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Vertebrate assemblages of the Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota: Comparisons and implications

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Abstract

Although both the Yanliao and Jehol vertebrate assemblages are known for exceptional preservation of feathered dinosaurs, mammals, pterosaurs, lizards, salamanders, and fish, the Early Cretaceous Jehol Biota also contains birds, choristoderes, frogs, and turtles that are currently lacking in the Jurassic Yanliao Biota. The vertebrate assemblages of the Yanliao and Jehol biotas are very distinct from each other, with the salamander *Liaoxitriton* being the sole unquestionably shared taxon on generic level. Both assemblages contain mainly stem relatives of major clades of extant vertebrates, with all genera and species extinct. Crown group taxa are restricted to some fishes, salamanders, frogs, and turtles.

In addition to its much greater taxonomic diversity, the Jehol vertebrate assemblage also shows a greater body size variation among dinosaurs, pterosaurs, and mammals (three major vertebrate groups shared by the two biotas); however, members of these groups are generally small in the Yanliao Biota. The Jehol aquatic vertebrates also show a much greater diversity, characterized by many large-sized forms such as acipenseriforms and choristoderes, possibly indicating growing and more expanded ecological adaptations of the Jehol vertebrates.

The relatively greater biodiversity of pterosaurs in the Yanliao Biota as compared to that in the Jehol Biota was due possibly to the lack of birds as a competitor then. Birds in the Jehol Biota had occupied much of the similar ecological niches (forest, lakes etc.) with more sophisticated and refined flight capability.

The Yanliao dinosaurs that were dominated by maniraptorans are either paravians or closely related species, possibly indicating that northeastern China could be an origin center of the earliest birds, consistent with the previous hypothesis that this area was probably also the origin and diversification center for many other biological groups.

The flourishing time of the Jehol Biota (125 Ma) appears to be coincident with the peak of the destruction of the North China Craton, and the flourishing time of the Yanliao Biota (160 Ma) is coincident with the initiation time of the destruction of the North China Craton or the beginning of the subduction of the Paleo-Pacific plate underneath the Asian continent that resulted a series of tectonic and palaeogeographic and palaeoenvironmental changes, confirming the co-evolution between the two biotas and their geological and palaeoenvironmental background. The frequent volcanic activities during the formation of both the Yanliao and Jehol biotas not only provided much nutrient to the lakes, but also were critical for the exceptional soft tissue preservation of the two lagerstätten.

The cold temperature or the fluctuation of temperature during the Middle Jurassic–Late Jurassic transition might be related to the first appearance of feathered dinosaurs and haired pterosaurs. The cold interval during the Early Cretaceous Jehol Biota could possibly partially explain the presence of many feathered dinosaurs including some large-sized theropods.

Keywords: Jehol Biota; Yanliao Biota; Vertebrates; Geological background; North China Craton

1. Introduction

The Middle–Late Jurassic Yanliao Biota (also known as the Daohugou Biota) and the Early Cretaceous Jehol Biota represent fossil assemblages of two of the most famous Mesozoic terrestrial lagerstätten from China, most notable for producing

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many rare and exceptionally preserved fossils (Zhou et al., 2003, 2010, in press; Ren et al., 2010; Zhang et al., 2010; Zhou and Wang, 2010; Lü et al., 2011; Pan et al., 2013, 2016; Sullivan et al., 2014; Zhou, 2014; Huang, 2015; Xu et al., 2015, in press). They are preserved in the lacustrine sediments (mainly tuffaceous shales or mudstones) often interbedded with tuffaceous layers. Both biotas preserved feathered dinosaurs and many other vertebrates such as fishes, salamanders, lizards, pterosaurs, and early mammals, and share a similar palaeogeographic distribution in northern Hebei, western Liaoning, and southwestern Inner Mongolia (Fig. 1) although the Jehol Biota seems to be more widely distributed (Meng et al., 2011; Pan et al., 2013; Bi et al., 2014; Sullivan et al., 2014; Xu et al., 2014, in press; Zhou, 2014; Zhou et al., in press) (Fig. 1); however, there existed a temporal hiatus between the Yanliao Biota (166–159 Ma) and the Jehol Biota (131–120 Ma), thus they comprise two very distinct and slightly related vertebrate assemblages.

It is notable that the definition of the Yanliao Biota referred to in this paper comprising fossil assemblages from both the Jiulongshan (or Haifanggou) and Tiaojishan (or Lanqi) formations (Zhou et al., 2010; Xu et al., in press), is slightly different from the Daohugou Biota as referred by Sullivan et al. (2015) that is defined as fossil assemblage from a set of localities, thought to be stratigraphically situated near the boundary between the Jiulongshan and Tiaojishan formations that were characterized by the presence of the salamander *Chunerpeton tianyiensis*. The definition of the Jehol Biota follows Pan et al. (2014) with the fossil-bearing deposits from the Huajiying, Yixian, and Jiufotang formations or equivalent ash-interbedding sediments in neighboring areas (Table 1).

The vertebrates from these two biotas provide the most compelling evidence for understanding the transitions from non-avian theropods to birds as the Yanliao Biota contains the earliest known feathered dinosaurs, many of which are close relatives of birds, and the Jehol Biota documents the earliest radiation of bird evolution and contains some of the basal-most lineages of early birds and many other more derived maniraptoran theropods (Xu et al., 2009, 2014, in press; Hu et al., 2010; Sullivan et al., 2014; Zhou, 2014; M. Wang et al., 2016a,b; Zhou et al., in press). In addition, many other groups of vertebrates, e.g., mammaliforms, pterosaurs, lizards, amphibians, and fishes also provide important information concerning their evolution in the Jurassic and Early Cretaceous.

Both the Yanliao Biota and Jehol Biota had witnessed a strong tectonic activity as shown by frequent volcanic eruptions, during the most active stage of the destruction of the North China Craton against the background of the Paleo-Pacific subduction underneath the eastern Asian continent (Davis et al., 2001; Wu et al., 2005, 2008; Jiang et al., 2011; Zhu et al., 2011, 2012a,b; Liu et al., 2015). The presence of volcanic ashes enables a comprehensive dating of the ages of the fossil-bearing deposits in addition to biostratigraphic and geochronological work (Swisher

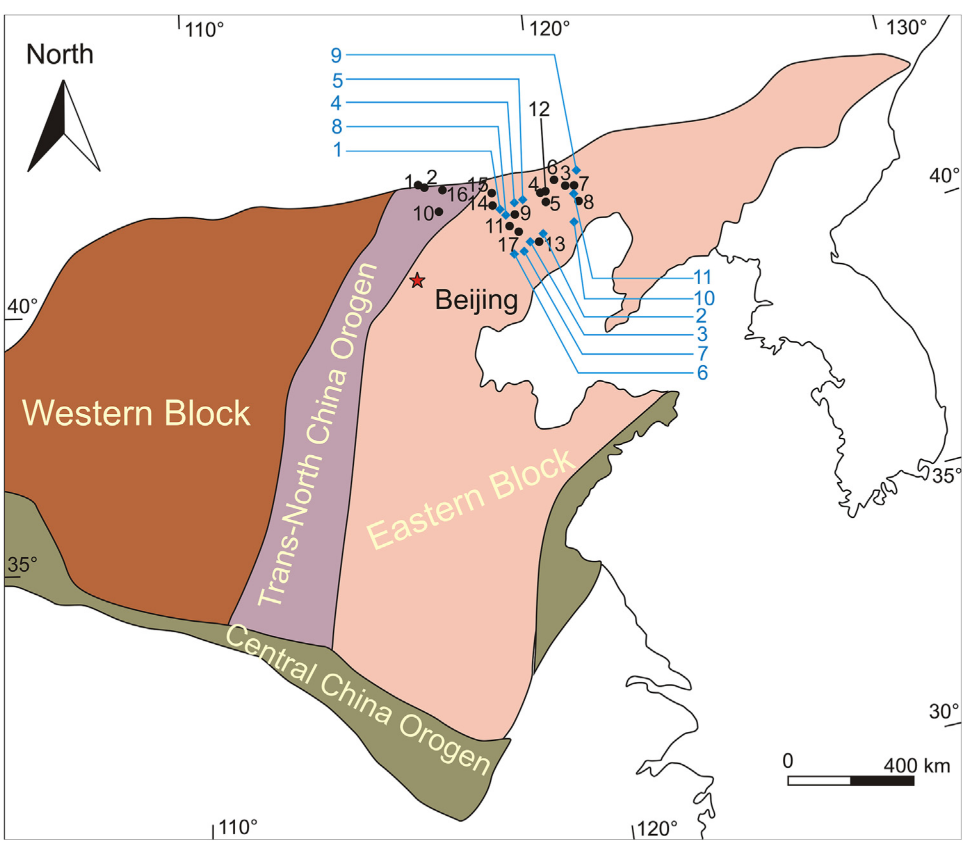

Fig. 1. Comparison of the major fossil sites of Yanliao and Jehol biotas (modified from Sullivan et al., 2014; Zhou, 2014; Xu et al., in press) and their distributions in areas of the North China Craton. Blue dots and dark dots represent the Yanliao Biota and Jehol Biota respectively. Note that the destruction of the North China Craton occurred mainly in the eastern block.

Table 1
Stratigraphic sequence of the fossil-bearing deposits of the Yanliao and Jehol biotas.

Age	Hebei Province	Liaoning Province	Biota
Early Cretaceous	Xiguayuan Formation	Jiufotang Formation	Jehol Biota
	Dadianzi Formation	Yixian Formation	
	Huajiying Formation (Dabeigou Formation)	Dabeigou Formation	
	Zhangjiakou Formation	Zhangjiakou Formation	
J3-K1	Houcheng Formation	Tuchengzi Formation	
Middle–Late Jurassic	Tiaojishan Formation	Lanqi Formation	Yanliao Biota
	Jiulongshan Formation	Haifanggou Formation	

et al., 2002; He et al., 2004, 2008; Chang et al., 2009a,b, 2014; Jiang et al., 2011; Liu et al., 2012, 2015; Sha et al., 2012; Wang et al., 2013; Wu et al., 2013).

However, the geological and palaeoenvironmental background of the two biotas also shows remarkable differences, which are worthy of discussion because they were clearly related to the development and flourishing of the two biotas that also include very important insect assemblages and floras (Sun et al., 2001, 2002; Ren et al., 2010; Huang et al., 2012; Huang, 2014, 2015).

It is also notable that due to the similar sedimentary features (fine-grained lacustrine sediments interbedded with tuffs) and taphonomic features (e.g., articulated skeleton associated with soft-tissue preservation) of the Yanliao and Jehol fossils (Fig. 2) and the unfortunate fact that many of the published specimens were not directly collected by the researchers, therefore some controversy and uncertainty on the locality and horizon of a few vertebrate fossils remain unsolved and deserve further investigation and discussion.

Despite the abovementioned issues and the sampling bias, a comparison of the vertebrate diversity of the Yanliao and Jehol biotas may shed light on our understanding of the Middle–Late Jurassic and Early Cretaceous terrestrial ecosystem in Northeast China and their relationships to the tectonic and palaeoenvironmental backgrounds in this region.

2. Vertebrate assemblages of the Yanliao and Jehol biotas

The Yanliao vertebrate assemblage contains two species of basal actinopterygian fishes (ray-finned fishes); one belongs to the acipenseriform genus *Liaosteus* and the other an unnamed ptycholepid (Duan et al., 2009), thus lacking any evidence of teleosts. The Jehol fish assemblage has a greater diversity, containing 15 species, most representing more derived taxa, i.e., teleosts, of which the best known taxon is the osteoglossomorph *Lycoptera* that is often abundant and regarded as a representative member of the Jehol Biota. Acipenseriforms are more diversified and common in the Jehol Biota, including the best known *Peipiaosteus* and paddlefish *Protopsephurus*. It is also notable that the Jehol fish assemblage also contains a fossil lamprey *Mesomyzon*, often represented by specimens of various developmental stages (M.M. Chang et al., 2014).

The Yanliao Biota contains six species of salamanders, including *Chunerpeton*, *Jeholotriton*, *Pangerpeton*, etc. Although some of them may represent the earliest known crown-group caudates (i.e., *Liaoxitriton*, *Chunerpeton*), others (i.e., *Pangerpeton*, *Jeholotriton*) are difficult to be referred to any living caudate family and may represent stem taxa (Wang and Rose, 2005; Dong et al., 2012; Sullivan et al., 2014; Y. Wang et al., 2016a). Two reports seem to confirm the presence of early members of Salamandroidea in the biota (Gao and Shubin, 2012; Jia and Gao, 2016) and suggest an early diversification of crown caudates. No evidence of anurans (frogs) has been confirmed from this biota. It is, however, notable that an insect specimen from the Yanliao Biota had been mistakenly described at one point as a froglet (Huang, 2013).

The Jehol Biota contains eight species of amphibians, including four species of frogs, belonging to the basal crown-anuran genus, *Liaobatrachus*, and four monotypic genera of salamanders, including *Liaoxitriton* that is particularly interesting as it was also found from the Yanliao Biota. The Jehol salamanders sometimes can be also very abundant as the Yanliao salamanders, while all are members of crown-group caudates (Gao and Shubin, 2001; Zhang et al., 2009; Dong et al., 2013).

The Yanliao Biota contains three different lizards. One is equivocally referred to *Yabeinosaurus* (Evans and Wang, 2012), and the other two are of uncertain systematic position due to their immature skeletons and limited anatomical information, although one of them might be referable to a scleroglossan (Sullivan et al., 2014). Lizards from the Jehol Biota are more diversified and abundant, comprising five species, including the common taxa *Yabeinosaurus*, *Dalinghosaurus* (Evans and Wang, 2005; Wang and Evans, 2006; for viviparity of *Yabeinosaurus*, see Wang and Evans, 2011) and the gliding *Xianglong* identified as an iguanian (Li et al., 2007). *Yabeinosaurus* represents a basal lizard unrelated to any living clade and may be a survivor of the Pan-Laurasian lizard fauna of the Jurassic (Evans and Wang, 2012), whereas *Dalinghosaurus* resembles in cranial morphology to some living anguimorphs (Evans and Wang, 2005).

No turtle or choristodere has been discovered from the Yanliao Biota, although they are common in the Jehol Biota. The Jehol Biota currently contains abundant turtle fossils. Most of them are referable to three genera and species, including *Ordosemys*, *Manchurochelys*, and *Liaochelys*, representing basal taxa of the Cryptodira, with implications for discussing the basal divergence of crown turtles (Tong and Brinkman, 2012; Zhou and Rabi, 2015). Currently only one specimen is referred to the soft shelled turtle, *Perochelys*, representing a stem or crown

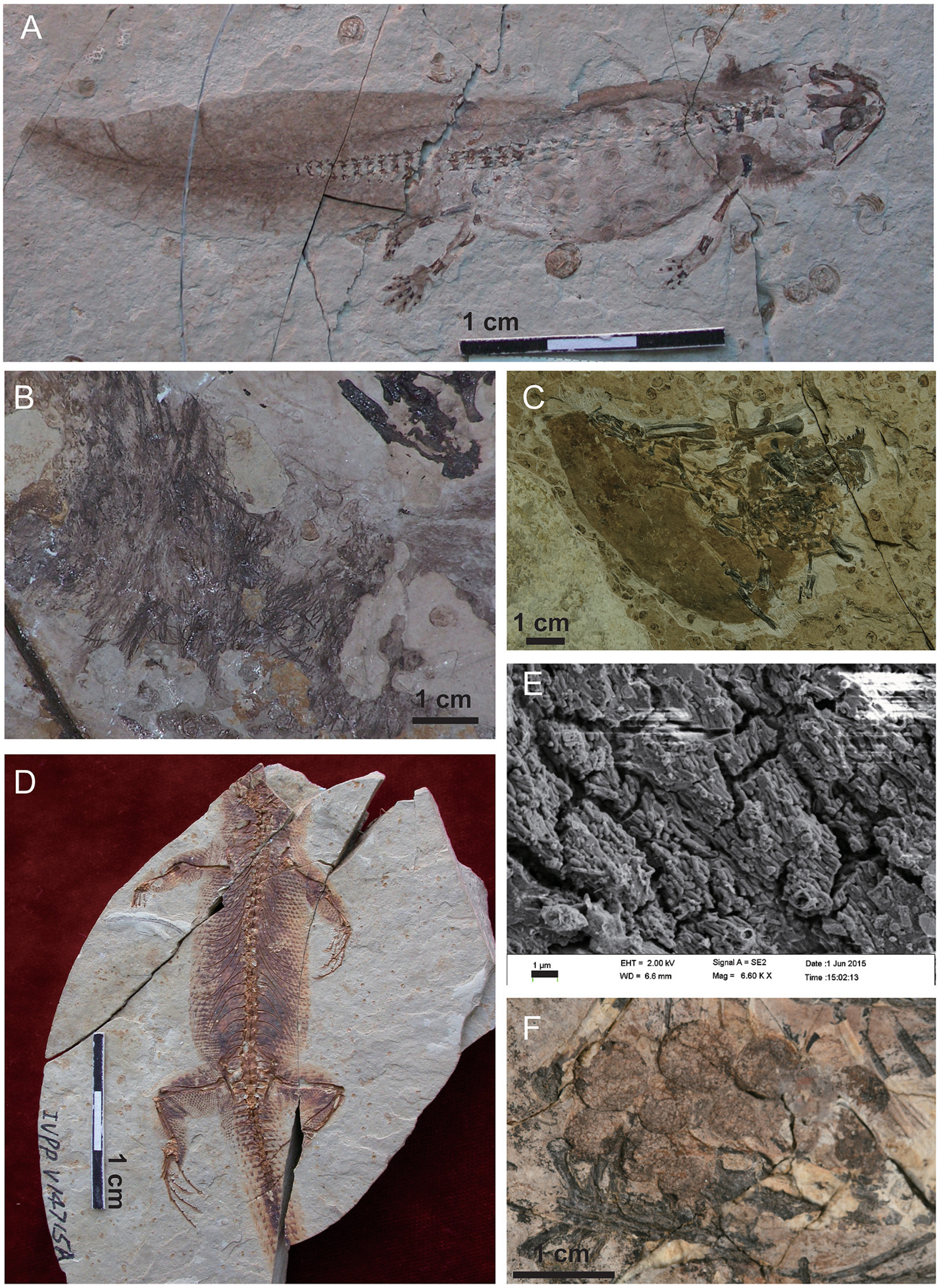

Fig. 2. Selected fossils from the Yanliao (A–C) and Jehol (D–F) biotas, showing exceptional preservations of soft tissues. (A) A salamander (*Chunerpeton*) showing gill arches and skins; (B) protofeathers of a short-headed pterosaur (*Jeholopterus*); (C) a gliding mammal (*Volaticotherium*) showing memberance; (D) a lizard (*Liushusaurus*) showing skins; (E) melanosomes of feathers from a basal bird (*Eoconfuciusornis*); (F) ovarian follicles in an unnamed enantiornithine bird.

trionychid (Li et al., 2015). The Jehol choristoderes represent an extinct lineage of diapsids and the top predators of the Jehol lake ecosystem, currently comprising five genera and seven species, belonging to three families. Most notable among them are the large-sized *Ikechosaurus*, the long-necked *Hyphalosaurus* and semi-aquatic *Monjurosuchus* (Gao and Fox, 2005). The latter two genera are often preserved in great abundance.

It is notable that a basal (i.e., non-crocodyliform) crocodylomorph represented by a complete skeleton with soft tissues from the Yanliao Biota was recently reported in an abstract (Sullivan et al., 2015). Yet, no crocodylomorph has been reported from the Jehol Biota to date. The absence, or at least rarity, of this group in the Jehol Biota may have been due to the similar niche shared by choristoderes and crocodylomorphs.

The Yanliao Biota is characterized by possessing diverse pterosaur taxa (at least 13 species) that are typically of Jurassic pterosaur assemblages, mostly belonging to non-pterodactyloids, including the short-tailed insectivorous anurognathids *Jeholopterus* and *Dendrorhynchoides*, the long-tailed rhamphorhynchine *Qinglongopterus* (Lü and Hone, 2012), several taxa that are tentatively recognized as the scaphognathines such as *Pterorhynchus*, the more derived wukongopterids *Wukongopterus* (Wang et al., 2009, 2010), *Darwinopterus* (Lü et al., 2010) etc., and the possible istiodactylid *Archaeoistiodactylus*. It is notable that the holotype and first known specimen of *Dendrorhynchoides* was reported from the Early Cretaceous Yixian Formation (Ji and Ji, 1998; Ji et al., 1999), and given that the holotype was collected by a farmer and that at that time of the publication of the holotype there was still little understanding of the Yanliao vertebrates and their fossil-bearing information, there is no strong evidence confirming that its provenance and stratigraphic information is correct. *Dendrorhynchoides mutoudengensis* is definitely from the Yanliao Biota, whereas *Dendrorhynchoides curvidentatus* was originally described as being from the Yixian Formation but may actually be from the Yanliao Biota as well. Also, *Archaeoistiodactylus* was suggested to be an unspecified kind of basal monofenestratan by Sullivan et al. (2014) and a wukongopterid by Witton (2015).

The Jehol pterosaur assemblage is equally abundant and more diverse than the Yanliao assemblage, with at least 24 reported species. However, it is generally similar to the Cretaceous assemblages as known from other regions, containing members of of Anhangueridae, Ctenochasmatidae, Ornithocheiridae, Gallodactylidae, Pteranodontidae, Tapejaridae, and Istiodactylidae. It also shows a greater size and dietary variation (Wang and Zhou, 2006; Wang et al., 2008, 2012; Jiang and Wang, 2011; Wang et al., 2012). In contrast, the Yanliao pterosaurs are generally small and lack any large sized species. All Jehol pterosaurs belong to pterodactyloids, and the only purported exception is *Dendrorhynchoides*, which belongs to the short tailed rhamphorhynchoid family Anurognathidae (Wang and Zhou, 2006), but this remains questionable.

The dinosaur fossils of the Yanliao Biota all represent maniraptoran theropods. The only possible exception is the heterodontosaurid ornithischian *Tianyulong* (Zheng et al., 2009) that was reported to come from the Early Cretaceous Jehol Biota, but it was suspected to be from the Yanliao Biota by some workers (Sullivan et al., 2014); however, we believe it most likely belongs to the Jehol Biota as on one specimen the dinosaur has been observed to associated with a teleost (possibly *Lycoptera*) typical of the Jehol Biota (Xiao-Lin Wang, pers. comm.; Zhong-He Zhou, pers. observ.). It is notable that the Yanliao maniraptorans are either paravians or closely related species. They include the scansoriopterygids *Epidendrosaurus* and *Epidexipteryx* (Zhang et al., 2008) and the paravians *Pedopenna*, *Anchiornis* (Xu et al., 2009; Hu et al., 2010), and *Xiaotingia* (Xu et al., 2011). With the dominant occurrence of many of the earliest feathered dinosaurs, including some of the most bird-related taxa, and considering its age (about 160 Ma, slightly older than the earliest (about 150 Ma) known bird *Archaeopteryx*), we are tempted to propose that the Yanliao Biota might be considered as the center for the origin of birds. However, such a hypothesis is still largely speculative as little is known about the distribution of feathered dinosaurs and birds around the Middle and Late Jurassic age in other areas except Yanliao and Solnhofen. However, it is safe to argue that the Yanliao can be viewed as the best current window for understanding the character evolution associated with the origin of Paraves.

The Jehol dinosaur assemblages are much more diverse than the Yanliao ones, comprising at least 31 genera and 38 species. Among them, 22 genera and species belong to the theropods, and they represent nearly all major Cretaceous coelurosaurian theropod lineages (Xu et al., 2014), only lacking the Alvarezsauroidea. Other major lineages include ornithopods (Xu et al., 2000), ankylosaurs (Xu et al., 2001), ceratopsians (Xu et al., 2002), and sauropods (Barrett and Wang, 2007; Wang et al., 2007) etc. Many of the Jehol dinosaurs are preserved with feathers and characteristic of arboreal or herbivorous adaptation. In addition to species diversity, the Jehol dinosaurs show great differentiation in dietary adaptation, body size, and locomotion (Zhou et al., in press). For example, the largest known Jehol dinosaur, *Dongbeititan*, could be well exceeding ten meters in length (Wang et al., 2007). In contrary, the Yanliao dinosaurs are generally small and lack any species that are larger than two meters. Like the Yanliao dinosaurs, the Jehol dinosaurs are mostly preserved with complete skeletons, and often associated with exceptionally preserved integuments, and sometimes with stomach contents (Xing et al., 2013). Unlike the Yanliao dinosaurs, some Jehol dinosaurs are three dimensionally preserved in sandstones or silt sandstones, providing more detailed information about their skeletal anatomy or behavior often inaccessible in compressed specimens in shales or mudstones.

The Yanliao mammaliaforms are diverse (11 species) and show a variety of ecological adaptations, in which terrestrial, swimming, arboreal, burrowing, and gliding species were present (Meng, 2014; Luo et al., 2015). Reported taxa include the triconodonts *Liaotherium* and *Manchurodon*, the yinotherian *Pseudotribos* (Luo et al., 2007), the gliding *Volaticotherium* (Meng et al., 2006), the swimming docodont *Castrocauda* (Ji et al., 2006), the subterranean docodont *Docofossor* (Luo et al., 2015), the haramiyidans *Arboroharamiya* (Zheng et al., 2013a) and *Megaconus* (Zhou et al., 2013), the euharamiyidans *Xianshou* and *Shenshou* (Bi et al., 2014), and the eutherian *Juramaia* (Luo et al., 2011).

The Jehol mammaliaforms are also diverse, comprising at least 17 species, which are dominated by the derived clades such as eutriconodontans and trechnotherians ("symmetrodonts and therians"), lacking the more basal clades docodontans and euharamiyidans (Meng, 2014). They can be referred to five major groups of Mesozoic mammals: Triconodonta, Multituberculata, Symmetrodonta, Metatheria, and Eutheria. Unlike the Yanliao mammals, some Jehol mammals, such as *Repenomamus*, are three dimensionally preserved containing information about their dietary behavior (Meng, 2014). Furthermore, the Yanliao mammals are generally small and lack any large-sized species; however, some Jehol mammals had already reached a relatively large body size (Hu et al., 2005; Meng, 2014).

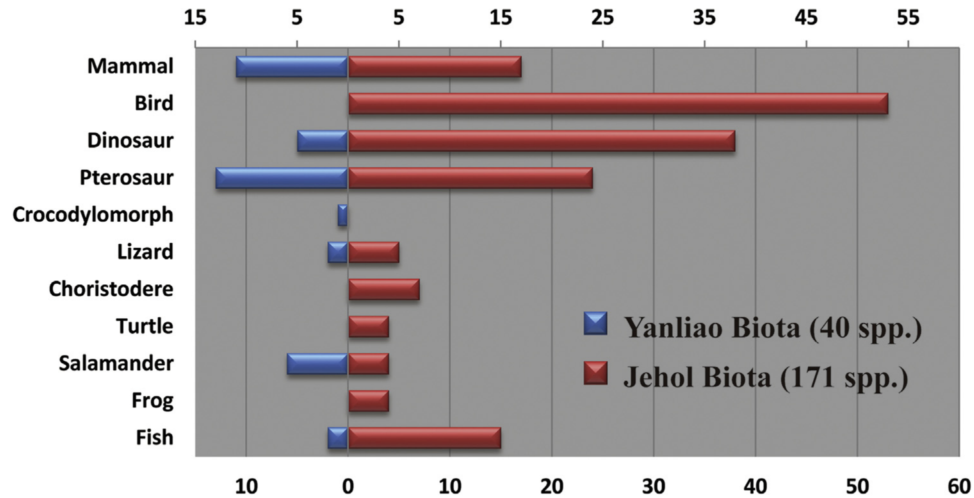

Fig. 3. Vertebrate diversity comparison of the Yanliao and Jehol biotas, showing species number of major vertebrate groups in both biotas.

Together with the Yanliao mammaliaforms, the Jehol fossils provided a great amount of information that has contributed to our understanding on some major issues in phylogeny and the early evolution of mammals, such as divergences of Mesozoic mammals and the evolution of the mammalian middle ear (Meng et al., 2011; Meng, 2014).

The Jehol vertebrate assemblage is probably most distinguishable from that of the Yanliao Biota by possessing the greatly diversified early birds (53 species known to date). Currently, it has more genera and species than any other vertebrate groups in the biota. It mainly includes many basal-most taxa such as *Jeholornis*, *Sapeornis*, *Confuciusornis* and the newly published *Chongmingia* (M. Wang et al., 2016a), and the relatively small-sized enantiornithines, such as *Protopteryx*, *Pengornis*, *Longipteryx* and *Bohaiornis* (X.L. Wang et al., 2014; Y. Wang et al., 2016b) and most derived Mesozoic birds ornithuromorphs, such as *Yanornis*, *Hongshanornis*, *Bellulia*, etc. (Wang et al., 2015; M. Wang et al., 2016b). These birds not only provided consecutive evidence on the transition from non-avian theropods to more advanced birds, but also greatly enriched our understanding of the biology of early birds in the Early Cretaceous, such as flight, feather, diet, reproduction, development, habitat, etc. (O'Connor et al., 2013, 2014, 2015; Zheng et al., 2013b,c, 2014a,b; Zhou, 2014; O'Connor and Zhou, 2015; Wang et al., 2015) .

In sum, the Yanliao vertebrate assemblage now contains at least 40 species, including 11 species of mammals, 5 species of dinosaurs, 13 species of pterosaurs, 2 species of squamates, 1 species of crocodylomorph, 6 species of salamanders, and 2 species of fishes. Among them, crocodylomorphs have not been reported from the Jehol Biota (Fig. 3).

The Jehol vertebrate assemblage obviously has a much greater diversity (partially because of a sampling bias because of longer and more extensive collecting over more sites), comprising at least 171 species, including 17 species of mammals, 53 species of birds, 38 species of dinosaurs, 24 species of pterosaurs, 5 species of squamates, 7 species of choristoderes, 4 species of turtles, 8 species of amphibians, and 15 species of fishes. Among them, lampreys, frogs, turtles, choristoderes, and birds have not been known from the Yanliao Biota. It is also notable that abundance of the fishes is much greater in the Jehol Biota than in the Yanliao Biota. Currently, only one genus of salamanders, *Liaoxitriton*, is believed to be shared by both the Yanliao and Jehol biotas. It is interesting to note that the Yanliao the Jehol assemblages also share only a few insect genera, and none on the species level (Huang, 2015).

Additionally, pterosaurs had the greatest diversity in the Yanliao vertebrate assemblage, and birds had the greatest diversity in the Jehol vertebrate assemblage, possibly indicating that adaptation of flight had played a key role in their diversification success. However, the birds had a greater diversity than pterosaurs in the Jehol Biota, showing that birds had become more successful in adaptation for new niches with a wide range of feeding styles, and it is also equally, if not more important, that early birds had diversified ornamental feathers for sexual selection that could also increased the speciation. Among the Jehol birds, although the basal-most taxa such as *Jeholornis* still retained a primitive flight capability as indicated by its retaining of a long skeletal tail and a sternum lacking a keel, enantiornithines already show improved flight as indicated by its shortened tail (with a pygostyle) and more bird-like wings (including the presence of the alula showing sophisticated flight), and the ornithuromorphs such as *Yanornis* had possessed the flight skill nearly identical to that of extant flying birds as shown by their elongated sternum with a large keel, pectoral girdle with triosseal canal, and fan-shaped tail feathers (Wang et al., 2015).

At the time of the Yanliao Biota, pterosaurs were probably the sole specialized predator of fish although some pterosaurs, particularly the anurognathids, probably had non-piscivorous diets. Yet, by the time the Jehol Biota, many birds, particularly ornithomorphs that mainly dwelled the lake shores, had become the strong competitors for pterosaurs in preying on fish. Some non-avian dinosaurs such as *Microraptor* had at least some limited aerial capability, and also known to have sometimes fed on fish (Xing et al., 2013). It might not be simply a coincidence that the diversity of pterosaurs is less than that of dinosaurs in the Jehol Biota, in contrast to the situation in the Yanliao Biota when dinosaurs were still generally small and less diversified.

The Jehol vertebrate assemblage also shows a greater body size variation among dinosaurs, pterosaurs, and mammals (three major vertebrate groups shared by the two biotas); however, these groups are generally small-sized in the Yanliao Biota, possibly reflecting a growing and expanded ecological adaptation of the Jehol vertebrates. It is also notable in the lake ecosystem the Jehol vertebrates also show a much greater diversity with the appearance of many larger sized forms, including the choristoderes that could reach more than one meter long. However, the possibility of taphonomic bias cannot be fully excluded for this difference, and obviously future statistic work is needed to further our understanding of such size difference.

3. A big gap between the two assemblages

There existed a long, nearly 28 million year's temporal gap between the Middle–Late Jurassic Yanliao Biota (166–159 Ma) and the Early Cretaceous Jehol Biota (131–120 Ma). What had happened between these two biotas when the fossil record was poorly known? The Tuchengzi Formation (called Houcheng Formation in Hebei Province) (about 156–136 Ma) that preserves the terrestrial Jurassic–Cretaceous boundary holds the key to understanding much of this mystery. Previously known vertebrates from this formation include the ceratopsian dinosaurs *Chaoyangosaurus* and *Xuanhuaceratops* as well as some theropod footprints (Zhao et al., 1999; Sullivan et al., 2009). Recently, a rhamphorhynchoid pterosaur, *Orientognathus*, was reported from the Tuchengzi Formation (Lü et al., 2015), filling the gap between the pterosaur assemblages of the Yanliao and Jehol biotas.

Orientognathus was reported as the largest Late Jurassic pterosaur with an estimated wing span of over one meter (Lü et al., 2015). The Tuchengzi Formation is composed mainly of sandstones with interbedding ashes. For a long time, relatively little work has been done on the vertebrates as well as other fossils from this formation. However, this stratigraphic unit has drawn more attention not only for its importance for studying the terrestrial Jurassic–Cretaceous boundary, but also for its temporal link between the Yanliao and Jehol biotas. Current studies have shown that the Yanliao Biota contains many of the transitional forms from non-avian theropods to the basal-most birds, and the Jehol Biota had already recorded the first major radiation in early avian evolution; therefore, it is highly expected that some of the basal-most birds are very much likely to be discovered from this formation in the future. In addition, we also predict that many other transitional forms of vertebrate groups such as mammaliforms, pterosaurs, squamates, and amphibians might have existed during this important geological interval.

It is also notable that the Early Cretaceous Zhangjiakou Formation (136–130 Ma) that underlies the Jehol fossil-bearing deposits is composed mainly of volcanic rocks (Liu et al., 2003; Zhang et al., 2005). And the Dabeigou Formation overlying the Zhangjiakou Formation in Luanping Basin in Hebei Province also contains some fossils that may potentially be important for understanding the origin and early evolution of the Jehol Biota as various invertebrates (such as conchostracans, ostracods etc.), plants and some fragmentary fishes have been recovered from the Dabeigou Formation in this basin (Wang and Ji, 2009). It is notable that the Dabeigou Formation in Luanping Basin is approximately contemporarily to the lower part of the Huajiying Formation that is exposed mainly in the Fengning Basin in Hebei Province (Fan Jin, pers. comm.). The Huajiying Formation in Fengning has produced the earliest known birds (e.g., *Protopteryx*, *Eopengornis*, *Archaeornithura*, *Eoconfuciusornis* etc.) from China (M. Wang et al., 2014, 2015; Pan et al., 2016).

4. Geological and palaeoenvironmental background

The geological backgrounds of the Yanliao Biota and Jehol Biota are worthy of discussion as both strong tectonic activity and active volcanic eruptions were apparent in association with the time of their duration (Fig. 4). The two biotas share a similar geographic distribution, mainly located in western Liaoning, northern Hebei, and southeastern Inner Mongolia in Northeast China, belonging to the Eastern block of the North China Craton. The North China Craton contains one of the longest, most complex records of magmatism, sedimentation, and deformation on Earth, with deformation spanning the interval from the Early Archaean (3.8 Ga) to the present, and it consists of two major blocks (named the Eastern and Western Blocks), separated by the Central Orogenic Belt (Kusky et al., 2007). The destruction of the North China Craton has been extensively studied in recent years (Zhu et al., 2012a). One of the major conclusions is about the timing of the destruction of the North China Craton. It is generally concurred that the destruction as characterized by the loss or thinning of the lithospheric mantle began in the Mesozoic, particularly in the Jurassic and Cretaceous. And it is interesting to note that the flourishing time of the Yanliao Biota (around 160 Ma) is coincident with the beginning of the Paleo-Pacific subduction underneath the eastern Asian continent (Zhu et al., 2012a,b), and the flourishing of the Jehol Biota (around 125 Ma) appears to be coincident with the peak of the destruction of the North China Craton, as represented by the most extensive development of Early Cretaceous magmatism (considered by some as "giant igneous event"), extensive deformation, and associated gold mineralization, with significant continental crust growth (Wu et al., 2005, 2008; Zhu et al., 2011, 2012a,b).

There is yet no evidence or study showing how this coincidence had occurred. The strong tectonic activity had resulted in the formation of wide-spread continental rift basins that hosted the fresh water lakes (Davis et al., 2001; Zhu et al., 2008; Liu et al., 2015). Recently Liu et al. (2015) discussed the evolution of the Mesozoic terrestrial basins and associated palaeogeography in North China. And according to Liu et al. (2015), during the Late Jurassic, a variety of faulted basins occurred, and in the Yanshan area (or Yan Mountains area, a major mountain range north of the North China Plain), these basins were filled with thickened intermediate volcanic rocks and purple-red coarse-grained clastic rocks. During the transition of the Late Jurassic and Early Cretaceous, northeastern and northern parts of the North China had experienced extensive movements as a result of the

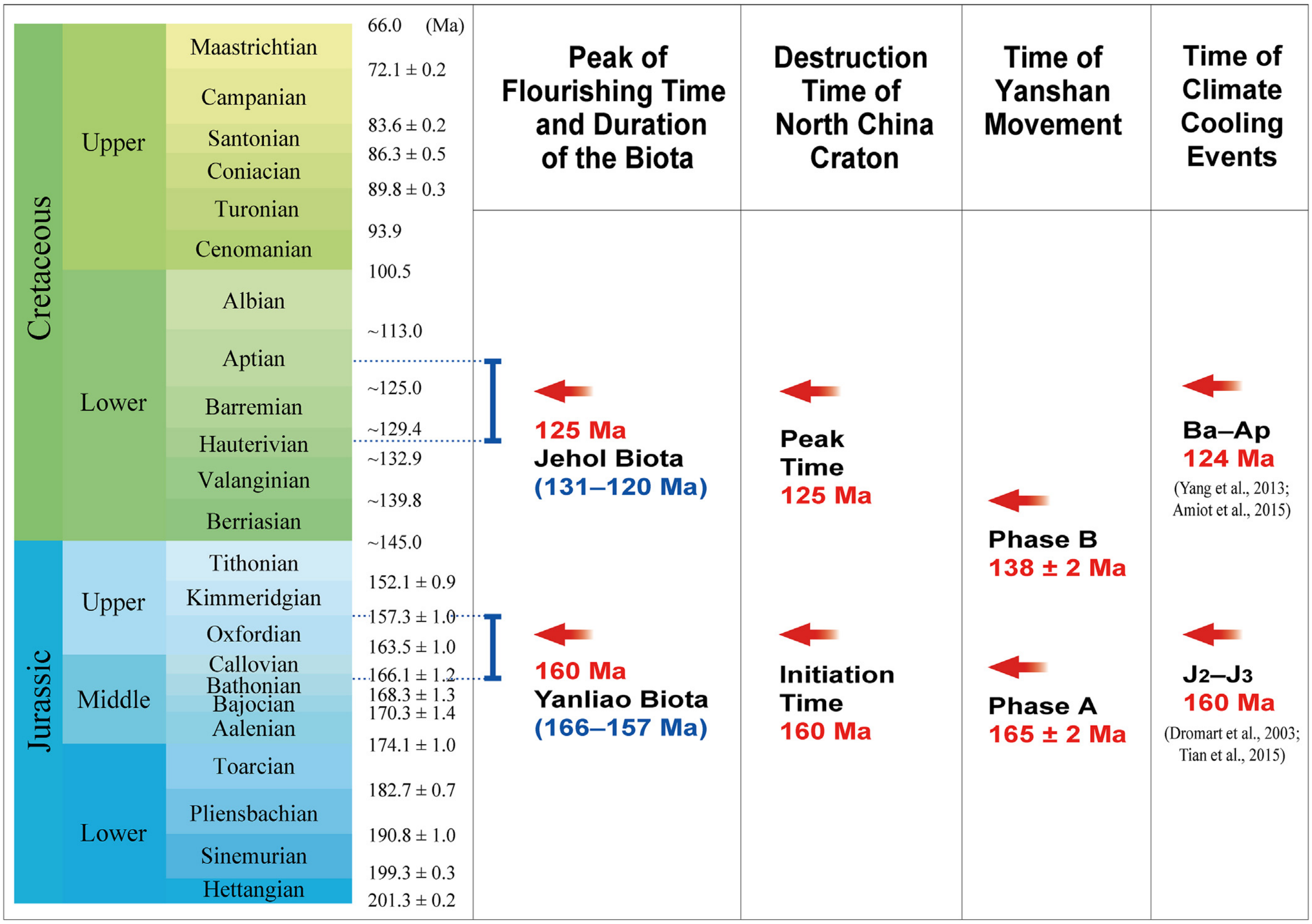

Fig. 4. Temporal range and flourishing time of the Yanliao and Jehol biotas and major geological and palaeoenvironmental events as imposed onto the Jurassic and Cretaceous sections of the International Chronostratigraphic Chart by Cohen et al. (2013), showing also the initiation and peak times of the destruction of North China Craton, two phases of the local Yanshan Movement, and two climatic cooling events (with citations) in correlations with the development of the two biotas. Abbreviations: Ap, Aptian; Ba, Barremian.

Paleo-Pacific subduction, the closure of the Mongolia-Okhotsk Ocean, and the subsequent Yanshan movement or Yanshanian orogeny. The extensive volcanic-magmatic-orogenic activities in the Mesozoic terrestrial environments of North China had resulted in the complex and diverse palaeogeography (notably the isolation mechanism), which might be related to the rapid biological differentiation and evolution. Huang (2015) also proposed that the first and second phases of the Yanshanian orogeny were related to the beginning of the Yanliao Biota and Jehol Biota, respectively.

It seems obvious that both the Yanliao Biota and Jehol Biota developed in a tectonically active geological background (North China Craton destruction, Yanshan Movement etc.) in association with a series of small rift basins in volcanic settings (Wei et al., 2012). The long gap between the two biotas possibly represents a tectonic hiatus that had controlled a different basin history.

In addition, in the Early Cretaceous of northeastern China there seems to exist an obvious eastward transition of both basin sedimentation and biotas with time, i.e., from Zhangjiakou to Chengde, Chaoyang, and Fuxin basins, we notice the occurrence of progressively younger deposits associated with later stage of the biotas (Fan Jin, pers. comm.) against the background of the progressive retreat of the west Paleo-Pacific subduction zone, the exact position of which remains unknown till now (Ri-Xiang Zhu, pers. comm.). This observation is consistent with the proposal that that the destruction of the North China Craton was controlled mainly by the Paleo-Pacific subduction (Zhu et al., 2012a,b). The Early Cretaceous Jehol fossil-bearing strata are widely distributed as deposition in the pull-apart basins, and contain a significant amount of volcanic rocks, i.e., basalt, andesite, dacite, and rhyolite, in addition to sedimentary rocks (Zhu et al., 2012b). During this period, the East China, Korean Peninsula, Japan, and the Far East of Russia shared the same palaeogeographic and palaeoecologic environments, which were habitable for terrestrial vertebrate and invertebrate faunas and floras (Liu et al., 2015).

Furthermore, the frequent volcanic activities not only provided a large amount of nutrient to the lakes, but also were critical for the exceptional preservation of complete articulated skeletons as well as soft tissues in the two lagerstätten (Jiang et al., 2011, 2014; Pan et al., 2013, 2014).

The reconstructions of the palaeoclimates, although often controversial, are important for understanding the evolution of the Yanliao and Jehol biotas. Recently, studies on the fossil woods (*Xenoxylon* and *Protaxodioxylon*) from the Tiaojishan Formation in Liaoning Province, Northeast China suggested a cool temperate, wet climate with seasonal changes (Tian et al., 2015). According to Tian et al. (2015), megafossil plants from this formation also indicate a cool temperate climate. The age (160 Ma) of the Tiaojishan Formation (Liu et al., 2012; Wang et al., 2013) is consistent with previous studies that suggested a severe global cooling event at the Middle–Late Jurassic transition (Dromart et al., 2003; Tian et al., 2015).

However, many other studies also show that the Jurassic is generally warm, and particularly during the time of the early stage of the Yanliao Biota, information on insects, mega-plants and palynology often imply a warm, seasonal and humid climate (Sun et al., 2008; Ren et al., 2010; Na et al., 2015) or even a hot, dry climate during the time of Lanqi Formation (a formation named in Liaoning Province, comparable to Tiaojishan Formation of Beijing and Hebei), possibly reflecting a fluctuation of the temperature during the Middle to Late Jurassic in Northeast China.

Although the Early Cretaceous is generally believed to be warm globally, there existed several cool intervals. Studies on the oxygen isotopes of dinosaurs and other vertebrates showed that cool temperate climate was dominant in the Early Cretaceous of East Asia (Amiot et al., 2011, 2015). Evidence of fossil plants from the Yixian Formation (such as the presence of the wood of *Xenoxylon*) also indicates a cool temperature (Tian et al., 2015). Interestingly, a recent isotope study based on extremely low δ^{18} (oxygen-18) values for the hydrothermal zircon has provided further evidence suggesting that continental glaciations might have occurred in the Early Cretaceous of Northeast China (Yang et al., 2013).

Based on above mentioned information, it can be tentatively suggested that the cold interval or the remarkable temperature fluctuation near the Middle–Late Jurassic transition might be related to the first occurrence of feathers in dinosaurs and hair-like integuments in pterosaurs and the cold intervals during the time of the Jehol Biota was related to the widespread appearance of (including a few giant) feathered dinosaurs (Xu et al., 2012) and the diversification of a variety of biological groups of the Cretaceous, many of which had become extinct by the end of the Cretaceous whereas some had finally surviced into the Cenozoic and given rise to some extant lineages (Fig. 3).

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