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Major Features of the Vertebrate Diversity of the Early Cretaceous Jehol Biota and Their Paleoecological Implications

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INTRODUCTION

The Early Cretaceous Jehol Biota represents one of the best preserved terrestrial lagerstätten. It is now best known for producing such extraordinary fossils as feathered dinosaurs, early birds, mammals, pterosaurs, lissamphibians, insects, and flowering plants. The Jehol fossils are also known to be exceptionally preserved, many of which are complete and articulated, often with preservation of soft tissues such as feathers, hairs, skins, muscles, and even melanosomes that contain information about color of integuments (Zhang et al., 2010).

The discoveries of the Jehol fossils provide important clues for understanding the evolution of many biological groups, e.g., particularly the origin of birds and their flight and feathers, the Cretaceous radiation of birds, dinosaurs, pterosaurs, amphibians, and mammals as well as insects and angiosperms (Benton et al., 2008; Zhou et al., 2003).

Despite over a century's history of fossil collecting in northeastern China, our knowledge of the Jehol Biota has only been significantly increased in the past twenty years thanks to recent intensive collecting and study as well as overwhelming scientific and public interest of the newly discovered fossils. As a result, the diversity of the Jehol Biota is now much better known than ever before, which has greatly improved our reconstruction of the Early Cretaceous terrestrial ecosystem. This short article is intended to provide a brief discussion of the vertebrate diversity of the Jehol Biota, its major features, and its paleoecological implications.

VERTEBRATE DIVERSITY OF THE JEHOL BIOTA

The vertebrate assemblage from the Jehol Biota in western Liaoning, northern Hebei, and southern Inner Mongolia in Northeast China currently comprises, at the generic count, approximately 31 birds, 30 dinosaurs, 16 pterosaurs, 13 mammals, 5 lizards, 5 choristoderes (extinct reptiles), 2 turtles, 8 amphibians, and 7 fishes as well as 1 agnathan, totaling 118 genera. All of them have been recognized as members of extinct genera and species, and only a few of them (e.g., some fishes and amphibians) can be referred to extant vertebrate families.

The Jehol vertebrate assemblage is known not only for its taxonomic diversity but also for its remarkable differentiation in diet, locomotion and habitat. For instance, among birds, there existed a great differentiation of flight capability, which can be related to their dietary and habitat preference, and ac-

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cordingly their structural innovations also appeared in mosaic and seem to be consistent with their locomotion styles. Remarkable size variations can also be found in birds, dinosaurs, pterosaurs and mammals, which also account for the radiations of the Jehol vertebrates.

The vertebrate diversity of the Jehol Biota exceeds that of other contemporaneous lagerstätten such as the Santana Fauna from Brazil, and the Las Hoyas Fauna from Spain (Herculano Alvarenga pers. comm. 2010; Buscalioni et al., 2008). In particular, the diversity of birds, dinosaurs, mammals, and pterosaurs is much greater than in any other areas. For instance, the Jehol birds make up more than one third of the total avian diversity in the Mesozoic; the Jehol mammals comprise representatives of nearly all major groups of Mesozoic mammals.

The Late Jurassic Solnhofen lagerstätte best known for preserving the oldest bird *Archaeopteryx*, comprises vertebrates from both marine and terrestrial habitats. The estimated total number of vertebrate genera and species is approximately equal to that of the Jehol Biota (Helmut Tischlinger, pers. comm. 2010); however, more than half of them are fishes, and no mammal or amphibian has been reported. Thus, it contains arguably less information than the Jehol Biota does about the Mesozoic vertebrate evolution and particularly the terrestrial ecosystem in which it occurred.

PALEOECOLOGICAL IMPLICATIONS

The vertebrate diversity of the Jehol Biota is an integral part of the Jehol ecosystem. Therefore, the interactions among various vertebrate groups as well as among the vertebrates, invertebrates, and plants had definitely played a key role in the succession of the Jehol ecosystem. One of the most distinctive features of the Jehol vertebrate assemblage is the presence of a high percentage of arboreal (or scansorial) and herbivorous forms including birds, pterosaurs, dinosaurs, mammals, and lizards, which strongly suggests that the forests were vital to the evolution and radiation of various important vertebrate groups at this stage (Zhou, 2004). For instance, approximately 75% of the birds lived an arboreal life, and less than 25% of them (mainly ornithurines with the most sophisticated flight capability) were terrestrial or lake shore dwellers. Most of the pterosaurs are believed to be arboreal. Many of the Jehol dinosaurs are known to be herbivorous, including a number of theropods such as oviraptorosaurs and ornithomimosaurs as well as nearly all ornithischians and titanosauriforms. Other arboreal or scansorial forms also include some, mammals (e.g., *Sinodelphys*), and lizards (e.g., *Xianglong*). The scansorial adaptation had probably played a key role in the origin of eutherians and metatherians.

The dietary differentiation of the Jehol vertebrates is equally significant. Thanks to the extraordinary preservation of the lagerstätte, the stomach contents of various vertebrates provided direct evidence for their dietary reconstruction, such as piscivorous birds, carnivorous dinosaurs and mammals as well as various herbivorous birds and dinosaurs.

Insects most likely are the prey of most amphibians, mammals, lizards, and many birds. Fishes as the most common vertebrates in the lakes also played an important role in the food web of the Jehol ecosystem. Many of the Jehol pterosaurs are believed to be piscivorous, and fishes are recognized as the major food source for the presumably hot-blooded ornithurine birds, one branch of which finally evolved into modern birds.

Current paleogeochronological work on the ash bed interbedded with the fossil-bearing Jehol lake deposits provided compelling evidence for the temporal distribution of the Jehol Biota, approximately from 131 to 120 Ma (Hauterivian to Aptian), and most developed at the duration of 125–120 Ma, which makes it possible to relate the evolution of the Jehol Biota to some major global or local geological events in the Early Cretaceous (Zhou et al., 2009; He et al., 2006) such as active tectonic activities, frequent volcanism (Guo et al., 2003), global warming and seasonal climatic changes (Steuber et al., 2005), the disappearance of geographic barriers between East Asia and European continent (Zhou, 2006), the North China craton destruction, and mantle thinning as well as the development of extensional basins in northeastern China (Wu et al., 2008).

Although the success of the Jehol vertebrate diversity must have had a complex geological, paleogeographical, and paleoenvironmental background,

our understanding of the biological evolution and paleoenvironmental background remains poor compared to our knowledge of the lagerstätte.

CONCLUSIONS

The Jehol lagerstätte is undoubtedly one of the best windows to look into the Early Cretaceous terrestrial ecosystem. It comprises nearly all major groups of vertebrates. Its vertebrate assemblage is characterized not only by its great taxonomic diversity but also by its remarkable differentiation in diet, locomotion, size, and habitat. The success of the Jehol vertebrate radiations is related to both the interactions among various vertebrate groups, invertebrates, and the flora, and the unique global and local paleoenvironmental and paleoecological background in the Early Cretaceous. Despite much progress made in the past twenty years concerning the biological aspects of the biota, more studies remain to be done in order to better understand the co-evolution of the organisms and their paleoenvironments.

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