



The Jehol Biota: Definition and distribution of exceptionally preserved relicts of a continental Early Cretaceous ecosystem

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ARTICLE INFO

Article history:

Received 22 January 2013

Accepted in revised form 23 March 2013

Available online 24 April 2013

Keywords:

Jehol Biota

Palaeoecology

Taphonomy

Konservat-Lagerstätten

Jehol Group

Early Cretaceous

Northeastern China

ABSTRACT

Fossils from the “Jehol Biota” have been studied for nearly 90 years, and the term “Jehol Biota” has been extensively used and is well known today, largely thanks to the discovery of feathered dinosaurs, angiosperms, and numerous other exceptionally preserved fossils in the Lower Cretaceous of northeastern China. Ironically, however, what exactly the Jehol Biota represents and how it is defined has hardly been discussed. The lack of a precise definition of the Jehol Biota has hindered our understanding of such important issues as its palaeodiversity, its spatial and temporal distribution, and the pattern of radiation of the biota. In this paper, we propose that the Jehol Biota is defined by using a palaeoecological concept, and by combining ecological and taphonomic aspects, i.e., as organisms that lived in the Early Cretaceous volcanic-influenced environments of northeastern China, and were buried in lacustrine and rarely fluvial sediments, where most turned into exceptionally preserved fossils. The relationship between the Jehol Biota and the Jehol Group is also clarified. According to the revised definition, the Jehol Biota is so far only discovered in deposits of the Yixian and Jiufotang formations of western Liaoning, adjacent Inner Mongolia, and northern Hebei, and the Huajiyang Formation of northern Hebei. Temporally it ranges from the Barremian to Aptian, i.e., for at least 10 Ma (130–120 Ma).

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1. Introduction

Understanding the history of any particular extant or extinct ecosystem represents one of the major topics of evolutionary studies. The Early Cretaceous “Jehol Biota”, as one of the best preserved continental ecosystems in earth history, witnessed many important evolutionary transitions, e.g. documents how feathers might have evolved and also shows an early burst of avian diversification, and the early diversification of angiosperms. The Jehol Biota has been studied for nearly a century, yet there is no generally accepted, unambiguous definition of the “Jehol Biota”. The composition and distribution of the “Jehol Biota” vary greatly according different authors. An overview of the history of the use of the term “Jehol Biota” shows that there exist at least four opinions. First, the Jehol Biota is understood on the basis of its traditional and oldest definition, i.e., as a lacustrine biota characterized by the *Eossetheria* – *Ephemeropsis* – *Lycoptera* (EEL)

fossil assemblage (e.g., Grabau, 1928; Gu, 1962; Chen, 1988). The second concept of the Jehol Biota involves a much more expanded distribution and composition, i.e. it represents a terrestrial and lacustrine biota comprising all fossils of the Lower Cretaceous Jehol Group or equivalent strata of adjacent areas in eastern and central Asia (e.g., Chang et al., 2003; Zhou et al., 2003; Zhou, 2006). The third use of the Jehol Biota includes all the fossils that co-occurred with *Lycoptera*, *Peipiaosteus*, and *Ephemeropsis* (e.g., Ji, 2002; Ji et al., 2004a). Finally, the fourth and last definition of the Jehol Biota recently proposed, refers to a fossil assemblage comprising all fossils from the large-scale tectonic-sedimentary cycle between the Shalei and Fuxin formations that is composed of fan-delta and lacustrine-swampy coal-bearing deposits and the Zhangjiakou Formation of acidic volcanic rocks (Jin et al., 2008).

As a result of the different definitions or understanding of the Jehol Biota, the geographic distribution of the biota also differs markedly, whereby mainly two opinions have been put forward. Some workers suggested that the Jehol Biota is widely distributed in central and eastern Asia, including northeastern China, the Korean Peninsula, Japan, Mongolia, Kazakhstan, and Siberia (e.g., Gu, 1962; Chen, 1988, 1999; Chang et al., 2003; Zhou et al., 2003).

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Other authors limited the composition and distribution of the Jehol Biota (or the Jehol Biota *sensu stricto*; Zhou and Wang, 2010) to a small area in northeastern China, including only northern Hebei, western Liaoning, and southeastern Inner Mongolia (e.g., Zhou, 2006; Zhou and Wang, 2010; Zhang et al., 2010b).

From this review it becomes clear that the current use of the Jehol Biota is both ambiguous and differs substantially: its definition is either based on the occurrence of the representative fossil assemblage, on the geographic distribution of representative fossil elements, or on the tectonic setting. Furthermore, only few workers have provided a clear definition of the Jehol Biota in their publications.

Lacking a precise and generally accepted definition of the Jehol Biota is becoming a problem when such important issues as its palaeobiodiversity, its spatial and temporal distribution, and the pattern of the radiation of the Jehol Biota are discussed, which are attracting more and more attention from workers in various areas (e.g., Chen, 1988, 1999; Zhou, 2006; Gao et al., 2009; Li et al., 2010b; Zhou and Wang, 2010; Zhang et al., 2010b; Chang et al., 2012).

In this paper, we aim to provide an unambiguous definition of the Jehol Biota based on ecological and taphonomic aspects, and further discuss the spatial and temporal distribution patterns of the Jehol Biota in terms of the new definition.

2. The development of the term “Jehol Biota”

The name “Jehol fauna” (spelled Jehol by later authors) was first coined by A.W. Grabau to refer to the fossil community from the lacustrine Jehol Series in Liaoning, northeastern China (Grabau, 1928, p. 674). In 1962, the Chinese palaeontologist Gu Zhiwei first proposed the name “Jehol Biota” in his monograph “Jurassic and Cretaceous of China” (Gu, 1962) after working on various *Lycoptera* (a fossil fish) – bearing deposits from different areas of western Liaoning. In the same monograph, he had actually used several names to describe the fossil community represented by “*Bairdestheria middendorffii* – *Ephemeropsis* – *Lycoptera*”, e.g. “Jehol fossils” (p. 11), “Tujiaer fossils” (p. 11), “*Lycoptera* layer biota” (p. 15), as well as the name “Jehol biota” which was the most frequently used term (p. 20, p. 50, p. 76).

Later, the genus *Eosestheria* Chen, 1976 was established based on material from western Liaoning (Zhang et al., 1976, p. 153), and it was further suggested that the fossil spinicaudatans (conchostracans) from the Jehol fauna previously identified as “*Bairdestheria middendorffii*” [the species was first described under the genus *Estheria* by Jones (1862), and was later revised into *Bairdestheria* by Raymond (1946)] should be referred to *Eosestheria middendorffii*. Since then, the Jehol Biota as a lacustrine biota represented by the “*Eosestheria* – *Ephemeropsis* – *Lycoptera*” (EEL) assemblage was gradually accepted and became well known (e.g., Chen, 1988).

Zhang et al. (1994) restudied the anatomical characters and morphological variation of the “*Lycoptera longicephalus*” material from the Jiufotang Formation, and revised it as *Jinanichthys longicephalus*. Thus, the temporal range of *Lycoptera*, which has often been regarded as a representative fossil of the Jehol Biota, is now actually limited to the Yixian Formation.

Recently, the taxonomic assignment of another classic representative of the Jehol Biota, *Ephemeropsis* (an insect) of the EEL assemblage has also been seriously challenged. Kluge (2004) treated it as a synonym of *Hexagenites* Scudder, 1880. Huang et al. (2007) compared “*Ephemeropsis*” from the Yixian Formation with *Ephemeropsis* Eichwald (1864) from the Lower Cretaceous strata of Transbaikalia and Mongolia, and found distinct differences in the membrane structures and veins. They also argued that the hind wing of specimens from the Yixian Formation is slightly more than half the length of the forewing, in contrast to *Hexagenites* Scudder

(1880), in which the length ratio of the hind wing to forewing is less than 0.5. Thus, Huang et al. (2007) proposed a new genus name, *Epicharmeropsis* for the specimens from the Yixian Formation. Considering the controversy on the taxonomy of the insects from the Yixian Formation, “*Ephemeropsis*” can probably no longer be regarded as an appropriate name of representative fossils for the Jehol Biota.

During the last two decades, the discoveries of many new taxa of terrestrial plants and vertebrates often represented by exceptionally preserved specimens, have provided opportunities to address some critical evolutionary topics, and the traditional representatives of the Jehol Biota, i.e., the aquatic *Eosestheria* – *Ephemeropsis* – *Lycoptera* (EEL) assemblage probably no longer well represents the composition of the Early Cretaceous terrestrial ecosystem in this region. Many workers have proposed that the Jehol Biota should include all aquatic and terrestrial fossils from the Lower Cretaceous Jehol Group or equivalent strata of the adjacent areas (e.g., Chen, 1999; Chang et al., 2003). Although it is now generally accepted that the Jehol Biota comprises fossil assemblages from both lacustrine and terrestrial ecosystems, it remains a controversial issue as to whether we should treat the Jehol Biota as an exact equivalent of fossil assemblages of the Jehol Group, of which the definition is also debatable (see discussion in later part of this paper).

Some workers suggested that the Jehol Biota should include all the fossils that co-occurred with *Lycoptera*, *Peipiaosteus*, and *Ephemeropsis* (e.g., Ji, 2002; Ji et al., 2004a). This proposal is a modified version of the traditional definition of the Jehol Biota, represented by the characteristic EEL assemblage, but with another common fish, *Peipiaosteus*, replacing *Lycoptera* as *Lycoptera* has a much more limited temporal distribution.

It is difficult to choose the diagnostic elements (e.g., EEL or LPE) while there are many other fossils that are equally common in the biota. Moreover, it is not common that the representatives occurred all together in the fossil assemblage of a specific locality or region. Generally, each of the representatives has its own special or temporal range.

Jin et al. (2008) provided a definition of the Jehol Biota that is completely based on the tectonic setting. They suggested that the definition of the Jehol Biota should be based on the large-scale tectonic-sedimentary cycle, including all fossils that occurred between the Shahai and Fuxin formations and the Zhangjiakou Formation, with the upper boundary defined by the commencing of fan-delta and lacustrine-swampy coal-bearing deposits and the lower boundary by the ending of the eruptive-sedimentary cycle. The large-scale tectonic-sedimentary cycle is recorded in the lithological and sedimentary features of the rocks, which to some extent exhibit a unique palaeoenvironmental background. Such a definition resembles some previous suggestions that the Jehol Biota is equivalent to fossil assemblages from deposits of the Jehol Group, while the lithostratigraphic units are used for definition. Yet, it remains questionable whether a fossil biota should be defined simply on the basis of a tectonic background.

In sum, it seems that despite the use of the term “Jehol Biota” for about half a century, a generally accepted and unambiguous definition of the biota is still lacking.

3. Definition of the Jehol Biota: from biota to a fossil biota

An ecosystem consists of a biotic community and its abiotic environment, interacting as a system (e.g., Tansley, 1935; McIntosh, 1986; Santra, 1994). The biotic community is an aggregate of organisms which form a distinct ecological unit, which is defined in terms of its flora, fauna or both (as biota) (e.g., Santra, 1994, p. 49). While the size of an ecosystem is not specifically defined, it usually encompasses a specific, limited area and time (e.g., Chapin et al.,

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