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Vertebrate radiations of the Jehol Biota and their environmental background

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Significant progress has been made in recent years in the studies of various groups of the Jehol Biota, particularly concerning the origin of birds and their flight as well as the evolution of Early Cretaceous birds, dinosaurs, mammals, insects and flowering plants[1—5]. As a result, the Jehol Biota has become well known to both the scientific community and the public. The studies on the Jehol Biota also revealed the patterns and processes of the evolutionary radiations of many major groups of Early Cretaceous animals and plants, such as the earliest known radiation of angiosperms and birds, early differentiation of mammals and many Cretaceous dinosaurian groups. Notably, the radiations of the Jehol vertebrates share some similar patterns attributable to the particular environmental background. For instance, the Jehol vertebrate radiations are highlighted by the presence of abundant arboreal adaptations and herbivorous forms, thus closely linked to the forest environments. In addition, the differentiation of habitats and diets is also characteristic of the evolutionary radiations of pterosaurs, dinosaurs, birds and mammals in the Jehol Biota.

The pterosaur radiation in the Jehol Biota was dominated by the short-tailed pterodactyloid pterosaurs[6—9]. The Yixian Formation and the overlying Jiufotang Formation represent the two successive stages of the radiation of the Jehol pterosaurs. These pterosaurs all possessed both arboreal adaptations and strong flying capability. Except a few insectivorous forms, most of them fed on fishes or other aquatic animals. Conceivably, the Jehol pterosaurs mainly lived in the forest near the freshwater lakes.

The Jehol Biota marks a significant radiation event in the evolutionary history of dinosaurs. The known dinosaurs from this biota can be referred to at least 14 families or higher categories of classification[10,11]. Many of them had occurred for the first time in the Early Cretaceous, and became further diversified in the Late Cretaceous. Among the Jehol dinosaurs, except a few carnivorous forms such as compsognathids, dromaeosaurids and troodontids, most are herbivorous, including oviraptorosaurids, ornithomimosaurids, psittacosaurids, ankylosaurids, neoceratopsians, iguanodontids, and ornithopods[11—14]. It is notable that the oviraptorosaurian *Incisivosaurus* represents the first known theropod with a specialized dental differentiation for herbivorous diet[14]. It is also noteworthy that most Jehol dinosaurs lived on ground, yet *Microraptor* represents the first known arboreal form in the evolutionary history of dinosaurs[1,15]. The discovery of arboreal dinosaurs are important because they represent not only a key transitional stage between terrestrial dinosaurs to birds, but also the expansion of the adaptive spaces of dinosaurs. Obviously, the success of the radiation of the Jehol dinosaurs was inseparable from the flourishing forest, which provided both the habitat and dietary resources for the dinosaurs to differentiate.

The Jehol Biota also encompasses the first important radiation in avian history. The Jehol birds comprise at least 13 families, 20 genera and 23 species whereas only one genus and two species of birds have been recorded in the Late Jurassic. The success of the early avian radiation was probably largely due to their possession of strong flying and arboreal capability with the development of such key structures as a keeled sternum and an opposing hallux of the foot. Birds could explore new adaptive zones and exploit more food resources with these major evolutionary innovations. Majority of the birds in the Jehol Biota are arboreal types, including the most basal birds such as *Jeholornis* and *Cofuciusornis*. Of the two major monophyletic avian groups (Enantiornithes and Ornithurae) in the Mesozoic, the Enantiornithes in the Jehol Biota inherited the ancestral arboreal life[16], while the much more advanced Ornithurae were mainly shorebirds[17], representing the exploitation of new ecological niches. The morphological differentiations and habitat selections in early birds were accompanied by a variety of dietary adaptations, exhibited by the frugivorous *Jeholornis*[2], piscivorous *Yanornis*[17] and *Longipteryx*[18], and many more insectivorous birds including most enantiornithines.

All of the eight known mammal species of the Jehol Biota were from the Yixian Formation. They are represented by fossils of several major mammalian groups, including Symmetrodonta, Triconodonta, Multituberculata, Eutheria and Metatheria. These early mammals diversified significantly in body size (from dozens grams to several kilograms) and locomotive styles due to adaptations to various ecological environments[19]. Among the Jehol mammals, *Jeholodens*, *Sinobaatar*, *Zhangheotherium*, and gobiconodontids all show terrestrial adaptation, while, *Sinodelphys*[19], the oldest known metatherian, and *Eomaia*[20], the oldest known eutherian, possess climbing and tree-living features in the skeleton, showing the trend of increasing scansorial and arboreal adaptations in the early mammalian evolution. The Jehol Biota has also been purported to be the center for the diversification of the earliest metatherians and eutherians during the Early Cretaceous[19], which was also related to the flourishing forest environment in this area.

Two prominent positive carbon excursions in the Early Cretaceous coincided with episodes of increased volcanic activities, and occurred in response to elevated atmospheric carbon dioxide levels and resulted climate changes[21], such as the rising atmospheric temperature that is conducive to the increased productivity and diversity of plants. The angiosperms first occurred in early Early Cretaceous, and had not begun to radiate significantly until in late Early Cretaceous[22]. Some advanced angiosperms had already appeared in the Jehol Biota, such as the basal eudicot *Sinocarpus*[23]. The increasing rate of diversification of angiosperms in the late Early Cretaceous may also be related to the elevated CO_2 level and the greenhouse temperature at the time.

The Early Cretaceous is generally characterized by high rates of sea floor spreading, volcanism, excess atmospheric CO_2, high surface temperature, and important paleogeographic changes. The relatively isolated freshwater lakes in the western Liaoning region during the Early Cretaceous provided a fundamental environmental background for explaining the patterns of the evolutionary radiations of the Jehol Biota. In addition, the presence of embayment and the damp climates in eastern Heilongjiang Province at the same time might have played an important role in the Jehol flora's flourishing[24].

The major paleogeographic changes during the Early Cretaceous in East Asia and neighboring areas may also provide clues to explaining the dispersals of the Jehol Biota. East Asia was isolated from the rest of the Laurasia since the Middle Jurassic. The paleogeographic framework at the time is as follows: East Asia was separated from the Siberia by the slender Mongol-Okhotsk Ocean; the Turgai Epicontinental Sea existed between Central Asia and Europe; the Mongolia-Tarium-Junggar land connections began to break up that had linked East Asia and Eurasia from Triassic to Early Jurassic; Asia was separated from North America by the ancient Pacific; and further, in China the North China block was separated from the South China block by the Qilian-Qinling-Dabie mountains. The isolation of East Asia from the rest of the world resulted in some local or endemic fossils in the Jehol Biota. By the early Cretaceous the Turgai Epicontinental Sea had regressed and the Mongol-Okhotsk Ocean was closed[25,26]. Incidentally, such a geographic isolation did not completely rule out biotic exchanges. Even in the Late Jurassic, there were probably frequent biotic exchanges between Asia and Europe, especially for those with powerful flight capability such as birds and pterosaurs, which were less susceptible to the geographic barriers. For instance, the pterosaur assemblage of the earlier stage of the Jehol Biota bears a close resemblance to that of the Late Jurassic in Europe[6,7]. Similar species of insects that possessed strong flying capability were also found in both Asia and Europe[27]. It appears that many biological species such as birds, pterosaurs and insects dispersed to East Asia from Europe at that time despite the geographic isolation of East Asia.

It is noteworthy that the pterosaur assemblage at the later stage of the Jehol Biota already shares many similarities with that of the late Early Cretaceous deposit in Brazil, and many of the taxa also had a global distribution[8,9]. Besides, the pterosaurs in the Jehol Biota are generally more primitive compared with those of Brazil and other Cretaceous deposits. In fact, many other vertebrates including dinosaurs, birds and mammals in the Jehol Biota often represent the most primitive member of their respective groups. It appears that with the regression of the Turgai Epicontinental Sea and closing of the Mongol-Okhotsk Ocean, and the consolidatation of the Eurasia, the Jehol Biota had more frequent and extensive exchanges with the outside world by the late Early Cretaceous. Besides, the birds and pterosaur with strong dispersal capability, more vertebrates such as dinosaurs and mammals were able to radiate and disperse into a larger area; some biological groups with a probable Asian origin, such as some dinosaur and pterosaur families, Enantiornithes, Eutheria and Metatheria, etc., had started their global geographic expansions and evolutionary radiations[10,19,28]. Admittedly, however, the reverse dispersal could as well have existed between the Jehol Biota and other areas in the Early Cretaceous.

In summary, the evolutionary radiations of birds, dinosaurs, pterosaurs and mammals in the Jehol Biota are undoubtedly closely related to the flourishing forest environment. As a result of the adaptation to the lives in trees or bushes, there appeared many arboreal and scansorial species, or vertebrates with herbivorous diets. Early birds in the Jehol Biota mainly lived in an arboreal life, and only advanced birds had exploited new niches outside the forest and became successful in the near-shore environment. The arboreal dinosaurs are not only critical to the radiation of dinosaurs but also to the origin of birds and their flight. Early mammals that were adapted to scansorial life had played an important role in the origin of both the Eutheria and Metatheria. By the late Early Cretaceous, a "thawing" of the isolation of the Jehol Biota from the outside world had laid the foundation for the further dispersal and radiation of the biota as well as its exchanges with other contemporaneous biota worldwide.

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