



Spatiotemporal evolution of the Jehol Biota: Responses to the North China craton destruction in the Early Cretaceous

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The Early Cretaceous Jehol Biota is a terrestrial lagerstätte that contains exceptionally well-preserved fossils indicating the origin and early evolution of Mesozoic life, such as birds, dinosaurs, pterosaurs, mammals, insects, and flowering plants. New geochronologic studies have further constrained the ages of the fossil-bearing beds, and recent investigations on Early Cretaceous tectonic settings have provided much new information for understanding the spatiotemporal distribution of the biota and dispersal pattern of its members. Notably, the occurrence of the Jehol Biota coincides with the initial and peak stages of the North China craton destruction in the Early Cretaceous, and thus the biotic evolution is related to the North China craton destruction. However, it remains largely unknown how the tectonic activities impacted the development of the Jehol Biota in northeast China and other contemporaneous biotas in neighboring areas in East and Central Asia. It is proposed that the Early Cretaceous rift basins migrated eastward in the northern margin of the North China craton and the Great Xing'an Range, and the migration is regarded to have resulted from eastward retreat of the subducting paleo-Pacific plate. The diachronous development of the rift basins led to the lateral variations of stratigraphic sequences and depositional environments, which in turn influenced the spatiotemporal evolution of the Jehol Biota. This study represents an effort to explore the linkage between terrestrial biota evolution and regional tectonics and how plate tectonics constrained the evolution of a terrestrial biota through various surface geological processes.

diachronous | Jehol Biota | North China craton destruction | paleo-Pacific subduction | spatiotemporal distribution

The Early Cretaceous Jehol Biota has been well known for producing hundreds of exceptionally preserved fossils, including feathered dinosaurs, birds, mammals, pterosaurs, lizards, turtles, choristoderes, amphibians, fishes, as well as abundant insects and flowering plants (1–5). Many vertebrate fossils are preserved as completely articulated skeletons, and some are even associated with gut contents, showing direct evidence of their diets (6, 7). It is most notable that the Jehol fossils often preserve soft tissues in great fidelity, such as skins, feathers, hairs, wing membranes, ovarian follicle, lung, and foot webs (8–10). Micro- or even nanoscale structures, including melanosomes and even beta keratins, have been reported (11–14). These fossils with superb quality have made them feasible to address a number of important issues on vertebrate evolution, e.g., the origin and early evolution of birds and their flight, origin of feathers, and origin and early evolution of mammals and their middle ear bones (15–17). The Jehol fossils also preserve much information about paleoecology of terrestrial biota, and thus can be used to investigate the Early Cretaceous terrestrial ecosystem (1, 18–20).

The Jehol Biota has been extensively studied. Understanding of its composition and distribution depends on how the Jehol Biota is defined. Traditionally, the Jehol Biota is defined by three typical elements: the conchostracan *Eosetheria*, the insect *Ephemeroptera*, and the fish *Lycoptera*. The Jehol Biota sensu stricto is normally

considered in the literature to have a limited paleogeographic distribution in northeast China, whereas the Jehol Biota sensu lato is distributed across the whole of northern China and neighboring regions in eastern and central Asia (21). The recent paleoecology-based definition of the biota is similar to the Jehol Biota sensu stricto (22) and is followed here. According to the new definition, the Jehol Biota only occurs, in ascending order, in the Huajiying, Yixian, and Jiufotang formations in northern Hebei, western Liaoning, and southeast Inner Mongolia (22), in which volcanic and volcanoclastic beds are commonplace (23, 24). The growing geochronologic data now put a tight constraint on the ages of the fossil-bearing units, which indicate that the Jehol Biota spanned from approximately 135 to 120 Ma (25–28).

The North China craton (NCC) is one of the key elements of eastern Asian continental geology and usually divided into the eastern and western blocks, which were welded by the Trans-North China Orogen in the Paleoproterozoic orogeny (~1.90 to 1.85 Ga) (29) (Fig. 1). The NCC had remained tectonically stable until the late Mesozoic when decratonization took place. The decratonization is accompanied by vigorous magmatism, rifting, strike-slip faulting, and transformation of lithospheric nature (30). It is generally regarded that the destruction of the NCC was triggered by the combined tectonic processes, including high-angle subduction, trench retreat, and rollback of the paleo-Pacific plate during the late Mesozoic (30–33).

It is worth noting that the Jehol Biota evolution is in accord with the NCC destruction in time and space (19, 20, 31, 33), with its flourishing period of around 125 Ma coincident with the peak

Significance

The Early Cretaceous Jehol Biota is a terrestrial lagerstätte that produces exquisitely preserved fossils that have furnished enormous evidence on the origins and early evolution of diverse vertebrate groups. On the basis of the latest paleontological and geochronologic evidence, we discuss the three stages of the biota, and suggest that the spatiotemporal evolution of the Jehol Biota coincides with the initial and peak stages of the North China craton destruction in the Early Cretaceous. Such linkage presents an example of how regional tectonics influence the terrestrial biota that points to a new path for future studies involving multidisciplinary methods to explore the biosphere in deep time.

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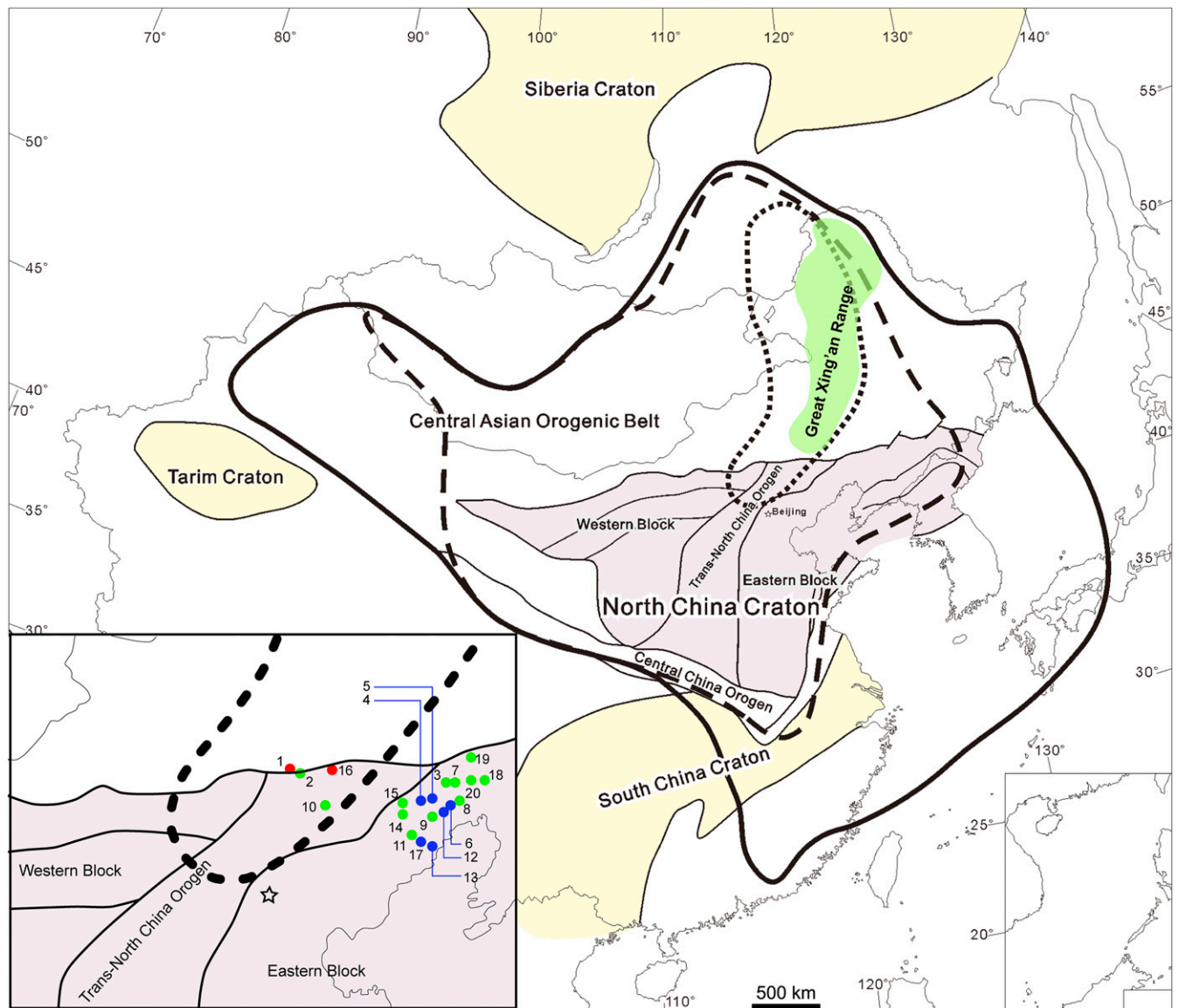


Fig. 1. Spatiotemporal distribution of the Jehol Biota and its contemporaneous or nearly contemporaneous biotas in East and Central Asia. The Jehol Biota and its contemporaneous biotas are largely north-southerly distributed during the first evolving stage, along the western margin of the east block of the North China craton (NCC) (dotted line), and expanded eastward, westward, and southward during the second (dash line) and third stages (solid line). The *Inset* shows the distribution of the major vertebrate-bearing horizons of the Jehol Biota in northern Hebei, western Liaoning, and southeast Inner Mongolia in the northern margin of central and eastern blocks of the NCC, with red, green, and blue circles denoting localities from the first, second, and third stages, respectively. 1, Sichakou; 2, Senjitu; 3, Lujiatun; 4, Boluochi; 5, Meileyingzi; 6, Shangheshou; 7, Sihetun; 8, Jinggangshan; 9, Daxinfangzi; 10, Fengshan; 11, Dawangzhangzi; 12, Dapingfang; 13, Xiaotaizi; 14, Shifo; 15, Liutiaogou; 16, Shixia; 17, Sihedang; 18, Wutun; 19, Dawujiazi; and 20, Baicaigou.

of the NCC destruction. Also noticeable is that the Jehol Biota is mostly distributed in the northern margin of the eastern NCC, where the destruction is most severe (19, 33). It is also shown that magmatism, sedimentation, and biota migrated toward the east with time during the Early Cretaceous, as indicated by the east-younging trends of volcanic eruption, basin initiation, and beginning of the Jehol elements in northeastern China (32). All the spatiotemporal changes in magmatism, stratigraphy, basin tectonics, and biota were possibly linked to the various subduction processes of the western paleo-Pacific plate, such as the trench retreat and slab rollback. This study aims to review the latest development in the study of the western paleo-Pacific plate subduction and its possible controls of the evolution and distribution of the Jehol Biota through various surface processes, such as basin development. The focus is on the spatiotemporal evolution of the

Jehol Biota and contemporaneous biotas in East and Central Asia, exploring their possible relationship with coeval destruction processes of the NCC.

Spatiotemporal Distribution of the Jehol Biota. Recent discoveries of fossils and newly obtained isotopic ages of the Jehol fossil-bearing stratigraphic units have significantly refined our understanding of the temporal (chronological) and spatial (geographic) distribution of the Jehol and contemporaneous biotas in East and Central Asia. The Jehol Biota is generally divided into three evolving stages, i.e., Jehol Biota stages I to III (JBS I to III), as represented by fossil assemblages from the Huajiyang, Yixian, and Jiufotang formations, respectively (18, 20, 22). More fossils are discovered in recent years not only from the Jehol Biota in northern China but also from contemporaneous deposits in Mongolia, Japan, Korea,

and Transbaikalia of Russia (18). An updated chronological framework has been built for more precise regional stratigraphic and biotal correlations. All the results help to elaborate the origin, evolution, and spatiotemporal distribution of various biological groups in the Jehol Biota during the Early Cretaceous (28).

The earliest occurrence of the Jehol Biota (JBS I) was best recorded in the Huajiyang Formation in Fengning (equivalent to the Dabeigou Formation in Luanping), northern Hebei Province (Fig. 1). The unit is composed mainly of thin-bedded mudstones with abundant tuff interlayers, and the fossils are exceptionally well preserved. Soft tissues can be recognized and are often associated with completely articulated vertebrate skeletons. In addition, there occur conchostracan (clam shrimp) assemblage *Nestoria-Keratestheria* and the ostracod assemblage *Darwinula-Luanpingella-Eoparacypris* (Fig. 2 A and B) (21), which are of significance in stratigraphic correlation. The vertebrate assemblages are also very common. The fossil birds *Protopteryx*, *Eoconfuciusornis*, and *Eopenomis* document the earliest and lowermost member of the Enantiornithes, Confuciusornithidae, and Pengornithidae, respectively (34–36). Other important vertebrate assemblages include acipenseriform fishes, a compsognathid dinosaur, and a newly discovered mammal. A recently described bird in the Huajiyang Formation in Weichang, northern Hebei can also be an early-stage representative of the Jehol Biota (37). The first stage (JBS I) spans from ~135 to 127 Ma (38) based on new geochronologic data, thereby recording the earliest avian radiation in the Early Cretaceous.

JBS II is represented by fossil assemblages in the Yixian Formation in western Liaoning and similar deposits in northern Hebei and southern Inner Mongolia (18, 20). The fossils are present in two different types of sedimentary facies. The first type of sedimentary facies is shales and thin-bedded mudstones with many tuff interlayers, making up the Jianshangou Bed of the lower Yixian Formation. This type of facies archives many well-preserved two-dimensional articulated skeletons often with soft tissues. The second type of sedimentary facies is characterized by massive, tuffaceous, pebbly sandstones, as represented by the Lujiatun Bed at the base of the Yixian Formation. Articulated vertebrate skeletons in this type of facies are usually three-dimensional and have no trace of soft tissues (18, 24). The Yixian Formation records the first great species diversification of the Jehol Biota. The second

stage of the Jehol Biota (JBS II) spans only 2 Ma from ~126 Ma to ~124 Ma (39). This short period, however, witnesses the second great species diversification, as indicated by the fossil assemblage containing diverse birds, dinosaurs, pterosaurs, mammals, lizards, turtles, choristoderes, amphibians, fishes, as well as insects and plants like angiosperms (18).

JBS III is best represented by fossil assemblages that primarily occur in the Jiufotang Formation in western Liaoning and in coeval stratigraphic units in northern Hebei and southern Inner Mongolia (18, 20). The units are mainly composed of interbedded mudstone, siltstone, and fine-grained sandstone, and tuffs are also common in the sequences. The fossils are mostly two-dimensional, but soft tissues are less well preserved compared with the fossils in the Huajiyang and Yixian formations. JBS III is roughly represented by fossils from 124 Ma to 120 Ma in western Liaoning (26). The fossil assemblage in the Jiufotang Formation also displays a remarkable differentiation of vertebrates, including birds, dinosaurs, pterosaurs, mammals, lizards, turtles, choristoderes, amphibians, and fishes (18).

The fossils of biostratigraphic significance (e.g., conchostracans and ostracods) in JBS II and III are hardly distinguishable but distinct from JBS I fossils that are characterized by the appearance of *Eosetheria* (Fig. 2C) in the conchostracan assemblage and *Cypridea* in the ostracod assemblage, respectively. Although JBS I is only distributed in northern Hebei Province, the contemporaneous units in Inner Mongolia, Heilongjiang, Mongolia, and Siberia contain some fossil elements (e.g., conchostracan *Nestoria* and *Keratestheria*) that are correlatable with JBS I. It is important to note that JBS I and contemporaneous biotas are distributed in many rift basins that develop in a NE- or NNE-oriented zone west of the Great Xing'an Range (38, 40). The earliest Cretaceous biotas are also found in the Transbaikalia in Siberia (41). JBS I contains several early birds, as discovered in the Huajiyang Formation in Hebei Province. However, there is yet no documentation of bird fossils in the contemporaneous strata in other areas of East Asia. Hence, the Jehol Biota and its contemporaneous biotas in eastern and central Asia exhibit a limited paleogeographic distribution in northeast Asia and Siberia during the earliest Cretaceous (Fig. 1). The JBS I vertebrate assemblage, particularly the bird assemblage that is mainly composed of stem members, is

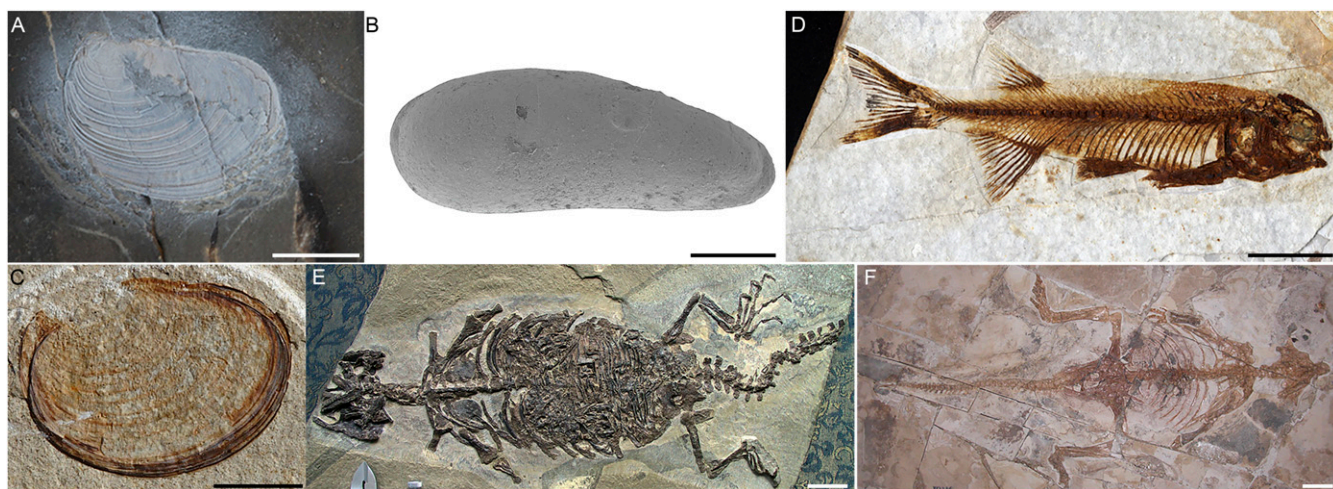


Fig. 2. Photographs of selected fossils of the Jehol Biota with biostratigraphic and paleogeographic significance. (A and B) Typical and common fossils of JBS I: *Nestoria* (A; Diplostraca: Spinicaudata), and *Darwinula* (B; Crustacea: Ostracoda), both mainly distributed in northern Hebei and the Great Xing'an Range of China and Transbaikalia of Russia. (C–F) Common fossils from JBS II and III: *Eosetheria* (C; Arthropoda: Conchostraca), and *Lycoptera davidi* (D; Osteichthyes: Osteoglossomorpha), both extensively distributed in northern and northeast China, Mongolia, Korea, and Transbaikalia of Russia; (E) *Monjurosuchus* (Reptilia: Choristodera), found in northern China and Japan; (F) *Psittacosaurus* (Dinosauria: Ornithischia), found in northern China, Mongolia, and Transbaikalia of Russia. (Scale bars: 5 mm [A], 100 μ m [B], 10 mm [C, D], 20 mm [E], 50 mm [F].)

basically less diverse than those of the two younger stages (Fig. 3), confirming that northern Hebei might be the center of the initiation, early differentiation, and evolution of the Jehol Biota.

Jehol Biota stages II and III start from the middle Early Cretaceous and the fossil assemblages are best preserved in western Liaoning. The contemporaneous or subcontemporaneous biotas occur in many other areas in NE Asia, such as Hebei, Inner Mongolia, Shandong, Jilin, and Heilongjiang provinces of China, Japan, Korea, and Transbaikalia of Russia, and share with the Jehol Biota more or less typical Jehol fossils. In addition to some biostratigraphically important invertebrates like *Eoestheria* and *Cypridea*, several other vertebrate taxa have also been reported in these regions, including the fishes

Acipenseriformes, Osteoglossomorphs (e.g., *Lycoptera*) (Fig. 2D), the aquatic or semiaquatic reptilian Choristoderes (e.g., *Monjurosuchus*) (Fig. 2E) (42–44), the Squamates, the dinosaurian Psittacosauridae (e.g., *Psittacosaurus*) (Fig. 2F), and the avians Confuciusornithidae (9, 45), Enantiornithes, and Ornithuromorpha, etc. (46). Obviously, the Jehol Biota and its contemporaneous biotas have significantly expanded laterally in East and Central Asia during the middle Early Cretaceous. Compared with the early Early Cretaceous fossil assemblages, some elements of the Jehol Biota have expanded toward the east, west, and south (Fig. 1). The study of biotic composition and phylogenetic relationships will help reveal the paleogeographic history of the biota.

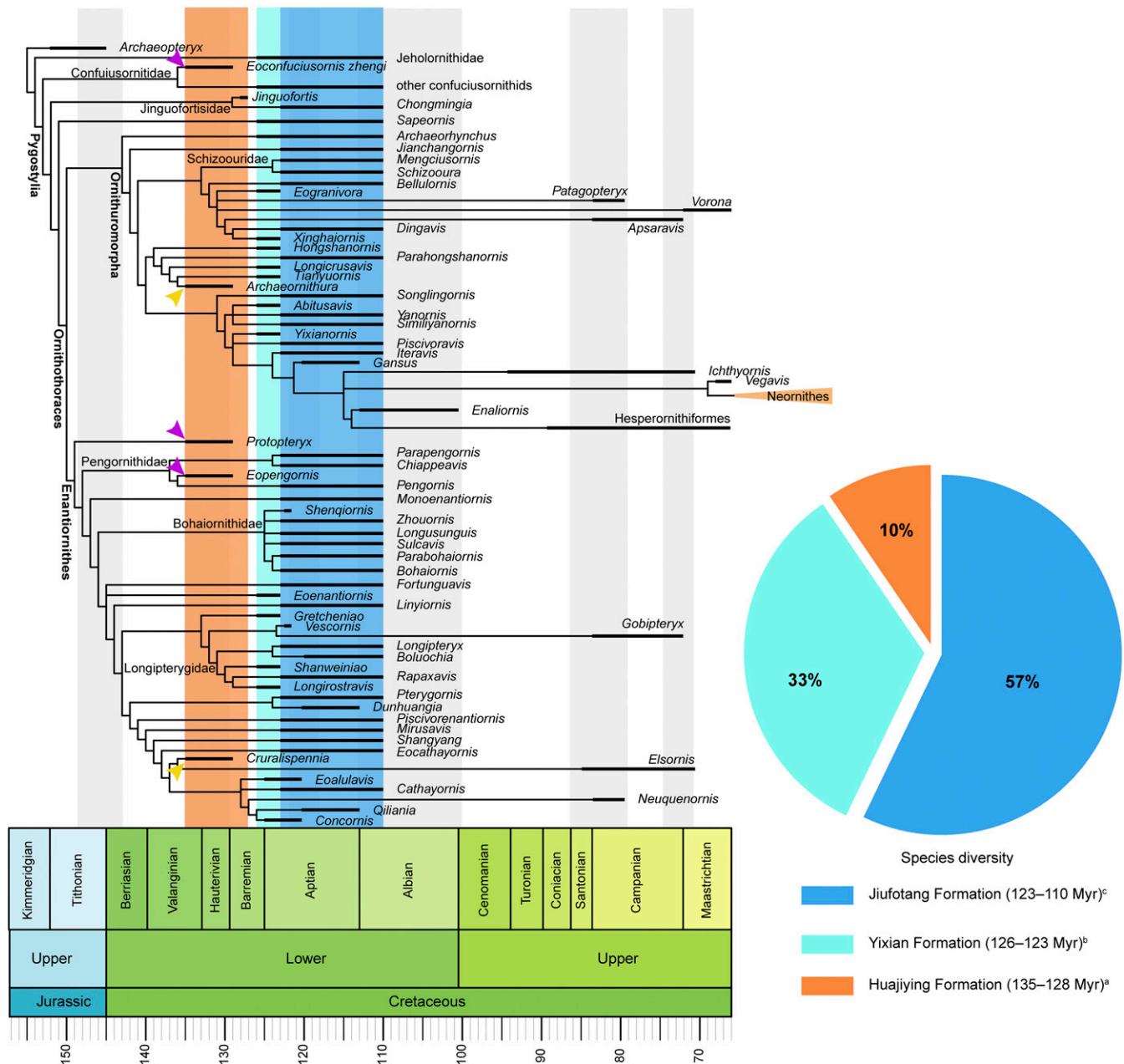


Fig. 3. Chronological distribution of Jehol birds. Time-scaled phylogeny of Mesozoic birds is modified with permission from ref. 54. Data from refs. 26–28. The purple arrowheads denote that taxa from the Huajiyang Formation often emerge as the basalmost phylogenetic position of corresponding clades, with two exceptions (yellow arrowheads). A simple count of avian species unearthed from the three formations (Huajiyang: 6 taxa; Yixian: 21 taxa; Jiufotang: 36 taxa) of the Jehol Biota shows that the youngest Jiufotang Formation yielded more species than the others (^aref. 28; ^bref. 27; and ^cref. 26).

Spatiotemporal Evolution of Rift Basins in Response to the NCC Destruction. It is generally accepted that the destruction of the NCC was triggered by the paleo-Pacific plate subduction (31–33). Trench retreat and slab rollback are considered as the main mechanisms for late Mesozoic lithospheric stretching of the NCC, as manifested by widespread magmatism and occurrences of rift basins and metamorphic core complexes (32, 33). It is hypothesized that the Jehol Biota evolution might have been born on these tectonic processes (19, 31, 33). The NCC experienced diachronous destruction in the late Mesozoic, as indicated by time-space variations of magmatism and rifting (33). The Middle Jurassic magmatism mainly occurred in the easternmost NCC and then migrated westward in the Late Jurassic. In contrast, the Early Cretaceous magmatism shows a younging trend from west to east across the eastern NCC (32, 33).

The eastern NCC destruction involves the thinning of the lithosphere from ~200 km in the Paleozoic to ~80 km in the Cenozoic. As a result, the NCC lithosphere displays rapid thickness change across the boundary between the eastern and western blocks of the NCC. The eastern block has been greatly attenuated and decratonized in the late Mesozoic, contrasting strikingly with the western block that has remained stable throughout the Mesozoic. Rift basins developed in the period from the Middle Jurassic to Early Cretaceous in the eastern NCC, and basin successions are well preserved in the northern margin of the NCC (29, 32). Three phases of crustal shortening, which are usually called phases A–C of the Yanshanian Movement in the literature. The three contractional events interrupted the rift basin development and resulted in three regional unconformities within Late Mesozoic strata. The first unconformity is between the Middle and Upper Jurassic, registering the phase A contraction from 170 to 165 Ma (32, 47). The second unconformity displays the marked change in timing and duration from west to east (Fig. 4). The Lower Cretaceous volcanics above the second unconformity are dated at 143 Ma in the west of the northern NCC and then gradually get younger to the east, spanning 136 to 123 Ma (Fig. 4). The third unconformity separates Lower from Upper Cretaceous strata. The three unconformities divide Late Mesozoic successions into three distinct sequences, which record three stages of rift basins in the northern NCC. In other words, Late Mesozoic rift basin development was punctuated by three phases of crustal shortening, leading to the sequential inversion of the Middle Jurassic, Late Jurassic, and Early Cretaceous rift basins, respectively (33). This study is mainly concerned with the development of rift basins after the phase B contractile event or the Early Cretaceous basins where the Jehol Biota dwelled. As indicated by the ages of basal volcanics of the Lower Cretaceous sequences, the rift basins in the northern NCC did not initiate simultaneously but occurred early in the west. The Jingxi basin initiated around 145 Ma, whereas the basins in eastern Liaoning had not started until ~125 Ma (Figs. 1 and 4).

Paleogeographic study suggested that from the Late Jurassic to early Early Cretaceous, the NNE-trending Great Xing'an Range-Yanshan Mountain area contrasts with the North China Highland (which had remained until the middle Early Cretaceous) on the east (40). By the late Early Cretaceous, the North China Highland disappeared and it was replaced by the Great Xing'an Range Highland on the west. It is also notable that during the Early Triassic, the Central Asian Orogenic Belt was formed with the closure of the paleo-Asian Ocean between the NCC and Siberian craton (29). The Great Xing'an Range, as part of the Xing'an Mongolian Orogenic Belt, which is the eastern part of the Central Asian Orogenic Belt, merged with the northern margin of the NCC and the southern margin of the Siberian craton. Therefore, the subduction of the paleo-Pacific Ocean had not only resulted in the destruction of the NCC, but also had greatly controlled tectonic activity, basin development, and biotal evolution of the Great Xing'an Range and the Transbaikalia since the early Early Cretaceous.

Discussion

The precise chronological framework has been built up for Late Mesozoic strata in recent years and puts a good constraint on the regional stratigraphic and biotal correlation (28, 39). The well-defined stratigraphic framework is essential for understanding the temporal evolution of the Jehol Biota and its links to other processes, such as volcanic eruption, rift basin evolution, crustal shortening, surface uplifting, and the paleo-Pacific plate subduction (19, 33). The paleo-Pacific plate subduction must have exerted first-order control over the evolution of the biotas through various surface geological processes. East-directed shifting of both volcanic eruptions and rift basins leads to the eastward younging of Lower Cretaceous stratigraphic and sedimentary sequences. The eastward migration of the above-mentioned geologic processes is in general consistent with the eastward expansion of the Jehol Biota in north and northeast China. This consistency suggests that the biotal evolution must have been connected with regional tectonic processes.

JBS I is distributed in a restricted region, being present only in northern Hebei. However, it is interesting to note that contemporaneous biotas also occur in the Siberia craton and the regions west of the Great Xing'an Range (40, 41, 48). Such spatial distribution is obviously related to earlier closure of the paleo-Asian Ocean, and the coalition between the NCC and Siberia craton by the Xing'an Mongolian Orogenic Belt that forms the eastern part of the Central Asian Orogenic Belt (Fig. 1). In contrast, the Jehol Biota extended outward significantly in JBS II and III, as evidenced by its widespread occurrence in western Liaoning, northern Hebei, and southern Inner Mongolia. The center of the Jehol Biota was in the northern margin of the central block of the NCC. The contemporaneous biotas in Korea, Japan, Mongolia, and Siberia contain fossils similar to the elements of the Jehol Biota, suggesting extensive faunal and floral exchange and paleogeographic links among these areas (9, 42, 44–46, 49). The development of wide rift systems, which consist of many small and isolated rift basins, might also have played a role in the flourishing of the Jehol Biota in the late Early Cretaceous (19).

It is noteworthy that the Jehol Biota is best preserved in the northern margin of the NCC, which implies that the Jehol Biota might have originated from the northern Hebei Province. However, the Jehol Biota and contemporaneous biotas are in practice distributed in a wide area. They might have been dwelling in the NCC, the Siberia craton, and the western Great Xing'an Range in the early Early Cretaceous, and then migrated toward east, west, and south in the late Early Cretaceous (Fig. 1).

The diachronous volcanic eruption, basin development, and biotal evolution are best constrained in northeast China on the basis of precise geochronological data and abundant diverse fossils (50, 51). The Jehol Biota is only present in the western segment of the northern margin of the NCC at JBS I and then migrated eastward and flourished in western Liaoning at JBS II. Abundant Jehol fossils in the Yixian Formation attest to the eastward expansion of the Jehol Biota. The Jehol Biota continued to thrive in the western Liaoning and further migrated to the east at JBS III, as evidenced by the presence of the Jehol elements in the Jiufotang Formation and the contemporaneous strata in eastern Liaoning and Jilin Province (52, 53) (Fig. 4).

In summary, the spatiotemporal evolution of the Jehol Biota is consistent with eastward shifting of volcanism and rift basins, which is in fact controlled by the paleo-Pacific plate subduction. Flourishing and vanishing of the biota appear closely related to volcanic intensity and rift basin development in space and time, implying a profound control of the NCC destruction on surface paleogeography and ecosystems. This study provides a unique example of how deep geology could have controlled the evolution of terrestrial biota from an Earth system view. More work is needed to comprehensively understand such a complex process,

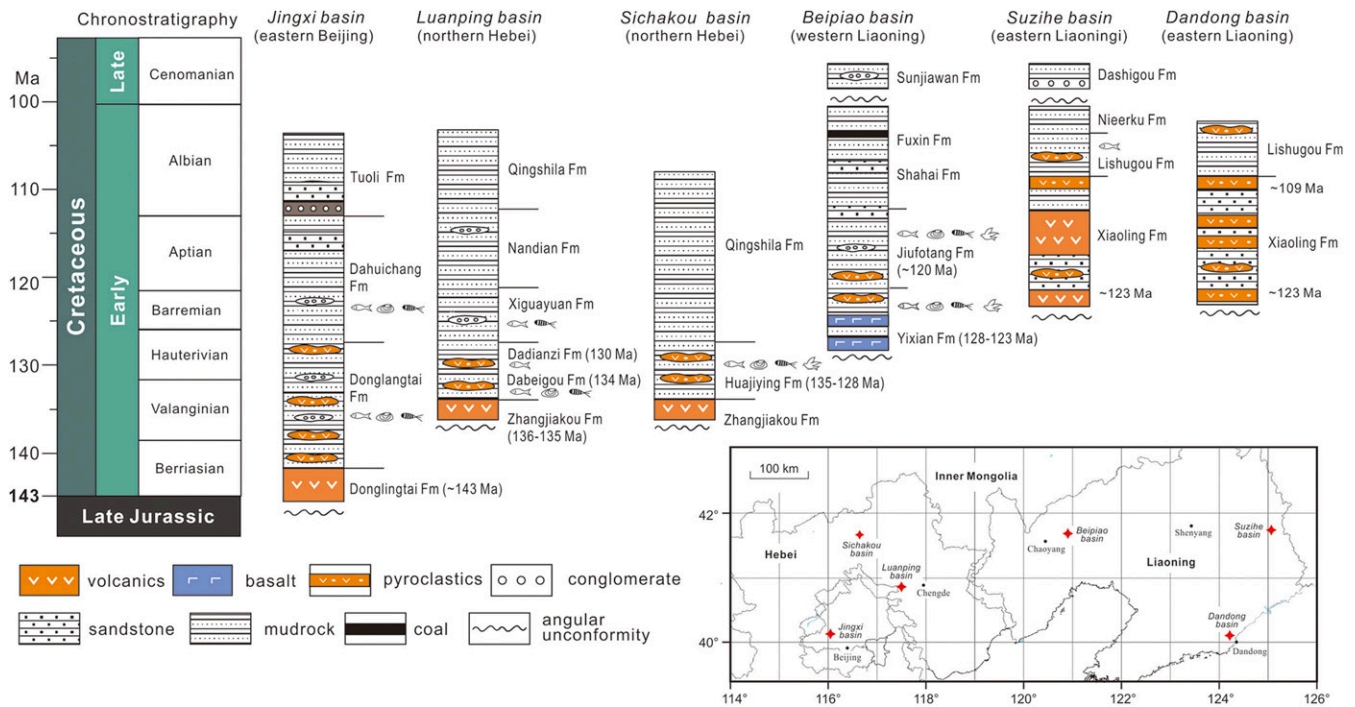


Fig. 4. Spatiotemporal distribution of the Early Cretaceous fossil-bearing volcanoclastic deposits and corresponding biotas in northeastern China, showing the progressive eastward younging trend.

e.g., how the deep geology in this region might have contributed to the generally warm and humid climate that is suitable for the flourishing of the Jehol Biota.

Data Availability. All study data are included in the article.

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- Zhou, P. M. Barrett, J. Hilton, An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807–814 (2003).
- M. A. Norell, X. Xu, Feathered dinosaurs. *Annu. Rev. Earth Planet. Sci.* **33**, 277–299 (2005).
- L. M. Chiappe, Q. Meng, *Birds of Stone: Chinese Avian Fossils from the Age of Dinosaurs* (Johns Hopkins University Press, Baltimore, 2016).
- J. Meng, Mesozoic mammals of China: Implications for phylogeny and early evolution of mammals. *Natl. Sci. Rev.* **1**, 521–542 (2014).
- D. Ren, C. Shih, T. Gao, Y. Wang, Y. Yao, *Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China* (John Wiley & Sons, 2019).
- X. Zheng *et al.*, New specimens of *Yanornis* indicate a piscivorous diet and modern alimentary canal. *PLoS One* **9**, e95036 (2014).
- J. K. O'Connor, The trophic habits of early birds. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **513**, 178–195 (2019).
- X. Zheng *et al.*, Preservation of ovarian follicles reveals early evolution of avian reproductive behaviour. *Nature* **495**, 507–511 (2013).
- J. K. O'Connor, A. O. Averianov, N. V. Zelenkov, A confuciosornithiform (Aves, Pygostylia)-like tarsometatarsus from the Early Cretaceous of Siberia and a discussion of the evolution of avian hind limb musculature. *J. Vertebr. Paleontol.* **34**, 647–656 (2014).
- X. Wang *et al.*, *Archaeorhynchus* preserving significant soft tissue including probable fossilized lungs. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 11555–11560 (2018).
- Q. Li *et al.*, Plumage color patterns of an extinct dinosaur. *Science* **327**, 1369–1372 (2010).
- F. Zhang *et al.*, Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature* **463**, 1075–1078 (2010).
- Y. Pan *et al.*, Molecular evidence of keratin and melanosomes in feathers of the Early Cretaceous bird *Eoconfuciosornis*. *Proc. Natl. Acad. Sci. U.S.A.* **113**, E7900–E7907 (2016).
- Y. Pan *et al.*, The molecular evolution of feathers with direct evidence from fossils. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 3018–3023 (2019).
- X. Xu *et al.*, An integrative approach to understanding bird origins. *Science* **346**, 1253293 (2014).
- H. Wang, J. Meng, Y. Wang, Cretaceous fossil reveals a new pattern in mammalian middle ear evolution. *Nature* **576**, 102–105 (2019).
- F. Mao, C. Liu, M. H. Chase, A. K. Smith, J. Meng, Exploring ancestral phenotypes and evolutionary development of the mammalian middle ear based on Early Cretaceous Jehol mammals. *Natl. Sci. Rev.*, 10.1093/nsr/nwaa188 (2020).
- Zhou, The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: New discoveries and implications. *Natl. Sci. Rev.* **1**, 543–559 (2014).
- Zhou, Y. Wang, Vertebrate assemblages of the Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota: Comparisons and implications. *Palaeoworld* **26**, 241–252 (2017).
- X. Xu, Z. Zhou, Y. Wang, M. Wang, Study on the Jehol Biota: Recent advances and future prospects. *Sci. China Earth Sci.* **63**, 757–773 (2020).
- P. Chen, Distribution and migration of the Jehol fauna with reference to the non-marine Jurassic-Cretaceous boundary in China. *Acta Palaeontologica Sin.* **27**, 659–683 (1988).
- Y. Pan, J. Sha, Z. Zhou, F. T. Fürsich, The Jehol Biota: Definition and distribution of exceptionally preserved relicts of a continental Early Cretaceous ecosystem. *Cretac. Res.* **44**, 30–38 (2013).
- B. Jiang, G. E. Harlow, K. Wohletz, Z. Zhou, J. Meng, New evidence suggests pyroclastic flows are responsible for the remarkable preservation of the Jehol Biota. *Nat. Commun.* **5**, 3151 (2014).
- C. S. Rogers *et al.*, The Chinese Pompeii? Death and destruction of dinosaurs in the Early Cretaceous of Lujiatun, NE China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **427**, 89–99 (2015).
- C. Swisher *et al.*, Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: New $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Yixian and Tuchengzi formations. *Chin. Sci. Bull.* **47**, 135–138 (2002).
- H. Y. He *et al.*, Timing of the Jiufotang Formation (Jehol Group) in Liaoning, north-eastern China, and its implications. *Geophys. Res. Lett.* **31**, L12605 (2004).
- S. Chang, H. Zhang, P. R. Renne, Y. Fang, High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Jehol Biota. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **280**, 94–104 (2009).
- S. Yang *et al.*, The appearance and duration of the Jehol Biota: Constraint from SIMS U-Pb zircon dating for the Huajiyi Formation in northern China. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 14299–14305 (2020).
- Q. Meng, G. Wu, L. Fan, H. Wei, Tectonic evolution of early Mesozoic sedimentary basins in the North China block. *Earth Sci. Rev.* **190**, 416–438 (2019).
- R. Zhu, Y. Xu, The subduction of the west Pacific plate and the destruction of the North China craton. *Sci. China Earth Sci.* **62**, 1340–1350 (2019).
- R. Zhu *et al.*, Destruction of the North China craton. *Sci. China Earth Sci.* **55**, 1565–1587 (2012).
- F. Wu, J. Yang, Y. Xu, A. S. Wilde, J. R. Walker, Destruction of the North China craton in the Mesozoic. *Annu. Rev. Earth Planet. Sci.* **47**, 173–195 (2019).

33. R. Zhu, Z. Zhou, Q. Meng, Destruction of the North China craton and its influence on surface geology and terrestrial biotas. *Chin. Sci. Bull.* **65**, 2954–2965 (2020).
34. F. Zhang, Z. Zhou, A primitive enantiornithine bird and the origin of feathers. *Science* **290**, 1955–1959 (2000).
35. F. Zhang, Z. Zhou, M. J. Benton, A primitive confuciusornithid bird from China and its implications for early avian flight. *Sci. China Ser. A* **51**, 625–639 (2008).
36. X. Wang *et al.*, Insights into the evolution of rachis dominated tail feathers from a new basal enantiornithine (Aves: Ornithothoraces). *Biol. J. Linn. Soc. Lond.* **113**, 805–819 (2014).
37. M. Wang, T. A. Stidham, Z. Zhou, A new clade of basal Early Cretaceous pygostylian birds and developmental plasticity of the avian shoulder girdle. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 10708–10713 (2018).
38. Y. Yang *et al.*, Distribution and time frame of *Nestoria* fauna and determination of Late Mesozoic volcanic-sedimentary strata in the Da Hinggan Mountains. *Geol. Bull. China* **39**, 827–838 (2020).
39. Y. Zhong *et al.*, High-precision geochronological constraints on the duration of 'Dinosaurs Pompeii' and the Yixian Formation. *Natl. Sci. Rev.*, 10.1093/nsr/nwab063 (2021).
40. Y. Liu *et al.*, Mesozoic basins and associated palaeogeographic evolution in North China. *J. Palaeogeogr. Palaeoclimatol. Palaeoecol.* **559**, 109951 (2020).
41. X. Li, R. Reisz, The stratigraphy and paleoenvironment of a 'Lycoperia Bed' site in eastern Inner Mongolia, China: Correlation with the fossiliferous Lower Cretaceous strata in western Liaoning. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **559**, 109951 (2020).
42. R. Matsumoto, S. Evans, Choristoderes and the freshwater assemblages of Laurasia. *J. Iber. Geol.* **36**, 253–274 (2010).
43. R. Matsumoto, S. E. Evans, M. Manabe, The choristoderan reptile *Monjurosuchus* from the Early Cretaceous of Japan. *Acta Palaeontol. Pol.* **52**, 329–350 (2007).
44. P. P. Skutschas, D. D. Vitenko, Early Cretaceous choristoderes (Diapsida, Choristodera) from Siberia, Russia. *Cretac. Res.* **77**, 79–92 (2017).
45. K. Gao, Q. Li, M. Wei, H. Pak, I. Pak, Early Cretaceous birds and pterosaurs from the Sinuiju Series, and geographic extension of the Jehol Biota into the Korean Peninsula. *J. Paleontol. Soc. Korea* **25**, 57–61 (2009).
46. S. Sano, A. Yabe, Fauna and flora of Early Cretaceous Tetori Group in Central Japan: The clues to revealing the evolution of Cretaceous terrestrial ecosystem in East Asia. *Palaeoworld* **26**, 253–267 (2017).
47. Q. Meng, H. Wei, G. Wu, L. Duan, Early Mesozoic tectonic settings of the northern North China craton. *Tectonophysics* **611**, 155–166 (2014).
48. X. Yang, B. Jiang, Y. Yang, Spatial-temporal distribution characteristics of the Early Cretaceous volcanic rocks in the Da Hinggan Mountains. *Earth Sci. (Paris)* **44**, 3237–3251 (2019).
49. Y. N. Lee, K. M. Yu, C. B. Wood, A review of vertebrate faunas from the Gyeongsang Supergroup (Cretaceous) in South Korea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **165**, 357–373 (2001).
50. Y. Wang, Isotope dating suggests the diachronous feature of the Jurassic volcano-sedimentary strata in the northern North China craton. *Acta Geol. Sin.* **89**, 33–34 (2015).
51. J. Zhang *et al.*, Large-scale Early Cretaceous volcanic events in the northern Great Xing'an Range, northeastern China. *Lithos* **102**, 138–157 (2008).
52. S. Chang, S. R. Hemming, K. Gao, C. Zhou, $^{40}\text{Ar}/^{39}\text{Ar}$ age constraints on Cretaceous fossil-bearing formations near the China–North Korea border. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **396**, 93–98 (2014).
53. D. Chen *et al.*, Timing of the late Jehol Biota: New geochronometric constraints from the Jixi Basin, NE China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **492**, 41–49 (2018).
54. M. Wang, G. T. Lloyd, C. Zhang, Z. Zhou, The patterns and modes of the evolution of disparity in Mesozoic birds. *Proc. R. Soc.* **288**, 20203105 (2021).