

GEOSCIENCES

Special Topic: Paleontology in China

The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and implications

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ABSTRACT

The study of the Early Cretaceous terrestrial Jehol Biota, which provides a rare window for reconstruction of a Lower Cretaceous terrestrial ecosystem, is reviewed with a focus on some of the latest progress. A newly proposed definition of the biota based on paleoecology and taphonomy is accepted. Although the Jehol fossils are mainly preserved in two types of sedimentary rocks, there are various types of preservation with a complex mechanism that remains to be understood. New discoveries of significant taxa from the Jehol Biota, with an updated introduction of its diversity, confirm that the Jehol Biota represents one of the most diversified biotas of the Mesozoic. The evolutionary significance of major biological groups (e.g. dinosaurs, birds, mammals, pterosaurs, insects, and plants) is discussed mainly in the light of recent discoveries, and some of the most remarkable aspects of the biota are highlighted. The global and local geological, paleogeographic, and paleoenvironmental background of the Jehol Biota have contributed to the unique composition, evolution, and preservation of the biota, demonstrating widespread faunal exchanges between Asia and other continents caused by the presence of the Eurasia–North American continental mass and its link to South America, and confirming northeastern China as the origin and diversification center for a variety of Cretaceous biological groups. Although some progress has been made on the reconstruction of the paleotemperature at the time of the Jehol Biota, much more work is needed to confirm a possible link between the remarkable diversity of the biota and the cold intervals during the Early Cretaceous. Finally, future directions for the study of the Jehol Biota are proposed that highlight the great potential of more comprehensive and multidisciplinary studies to further our understanding of the biological and geological implications of the Jehol Lagerstätte.

Keywords: Jehol Biota, Early Cretaceous, Lagerstätte, China, terrestrial, ecosystem

The Early Cretaceous terrestrial Jehol Biota is distributed mainly in western Liaoning Province and neighboring areas in northeastern China (Fig. 1). It has been famous since the early 1990s for producing feathered dinosaurs and many other exceptionally preserved vertebrate fossils such as early birds, mammals, pterosaurs, and amphibians, as well as abundant insects and early flowering plants. These fossils have significantly increased our understanding of the biological evolution of a number of taxonomic groups. Furthermore, thanks to its unique taphonomy in the context of a volcanism-prevalent geological background, many soft tissues or stomach contents are well preserved

together with often fully articulated skeletons of vertebrates, enabling a more complete reconstruction of the paleoecology of a Lower Cretaceous terrestrial ecosystem [1–4].

Newly discovered fossils continue to add to the already long list of taxa in the Jehol Biota and provide fresh evidence on the phylogeny of various vertebrate groups such as amphibians, pterosaurs, dinosaurs, birds, and mammals, as well as insects and plants. The diversity of the Jehol Biota is still increasing rapidly as new species of Jehol fossils (e.g. birds and insects) are being or will be reported. According to an earlier estimate [3], the vertebrate assemblage contains at least 121 genera

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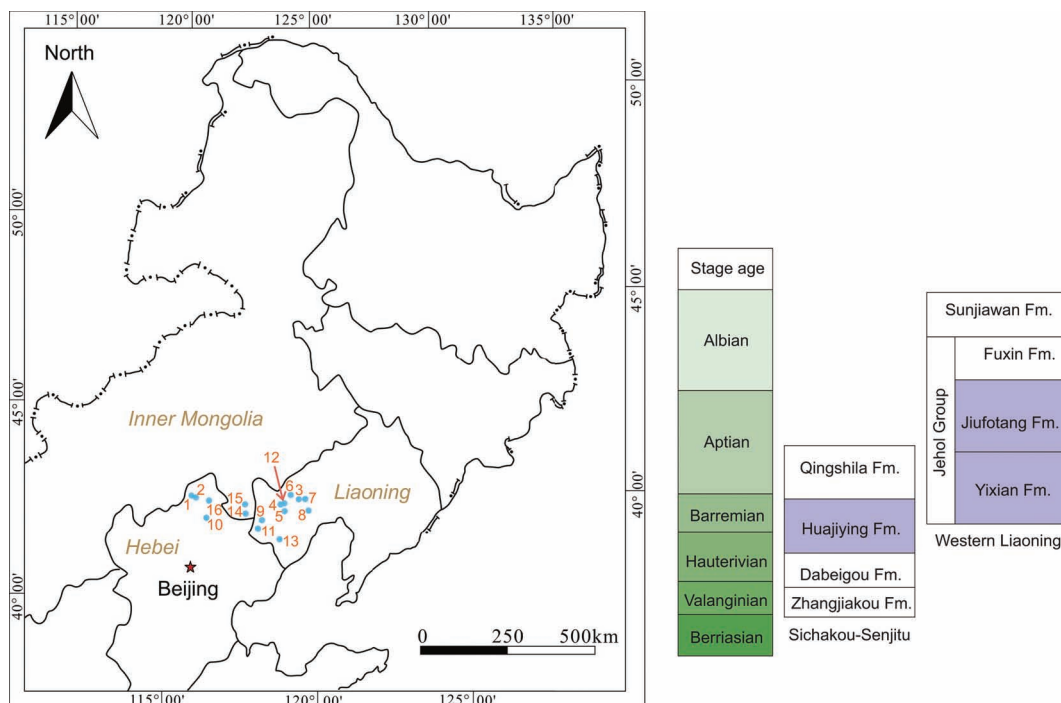


Figure 1. Distribution of the Jehol Biota and stratigraphic correlation of the Jehol Biota-bearing deposits in western Liaoning, northern Hebei (modified from [40]). Numbers indicate some of the major vertebrate fossil localities of the Jehol Biota. (1) Sichakou, (2) Senjitu, (3) Lujiatun, (4) Boluochi, (5) Meileyingzi, (6) Shangheshou, (7) Sihetun, (8) Jingangshan, (9) Daxinfangzi, (10) Fengshan, (11) Dawangzhangzi, (12) Dapingfang, (13) Xiaotaizi, (14) Shifo, (15) Liutiaogou, and (16) Weichang.

and 142 species, which already exceeds the diversity of contemporaneous Lagerstätten such as the Santana Fauna of Brazil and the Las Hoyas Fauna from Spain, and is nearly as large as that of the Jurassic Solnhofen Fauna and the Eocene Messel Fauna from Germany.

Additionally, the exceptional preservation of some Jehol fossils enables recognition of a large amount of rare information about the biology of Early Cretaceous vertebrates, e.g. the early evolution of feather color in birds and dinosaurs [5–7], the feeding behavior of dinosaurs and birds [8–14], the digestive system of early birds [15,16], and even the reproductive behavior of early birds, amphibians, chorisoteres, and pterosaurs [17–22].

Further, important progress from the study of the Jehol Biota has been on the coevolution of insects and plants [23], and possible coevolution of some insects and mammals/feathered dinosaurs/birds, e.g. the discovery of ectoparasitic blood-feeding giant fleas or flea-like ectoparasites [24–28].

In addition to new fossil discoveries that directly add to our understanding of an improved reconstruction of the diversity and the early evolution of various lineages of vertebrates, insects, and plants, studies on the paleoenvironmental background of the Jehol lakes and the taphonomy of the exceptionally preserved fossils have provided new insights into

the interaction between the environment and the evolution of life, which is fundamental to deciphering the terrestrial ecosystem in the Early Cretaceous [29–42].

Although significant progress has been made on the study of the Jehol Biota, many new exciting fossils (e.g. insects, the earliest known feathered dinosaurs, pterosaurs, and early mammals) have been recovered from the Middle–Late Jurassic Yanliao (or Daohugou) Biota (about 160 Ma) from approximately the same region in northeastern China. Although it is now apparent from recent and extensive dating of the fossil-bearing deposits and more detailed biostratigraphic correlation [3,4,43–46] that these deposits represent two distinct terrestrial biotas, it should be noted that in some previous publications, some elements of the Yanliao Biota were incorrectly referred to the Jehol Biota.

DEFINITION AND TAPHONOMY

The study of the fossils of the Jehol Biota has had a relatively long history, with the teleost fish *Lycoptera davidi* being the first scientifically named vertebrate species. The name Jehol Fauna was first proposed by Amadeus William Grabau [47] to refer to the fossil community of the fossil fish-bearing lacustrine

deposits in western Liaoning Province. Gu [48] first proposed the name Jehol Biota for the ‘*Eosestheria* (conchostracan)–*Ephemeropsis* (insect)–*Lycoptera* (fish)’ (EEL) lacustrine fossil assemblage [49].

With increasing numbers of new fossil discoveries, in particular since the early 1990s, e.g. early birds, feathered dinosaurs, mammals, pterosaurs, amphibians, flowering plants, and insects [1,50–52], the Jehol Biota has become better known to the scientific community as a world-class terrestrial Lagerstätte. Its distribution is now known to extend beyond western Liaoning and, furthermore, its composition can no longer be appropriately defined by the lacustrine EEL assemblage.

Admittedly, there is as yet no consensus on the definition or the distribution of the Jehol Biota, which would, however, further confuse our study of the diversity and the pattern of the radiation of the Jehol Biota. Most workers have accepted that the Jehol Biota is mainly distributed in western Liaoning and neighboring regions such as northern Hebei and southeastern Inner Mongolia, as many typical Jehol fossils are also known from these regions [3,53,54]. However, some workers have argued for an even more inclusive paleogeographic distribution of the biota, i.e. fossil assemblages from the Lower Cretaceous Jehol Group (Yixian and Jiufotang formations) or equivalent strata of adjacent areas in eastern and central Asia, including northern China, the Korean Peninsula, Japan, Mongolia, Kazakhstan, and Siberia [1,48–50,52,53].

Zhou and Wang proposed the Jehol Biota *sensu stricto*, with a limited distribution in northern Hebei, western Liaoning, and southeastern Inner Mongolia, as distinct from the Jehol Biota *sensu lato*, which is more widely distributed in eastern and central Asia, including northern China, the Korean Peninsula, Japan, Mongolia, Kazakhstan, and Siberia [3].

A recent proposal by Pan *et al.* [40] for a definition of the Jehol Biota that combines ecological and taphonomic aspects i.e. ‘organisms that lived in the Early Cretaceous volcanic-influenced environments of northeastern China, and were buried in lacustrine and rarely fluvial sediments, where most turned into exceptionally preserved fossils’ is accepted in this paper as it best describes the features of the Lagerstätte. According to this definition, the biota contains fossils from the Yixian and Jiufotang formations of western Liaoning and adjacent Inner Mongolia and Hebei, and the Huajiying Formation of northern Hebei, which is also consistent with the definition of the Jehol Biota *sensu stricto* [3]. The biota’s temporal distribution is from the Barremian to Aptian, i.e. a time span of about 10 Myr, as is known from extensive dating of the Jehol fossil-bearing deposits [53,55–60].

As a Lagerstätte, the Jehol Biota continues to produce exceptional preservation of fossils (Figs 2 and 3), in addition to the common occurrence of integument such as the feathers of birds and dinosaurs, mammal hair, fibers and hair-like structures of pterosaurs, soft tissues such as skin [61–65], fish muscles and eyes [66], the melanosomes of birds and dinosaurs [5–7], and the ovarian follicles of birds [22] (Figs 2–5).

The Jehol fossils are mainly preserved in two types of sedimentary rock. One is composed of finely laminated sediments (shales or mudstones) interbedded with ash layers, as is typical in the Jianshangou Bed of the Yixian Formation at the Sihetun locality in Beipiao, Liaoning. The second type is composed of massive, tuffaceous, pebbly sandstones, commonly yielding articulated vertebrate skeletons without any trace of soft tissues, sometimes isolated teeth, fragmentary postcranial elements [67,68], and plant fragments, but lacking invertebrates and flying vertebrates [40]. This rock type is typically developed in the Lujiatun Bed of the Yixian Formation at Lujiatun and several other localities in Beipiao, Liaoning. The second type obviously represents a lahar deposit, and is known for preserving sleeping or resting postures, post-nesting gregarious behavior of dinosaurs, frogs, and lizards [69–71], and evidence of a mammal that ate baby dinosaurs [72].

Stomach contents are preserved in a wide range of vertebrate groups and have been reported from both types of deposit (Fig. 4). For instance, dinosaurs have been reported with stomach contents suggesting either carnivorous, piscivorous, [12,14,73,74] or herbivorous diets [53,75], and early birds are known with stomach contents indicating piscivorous or herbivorous diets [8,9,13,15,16,76–78], in addition to a report of a large mammal feeding on a baby dinosaur [72].

Some birds have preserved evidence of the crop. For example, seeds have been reported to be preserved in the crops of several birds (*Sapeornis*, *Hongshanornis*), suggesting a modern digestive organ similar to that of extant birds [15] and new specimens of *Yanornis* contain preserved fish in the crop, indicating a modern alimentary canal [16].

Evidence of reproductive behavior is also not rare in the Jehol Biota (Fig. 5). For instance, *Monjurosuchus* (contrary to the cannibalism explanation by Wang *et al.* [19]) and *Yabeinosaurus* [21] specimens contain preserved babies in their bodies. Additionally, *Sinosauropteryx* with eggs [73] and early birds with follicles in the uterus [22] have been reported. The deposits have also produced choristodere [20] and pterosaur [17] embryos and the earliest bird embryo [18]. The eggs of frogs have also been

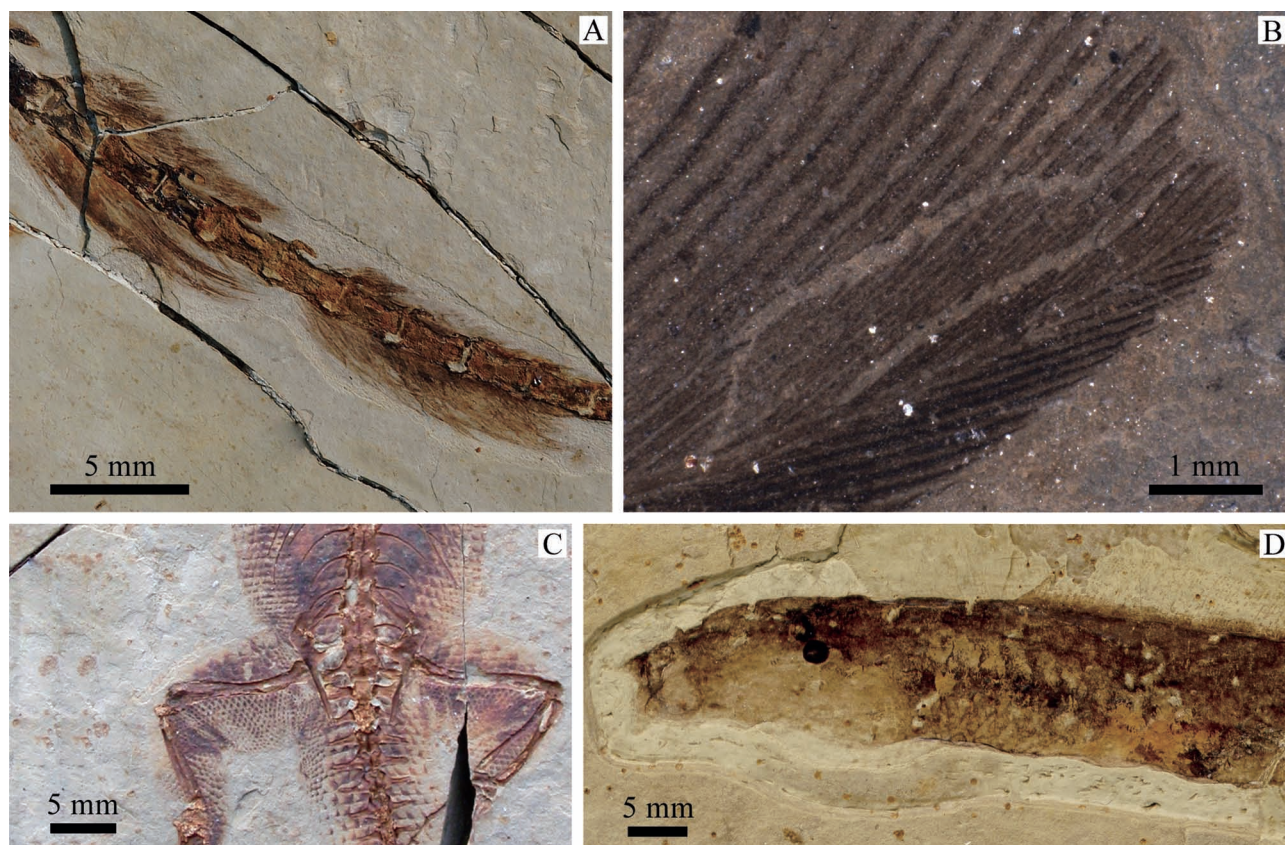


Figure 2. Exceptional preservation of soft tissues in Jehol vertebrates. (A) Tail feathers of a *Sinosauropteryx* (courtesy of X. Wang), (B) flight feather of a *Confuciusornis* (courtesy of X. Zheng), (C) skin of a lizard *Liushusaurus* (courtesy of Y. Wang), and (D) eyes, muscles, and gonads of a lamprey *Mesomyzon* (courtesy of J. Zhang).

discovered or reported in recent years (personal observation).

Leng and Yang [79] first discussed the role of pyritization in the preservation of the plant and insect fossils from the freshwater Jehol Biota, which was later confirmed by [80] as a common phenomenon in insects. Previous studies on the benthic fossil assemblages and framboid size in the sediments suggested that the paleolake system was governed by dysoxic bottom waters with spells of anoxia [31,39,42,79]. The active volcanic activity in the region of the Jehol Biota obviously contributed to a high abundance of sulfur compounds and iron minerals. It has also recently been suggested that both clay and pyrite played a key role in the soft-tissue preservation in the Jehol Biota [81].

One of the interesting taphonomic questions about the Jehol Biota is how and why many terrestrial animals (e.g. birds, dinosaurs, pterosaurs, and lizards) were transported to the Jehol lake and were preserved so well together with aquatic animals (abundant fish, chorisoderes) in the first (and most common) type of Jehol deposit, while the second type of deposit seems now to have been obviously caused by lahar or ash flow [1,53,71]. What geologi-

cal process and mechanism can explain such unusual preservation?

Volcanic eruptions have often been invoked to explain the mass mortality and exceptional preservation of the Jehol fossils [38,82]. However, Pan *et al.* [39] noted that, although aquatic invertebrates also suffered mass mortality, in the majority of cases individuals tend to occur on bedding planes in finely laminated sediments, suggesting that each mass mortality event was not related to volcanic activity. Thus, they proposed that oxygen-level fluctuations were probably responsible for the existence and distribution of the fossil communities, as well as the unfossiliferous layers.

It is notable that plant charcoal has often been observed in the Jehol sediments, although there has as yet been no comprehensive description or study. There appears to be some evidence of charring on terrestrial vertebrates, such as birds [65], while no charring has been observed on aquatic animals, which probably suggests that volcanic activity had indeed resulted in the mass mortality and rapid burial of terrestrial animals in the first type of Jehol fossil deposit. Recently, Jiang *et al.* [38] have further proposed that the events were

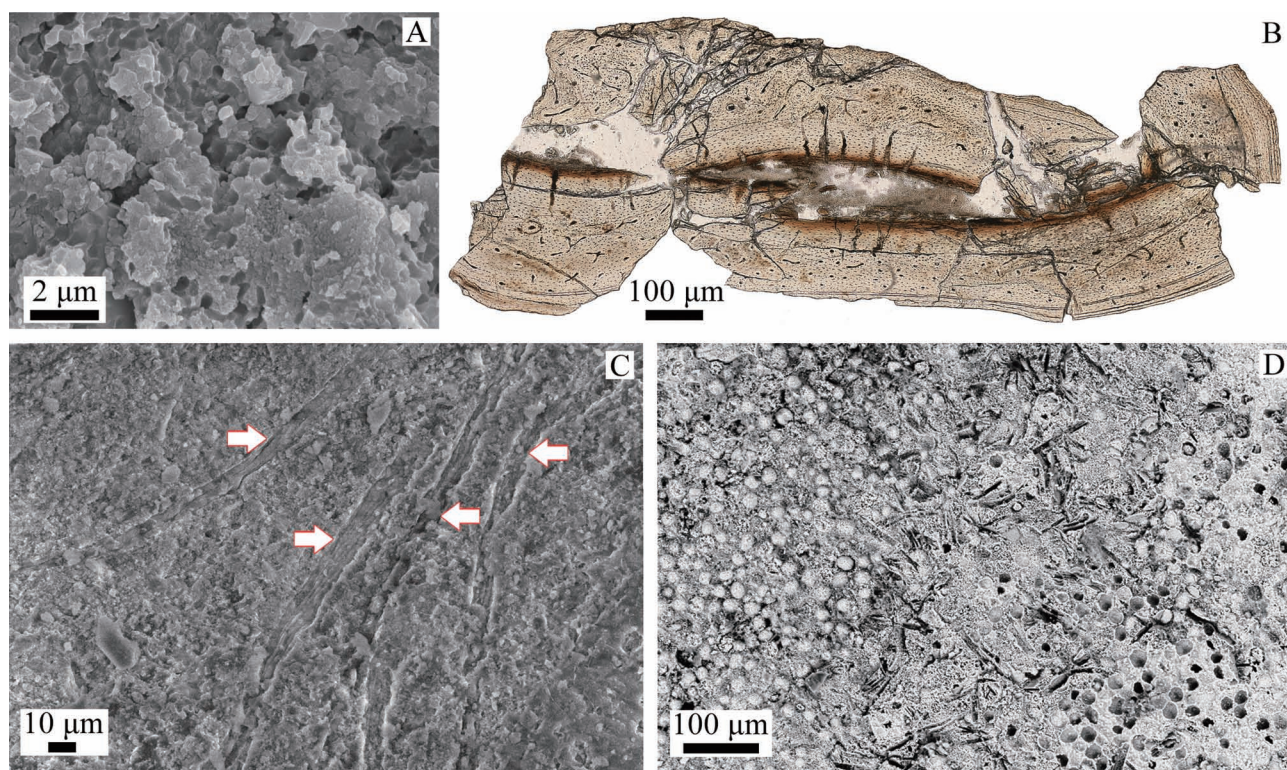


Figure 3. SEM photos of Jehol fossils and preservation. (A) Melanosomes of feathers of a *Sinosauropteryx*, (B) histology of the ulna of *Jeholornis*, (C) 'hairs' of an insect (courtesy of D. Huang), and (D) pyritization observed in a plant seed (courtesy of Y. Pan).

mainly caused by phreatomagmatic eruptions that were responsible for major casualties and for transporting most of the terrestrial vertebrates, such as lizards, birds, non-avian dinosaurs and mammals, into the lacustrine environment for burial. Their evidence for pyroclastic density currents (PDC) from phreatomagmatic eruptions includes a detailed analysis and comparison of the sedimentary features of the matrix in which the vertebrate fossils are directly embedded from several localities, the charring or carbonized bone surface of skeletons, as well as the postures of Jehol vertebrates such as *Confuciusornis* that are comparable to PDC victims, which resulted from postmortem shortening of tendons and muscles [38]. It is notable that Faux and Padian [83] explained the opisthotonic posture seen in many fossil amniotes as the consequence of 'death throes' (related to dysfunction of the central nervous system caused by hypoxia or poisoning) and not of postmortem processes. In other words, rapid burial of recently deceased carcasses is key to retaining an opisthotonic posture in articulated vertebrates (e.g. birds, dinosaurs, and pterosaurs).

Finally, it should be mentioned that compared with the study of the taphonomy of marine Lagerstätte such as the Burgess Shale, the taphonomy of the Jehol Lagerstätte is not yet well understood. It must also be noted that there are

various styles of preservation of fossils in the biota; therefore, it would be difficult to explain the Jehol taphonomy by a simple hypothesis concerning the death and transport of Jehol animals. Volcanic eruptions were most likely related to the exceptional preservation of the Jehol vertebrates; however, in addition to lahar deposits [1,71], whether pyroclastic flows or poisoning were more responsible for the mass mortalities of the majority of Jehol terrestrial vertebrates remains to be investigated. Many more questions remain to be answered than we can probably realize at this stage of the study of the Jehol Biota [2].

RECENT DISCOVERY AND PALEOBIODIVERSITY

Since the review by Zhou *et al.* [1] of the study of the Jehol Biota as part of the Lower Cretaceous terrestrial ecosystem, many new and exciting fossils have been added to the Jehol assemblages. This chapter will thus focus on those reported after 2003.

According to a recent study [4], the Jehol vertebrate assemblage contains at least 129 genera and 155 species. The most primitive known vertebrate from the Jehol Biota is *Mesomyzon*, the earliest representative of freshwater lampreys [66]. Seven

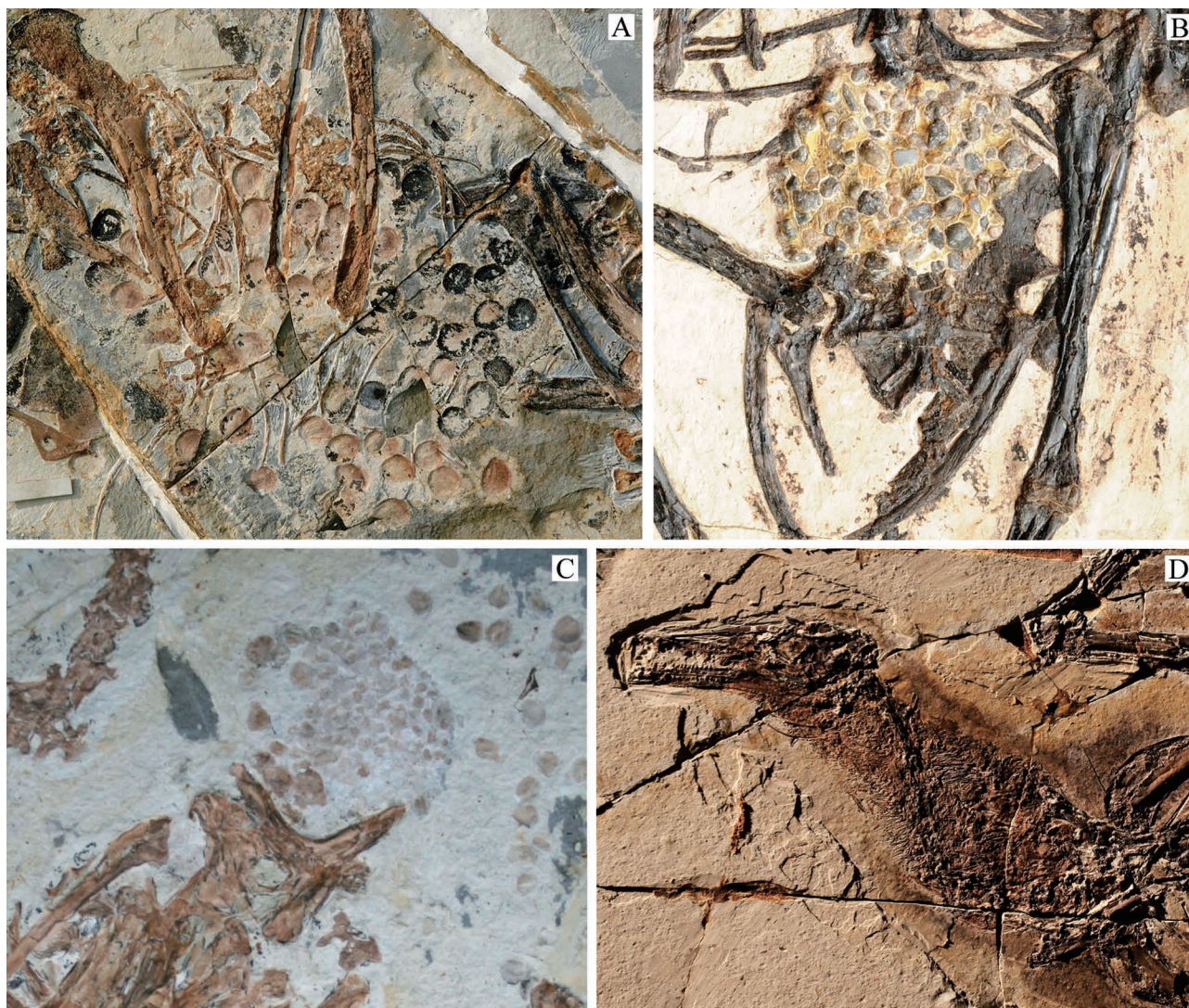


Figure 4. Stomach and crop contents of Jehol birds, indicating various dietary adaptations. (A) Seeds in the stomach of the holotype of *Jeholornis*, (B) gizzard stones of an *Archaeorhynchus*, (C) seeds in the crop of a *Sapeornis*, and (D) fish in the crop of a *Yanornis*.

genera and fourteen species of fish are currently known from the biota, and include fossil acipenseriforms, basal bowfins, and basal teleosts [3].

At least five genera and eight species of lissamphibians are known from the Jehol Biota [84,85], including four species of the basal crown-anuran *Liaobatrachus* [86], and salamanders such as *Liaoxitriton* and *Regalrpeton* [87,88].

Of the Jehol non-dinosaurian reptiles, the choristoderes represent the top predators of the Jehol lake ecosystem, with five genera and seven species currently known, e.g. *Ikechosaurus* [89], *Hyphalosaurius*, and *Monjurosuchus* [90]. Turtles from the Jehol are less diversified but often abundant, with only three genera and species reported, including *Ordosemys*, *Manchurochelys*, and *Liaochelys*, which are basal taxa of the crown group Cryptodira [91,92]. There are five genera and species of Jehol lizard, including

Yabeinosaurus and *Dalinghosaurus* [93,94], and the earliest known gliding lizard *Xianglong* [63], demonstrating adaptation to diversified niches.

Recent discoveries of Jehol pterosaurs have documented several new taxa, including the smallest arboreal pterosaur *Nemicolopterus crypticus* [95] and the toothed *Guidraco venator* [96]. The Jehol pterosaurs probably represent the most diverse pterosaur assemblages in the Mesozoic, currently containing at least 10 families and 21 genera and species, with also a great degree of differentiation in body size, skull morphology, and diet.

One of the most important recent discoveries of the Jehol dinosaurs is *Tianyulong*, a heterodontosaurid, representing the first ornithischian dinosaur with filamentous integumentary structures [97]. Another interesting discovery is the discovery of some large tyrannosauroid theropods [98,99]

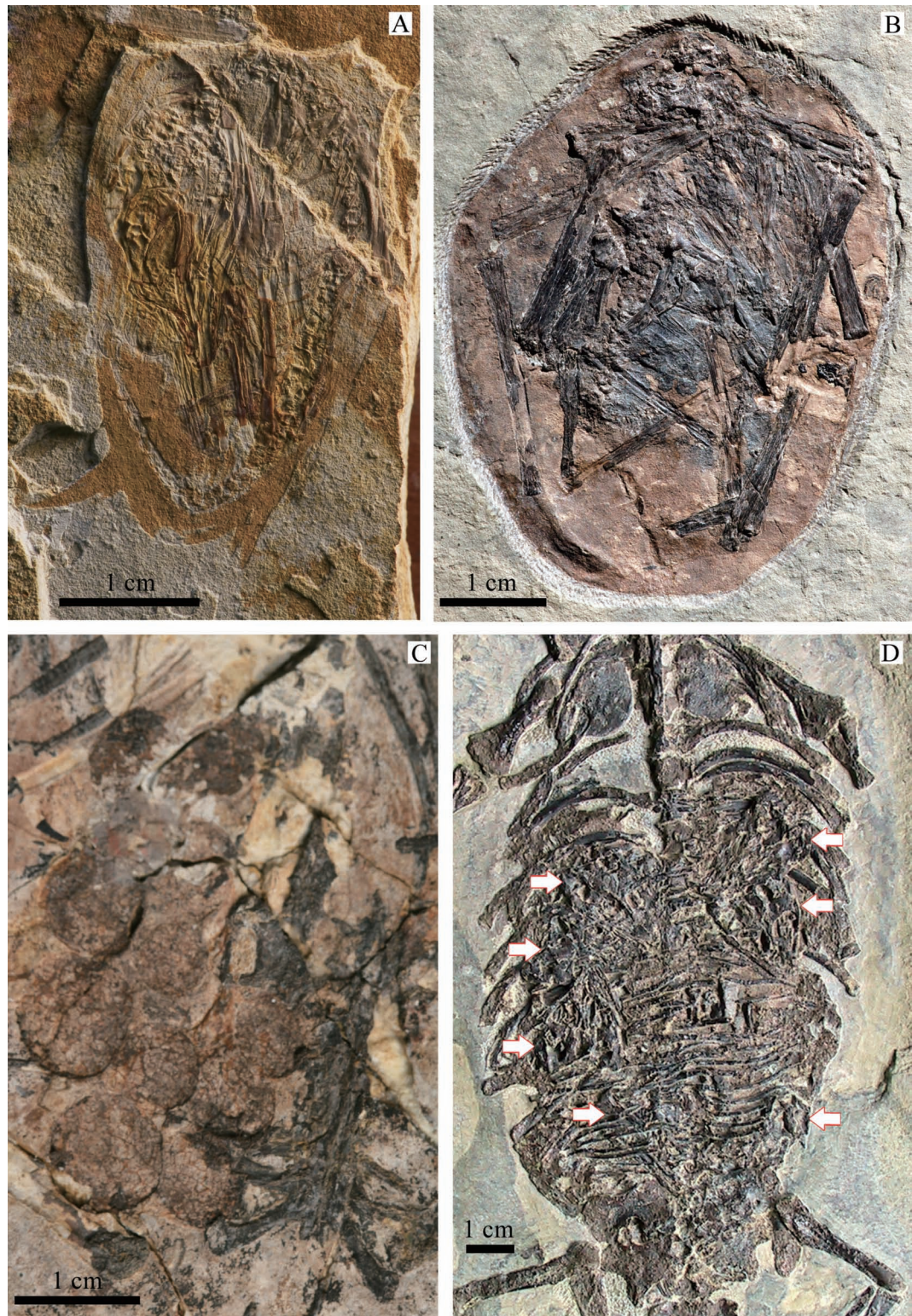


Figure 5. Exceptional preservation of reproductive behavior of Jehol vertebrates. (A) Embryo of an enantiornithine bird, (B) embryo of a pterodactyloid pterosaur, (C) ovary follicles of an enantiornithine bird, and (D) a pregnant choristodere.

including the basal tyrannosauroid, *Yutyrannus*, which is the largest known feathered dinosaur. The Jehol dinosaurs are obviously the most diversified reptilian group. They consist of at least 31 genera and 37 species, 22 genera and species of which belong to the theropods, representing nearly all major Cretaceous coelurosaurian theropod lineages. The Jehol dinosaurs also show a great degree of differentiation in locomotion, diet, ornamentation, and body size [69,100]. Furthermore, the appearance of a variety of feathers in the Jehol dinosaurs was probably also responsible for their great diversity.

Recent discoveries of Jehol birds include many new forms belonging to both enantiornithines and ornithurines, as well as basalmost birds such as the Confuciusornithidae [4,54,101]. Several lineages of enantiornithines, such as Longirostridae, Bohaiornithidae, and Pengornithidae, have been recognized [101–103], further confirming the differentiation of the enantiornithines. The recent discovery of *Eoconfuciusornis* as the earliest known confuciusornithid has extended the temporal range of this clade of avian lineage to at least 11 Myr [54]. The Jehol birds consist of at least 38 genera and 44 species, showing significant differentiation in morphology, size, flight, diet, locomotion, and habitat, and representing the first major radiation in avian evolutionary history. Enantiornithines and basalmost birds seem to be mostly arboreal, and ornithurines are mainly terrestrial forms.

The newly reported mammals from the Jehol include the largest known Mesozoic mammal *Repenomamus*, which could feed on baby dinosaurs [72], the eutriconodont *Yanoconodon* [104], and *Liaotherium* [105], which provides much new information on the evolution of the middle ear. Currently, the Jehol mammal assemblage contains 14 genera and 16 species referable to five major groups of Mesozoic mammals: Triconodonta, Multituberculata, Symmetrodonta, Metatheria, and Eutheria.

The diversity of the Jehol invertebrates has not been well studied. Zhang *et al.* [106] summarized the diversity of the insects, which include 150 species belonging to about 40 families and 11 orders in the early phase, about 500 species in about 100 families and 16 orders in the middle phase, and about 300 species belonging to about 80 families and 14 orders in the late phase. However, D. Ren (personal communication) estimated a total of only 467 species belonging to 327 genera, 143 families, and 15 orders of insects in the Jehol Biota. Considering the large number of new taxa reported in recent years, there is no doubt that giving a final estimate of Jehol insect diversity now would be premature. More information on some new insect discoveries will be provided in a later chapter.

Wu [107] provided an estimate of 31 genera and 51 species for the diversity of the Jehol Flora, which is dominated by Gymnospermae, including cycadophytes, ginkgophytes, conifers, and Gnetales. Since then, several new taxa have been reported, including the basal angiosperms *Archaeofructus* and *Sinocarpus* [108–112]. Pott *et al.* [112] described two fossil seed plants, *Baikalophyllum* and *Rehezamites*, with ‘cycadophyte’ foliage from the Yixian Formation. New information on the evolution of the Gnetales has been discovered. *Siphonospermum* was described as an Early Cretaceous relative of Gnetales [113], such as *Chengia* [114]. The report of a fleshy cone of *Ephedra* further confirmed the high diversity of Gnetales in the Jehol Flora [115].

EVOLUTIONARY IMPLICATIONS OF THE JEHOI BIOTA

Many of the recently discovered Jehol fossils have important implications for the study of the origin and evolution of various biological groups, but this chapter will focus on the vertebrate, insect, and plant fossils.

Vertebrate evolution

The Jehol vertebrate assemblage is undoubtedly the highlight of the Jehol Biota and contains the most significant information on the origin and early evolution of many groups of vertebrate lineages, e.g. dinosaurs, birds, pterosaurs, and mammals.

Study of the origin of birds, their flight, and feathers is probably one of the most debated and stimulating issues in paleontology over the past two decades. Thanks to the remarkable discoveries of many feathered dinosaurs from the Jehol Biota (and more recently also from the Jurassic Yanliao Biota, the feathered dinosaurs of which have solved the temporal paradox in the study of the bird origins), a great deal of significant progress has been made and can be briefly summarized as consisting of the following major aspects.

(i) Feathers or protofeathers have been confirmed to be a common feature of theropods, indicating that feathers are not a feature unique to birds [50,100]. (ii) Protofeathers were not restricted to saurischian dinosaurs, but are also found in ornithischians [97], and they probably first occurred at the beginning of dinosaur evolution. (iii) A comprehensive phylogenetic study including many complete articulated skeletons of dinosaurs has provided solid evidence in support of the dinosaurian origin of birds [116,117]. (iv) Many theropods have been confirmed to have possessed arboreal

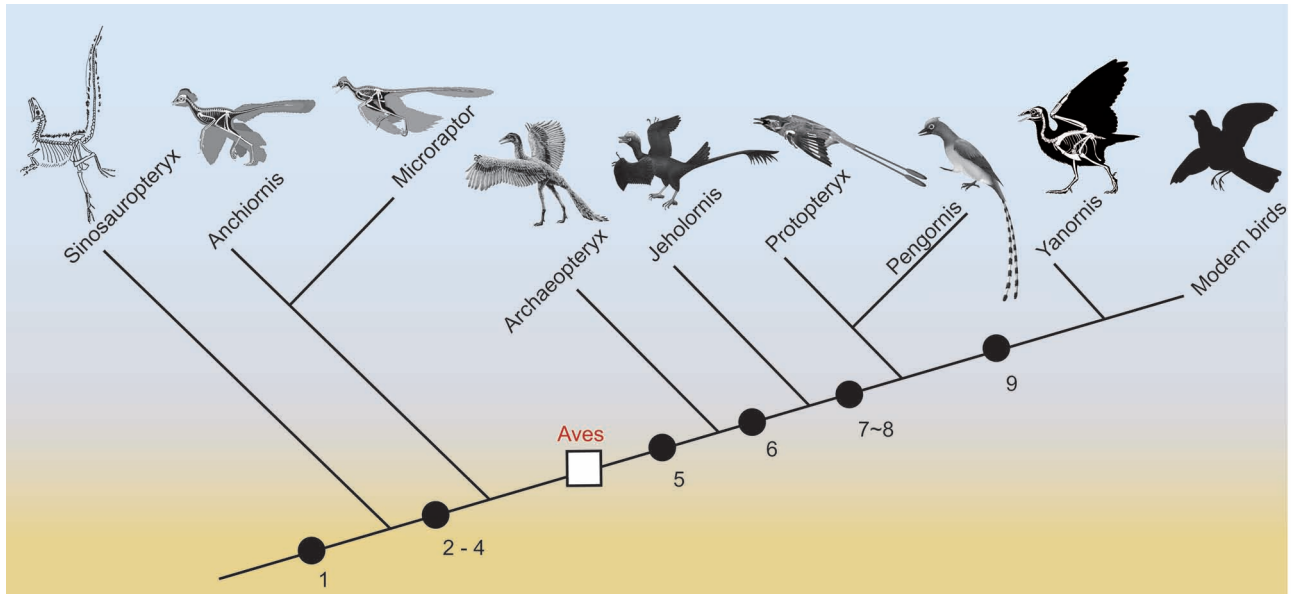


Figure 6. Cladogram outlining the transition from non-avian theropods to birds, with indication of major stages in feather evolution. (1) Unbranched feathers, (2) branched feathers, (3) asymmetric vanes, (4) four wings, (5) reduction of hind-wing, (6) proximal fan-shaped tail feathers, (7) alula, (8) fully pennaceous rachis-dominated tail feathers, and (9) fan-shaped distal tail feathers.

adaptations, lending some support to the arboreal hypothesis of bird flight [12,100]. (v) The discovery of four-winged dinosaurs and a four-winged bird (*Sapeornis*) indicates that the ancestor of birds experienced a four-winged stage during the origin of flight [118]. (vi) The discovery of melanosomes in feathered dinosaurs further confirms the homology between their integument and the feathers of modern birds and has for the first time provided direct fossil evidence of the color of dinosaurs (including birds) [5–7]. (vii) The dinosaur feathers reveal critical information not only on the origin and early evolution of feathers, but also on the ontogenetic development of protofeathers [68,119,120]. (viii) Some bird-like dinosaurs already possessed a sleeping posture similar to that of birds [69]. (ix) Although many Jehol theropods were proposed to be dangerous predators feeding on a variety of vertebrates [12,14,50,121], some groups of theropods had become specialized herbivores in the Early Cretaceous, such as the oviraptorosaurid *Incisivosaurus*, which has a pair of premaxillary teeth resembling rodent incisors and small, lanceolate cheek teeth with large wear facets previously unknown in theropods [122]. (x) The Jehol dinosaurs have provided some of the most detailed evidence for the discussion of character evolution during the transition from dinosaurs to birds (Fig. 6).

The Jehol birds represent the second most important stage in early avian evolution. Like the Jehol dinosaurs, the evolutionary significance of all these early bird fossils would deserve a whole chapter to

discuss; however, only a brief summary of their major significance is listed here.

(i) *Jeholornis* has a long skeletal tail containing more caudal vertebrae than that of *Archaeopteryx* and a partially reversed hallux, and thus represents the second most primitive bird in early avian evolution [8]. (ii) The Jehol Biota preserves the basalmost enantiornithine *Propteryx* [123] and other basal enantiornithines such as *Pengornis* [103, 124,125], suggesting an origin center of Enantiornithes in northeastern China. (iii) The Jehol Biota also preserves some of the basalmost ornithurines such as *Archaeorhynchus* [77,78] and hongshanornithids [126], also indicating a northeastern China origin. (iv) Confuciusornithids are the oldest known birds with a horny beak and also represent an avian lineage with a temporal range of at least 11 Myr; the loss of teeth has probably occurred several times in early bird evolution [10]. (v) The Jehol birds record the earliest known evidence of specialized seed-eating birds (e.g. *Jeholornis*, *Sapeornis*) and piscivorous birds (e.g. *Yanornis*). Additionally, there is preserved evidence of a crop in several birds (e.g. *Sapeornis*, *Hongshanornis*, *Yanornis*) indicating the presence of a modern digestive system in Early Cretaceous birds [15,16]. (vi) A long pygostyle first evolved in *Sapeornis*, but a short pygostyle similar to that of modern birds only appeared in ornithurines. (vii) The Jehol ornithurines appear to have mainly occupied a terrestrial habitat, in contrast to enantiornithines and more basal birds, indicating a remarkable ecological differentiation in early bird

evolution. (viii) The discovery of an enantiornithine embryo showed that early birds had a precocial embryological developmental mode [18] much like dinosaurs and pterosaurs [17]. (ix) The Jehol birds provide a large amount of information on the evolution of feathers in early birds, for instance, the alula seems to have appeared in the basalmost enantiornithine but was absent in more basal birds. Fan-shaped tail feathers first occurred in *Jeholornis* and became a common feature in ornithurines, but were lost in the majority of more basal forms, indicating complex evolution of this derived bird feature [127]. (x) The sternum is absent in *Sapeornis*, as in *Archaeopteryx* and *Anchiornis*, but is present in all other known birds. The Jehol birds display a great diversity of sternum morphology, and a sternal keel is present only in ornithurines. It is most notable that enantiornithines seem to have a unique sternal development different from that of other birds and dinosaurs, based on a recent study of a number of juvenile specimens [128].

The mammals from the Jehol Biota are most notable for their nearly complete articulated skeletons and contain some of the most significant information on the early radiation and differentiation of mammals in the Mesozoic.

One of the most interesting discoveries is the largest known Mesozoic mammal, which may indicate that early mammals were no longer living in the shadow of dinosaurs by the Early Cretaceous, and that at least some taxa were probably not limited to nocturnal life. One nearly three-dimensionally preserved skeleton of *Repenomamus* preserves the remains of a baby dinosaur *Psittacosaurus*, providing the first direct evidence that early mammals ate dinosaurs [72].

The ossified Meckel's cartilage in mammals is undoubtedly one of the most significant discoveries in the study of the Jehol mammals concerning the origin of definitive mammalian middle ears [129]. The recently reported exceptionally preserved eutriconodont *Liaotherium* [105] preserves much key information about the transference of post-dentary jaw elements to the cranium of mammals as auditory ossicles, including the first unambiguous ectotympanic (angular), malleus (articular and prearticular), and incus (quadrate). Their study also showed that in *Liaotherium* the ectotympanic and malleus had lost their direct contact with the dentary bone, but still connected the ossified Meckel's cartilage.

The pterosaur assemblage of the Jehol Biota is also much better known as the result of many new discoveries and studies. Among these, the discovery of the first pterosaur egg clearly showed that they had a precocial embryological mode as in dinosaurs

and early birds [17], and their eggs were most likely soft-shelled or with a very thin external hard shell [130,131]. The Jehol pterosaur assemblage contains many Cretaceous pterodactylid groups, such as Anhangueridae, Ctenochasmatidae, Ornithocheiridae, Gallodactylidae, Pteranodontidae, Tapejaridae, and Istiodactylidae [95,96,132–134], showing a great differentiation of body size, jaw morphology, and dietary adaptations ranging from piscivory and insectivory to filter-feeding. Pterosaurs seem to have been the dominant vertebrates in the Jehol sky, and in comparison, the Jehol birds were generally relatively small, with their large-sized forms mainly adapted to herbivorous life.

The Jehol pterosaurs also have paleogeographic implications. Many of the Jehol pterosaurs are closely related to cosmopolitan groups reported from South America and Europe, suggesting that there were few paleogeographic barriers to their global distribution. Furthermore, northeastern China probably represents an origin and early diversification center for the Cretaceous pterosaur radiation [96,132,133], a conclusion similar to that drawn from the study of Jehol birds and other fossils [1,53].

Other vertebrates from the Jehol Biota include lampreys, fish, amphibians, turtles [91,92,135], lizards, and choristoderes, which also have great evolutionary significance (for more discussion of these taxa, see Zhou *et al.* [4]).

Insect evolution

Probably more papers have been published on insects than on any other Jehol fossil group. The exceptional preservation and endless discoveries of new species have not only greatly increased the diversity of the Jehol insect assemblage, but have also added much new information on the origin and evolution of a variety of insect lineages. Although most of the Jehol insects can be assigned to extant families [106], others are referable to extinct families; thus, together with studies on the Jurassic Yanliao Biota, the first appearances of many insect families or higher ranking taxa have been pushed back to the Early Cretaceous or Middle–Late Jurassic.

One of the most exciting aspects of the study of the Jehol insects is the fossil evidence for co-evolution of insects and plants. Since the first report on fossil evidence of pollinating insects (short-horned flies) from the Jehol Biota [136], there have been more such examples discovered [23], confirming that pollinating insects probably played a decisive role in the origin and early evolution of the angiosperms.

Further, major progress made on the Jehol insects has been on the study of the coevolution of insects and vertebrates. Huang *et al.* [24,25] and Gao *et al.* [26,27] reported evidence for ancient fleas from the Early Cretaceous Jehol Biota and the Jurassic Yanliao Biota, respectively, suggesting the presence of diverse ectoparasitic insects in the Mesozoic. As these fleas have stout and elongated sucking siphons for piercing the hides of their hosts, it was suggested that they were probably rooted among the pollinating 'long siphonate' scorpionflies of the Mesozoic. A recent study that used geochemical methods to determine diet and combined both morphological and taphonomic data reported a new family of true bugs, and argued that they represent the earliest evidence of blood feeding among true bugs that may have fed on the blood of mammals, birds, and feathered dinosaurs [28]. Furthermore, despite the lack of direct evidence, the potential hosts for these fleas could have been early mammals, hairy or feathered dinosaurs, or pterosaurs [137].

Plant evolution

Although the Jehol Flora is best known for producing some of the earliest known flowering plants including basal eudicots [51,108–111], some progress has been made on the early evolution of *Ephedra* and ephedroid fossils, such as the report of the earliest fleshy cone of *Ephedra* from the Jehol [115] and *Chengia*, a newly reported ephedroid that represents a part of a leafy shooting system with reproductive organs attached, providing a missing link between archetypal fertile organs in the crown lineage of the Gnetales and compound female cones of the extant Ephedraceae [114]. These findings seem to have demonstrated the presence of a considerable diversity of the basal family Ephedraceae in the Early Cretaceous and show that northeast China and adjacent areas might represent either the center of origination or one of the centers for early diversification of the family [114].

Pott *et al.* [112] recently also reviewed two seed plants, *Baikalophyllum lobatum* and *Reheza-mites anisolobus*, with 'cycadophyte' foliage from the Jehol Biota and other areas in Eastern Asia based on some new fossils. They concluded that the leaf morphologies and venation patterns of these two genera generally resemble those of leaves traditionally assigned to extinct members of Cycadales, Bennetitales, and Pentoxylales, but did not assign these leaves to any specific group.

Leefructus was recently reported by Sun *et al.* [138] as a new eudicot, represented by a nearly per-

fectly preserved specimen. This suggests that basal eudicots were already present and diverse by the latest Barremian and earliest Aptian; however, caution should be taken when discussing this new plant before the hypothesis of the authenticity of the specimen is completely clarified.

GEOLOGICAL, PALEOGEOGRAPHIC, AND PALEOENVIRONMENTAL BACKGROUND

The Early Cretaceous was among the most tectonically active times in Earth's history, with enhanced sea-floor spreading accompanied by the breakup of Pangea, the presence of a large igneous province, and frequent volcanic activity [139–142]. While Mesozoic igneous rocks are widespread throughout eastern China, the Early Cretaceous was a particularly significant period of igneous activity (131 to 117 Ma, nearly corresponding to the duration of the Jehol Biota). It was proposed that this giant igneous event in the Early Cretaceous was related to coeval lithospheric delamination in eastern China, which resulted from Kula–Pacific Plate subduction, possibly aided by major superplume activity associated with global-scale mantle upwelling [29]. Northeast China also experienced severe destruction of the North China Craton in the Early Cretaceous [30]. Against such a tectonic background, extensive fault basins and freshwater lakes were present in northeast China in the Early Cretaceous, in which the sediments preserving the Jehol Biota were deposited. A recent study by Zhang and Sha [41] on the fine sedimentary laminations of the Yixian Formation in the Sihetun locality in Liaoning concluded that the sedimentation rate for the majority of the mudstones and shales was 0.2–0.7 mm/yr. Conversely, Wu *et al.* [143] studied the same section and concluded that the average depositional rate was ~1.70 cm/kyr, an estimate similar to that of Zhu *et al.* [59], and further suggested that climate fluctuations might have been controlled by orbital forcing during the Early Cretaceous.

Many of the Jehol fossils (e.g. *Lycoptera*, *Monjuro-suchus*, and *Psittacosaurus*) in northeast China have also been found in many other areas of East and Central Asia, including northern China, the Korean Peninsula, Japan, Mongolia, Kazakhstan, and Siberia [144–147].

Paleogeographically, East Asia has been argued to have been isolated from the rest of Laurasia from the Middle Jurassic until the early part of the Cretaceous [1,148,149], which resulted in some endemism, or a 'refugium for relics', in the Jehol Biota [150]. In the Early Cretaceous, there were three large continental blocks (masses): Laurasia (North

America–Eurasia), Western Gondwana, and Eastern Gondwana [151,152]. The freshwater connection of Asia and Europe existed no later than late Hauterivian, as the non-marine Cretaceous index trigonoioid bivalves have been recorded from the late Hauterivian/Barremian Wessex Formation of the Wealden Group in the Isle of Wight, southern England [33].

The disappearance of the paleogeographic barrier that existed between Asia and Europe was probably partly caused by regression of the Turgai Sea, which resulted in the formation of a Europe–Asia ‘land bridge’ during the Aptian–Albian [153]. The final formation of the Eurasian Continent in the Early Cretaceous as well as possible links between this and other continents made more frequent and free faunal and floral exchanges possible. This is demonstrated by the recognition of many cosmopolitan taxa in the Jehol Biota, particularly vertebrates such as dinosaurs, birds, pterosaurs, mammals, and amphibians [1,53,96]. For instance, some pterosaurs are now well known from both China and Brazil, with many taxa distributed in both regions, indicating a close phylogenetic relationship. The recently reported *Guidraco* was found to have a sister-group relationship with the Brazilian *Ludocactylus*, suggesting significant faunal interchange between continents in this period. It has been further suggested that at least some Early Cretaceous pterosaur clades, such as the Tapejaridae and the Anhangueridae, might have originated in Asia [96]. The widespread faunal exchanges might reflect a close paleogeographic link between the Eurasia–North America continental mass and South America.

Many of the most basal representatives of various dinosaurian, mammalian, lizard, pterosaur, bird, and plant groups have been reported from the Jehol deposits, which lends support to the hypothesis that the Jehol area represents an origin and diversification center for many biological groups [1,96,114,132,154].

The paleoenvironments of the Cretaceous have been studied more extensively from marine deposits than from terrestrial deposits. Oceanic anoxic events (OAEs) have been regarded as geologically brief intervals reflecting a serious major perturbation in the global carbon cycle [155, 156]. The Aptian Oceanic Anoxic Event 1a (OAE1a, ca. 120 Ma) corresponds approximately to the age of the Jehol Biota. Wortman *et al.* [157] concluded that the large Aptian carbon isotope anomaly records the response of the biosphere to widespread volcanic activity and probable resulting changes in atmospheric paleo-CO₂ levels. Millán *et al.* [155] suggested that a condensed interval rich in ammonites (the Selli level) corresponding with the beginning of OAE1a is observed and linked with a major transgression with

high biodiversity in the Basque–Cantabrian Basin (Aralar, northern Spain). The terrestrial response to the OAEs was recently studied by Hu *et al.* [158] using the fluctuation of organic carbon isotopes of the Lower Cretaceous deposits of coastal southeastern China.

It is generally accepted that the mid-Cretaceous was an extremely warm period (Aptian–Turonian: 125–89 Ma) and had higher atmospheric CO₂ levels [159–161]. Wang *et al.* [156] recently concluded that CO₂ concentrations were at a relatively high level throughout the Cretaceous, but at lower levels in the early Cretaceous, higher in the mid-Cretaceous, and showed a gentle decline during the late Cretaceous. They further pointed out that these trends were punctuated at several intervals by rapid paleo-CO₂ changes, often associated with critical events such as OAEs and the Cretaceous–Tertiary boundary. They also argued that the relatively low paleo-CO₂ levels (even in the Aptian–Albian interval) and the reduction in paleo-CO₂ after OAE1a are consistent with compilations of oxygen isotope data, which indicate a relatively cool mid-Cretaceous.

The paleoclimate of the Early Cretaceous in the Jehol region has not been substantially studied, although globally the climate was generally warm and interrupted by cold intervals [139, 162]. A recent study based on the oxygen isotope composition of vertebrate apatite has proposed that globally cold climates existed during the deposition of the Jehol Biota, with mean air temperatures of about $12 \pm 3^\circ\text{C}$ in Liaoning Province [35]. Fossil evidence consistent with this conclusion includes the occurrence of the temperate to cool temperate fossil wood genus *Xenoxylon* in northeast China and the absence of crocodylians. Amiot *et al.* [35] also argued that the integument of various Jehol vertebrates might have been an insulation advantage, helping them to maintain sustained activity during cold winters when other reptiles hibernated. This idea was further supported by the discovery of a giant feathered tyrannosauroid, *Yutyrannus* [99]. However, it remains to be investigated whether the temperature was in general cold or warm and/or how many intervals of cold temperature occurred during the time of the Jehol Biota.

Finally, it has been proposed that during the late Early Cretaceous (Barremian–Albian), the long-term existence of a marine embayment in eastern Heilongjiang, successive marine transgressions, and flooding along the Tan-Lu fault system in northeast China was possibly responsible for a humid climate across the whole of northeast China. These transgression and climatic conditions produced a number of extensive and long-lasting swamps and marsh

lands in both paralic and limnic environments [32]. However, there is as yet no evidence showing that the Jehol Biota lived near the sea.

PROBLEMS AND FUTURE RESEARCH DIRECTIONS

The discovery of new fossils from the Jehol Biota has proceeded at an unprecedented rate for a variety of reasons. Many new taxa have been reported, yet most of them lack a detailed description and are yet to be placed in a satisfactory systematic position. Additionally, as a result of competition between research groups from different institutions on fossils from the Jehol Biota, many synonyms have been created. Many systematic revisions based on solid and detailed morphological and comparative work will be needed in the future, after the desire for naming new species has become less intense.

Although remarkable progress has been made on the age and correlation of the Jehol fossil-bearing deposits in various basins of western Liaoning, northern Hebei, and southern Inner Mongolia, higher resolution chronostratigraphy using new technology and more biostratigraphic correlation may help to elucidate the origin and dispersal process of the biota and the macroevolutionary pattern of various biological groups. Furthermore, a more extensive comparison of the Jehol Biota with those from neighboring areas in East and Central Asia (see Sha *et al.* [34] for a discussion on the non-marine and marine correlation of the Early Cretaceous deposits in northeast China, southeast Korea, and southwest Japan and their paleogeographic implications) remains an important issue to be considered, as it is important for the faunal migrations and exchanges among this region and beyond. For instance, with the evidence of feathered dinosaurs from both the Middle–Late Jurassic and Early Cretaceous of northeast China, plus the occurrence of abundant birds in the Early Cretaceous and the earliest known birds from Germany, potentially it would be interesting to combine the process of the origin of birds with the paleogeographic changes, e.g. how exactly East Asia was connected to Europe during the transition from the Middle Jurassic to the Early Cretaceous.

Many of the Jehol fossils have not been recovered from younger late Early Cretaceous deposits in northeast China. Was there a major biological extinction after 120 Ma, or does this observation simply reflect a preservational bias?

Although the general geological background of the Jehol Biota is known, there is more to explore. Did global tectonics or regional geology have a larger contribution to the paleoenvironment of the Jehol

Biota? Was it generally warm or cold during the time of the Jehol biota? Further work is necessary to propose a possible link between the cold intervals and the remarkable diversity of the Jehol Biota in the Early Cretaceous of northeast China.

Many more questions remain to be answered as to how exactly tectonic activity contributed to the success of the Jehol ecosystem or how the paleoenvironment in the Jehol controlled the preservation of the Jehol fossils. In other words, despite some progress having been made in recent years, the taphonomy of the Jehol Lagerstätte is not yet well understood. More research is needed to determine the preservation of the microstructures of soft tissues of the Jehol fossils. Is there any evidence for fossilized microbes in the biota? Although volcanic activity has often been used as an explanation for the mortality and preservation of many terrestrial vertebrates, little is known about the distribution of charcoal in the biota, considering the fact that the Early Cretaceous has been proposed to have been a period of high oxygen and fire [163,164].

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