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A Mesozoic Pompeii: History of the Jehol Biota's Rise and Fall

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Abstract: The Jehol fauna was initially represented by a bony fish, concostracan and an insect, as a *Lycoptera davidi–Eosestheria–Ephemeropsis trisetalis* association, but since the researches of recent decades, the Jehol Biota is now completely different from the past low-diversity, and encompasses a native terrestrial biota that includes many well-preserved vertebrates, invertebrates and plants. There are more than 20 important biological categories, thousands of taphonomically unusual fossils, especially noted for the wide variety of biological tissues. The Jehol Biota has caused a sensation in the world with its wide distribution, large quantity, great variety, fine preservation and detailed information, which records the rise and fall of the numerous taxa, and provides significant evidence for three origins: of birds, eutherian mammals, and angiosperms. The Jehol Biota is a highlight of basic scientific research in China, and we honor it as a world–class fossil treasury and "a Mesozoic Pompeii".

Key words: geoheritage, paleontology, Jehol Biota, evolutionary origins, Jurassic–Cretaceous, Northeast Asian region, Liaoning province

1 Research Situation

The "Jehol Biota" was named by paleontologist Academician Gu Zhiwei in 1962 based on research on invertebrates and biostratigraphy(Gu, 1962), and it was named for the first discovery in the old Jehol province of China. The "Jehol Series" and the "Jehol Fauna" were established by Grabau (Grabau, 1923, 1929) and then developed by Gu Zhiwei. The "Jehol Biota" refers to a flora and fauna that thrived in the early Cretaceous (late Mesozoic, 145–120 million years ago) and was distributed throughout East Asia, primarily in North China, Mongolia, Siberia, Korea and Japan. The western Liaoning region is the typical area for Jehol Biota research, which comprises fossils from the Yixian Formation and Jiufotang Formation that span 18 million years. Since the 1990s, more than 20 higher taxa with thousands of beautiful fossils have been discovered in western Liaoning.

This biota was initially based on a conchostracan, an insect, and a bony fish—*Eosestheria–Ephemeropsis–Lycoptera*—faunal association, but continuous research for about half of a century, especially in recent decades, has shown the Jehol Biota to encompass a complex native terrestrial biota that is widely distributed in northeastern Asia and which comprises vertebrates, invertebrates and plants. The Jehol Biota contains more than 20 important biological categories, especially a large number of organisms with soft tissues such as feathers, trichomes, hair, and soft tissues of dinosaurs, birds, pterosaurs and mammals (Fig. 1).

The Jehol Biota has caused a sensation around the world in both the academic community and popular press. The wide distribution, enormous quantity, great variety, and unusually good preservation of the fossils giving full information has provided increasingly significant evidence to answer a series of problems, such as the origins, radiation and evolutionary relationships of various groups, for example the origin of birds, the origin and early evolution of flight and feathers, the origin and evolution of angiosperm plants. The biota provides a window into the environment of life on the later Mesozoic earth. There have been some 30 articles published in top journals (e.g. Zhang and Zhou, 1976; Chen et al. 1998; Ren, 1998; Wang et al., 1998; Chang et al., 2006), contributing significantly to world science. The Jehol Biota is now honored as "a world–class fossil treasury" and "a Mesozoic Pompeii" (Zhang, 2001).

At the time the Jehol Biota lived, Early Cretaceous volcano activities were frequent. Thus, organisms were buried periodically by volcanic products and deposits into rivers and lakes, forming the Jehol Biota that we see

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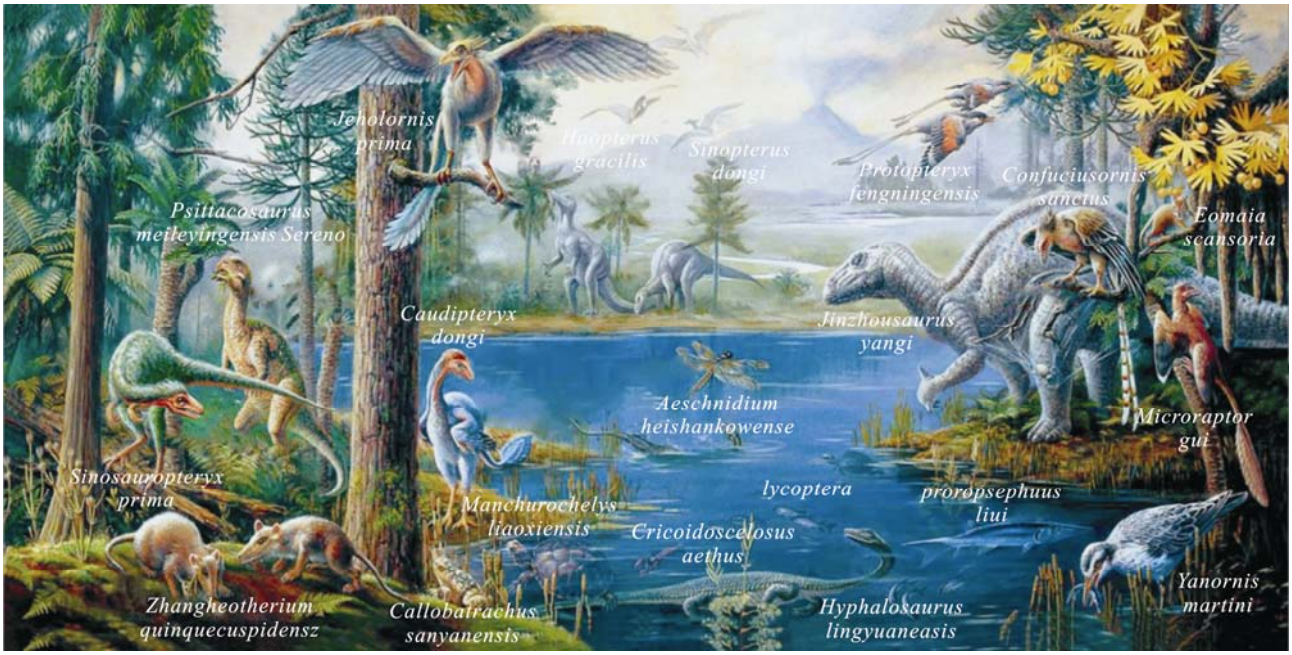

Fig. 1. Ecological Reconstruction of the Jehol Biota (from Baidu Wikipedia).

today. Hence the comparison has been made with the volcanic cataclysm of 79AD when Pompeii in Italy was devastated (Zhang, 2001).

2 Biotic Components

Since the 1990s, the earlier *Lycoptera davidi–Eosestheria–Ephemeropsis trisetalis* association was no longer able to generalize for of Jehol Biota. Presently incomplete statistics show that there are more than 20 categories (major taxa) in the biota, including mammals, dinosaurs, lizards, crocodiles, pterosaurs, birds, chelonians, frogs, salamanders, fish, conchostracans, ostracods, bivalves, gastropods, arthropods such as insects and decapods, limulaceans, arachnoideans, all kinds of terrestrial plants (including angiosperms), sporopollen and algae. Each category includes multiple subunits (genera, species).

At present, there are known dozens of fossil mammal sites found in the Jehol Formation: in 2002, P. Sereno et C. G. Rao found and described *Sinornis santensis* from Shengli Township, Chaoyang County, Liaoning Province; in 1992, Zhou Zhonghe found *Cathayornis yandica* in the Jiufotang Formation at Boluochi, Chaoyang; in 1995, Hou Lianhai *et al*. found the primitive birds *Confuciusornis sanctus* and the Prasavci *zhangheotherium quinquecuspidens* in lower part of the Yixian Formation at Jianshangou, Shangyuan Town, Beipiao County, in Liaoning (Zhou, 1992; Hou et al. 1995a, 1995b; Sereno et al., 2002).

Jehol Flora is equally abundant as the Jehol Fauna. The plants that have been found include mosses, ferns, ginkgos, cycads, conifers and flowering plants, among which, the ginkgo, cypress, and conifers are particularly rich. Angiosperms were also emerging at this period, epitomized by species *Archaefructus liaoningensis* and *Archaefructus sinensis* (e.g. Sun et al., 1998).

The Jehol Biota was distributed throughout eastern Asia area in the late Mesozoic. In recent years, the discoveries of primitive bird fossils (Zhou and Jin, 1992; Hou, 1994; Hou et al., 1995a, 1996), Theropoda with feathers (Ji and Ji, 1996, 1997a, 1997b; Ji, 1999; Chen et al., 1998; Xu et al., 1999, 2001; Zhou and Wang, 2000; Wang and Lv, 2001), early Mammalia (Hu et al., 1997; Hu et al.,1998; Wang et al., 1998; Ji et al., 1999, 2002) and early angiosperms and pollen (Ren and Hong, 1998; Sun et a1., 1998, 2002; Wu, 1999; Sun Ge and Zheng, 2000) make the Liaoxi area a good place for the research on the evolution of early birds, primitive mammals and the origin and evolution of early angiosperms in China, and even the world. The Jehol Biota is now the focus of paleontology fieldwork, and has given us a huge fossil treasury such as conchostracans, insects, bivalves, gastropods, Ostracoda, fish, amphibians, reptiles, birds, mammals and plants and sporopollen (Fig. 2). The main fossil categories and their preservation features from the Yixian Formation are discussed below.

2.1 Bivalvia

The bivalves of the Jehol Biota were first reported by Grabau, and then researchers such as Gu (1962), Hao et al. (1982), Wang (1990), and Chen (1999a) studied them.

Fig. 2. Fauna and flora and restorations of the Jehol Biota.
(a), the holotype of *Sinosauropteryx*; (b), the holotype of *Protarchaeopteryx*; (c), the holotype of *Caudipteryx zoui*; (d), ecological restoration of *Zhangheotherium quinquecuspidens*; (e), restoration of the oldest placental mammals—*Eomaia scansoria*; (f), *Confuciusornis*; (g), *Archaefructus Liaoning*; (h), *Archaefructus sinensis*. a, b, c, d, e, f, g, h from Ji Qiang , 2004; d drew by M. A. Klingler.

Seven species from two genera have been reported to date: *Ferganoconcha sibirica*, *F*. cf. *burejensis*. *Arguniella lingyuanensis*, *F*. *quadrata*, *Sphaerium selengiensis*, *S. jeholense*, and *S*. *subplanum*. Copious amounts of tuff in the sediments reflect the fact that these creatures died as a result of volcanic eruptions.

2.2 Gastropoda

Wang Huiji (1984) reported two species of *Probaicalia*. Yu Xihan (1987) identified seven genera in the Jehol Biota: *Viviparus*? *Probaicalia*, *Galba*, *Bithynia*, *Zaptychius* (*Omozaptychius*), *Eozaptychius*, and *Hippeutis*. Pan and Zhu (1999) described 5 species in 4 genera: *Amplovalvata* sp., *Probaicalia vitimensis*, *Ptychostylus harpaeformis*, *P*. cf. *philippii* and *Gyraulus* sp. as a total of 15 species in 10 genera.

2.3 Ostracoda

Zhang Lijun (Zhang et al., 1985) described two combinations of ostracod taxa in the formation (29 species in 9 genera): *Cypridea* (*Cypridea*) *liaoningensis–C*. (*Ulwellia*) *muriculata–Djungarica camarata* in the lower Yixian Formation and *Cypridea* (*Cypridea*) *veridical arquata–C*. (*C*.) *zaocishangensis* in the Jingangshan layer of the upper Zaocishan area. Cao Meizhen (1999) described 16 species in 9 genera, as a total of 24 species of 12 genera.

2.4 Conchostraca

The conchostracans in western Liaoning were studied by Zhang Wentang et al. (1976), Wang Wuli (1987), Chen Piji and Shen Yanbin (1985), and Chen Pijii (1999b) in succession, as a total of more than 40 species in 7 genera: including *Eosestheria*, *Diestheris*, *Longjiangestheria?*, *Filigrapta*, *Clithrograpta*, *Chaoyangestheria*, *Eosestheriopsis*, *Yanjiestheria*. The Conchostraca of the Yixian Formation are widespread, appearing from the early stage and lasting to the late stage of the formation at Lake Basin.

2.5 Insecta

Most fossils are preserved perfectly with soft tissue imprinting, intact wings and clear veins, as in *Sinaeschnidia cancellosa*, *Rudiaeschna limnobia*, odonatan *Aeschnidium heishankowense*; phasmatodean *Hagiphasma paradoxa*; raphidiodeans *Caloraphidia glossophylla* and *Siboptera fornicata*; orthopteran *Habrohagla curtivenata*; *Caloraphidia glossophylla*, *Siboptera fornicata*, *Sibirobittacus atalus*, *Hagiphasma paradoxa*, *Karatavoblatta formos*, *and Coptoclava longidopa* (needs references here). The *Ephemeropsis trisetalis* are always well preserved including three tails, and often appear in large numbers in the same layer, associated with other fossils (Ji, 2004).

2.6 Arachnida

The spiders of the Jehol Biota are limited in number and species, and the common representatives are species of Araneidae (Araneida). Spiders are difficult to preserve as fossils because of their special software structure. One of the unknown species of Araneidae is preserved as a complete individual in life position with eight spread out feet visible; it was fast buried (Ji, 2004).

2.7 Agnatha and Fish

The fish fossils were successively studied by many scholars (Liu and Zhou, 1965; Zhang and Zhou, 1976; Ma and Sun, 1988; Su, 1991; Jin et al., 1993; Bai, 1983; Zhou, 1992; Jin et al., 1995; Zhang et al., 2001; Chang et al., 2006), the research on fish in the Jehol Biota has entered a new stage. Nowadays there are 15 species in 8 genera found in the Yixian and Jiufotang formations of western Liaoning.

2.8 Tetrapoda

The amphibians reported in the Jehol Biota all belong to the Lissamphibia. *Liaobatrachus grabaui* and *Callobatrachus sanyanensis* of the Yixian Formation are both also found in the Jianshangou sediments of the lower Yixian Formation in Sihetun village, Beipiao (Ji and Ji, 1998).

2.9 Chelonia

Up to date, the turtles *Manchurochelys manchouensis* and *Manchurochelys Liaoxiensis* have been reported, and most fossils are well preserved. The chelonian fossils often appear densely packed and are preserved along the bedding plane, indicating that they were concentrated together when they died in a catastrophe, being fast buried by volcanic ashes (Ji, 2004).

2.10 Choristoderes

Monjurosuchus splendens fossils were all found in the same horizon of the same basin. Two individuals found near Niuyingzi, Lingyuan, have been described as of different size; many well-preserved adult and juvenile *Monjurosuchus* fossils were found in recent years, with their toes on the foreleg digging into the soft layer, showing that they had a painful struggle before death (Ji, 2004).

2.11 Lepidosauria

The lepidosaurs of the Yixian Formation in western Liaoning are *Yabeinosaurus tenuis* and *Dalinghesaurus longidigitus*. The fossils are of almost complete bodies

Table 1 Main fossil tetrapod categories and their occurrence horizon in the Jehol Biota

Categories	Fossils	Yixian Formation	Jiufotang Formation
Amphibians	*Liaobatrachus grabaui*	Lower Sihetun layer	
	Callobatrachus sanyanensis	Lower Sihetun layer	
	Liaoxitriton zhongjiani		Huludao
Chelonia	*Manchurochelys liaoxiensis*	Upper Jianshangou layer	
	Manchurochelys sp.	Lower Jianshangou layer	
	Manchurochelys manchouensis	Zaocishan	
Saurian	*Yabeinosaurus tenuis*	Jingangshan layer	
	Dalinghesaurus longidigitus	Sihetun layer	
Theropoda	*Sinosauropteryx prima*	Sihetun layer	
	Protarchaeopteryx robusta	Sihetun	
	Caudipteryx zoui	Zhangjiagou layer	
	Sinornithosarus millenii	Sihetun layer	
	Sinornithosarus sp.	Sihetun layer	
	Dromaeosauridae gen. et sp. indet.	Fanzhangzi layer	
Choristoderes	*Beipiaosaurus inexpectus*	Sihetun layer	
	Microraptora zhaoianus		Shangheshou
	Microraptora gui		Dapingfang
	Shenzhouraptor sinensis		Baitaigou
	Hyphalasaurus lingyuanensis	Fanzhangzi	Baitaigou
Horned dinosaur	*Monjurosuchus splendens*	Danangou	
	Psittacosaurus sp.	Sihetun	Meileyingzi
	Psittacosaurus meileyingensis		
Pterosaur	*Eosipterus yangi*	Jianshangou	
	Dendrorhynchus curvidentatus	Lower Sihetun	
	Haopterus gracilis	Lower Sihetun	
	Chaoyangopterus zhangi		Xiaoyugou
	Liaoningopterus gui		Lamagou
	Sinopterus dongi		Baitaigou
Aves	*Confuciusornis sanctus*	Jianshangou	
	Changchengornis hengdaoziensis	Sihetun	
	Jinzhouornis yixianen	Wutun	
	Jinzhouornis zhangjiyingia	Heitizigou	
	Eoenantiornis buhleri	Bottom of Heitizigou	
	Liaoningornis longiditris	Lower Sihetun	
	Liaoxiornis delicatus	Dawangzhangzi	
	Lingyuanornis parvus	Dawangzhangzi	
	Longipteryx chaoyangensis	Sihetun	
	Cathayornis yandica		Qidaoquan
	Cathayornis cardatusis		Boluochi
	Cathayornis aberrantsis		Boluochi
	Longchengornis sanyansis		Boluochi
	Cuspirostriornis Houi		Boluochi
	Largirostres sexdentornis		Boluochi
	Chaoyangia beishanensis		Boluochi
	Sinornis santens		Boluochi
	Boluochia zhengi		Meileyingzi
	Yanornis martini		Boluochi
	Yixianornis grabaui		Yixian, Chaoyang
	Jeholornis prima?		Qianyang, Yixian
	Songlingornis linghensis		Dapingfang
Mammalia	*Maotherium sinensis*	Jianshangou	
	Zhangheotherium quinquecuspidens	Jianshangou	
	Sinobaatar lingyuanensis	Dawangzhangzi	
	Eomania scansoria	Dawangzhangzi	
	Jeholodens jenkinsi	Sihetun	

with twisted gestures, showing that there was a painful struggle before death (Ji, 2004).

2.12 Pterosaurs

There are tens of pterosaur fossils found in the Jehol Biota, and among them *Eosipterus yangi*, *Dendrorhynchus curvidentatus* and *Haopterus gracilis*, found in the Yixian Formation. The *Haopterus gracilis* fossil was found in a gesture that looks like its right forearms were tightly bitten by itself, which might have been caused by the toxic fumes from a volcanic eruption (Ji, 2004).There are also new findings in recent years (e.g. Jun et al., 2016).

2.13 Dinosaurs

Most of the theropod fossils are well preserved, with feathers, feather-like integumentary structures and skin impressions. *Sinosauropteryx* specimens have undigested food—lizard and mammalian skeletons in the stomach and

an intact egg in the abdomen. *Sinosauropteryx prima* is laterally preserved; a small individual was about 65 cm long, with sharp teeth and basically complete caudal vertebra preserved. It also has primitive feathers or fibrous skin derivatives on the back and tail, as well as gastric contents in the stomach. The neck is high and its tail is tilted. The adult *Sinosauropteryx* is a well-preserved specimen of about 1.06 m, squashed but in good integral shape. The 2-cm long ulnar and teeth of primitive mammals found between two ulnae of *Sinosauropteryx* provide direct evidence for its carnivorous nature. The fossils are locally preserved with pristine feathers, and the head and neck are twisted into the back.

The skull of *Protarchaeopteryx robusta* is broken. The tail vertebra are preserved, and the front hind limbs and the belt are intact and clear; the left femur proximal lateral has well preserved feathers.

Caudipteryx zoui is almost intact; the girdle is complete, the tail almost complete but warped, and the hind limbs are almost connected with body. The head is tilted back, the hind legs extended.

Dromaeosaurids exhibit preserved fine skeletons and filamentous skin derivatives. *Sinornithosarus millenii* is preserved with an almost complete skeleton, skull, waisted mid-section and many original slender feather impressions (skin derivatives) (Ji, 2004; Hao et al., 2015).

2.14 Birds

The avian fossils of the Jehol Biota were mainly discovered as a *Confuciusornis* flock and a *Liaoxiornis* flock in the Yixian Formation, and a *Cathayornis–Chaoyangia* flock in the Jiufotang Formation. The taxa comprise mainly *Confuciusornis sanctus*, *C. sunae*, *C. chuonzhou*, *C. dui*, *Changchengornis hengdaoziensis*, *Jinzhouornis zhangjiyingia*, *Eoenantiornis buhleri*, and *Liaoningornis longiditris* among others.

Confuciusornis is exquisitely preserved. The bones are intact, and the pinnule and pinna rachis of its flight feathers are clearly visible. Some individuals have long tail feathers preserved, presumably a secondary characteristic of males, indicating that there was sexual differentiation in appearance. A large number of *Confuciusornis* are preserved in one layer, and so Zhou and Hou (1998) speculated that this species was characteristically gregarious.

Liaoxiornis delicatus is almost complete with bones and impressions. The jaw, trunk, limbs and caudal vertebra are basically all preserved, shaped like wings, and graceful. The fossil is found in a tuffaceous shale interlayer of the Upper Jurassic Yixian Formation in Dawangzhangzi, Lingyuan city, Liaoning province.

Eoenantiornis buhleri from Heitizigou is a fossil with an almost complete skeleton and the impression of a ventral visual burial suggesting an autochthonous burial.

Liaoningornis longgiditris was found in Sihetun; it is the only member of the Neornithes in the Yixian Formation. The forearm, shoulder girdle, sternum, rib and part of its hind legs are preserved (Ji, 2004).

2.15 Mammals

The mammals include: *Zhangheotherium quinquecuspidens* and *Maotherium sinensis* from Jianshangou; *Jeholodens jenkinsi* from Sihetun; *Sinobaatar lingyuanensis*, and *Eomania scanaoria* from Dawangzhangzi, Lingyuan. The placental mammals *Eomaia scansoria* from a tuffaceous shale in the Yixian Formation at Dawangzhangzi is almost intact with preserved clear hair impressions or carbonized membranes, which are regularly distributed over the head and four limbs to the tail (Ji, 2004).

2.16 Algae, plants and sporopollen

Algal fossils are rare in the Yixian Formation in western Liaoning. Lu Huinan and Wang Qifei (1999) described 4 species in 2 genera from the Yixian Formation in northern Hebei and western Liaoning. *Minhechara* sp. is the only algae fossil from western Liaoning, where the age of the formation is speculated to be Early Cretaceous.

In 1934–1935, Yabe and Endo first reported the conifer *Schizolepis jeholensis* and an angiosperm *Potamogeton jeholensis* from the Yixian Formation of Lingyuan. In 1964, Miki described a small number of plant fossils, a total of 10 species in 10 genera, and established a new genus for the purpose of Gnetales, describing and establishing a new combination species. In 1980, Chen Piji initially identified *Equisetites* sp., *Phoenicopsis* cf. *angustifolia*, *Solenites* sp. and *Potamogeton*? sp. (Chen et al., 1980).

In recent years, many plant fossils have been found in the Jianshangou layer of the lower Yixian Formation of Huangbanjigou, Shangyuan, Beipiao. Cao Zhengyao and colleagues (1998), Duan Shuying (1997), and Sun Ge et al. (1998, 2002) first reported *Liaoxia chenii* Cao et Wu (Cao et al., 1998), *Eragrosites changii* Cao et Wu, fossilized leaves of the monocotyledons, *Chaoyangyia liangii* Duan (Duan, 1998), *Archaefructus liaoninggensis* Sun et al., and *Archaefructus sinenesis* Sun et al. Wu Shunqing (1999) described 50 species in 31 genera from this horizon, mainly including: Bryophyta, lycopods, Articulatae and Filicinae of Pteridophyta, cycad, Ginkgopsida, conifers of Spermatophyta, questionable gymnosperm Gnetales, Dicotyledoneae and Monocotyledoneae of Angiospermae and so on. Sun and Zheng (2001) reported 88 species from 56 genera out of

the Jianshangou layer in western Liaoning; Ding Qiuhong et al. (2003) reported 90 species in 52 genera in 2003.

3 Scientific Significance: Three Origins

The reason why the Jehol Biota has gained great attention is that the fossil species are extremely rich and unusually buried, and many of them involve some major problems of biological evolution. The palaeobios of western Liaoning covers almost all the transitional categories from the Mesozoic to the Cenozoic, providing great significance for the discussion and research of three origins: that of birds, of eutherian mammals, and of angiosperms.

3.1 Origin of birds

Birds are one of the most prosperous terrestrial vertebrates nowadays, with a total of more than 9000 species. The origin of birds has always been one of the major scientific concerns of the international scientific community. In the mid-19th century, *Archaeopteryx lithographica* was discovered in the Solnhofen region of Germany (1860), the Latin name of it originally intended for an ancient feathered animal, and it was considered as the ancestor of birds. Actually, *Archaeopteryx* is a transitional creature between dinosaurs and birds, the relationship of which scientists of that time did not realize. One of the greatest scientists of the 19th century, Thomas Henry Huxley was the first person who came up with the idea that “birds were descended from dinosaurs”. While the international scientific community did not accept Huxley's ideas at that time, “non-dinosaur–origin” hypotheses such as the “Thecodontia–origin” theory became the dominant idea. A century later, Professor J. H. John Ostrom (1973) came up with the idea that “birds evolved from a small theropod dinosaur”, and considered the relationship between birds (including Archaeopteryx) and theropod dinosaurs (such as *Deinonychus*) as more closely than that with other reptiles (Ji, 2004).

In 1995, Hou Lianhai et al. (1995b) first reported the first primitive bird fossil—*Confuciusornis sanctus*. The *Confuciusornis*, known as the *Archaeopteryx* of China, kicked off the study of bird origins in China.

The world's first feathered dinosaur, *Sinosauropteryx prima* Ji and Ji, 1996, a typical small theropod dinosaur, was discovered in Sihetun, Beipiao, western Liaoning (Ji and Ji, 1996). Because of these rare fossils, the international scientific communities have generally accepted that birds were evolved from small theropods, and scientists all over the world have agreed with Ji Qiang and Ji Shu’an, whereas some still assert different views. At the height of the controversy, Ji and Ji found a second feathered dinosaur—*Protarchaeopteryx robusta* in western Liaoning (Ji and Ji, 1997a), once again proving that many of the theropods animals in were feathered, and strongly supported the theory that birds evolved from small theropod dinosaurs.

Ji Qiang, P. J. Currie, M. A. Norell and Ji Shu’an (2013) then wrote a cover article in *Nature* about newly discovered feathered dinosaurs—*Caudipteryx zoui* Ji et al., 1998 and *Protarchaeopteryx* (Ji et al., 1998). And two comments were made specifically as “Dinosaurs and birds: the debate is over” and “When is a bird not a bird?”.

In February 1999, the Osterlung International Symposium on the origin and early evolution of birds was held in Yale University, and a landslide participation of more than 500 scientists accepted the idea that "birds evolved from small carnivorous dinosaur", and the "discovery of *Sinosauropteryx* and other rare fossils in western Liaoning, China is one of the most important scientific discoveries of the 20th century", "the most important event in international life evolution research field since Darwin put forward the theory of evolution". The Yale conference is an important symbol of the international scientific community's recognition of the value and research achievements of the feathered dinosaurs in China. The discovery of fossils such as *Sinosauropteryx*, *Protarchaeopteryx* and *Caudipteryx* provided solid evidence to prove Huxley's hypothesis into a theory. The research achievements of Ji Qiang et al. have basically solved the problem of the origin of birds that had not been solved for more than 140 years, and they have had a significant impact on the academic community and the public.

After the Yale conference, many feathered dinosaurs such as *Beipiaosaurus*, *Sinornithosaurus*, *Microraptor*, *Sinovenator*, provided new evidences for the “Thecodontia -origin” theory of birds (Xu et al., 1999, 2000, 2002).

3.2 Origin of eutherian mammals

About 220 million years ago, the earliest mammals appeared on earth almost simultaneously with the earliest dinosaurs. The mammals of that time were in low numbers but varied, including a few early mammalian higher taxa such as symmetrodonts, lasting from the late Triassic until the late Cretaceous and then they went extinct.

The Mesozoic mammal fossils of the Jehol Biota in western Liaoning are also rare, comprising *Zhangheotherium quinquecuspidens*, *Maotherium sinensis*, *Jeholodens jenkinsi*, *Eomaia scansoria*, *Sinodelphys szalayi* among others.

3.2.1 *Zhangheotherium quinquecuspidens*

Hu Yaoming and others described and named the *Zhangheotherium quinquecuspidens* Hu et al., 1997 (Hu et al., 1997). They was classified it as within the Symmetrodonta, an important clade of early mammals, and was donated to Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica by Mr. Zhang He, the rock collector of Jinzhou. It was named based on its dental structure where all upper and lower molars have five tips, and reported in the journal *Nature*. *Z. quinquecuspidens* was the first mammal found in the Jehol Biota, and the best Mesozoic mammalian fossil preserved in the world. It is about the size of a rat and placed in a basal position in the phylogeny of mammals, which leaves the phylogenetic relationship of early mammals to be further explored.

3.2.2 *Jeholodens jenkinsi*

Ji Qiang, Luo and Ji (1999) found the triconodont mammalian fossil—*Jeholodens jenkinsi*, the oldest, the most complete, and most exquisite fossil of the Mesozoic triconodont fossils in the world. *J. jenkinsi* has three-cusped teeth, which are very good for an insectivore.

3.2.3 Placental *Eomaia scansoria*

Ji Qiang, Luo Zhexi et al. (2002) reported the finding of placental mammal specimens in the Jehol Biota and named the new taxon *Eomaia scansoria*. This is the earliest and the most primitive placental mammal known, providing new evidence for the origin and early evolution of eutherian mammals. The geological age of *E. scansoria* should be 125 to 130 Ma, which pushed forward the origin of eutherian mammals at least 1 million to 1.5 million years earlier.

3.2.4 Marsupialia *Sinodelphys szalayi*

In 2003 in the journal *Science*, Luo Zhexi, Ji Qiang et al. (2003) reported the earliest marsupial fossils known—*Sinodelphys szalayi*. This taxon represents the most primitive species of all Metatheria (including marsupials), which provides valuable scientific information for the early evolution of the marsupial mammals.

The Marsupialia and Placentalia are all viviparous, and their origin and early evolution have important scientific significance. The differentiation between eutherian mammals and Metatheria may have been earlier than previously thought. In addition to the fact that they originated in the northern hemisphere, the fossils from the Jehol Biota suggest that northern China was likely the center of their origin.

3.3 Origin of angiosperms

Angiosperms, also known as flowering plants, are known currently in the world from more than 234000 described species in 437 families. Their origin has been one of the major scientific concerns of the international scientific community, and many published hypotheses have had inescapable weaknesses.

Chinese scholars have also been trying to solve this problem. Dr. Ren Dong published a study on the coordinated evolution of anthophilous insects and flowering plants in *Science* (Ren, 1998), which kicked off our research on the origin of angiosperms, based on the appearance of the numerous anthophilous insects in the Jehol Biota in western Liaoning. Ren and Hong (1998) published the study on the coordinated evolution of flower insects and flowering plants, which kicked off our research on the origin of angiosperms, from which it can be speculated that flowering plants should have existed during the late Jurassic to early Cretaceous periods. In the same year, Sun Ge et al. (1998) also reported in *Science* a fossil fruit with seeds and female reproductive branches in the Jehol Biota—*Archaefructus liaoningensis*, which has greatly driven the study of the origin of angiosperms in China.

In 1999, based on the discovery of new fossils, Ji Qiang et al. (2004) suggested that whether the angiosperms are of terrestrial or aquatic origin should be reconsidered and a collaboration on this study began with the Nanjing Institute of Geology and Palaeonotology, Chinese Academy of Sciences. Then Sun Ge et al. (2002) insisted that the newly found plant fossils should be classified as "*Archaefructus*"; they established a new species—*Archaefructus sinensis* (Sun Ge et al., 2002) and a new higher taxon of primitive angiosperms—Archaefructaceae, and considered that they were herbaceous aquatic vegetation.

The *Archaefructus* fossils found in the Jehol Biota in western Liaoning are still the most complete and earliest angiosperms to date. They have greatly promoted international scientific research on the origin and early evolution of angiosperms, and suggest that angiosperms might have originated in western Liaoning province. It also provides solid fossil evidence for proving the theory that East Asia is the center of angiosperm evolution, which has great significance for the restoration of paleogeography, paleoclimate and the search for sedimentary minerals in China and eastern Asia.

4 Conclusions

After the research of about half of a century, especially in recent decades, the Jehol Biota is now much enhanced from the simple original "*Eosestheria–Ephemeropsis–Lycoptera*" association, and has become the focus of

international paleontological fieldwork. The Jehol sequence has uniquely complete Mesozoic continental strata. The unique feathered dinosaur fossils, the abundant primitive bird fossils and plant fossils make this region the center of the study for “three origins” in the scientific community. If the eutherian mammals are found in the Jehol Biota, that means they can mount a challenge to the current ideas about the origin of eutherian mammals, which also are very controversial, and deepen the study of Mesozoic mammals.

Since 1995, Chinese scholars have published more than 30 papers about studies on the Jehol Biota in such international journals as *Nature* and *Science*, some with western colleagues. Thus, such work has great influence both in academia and with the public, and represents a unique research field in Chinese geological scientific research and one of the highlights of basic scientific research in China.

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