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

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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 Huajiying Formation of northern Hebei. Temporally it ranges from the Barremian to Aptian, i.e., for at least 10 Ma (130–120 Ma).

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 *Eosestheria* – *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 Shahai 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 "Johol fauna" (spelled Jehol by later authors) was first coined by A.W. Grabau to refer to the fossil community from the lacustrine Johol 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 middendorfii* – *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 middendorfii*" [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 middendorfii*. 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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2002, p. 380), occasionally up to planet- and whole-time-scale scales, e.g. the biosphere. Thus there are three principal restrictions to distinguish a biota: a particular geographic region, a specific time, and a certain ecological habitat.

"In dealing with distribution and succession of major faunas and floras, as well as in tracing the development of environments and habitats, the ecologist must use the geological data" (Fenton, 1934, p. 64). The first integrated discussion of palaeocommunities was presented by Elias (1937), who analysed the Carboniferous faunas of the Big Blue Group in Kansas. Gradually, the terms of fauna, flora, and biota were applied to palaeontological studies, especially with the progress of community palaeoecology.

Most palaeontologists use biota to refer to a typical collection of a fossil community occurring in a specific time slice and area, or in a specific stratigraphic unit. Mostly they are only represented by the shelly or bony relicts of a life biota, and they are far from representing a whole biota. It is almost impossible for a life biota to be completely preserved in the fossil record. Thus, a direct copy or application of the definition of an ecological biota to palaeontology is not desirable. A fossil biota, composed of a fossil fauna and a fossil flora confined to a particular region and time should comprise as much information about its former life biota as possible. A fossil biota is expected to contain the best record or source for reconstructing a life biota or even an ecosystem in a particular region and time. However, one of the most serious problems encountered in palaeoecological reconstruction is assessing to what extent the fossil record faithfully records that of the original life community. The formation of the fossil record experiences two transitions: transition from life to death assemblage and from death to fossil assemblage (e.g., Fürsich and Flessa, 1991; Kidwell and Flessa, 1995; Kidwell, 2001). Meaningful interpretation of the fossil record requires the identification of contributing taphonomic pathways and their differential distribution in both time and space (Butterfield, 2003).

"Konservat–Lagerstätten" i.e., "conservation deposits" (Seilacher, 1970), characterized by a high preservation quality, are believed to be the best sources to reconstruct palaeoecosystems. They provide relicts of soft part substances and fully articulated skeletons (e.g., of arthropods, echinoderms, and vertebrates). Moreover, decomposition may be prevented (Seilacher, 1970; Seilacher et al., 1985; Allison, 1988; Briggs, 2003). These exceptionally preserved fossil communities provide a considerably more complete information of the life communities than do normal shelly fossil communities. Konservat–Lagerstätten that are unevenly distributed through geologic time (Allison and Briggs, 1993) offer unique glimpses of diversity, disparity, and biology (Schiffbauer and Laflamme, 2012). For example, the Lower Cambrian Maotianshan Shales (e.g., Chen and Zhou, 1997), the Middle Cambrian Burgess Shale (Conway Morris, 1986), the Ordovician Beecher's Trilobite bed (e.g., Cisne, 1973), the Devonian Rhynie chert (e.g., Trewin, 1996), the Jurassic Solnhofen limestone (e.g., Barthel et al., 1990), and the Eocene Messel Oil shale (e.g., Hoch, 1988) are all well known examples of such unique fossil preservation.

In conclusion, besides a particular geographic region, a specific time slice, and a certain habitat, to define a biota, preservation quality should be taken into account. Therefore, the Jehol Biota is defined here as organisms that lived in Early Cretaceous volcanic-influenced environments of northeastern China, and were buried in lacustrine and, rarely, fluvial sediments, where many of them turned into exceptionally preserved fossils.

4. The exceptional preservation of the Jehol Biota

The exceptionally preserved Jehol Biota is contained in sediments characteristic of a "Konservat–lagerstätte". The sedimentary rocks in which it occurs can be roughly divided into two types:

Type A consists of finely laminated sediments, characterized by exceptional preservation of soft tissues, as body outlines, skin casts (the external morphology can be preserved in three-dimensions with no internal structure), wing membranes, scales, integumentary filaments and colour patterns (original melanin-containing intracellular organelles, or melanosomes), feathers and furs (Fig. 1) (e.g., Evans and Wang, 2005, 2010; Norell and Xu, 2005; Xu and Norell, 2006; Ji et al., 2001, 2004b; Li et al., 2010a; Wang and Evans, 2011; Zhang et al., 2010a; Huang et al., 2012). The occasional preservation of stomach contents (e.g., Chen et al., 1998; Zhou and Zhang, 2001, 2002; Zhou, 2004; Hu et al., 2005; Ji et al., 2007; Zheng et al., 2011b; O'Connor et al., 2011), is not a case of soft tissue preservation since these remains are represented by bones and/or hard fragments or seeds (Schweitzer, 2011).

Type B consists of massive, tuffaceous, pebbly sandstones, yielding commonly articulated vertebrate skeletons without any soft tissues traces, occasionally isolated teeth and fragmentary postcranial elements (e.g., Barrett and Wang, 2007; Xu and Norell, 2006; Wang et al., 2007), a few plant fragments, but with no invertebrates or flying vertebrates (birds and pterosaurs). In some cases, these articulated three-dimensional fossils yielded behavioural information, which is usually not preserved. For example, the holotype of the dinosaur "*Mei Long*" displays the stereotypic sleeping or resting posture found in living birds (Xu and Norell, 2004), a single individual adult of the small ornithischian dinosaur *Psittacosaurus* sp. clustered with 34 juveniles was proposed as evidence for post-hatching parental care (Meng et al., 2004), and a herd of the ceratopsian dinosaur *Psittacosaurus* provides evidence of post-nestling gregarious behaviour (Zhao et al., 2007) (Fig. 2). Though some of these hypotheses need to be substantiated by more detailed and careful investigations to exclude taphonomic and artificial biases, they are wonderful fossil materials demonstrating how much information can be extracted from the fossil record under special circumstances.

5. Relationship between the Jehol Biota and the Jehol Group

Gu (1962) first introduced the term "Jehol Group" into the literature, replacing the term "Jehol Series" used by Grabau (1923, p. 184) for the Lower Cretaceous continental sedimentary strata in Lingyuan County, western Liaoning. The Jehol Group comprises not only the fossil-bearing sediments but also the volcanic rocks in the region (Gu, 1962). Subsequently, the "Jehol Group" has been used as a major stratigraphic unit to refer to the coal-bearing beds, oil shale strata, and volcanic rocks in western Liaoning (e.g., Gu, 1982a,b, 1983, 1998). After a long standing debate on the stratigraphic subdivision and correlation of the Mesozoic strata in western Liaoning (see Jiang and Sha, 2006; Sha, 2007), there exist now two major opinions on the composition and subdivisions of the "Jehol Group": According to some workers the Jehol Group comprises, in ascending order, the Yixian and Jiufotang formations (Wang and Zhou, 2003), and more recently also "the Dabeigou Formation" as its lowest part (e.g., Wang and Zhou, 2006; Zhou, 2006; Zhou and Wang, 2010; Zhang et al., 2010b). According to some other workers the Jehol Group comprises, in ascending order, the Yixian, Jiufotang, and Fuxin formations (e.g., Sha, 2007; Sha et al., 2007; Jiang et al., 2007; Jiang and Sha, 2006; Sha et al., 2012).

According to the first opinion, the lithological features and fossil assemblages of the Shahai and Fuxin formations differ distinctly from those of the Yixian and Jiufotang formations which contain the most typical Jehol fossils. Therefore, they should be excluded from the Jehol Group (Wang and Zhou, 2003). "The Dabeigou Formation" is added to the Jehol Group based on the same argument that its fossil assemblage and lithologic features are largely consistent with those of the Yixian and Jiufotang formations (e.g.,

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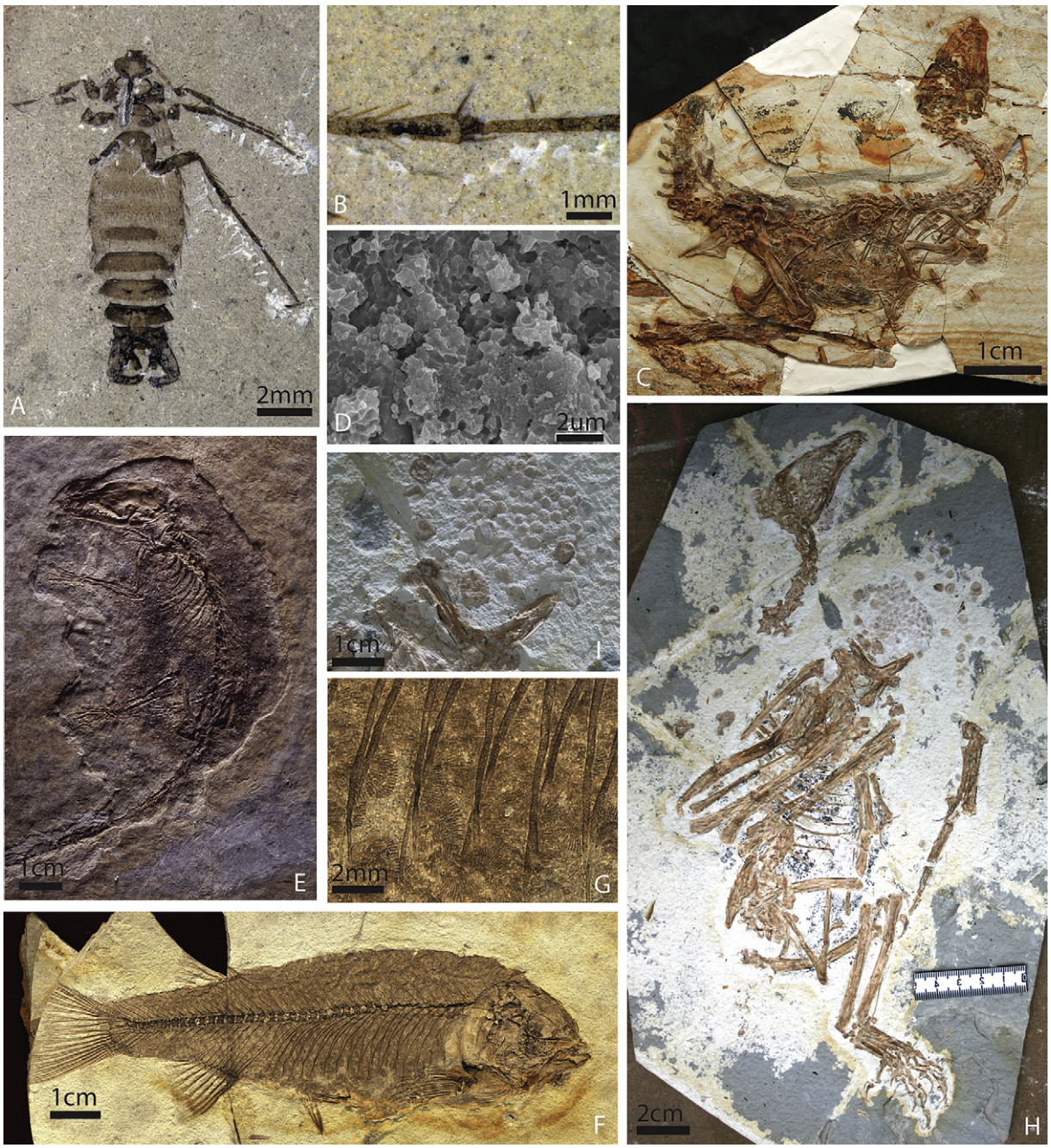

Fig. 1. The exceptional preservation of fossils from the finely laminated sediments (preservational type A of the Jehol Biota). **A**–**B**, A giant flea from the Yixian Formation (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, NIGP 154249) (Photographs provided by Huang Diying, also see Huang et al., 2012, fig. 3, a-c), A, general habitus, B, detail of A, close view of the leg; **C**–**D**, Melanosomes in the integumentary filaments of the dinosaur *Sinosauropteryx* (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, IVPP V14202, also see Zhang et al., 2010a, fig. 3, a-c), C, optical photograph of the specimen, D, SEM sample of integumentary filaments; **E**, *Eomaia* with hairs (Chinese Academy of Geological Sciences, Institute of Geology, CAGS01-IG1) (Photographs provided by Luo Zhexi); **F**–**G**, Specimen of *Lycoptera*, with scales preserved (IVPP-V11982.17), F, general habitus, G, detail of F, close view of the scales (Photographs provided by Zhang Jiangyong); **H**–**I**, Specimen of *Sapeornis chaoyangensis* with preservation of a crop (Shandong Tianyu Museum of Nature, STM 15-29, also see Zheng et al., 2011b, fig. 2, A-B), H, general habitus, I, detail of H, close view of the crop region.

Wang and Zhou, 2006; Zhou, 2006; Zhou and Wang, 2010). According to the second opinion, the concept of the Jehol Group should be consistent with the original definition by Gu (e.g, 1962, 1983). Lithostratigraphically, the "Jehol Group" was subdivided into the Yixian, Jiufotang and Fuxin formations in the Fuxin and Beipiao basins in western Liaoning (Sha, 2007; Sha et al., 2007). The Yixian Formation is characterized by volcanic rocks, the Jiufotang Formation by coal beds and oil shales in the upper part [the Shahai Formation was regarded as equivalent to the Jiufotang Formation according to Jiang and Sha (2006)], and the Fuxin Formation is characterized by coal-bearing silicilastic rocks.

Group as a lithostratigraphic unit should be defined and recognized on the basis of its lithologic properties or combination of lithologic properties and stratigraphic relations, not by their inferred age, the time span they represent, inferred geologic history, or manner of formation (Murphy and Salvador, 1999). Thus, the different fossil assemblages should not be used for distinguishing a lithostratigraphic unit. Besides, the strata referred to

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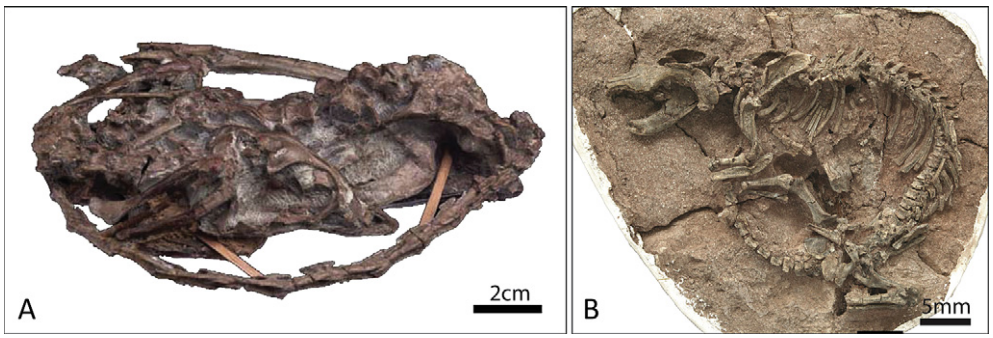

Fig. 2. The exceptional preservation of fossils from the massive tuffaceous pebbly sandstone (preservational type B of the Jehol Biota). **A**, Holotype skeleton of "*Mei long*" (IVPP V12733) (Courtesy of Xu xing, also see Xu and Norell, 2004, fig. 1, a-c), dorsolateral view; **B**, Holotype skeleton of *Repenomamus giganticus* (IVPP V14155) (Courtesy of Meng Jin, also see Hu et al., 2005, fig. 2), lateral view.

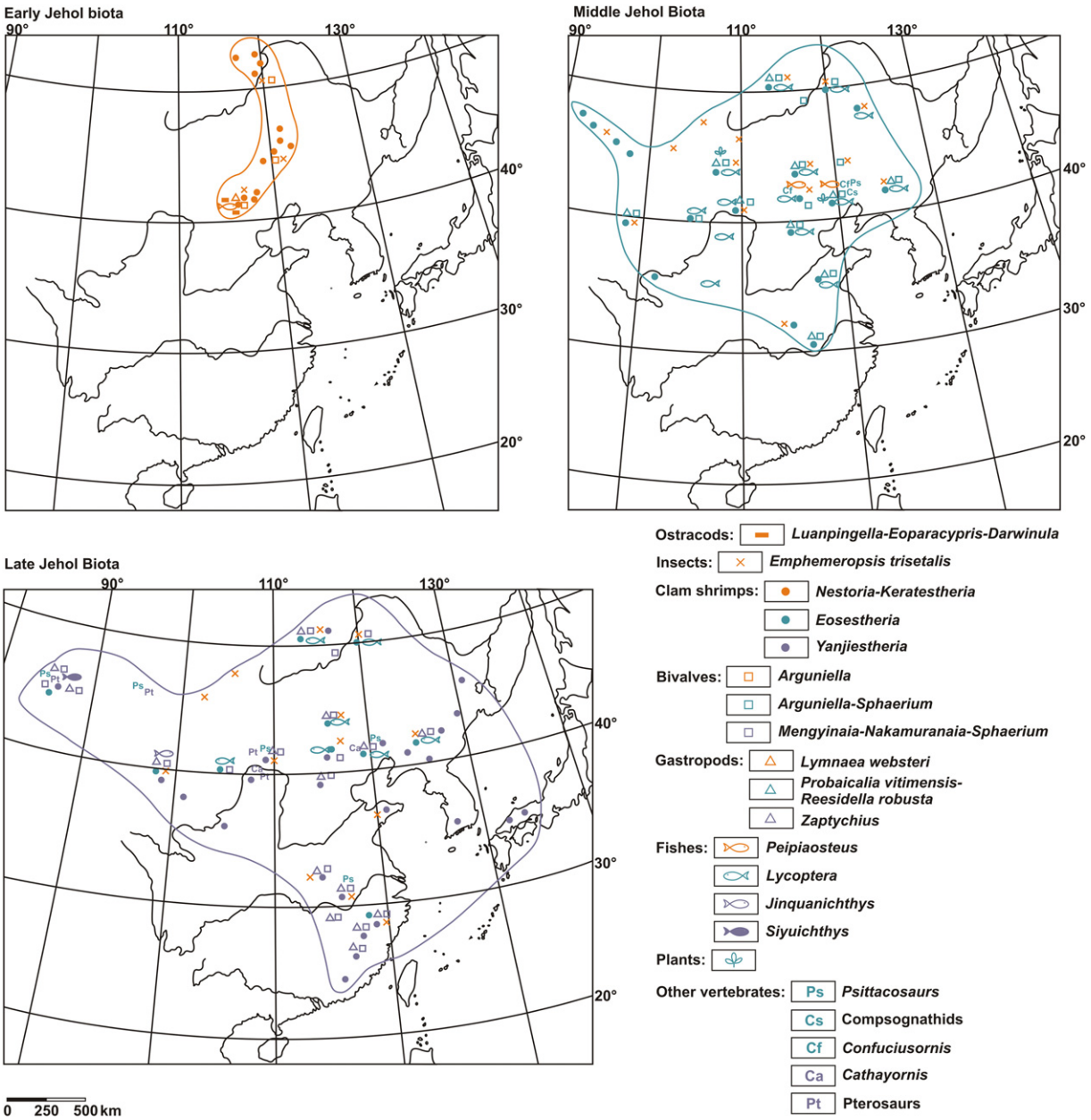

Fig. 3. The distributional patterns of the early, middle, and late Jehol Biota proposed by Chen (1988).

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"the Dabeigou Formation" that was combined into the Jehol Group by some workers (e.g., He et al., 2006a; Wang and Zhou, 2006; Zhou, 2006; Zhou and Wang, 2010) most likely corresponds to the Huajiying Formation in the Sichakou–Senjitu Basin (Jin et al., 2008). The original Dabeigou Formation is a lithostratigraphic unit recognized in the Luanping Basin of northern Hebei, representing the lower part of the Luanping Group (Wang, 1986, 1990). The geographic extent of a lithostratigraphic unit is more controlled by the continuity and extent of its diagnostic lithologic features rather than by the diagnostic lithologic features themselves. As the lithologic character is influenced more by conditions of formation than by time of origin, nearly identical rock types are often repeated over time. Since there is no evidence indicating the Dabeigou Formation continuously extended to the Sichakou–Senjitu Basin, it is more appropriate to use the Huajiying Formation to refer to the fossil-bearing deposits in the Sichakou–Senjitu Basin (also see discussion in Jin et al., 2008).

Based on these arguments, we suggest that it is more appropriate to keep the traditional composition of the Jehol Group as comprising, in ascending order, the Yixian, Jiufotang, and Fuxin formations.

Fossils of the Jehol Biota were first discovered in the "Jehol series", which was later modified into the Jehol Group. Moreover, the majority of the fossils of the Jehol Biota are also from the Yixian and Jiufotang formations. The question then is: should all the Jehol Biota fossil-bearing deposits be referred to the Jehol Group? As the Jehol Biota is a palaeoecological concept, while the Jehol Group is a lithostratigraphic unit, we argue that these two concepts do not need to exactly correspond to each other. In other words, it is not reasonable to suggest that "the Jehol Biota is the fossil community from the Jehol Group" or "the Jehol Group is the strata yielding the Jehol Biota".

6. The spatial and temporal distribution of the Jehol Biota

The spatial and temporal distribution of the Jehol Biota was first outlined by Chen (1988), who also proposed that the Jehol Biota displays early, middle and late evolutionary stages with a progressive expansion of its palaeogeographic distribution (Fig. 3). Subsequent studies on the palaeobiogeography and evolutionary stages of the Jehol Biota are more or less based on this original proposal (e.g., Wang, 1990; Chen, 1999; Zhou, 2006). These authors

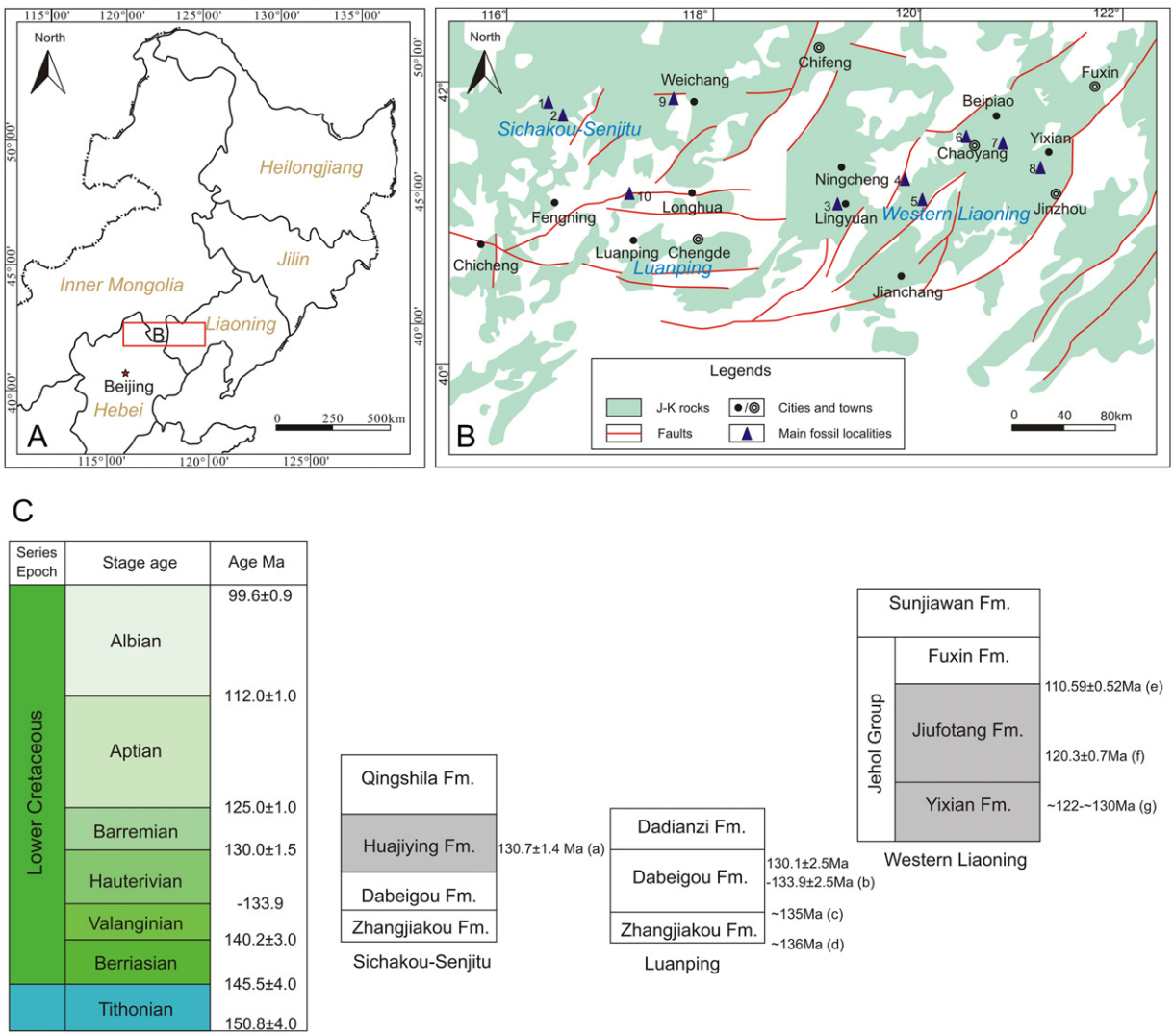

Fig. 4. The updated spatial and temporal distribution of the Jehol Biota based on its new definition of this paper. **A**, Location of the updated Jehol Biota: western Liaoning, northern Hebei and adjacent Inner Mongolia; **B**, Geologic map of western Liaoning, northern Hebei and adjacent Inner Mongolia showing the main fossil localities of the Jehol Biota (1, Sichakou; 2, Senjitu; 3, Fanzhangzi; 4, Boluochi; 5, Meileyingzi; 6, Shangheshou; 7, Sihetun; 8, Jingangshan; 9, Weichang; 10, Fengshan); **C**, Chronostratigraphic and lithostratigraphic position and the age of the Jehol Biota. Based on Eberth et al. (1993), He et al. (2006a), Swisher et al. (1999, 2002), Liu et al. (2003), Chen and Zhang (2004), He et al. (2004), Zhao et al. (2004), Zhang et al. (2005), He et al. (2006b), Zhu et al. (2007), Yang et al. (2007), Chang et al. (2009).

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generally agree that the first phase of the Jehol Biota was geographically restricted to a relatively small area in NE China and Siberia, and that the biota expanded in the second phase, and even more so in the third phase, when it extended further west to Xinjiang, south to southwestern China, and east to the Korean Peninsula and southwestern Japan (Fig. 3). Furthermore, these workers also related the three evolutionary stages of the Jehol Biota to the Dabeigou, Yixian and Jiufotang formations, respectively.

According to our new definition, the Jehol Biota are currently known only from the Huajiying Formation of northern Hebei, and the Yixian and Jiufotang formations of western Liaoning, as well as from corresponding deposits in southern Inner Mongolia and northern Hebei.

Contrary to previous studies, we propose that the fossil assemblages of the Dabeigou and Dadianzi formations of the Luanping basin in northern Hebei should be excluded from the Jehol Biota, although biostratigraphy (e.g., Pang et al., 2006; Zheng et al., 2011a; Wang et al., 2012) and radiogenic isotope geochronology results also indicate an Early Cretaceous age in the case of the Dabeigou Formation, about 130–135 Ma, see Chen and Zhang (2004); Liu et al. (2003); Zhao et al. (2004); Zhang et al. (2005). The fossil assemblages in these two formations were preserved in lacustrine and fluvial sediments, rarely affected by volcanic activities, indicating that their habitat differed from that of the Jehol Biota. It is also worth noting that the fossils from the Dabeigou and Dadianzi formations only constitute a very small portion of the former life ecosystem, though some fossil elements of the Jehol Biota were also recorded (e.g., Wang et al., 1984; Wang, 1999; Pang et al., 2002, 2006; Niu et al., 2002, 2003).

The new definition of the Jehol Biota requires a new look at its distribution (Fig. 4). In the basins of northern Hebei, the Jehol Biota is represented by lacustrine and fluvial sediments of the Huajiying Formation (previously called the Dabeigou Formation, see discussions referred in chapter 5), which have been dated about 130 Ma (He et al., 2006a). Biostratigraphically, the formation is slightly older than the Yixian Formation (Jin et al., 2008). In the basins of western Liaoning and adjacent Inner Mongolia and northern Hebei, the Jehol Biota occurs in lacustrine and, rarely, fluvial sediments of the Yixian and Jiufotang formations, which have been dated from about 130 Ma to about 120 Ma (Swisher et al., 1999, 2002; He et al., 2004, 2006b; Zhu et al., 2007; Yang et al., 2007; Chang et al., 2009); biostratigraphic data also shows a Barremian to Aptian age for the deposits (Sha, 2007; Sha et al., 2007). We agree with the previous suggestion that the Huajiying Formation currently contains the oldest fossil assemblage of the biota, while the Yixian and Jiufotang formations yield younger fossil assemblages.

Admittedly, some elements of the Jehol Biota have been found in localities of many other regions (e.g. northwestern China, southwestern China, Siberia, Korea, and Japan), which has been used as evidence that the Jehol Biota extended to these areas (e.g., Chen, 1988, 1999; Li and Gao, 2007; Gao et al., 2009; Li et al., 2010b; Chang et al., 2012). However, some elements of the Jehol Biota evidently must have had migrated to a greater area. It is also important to differentiate between the distribution of a single fossil element and the distribution of the whole biota. Furthermore, the palaeoecological and taphonomic background of many of these localities seems to differ from that in western Liaoning, northern Hebei, and southern Inner Mongolia.

7. Conclusions

The Jehol Biota are defined as the organisms that lived in Early Cretaceous volcanic-influenced environments of northeastern China, and were buried in lacustrine and, rarely, fluvial sediments, where most turned into exceptionally preserved fossils. Up to now, it has only been discovered in the Yixian and Jiufotang formations of western Liaoning and adjacent Inner Mongolia and Hebei, and in the Huajiying Formation of northern Hebei. It is limited to a comparatively small area throughout the Barremian and into the Aptian, i.e. for about 10 Ma.

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