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Jurassic-Cretaceous Herpetofaunas from the Jehol Associated Strata in NE China: Evolutionary and Ecological Implications

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Jurassic-Cretaceous herpetofaunas have recently been recovered from tuff-interbedded lacustrine strata in northeastern (NE) China. Most of them are from the Early Cretaceous Jehol Group (131–120 Ma), which has yielded a diverse and important fossil assemblage including insects, plants, fishes and tetrapods. Work on the Jehol Biota has been ongoing for more than a century, but the discovery of important new localities, particularly in western Liaoning, northern Hebei and southeastern Inner Mongolia in the past decade, has fuelled a resurgence of interest and a stream of spectacular finds. The fossils found at these localities are often characterized by articulated skeletons and even exquisite soft tissue preservation.

Associated with the Jehol Group, another important fossil horizon, the Daohugou Fossil Bed, was also identified in the same areas. It predates the Jehol Group, and may be of Late Jurassic age. Findings from this horizon include a diverse caudate assemblage and many insects. Both the Jehol Biota and the Daohugou Fossil Bed are justly famous for their feathered dinosaurs and mammals, whereas their herpetofaunal components, including salamanders, frogs, turtles, choristoderes and lizards, 26 species in total, also play an important role in phylogenetic and paleoenvironmental analyses.

Amphibians

Frogs and salamanders have been collected from more than 15 localities of the Jehol Group and Daohugou Fossil Bed. *Jeholotriton* and *Chunerpeton* (Daohugou Bed, Inner Mongolia) are paedomorphic caudates (animals whose adults resemble juveniles). Phylogenetic analysis suggests *Jeholotriton* is a primitive taxon lying at the base of the crown-group Urodela. *Chunerpeton* is the only Chinese Mesozoic

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salamander taxon that can be classified at a familial level (Cryptobranchidae) and one of the earliest crown-group caudates found in the world. *Liaoxitriton* (Daohugou Bed, Inner Mongolia; Yixian Fm, Liaoning) is a fully metamorphosed salamander similar to modern hynobiids and with its two species, links the Daohugou Fauna (*L. daohugouensis*) to the Jehol Biota (*L. zhongjiani*). *Laccotriton* and *Sinerpeton* are hynobiid-like salamanders from the same quarry (Yixian Fm, Hebei), the former being the first Mesozoic caudate reported from China (in 1998). *Pangerpeton* (Daohugou Bed, Liaoning) is a metamorphosed salamander having a close affinity with *Jeholotriton*, and it is one of the shortest-bodied salamanders known. The newly named *Regalerpeton* (Dabeigou Fm, Hebei) is the sister taxon to *Chunerpeton* but it is metamorphosed and bears characteristics of *Liaoxitriton*.

The basal frog *Mesophryne* is an exception among the four Jehol frogs in being represented by more than one specimen, and it is the sister taxon to the archaeobatrachian (archaic frogs) clade. At some localities, it is found as well preserved, three-dimensional skeletons, unusual for Mesozoic anurans known from around the world. *Yizhoubatrachus* should be a subadult, affecting some diagnostic characters. Together with *Mesophryne* and *Liaobatrachus* (referred to the family Pelobatidae on questionable characters), these genera form successive sister groups to Archaeobatrachia. *Callobatrachus*, from the same locality and horizon as *Liaobatrachus*, represents the earliest discoglossid frog from China, and the most primitive discoglossid known to

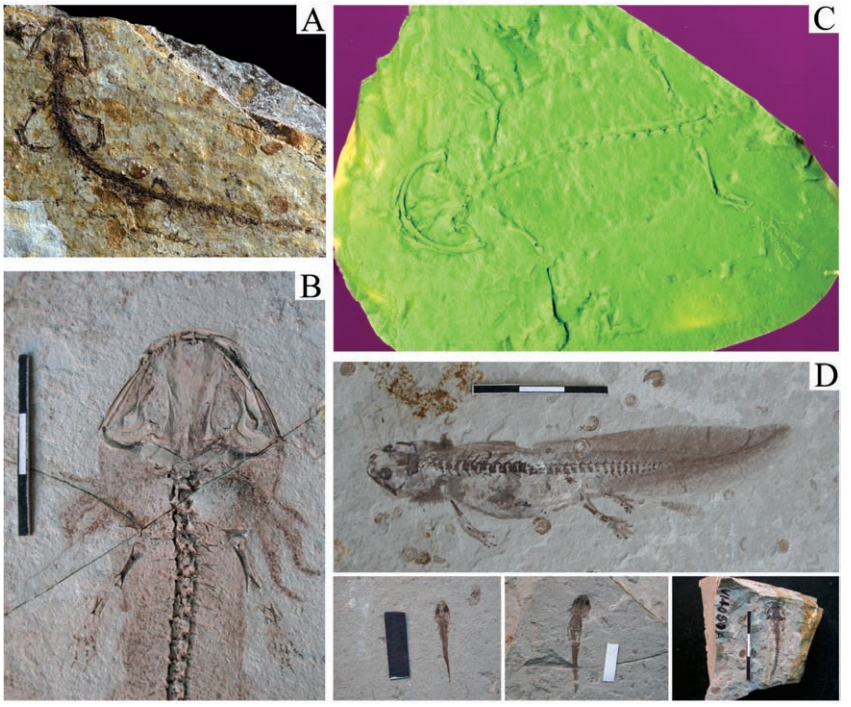


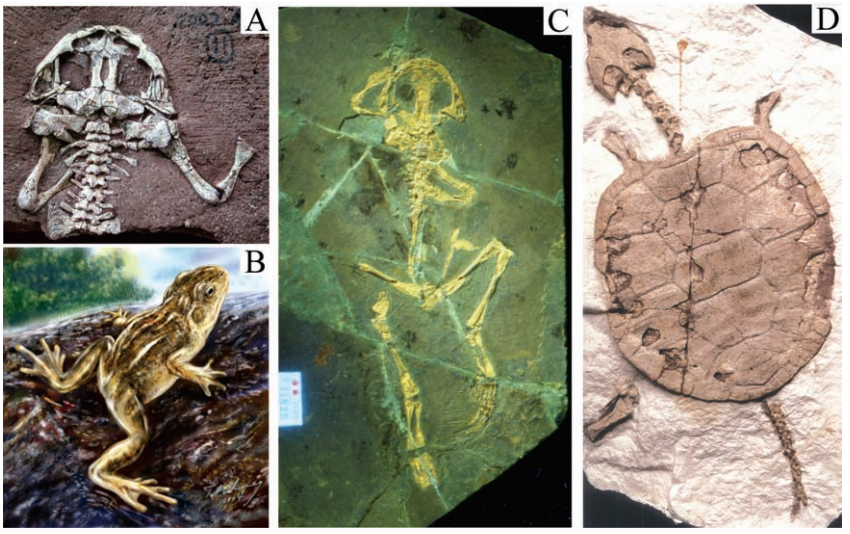
Fig.1 Jehol-associated fossil salamanders: (A) *Laccotriton subsolanus* (Holotype); (B) *Chunerpeton tianyiensis*, showing well-preserved impressions of external gills; (C) *Pangerpeton sinensis* (a high fidelity cast of the holotype, showing a "fat" body outline and warty skin impressions); and (D) *Jeholotriton paradoxus*, showing ontogenetic series, and an exquisite tail imprint in the adult.

date. It extends the temporal range of the group in Asia back by at least 120 Ma, and provides valuable anatomical information on early anurans. An unnamed tadpole from Daohugou represents the earliest anuran from China, and signals the possibility of finding adult specimens in the same fossil horizon.

The salamanders and frogs from the Jehol-associated faunas are important in resolving the highly problematic phylogeny of caudates and anurans. Their fine preservation, high taxonomic diversity and crucial geological age (Jurassic to Cretaceous) can help to elucidate the early evolution and diversification of lissamphibians. However, frogs and salamanders are represented by disproportionate numbers of specimens, reflecting differences in depositional environments. Adult frogs are common only in the more terrestrial deposits and are rare in the fully aquatic environments. By contrast, salamanders are found only in the aquatic facies, and paedomorphic taxa predominate. Several localities even preserve salamanders at different growth stages, a situation unique amongst Mesozoic localities around the world. They thus provide a wonderful opportunity for ongoing ontogenetic studies.

Turtles

Turtles are rare in the Jehol-associated faunas of NE China. Until recently, only one genus was recognized, *Manchurochelys*, with two species, but one of these, M. *liaoxiensis*, was lately reassigned to the genus *Ordosemys*. Turtles are known from only two horizons of the Jehol Group and show obvious aquatic adaptations. New



material under study (by present authors) from the Yixian Fm of Inner Mongolia may reveal more cranial characters.

Fig. 2 Jehol-associated fossil frogs and turtles: (A) The three dimensional preservation of a frog skeleton from Lujiatun Locality, Liaoning; (B, C) *Callobatrachus sanyanensis* (a life reconstruction, and a holotype skeleton under UV light showing eye imprints); and (D) *Ordosemys liaoxiensis* (a compressed skeleton prepared from two sides).

Choristoderes

Choristoderes are an extinct group of freshwater reptiles (170–15 Ma). They are much more common in the Jehol-associated faunas than turtles and some choristoderan taxa are represented by a full range of growth stages. Three ecomorphic types have been recognized: a long-snouted gavial type (*e.g.*, *Ikechosaurus*), a short-snouted crocodile type (*e.g.*, *Monjurosuchus*), and highly aquatic long-necked type (*e.g.*, *Hyphalosaurus*). Choristoderes appear to have thrived and diversified in East Asia during the Early Cretaceous. They are thought to have dispersed into western North America when it became connected to East Asia about 110 million years ago, but then disappeared from the Asian record, possibly due to climate change.

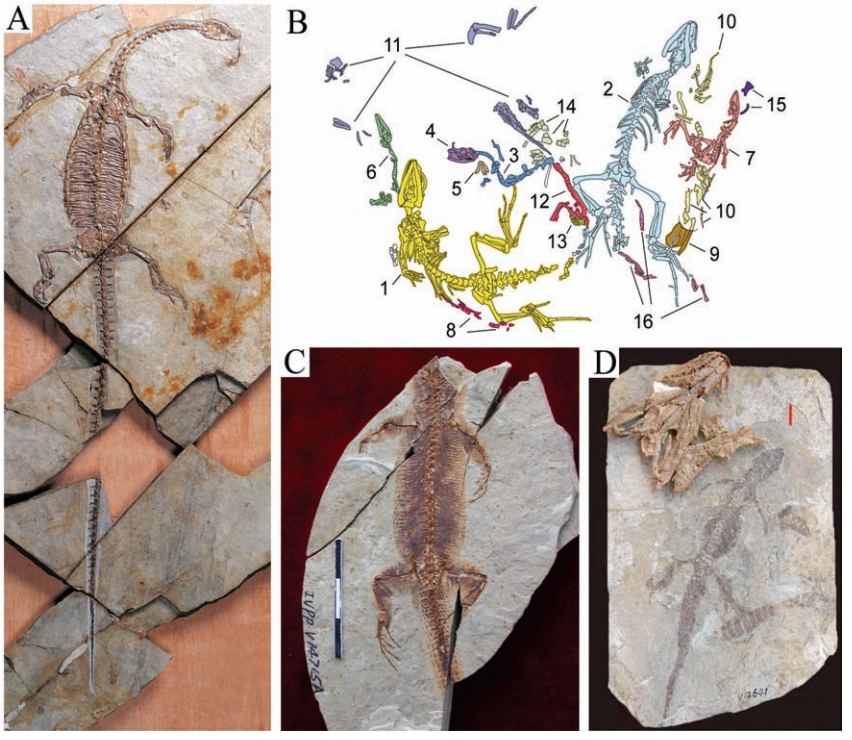


Fig. 3 Jehol-associated fossil choristoderes and lizards: (A) *Hyphalosaurus lingyuanensis* (Holotype, 1.16 m long); (B) Colored outline drawing of 16 *Dalinghosaurus* lizards buried in aggregation on a block of rock; (C) *Liushusaurus acanthocaudata* showing exquisitely preserved scalation; (D) *Yabeinosaurus tenuis* (a juvenile skeleton and an adult skull for size comparison).

Lizards

Lizards are relatively rarer than salamanders in the Jehol-associated strata, but are quite diversified in terms of ecomorphs. *Yabeinosaurus* (Yixian Fm, Liaoning) is a large, robust, terrestrial squamate with conservative body proportions. Newly found specimens have allowed a revision of previous descriptions, which were

all based on juvenile specimens. *Dalinghosaurus* is a scleroglossan lizard that is smaller and more gracile than *Yabeinosaurus*, and has longer hind limbs. It may have been a runner and/or climber. *Liaoningolacerta* and *Xianglong* are both from the Yixian Fm of Liaoning. The former is a juvenile named on the basis of an indeterminate specimen with scale impressions. The latter is a gliding lizard with long ribs. Two unnamed lizard specimens were recently described from Daohugou, both immature. One has well-preserved skin impressions and the other represents a distinct long-limbed form. The recently named *Liushusaurus* (Yixian Fm, Inner Mongolia) shows exquisite preservation of the scales and other integumentary structures, as well as sexually dimorphic traits. Like *Yabeinosaurus*, it may be a survivor from an older, Jurassic, squamate lineage.

Discussion

The herpetofaunas recently recovered from the Late Jurassic to Early Cretaceous strata of NE China represent a paleontological legacy of unrivalled importance for our understanding of vertebrate evolution, particularly with respect to the smaller species living in terrestrial–freshwater ecosystems (birds, mammals, frogs, salamanders, lizards, *etc*). Comparisons with contemporaneous deposits in neighboring countries (*e.g.* Japan, Korea) show biotic similarities that reflect the geographic continuity of these regions until 120 million years ago. Wider global comparisons suggest that Eastern Asia at this time was isolated from the rest of the world and had a unique fauna that later spread to other regions. Phylogenetic analysis of selected taxa shows the presence of both survivors of older, Jurassic, lineages and representatives of newer clades. It also provides new information on disputed family-level relationships, *e.g.*, within Amphibia and Squamata.

The exquisite preservation of many of the Jehol specimens also allows real insights into the biology of these extinct organisms. One interesting topic under study is the influence of volcanic activity on the herpetofaunas and their preservation. The prevalence of paedomorphic salamanders at Daohugou may imply unfavorable terrestrial conditions of high surviving pressure caused by frequent volcanic eruptions at the time. Some polydactylous caudate specimens found in Liaoning may also result from water toxicity related to volcanic activity. At some localities, volcano-triggered mudslides may be responsible for mass mortality events such as those represented in the Lujiatun Bed, where three dimensional skeletons of frogs, lizards and even dinosaurs (psittacosaurs) are buried in aggregation. It is remarkable that after more than a decade of extensive excavation and collecting, new herpetofaunal localities and new taxa are still being found. We can therefore anticipate that our understanding of the early evolutionary history of these amphibians and reptiles will continue to improve as a result of the Chinese finds, with more interesting fossils being recovered in the future.

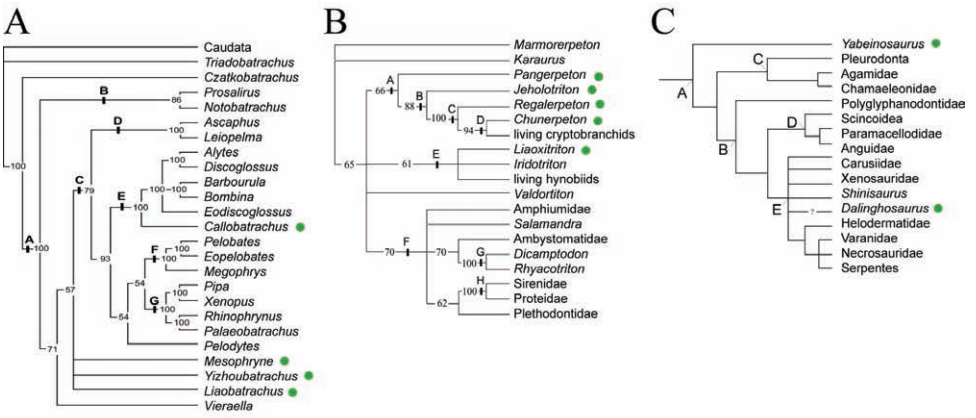


Fig. 4 Phylogeny of (A) basal anurans at generic level; (B) caudates at familial level; and (C) squamates from China. Green dots denote Mesozoic taxa from China.

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