



Study on the Jehol Biota: Recent advances and future prospects

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Abstract The Jehol Biota is an Early Cretaceous terrestrial fossil assemblage of paramount significance, and its core distribution areas are western Liaoning, northern Hebei, and southeastern Inner Mongolia. Despite with a research history of more than 150 years, it started yielding important fossils until early 1990s, which include feathered dinosaurs, early birds, early mammals, flower-visiting insects, and early angiosperms. These discoveries have implications for understanding the origins and early evolution of several major organismal groups, as well as the origin and initial formation of modern terrestrial ecosystem. This review presents a brief introduction of the major discoveries, research history, and current understanding of this biota, and also provides future prospects for studying the Jehol Biota.

Keywords Jehol Biota, Early Cretaceous, Terrestrial ecosystem, Origin, Evolution

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1. Introduction

The Jehol Biota existed in the middle Early Cretaceous, with its known fossil localities mainly distributed in western Liaoning, northern Hebei and southeastern Inner Mongolia of China (Figure 1), yielding a large amount of well-preserved fossils of various terrestrial organisms. It represents the best-preserved terrestrial fossil assemblage from the Cretaceous, opening a window into the Mesozoic terrestrial ecosystem (Chang et al., 2003; Ji et al., 2004a; Zhou et al., 2017). The research of this biota bears great significance on our understanding of the origin and early evolution of some major groups, e.g., eutherian and metatherian mammals, birds, many subgroups of insects, and angiosperms (Chang et al., 2003; Zhou and Hilton, 2003; Ji et al., 2004a; Zhou et al., 2017). Despite with a long research history, until early 1990s has it gradually become a hotspot in paleontology and evolutionary biology. The past three decades have witnessed

numerous new discoveries and significant advances in our understanding of the Jehol Biota. This paper will briefly review the discovery and research history of the Jehol Biota and discuss the present research status and provide a forecast to its future study.

2. The discovery and early researches of the Jehol Biota

American paleontologist AW Grabau first proposed the “Jehol Series” in 1923 to refer to a set of lacustrine deposits exposed near the Lingyuan County of the Jehol Province (now Lingyuan City of Liaoning Province) that had yielded the fish *Lycoptera*, and he regarded the strata as Lower Cretaceous (Grabau, 1923). In 1928, he used “Jehol Fauna” for the animal fossil assemblage preserved in the Jehol Series. The Chinese paleontologist Gu Zhiwei proposed the terms “Jehol Group” and “Jehol Biota” in 1962, with the former derived from Jehol Series, covering not only the fish-

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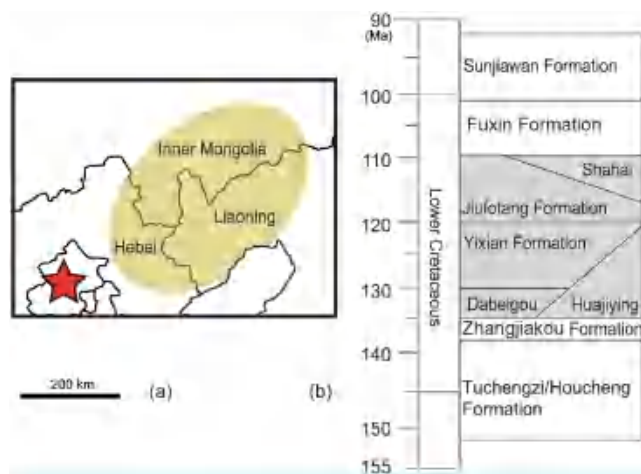


Figure 1 The Jehol Biota *sensu stricto* geographical and stratigraphic distribution. (a) Geographical distribution, read star for Beijing and yellow color for the Jehol Biota *sensu stricto*. (b) Stratigraphic distribution, gray color for stratigraphic distribution of the Jehol Biota *sensu stricto*. Note that there are still debates on the correlation and division of some lithostratigraphic units such as Huajiying and Yixian formations and Shahai and Jiufotang formations.

bearing lacustrine deposits but also the contemporaneous volcanic rocks, and the latter representing a fossil assemblage of both animals and plants from the Jehol Group (Gu, 1962). But different from Grabau's opinion, Gu regarded the strata as from Middle to Upper Jurassic.

The earliest studies considered *Bairdestheria*, *Ephemeropsis* and *Lycoptera* (Grabau, 1928; Gu, 1962) as representative members of the Jehol Biota, but the fossils identified as *Bairdestheria* were later re-identified as *Eosestheria* (Zhang et al., 1976). Consequently, the representative members of the biota were revised to

Eosestheria -*Ephemeropsis*-*Lycoptera* (Figure 2), which was a mainstream view in the early research of the biota (Chen, 1988).

Among the above three representative elements of the Jehol Biota, *Eosestheria* was a crustacean arthropod named in 1976 (Zhang et al., 1976), but the history of its relevant researches is more than 150 years (Jones, 1862; Zhang et al., 1976). *Ephemeropsis* was an aquatic insect belonging to the Ephemeroptera and it was first discovered from the Lower Cretaceous of Trans-Baikal region, Russia and the Republic of Mongolia (Eichwald, 1864) and then from the Jehol Biota as early as 1928 (Bing, 1928). The first fossils of the fish *Lycoptera* were discovered in 1860s, named in 1880 as *Prolebias davidi* (Sauvage, 1880), and revised in 1901 to *Lycoptera davidi* (Woodward, 1901).

Beside the above representative elements, other important early discoveries of the biota include three reptiles named by Japanese scholars, i.e., the choristodere *Monjurosuchus splendens* (Endo, 1940), the lizard *Yabeinosaurus tenuis* (Endo and Shikama, 1942), and the turtle *Manchurochelys manchoukuoensis* (Endo and Shikama, 1942). After 1949, more Jehol vertebrate fossils have been discovered, including the acipenseriform fish *Peipiaosteus pani* (Liu and Zhou, 1965) and the ceratopsian dinosaur *Psittacosaurus meileyingensis* (Sereno et al., 1988).

The three typical elements and some other fossils of the Jehol Biota had a distribution not only in western Liaoning, but also in northern Hebei and southeastern Inner Mongolia, and even beyond. Some of the elements have been found in temporally earlier deposits (Chen, 1988). Therefore, some studies have employed the Jehol Biota *sensu lato* to refer to a geographically larger biota, i.e., covering northern China,



Figure 2 Previously considered representative species of the Jehol Biota: *Lycoptera* (a), *Ephemeropsis* (b) and *Eosestheria* (c). Without scale. Note that the supposed *Ephemeropsis* in the Jehol Biota is now considered to be *Epicharmeropsis* (Huang and Ren 2008).

Korean Peninsula, Japan, Mongolia, Kazakhstan and Siberia (Chang et al., 2003; Zhou and Hilton, 2003). Some studies also divided the biota into three evolutionary phases: the first phase is represented by fossils from the Dabeigou Formation and equivalents of northeastern China and part of Siberia; the second phase witnessed the gradual extension of the biota to the Yixian Formation and equivalents; in the last phase, the Jehol Biota extended to northwestern China (Xinjiang) and coastal regions in the southeast of China, as well as to Korean Peninsula and southwestern Japan, being represented by fossils from the Jiufotang Formation and equivalents.

Although some consensuses were reached on several aspects of the Jehol Biota research, others were still in debate. For example, some work regarded the age of the biota as Late Jurassic (Zhang et al., 1976; Chen, 1988), and some others, in support of Grabau's view, considered the biota to be an Early Cretaceous terrestrial biota (Hao et al., 1982). In general, early studies made few important discoveries but had hot debates on the geological age of the biota.

3. Research bloom of the Jehol Biota

Studies of the Jehol Biota have been explosive ever since 1990s, initiated by the discoveries of bird fossils. The enantiornithines *Cathayornis yandica* and *Sinornis santensis* are the first birds uncovered from the Jehol Biota (Sereno and Rao, 1992; Zhou et al., 1992), along with *Confuciusornis sanctus* reported later (Hou et al., 1995a, b), which received great attention across the world. In addition, key vertebrate and plant fossils have also been found from this biota in tandem such as the early mammal *Zhangheotherium quinquecupidens* (Li et al., 1995; Hu et al., 1997), the first feathered dinosaur *Sinosauropteryx prima* (Ji and Ji, 1996; Chen et al., 1998), and the flowering plant *Archaeofructus liaoningensis* (Sun et al., 1998). These fossils provide unprecedented information regarding the origin and early evolution of certain groups of vertebrates and plants, making the Jehol Biota a research focus in paleontology (Chang et al., 2003; Zhou and Hilton, 2003; Ji et al., 2004a). Apart from great progress made in the studies of vertebrate and plant evolution, significant advance has also been made in geochronology and taphonomy of the Jehol Biota (Swisher et al., 1999, 2002; Wang et al., 1999; Ji et al., 2004a; Zhou, 2006; Jiang and Sha, 2007).

The bird fossils of Jehol Biota form arguably the most important Mesozoic bird assemblage, which includes species that record different stages in early bird evolution, including *Jeholornis*, *Confuciusornis*, *Protopteryx*, and *Yixianornis* (Zhou, 2004; Zhou and Zhang, 2006a). Similar to *Archaeopteryx*, *Jeholornis* had a long bony tail, together with the former representing an early phase in bird evolution (Zhou and Zhang, 2002). In contrast, *Confuciusornis* had a tooth-

less, beaked jaw and a pygostyle as in modern birds, although retaining the primitive diapsid skull (Hou et al., 1995a, 1999). *Protopteryx* and *Yixianornis* are the early members of the two dominating clades of Mesozoic birds, the Enantiornithes and Euornithes, respectively, which provide important data pertaining to the evolution of feathers and modern birds' osteological characteristics (Zhang and Zhou, 2000, 2001).

Needless to say, dinosaur fossils preserving feathers are the most attractive ones of the Jehol Biota, including *Sinosauropteryx*, *Beipiaosaurus*, *Caudipteryx*, *Microraptor* and some other species (Norell and Xu, 2005; Xu and Norell, 2006). The compsognathid theropod *Sinosauropteryx* is the first known dinosaur that bears feathers (Ji and Ji, 1996; Chen et al., 1998). The discovery of the feathered therizinosauroid *Beipiaosaurus* indicates that primitive feathers were widely distributed among theropods (Xu et al., 1999a); the oviraptorosaurian theropod *Caudipteryx* had pennaceous flight feathers (Ji et al., 1998); the dromaeosaurid theropod *Microraptor* had asymmetrical flight feathers in both fore- and hindlimbs (Xu et al., 2000), forming a four-winged condition probably having played a key role in bird flight origins (Xu et al., 2003). In addition, many other important dinosaurs have been found in the Jehol Biota (Xu and Norell, 2006), e.g., *Incisivosaurus*, *Dilong*, and *Liaoceratops*. The oviraptorosaurian *Incisivosaurus* demonstrates that some theropods were herbivorous and that oviraptorosaurians independently evolved a few bird characteristics (Xu et al., 2002a); the discovery of *Dilong* for the first time directly shows the presence of feathers in tyrannosauroids (Xu et al., 2004); the ceratopsian ornithischian *Liaoceratops* demonstrates the mosaic evolution in early history of the group (Xu et al., 2002b).

The Jehol mammals are represented by *Zhangheotherium*, *Repenomamus*, *Eomaia*, *Sinodelphys* and several other species. The symmetrodont *Zhangheotherium* is of importance for the reconstruction of mammal phylogeny, and in particular demonstrates that early mammals have yet to evolved the derived mammalian middle ear (Hu et al., 1997); the triconodont *Repenomamus* is probably the largest known Mesozoic mammal, demonstrating that some mammals could be higher in the food chain of the Mesozoic ecosystem (Hu et al., 2005); the eutherian *Eomaia* displays morphologies suggesting arboreal habit (Ji et al., 2002); *Sinodelphys* is the oldest known metatherian, together with other Mesozoic therians such as *Eomaia*, shedding new lights on the therian ecological diversity in Early Cretaceous (Luo et al., 2003), though a recent study argued that *Sinodelphys* should be assigned to the Eutheria (Bi et al., 2018).

The most important discoveries of Jehol plant fossils are the angiosperms *Archaeofructus* and *Hyracantha* (Sun et al., 1998, 2002; Leng and Friis, 2003; Dilcher et al., 2007). *Archaeofructus* is an aquatic herbaceous plant, which was

considered to represent the earliest stage in angiosperm evolution by some studies (Sun et al., 1998, 2002), but was argued to be a specialized early angiosperm by others (Friis et al., 2003). Other important plant fossils include a ginkgo species that fills the morphological gap between the Jurassic and Cenozoic ginkgoes, suggesting that the female reproductive organ had changed little during the 120-million-year-long evolution (Zhou and Zheng, 2003).

In addition to aforementioned dinosaurs, birds, mammals, and angiosperms, other important fossils include the earliest known freshwater lamprey *Mesomyzon* (Chang et al., 2006), the crown-group urodeles *Liaoxitriton* (Dong and Wang, 1998) and *Sinerpeton* (Gao and Shubin, 2001), the gliding lizard *Xianglong* (Li et al., 2007), the early members of various pterosaurian subgroups (Wang and Zhou, 2006), the flower-visiting insects (Ren, 1998), the early fleas (Gao et al., 2012, 2013; Huang et al., 2012), etc. These recently-reported species have become the new representative mem-

bers of the Jehol Biota (Figure 3) (Zhou and Wang, 2010; Zhou et al., 2017).

The Jehol Biota has also produced other rarely preserved fossils (Figure 4). For instance, embryonic skeletons were preserved *in vivo* in the female adults of *Monjurosuchus* (Wang et al., 2005b) and *Yabeinosaurus* (Wang and Evans, 2011), indicating the presence of viviparity in these species; a *Sinosauropteryx* specimen preserves two eggs inside the body cavity (Chen et al., 1998); ovarian follicles have been found in several Early Cretaceous birds (Zheng et al., 2013a); separately preserved embryo fossils of choristodere (Ji et al., 2006), birds, and pterosaurs (Wang and Zhou, 2004; Zhou and Zhang, 2004), and soft-shelled pterosaur egg fossils, have also been found (Ji et al., 2004b). Stomach contents have been identified in a few Jehol tetrapods: partial skeleton of a juvenile *Psittacosaurus* in *Repenomamus* (Hu et al., 2005), lizard and mammal bones in *Sinosauropteryx* (Currie and Chen, 2001; Xing et al., 2012), bird and fish bones in



Figure 3 Newly recognized representative species of the Jehol Biota: The early birds *Confuciusornis* (a), *Jeholornis* (b), *Protopteryx* (c) and *Yixianornis* (d); feathered dinosaurs *Sinosauropteryx* (e), *Caudipteryx* (f), and *Microraptor* (g); early mammals *Zhangheotherium* (h) and *Eomaia* (i); early flea *Tyrannosylla* (j); early flowering plant *Archaeoartus* (k). Not to scale.

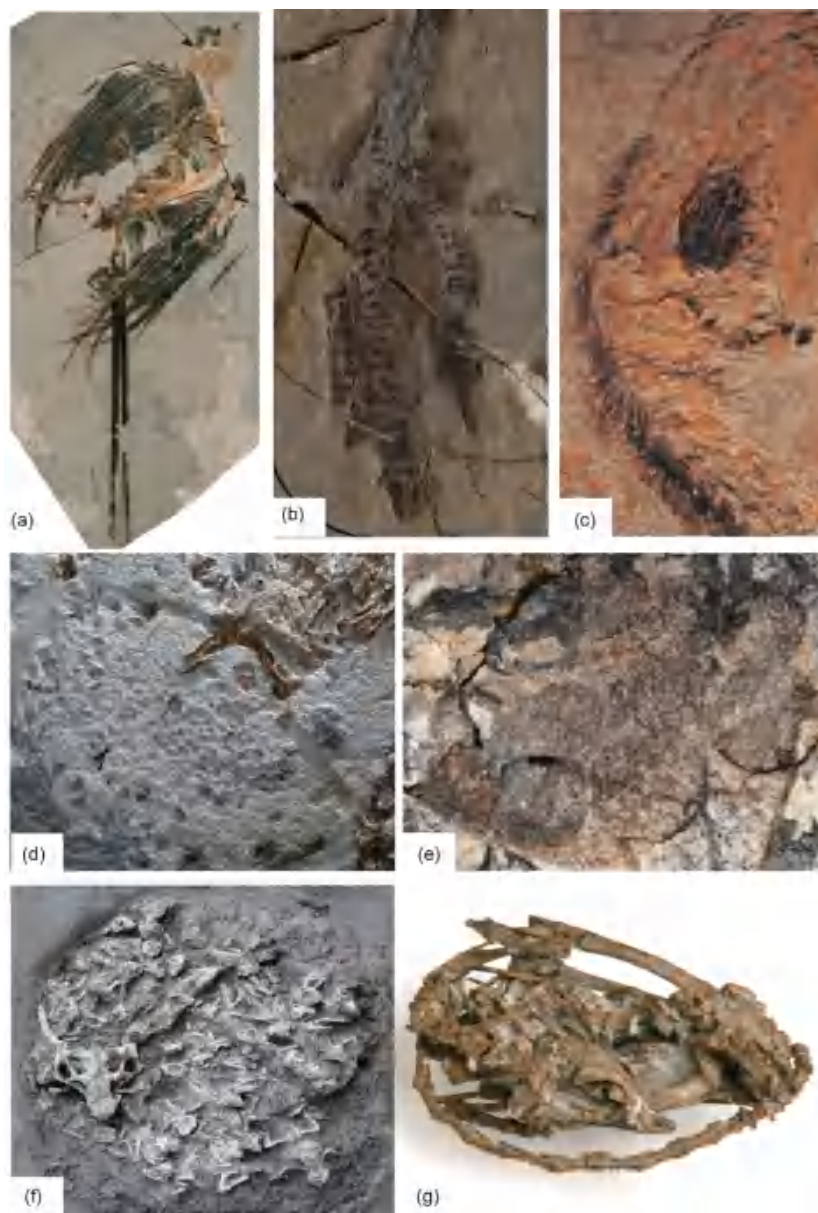


Figure 4 Selected Jehol fossils of exceptional preservation. (a) *Eoconfuciusornis* fossil preserving feathers; (b) *Yanornis* fossil preserving pedal integuments; (c) *Sinosauropteryx* fossil preserving primitive feathers and ocular soft tissues; (d) *Sapeornis* fossil preserving crop containing seeds; (e) Enantiornithine fossil preserving ovarian follicles; (f) *Psittacosaurus* fossil preserving parental care behavior; (g) *Mei* fossil preserving sleeping behavior. Not to scale.

Microraptor (O'Connor et al., 2011; Xing et al., 2013), seeds in *Jeholornis* (Zhou and Zhang, 2002), crop containing seeds in *Sapeornis* and *Hongshanornis* (Zheng et al., 2011), fish remains in *Piscivoravis* and *Yanornis* (Zhou et al., 2002, 2014), and the gastric pellet consisting of fish bones in the enantiornithine *Piscivorenanthornis* (Wang et al., 2016). Additionally, a few other exceptionally preserved fossils preserve information on animal behavior: for example, the troodontid *Mei long* fossil displays bird-like sleeping posture (Xu and Norell, 2004); *Psittacosaurus* fossils exhibit parental care and gregarious habit (Meng et al., 2004; Zhao et al., 2007); and the lizard *Dalinghosaurus* was also argued to

be gregarious (Evans et al., 2007).

The large amount of new fossil discoveries have not only greatly improved our understanding of the evolution of many organismal groups, but also added to our knowledge of the geological and stratigraphic distribution, chronology, and taphonomy of the Jehol Biota. The biota is featured by the sheer amount and completeness of fossils as well as exquisitely preserved soft tissues, providing unprecedented information not available from other Cretaceous terrestrial fossil assemblages (Chang et al., 2003; Zhou et al., 2017).

Fossils preserving soft tissues are mainly from the tuffaceous deposits or the shales intercalated within tuffs, which

represent the main fossiliferous beds of the Jehol Group (Jiang and Sha, 2007; Jiang et al., 2011, 2012, 2014; Pan et al., 2012). These fossils are usually complete, and the preserved soft tissues and microstructures (Zhang et al., 2010a) include wing veins, mouthparts, and bristles of insects (Ren et al., 2010), impressions of skin and/or scales of amphibians, choristoderes, lizards (Evans and Wang, 2010), and dinosaurs, membranes and fibrous skin tissues of pterosaurs, feathers of dinosaurs and birds (Norell and Xu, 2005; Xu and Norell, 2006), and hairs of mammals (Rougier et al., 2003; Zhou and Wang, 2010; Zhou et al., 2017). The shales not only contain abundant fossils of aquatic vertebrates such as fishes, urodeles, turtles, and choristoderes, but also a large number of bird fossils. Although other vertebrates are relatively less common in the shales, they are also well-preserved. The mass mortality of these vertebrates has been often ascribed to the frequent volcanic eruptions: specifically, the hot ashes and poisonous gas released by volcanic eruptions resulted in the sudden death and rapid burial of the animals (Wang et al., 1999; Guo and Wang, 2002; Guo et al., 2003; Jiang et al., 2011); whereas, some other studies suggested that the collapse of the aquatic ecosystem induced by the volcanic eruptions rather than the eruptions themselves was the direct cause of the mortality (Pan et al., 2012), but this hypothesis could not explain the mass mortality of terrestrial animals, especially birds and pterosaurs that could fly. In terms of taphonomy, the rapid burial and the high quality of preservation also relate to volcanic activity (Wang et al., 1999; Guo and Wang, 2002; Guo et al., 2003; Jiang and Sha, 2007; Jiang et al., 2011, 2012, 2014; Pan et al., 2012, 2013). Still other studies suggested that the widely distributed volcanogenic lakes in the Jehol area might have formed a special taphonomic settings in favor of soft tissues preservation, contributing to the well-preserved Jehol fossils (Jiang et al., 2011); meanwhile, pyritization was also considered to play a central role in fossilization of soft tissues (Leng and Yang, 2003).

The other fossil-bearing beds consist of tuffs, and volcanic ash-rich sandstone with conglomerates. The most typical one is the “Lujiatun bed” (Chang et al., 2003), which is generally considered resultant from pyroclastic flows or volcanic related mud flows (Xu and Norell, 2004; Evans et al., 2007; Zhao et al., 2007; Jiang et al., 2014). This bed has produced abundant three-dimensionally preserved fossils of anurans, lizards, and *Psittacosaurus*, some of which also preserve behavioral information, but the soft tissues are rarely preserved.

Chronologic studies of the Jehol Biota have been greatly advanced. The age of the Yixian Formation and a few important Jehol fossils (e.g., *Confuciusornis*, *Sinosauropteryx*, *Sinerpeton*, and *Archaeofructus*) was suggested to be the Late Jurassic in earlier studies, but a growing body of evidence from biostratigraphic and other stratigraphic studies, espe-

cially combined with isotope dating results, provides strong support for the Early Cretaceous age of the Jehol Biota (Swisher et al., 1999, 2002; He et al., 2004, 2006; Chang et al., 2009). Because the exceptionally well preserved fossils such as fossils of birds, dinosaurs, and mammals with soft tissues are restricted only to the Jehol area, some studies proposed the Jehol Biota *sensu stricto*, referring to a middle Early Cretaceous terrestrial biota preserved in the Dabeigou, Yixian, Jiufotang formations of the Jehol area, and their equivalent deposits nearby (Zhou and Wang, 2010). These three lithographic unites were formed during 135~110 million years ago (Swisher et al., 2002; Liu et al., 2003; Ji et al., 2004a; Zhang et al., 2005).

4. The current research status of the Jehol Biota

Although great progresses have been made on the research of the biota, some problems such as how to define the Jehol Biota (Jin et al., 2008; Pan et al., 2013) exist. Obviously the traditional definition of the biota based on the presence of *Eosestheria*, *Ephemeropsis* and *Lycoptera*, is problematic: later studies have shown that *Lycoptera* is confined only in the Yixian Formation (absent from the Dabeigou Formation and revised to *Jinanichthyes* in the Jiufotang Formation (Zhang et al., 1994)). *Ephemeropsis* may be also absent in the Jehol Biota as the relevant fossils have been referred to *Epicharmeropsis* (Huang et al., 2007; Huang and Ren, 2008). There were suggestions to use some other species to define the biota, e.g., to replace *Ephemeropsis* with *Epicharmeropsis* (Huang and Ren, 2008) and *Lycoptera* with *Peipiaosteus* (Ji et al., 2004a). However, there is no species or a species combination present in all the fossiliferous strata of the Jehol Biota, so the definition of the biota based on typical fossils is not applicable (Pan et al., 2013).

Defining the Jehol Biota based on the lithostratigraphic unit “Jehol Group”, i.e., regarding the Jehol Biota as a fossil assemblage preserved in the Jehol Group, is also questionable. In lithostratigraphic concept, the Jehol Group represents the Yixian, Jiufotang and Fuxin formations from the Beipiao-Fuxin Basin from western Liaoning, but the traditional Jehol Biota was not preserved in the Fuxin Formation from the upper part of the Jehol Group, and the biota has a larger geographic distribution than the group (Pan et al., 2013). Some studies have emphasized the importance of taphonomy and paleo-ecology in the definition of the Biota, and restricted the distribution of the biota to the Huajiying Formation of northern Hebei and Yixian and Jiufotang formations of western Liaoning, northern Hebei and southeastern Inner Mongolia and their equivalents in the same region. This biota thus represents a volcanic-influenced one with a duration from 131 to 120 Ma (Pan et al., 2013), an

opinion supported by some studies (Zhou et al., 2017). It needs to be emphasized that, due to temporal and spatial spans, a fossil assemblage is hard to be strictly defined, especially for terrestrial biota which is more influenced by the complexity of the deposits formed in terrestrial environments. So the definition of fossil assemblage is destined to be an artificial one.

To date, the Jehol Biota *sensu stricto* has produced invertebrates such as gastropods, bivalves, crustaceans (e.g., conchostracans, tadpole shrimps, ostracods and shrimps), insects and spiders, vertebrates such as agnathans, chondrichthyes, osteichthyes (e.g., acipenseriforms, bowfins and osteoglossiforms), amphibians (e.g., anurans and urodelans), reptiles (e.g., turtles, choristoderes, lizards, pterosaurs, ornithischian and saurischian dinosaurs), birds including non-ornithothoracine birds, enantiornithines and euornithines, and mammals (e.g., multituberculates, symmetrodonts, eutriconodonts, metatherians and eutherians), and algae, moss, ferns, gymnosperms and angiosperms (Zhou et al., 2017). The plant assemblage of the Biota is mainly characterized by a high diversity of gymnosperms and by the occurrence of early angiosperms (Figure 5). The invertebrate fauna is most abundant in insect fossils (Figure 6), which is far more than

other groups in species diversity (Zhou et al., 2017). The vertebrate fauna is highest in bird diversity, with dinosaurs and pterosaurs ranked at the second level. Several aquatic groups, such as fish, urodelan amphibians and choristoderes, are not relatively high in taxonomic diversity, but are great in abundance (Figure 7) (Zhou et al., 2017).

The Jehol biota has significantly advanced our understanding about the origins and early evolution of many organismal groups, the evolution of some key biological structures and organs, and particularly the origin of some vertebrate subgroups (Figure 8). Specifically, theropod fossils unearthed from the Jehol Biota nearly span the whole spectrum of the coelurosaur theropods, which provide solid and comprehensive evidence supporting the hypothesis that birds were descended from dinosaurs (Norell and Xu, 2005; Xu and Norell, 2006; Xu et al., 2014). For instance, such dinosaurs as dromaeosaurids and troodontids from Jehol show that they are nearly as small as *Archaeopteryx* (Xu et al., 2000; Ji et al., 2005; Xu and Norell, 2006), a few bird-like dinosaurs (e.g., *Caudipteryx*) have an abbreviated tail that is even shorter than that of some early birds (Ji et al., 1998; Jones et al., 2000), and some dromaeosaurids such as *Sinornithosaurus* have *Archaeopteryx*-like pectoral girdle



Figure 5 Selected Jehol plant fossils. The fern *Xitajiaenia* (a); the gymnosperms *Williamsonia* (b), *Rehezamites*(c), *Czekanowskia* (d), *Podocarpus* (e) and *Liaoningocladus* (f); the angiosperms *A. sinensis* (g) and *Hyrcantha* (h). Not to scale.



Figure 6 Selected Jehol invertebrate fossils. The insects *Sinaeschnidia* (a), *Parahagla* (b), *Sophogramma* (c), *Sinochresmoda* (d), *Siboptera* (e), *Vitimopsyche* (f), *Florinemestrius* (g), *Coptoclava* (h); unnamed scavenging silphid (i); mushroom-eating *Protoxyporus* (j); the crustacean *Liaoningogriphus* (k). Not to scale.

and robust elongate forelimb (Xu et al., 1999b, 2011). Many bird-like dinosaurs such as *Sinovenator* have *Archaeopteryx*-like pelvis (Xu et al., 2002c), and troodontids such as *Mei long* have already evolved bird-like sleeping posture (Xu and Norell, 2004). Importantly, the feathered dinosaurs from the Jehol Biota demonstrate that feathers appeared at least in the early history of theropod dinosaurs (Chen et al., 1998; Ji et al., 1998, 2001, 2005; Xu et al., 1999b, 2003, 2004, 2010, 2012; Norell et al., 2002). The initial functions of feathers are not related with flight, and complex feathers including the asymmetrical flight feathers have already evolved within dinosaurs (Zhang and Zhou, 2006; Xu and Guo, 2009).

The Jehol bird assemblage is mainly composed of the Enantiornithes and Euornithes, in addition to a few earlier-branching taxa, which together document the earliest known radiation in the evolution of birds (Zhou, 2004; Zhou and Zhang, 2006a; Wang and Zhou, 2017). Jehol bird fossils exhibit morphological (body size, beaked/toothed, long/short tail, etc.) and ecological (arboreal, terrestrial, aquatic, herbivory, omnivory, carnivory, etc.) diversity (Zhou, 2004; Zhou and Zhang, 2006a), and also evolved many modern bird characteristics (Zheng et al., 2011, 2013a; Wang et al.,

2016). In particular, significant advances have been made in the study on the evolution of important organs and structures, such as the integument structures (e.g., feathers used in display widely distributed in early birds), digestive system (e.g., stomach divided into the proventriculus and gizzard, presence of crop and regurgitation) (Zheng et al., 2011; Wang et al., 2016), and the reproductive systems (e.g., reduction of the right ovary, follicular hierarchy less distinct than in modern birds) (Zheng et al., 2013a). Meanwhile, these fossils shed new lights on growth and development (for example, these early birds grew relatively slower than most modern birds and reached sexual maturity before somatic maturity, as opposed to modern birds) (Zhang et al., 1998; Zheng et al., 2014), and the skeletal system (e.g., the cranial kinesis, the abbreviation of the bony tail and the pygostyle evolution, and the modifications of the girdles and appendages) (Wang and Zhou, 2017).

The feathered dinosaurs and early birds from Jehol also have advanced our understanding of another important question about the origin of birds, that is, the origin and early evolution of bird flight. The Jehol Biota has produced a few arboreal dromaeosaurids such as *Microraptor* (Xu et al.,

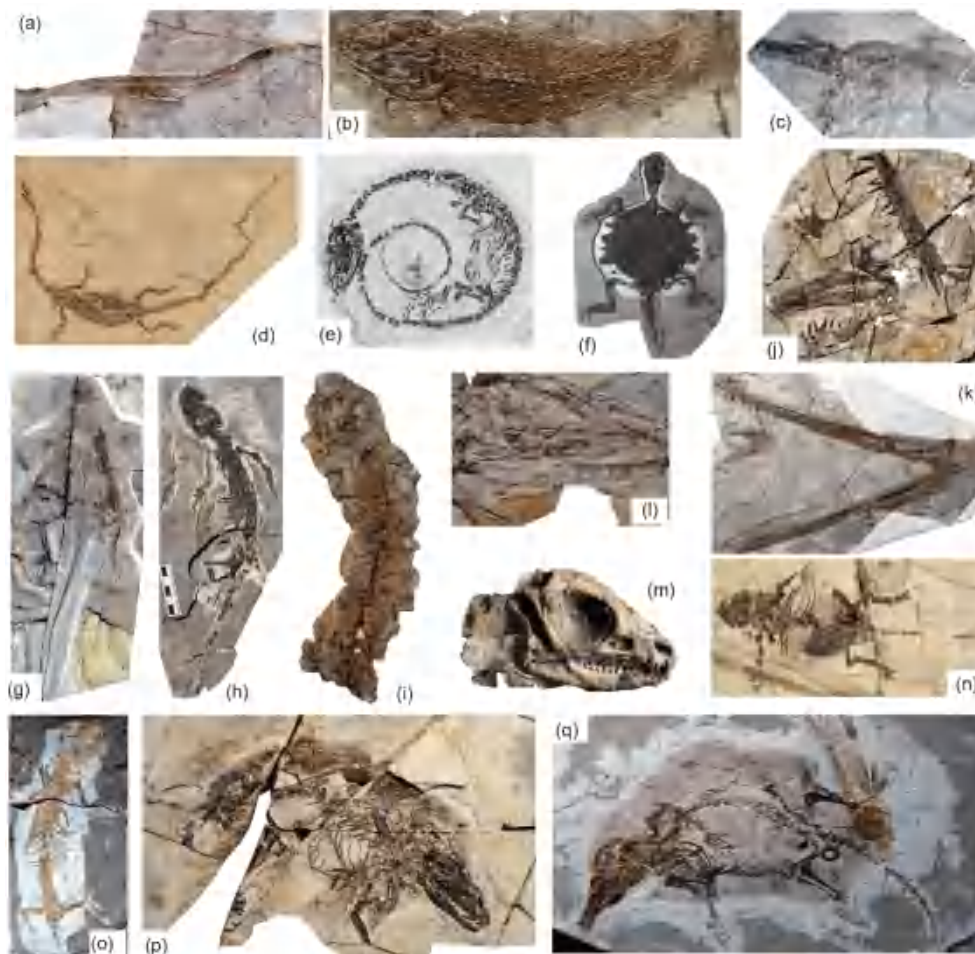


Figure 7 Selected Jehol vertebrate fossils. (a) The agnathan *Mesomyzon*; (b) the fish *Sinamia*; (c) the salamander *Regalerpeton*; the adult (d) and juvenile (e) of the choristodere *Hyphalosaurus*; (f) the turtle *Perochelys*; the lizards *Xianglong* (g) and *Yabeinosaurus* fossils (h, with fish bones in stomach) and (i., preserving embryonic skeletons); the pterosaurs *Liaoningopterus* (j) and *Feilongus* (k); the dinosaurs *Yutyrannus* (l), *Jeholosaurus* (m) and *Liaoningosaurus* (n); the mammals *Yanoconodon* (o), *Sinodelphys* (p), and *Akidolestes* (q). Not to scale.

2000), as well as other dinosaurs and birds that bear flight feathers on their hindlimbs (Xu et al., 2003; Zhang and Zhou, 2004; Zheng et al., 2013b). These fossils support the arboreal origin hypothesis and indicate that the bird flight likely evolved through a four-winged stage. Morphological analyses of the feathers of the Jehol bird fossils reveal that early flight is primitive and complicated (Zheng et al., 2010; O'Connor et al., 2013). All these aforementioned discoveries triggered numerous functional morphology and biomechanic discussion about the origin of bird flight, which open a new direction for the study of the origin and early evolution of bird flight.

The Jehol pterosaurs contribute to the taxonomically and ecologically most diverse pterosaur assemblage (Zhou et al., 2017). Nearly all reported Jehol pterosaurs belong to the Pterodactyloidea and many of them represent the earliest known members of their respective pterodactyloid subgroups. The Jehol pterosaurs display significant differences in their body size, diet, habitats and other aspects (Wang et

al. 2005a, 2008). Some Jehol fossils provide key information on several important biological traits. For example, fossils of pterosaur egg with embryos indicate that pterosaur eggs are soft-shelled (Ji et al., 2004b), and that pterosaurs are precocious in embryonic development (Wang and Zhou, 2004). Some other reptilian fossils also display the biological and ecological diversity of their respective groups. For example, the semiaquatic choristoderes display some morphological and reproductive disparity: the long necked *Hyphalosaurus* was oviparous, but the short necked *Monjurosuchus* was ovoviviparous (Wang and Evans, 2011); the lizard *Xianglong* was capable of gliding, and the large terrestrial lizard *Yabeinosaurus* was ovoviviparous, thus extending back the fossil record of ovoviviparous behavior in squamates by at least 30 million years (Wang and Evans, 2011).

The Jehol mammalian fauna lacks a high taxonomical diversity, but the reported species cover the two of the three major mammalian lineages—metatherians and eutherians (but see Bi et al., 2018 for different opinion), as well as stem

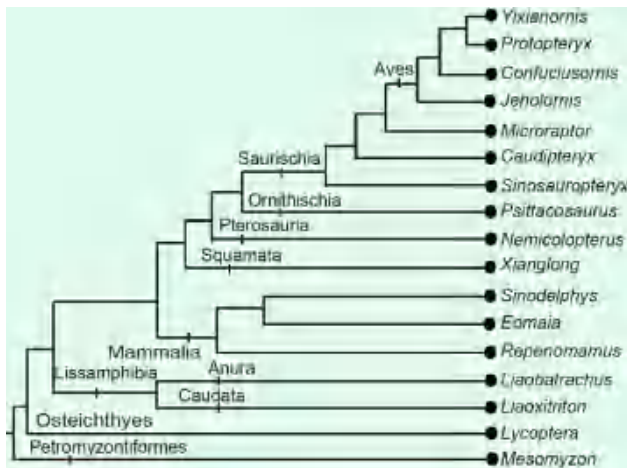


Figure 8 Simplified vertebrate phylogeny highlighting the Jehol species. Jehol contains the key taxa for understanding vertebrate evolution.

therian mammals (e.g., eutriconodontans, multituberculates, and symmetrodontans) (Luo, 2007; Zhou et al., 2017), and their discoveries have significant implications for understanding the origins of the crown group mammals (Luo, 2007). Unlike most Mesozoic mammal fossils which are fragmentary, Jehol fossils are represented mostly by nearly complete skeleton, and even fur and other soft tissues in some cases (Hu et al., 1997; Ji et al., 1999; Ji et al., 2002; Luo et al., 2003; Li and Luo, 2006; Luo et al., 2007; Ji et al., 2009). These fossils have not only provided previously unknown morphological information, shedding light on the evolution of middle ear and other biological structures (Wang et al., 2001; Luo, 2007; Meng et al., 2011), but also displayed the locomotion and ecological diversity (Luo, 2007; Zhou et al., 2017), and they are among the most important discoveries in studying early mammal evolution (Luo, 2007).

The discoveries of Jehol insect fossils have advanced many aspects of our understanding of insect evolution, for example, the appearance of pollinating structures, the evolution of insect mimicry and parasitism (Ren et al., 2010), and the origins of several insect clades (Ren et al., 2010; Gao et al., 2012; Huang et al., 2012; Gao et al., 2013; Gao et al., 2014). In particular, the discoveries of flea fossils reveal the plesiomorphic features for fleas and support the phylogenetic hypothesis that fleas are the descendants of panorpids.

The Jehol plant fossils cover nearly all major plant groups, but they have not yet been systematically studied with in-depth analysis (Sun et al., 2001; Sun et al., 2011). Angiosperm fossils recovered from the Jehol are few in numbers, but they have significant evolutionary implications (Dilcher, 2000; Leng and Friis, 2006), indicating that earliest angiosperms are probably aquatic plants (Sun et al., 2002; Sun et al., 2008).

From the perspective of paleoecology, many Jehol species are known in their habitats and diets (Zhou et al., 2017). For

example, there are predatory and filter-feeding fishes in the biota; the top predator of Jehol lake ecosystem is the choristodere *Ikechosaurus* (Liu and Wang 2003; Liu 2004); the lizard *Dalinghosaurus* is tree-climbing (Evans and Wang, 2005) and gregarious in habit (Evans et al., 2007), and the lizard *Yabeinosaurus* is known to have a feature rarely present in terrestrial lizards: its diet includes fish, suggesting that this species has foraged near the water; most Jehol pterosaurs are fish-eaters and some are filter-feeding (e.g., *Gegepterus* and *Pteroflitus*) (Jiang and Wang, 2011), and some species such as *Sinopterus* displays features for climbing (Wang et al., 2008).

Among the Jehol dinosaurs, *Yutyranus* and *Sinotyrannus* represent the top predators of the Jehol ecosystem, but many theropods such as *Caudipteryx* and *Beipiaosaurus* are secondarily herbivorous; the biota is characterized by small dinosaurs, though a few large sized species are also known; most species are ground-dwelling, but some are arboreal (Xu and Norell, 2006); some Jehol dinosaurs are known to be nocturnal (Schmitz and Motani, 2011). Among the Jehol birds, the majority are arboreal species, but some euornithines are probably ground-dwelling (Zhou and Zhang, 2006b), and a few are likely to be semiaquatic. There is a considerable diet differentiation, including carnivorous (also fish-eating), herbivorous (also seed-eating), and omnivorous (Zheng et al., 2018), and even filter-feeding (Hou et al., 2004).

The Jehol mammals are in general similar to other Mesozoic mammals in having a small body size and mainly feeding on insects, but they do exhibit apparent size and diet variations, as indicated by the largest known Mesozoic mammal *Repenomamus*, which even fed on juvenile dinosaurs (Hu et al., 2005). In terms of habitats, Jehol mammals also display a high diversity, with ground-dwelling, arboreal, semiaquatic, and semi-fossorial representatives (Chen et al., 2019).

The discoveries of flower-visiting insects provide key evidence for the co-evolution between insects and plants in the Jehol Biota (Ren 1998); the discoveries of fungus-eating insects indicate the presence of a trophic relationship between these two major groups in the Jehol Biota (Cai et al., 2017); the discoveries of multiple ectoparasitic insect species reveal the host-ectoparasite relationships of vertebrates and insects in the Jehol Biota (Ren et al., 2010; Gao et al., 2012; Huang et al., 2012; Gao et al., 2013; Gao et al., 2014). Meanwhile, insects are food resources of many vertebrate species. From the perspective of habitats, forest insects exhibit the highest taxonomic diversity in the Jehol insect fauna, aquatic insects, soil insects, and mountain insects display sequentially lower diversity; in terms of diet, herbivorous insects are the highest in taxonomic diversity, and then followed by carnivorous, parasitic, scavenging, and omnivorous insects (Zhang et al., 2010b).

There have been some advances in the study of the paleoenvironment and paleoecology of the Jehol Biota *sensu stricto* (Zhou et al., 2017). It is widely accepted that numerous lakes, particularly volcanogenic lakes, and even large lakes, are distributed in the Early Cretaceous Jehol area. Plant fossils indicate the presence of sloping fields and forests (Sun et al., 2001; Sun et al., 2011). This has been also supported by the reconstructed body color pattern of psittacosaur, which suggests that this species lived in a relatively closed forest habitat (Vinther et al., 2016). The discoveries of arboreal dinosaurs, birds, mammals and pterosaurs (*Nemicolopterus*) also support the presence of forests. The discoveries of many mountain insects suggest the presence of relatively high-altitude areas such as mountains. The inference of the presence of cool climate and even cold climate has been further supported by some paleontological and isotopic data. The wide distribution of conifers and wood fossils indicate the seasonal climatic changes; the presence of *Xenoxylon* in the Yixian Formation suggests a cool climate (Tian et al., 2015). The absence of crocodyliforms also suggests a relatively cold climate, which is consistent with the presence of gigantic feathered dinosaurs such as *Yutyrannus* (Xu et al., 2012). Stable isotope data indicates as well that there was a cold interval during the period when the Jehol Biota existed (Amiot et al., 2011, 2015), and that continental ice sheet was even present in northeastern China (Yang et al., 2013). Globally the Early Cretaceous represents a warm and humid period, but since middle Early Cretaceous, there has been dramatic climatic changes at least in East Asia, being increasingly drier and with more evident seasonal changes. The evidence for a warm and humid climate include the wide distribution of ferns, cycads, and ginkgoes and the presence of the gliding lizard (extant gliding lizards are known only in tropics and subtropics (Li et al., 2007), but evidence for dry climate is also present, for example, the flourishing gnetophytes. The habitats of the Jehol Biota are probably geographically highly variable, with both high mountains and deep valleys, being dry and cold particularly in higher altitude, as in today's northern Yunnan, China. The Jehol fossils are also suggestive of dramatic climate changes, e.g., the air temperature being considerably lower in *Yutyrannus*'s living period than in other Jehol periods. However, plant fossil data and other data indicate that the global air temperature had been rising since the Jehol period, and the global climate was warm and even hot.

Some studies suggested that Jehol Biota was endemic, but others proposed that Jehol area was in fact a place for the origins of many organismal groups. There are apparently many endemic species in Jehol Biota (Sereno, 1990; Sychevskaya, 2001a; Chang et al., 2003; Averianov et al., 2006; Gao et al., 2009), such as the vertebrates *Lycoptera*, *Monjurosuchus*, some turtle species, psittacosaurids, and confuciusornithids, which are known only in Jehol and the

neighboring Siberia, Korean peninsula and Japan, so are many invertebrate species. Invertebrate fossils indicate that the northeastern part of China, Korean peninsula, Siberia and Japan belong to the same river systems in Early Cretaceous (Sha et al., 2012); these areas are also similar to each other in paleogeography and paleoenvironment (Liu et al., 2015), supporting that the Jehol Biota is an endemic biota, which is consistent with the tectonic and geographical background of the Jehol Biota: East Asia had been isolated from other continents from Middle Jurassic to Early Cretaceous, and was connected to the latter until Aptian and Albian when the Eurasian land bridge appeared (Upchurch et al., 2002). However, many Jehol dinosaurs, mammals, and amphibians have a global distribution (Zhou and Hilton, 2003), birds and pterosaurs display European and American affinities (Zhou, 2006; Zhou and Zhang, 2006a; Wang et al., 2012), and some turtle species are also closely related to European ones (Tong and Brinkman, 2012). Many Jehol species represent the relatively early-branching ones of their respective lineages, leading to the suggestion that Jehol represents the origination and diversification center for many terrestrial organismal groups (Manabe et al., 2000; Zhou and Hilton, 2003; Wang et al., 2005a; Zhou and Zhang, 2006a; Zhou and Zhang, 2006b), but which was interpreted differently, i.e., that Jehol is in fact a "refugee" for those relatively early-branching species which are isolated from their close relatives for a long time (Luo, 1999).

The available data support the traditional three-evolutionary-phase model for the Jehol Biota (Chen, 1988), but with some revisions: the first phase is restricted to northern Hebei (the Huajiyang Formation), and its main features include a small number of component species and without widely known typical elements; the second phase (the Yixian Formation) is the peak in terms of taxonomical diversity; the third phase (the Jiufotang Formation) is featured by the maximum geographical distribution of the biota (Zhou et al., 2017). For example, bivalves (Chen J H, 1999), conchostracans (Chen P J, 1999), ostracods (Cao and Hu, 2003), insects (Zhang et al., 2010b) and several other groups all display a relatively evident three-phase evolution, so do acipenseriforms (Zhou et al., 2010), salamanders (Zhang et al., 2009), pterosaurs, and birds (Zhang and Zhou, 2000; Wang and Zhou, 2006; Zhang et al., 2008).

5. Future prospects of research on the Jehol Biota

As a window into the initial development of the modern terrestrial ecosystem, the Jehol Biota will continue to provide significant information on a series of important questions such as how the Jehol Biota helps to reveal the origins of major organismal groups, how the paleoenvironment and

paleoclimate affected the evolution of the Jehol Biota, and what the similarities and differences the Early Cretaceous and modern terrestrial ecosystems share and have. Answering these questions are important for our understanding of the evolution of modern terrestrial ecosystem.

The core research topic of Jehol Biota is still the geographic and temporal distribution of the biota, i.e., the geographic distributions of the compositional species and individuals across the time slices of the biota. This requires the collection of more specimens, in particular, those with accurate provenance information, as well as more in-depth morphological and taxonomic studies. The latter needs not only the traditional methods, but also new analytic methods and imaging techniques. Worthy of mention is that some vertebrate groups (e.g., psittacosaur, dromaeosaur, and confuciusornithids) have a large number of samples, and some species of these groups, such as, *Liaobatrachus* (Dong et al., 2013), *Hyphalosaurus* (Ji et al., 2006), *Dalinghosaurus* (Evans and Wang, 2007), and *Psittacosaurus* (Zhao et al., 2013), are represented by numerous fossils, and in some cases, of different ontogenetic stages. This is rarely seen in terrestrial vertebrate fossil records, but provides an opportunity for understanding morphological variations of terrestrial vertebrate clades and species both within the species and through the ontogeny. In combination with other data such as fossil distribution, paleoenvironment, paleoclimate, and paleoecology, these fossils will provide unprecedented new insights into evolutionary phenomenon.

The exceptionally well preserved Jehol fossils provide a rare opportunity for studying the soft tissues and in particular the preserved nanostructures. For example, by studying the melanosomes preserved in feathered dinosaur fossils (Zhang et al., 2010a), the body color of some dinosaurs has been reconstructed (Li et al., 2012); by collecting and comparing the melanosome data from dinosaurs, early birds, and some other groups, the phylogenetic distribution pattern of these structures and even some ecological signals (e.g., psittacosaurid countershading camouflage) have been recovered (Vinther et al., 2016), and discussions were made about the evolution of integumentary microstructures and even of physiological features (Li et al., 2014). In the future, we need to collect more specimens including the ones preserving melanosomes in three-dimensional distribution on the body, study three-dimensional melanosomes, conduct more chemical analyses on soft tissue fossils, and analyze other pigments. The other research topic is about the ancient proteins. Some studies demonstrate the potential of preserving protein fragments in Jehol fossils, and a few proteins have been identified and even been observed directly (Pan et al., 2016; Pan et al., 2019). Although studying ancient proteins face many challenges, it nevertheless represents a promising research area, and provides us with a new way of understanding evolution.

The paleoecology research of the Jehol Biota has significant implications for our understanding of the initial development of modern terrestrial ecosystem. Most previous studies are qualitative ones (Chen et al., 2019), and are also flawed by a lack of accurate paleogeographic, paleoclimatic and paleoenvironmental information. Future studies in this regard will be based on more accurate taxonomical and fossil distribution information in combination with better paleogeographic, paleoclimatic and paleoenvironmental data, and importantly will adopt quantitative approaches. A key study is to establish the high-precision temporal and geographical framework for the Jehol Biota, and to put individual specimens into this framework, and based on this, to conduct quantitative analysis of the Jehol ecosystem. One study has attempted to reconstruct the Jehol Biota ecosystem based on food web and energy flow model (Healand MacLean, 1975), which quantitatively estimated the biodiversity and biostructure of the Jehol Biota (Matsukawa et al., 2014). This study would be much improved if more samplings with more accurate geographic and stratigraphic information can be added. The other promising modeling method is the general ecosystem models (Harfoot et al., 2014). These modeling methods can provide more reliable estimation of the biodiversity and biostructure of the ecosystems in question and estimate their stability and resilience.

Relative to the research on taphonomy of the Jehol fossil assemblage, finding the external driving forces of the evolution of the Jehol Biota is a more challenging task (Zhou and Wang, 2017). Recent discussions involve the environmental effect on the evolution of the Jehol Biota caused by the North China Craton destruction (Zhou and Wang, 2017). The latter started about 160 million years ago, reached to its peak about 125 million years, and was correlated to the Paleo-Pacific subduction and retreat underneath the eastern Asian Continent (Wu et al., 2008; Zhu et al., 2011; Zhu et al., 2012). The tectonic activity resulted in the formation of numerous continental rift basins (Wu et al., 2008; Liu et al., 2015), which housed fresh-water lakes (Zhu et al., 2008; Liu et al., 2015). The tectonic activity is most active around the booming time of the Jehol Biota (i.e., about 125 million years ago), and it is accompanied with magmatic activities and volcanic eruptions (Wu et al., 2008; Zhu et al., 2011; Zhu et al., 2012). Environmental effects caused by North China Craton destruction also include geothermal increase and the formation of complex geography. The former leads to regional ecological changes and in particular the change of biomass, and the latter is probably contributable to the formation of the isolation mechanism which is important for speciation. Some studies suggest that the volcanic-magmatic-orogenic activities starting in the Late Jurassic lead to the complex and diverse paleogeography in North China (Liu et al., 2015). The available data does show that the environmental effects caused by the North China Craton

destruction affected the Jehol Biota. There is a trend of eastward-moving of the sedimentary basins and biotas in the Early Cretaceous of northeastern China, which is consistent with the expected geographic and environmental results from the Paleo-Pacific subduction and retreat underneath the eastern Asian Continent (Zhou and Wang, 2017). The frequent volcanic activity is not only responsible for the preservation and fossilization of the Jehol Biota, but also plays an important role in the formation and evolution of the biota, representing an important external driving force. It brings the lake a large amount of nutrition (Jiang et al., 2011; Pan et al., 2013; Jiang et al., 2014; Pan et al., 2014) as well as harsh environmental condition, which contribute to a strong selection pressure. How the North China Craton destruction affected the speciation and extinction of Jehol organisms is an important topic for future research (Zhou and Wang, 2017).

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