

Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives

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The Jehol Biota, preserved in the lacustrine sediments of Liaoning Province, northeast China, has provided a new window for understanding Early Cretaceous terrestrial ecosystems. Based on recent geochronological and biostratigraphic studies of the fossil-bearing deposits, a preliminary temporal framework has been established and suggests that the Jehol Biota had lasted for at least 11 Ma during the late Early Cretaceous (131–120 Ma). The development of the Jehol Biota can be divided into three major phases, with the most significant biological radiations occurring in the second phase between the Barremian and Aptian (approximately 125 Ma). Thanks to a diverse forest environment, major vertebrate groups, i.e. pterosaurs, dinosaurs, birds and mammals, in the Jehol Biota are characterized by a remarkably high percentage of arboreal and herbivorous forms. In addition to strong phylogenetic and morphological differentiation and high taxonomic diversity, the Jehol Biota is also characterized by significant dietary differentiation and biological interactions, i.e. competition and co-evolution between various animal groups, in an environment shaped by tectonic activities and palaeoclimatic changes both at a global and local scale. Copyright © 2006 John Wiley & Sons, Ltd.

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1. INTRODUCTION

Although the Jehol Biota has been studied since the 1920s, major discoveries of early birds, feathered dinosaurs, pterosaurs, early mammals, amphibians, pollinating insects and angiosperms, and international awareness of these findings are relatively recent events, particularly since the early 1990s (Chang 2003; Zhou *et al.* 2003; Barrett and Hilton 2004). The new discoveries have not only significantly expanded our knowledge on the evolutionary history of many important groups of organisms, but have also contributed greatly to biostratigraphic correlation of the fossil-bearing lacustrine deposits of the Jehol Group sequence and thus to the understanding of the age of the Jehol Group, a long standing controversy that has lasted for over half a century.

Both biostratigraphic and palaeochronological studies of the Jehol Group sequence indicate a late Early Cretaceous age for the whole biota, and enable a more precise global correlation of the Jehol Biota with its equivalents elsewhere. With increased knowledge of the composition of the biota and better understanding of the geological and palaeogeographic framework, it is now generally agreed that the Jehol Biota is not simply a 'refugium for relics' as suggested earlier (Luo 1999), but mainly a cradle and centre of diversification for many groups of animals that prevailed in the Cretaceous (Manabe *et al.* 2000; Barrett *et al.* 2002; Zhou *et al.* 2003; Barrett

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and Hilton 2004; Zhou 2004a). Further, the temporal framework has enabled the establishment of a preliminary synthesis on the radiation of the Jehol Biota (Zhou 2006). Thus, the extraordinary Jehol Biota is a unique source for studying Early Cretaceous terrestrial ecosystems and the emergence of modern ecosystems (Zhou *et al.* 2003; Friis *et al.* 2005).

This paper aims to provide an overview of the evolutionary radiation of the Jehol Biota based on evidence from recent chronological results and an analysis of the fossil assemblages of major biological groups and their interactions in the biota from the perspective of an Early Cretaceous terrestrial ecosystem.

2. CHRONOLOGICAL BACKGROUND

2.1. Stratigraphy and volcanism

The Jehol Biota is preserved in the lacustrine Jehol Group, which was usually considered to comprise the Yixian Formation and overlying Jiufotang Formation in western Liaoning Province, northeast China. Recently, the Dabeigou Formation in Fengning, northern Hebei Province, has been suggested as the lowest part of the Jehol Group below the Yixian Formation, although it has also been considered as equivalent to the lower part of the Yixian Formation in Liaoning Province (see further discussion below). Comparable deposits of similar age throughout northern China and adjacent areas of eastern and central Asia, including Kazakhstan, Mongolia, Siberia, Japan and Korea, have yielded biota very similar to the Jehol Biota (Chang 2003; Zhou *et al.* 2003).

Volcanic eruptions frequently occurred during the time of deposition of the Dabeigou and Yixian formations and became only slightly weaker by the time of the Jiufotang Formation. As a result, tuffs are commonly interbedded with the shales or mudstones of these formations, and even the normal lake sedimentation contains tuffaceous components (Figure 1). The Yixian Formation mainly comprises basalts with interbedded siliciclastic sediments, and can be divided into several beds: from bottom up, they are the Lujiatun Bed, Jianshangou Bed, Dawangzhangzi



Figure 1. Stratigraphic section (about 2M thick) of the lower Yixian Formation at the Zhangjiagou locality in Beipiao, western Liaoning Province, showing the shale and mudstone sediments interbedded with tuffs (orange and brown beds).

Bed, and Jingangshan Bed, respectively. The presence of volcanic tuffs in the Jehol deposits is important as it has permitted high-resolution dating of the fossiliferous horizons (Wang and Zhou 2003a,b,c).

2.2. Dating of the Yixian Formation

In the past, the age of the Jehol Group was contentious among palaeontologists, and varied from the Late Jurassic to Early Cretaceous. Before the use of ^{40}Ar - ^{39}Ar dating on the tuffs, radiometric dating on the age of the Yixian Formation was never generally accepted because K-Ar and Rb-Sr dates on biotite and whole-rock samples usually produced slightly older ages than the actual age of the deposits. ^{40}Ar - ^{39}Ar dates are arguably more reliable, particularly in the case of the interbedded tephra from the lower Yixian Formation, which provides the most direct age for the fossil-bearing sediments (Swisher *et al.* 1999, 2002).

The ^{40}Ar - ^{39}Ar method was first used to determine the age of the Jehol Biota using samples of volcanic breccia, diabase, and basalt from the upper part of the Yixian Formation (Jingangshan Bed), which produced an age of 121 ± 0.2 Ma (Smith *et al.* 1995).

The first ^{40}Ar - ^{39}Ar dates on tuffs interbedded with the fossiliferous horizons of the Jehol deposits was published shortly thereafter. Swisher *et al.* (1999) used replicate Ar-ion-laser total-fusion analyses of single sanidine feldspar crystals and CO_2 -laser incremental heating of a bulk sanidine separate to obtain a result of 124.6 ± 0.3 Ma for the Jianshangou Bed of the lower Yixian Formation. This result is more reliable than prior K-Ar and Rb-Sr dates on biotite and whole rock because of the superior argon retentivity of sanidine and the unambiguous relationships of the dated units with the fossiliferous horizons of the Yixian Formation (Swisher *et al.* 1999).

The work by Swisher *et al.* (1999) was challenged by Lo *et al.* (1999), who reported an age of 147.1 ± 0.18 Ma using ^{40}Ar - ^{39}Ar dating of biotite crystals from a tuff in the lower Yixian Formation. However, this result was questioned by other workers, as it was reported that the biotite in western Liaoning had been heavily altered into vermiculite, and because of the loss of potassium in the alteration the ^{40}Ar - ^{39}Ar dating of the biotite thus became problematic (Wang *et al.* 2001a).

Subsequently, recent U-Pb dating from zircons in the tuffs of the lower Yixian Formation at the Sihetun locality resulted in an age of 125.2 Ma, confirming the previous results from ^{40}Ar - ^{39}Ar dates on sanidine feldspar from the same bed (Wang *et al.* 2001a). Furthermore, given the controversy regarding ^{40}Ar - ^{39}Ar dating of the Yixian Formation, Swisher *et al.* (2002) recollected tuff samples from the lower Yixian Formation in Sihetun and the nearby Hengdaozi localities. Analyses of these new samples using single crystal total-fusion analyses of sanidine showed homogeneous radiogenic Ar, Ca/K ratios and excellent reproducibility, and the single sanidine crystal total-fusion ^{40}Ar - ^{39}Ar analyses of the Sihetun and Hengdaozi tuffs gave a mean age of 125.0 ± 0.18 Ma and 125.0 ± 0.19 Ma, respectively. They also performed detailed laser incremental-heating analyses of biotite from Sihetun and Hengdaozi, which suggested that the total fusion dates of Lo *et al.* (1999) were erroneously old.

The Lujiatun Bed of the Yixian Formation represents the lowest horizon of the formation in western Liaoning Province. The basalt capping the tuffaceous deposits was dated as 128.4 ± 0.2 Ma with ^{40}Ar - ^{39}Ar total-rock dating (Wang *et al.* 2001b). This result was used as a proxy for the oldest age of the Jehol Biota (Zhou *et al.* 2003). However, recently obtained ^{40}Ar - ^{39}Ar dates on a single crystal of feldspar from the tuffs of the Lujiatun Bed produced a younger age, almost identical to that of the Jianshangou Bed of the Yixian Formation, suggesting that these two beds were probably deposited at approximately the same time (He *et al.*, 2006). The younger age appears more reasonable considering that the Lujiatun Bed sequence is relatively thin, and composed completely of tuffaceous sediments that were probably deposited during a very short time interval.

It is noteworthy that although the ages of various beds of the Yixian Formation range from approximately 125 Ma to 120 Ma, the Jianshangou Bed remains the only bed with a ^{40}Ar - ^{39}Ar age derived directly from the crystals of the tuffs interbedded within the fossil-bearing sediments. The dates of other beds were either from the basalts or from glauconite (Smith *et al.* 1995). The ^{40}Ar - ^{39}Ar results of Smith *et al.* (1995) would be approximately between 124–122 Ma (Swisher *et al.* 1999) after correcting to the standards of the Berkeley Geochronology Center (H. He, personal communication).

In summary, despite the remarkable progress in dating of the Yixian Formation during the last 10 years, more work is needed to further determine the age of the various beds of the formation and to provide a more precise estimate of its duration. Current evidence appears to indicate a minimum age of 125 Ma for the beginning the deposition of the Yixian Formation.

2.3. Dating of the Jiufotang Formation

Compared to the Yixian Formation relatively few studies have focused on dating the Jiufotang Formation, the upper part of the Jehol Group. This may be explained partly by the fact that volcanic components are more abundant in the Yixian Formation, and also because more of the most spectacular fossils are from the Yixian Formation. More recently, however, major fossil discoveries have been reported from the Jiufotang Formation. These findings include such fossils as the four-winged dinosaur *Microraptor gui* (Xu *et al.* 2003), the long tailed seed-eating bird *Jeholornis* (Zhou and Zhang 2002a), and a more diverse and richer bird and pterosaur assemblages than from the Yixian Formation (Wang *et al.* 2005).

The first published radiometric date for the Jiufotang Formation was gained from Tebch, Inner Mongolia, with a ^{40}Ar - ^{39}Ar date of 110.59 ± 0.52 Ma obtained from an intrusive basalt within the formation (Eberth *et al.* 1993). However, this date, at best, provides a minimum age for the Jiufotang Formation, and there is no evidence indicating how much younger the basalt is than the fossil-bearing sediments, although pollen from the clastic deposits at Tebch, Inner Mongolia supports a Barremian or early Aptian age for the fossil-bearing sediments (Eberth *et al.* 1993).

The first direct age for the Jiufotang Formation was recently published and gave an age of 120.3 ± 0.7 Ma based on ^{40}Ar - ^{39}Ar dating on sanidine crystals from tuffs found interbedded within the fossil-bearing deposits of the Jiufotang Formation at the Shangheshou locality in Chaoyang, Liaoning (He *et al.* 2004). This date indicates that the Jiufotang Formation is not as young as had been previously assumed. However, the duration of sedimentation of the Jiufotang Formation is uncertain, and further work is needed.

2.4. Dating of the Dabeigou Formation and the duration of the Jehol Biota

Estimates of the temporal distribution of the Jehol Biota have been difficult due largely to a lack of sufficient and precise isotope dating of all the fossil-bearing beds of the Jehol Group. It was proposed that the Jehol Biota had probably existed for about 18 Ma (Zhou *et al.* 2003). This estimate was based on some indirect evidence, and needs to be updated on the basis of several new palaeochronological studies.

First, the recent dating of the tuffs in the Lujiatun Bed of the lowest part of the Yixian Formation indicates that the previous date, 128.4 ± 0.2 Ma, from the basalt overlying the deposits, was probably too old because the dating was based on the ^{40}Ar - ^{39}Ar total-rock method (Wang *et al.* 2001b; H. He, personal communication).

Second, recently determined dates for the Dabeigou Formation in Fengning, northern Hebei Province (west of Liaoning Province) have resulted in an age of about 131 Ma (Liu *et al.* 2003; Niu *et al.* 2003; He *et al.* in press). This represents the earliest known age for the Jehol Biota. The Dabeigou Formation comprises lacustrine tuffaceous shales and mudstones, much like the Yixian and Jiufotang formations in western Liaoning Province. It is generally believed to be the basalmost horizon of the Jehol Group. Major vertebrate fossils from the Dabeigou Formation include the enantiornithine bird *Protopteryx* (Zhang and Zhou 2000), and the acipenseriform fish *Peipiaosteus fengningensis* (Jin 1999).

Third, the recently published date (120.3 ± 0.7 Ma) for the Jiufotang Formation has for the first time produced a direct age for the upper part of the Jehol Group (He *et al.* 2004). This age provides a more precise estimate for the latest phase of the Jehol Biota.

Finally, the andesite underlying the Dabeigou deposits was dated by the SHRIMP U-Pb method as 130–136 Ma (Liu *et al.* 2003; Niu *et al.* 2003), which arguably provided a maximum age for the start of the Jehol Biota. Although the exact temporal range of the Jehol Group deposits and biota remains to be determined, we have now at least obtained an approximate or minimum estimate of the duration of the Jehol Biota as from Barremian to Aptian or

approximately 11 Ma (131–120 Ma) in the late Early Cretaceous, a preliminary but more reliable geochronologic framework for understanding the evolutionary radiation of the Jehol Biota. Admittedly, with more precise dating of the Jehol horizons in the future, the duration of the Jehol Biota might be expanded. Furthermore, our current conclusion is generally consistent with the proposal of a late Early Cretaceous age that has emerged from recent vertebrate biostratigraphic studies such as consideration of the mammal and pterosaur assemblages from the biota, which contain many Early Cretaceous members with a cosmopolitan distribution (Unwin *et al.* 2000; Hu and Wang 2002; Li *et al.* 2003; Wang and Zhou 2003a,b,d).

3. PHASES AND DISTRIBUTION OF THE JEHOL RADIATION

3.1. Three phases of the Jehol radiation

Although the majority of birds, feathered dinosaurs, mammals and flowering plants have been discovered from the lower Yixian Formation and the Jiufotang Formation of the Jehol Group, several other horizons have also preserved important members of the Jehol Biota. Each formation has preserved a distinct assemblage of invertebrate and vertebrate fossils.

Division of the evolutionary history of the Jehol radiation into three major phases was first proposed based on some of the major invertebrate groups such as conchostrachans, gastropods, bivalves, ostracods and insects (P. Chen 1988). Each phase has a distinct invertebrate assemblage corresponding to the Dabeigou, Yixian and Jiufotang formations (P. Chen 1988). There is a clear progression in diversity through the three phases and this also corresponds to a progressive palaeogeographic expansion up through the sequence (P. Chen 1988, 1999, 2003).

The first phase of the Jehol radiations is recorded from the Dabeigou Formation, approximately 131 Ma (Liu *et al.* 2003; Niu *et al.* 2003; He *et al.* in press). The typical assemblages from this formation include the *Nestoria-Keratetheria* conchostrachan assemblage, the *Luanpingella-Eoparacypris-Darwinula* ostracod assemblage, the *Arguniella* bivalve assemblage, the *Lymnaea websteri* gastropod assemblage, and the *Peipiaosteus fengningensis-Yanosteus longidorsalis* acipenseriform fish assemblage. The assemblages are characterized by relative few taxa and the lack of some of the most typical elements of the later Jehol Biota, such as the fish *Lycoptera* and the ostracod *Cypridea*. The only bird known from this assemblage is *Protopteryx fengningensis*, the most primitive enantiornithine bird known (Zhang and Zhou 2000).

The second phase of the Jehol radiation is typically preserved in the Yixian Formation. The fossil assemblages include the characteristic *Eosestheria-Lycoptera-Ephemeropsis trisetalis* assemblage, the *Cypridea (Cypridea) liaoningensis-C. (Ullwellia) muriculata-Djungarica camarata* and *Cypridea (C.) veridica orguata-C. (C.) jingangshanensis-C. (C.) zaocishanensis* ostracod assemblages, the *Arguniella-Sphaerium* bivalve assemblage, the *Probaicalia vitimensis-Reesidella robusta* gastropod assemblage, and the *Aeschnidium-Manlayamia dabeigouensis* insect assemblage (P. Chen 1999). These assemblages represent the most important and largest radiation of the Jehol Biota. Many of these radiations occurred for the first time during the time of the lower Yixian Formation (Jianshangou Bed) at an age of about 125 Ma. A diverse vertebrate assemblage has been recovered from the lower Yixian Formation in recent years, including many well-known assemblages of dinosaurs, birds, pterosaurs and mammals. The Jehol flora also witnessed its greatest diversity at this time, and was represented by nearly all Mesozoic plant groups, including some of the early angiosperms (Sun *et al.* 1998, 2001, 2002; Leng and Friis 2003; Friis *et al.* 2003, 2004, 2005).

The third phase of the Jehol radiation is mainly recorded in the Jiufotang Formation and other similar strata from northern China deposited around 120 Ma or slightly younger. The invertebrate assemblages are characterized by the appearance of the *Yanjiestheria* conchostrachan assemblage, the *Mengyinaia-Nakamuranai-Sphaerium* bivalve assemblage, and the *Cypridea (Cypridea) veridica veridica-C. (C.) trispinosa-C. (Yumenia) acutiuscula* and *C. (Ullwellia) koskulensis-C. (Yumenia) casta-Limmocyprideaabscondida-Djungarica* ostracod assemblages. Both bird and pterosaur assemblages are distinct from those recorded in the Yixian Formation, and are characterized by the presence of more cosmopolitan Early Cretaceous members (Unwin *et al.* 2000; Zhou *et al.* 2003; Wang and Zhou 2003d).

3.2. Phases of the radiations of different Jehol groups

It is notable that the radiation patterns vary significantly between taxonomic groups of the Jehol Biota. For instance, gastropods from the second phase (lower Yixian Formation) show a large concentration of individuals but low systematic diversity (Pan and Zhu 1999, 2003). Bivalves in the first and second phases of the Jehol radiation, dominated by *Arguniella*, also show a low diversity, and only with a significant increase in generic and species richness in the third phase (J. Chen 1999, 2003).

Conversely, despite a low diversity in the first phase, ostracods had already radiated significantly in the second phase, and attained their greatest diversity in the third phase (Cao 1999; Cao and Hu 2003). Similarly, significant insect and conchostrachan radiations took place during the time of the second phase. In particular, the insect assemblage of the second phase represents the largest known radiation of Mesozoic insects (Zhang and Zhang 2003). Therefore, among the major invertebrate groups of the Jehol Biota, ostracods, insects and conchostrachans radiated earlier than both gastropods and bivalves.

It is also noteworthy that the plants show maximum abundance and diversity in the second phase of the Jehol radiation (P. Chen 1988, 1999; Wu 1999, 2003; Sun *et al.* 2001), and this is likely to have been closely related to the radiation of many animal groups at that time. The angiosperms in the Jehol flora currently comprise three species of *Archaeofructus* and one species of the putative basal eudicot *Sinocarpus* (Leng and Friis 2003). Gnetales and sphenopsids (horsetails) show strong resemblance to their living descendants, indicating that the radiation of the Jehol plants played an important role in the development of modern plant ecosystems from their Mesozoic predecessors (Zhou *et al.* 2003; Zhou 2006).

Recent discoveries and studies on vertebrates such as fish, pterosaurs, dinosaurs, birds and mammals generally support the division of the Jehol radiation into three major phases (Zhou 2006). For instance, the fish assemblages are distinctive in each of the three phases. In the first phase, the only known fish taxa are the basal acipenseriforms *Peipiaosteus fengningensis* and *Yanosteus longidorsalis*. In the second phase, the most common fish is *Lycoptera*, a primitive teleost and the best-known fish in the Jehol Biota. By the time of the third phase of the Jehol radiation, *Lycoptera* had been replaced by another teleost, *Jinanichthys* (Zhang and Jin 2003).

The Jehol Biota records the largest radiation in Mesozoic avian evolutionary history. A total of 23 avian genera have been identified, including 12 enantiornithines, six ornithurines and five more basal birds (Zhou 2006). The bird assemblages had also changed significantly through the three phases of the Jehol Biota. In the first phase, the enantiornithine *Protopteryx engningensis* represents the only known avian (Zhang and Zhou 2000). Jehol birds had their first major radiation at the second phase; the avian assemblage at this phase is represented by the basal bird *Confuciusornis* (Hou *et al.* 1995), the enantiornithines *Eoenantiornis* (Hou *et al.* 1999) and *Longirostravis* (Hou *et al.* 2004), and the basal ornithurine *Liaoningornis*. The avian radiation at the third phase is characterized by a combination of basal birds, such as *Jeholornis* (Zhou and Zhang 2002a, 2003a) and *Sapeornis* (Zhou and Zhang 2002b, 2003b), more enantiornithines, such as *Sinornis* (Serenó and Rao 1992), *Boluochia* and *Longipteryx* (Zhang *et al.* 2001), and derived ornithurines, such as *Yixianornis* and *Yanornis* (Zhou and Zhang 2001).

Jehol dinosaurs comprise at least 27 genera, with 9 belonging to the Ornithischia and 18 to the Saurischia, representing a major dinosaurian radiation in the Early Cretaceous. Most of them are known from the second phase, which represents the largest radiation of dinosaurs in the Jehol Biota. No dinosaur has yet been reported from the first phase. The dinosaurs from the third phase are known from various regions of northern China, e.g. Liaoning, Inner Mongolia, and Gansu Province (You and Dodson 2003; You *et al.* 2003, 2005), representing the second dinosaur radiation of the Jehol Biota, which is accompanied by an increased geographic distribution (Zhou 2006).

Jehol pterosaurs are known mainly from two distinctive assemblages occurring in the second and third phases of the Jehol radiation, respectively. These two assemblages represent two major radiations of pterosaurs in the Early Cretaceous and are characterized by the appearance of several new and predominant pterodactyloids in the pterosaur radiation of the Jehol Biota. The pterosaurs from the third phase comprise members of more advanced and more cosmopolitan clades than those from the second phase of the Jehol radiation (Wang and Zhou 2003a,b, 2006a,b; Wang *et al.* 2005).

Jehol mammals are known only from the Yixian Formation. A total of 9 species have been reported, representing a great mammalian radiation in the Early Cretaceous, which includes representatives of many of the major lineages of Mesozoic mammals, such as Symmetrodonta, Triconodonta, Multituberculata, Eutheria and Metatheria (Luo *et al.* 2003; Hu *et al.* 2005). No mammal has been reported from the Dabeigou Formation. Mammals have been found from the Jiufotang Formation, but none of them has been formally reported.

In summary, various organism groups show their own patterns of radiation. Like ostracods, insects and conchostrachans, plants and many vertebrate groups (pterosaurs, dinosaurs, birds and mammals) had their first radiation in the second phase of the Jehol evolution, while the radiation of some other groups such as gastropods and bivalves did not begin until the third phase. The lower Yixian Formation (125 Ma) records the most significant radiation of the Jehol Biota, although several animal groups probably attained their greatest diversity at the time of the Jiufotang Formation.

3.3. Distribution of the Jehol Biota

The changing nature of the Jehol Biota is expressed not only by increased taxonomic diversifications but also by a progressive geographic expansion (Figure 2).

The first phase of the Jehol Biota, typically known from the Dabeigou Formation in northern Hebei Province, northeast China, is characterized by a fossil assemblage of relatively low systematic diversity and forms with more plesiomorphic features. The fossil assemblages are geographically restricted to a relatively small and strap-like north-south distributed area that includes northern Hebei Province, eastern Inner Mongolia and Siberia (P. Chen 1999).

The second phase of the Jehol radiation had a broad palaeogeographic distribution. Its fossil assemblages are mainly known from the Yixian Formation or equivalent sediments in northern Hebei, Inner Mongolia and western Liaoning, and Siberia (P. Chen 1999).

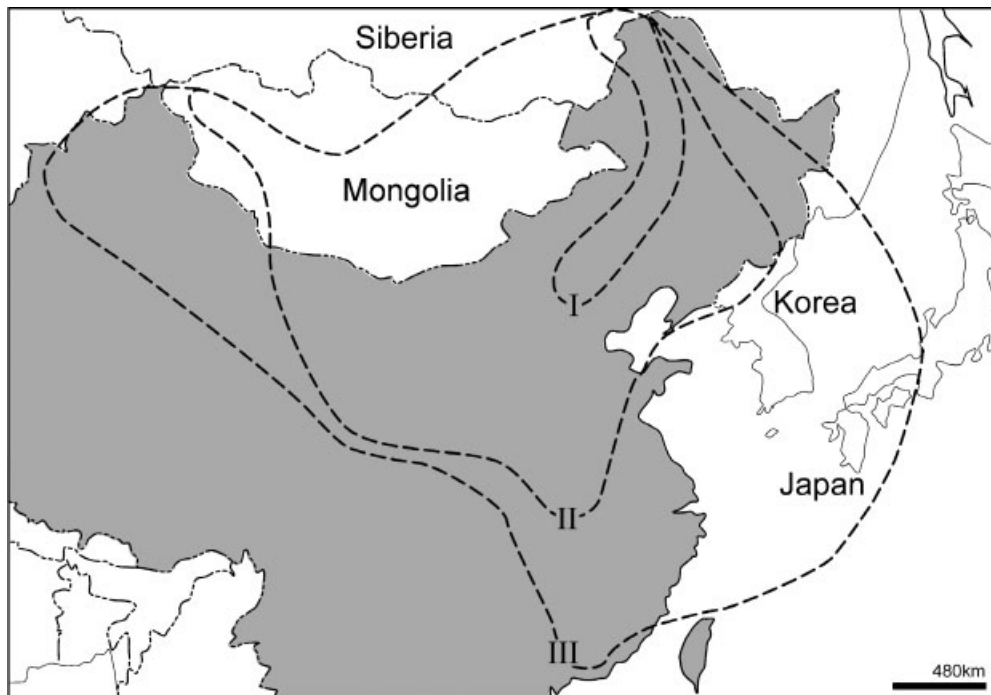


Figure 2. Distribution of the three phases of the Jehol radiation. The dotted area represents part of China. I, II and III defines the geographic range of the first, second and third phase of the Jehol Biota, respectively. Stratigraphically I, II and III correspond to the Dabeigou, Yixian and Jiufotang formations or equivalent deposits, respectively. (Modified from P. Chen 1999).

The third phase of the Jehol radiation is characterized by deposits equivalent to the Jiufotang Formation. The assemblages of the third phase were also distributed over a larger geographic area than earlier assemblages, having expanded further west to Xinjiang, to southeast China, and to the Korean Peninsula and southwest Japan in the east (P. Chen 1999). For instance, in western Gansu Province, northwest China, the Early Cretaceous terrestrial deposits contain a fossil assemblage very similar to that of the Jiufotang Formation, with some dinosaurs and birds showing more advanced features (Hou and Liu 1984; Ma 1993; Lü 1997; Xu 1997; Dong 1997a,b; Tang *et al.* 2001; You and Dodson 2003; You *et al.* 2003, 2005; Zhou 2006). Volcanism was much weaker in Gansu, and no absolute age has been reported for deposits in this region. As a result, it remains unclear whether the Gansu fossil assemblage is equivalent to or slightly younger than the Jiufotang Formation. The Jehol Biota has also been reported from the Junggar Basin in Xinjiang, northwest China, where it includes such important vertebrate fossils as *Psittacosaurus* and *Dsungaripterus*. Jehol fossils such as *Psittacosaurus* were also reported from Thailand (Buffetaut *et al.* 1989; Buffetaut and Suteethorn 1992).

Early Cretaceous palaeogeographic changes at a more global scale also played an important role in dispersal of the Jehol Biota into other regions. Because East Asia was nearly completely isolated from the rest of Laurasia from the Middle Jurassic until the early part of the Cretaceous (Enkin *et al.* 1992; Russell 1993; Upchurch 1995; Barrett *et al.* 2002; Zhou *et al.* 2003), a number of endemic forms had evolved in the Jehol Biota (Chang 2003). East Asia was even proposed to be a 'refugium for relics' (Luo 1999); however, the refugium hypothesis can, at best, only partly explain the features of the biota. Current evidence suggests instead that the Jehol Biota was a cradle or a centre for the diversification of many groups (Manabe *et al.* 2000; Zhou *et al.* 2003). With the Aptian-Albian regression of the Turgai Sea resulting in the formation of a Europe-Asia 'land bridge' (Upchurch *et al.* 2002) no significant palaeogeographic barrier existed between Asia and Laurasia at the times of the second and third phase of the Jehol Biota. For vertebrates such as birds and pterosaurs dispersal to Europe and America would have probably been easier than for other animals (Wang and Zhou 2003b,d; Zhou 2004a, 2006). In addition, many dinosaurian, mammalian or amphibian groups in the Jehol Biota also showed cosmopolitan distribution (Li *et al.* 2003; Zhou *et al.* 2003). Therefore, despite the fact that the Jehol Biota had retained some primitive forms that probably had an earlier origin in Europe, by the second, and particularly the third, phase of the Jehol Biota, the Jehol Biota must have had a significant dispersal to other regions. The presence of many of the most basal representatives of various dinosaurian, mammalian, lizard and avian groups supports this scenario (Manabe *et al.* 2000; Luo *et al.* 2003; Wang and Zhou 2003a,b,d; Zhou 2004a,b, 2006; Wang *et al.* 2005; Evans and Wang 2005).

4. ECOLOGICAL PERSPECTIVE ON THE EVOLUTION OF THE JEHOL BIOTA

4.1. Environmental background and biological adaptations

The radiation of the Jehol Biota coincided approximately with several major global geological events (Figure 3), including high tectonic activity, frequent volcanic eruptions (Ingle and Coffin 2004), increase of atmospheric CO₂ and the greenhouse climate in the middle Cretaceous (Larson and Erba 1999; Wilson and Norris 2001; Pearson *et al.* 2001) and the Cretaceous Normal Superchron (CNS) that lasted for about 37 Ma (120–83 Ma, Gradstein *et al.* 1995). A recent study has also indicated the presence of a large seasonal variability of temperatures in cold episodes in the Early Cretaceous (Steuber *et al.* 2005). The local geology in Liaoning reflects the impact of the increasingly active West Pacific tectonics on northeast China in the Early Cretaceous (X. Wang *et al.* 1999, 2000; Wang and Zhou 2003c). The increase of palaeotemperature had a positive impact on the productivity of plants and was directly responsible for the flourishing of the Jehol flora. For instance, angiosperms probably first appeared in the early Early Cretaceous with a low evolutionary rate, but its radiation (diversity, complexity and abundance) began to increase rapidly over a short interval through the middle and late Early Cretaceous, containing a diverse angiosperm assemblages including members of both monocots and eudicots (Leng and Friis 2003; Friis *et al.* 2004, 2005). The first evolutionary radiation of angiosperms may have been fostered by co-evolution with insects (Crepet and Friis 1987; Farrell 1998; Ren 1998; Grimaldi 1999), and closely related to the increase of atmospheric CO₂ and the greenhouse climate in the middle Cretaceous (Barrett and Willis 2001; McElwain *et al.* 2005).

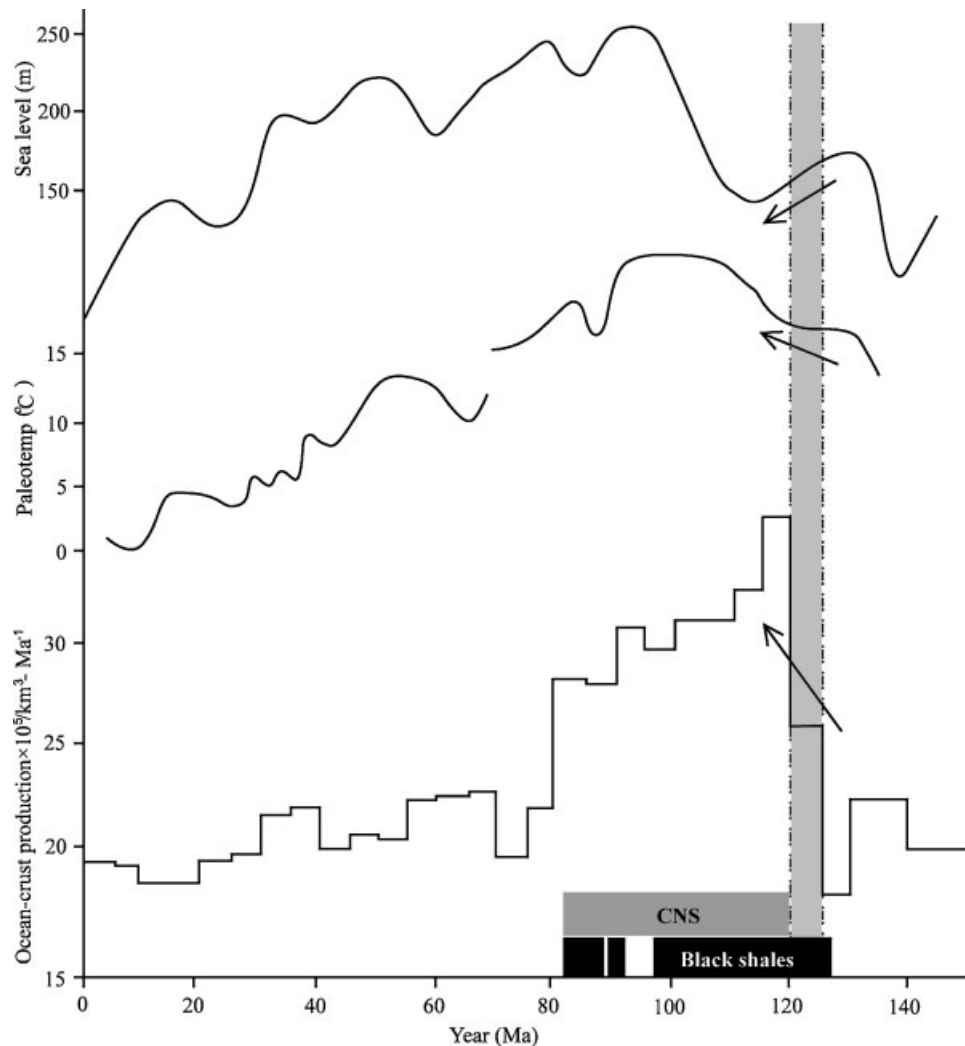


Figure 3. Correlation of the radiation of the Jehol Biota and some major global geological events in the Early Cretaceous. (Modified from Larson 1991; Gradstein *et al.* 1995; Zhou 2006).

Jehol plants are found mainly in the lower Yixian Formation, and include Bryophyta, Lycopsidea, Sphenopsida, Filicopsida, Ginkgoales, Czekanowskiales, Coniferales, Bennettiales, Gnetales and Angiospermae (Wu 1999, 2003; Sun *et al.* 2001). The vegetation included forest trees such as ginkgoes (Zhou and Zheng 2003), cycads, seed ferns and conifers, and an herbaceous groundcover of lycopods, horsetails and ferns (Wu 2003). Angiosperm were sparse and apparently also all small plants.

The frequent volcanic eruptions, while producing mass-mortality events, also introduced abundant minerals with the tuffs into the freshwater lakes (Wang 1990). Volcanic eruptions coupled with forest fires and poisonous gases may also have repeatedly destroyed biotic components in the existing ecosystem, resulting in its frequent destructions/reconstructions (Wang *et al.* 1999; Guo and Wang 2002; Guo *et al.* 2003; Wang and Zhou 2003c; Zhou 2006). Furthermore, a great diversity of habitats in the region may have contributed to accelerated speciation and radiation.

One of the characteristics of the Jehol Biota is the presence of many arboreal (or scansorial) and herbivorous dinosaurs, pterosaurs, birds and mammals (Zhou 2004a). For instance, *Microraptor* is an arboreal theropod (Xu

et al. 2000b). About half of the Jehol dinosaur taxa were herbivorous (Zhou 2006). Most of the avian genera of the Jehol Biota were arboreal, including nearly all enantiornithines and basal birds *Jeholornis*, *Sapeornis* and *Confuciusornis* (Zhou and Farlow 2001). Only some ornithurines were terrestrial and occupied an ecological niche near the water. The possession of the opposing hallux in birds, as compared to dinosaurs, is probably a key feature that had enabled the early birds to adapt well to a perching life (Zhou 2004b). Although the diets of birds are usually difficult to determine, many of them show evidence (gizzard stones or seeds, see Figures 4 and 5) for a distinctive herbivorous habit (Zhou *et al.* 2002; Zhou *et al.* 2003; Zhou *et al.* 2004).



Figure 4. Gizzard stones preserved in the feathered oviraptorid theropod *Caudipteryx* (IVPP V 12344), indicating a herbivorous diet.



Figure 5. Seeds preserved in the stomach of a basal bird *Jeholornis prima*, from the Early Cretaceous Jiufotang Formation in Chaoyang, western Liaoning, northeast China (IVPP V13274), suggesting seed-eating adaptation.

Nearly all known Jehol pterosaurs were arboreal. In addition, the Jehol Biota contains some scansorial mammals including the most primitive known eutherians (Ji *et al.* 2002) and metatherians (Luo *et al.* 2003). Their scansorial adaptations created a completely new niche for these mammalian groups, which distinguished them from other Mesozoic terrestrial mammals, and was possibly critical to their origin in East Asia (Luo *et al.* 2003). A recent study of the Jehol lizard *Dalinghosaurus* also suggests it as a climber rather than a facultative bipedal runner (Evans and Wang 2005). Therefore, the major land vertebrate groups all show a strong tendency towards an adaptation to living in forest habitats. Vertebrates with such an adaptation not only had the benefit of access to more food resources, but also became less vulnerable to the predation of ferocious terrestrial animals such as carnivorous dinosaurs. For instance, enantiornithines and more basal birds are relatively primitive forms with rather poorly developed flight capability, and living in trees might have been safer than living in a more open habitat near the water. In contrast, ornithurines with nearly modern flight capability could more easily escape from predating carnivorous animals and might have occupied more open habitats.

Size differences among the Jehol vertebrates also reflect the diverse niches they occupied. For instance, basal birds such as *Jeholornis* and *Sapeornis* are generally large (Zhou and Zhang 2002a,b, 2003a,b), and probably occupied a more open forest habitat, while small-sized enantiornithines could have lived in denser forests. Ornithurine birds living near the shore were larger than enantiornithines and better adapted for piscivorous habit (Zhou and Zhang 2001; Zhou *et al.* 2002). Pterosaurs also vary greatly in body size. Many large-sized forms with estimated wing span of up to 5 metres most likely lived in open forest close to water while they fed on fish.

4.2. Dietary differentiation and the Jehol radiation

The Jehol radiation may be linked also to the dietary differentiation among the Jehol animals. Birds and pterosaurs show significant dietary differentiation that may be coupled to arboreality and good flight capability. Among the Jehol birds, most of the enantiornithines probably ate insects, while *Longipteryx* was piscivorous (Zhang *et al.* 2001) and *Longirostravis* probed in soft sediment with elongated and pointed jaws that had teeth restricted to the rostral end (Hou *et al.* 2004); *Jeholornis* was a specialized seed-eating bird with nearly edentulous robust jaws (Zhou and Zhang 2002a); *Sapeornis* preserved gizzard stones indicating an herbivorous habit (Zhou and Zhang 2003b); and *Yanornis* was mainly a fish-eating bird, as indicated by fish remains in the stomach (Zhou and Zhang 2001; Zhou *et al.* 2002), and could also have switched to a vegetarian diet due to the seasonal shortage of their normal food resources (Zhou *et al.* 2004), which is consistent with a recent conclusion of the presence of large seasonal variability of temperatures in the Early Cretaceous (Steuber *et al.* 2005).

Jehol pterosaurs were mainly piscivorous or carnivorous while a few others were probably herbivorous such as *Sinopterus* (Wang and Zhou 2003a; Wang and Zhou 2006). Most of the known Jehol pterosaurs have a long and pointed snout with slender and densely distributed teeth. The diet differentiation of the pterosaurs is recognized by a great size range of the jaws and dentitions (Wang *et al.* 2005; Wang and Zhou 2006a,b). The presence of a variety of abundant fish and invertebrates in the lakes probably provided the main food resources.

Barrett (2005) provided a recent review of the herbivores in theropods, and concluded that herbivorous and omnivorous forms are rare among the non-avian Theropoda, but are more common than previously suspected. This conclusion is obviously consistent with the recent discoveries of non-avian theropods in the Jehol Biota. One of the unique characteristics of the Jehol dinosaur assemblages is the presence of many herbivorous theropods such as the oviraptorosaurids *Caudipteryx* (Ji *et al.* 1998) and *Incisivosaurus* (Xu *et al.* 2002a), and the ornithomimosaurid *Shenzhousaurus* (Ji *et al.* 2003). Many of these herbivorous dinosaurs also display structural specializations as seen, for instance, in *Caudipteryx* that has robust, short and high jaws with much reduced teeth, and nearly all specimens currently known have gizzard stones (Ji *et al.* 1998; Zhou and Wang 2000; Ji *et al.* 2003). *Incisivosaurus* has a pair of premaxillary teeth resembling rodent incisors and small, lanceolate cheek teeth with large wear facets, suggesting an herbivorous adaptation previously unknown in theropods (Xu *et al.* 2002a). Therizinosaurids (Xu *et al.* 1999a) are probably also herbivores (Paul 1984). Other herbivorous dinosaurs include sauropods, iguanodontids (Wang and Xu 2001; You *et al.* 2005), hadrosauroids (You *et al.* 2003), ankylosaurids (Xu *et al.* 2001), neoceratopsians (Xu *et al.* 2002b; You and Dodson 2003), and basal ornithischians (Xu *et al.* 2000a).

The most famous carnivorous dinosaur from the Jehol Biota is *Sinosauropteryx*, which is usually found with mammal or lizard remains preserved in their stomach (Chen *et al.* 1998; personal observation). Other carnivorous forms include troodontids (Xu *et al.* 2002c), dromaeosaurids (Xu *et al.* 1999b, 2000b, 2003), tyrannosauroids (Xu *et al.* 2004), and may also include other basal coelurosaurids such as *Protarchaeopteryx* (Ji *et al.* 1998).

Although Jehol mammals are usually small and probably mainly fed on insects or lizards, they also show great variation in size, ranging from a few grams to over a dozen kilograms (Luo *et al.* 2003; Hu *et al.* 2005). *Repenomamus* represents the largest mammal of the Mesozoic (Y.Q. Wang *et al.* 2001). Interestingly, a recently found specimen of *Repenomamus* represents the first fossil evidence of a mammal eating dinosaur, which is consistent with the increased body size in some mammals, and further illustrates the dietary differentiation of the Jehol mammals (Hu *et al.* 2005). The dietary differentiation of mammals is best displayed in the diversity of the dentition types. For instance, the recently described *Repenomamus giganticus* has large and sharp incisors and molars, and robust mandibles (Hu *et al.* 2005).

Finally, invertebrates dominate the Jehol Biota in terms of both abundance and diversity. For instance, insects are represented by hundreds of species, with habitats ranging from the water, soils, thickets, forests, marshes, and mountains to trees (Ren 2002). Many insects fed on plant leaves, seeds or fruits; some were saprophagous, some preyed on other insects or sucked blood of vertebrates; and others were pollinators with elongate mouthparts (Zhang and Zhang 2003). Their success may be directly responsible for the great diversification of the Jehol vertebrates. Most of the invertebrates were in the bottom or middle of the food chain and were the prey of many upper food chain vertebrate predators. Carnivorous dinosaurs, birds and mammals were at the top of the food chain of the Jehol ecosystem, with many other animals such as fish, amphibians and lizards (Wang and Gao 1999; Y. Wang *et al.* 2000; Gao and Shubin 2001; Gao and Wang 2001) in the middle of the food chain (Figure 6).

4.3. Competition and coevolution within the Jehol Biota

The Jehol Biota represents one of the best case studies for understanding Early Cretaceous terrestrial ecosystems. Interspecific relationships in the Jehol Biota including the competition, predator-prey relationship, and/or co-evolution of various organism groups may have played a key role in the radiation of the Jehol Biota (Zhou 2006).

Among the terrestrial vertebrates, dinosaurs, birds, pterosaurs and mammals were probably the major competitors for niches and food resources in the Jehol Biota. Interactions among these groups may have played a key role in the radiation of each group and also in the establishment of new lineages that further diversified successfully in the Late Cretaceous or in the Cenozoic.

Birds and pterosaurs are the only two flying vertebrate groups at the time. Arboreality was the dominant life-style for both groups. Due to the similarity in many ecological aspects they were probably major competitors in the Jehol Biota (Wang *et al.* 2005). The ornithurine birds, with the best flight ability at that time, were living near the water and fed on fish but many arboreal pterosaurs were also piscivorous (Wang and Zhou 2006a,b). Despite the similarity in piscivorous diet ornithurine birds and pterosaurs had avoided a direct competition against each other by occupying different niches, i.e. in terrestrial and arboreal environment, respectively (Zhou 2006).

Like other Mesozoic mammals, the Jehol mammals were generally small and lived in the shadow of the dinosaurs. Many were ground dwelling, but a few of them were scansorial (Ji *et al.* 2002; Luo *et al.* 2003). As in the case of small-sized enantiornithine birds they probably also lived in dense forest or thickets to avoid predation of carnivorous dinosaurs. With the increased body size, at least some mammals had already become a competitor for the carnivorous dinosaurs in the Jehol Biota.

The largest birds from the Jehol Biota are *Jeholornis* and *Sapeornis*, and both are arboreal and herbivorous forms. Nearly all Jehol pterosaurs are arboreal and live in the forest. Many of them are also large, probably occupying an open forest similar to most basal birds (Wang and Zhou 2006a,b), and fed on fish while some were herbivorous (Wang and Zhou 2003d). Nearly half of the Jehol dinosaurs are herbivorous and some of them even became arboreal. The appearance of many arboreal vertebrates reflects the severe competition on the ground, where the dinosaurs still dominated (Zhou 2006).

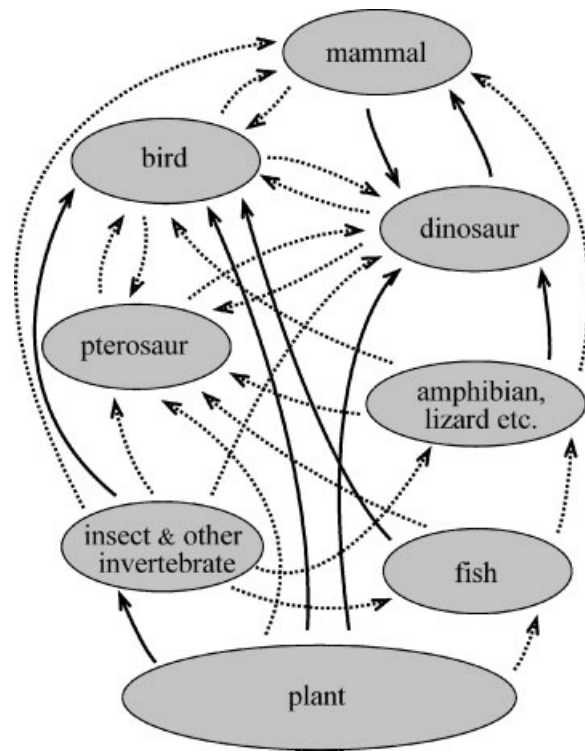


Figure 6. Simplified food chain of the Jehol Biota (Modified from Zhou 2006).

Competition among vertebrates also existed in the water where there were several kinds of fish, including the acipenseriform *Protosephurus* which could reach a length of over 1 m (Jin 1999; Grande *et al.* 2002). Several aquatic choristoderan reptiles became the rulers in the lakes, with the largest form reaching 2 m long (Gao *et al.* 1999; Liu and Wang 2003; Liu 2004). It is generally believed that the choristoderes ecologically overlapped with other aquatic reptiles (Gao *et al.* 2000), particularly *Ikechosaurus*, the largest aquatic reptile in Jehol lakes with an elongated snout and a maximum length of over 2 m, shared a similar habit with crocodiles (Liu 2004). This might in turn explain why crocodiles have not been discovered from the Jehol Biota in Liaoning Province, especially considering the fact that crocodiles are known from the Early Cretaceous deposits in Jiuquan Basin (Gansu Province) while no choristodere has been reported from that region.

The early angiosperm *Archaeoartus* was adapted to life in an aquatic environment. This fact, together with the existence of multiple early trends toward an aquatic habit in early angiosperms (Friis *et al.* 2003), emphasizes the importance of aquatic adaptation in the early radiation of the group. Similarly, ornithurine birds probably represent the first attempt of early birds to substantially exploit an aquatic resource (Zhou and Zhang 2001). The competition between angiosperms and other seed plants and that between ornithurines and other early birds may have contributed to the expansion and adaptation of angiosperms and ornithurine birds to new ecological vicinity.

Despite the competition among major Jehol vertebrate groups, examples of co-evolution were also common. For instance, pollinating insects probably played a key role in the origin and early evolution of the angiosperms (Ren 1998), and their subsequent co-evolution has been documented (Leng *et al.* 2003; Zhang and Zhang 2003). The major radiation of the Jehol insects occurred at the time of the lower Yixian Formation, which coincides with the major radiation of the Jehol flora. Pollinating orthorhaphous brachyceran fossils (short-horned flies) were proposed to be among the most ancient pollinators (Ren 1998). Studies of the mouthparts of pollinating insects indicate that in the Jehol biota there existed at least two forms, suggesting their adaptations to at least two different flower types (Ren 2002).

In addition to the obvious insect-flower interactions, animal-plant coevolution was probably much more common than we would normally believe. Plants were the food resources for a majority of animals in the Jehol

Biota. On the other hand, flying animals such as insects, pterosaurs and birds probably all played a significant role in the dispersal of the seed plants including angiosperms. The long-tailed bird *Jeholornis* displays seeds in the stomach, providing the first direct evidence for a possible bird-plant co-evolution (Zhou and Zhang 2002a). Furthermore, non-flying animals such as herbivorous dinosaurs and scansorial mammals could have contributed to the dispersal of seed plants as well (Barrett and Willis 2001).

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