. huxleyi* (Lü et al., 2011). Feathered theropods and ornithischians and transitional forms of pterosaurs were all excavated from sediments interbedded with volcanic rocks from the Jurassic Lanqi Formation (called the Tiaojishan Formation in Hebei Province) in Jianchang, western Liaoning, China. Though many dated results have previously been attained for this formation elsewhere (Gao et al., 2004; Davis, 2005, Davis et al., 2001; Zhang et al., 2005, 2008a, 2008b, 2008c; Liu and Liu, 2005; Liu et al., 2004, 2006; Liu J et al., 2006; Hu et al., 2007; Chang et al., 2009) with a rough estimation of 152–165 Ma, a precise date for the fossils has not been determined. Here, this study reports SHRIMP U–Pb zircon ages for the fossil horizons and for the feathered species of theropods and ornithischians and transitional forms of pterosaurs, emphasizing the timing of the first appearance of feathered dinosaurs and transitional pterosaurs previously not well determined.

2. Geological background

During the Late Mesozoic period, the sampling location and the surrounding area were located in northeastern part of the North China Craton, in a terrestrial environment at a paleolatitude of approximately 45°N (Smith et al., 1994). The Late Mesozoic terrestrial strata of the northeastern China , in ascending order, are the Middle Jurassic Haifanggou Formation (called the Jiulongshan Formation in Hebei Province) and Lanqi/Tiaojishan Formation, the Upper Jurassic-Lower Cretaceous Tuchengzi Formation (called the Houcheng Formation in Hebei Province), the Lower Cretaceous Zhangjiakou Formation (called as Tamulangou Formatio in the Great Xinganling Mountain, and Maketouebo,Manitu and Baiyingaolao Formations in an ascendering order in southeastern Inner Mongolia), the Dabeigou Formation, the Yixian Formation and the Jiufoutang Formation, which are widely distributed in western Liaoning, northern Hebei, and southern Inner Mongolia of northeastern China (Fig. 1,Table 1) and contain two well preserved terrestrial biotas (the Daohugou Biota and the Jehol Biota). Both the Haifanggou Formation and Lanqi/Tiaojishan Formation yielded fossils of the Daohugou Biota. The fossils of the Jehol Biota occurred within the Lower Cretaceous Zhangjiakou Formation, Dabeigou Formation, Yixian Formation and Jiufoutang Formation.

The Haifanggou/Jiulongshan Formation of western Liaoning and northern Hebei of China, containing fauna including conchostracans *Euestheria ziliujingensis*, bivalves *Ferganoconcha* spp., insects *Mesoneta beipiaoensis* Wang, *Mesoblattina* sp., *Sinoplecia protansa* Wang, *Platyperla plotypoda* B. R. et G., and *Lycoriomimodes ruida* Wang, and abundant plants (Chen, 2003), is mainly composed of sandstones, conglomerates, shales, and interbedded pyroclastic rocks (tuffs) and occasional poor coal seams and has a thickness of more than 200 m. The Lower Haifanggou/Jiulongshan Formation has more conglomerates, and the proportion of pyroclastic rocks increases upward.

Limited radioisotopic studies for the Haifanggou/Jiulongshan Formation have been reported. K/Ar whole rock analyses from the Haifanggou/Jiulongshan Formation yielded ages of 146 Ma for a volcanic rock at 900 m depth, 162 Ma for one at 1300 m depth and 178 Ma for one at the base (Chen et al., 1997). Wu et al. (2004) reported Rb/Sr isochron ages of 177 Ma from three samples and 188 Ma from four samples. The large uncertainties of most of these data and the incomplete stratigraphic descriptions of the samples limit their value for high-resolution chronostratigraphy (Chang et al., 2009).

The 200–800 m thick Lanqi/Tiaojishan Formation of western Liaoning and northern Hebei, mainly consists of basalts, with andesites in the lower and middle of the formation and rhyolites, acid tuffs, and purple-red tuffaceous siltstones, sandstones, and conglomerates. Besides the abundant conchostracans and plants (Zhang, 2002; Duan et al.,

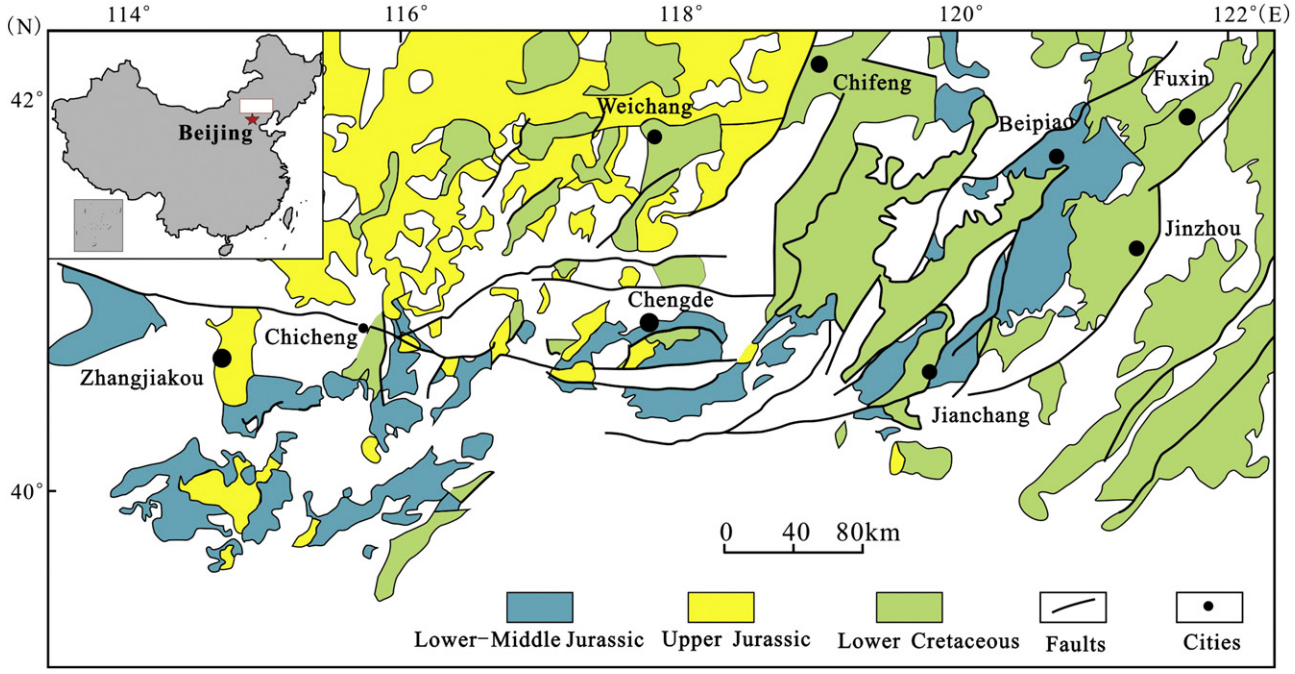

Fig. 1. Distribution of Late Mesozoic terrestrial strata and tectonics in northeastern China.