THE JEHOL FOSSILS

The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants

Editor-in-Chief: Mee-mann Chang
Co-editors: Pei-ji Chen
Yuan-qing Wang
Yuan Wang
English editor: De-sui Miao

CONTRIBUTORS

Cao, Mei-zhen	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Chang, Mee-mann	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Chen, Jin-hua	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Chen, Pei-ji	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Friis, Else Marie	Swedish Museum of Natural History; Box 50007, SE-104 05 Stockholm, Sweden
Gao, Ke-qin	School of Earth and Space Sciences, Peking University; Building Yifu No. 2, Peking University, Beijing 100871, China
Hou, Lian-hai	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Hu, Yan-xia	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Hu, Yao-ming	American Museum of Natural History; Central Park West at 79th Street, New York, New York 10024, USA Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Jin, Fan	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Leng, Qin	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Li, Chuan-kui	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Li, Wen-ben	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Liu, Jun	American Museum of Natural History; Central Park West at 79th Street, New York, New York 10024, USA Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China

CONTRIBUTORS

Lu, Hui-nan	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Pan, Hua-zhang	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Shen, Yan-bin	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Wang, Qi-fei	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Wang, Xiao-lin	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Wang, Yuan	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Wang, Yuan-qing	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Wu, Shun-qing	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Xu, Xing	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Yang, Jing-lin	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Zhang, Fu-cheng	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Zhang, Hai-chun	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Zhang, Jiang-yong	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Zhang, Jun-feng	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China
Zhou, Zhong-he	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; No. 142, Xi-Zhi-Men-Wai Street, Beijing 100044, China
Zhu, Xiang-gen	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; No. 39, East Beijing Road, Nanjing 210008, China

Sibetun Village
Photo: Jie Zhang/ IVPP

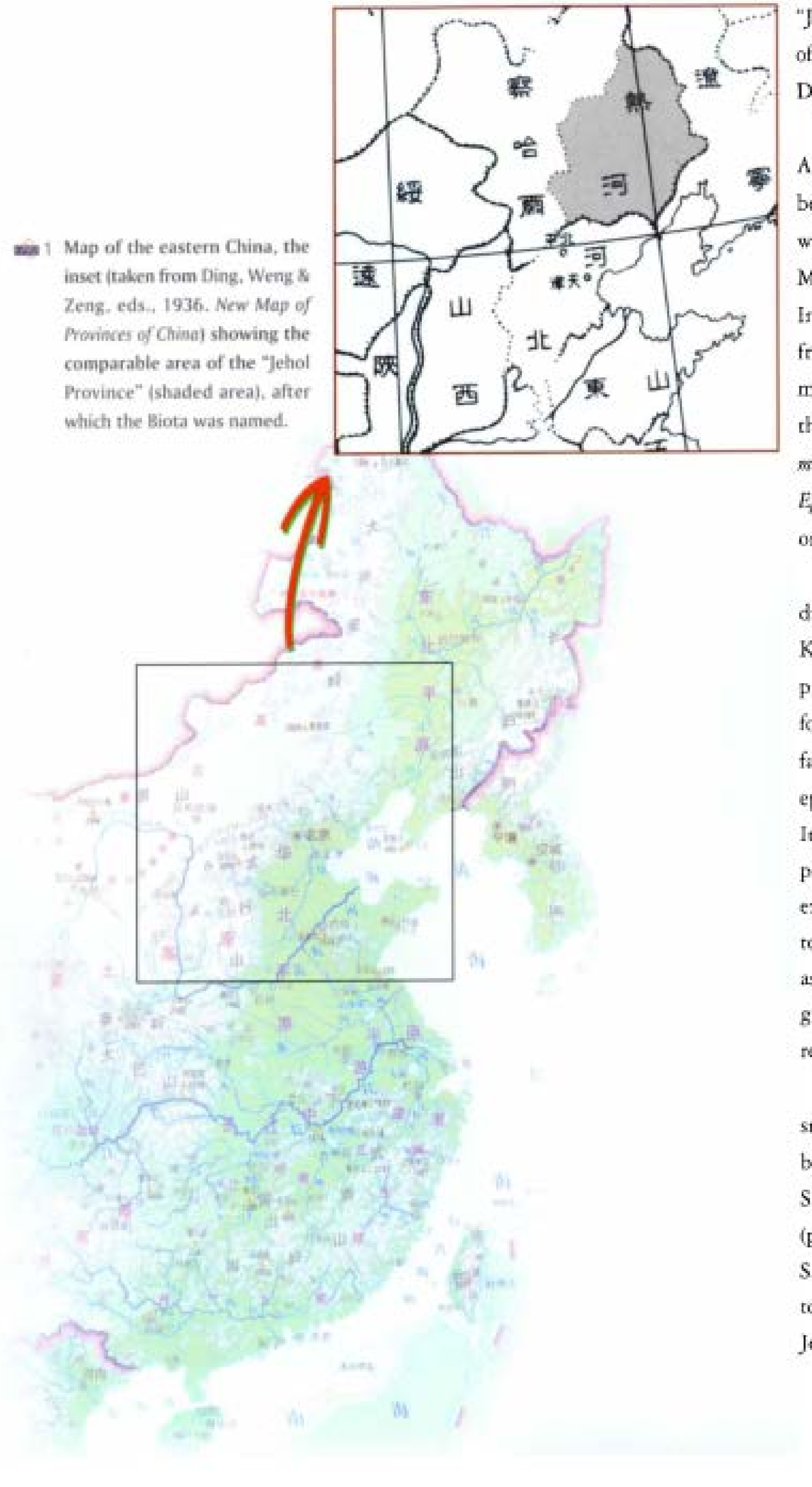
INTRODUCTION

Mee-mann Chang

Last decade has witnessed a renewed interest in the Jehol Biota both within the scientific community and among the general public worldwide. The numerous research papers on the Jehol Biota, published in the prestigious journals such as *Nature* and *Science*, have generated heated controversies among scientists and gained a widespread media frenzy. Here is a perfect example of Stephen J. Gould meeting Thomas S. Kuhn: a sudden "scientific revolution" has punctuated a long period of "normal science," with John Ostrom's revival of Thomas H. Huxley's theory of dinosaurian origin of birds as the new (or more precisely, renewed) paradigm. The discoveries of "feathered" dinosaurs in the Jehol Biota appear to have provided the direct evidence in support of the paradigm and therefore aroused public's intrigue in the notion of dinosaurs still being with us. Scientifically even more important is the Jehol Biota's well-preserved ancient biodiversity, which contains enormous amount of information on the paleoecosystem as well as many evolutionary issues.

We Chinese paleontologists have also had our turn of the wheel not only in those fabulous fossil finds but also in our poise to join our country's drive toward excellence in scientific research. To that end, I hope that this book bears some fruits. In the remainder of this chapter, I will present a brief history of the studies on the Jehol Biota, an outline of its main components, and a highlight of its scientific import.

"Jehol" is the transliteration of the two Chinese characters "熱河" in the Wade-Giles romanization system of the Chinese language, which was used until 1979 when the spelling of proper nouns were officially adopted using the Pinyin (Chinese phonetic alphabet) system of romanization in the mainland of China. In the Pinyin system, these two characters are transliterated to "Rehe". However, we must abide by the "International Stratigraphic Guide" (1976) to continue to use the terms of Jehol Group and Jehol Biota (or Fauna). The literal meaning of the two Chinese characters "熱河" is "Hot River", derived from many hot springs in the area. What are now called western Liaoning, northern Hebei and southeastern Inner Mongolia were municipally included in Jehol Province (Fig. 1) before 1956, when the provincial name was abolished. At present, the only historical reminder of the



1 Map of the eastern China, the inset (taken from Ding, Weng & Zeng, eds., 1936. *New Map of Provinces of China*) showing the comparable area of the "Jehol Province" (shaded area), after which the Biota was named.

"Jehol" is the two characters engraved on a stone tablet in Rehe Hot Spring of the Chengde summer resort, originally built for the emperors of the Qing Dynasty to escape the midsummer heat in the Forbidden City (Fig. 2).

In his paper "Cretaceous Mollusca from North China" (1923), the American geologist Prof. Amadeus W. Grabau (Fig. 3) named the fossil-bearing strata in the vicinity of Lingyuan County (now Lingyuan city in western Liaoning Province) as "Jehol Series". And while studying the Mesozoic stratigraphy of China in 1928, he first used the name "Jehol Fauna". In 1962, after working on various deposits bearing the fossil fish *Lycoptera* from different areas of western Liaoning, Prof. Zhi-wei Gu (Fig. 4), a malacologist from the Nanjing Institute of Geology and Palaeontology, used the name "Jehol Group" for the strata containing the conchostracan *Eosestheria middendorfii* (previously known as *Bairdestheria middendorfii*), insect larva *Ephemeropsis* and fish *Lycoptera*. Accordingly, he called the biota "Jehol Biota" or, in short, the E.-E.-L. Biota (Fig. 5).

The late Mesozoic Jehol Biota and those comparable to it had a wide distribution over northern China, Mongolia, Transbaikalian region of Siberia, Korea, and Japan (Fig. 6). The size of this area almost approaches that of the present-day Europe. This late Mesozoic oasis provided favorable conditions for many ancient animals and plants to thrive. A series of NE/SW- oriented fault basins developed during the Yanshan Orogeny (mountain-building episode), and were filled with thick volcanic and fluvial-lacustrine deposits. It was probably because of the frequent volcanic eruptions that numerous plants and animals were rapidly buried and consequently, preserved as exquisite fossils. Their catastrophic misery has turned into our best luck today: we have collected not only complete skeletons but also soft parts , such as feathers, and featherlike structures preserved as impressions, and not only gizzard stones but also stomach contents, especially in Chaoyang and Beipiao regions of western Liaoning.

The earliest studied fossil from the Jehol Biota in western Liaoning is a small fish found in the vicinity of Lingyuan City. The material was collected by L'Abbé David, and named in 1880 by a French ichthyologist, H. E. Sauvage, as *Prolebias davidi*, then thought to be a Tertiary cyprinodont (pupfish). It was not until 1901 when the renowned British ichthyologist A. S. Woodward reassigned the fish to the Mesozoic *Lycoptera*, a genus endemic to Siberia, Mongolia, and northern China. To date, the described fossils of the Jehol Biota include over 60 species of plants, nearly 90 species of vertebrates,

2 The Rehe Hot Spring in the Chengde summer resort. The two red characters on the stone tablet are "Jehol" in traditional Chinese.

and almost a thousand species of invertebrates. With the Jehol Biota being a hotbed of paleontological research at present, that number is increasing rapidly.

The Jehol Biota possesses the dual qualities that entice an unbridled enthusiasm from professionals and lay persons alike. The fossils are extremely well preserved, beautiful, and abundant. They have important implications on some key issues in evolution such as origin and early diversification of major groups like birds (Hou et al.,1995), mammals, and angiosperms (flowering plants), origin of avian flight, tempo and mode of evolution, paleobiogeography, paleoecology, and paleoenvironments.

The most notable among the recent fossil findings from western Liaoning are of course the "feathered" dinosaurs. Feathers had never been

3 Amadeus W. Grabau (1870–1946), an American geologist who proposed the Jehol Fauna in 1928. (Courtesy: Yuan-lin Sun/ PKU)

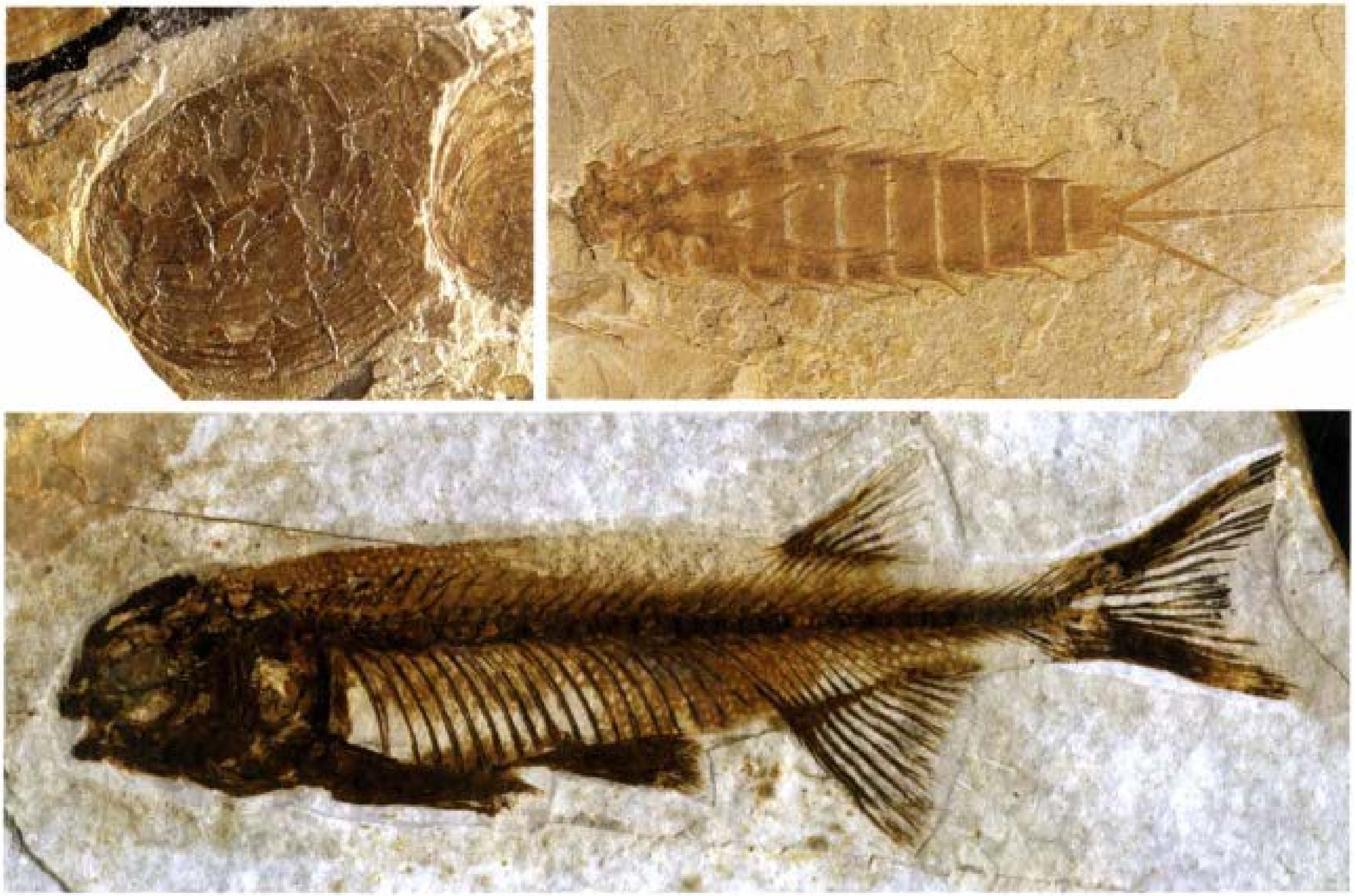
4 Zhi-wei Gu (b.1918), a Chinese malacologist of the NIGP who proposed the E.-E.-L. Biota in 1962.

discovered previously in animals other than birds. Yet, feathers or featherlike structures have been found abundantly associated with a number of dinosaurs from Liaoning such as *Sinosauropteryx* (Chen et al.,1998), *Caudipteryx*, *Beipiaosaurus*, *Protarchaeopteryx*, *Sinornithosaurus*, and *Microraptor*. If we only look at the skeletons of these creatures, dinosaur workers would say without hesitation that they are dinosaurs. Yet all of them bear feathers or featherlike structures. Though somewhat bewildered at first, many paleontologists soon realized how significant these discoveries were: the feathers and featherlike structures found in those dinosaurs betrayed the dinosaurs' affinity to birds!

In fact, about 130 years ago, Thomas H. Huxley thought the dinosaur was the direct ancestor of birds. And a few daring scientists even predicted that feathers would sooner or later be found on dinosaurs. But that point of view had not received general acceptance. It was not until 1973 when Prof. John Ostrom at the Yale University studied the small theropod *Deinonychus*, and found that its skeleton was astonishingly similar to that of *Archaeopteryx*, the earliest bird. And he suggested that small theropods might be the ancestors of birds. Despite the many skeletal characters that relate dinosaurs with birds, for most people, nothing can be more convincing than actually seeing the dinosaurs covered with feathers. To those who are convinced that birds are direct descendants of dinosaurs, the feathered dinosaurs from western Liaoning are nothing but the "smoking gun". However, a vocal minority of leading paleornithologists still insists that birds came from a primitive group of reptiles called thecodonts. Besides, feathers and featherlike structures were found on dinosaurs that apparently could not fly. Then what are those feathers for? Were they for insulation, for camouflage, for courtship, or for defense? And how did the avian flight originate? Did the proto-birds attain their flight capability by walking and running on the ground and then raising their wings to fly ("ground-up" theory), or by gliding from the tree to learn how to fly ("tree-down" theory)? We cannot expect that all these questions, together with the origin of birds, be answered just with the discoveries of new materials. More careful and synthetic work has to be done before more persuasive hypotheses emerge on more solid ground. Admittedly, this kind of work is more tedious and less sensational, but it is truly exciting and intellectually stimulating. Contrariwise, clever argumentation and religious war are bound to be detrimental to the progress in science.

The fossil plants, especially angiosperms, from western Liaoning are also very interesting. The records of angiosperms can be traced back to the works of H. Yabe and S. Endo in 1930s. They described *Potamogeton jeholensis*. Due to the poor preservation of the material, little attention was paid to their work. Later, S. Miki (1964) questioned the identification of *Potamogeton*, and considered the plant as *Ranunculus* instead. More recently, Zheng-yao Cao and others (1997) and Shu-ying Duan (1997) reported monocots and fructification with carpels. Cao et al.'s *Liaoxia chenii* (Cyperaceae) and *Eragrosites changii* (Gramineae) were later designated as gnetales, a group of gymnosperm, by Shun-qing Wu (1999) and Shuang-xing Guo and Xiang-wu Wu (2000) while Duan's *Chaoyangia liangii* is probably also a gnetalean, not an angiosperm. Similar forms have been found in the Lower Cretaceous strata of Mongolia and were described by V. A. Krassilov (1982) under other names: *Cyperacites* sp., *Potamogeton*-like spike, and *Gurvanella dictyptera*.

Archaefructus liaoningensis was described by Ge Sun, D. L. Dilcher and others (1998) as an angiosperm although this is not yet unquestionably accepted by most paleobotanists. Its age, however, may not be the Late Jurassic, as these authors suggested, but is more likely to be the same, i.e., the Early Cretaceous, as that of the early angiosperms previously discovered from Europe, Mongolia and western North America. A more definite angiosperm *Sinocarpus decussatus* was described recently by Qin Leng and E. M. Friis (2003). Another significant plant from the Jehol Biota is a gymnosperm *Sequoia jeholensis*. And it is regarded as the oldest record of the genus. The genus is at present surviving only in California. For lacking cone and the leaf cuticular structure, it must be treated with caution at present. More recently, Zhi-yan Zhou and Shao-lin Zheng (2003) reported that the ovulate organs of *Ginkgo* from the Yixian Formation show striking similarities to those of the extant species *Ginkgo biloba*, indicating a morphological stasis in *Ginkgo's* reproductive structure for over 100 million years. With ever increased and better-preserved specimens, we anticipate more thorough paleobotanical research of the Jehol

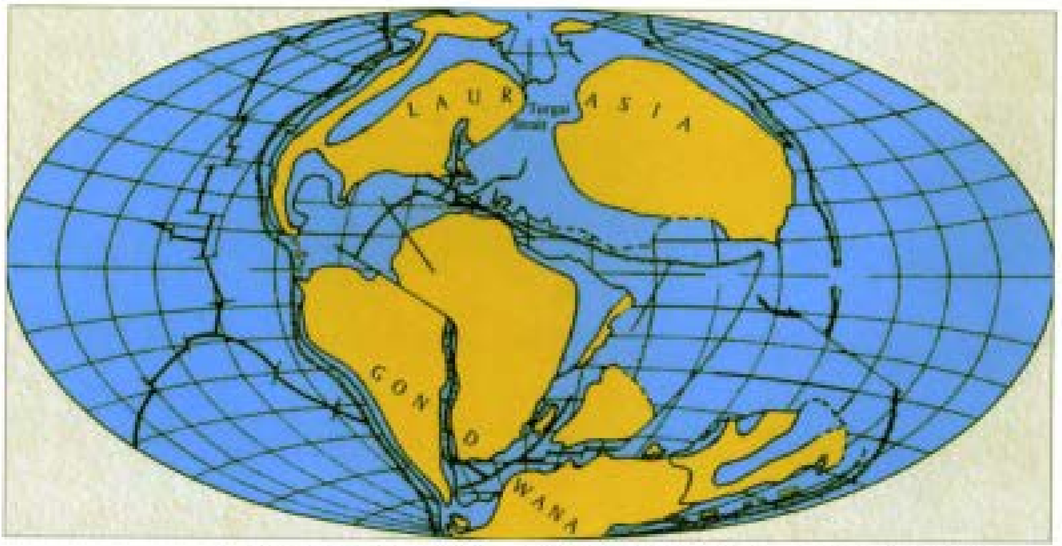


5 Three representatives of the Jehol Biota in the early studies, the conchostracan *Eosestheria* (**Upper left**), insect larva *Ephemeropsis* (**Upper Right**) and fish *Lycoptera* (**Lower**). (Photo: IVPP)

Biota in the near future as well.

The diversity, abundance, and exquisite preservation of the Jehol Biota make it one of a handful of extraordinary "Fossil-Lagerstätten" (strata containing abundant and well preserved fossils) in the world. Recently described vertebrate fossils include bony fishes, archaic frogs, salamanders, aquatic reptiles, lizards, turtles, dinosaurs, early mammals, etc. There are also abundant invertebrates: mollusks, ostracods, conchostracans, insects and others. Although this faunal list is far from complete, it catches a glimpse at the vast panorama of the Jehol Biota, which awaits further exploration.

6 Distribution of the Jehol Biota (green area) at its peak period.



7 Paleogeographic map of the world in the Early Cretaceous. (Modified from Fenton, Rich & Rich, 1989)

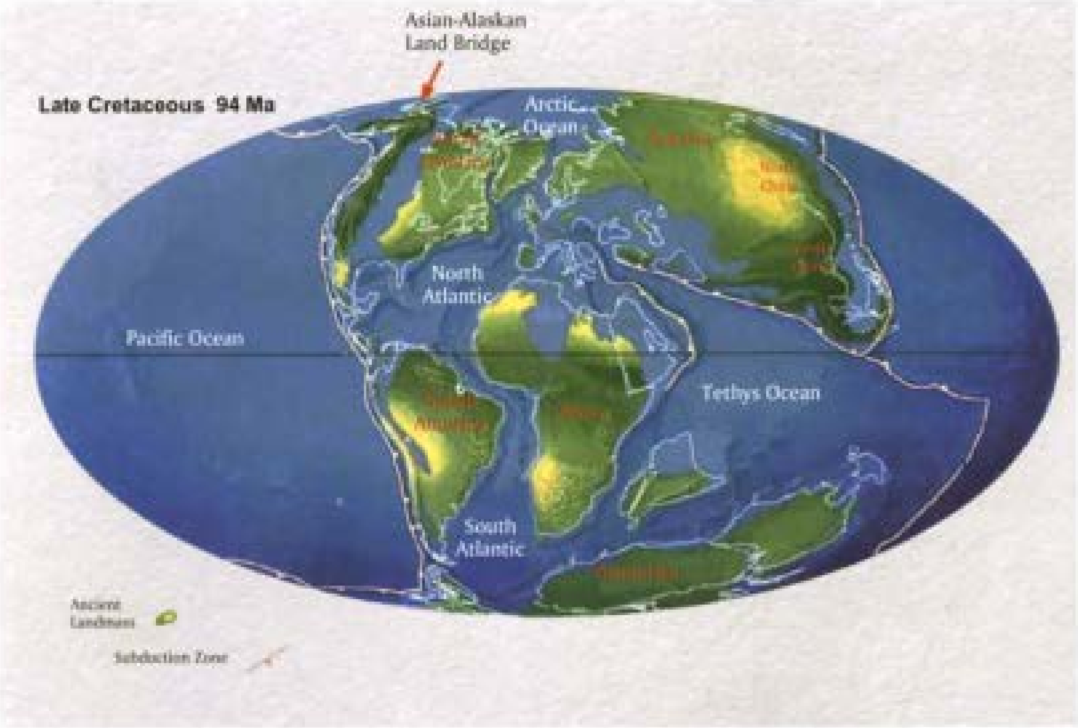
The Jehol Biota also has significant bearings on reconstructing the relationships among the ancient landmasses, i.e., paleobiogeography. During the lifetime of the Jehol Biota, the eastern part of Eurasia was an isolated area. It was separated from the western part of Eurasia by the Turgai Strait, and from North America by the comparatively wide Bering Strait (Fig. 7). Paleo-Qinling and Dabie Mountains on the southern border of this area must have acted as some kind of barrier that prevented the exchange of organisms between the north and south. Owing to this isolation, the Jehol Biota consists of many endemic forms, not seen on other continents, and not even seen in the southern part of China. For example, *Lycoptera* is a fish never found in any other places out of the distribution area of the Jehol Biota. Fishes such as polyodontid *Protopsephurus* and *Yanosteus* as well as amiiformes *Sinamia* were never found in their contemporaneous deposits anywhere else. In Late Cretaceous, however, when the Asian-Alaskan Land Bridge came into existence, many forms related to the aforementioned fishes started to appear and develop in North America (Fig. 8). Some of their close relatives still survive in North America as relics even today. For instance, *Hiodon* (mooneye) is related to *Lycoptera*, *Amia* (bowfin) to *Sinamia*, *Polyodon* (paddlefish) to *Protopsephurus* and *Yanosteus*; and a few other fishes seem to adopt the North American freshwater system as their present day refugium. You can find them nowhere else nowadays, and you can hardly find their ancient relatives in other parts of the world, either. Yet they occurred in the Jehol Biota. This is another aspect showing the Jehol Biota's scientific importance.

As for the age of the Jehol Biota, the debate has lasted for several decades. There are mainly two different opinions about the age: the Late Jurassic (ca. 145 millions years before present, or 145 Ma) versus the Early Cretaceous (ca. 125 Ma). Recently, C. C. Swisher III et al. (1999, 2002) and Ching-hua Lo et al. (1999) dated the Yixian Formation respectively. The former suggested an age of around 125 Ma (Early Cretaceous) using single sanidine crystal ^{40}Ar/^{39}Ar dating. And the latter used biotite for the ^{40}Ar/^{39}Ar laser single-grain fusion method and came up with an age of around 147 Ma (Late Jurassic). Many workers from various institutions are interested in the dating, and the work is still underway. The debate would probably go on for some time. But we can expect better results with more refined dating techniques and careful sampling and laboratory work in the near future.

This book provides the Biota's temporal and spatial relationships, showcases some of its most wonderful fossils, and summarizes our preliminary understandings of them. In a book that involves many authors and covers many taxonomic groups, it is almost inevitable that inconsistencies in age assignments and stratigraphic correlations exist. In most chapters, the Jehol Group includes the Yixian and Jiufotang Formations only, whereas in a few other chapters the scope of the Group varies to include certain strata either overlying or underlying those formations. We cannot overstate scientific impacts of the Jehol Biota on recent progress in paleontology. We hope that our readers will find the following pages visually pleasing, scientifically interesting, and intellectually rewarding.

It is worth noting that the Chinese names have, over the years, confused our overseas colleagues and bibliographers alike. To ease the situation, we decide to list the Chinese names according to the English convention, i.e., the first name first — a reversal of the Chinese custom with surname first. To further ease the pronunciation and potential confusion, we hyphenate the first name with two characters, e.g., Shu-an Ji. Without the hyphen, "Shuan" could be misconstrued as a single syllable, i.e., a first name with only one character.

ACKNOWLEDGMENTS: Needless to say, in a project as vast as this, there are numerous unsung heroes behind the contributors to this volume. I would like to name just a few whose assistances are particularly appreciated: E. M. Friis for her help with Chapter 19 and her willingness in joining in to add Chapter 20, Zhi-yan Zhou for his generosity in providing much-needed consultation on fossil plants, Er-mi Zhao, Zhe-xi Luo, and Ke-qin Gao for helping with figures for amphibian, mammal, and choristodere chapter, respectively, Dong Ren for supplying information and providing figures on insects, and Shu-an Ji for offering figures for some of the Jehol lizards. We express our heartfelt appreciation to Xiao-lian Zeng and Anderson Yang for their elegant artwork. We would also like to express our gratitude to the Chaoyang City Government and Land and Resources Bureau of Liaoning Province for their support in facilitating our fieldwork, and to the Museum of Natural Science (Taiwan) for supporting and participating in our research work (Fig. 9). This project is financed by the grants from the Chinese Academy of Sciences, the National Natural Science Foundation of China, the Ministry of Science and Technology of China, and the National Geographic Society of the US.



8 Paleogeographic map of the world in the Late Cretaceous. (From: http://www.scotese.com)

9 The IVPP field team joined by Prof. Yen-nian Cheng (back row, 2nd from the right) and his crew from the Museum of Natural History (Taiwan) in an excavation at Jianshangou, western Liaoning in May, 1999, when the vice president of the CAS, Prof. Yi-yu Chen (back row, 6th from the right) and the deputy mayor of the Chaoyang City, Mr. Xiao-kun Chen (back row, 7th from the right) visited the fossil site.

Site 1. Sihetun locality
Photo: Jie Zhang/ IVPP

MESOZOIC POMPEII

Xiao-lin Wang, Zhong-he Zhou

The eruption of Mount Vesuvius in 79 AD not only destroyed the historical city Pompeii but also caused the death of many people. When the lost city was rediscovered in 1748, the people and animals were still found lying in the thick ashes of the volcanic eruptions. Just as Pompeii's residents were victimized by the volcanic eruprions of 79 AD, so were the members of the Jehol Biota in the Early Cretaceous. This "Mesozoic Pompeii" has provided us a window through which we can observe the wonderful life that lived over one hundred million years ago.

Geologically speaking, the Jehol Biota developed in a relatively short time and quickly radiated in a large area in East Asia. It represents one of the largest radiations of terrestrial vertebrates during the Cretaceous period. The Jehol Biota has produced numerous beautifully preserved fossils, and thus revealed many evolutionary events of the terrestrial life.

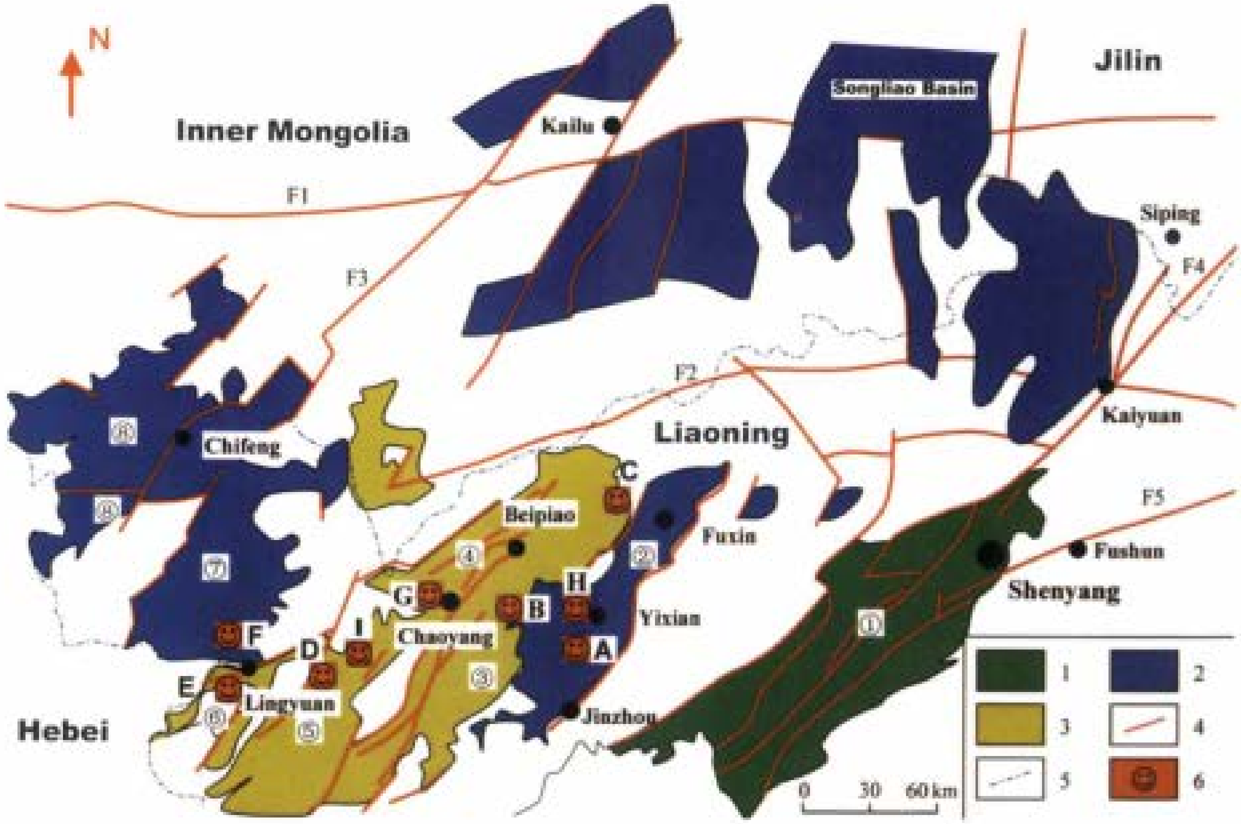
The discoveries of birds and feathered dinosaurs in the western part of Liaoning Province in late 1980s and 1990s attracted enormous attention of paleontologists worldwide. In the last decade, several dozens of major bird and dinosaur localities have been found in this region by workers mainly from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences. In the neighboring areas of northern Hebei Province and the southeastern Inner Mongolia (Nei Mongol Autonomous Region), there were also important discoveries similar to those from Liaoning. Since 1997, the field crews of the IVPP have launched about half a dozen large-scale excavations in Beipiao, Chaoyang, Fuxin in Liaoning, Fengning in Hebei and Ningcheng in Inner Mongolia, and collected hundreds of significant vertebrate specimens including fishes, amphibians, turtles, aquatic reptiles, lizards, pterosaurs, dinosaurs, birds, and mammals. Western Liaoning has since hosted hundreds of visitors each year worldwide and paleontologists and laypersons alike.

The Jehol Biota emerged at a time when the climate in the area was warm, with ample rainfall for most of the seasons. Such climatic background provided an ideal environment for animals and plants to thrive and differentiate. Lakes were widespread. Some of the water bodies were probably wide and deep. The plants were flourishing along the margins of the lakes. Volcanic eruptions were frequent at that time. Most vertebrates were preserved in rather deep lake deposits.

Throughout the Early Cretaceous, the Jehol Biota witnessed the increased volcanic activities. At least three major eruptions occurred during the deposition of the Yixian Formation and were responsible for the four significant lake deposit-volcanic eruption cycles. The volcanic rocks of the Yixian Formation mainly consist of basalts and andesites. The lake deposits of the Yixian Formation were mainly formed at the intervals between the major intermediate-basic eruptions although small-sized intermediate-acid volcanic eruptions occurred occasionally. The volcanic activities were less frequent and relatively weak at the time of the Jiufotang Formation.

The volcanic eruptions had long-lasting impact on the development and evolution of the Jehol Biota. With the intermediate-acid eruptions, a lot of poisonous gases were spread to the air, which could have caused the deterioration of the whole ecological system. For instance, at the Sihetun locality, several highly fossiliferous layers with exquisitely preserved fossils indicated some major mass mortality events of birds and feathered dinosaurs. The vertebrate fossils are mainly preserved in grayish black lacustrine shale and mudstone. They are frequently covered by a layer of volcanic ashes (tuff) (Fig. 10). Nearly all fossils are preserved in articulation; birds and dinosaurs often with feathers, skins and other soft tissues in the form of impression or

10 Stratigraphic section at the Sihetun locality, showing lacustrine deposits (gray layers) with intercalated tuffs (yellow layers).



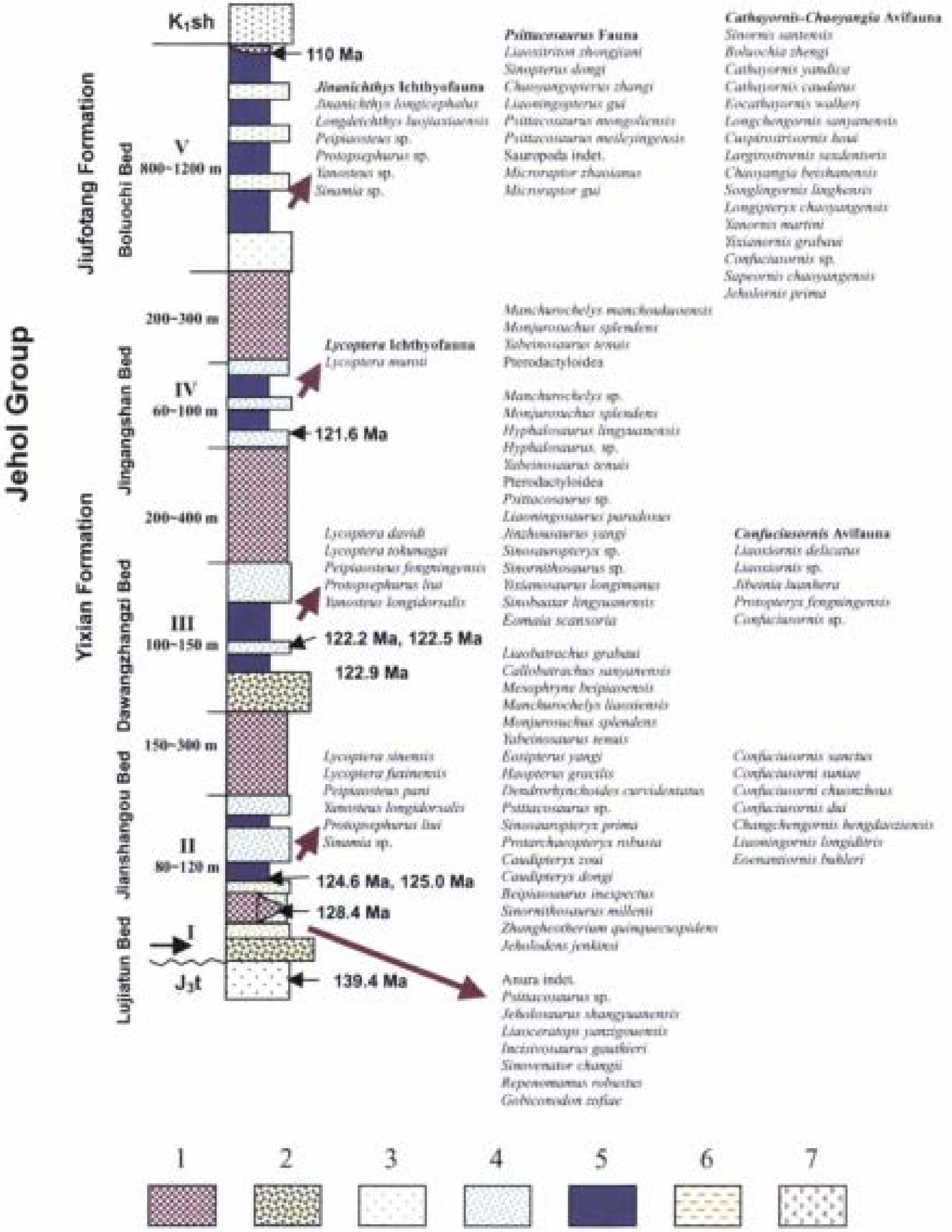
11 Distribution of major fossil vertebrate localities in western Liaoning and the neighboring areas. 1, Tertiary basins; 2, Cretaceous basins; 3, Jurassic-Cretaceous basins; 4, faults (F); 5, Provincial boundary; 6, Vertebrate sites. A, Jingangshan, Yixian; B, Sihetun, Beipiao; C, Dawujiazi, Fuxin; D, Boluochi, Chaoyang; E, Fanzhangzi, Lingyuan; F, Daohugou, Ningcheng; G, Shangheshou, Chaoyang; ①, Liaohe Basin; ②, Fuxin-Yixian Basin; ③, Jinlingsi-Yangshan Basin; ④, Beipiao-Chaoyang Basin; ⑤, Jianchang-Kazuo Basin; ⑥, Lingyuan-Sanshijiazi Basin; ⑦, Pingzhuang-Ningcheng Basin; ⑧, Chifeng-Yuanbaoshan Basin. (Geologic information of basins partly from Liaohe Petroleum Administration Bureau)

imprint with organic traces. Some specimens of dinosaurs were found with eggs, gastroliths and the stomach contents with remains identifiable as plant seeds, lizard and mammal skeletons. It is most likely that the environmental changes resulted from the volcanic eruptions caused the mass mortality of birds and other vertebrates. After a brief floating transportation on the surface of the lakes, the dead bodies quickly descended into, and were buried in, the deep water. The abundant volcanic ashes speeded up the deposition process; therefore the dead bodies were preserved rapidly and completely. In a sense, this is no different from the great burial of Pompeii.

Among the famous vertebrate fossil localities of the Jehol Biota are: Sihetun and Lujiatun localities in Beipiao; Fanzhangzi and Shanzui (Dawangzhangzi) localities in Lingyuan; Wanfotang, Hejiaxin, Wujiatun and Xierhuqiao localities in Yixian, Jinzhou; Shangheshou, Dapingfang, Lianhe and Dongdadao localities in Chaoyang, western Liaoning Province; Sichakou and Senjitu localities in Fengning, northern Hebei Province; and Daohugou and Xitaizi localities in Ningcheng, southeastern Inner Mongolia (Fig. 11).

In sum, after over half a century's study of the Jehol Biota and especially the unusual discoveries of the past ten years, our knowledge of the Jehol Biota has increased greatly compared with what was known in the past as represented by the *Eosestheria-Ephemeropsis-Lycoptera* assemblage (E.-E.-L. fauna as traditionally defined). The recent finds of the vertebrate fossils in western Liaoning have shed new light on the study of the origin of birds and their flight, the origin of feathers, early radiation of birds, mammals and angiosperms, and also furthered our understanding of the Early Cretaceous continental ecosystem.

Like the meticulous grid system at archaeological excavation sites, the rock layers have to be systematically studied in order to determine where the fossils are and decipher the geological age of the fossils embedded in them. Long before the recent discoveries of birds and feathered dinosaurs, the rocks producing them have been studied by several generations of paleontologists and geologists. It was the American geologist Amadeus W. Grabau who first proposed the "Jehol Series" and "Jehol Fauna" in 1920s. In 1962, Prof. Zhi-wei Gu introduced the Jehol Group into the literature. The Jehol Group is



1, basalt and andesite with volcanic breccia (lava); **2**, conglomerate with volcanic breccia; **3**, sandstone and conglomerate; **4**, tuffaceous sandstone and tuff; **5**, shale and tuff; **6**, silt and silty mudstone; **7**, subvolcanic rock

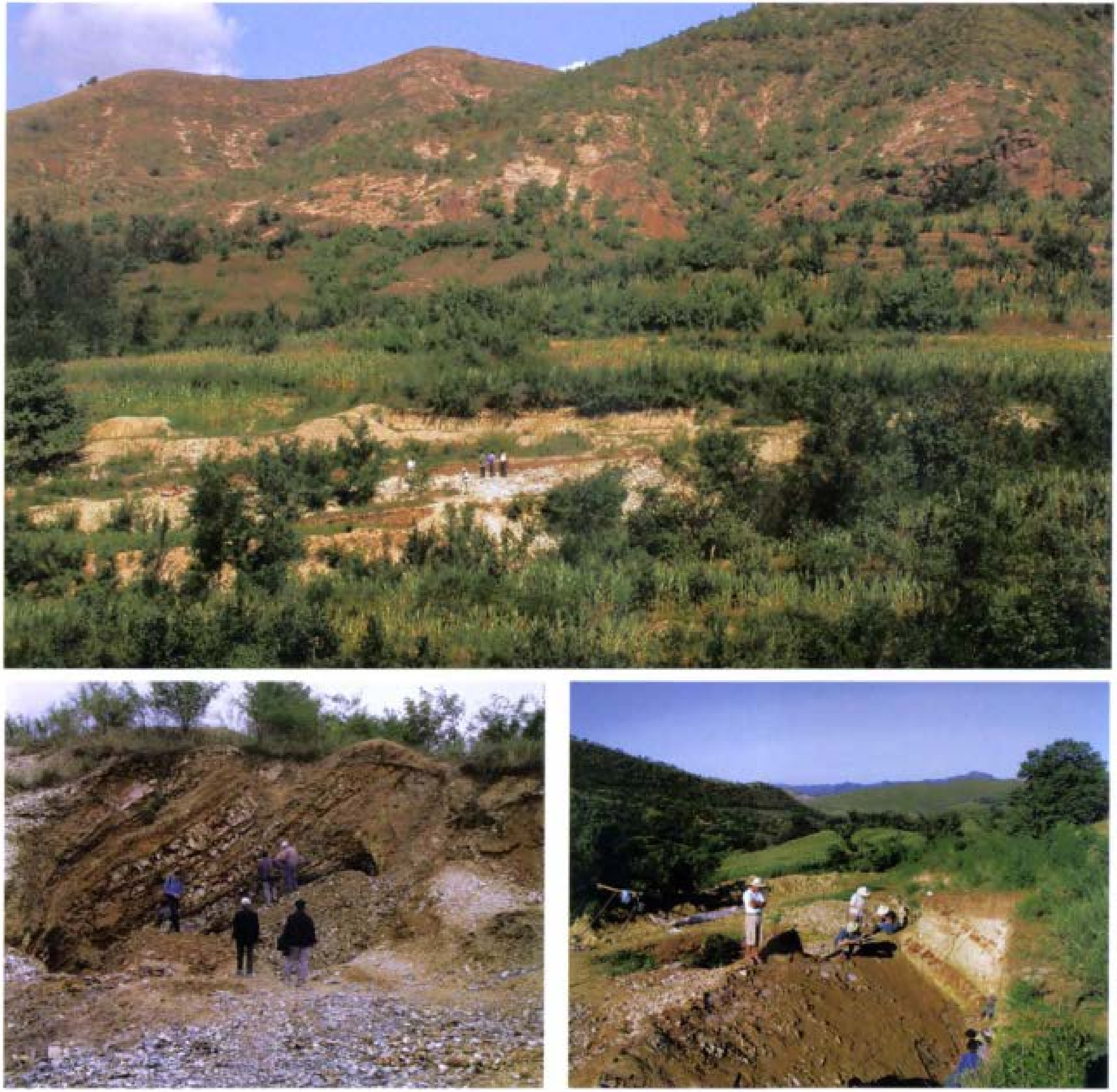
12 Biostratigraphic sequences of the Jehol Group.

a set of late Mesozoic rocks consisting of intercalated volcanic and lacustrine deposits rich in tuffaceous materials. The group comprises the Yixian Formation and the overlying Jiufotang Formation.

The Jehol Group is mainly distributed in northern Hebei Province, western Liaoning Province and southeastern Inner Mongolia in Northeast China. The deposits were formed in a series of northeast faulting basins in the late Mesozoic of northeastern Asia. Among the major basins are the Fuxin-Yixian Basin, Jinlingsi-Yangshan Basin, Beipiao-Chaoyang Basin, Jianchang-Kazuo Basin, Lingyuan-Sanshijiazi Basin, Pingzhuang-Ningcheng Basin, and Chifeng-Yuanbaoshan Basin. The vigorous collisions of plates in the western rim of the Pacific have resulted in the intensive tectonic activities in the eastern margin of the Eurasian continent at that time. Consequently, tectonic activities and frequent volcanic eruptions complicated the depositional history in different basins; hence the correlation of the deposits in these basins often becomes difficult.

The traditional Jehol Group, chronologically from old to new, comprises the Yixian Formation, Jiufotang Formation, Shahai Formation and Fuxin Formation. Recent studies show that the lithographic characteristics and the fossil assemblages of the Shahai and Fuxin Formations are much different from those of the Yixian and Jiufotang Formations. The Yixian Formation mainly comprises basalts and andesites, with interbedding lacustrine sediments (tuffaceous sandstones, gray and gray-black shales, mudstone and tuffs). Four fossil-bearing beds can now be recognized from the Yixian Formation. The Jiufotang Formation mainly comprises lacustrine sediments (grayish, gray-yellow, and gray-black sandstones, siltstones, shales and mudstones, with intercalated tuffs). The Shahai and Fuxin Formations are mainly composed of coal deposits and clastics, seldom with volcanic contents. The typical Jehol elements such as the *Eosestheria-Ephemeropsis-Lycoptera* assemblage as well as the feathered dinosaurs, early birds and some other distinctive vertebrates are only found in the Yixian and Jiufotang Formations. Their appearance in the Yixian Formation or slightly earlier deposits represents a major biological radiation event in the Early Cretaceous, and most of them existed until the Jiufotang time. Therefore, the Yixian and Jiufotang Formations record a complete history of the Jehol Biota. Currently, the Jehol Group is generally accepted as only to comprise these two

13 Lujiatun locality (basal part of Yixian Formation) in Shangyuan, Beipiao, Liaoning, showing tuffaceous sandstones, mudstones and overlying basalts (Lava, 128.4Ma).



14 Daohugou locality (basal part of Yixian Formation, but also arguably as Middle Jurassic Jiulongshan Formation by some other researchers) in Shantou, Ningcheng, Inner Mongolia, showing IVPP excavation sites of the year 2003.

formations.

Recently, we have recognized five fossil-bearing beds (or "members") of different age, with distinctive vertebrate assemblages (Fig. 12). They are, from the bottom to top: Lujiatun Bed of the lowest Yixian Formation (*Jeholosaurus-Repenomamus* assemblage), Jianshangou Bed of the lower Yixian Formation (*Lycoptera sinensis-Confuciusornis* avian fauna assemblage), Dawangzhangzi Bed of the middle Yixian Formation (*Lycoptera davidi-Hyphalosaurus* assemblage), Jingangshan Bed of the upper Yixian Formation (*Lycoptera muroii-Manchurochelys manchoukuoensis* assemblage), and the Boluochi Bed of the Jiufotang Formation (*Jinanichthys-Cathayornis* avian fauna assemblage). Most of the fossil localities of the Jehol Group can be referred to one of the above five beds.

Lujiatun Bed (Member) of the lowest Yixian Formation This bed is mainly distributed in the Sihetun and neighboring areas of the Jinlingsi-Yangshan Basin, representing a newly recognized fossil-bearing horizon of the Yixian Formation. It corresponds to the lowest bed (Member 1) in the composite stratigraphic section at the Sihetun area. The main localities where the Lujiatun Bed is exposed include Lujiatun, Xiaobeigou, Shuiquan and Sihetun of Beipiao City and Liutai of Yixian County, Jinzhou City. It is best represented in the Lujiatun locality.

The Lujiatun alluvial deposits were formed in the margin of early developing stages of the basins. They mainly comprise tuffaceous conglomerate, sandstones and silty mudstones about 20~40 meters thick (Fig. 13). This bed represents a nearly simultaneous mass mortality event that wiped out numerous adult and juvenile individuals of vertebrates, including the small-sized ornithischians such as *Jeholosaurus*, *Psittacosaurus* and *Liaoceratops*, the small-sized theropods like *Sinovenator* and *Incisivosaurus*, the primitive mammals *Repenomamus* and *Gobiconodon*, and frogs. No invertebrate fossil has been recognized. A few plant fragments and spore-pollen samples have been collected. Most of the Lujiatun fossils were collected in 2000 and 2001.

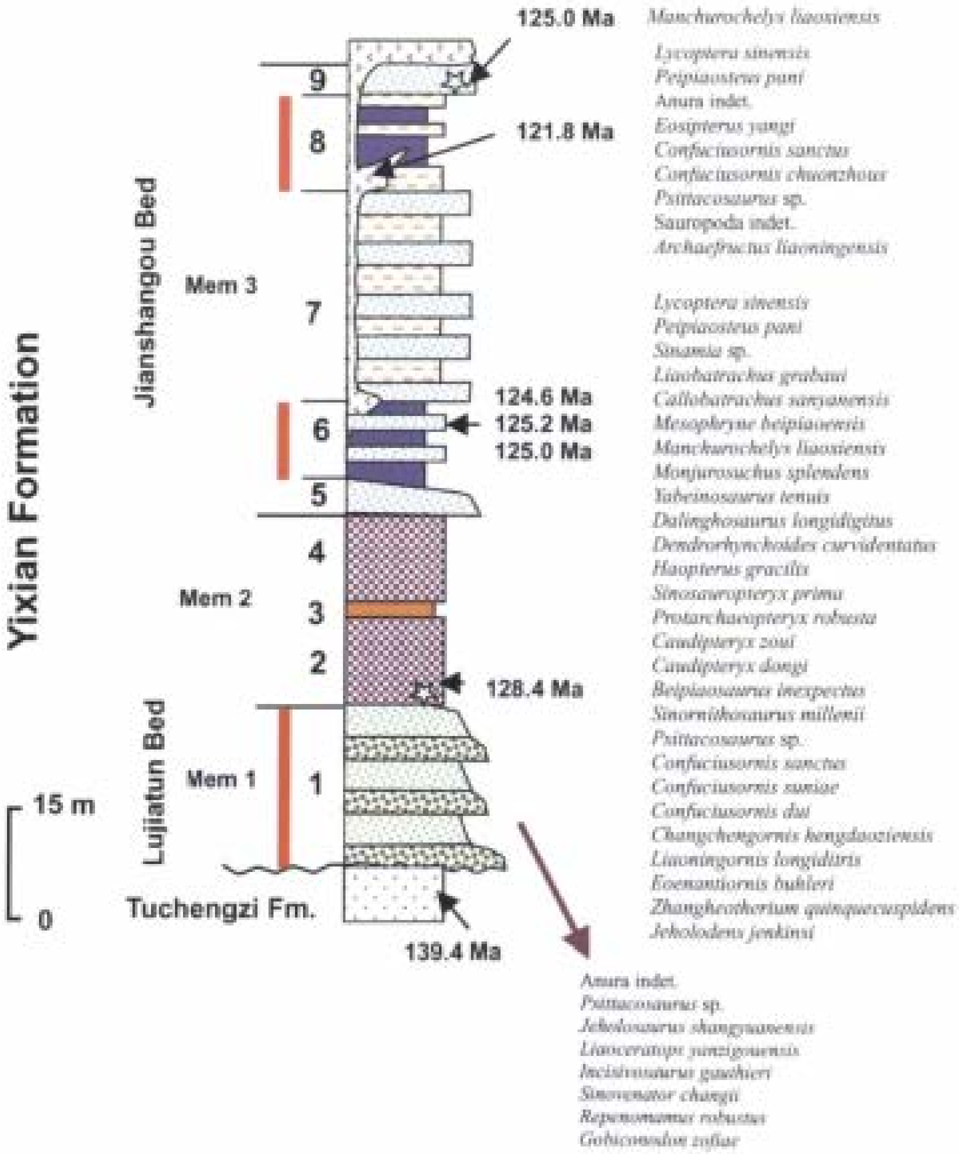
Since the fall of 1998, the Daohugou locality (Fig. 14) in Ningcheng County, Chifeng City, Inner Mongolia, adjacent and north to Lingyuan City, Liaoning, has produced abundant salamanders such as *Jeholotriton paradoxus* and *Chunerpeton tianyiensis*, the haired pterosaur *Jeholopterus ningchengensis* and feathered theropods such as the arboreal maniraptoran *Epidendrosaurus ningchengensis* and other vertebrates. It is noteworthy that thousands of beautifully preserved insects and plants have also been collected from this locality, yet the age of this deposit is still controversial, ranging from the Middle Jurassic to the Early Cretaceous according to different workers. We now regard the bed at Daohugou comparable to the Dabeigou Formation in northern Hebei, and it might be comparable to or slightly lower than the Lujiatun Bed in western Liaoning. At the neighboring Xitaizi locality (Fig. 15) with its statra overlying the Daohugou fossil horizon, abundant acipenseriform fishes *Protopsephurus* and *Yanosteus*, bird *Confuciusornis* and dinosaur *Psittacosaurus* have been collected, and this horizon is clearly comparable to the lower part of the Yixian Formation.

Jianshangou Bed (Member) of the lower Yixian Formation The Jianshangou Bed is mainly distributed in Sihetun and the neighboring areas, corresponding to Member 3 of the Sihetun composite section (Fig. 16). It is best represented in the Sihetun and Jianshangou localities. Around 20 localities in Sihetun and the neighboring areas are mainly distributed in an area about 12—14 km from north to south and 4~5 km from east to west.

15 Xitaizi locality (lower part of Yixian Formation) in Ningcheng, Chifeng, Inner Mongolia.

The most notable among these localities are Sihetun, Jianshangou, Zhangjiagou, Huangbanjigou, Hengdaozi, Libalanggou, Heitizigou, etc. Fossil-bearing beds comparable to the Jianshangou Bed are also found in other basins of western Liaoning, northern Hebei and southeastern Inner Mongolia, including Shangyuan Bed in Beipiao, and Zhuanchengzi Beds in Yixian County.

The Jianshangou Bed represents 2～3 sedimentary cycles of coastal lake, shallow lake, semi-deep lake to deep lake. The sediments comprise mainly gray, gray-black sandstones, shales and mudstones with rich tuffaceous components. This bed also represents the most important horizon preserving birds and feathered dinosaurs.



16 Stratigraphic sequences of the lower part of the Yixian Formation in Sihetun and the neighboring areas Legends see Fig. 12.

Nearly 40 genera and species of vertebrates have been discovered from the Jianshangou Bed, including birds such as *Confuciusornis* and *Liaoningornis*, feathered dinosaurs *Sinosauropteryx*, *Beipiaosaurus*, *Sinornithosaurus*, *Caudipteryx* and *Protarchaeopteryx*; ornithischian dinosaur *Psittacosaurus*, pterodactyloids *Haopterus* and *Eosipterus*, rhamphorhynchoid pterosaur *Dendrorhynchoides*; amphibians *Callobatrachus* and *Mesophryne*; primitive mammals *Zhangheotherium* and *Jeholodens*, and fishes *Lycoptera sinensis*, *L. fuxinensis*, *Peipiaosteus pani*.

Among them, *Lycoptera sinensis*, *L. fuxinensis*, *Peipiaosteus pani*, *Confuciusornis* and feathered dinosaurs are most abundant and notable. The *Confuciusornis* avian fauna in the Jianshangou Bed represents the earliest known avian fauna in the Jehol Biota. Invertebrates are also abundant in this bed including gastropods, bivalves, conchostracans, ostracods, insects as well as numerous plants (e.g., stoneworts, spores and pollen).

Due to the fragmentary material of *Sinornis* and *Cathayornis* (both described in 1992), the most remarkable vertebrate discovery in the Jehol Biota of Liaoning had not been made until 1993 when the earliest beaked bird *Confuciusornis sanctus* was discovered at the Jianshangou locality in Beipiao City (Fig. 17). The first important mammal fossil from this region, *Zhangheotherium quinquecuspidens*, a symmetrodon, was also collected at approximately the same time. And the putative angiosperm *Archaefructus liaoningensis* was found in the neighboring Huangbanjigou locality. In the following years, about 20 new localities such as Sihetun, Zhangjiagou, Heitizigou have been found in the nearby areas, preserving vertebrate-bearing deposits belonging to the Jianshangou Bed of the lower Yixian Formation.

Starting from 1995, the farmers of the Sihetun Village, Beipiao City have also been involved in fossil digging. They have come across some primitive birds near their village. Most of the fossil birds were later recognized as *Confuciusornis*. The field crew of the IVPP began large-scale excavations at this locality in 1997, and in the four consecutive seasons, we collected hundreds of vertebrate fossils as well as numerous invertebrates and plants. Many findings have drawn worldwide attentions, and the Sihetun locality immediately became the spotlight in paleontological community (Fig. 18). Among the many interesting vertebrates from this locality are primitive birds such as *Confuciusornis* and *Liaoningornis longiditris*, feathered dinosaurs such as *Sinosauropteryx prima*, *Beipiaosaurus inexpectus*, *Sinornithosaurus millenii* and the common ornithischian dinosaur *Psittacosaurus*, pterosaur such as *Haopterus gracilis*, amphibian *Callobatrachus sanyanensis* and the primitive mammal *Jeholodens jenkinsi*. Amazingly, all these fossils are primarily preserved in the shale of about seven meter's thick (Fig. 19).

The colleagues of the Museum of Natural Science (Taiwan) joined the IVPP field crew for the 1999 long field season in the Sihetun area, and collected lots of fishes, dinosaurs, birds, insects and plants. In order to better understand the biostratigraphic framework, we also collected about 150 meters of the core samples from the drillings done at Sihetun, Hengdaozi and Zhangjiagou. Some of the samples are currently under study at the Museum.

The Zhangjiagou locality (Fig. 20) is about three kilometers north of the Sihetun locality, and has produced important feathered dinosaurs such as *Caudipteryx zoui*, *C. dongi* and *Protarchaeopteryx robusta*. We carried out two large-scale excavations in 1998 and 2001, and collected, in addition to the aforementioned taxa, *Confuciusornis*, *Psittacosaurus*, turtles and rhamphorhynchoid pterosaur *Dendrorhynchoides curvidentatus*.

Dawangzhangzi Bed (Member) of the middle Yixian Formation The Dawangzhangzi Bed is best represented by the Fanzhangzi and Shanzui localities in Dawangzhangzi, about 20 km southwest of the town of Lingyuan City (Fig. 21).

The Dawangzhangzi Bed is approximately equivalent to the "Jehol Series" proposed by A. W.

17 Jianshangou locality (lower part of Yixian Formation) in Beipiao, Liaoning.

18 Site I of Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning.

19 Close-up view of Site 1, showing IVPP excavation of the year 2000, where a complete *Confuciusornis* specimen was discovered during the excursion of the 5th International meeting of SAPE and the symposium on the Jehol Biota.

20 IVPP excavation site of the year 2001 at Zhangjiagou locality (lower part of Yixian Formation) in Beipiao, Liaoning.

21 Shanzui site (vicinity) and Fanzhangzi site (beyond) in Dawangzhangzi (middle part of Yixian Formation) of Lingyuan, Chaoyang, Liaoning.

22 Hejiaxin locality (middle part of Yixian Formation) in Toutai, Yixian, Liaoning.

Grabau (1923). The sediments comprise mainly gray, gray-black sandstones, shales and mudstones with rich tuffaceous components. Fossil-bearing beds comparable to the Dawangzhangzi Bed are the Daxinfangzi Bed in Lingyuan, Dakangpu and Hejiaxin beds in Yixian, Liaoning; and Sichakou and Senjitu beds in Fengning, Hebei. Among the known vertebrate fossils are *Lycoptera davidi* and *L. tokunagai*, ascipenseriform *Peipiaosteus fengningensis* and *Protopsephurus liui*, turtle *Manchurochelys*, choristoderes *Monjurosuchus* and *Hyphalosaurus*, dinosaurs *Sinosauropteryx*, *Sinornithosaurus*, and *Jinzhousaurus*, birds *Liaoxiornis*, *Protopteryx* and a few *Confuciusornis*, mammals *Sinobaatar* and *Eomaia*, as well as the putative angiosperm *Archaefructus sinensis*. *Lycoptera davidi* and *Hyphalosaurus* are most abundant in this bed.

Since 1998, important vertebrate and plant fossils have been discovered from the Dawangzhangzi Bed of the middle Yixian Formation at the Fanzhangzi and Shanzui localities of Lingyuan City. The main fossils from this bed include the juvenile enantiornithine *Liaoxiornis delicatus*, the choristodere reptile *Hyphalosaurus lingyuanensis*, the multituberculate mammal *Sinobaatar lingyuanensis*, the earliest known eutherian mammal *Eomaia scansoria*, the primitive compsognathid *Sinosauropteryx* and putative angiosperm *Archaefructus*

23 Dongtuyao site, Senjitu (**Left**) and Jiecaigou site, Sichakou (**Right**) (middle part of Yixian Formation) in Fengning, Hebei.

sinensis as well as some unpublished materials of feathered theropods, pterodactyloids, *Confuciusornis*, insects and plants.

Various fossil vertebrates have been also known from the Dawangzhangzi Bed of Yixian Formation at the Hejiaxin, Wangjiagou, and Wanfotang localities, Yixian County, Jinzhou, Liaoning (Fig. 22). They include hundreds of *Hyphalosaurus*, the iguanodontid *Jinzhousaurus yangi*, birds, pterodactyloids and feathered dinosaur *Yixianosaurus longimanus*.

The primitive birds discovered from the Yixian Formation in the Senjitu-Sichakou Basin, Fengning County, northern Hebei Province (Fig. 23) include *Jibeinia luanhera* and the most primitive enantiornithine *Protopteryx fengningensis*. Some very primitive acipenseriform fishes, *Protopsephurus liui* and *Yanosteus longidorsalis*, were also found from these localities.

24 Jingangshan locality (upper part of Yixian Formation) in Yixian, Jinzhou, Liaoning.

25 Field excursion to the Boluochi locality (Jiufotang Formation) in Chaoyang, Liaoning, the 5th International meeting of SAPE and the symposium on the Jehol Biota (May, 2000).

26 IVPP excavation sites of the year 2000 (**Below**) and 2001 (**Right**) at Shangheshou locality (Jiufotang Formation) in Qidaoquanzi, Chaoyang, Liaoning.

Jingangshan Bed (Member) of the upper Yixian Formation The Jingangshan fossil Bed consists of the lake deposits of the upper Yixian Formation at the Jingangshan locality in Yixian County (Fig. 24). The sediments are mainly gray, gray-black sandstones, shales and mudstones with rich tuffaceous components. The vertebrate assemblage here includes only a few taxa such as *Lycoptera muroii*, *Manchurochelys manchoukuoensis*, *Yabeinosaurus tenuis*, some undescribed pterodactyloid pterosaurs, and birds. *Lycoptera muroii* is especially abundant in this bed.

Boluochi Bed (Member) of the Jiufotang Formation The Boluochi fossil bed is represented by the deposits at the Boluochi, Dapingfang, Dongdadao, Lianhe and Shangheshou localities in Chaoyang City (Fig. 25). The Boluochi locality is about 50 km west to Chaoyang. The Shangheshou locality lies in the west suburb of the Chaoyang City. Other localities with comparable fossil-bearing deposits include Meileyingzi and Shengli, Chaoyang; Wujiatun and Xierhuqiao, Yixian. The vertebrate assemblage comprises more than 20 genera and species including *Jinanichthys*, *Sinopterus dongi*, *Chaoyangopterus zhangi*, *Liaoningopterus gui*, *Microraptor zhaoianus*, *M. gui*, *Cathayornis*, *Chaoyangia*, *Longipteryx*, *Yanornis*, *Yixianornis*, *Sapeornis* and *Jeholornis*. The *Cathayornis* avian fauna from this bed represents the second avian fauna of the Jehol Biota.

In 1987, a farmer in Shengli, Chaoyang, Liaoning Province discovered the first fossil bird in the Province, later studied by Paul Sereno and Cheng-gang Rao and named as *Sinornis santensis*. In 1990, Zhong-he Zhou, then a paleoichthyologist working at the IVPP found several bird specimens from the Lower Cretaceous Jiufotang Formation in the locality of Boluochi, Chaoyang while collecting fishes. Among them was a rather complete bird and was described by Zhou and his colleagues in 1992 as *Cathayornis yandica*. This was the first bird from the Jehol Biota collected by a professional paleontologist in this region. More than three dozens of bird specimens were unearthed from Boluochi in the following four years by the IVPP field crew.

In 2000, the IVPP team excavated abundant birds, fishes and insects in the Jiufotang Formation at the Shangheshou locality, Chaoyang (Fig. 26). The following year, another even larger-scale excavation there resulted in the discoveries of over a dozen birds, feathered theropods, pterosaurs and turtles as well as abundant fishes. The Shangheshou locality has since become one of the most productive localities of the Jiufotang Formation, much like the Sihetun locality of the Yixian Formation. At the same time, various important vertebrate fossils were also collected in the neighboring areas. Consequently, several new vertebrate taxa have been recognized such as the birds *Longipteryx chaoyangensis* and *Yanornis martini*. It is worth noting that the smallest dinosaur *Microraptor zhaoianus* as well as the infamous specimen "*Archaeoraptor*" that was composed of the tail of the dinosaur *Microraptor zhaoianus* and the body of the bird *Yanornis martini* were also collected from the Jiufotang Formation in these areas.

During the past three years (2001~2003), hundreds of beautifully preserved vertebrate fossils have been collected from the Dapingfang and the neighboring Dongdadao and Lianhe localities, Chaoyang (Fig. 27). These fossils include birds *Sapeornis* and *Jeholornis*, pterosaurs *Sinopterus*, *Chaoyangopterus* and *Liaoningopterus* and dromaeosaur *Microraptor gui*.


27 Dapingfang locality (Jiufotang Formation) in the vicinity of Chaoyang, Liaoning.


28 Wujiatun locality (Jiufotang Formation) in Yixian, Jinzhou, Liaoning.

At approximately the same time, many important vertebrate fossils were collected from the Wujiatun and Xierhuqiao localities (Fig. 28), also of the Yixian County. They include fishes *Protopsephurus*, *Yanosteus* and *Sinamia*, the ornithurine bird *Yixianornis grabaui*, the turtle *Manchurochelys*, the feathered caudipterid as well as pterodactyloids and some other birds.

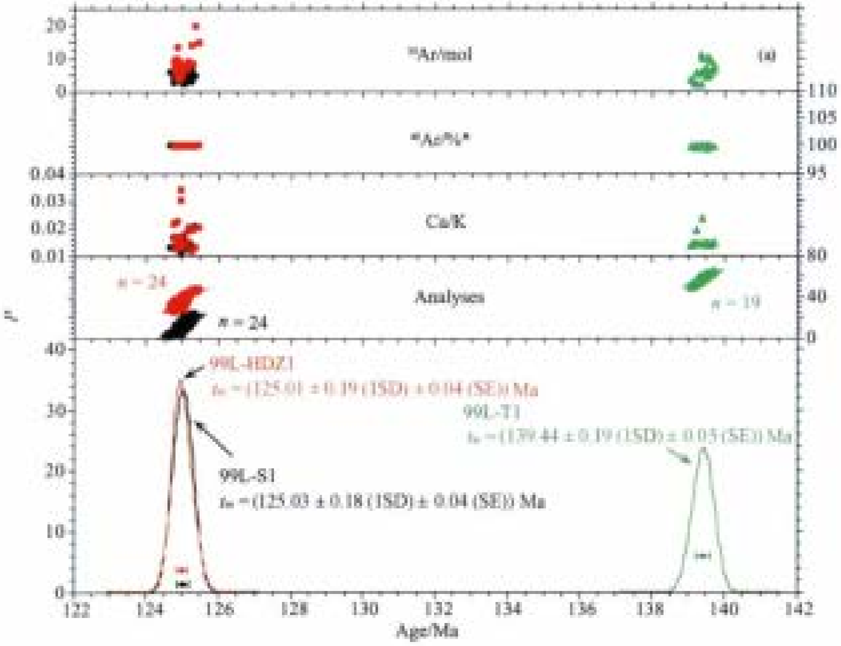
Despite the extensive paleontological research on the Jehol Biota in the last decade, the precise age of the Biota remains to be an enduring problem as well as an inherited one. Currently, there are three different opinions as regard to the age of the Jehol Biota, i.e., the Late Jurassic, Late Jurassic to Early Cretaceous, and Early Cretaceous. Paleontologists and geologists base their age determination mainly on paleontological and stratigraphic comparisons as well as isotope dating. Recently, using the biostratigraphic work in concert with the dating of the tuff samples in the sediments, most workers have agreed that the whole Jehol Biota belongs to the Early Cretaceous. However, still some workers argue otherwise. For instance, Lo et al. (1999) proposed the Late Jurassic age for the lower part of the Yixian Formation, based on the ^{40}Ar/^{39}Ar dating of the biotite (147 Ma).

In 1995, a joint project by the scientists from both the IVPP and Canada used the laser ^{40}Ar/^{39} Ar method for the first time to date the major horizons of the Jehol Group. They successfully obtained the age (from volcanic deposits) of the Dawangzhangzi and Jingangshan beds of the Yixian Formation as 122.2±0.2~122.5±0.3 Ma, and 121.4±1.1~121.6±0.4 Ma, respectively. It is noteworthy that in 1993, the age of the basalts overlying the Jiufotang Formation in Inner Mongolia was dated as 110±0.52 Ma.

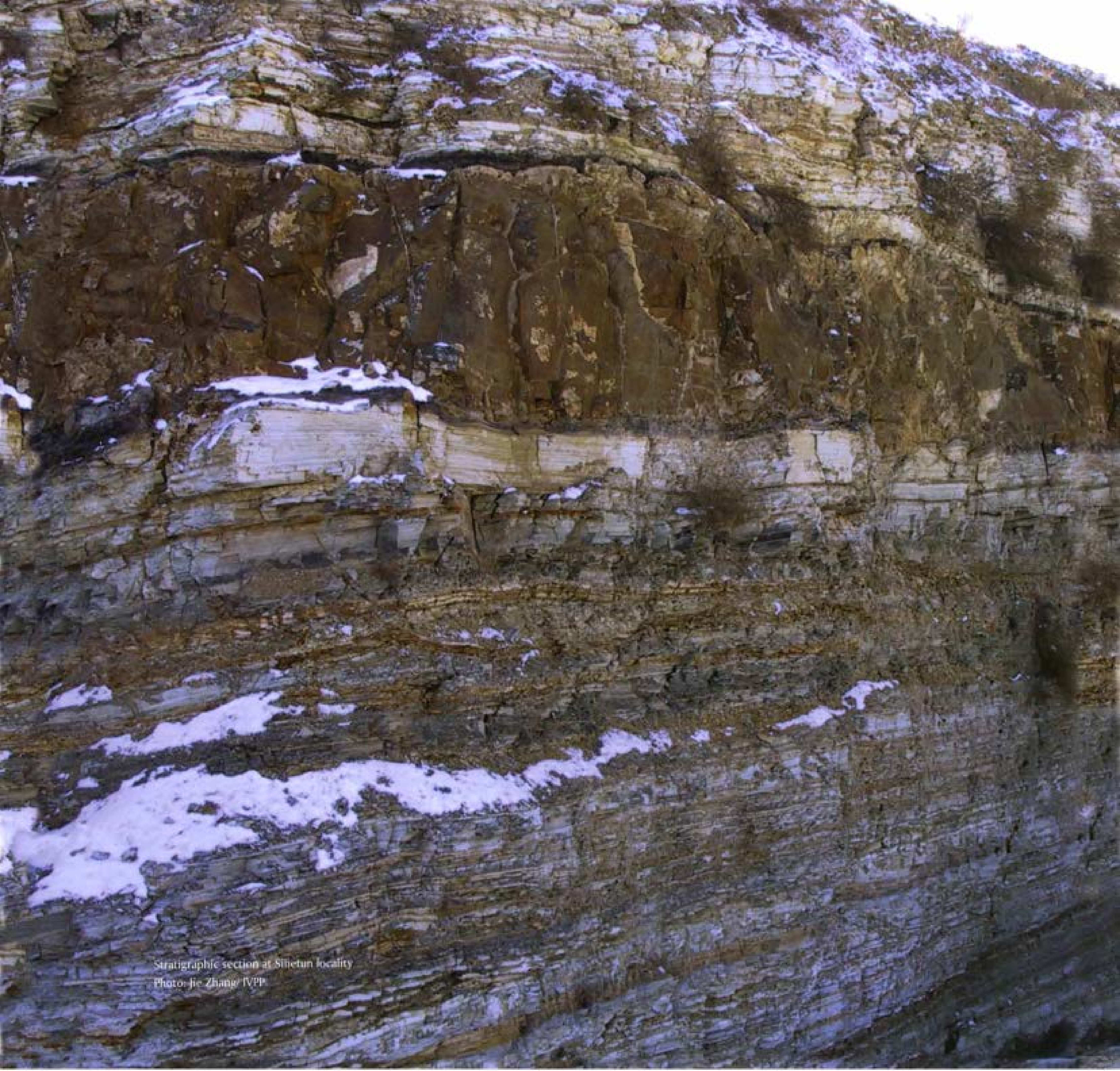
In 1999, paleontologists from the IVPP cooperated with C. C. Swisher III from the Berkeley Geochronology Center on the dating of the Yixian Formation. They dated single crystal sanidine from the tuffs of the sediments, thus obtaining a direct age of the sediments for the first time in the Jianshangou Bed of the Yixian Formation. According to their study, the lower part of the Yixian Formation is 124.6 ± 0.2~124.6 ± 0.3 Ma. In 2001, Wang et al. (2001) dated with zircon crystal from the tuffs of the same locality using U-Pb method, resulted in an age of 125.2 ± 0.9 Ma. These works further confirmed the Early Cretaceous age for the Jehol Biota, and indicated that the Jianshangou Bed that bears *Confuciusornis*, *Zhangheotherium* and feathered dinosaurs is about 125 Ma, about 20 Ma younger than the oldest bird *Archaeopteryx*.

In 2001, Swisher and his Chinese collaborators re-dated new samples using ^{40}Ar/^{39}Ar method, with total fusion and incremental-heating analysis of sanidine and biotites from the tuff samples from the Sihetun locality and the Hengdaozi locality where Lo et al. (1999) collected their biotite samples. The result not only confirmed the 125 Ma age for the Jianshangou Bed, but also indicated the presence of trapped Ar in the biotites, which helped explain why the biotite age was not geologically meaningful. Further, they also dated sanidine from tuff samples from the Tuchengzi Formation, which underlies the Yixian Formation unconformably. The 139.4 Ma age for the upper part of the Tuchengzi Formation lends further credence for the Early Cretaceous age of the Jehol Biota (Fig. 29).

Now, the isotope ages for all the Lujiatun, Jianshangou, Dawangzhangzi, Jingangshan Beds and the Jiufotang Formation are available. The Yixian Formation ranges approximately from Valanginian to Barremian, and the Jiufotang Formation corresponds to the Aptian. Recent vertebrate discoveries have provided further evidence supporting the Early Cretaceous age of the Jehol Biota. Although most workers now have accepted the Early Cretaceous age for the Jehol Biota, more stratigraphic work remains to be done and it will probably be a debatable issue for many years to come.



29 **Graphics showing results of a recent isotopic dating on the lower part of the Yixian Formation (125.0 Ma) and the underlying upper part of the Tuchengzi Formation (139.4 Ma) in Beipiao, Liaoning. (See Swisher III et al., 2002 for details)**



Stratigraphic section at Sihetun locality
Photo: Jie Zhang/ IVPP

GASTROPODS

Hua-zhang Pan, Xiang-gen Zhu

Gastropods (snails and slugs) are the most abundant, most diverse, and perhaps the best known of extant mollusks. They have approximately 37,500 living species, and represent some 80 percent of the living mollusks, only less than insects in number among all invertebrates. More than half of these snails and slugs are marine animals, and they are the only molluscan class to have spread both into freshwater and on land. Gastropods include three subclasses: Prosobranchia, Opisthobranchia, and Pulmonata. Both the prosobranchs and the opisthobranchs are mostly marine inhabitants with high diversity and wide distribution. Generally, many marine prosobranchs have well-developed and colorful shells with beautiful sculptures. A great number of them are found on rocky, sandy, and muddy bottoms in the shallow sea areas. The Pulmonata are the only molluscan subclass that lead a successful life on land, with some returning to a secondarily freshwater dwelling. Some gastropods burrow into the soft bottoms, while others swim or float at the surface, often forming a conspicuous part of the plankton, but the overwhelming majority of snails are crawling on the bottoms. In the inland freshwaters, gastropods are also common, and they are represented by some forms of the Prosobranchia as well as the Basommatophora from the Pulmonata, e.g., viviparids, bithynids, planorbids, lymnaeids, etc., commonly found in lakes or rivers. Their fossils often occurred in non-marine deposits from the Mesozoic to Cenozoic. Some forms of Stylommatophora may be seen in terrestrial habitats from deserts to tropical rainforests and montane altitudes of nearly 5,000 m above the sea level. The variations and special adaptations of these snails reflect a wide range of habitats. The majority of gastropods are carnivores, herbivores or occasionally, scavengers. Identification of fossil gastropod taxa mainly depends on protoconch characters, shape of shell, aperture and ornamentation.

Fossil gastropods are very common in the Jehol Biota, and widely

30 Shell of *Probaicalia gerassimovi* (3.34 mm long, 1.3 mm wide), a micromelaniid snail in apertural and ventral views, from Jianshangou locality (Yixian Formation) in Beipiao, Liaoning. (**Left**)

31 Shell of *Pseudarinia yushugouensis* (1.81 mm long, 0.80 mm wide), a cyclophorid snail in apertural view, from Pijiagou locality (Jiufotang Formation) in Yixian, Liaoning. (**Right**)

32 Shells of *Ptychostylus philippii* (2.58 mm long, 1.00 mm wide), an ellobiid snail in apertural, ventral, apertural and apical views, from Sihetun locality (Yixian Formation) in Beipiao, Liaoning.

33 Shell of *Gyraulus* sp. (0.75 mm long, 2.25 mm wide), a planorbid snail in apertural, apical and basal views, from Sihetun locality (Yixian Formation) in Beipiao, Liaoning.

distributed in eastern Asia (including Transbaikalian area of Russia; southeastern Mongolia; Zhejiang, Anhui provinces, southern China and Hebei, Shandong, Henan and some other provinces of northern China). They are mainly found in the Dabeigou, Yixian and Jiufotang Formations of northern Hebei and western Liaoning, and equivalent horizons of other areas. The fauna is largely represented by *Probaicalia* (Fig. 30), *Pseudarinia* (Fig. 31), opercula of *Reesidella*, viviparids of the Prosobranchia, *Ptychostylus* (Fig. 32) and *Zaptychius* of Ellobiidae, *Gyraulus* (Fig. 33) of Planorbidae and *Galba sphaira* of Lymnaeidae (Fig. 34). Sometimes the faunas are relatively low in diversity or even absent in some horizons. Once they were found they were always found in a large number of individuals. The gastropod fauna, scattered in the tuffaceous siltstone of Bed 9 below bird-bearing rocks of the lower part of the Yixian Formation near Sihetun village, western Liaoning, has a low diversity and a high density, e.g., one specimen (227 cm^2 in area) with 117 individuals. The fauna contains *Amplovalvata* sp., *Probaicalia vitimensis*, *Probaicalia gerassimovi*, *Ptychostylus philippii*, *Ptychostylus harpaeformis* and *Gyraulus* sp., but it is dominated *overwhelmingly* by *Ptychostylus*, constituting about 66.5% of the total number of specimens in the gastropod fauna. *Pseudarinia yushugouensis*, *Gyraulus loryi* and *Galba* from the Jiufotang Formation of the Pijiagou section in Yixian, western Liaoning are persevered in purple siltstone. It is noteworthy that these gastropod faunas include mostly very tiny forms, in general less than 5 mm long.

Based on its stratigraphic distribution and fossil characteristics, the gastropod fauna of the Jehol Biota is closely related to those of the Middle Purbeck Bed of Dorset, southern England, the Serpulit Formation of northwestern Germany, the Lower Cretaceous of southeastern Mongolia and Russian Transbaikalia. This indicates that the gastropod fauna bears obviously characteristics of those of the Early Cretaceous.

Gastropods have wide range of habitats, but they are sensitive to slight changes in environment, such as stability of the bottom, type of sediments, salinity, food supplies, water depth, temperature, oxygen content, and turbidity. Thus, there are different gastropod assemblages in different settings. Many scholars have examined the environments of modern snails, so the habitats of fossil gastropods can be extrapolated from the comparisons with their living counterparts. Different assemblages of fossil gastropods are found in several deposits that are interpreted to represent different kinds of habitat areas.

Analogous to their modern counterparts, population of the fossil gastropods *Ptychostylus* increased individual in number but decreased body in size usually indicates a brackish water living environment. *Ptychostylus* mainly occurred in the Serpulit Formation of North-West Germany associated with *Hydrobia* and neomiodontids (bivalve), showing the brackish water environment; *Ptychostylus* from Inter-marine Beds or Upper Building Stone near marine Cinder Beds, and Corbula Beds of Middle Purbeck Beds in Durlston Bay, England is associated with turtles, fish and bivalve *Neomiodon* of brackish water affinities. There are a few gypsum beds in the lower part of the Yixian Formation near Sihetun village, western Liaoning. All the factors indicate that *Ptychostylus*-dominated assemblage from the lower part of the Yixian Formation near Sihetun Village, w. Liaoning might be of brackish water setting, but *Gyraulus loryi*- and *Galba*-dominated assemblage from the Jiufotang Formation may represent a drifting assemblage frequently occurred along the shore of a river or lake.

(All photographs in this chapter were taken by Liu-Ping Yuan/ NIGP)

34 **Shell of *Galba sphaira* (1.20 mm long, 0.74 mm wide), a lymnaeid snail in apertural, ventral and apical views, from Pijiagou locality (Jiufotang Formation) in Yixian, Liaoning.**

35 Multiple species of *Arguniella* (15—25 mm long of the individuals), a sibireconchid bivalve in aggregation, from the roadside of Sihetun to Libalanggou (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: Da-jian Li/ CAS)

BIVALVES

Jin-hua Chen

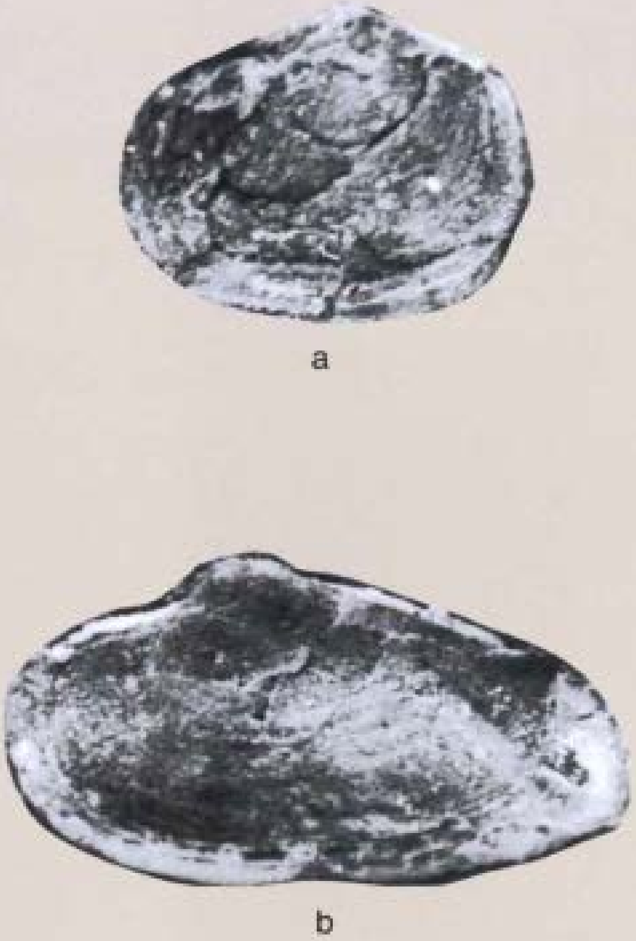
Bivalvia are a class of bivalved mollusks, also known as Pelecypoda and Lamellibranchiata in the literature. The bivalves are aquatic animals with a shell consisting of two matching lateral valves united by a dorsal horny ligament. The valves can be drawn together by a pair of adductor muscles (reduced to one in some) against the opening counter-force of the ligament. Today the bivalves are among the most common benthic invertebrates, especially on marine shelves, although there are many species in fresh-water or brackish-water environments and even in abyssal habitats. The laterally compressed shape characteristic of the great majority of bivalves renders them well adapted for burrowing in sandy or muddy substrates. Some bivalves are borers in solid or soft rocks, whereas the most highly specialized boring forms are wood-borers ("shipworms"). Among the benthic epifauna, bivalves form an important element. Some rely on the weight or the shape of their shell to maintain their position on the seafloor; others attach themselves to stationary objects by means of their byssus or by cementation of one of the valves. Some highly mobile bivalves, for example the pectinids, can "hop" near the sea bottom for short distances. No living bivalves are pelagic, except for larval stages and very few species with strongly reduced shells. However, some extinct thin-shelled bivalves are considered to have possibly lived pelagically.

The first occurrences of Bivalvia are known from the Lower Cambrian at a few localities in the United States, southern Australia, and China. During the Early Paleozoic periods, bivalves were not abundant. Since the Devonian, bivalves became very frequent and diversified. The class reached the acme of its development in the Mesozoic and Cenozoic. In most instances, Mesozoic bivalves are useful for stratigraphical correlation.

The Jehol Fauna arose after an important biotic extinction event, which took place between the latest Middle Jurassic and early Late Jurassic in China, accompanied by the strong tectonic movements during the Oxfordian and early Kimmeridgian (Late Jurassic). Owing to this extinction event, the *Eolamprotula-Psilunio* fauna and the *Pseudocardinia* fauna, flourished in the Middle Jurassic of the Chinese continent, are missing from the Jehol Fauna. The bivalves of the Jehol Fauna manifested themselves with a new feature

Internal moulds of *Mengyinaia*, a unionid bivalve, from Ningjiagou locality (Mengyin Formation) in Mengyin, Shandong. a, *Mengyinaia mengyinensis* (65 mm long); b, *Mengyinaia tugrigensis* (90 mm long). (Photo: Zhou-qing Chen/ NIGP)

Shell of *Nakamuranaia chingshanensis* (51 mm long), a nippononaiid bivalve, from Jiazhangzi locality (Jiufotang Formation) in Jianchang, Liaoning. (Photo: Zhou-qing Chen/ NIGP)



Internal moulds of *Sphaerium*, a small-sized pisidiid bivalve, from Xiwa locality (Xiwa Formation) in Mengyin, Shandong. a, *Sphaerium jeholense* (3 mm long); b, *Sphaerium pujiangense* (7 mm long). (Photo: Zhou-qing Chen/ NIGP) greatly differing from the Middle Jurassic ones. Among them, three freshwater assemblages are recognizable on the basis of bivalve samples respectively from the formations yielding the indices of the Jehol Fauna. The three assemblages are as follows.

1. *Arguniella* assemblage. The assemblage includes two species of a single genus, i.e., *Arguniella lingyuanensis* and A. *yanshanensis*, found from the Dabeigou Formation in eastern Hebei province, showing a very low diversity of the bivalves at the beginning or the early phase of the faunal development of the Jehol Fauna. The assemblage is comparable with that in the Upper Jurassic Mayakskaya Formation in the upper reaches of the Argun River, eastern Siberia, Russia.

2. *Arguniella-Sphaerium* assemblage. This bivalve assemblage belongs to the main phase of the Jehol Fauna, found from the lower Yixian Formation in western Liaoning and northern Hebei provinces. Particularly rich bivalves of the assemblage occur just below the bird (*Confuciusornis*)-bed at the type locality of this primitive fossil bird (Fig. 35). Although it is very abundant in number of individuals, the assemblage possesses only four species in two genera, *Arguniella lingyuanensis*, *A. yanshanensis*, *Sphaerium jeholense* and *S. anderssoni*, indicating emerging but still low diversity compared with some other groups of invertebrates (e.g., ostracods and insects) and some vertebrates (e.g., birds) in the same phase. Therefore, the bivalve radiation in the Jehol Fauna was delayed, probably owing to the slow evolutionary rates of these bivalve mollusks, which were protected by their solid shells and most probably had adapted to the adverse environments at that time.

3. *Mengyinaia-Nakamuranaia-Sphaerium* assemblage. It is from the fossiliferous horizons of the late phase of the Jehol Fauna, the Jiufotang Formation in western Liaoning and its coevals. The assemblage is more abundant and diverse in bivalves than the above two, consisting of more than 30 species designated to five genera including five species to *Mengyinaia* (Fig. 36), three to *Nakamuranaia* (Fig. 37), 12~13 to *Sphaerium* (Fig. 38), six to *Arguniella* and five to *Weichangella* (Fig. 39), representing a distinct faunal radiation. This assemblage was succeeded by the *Nippononaia sinensis*-N. cf. *tetoriensis*-*Tetoria* cf. *yokoyamai* assemblage found from the Shahai Formation in Liaoning, which overlays the Jiufotang Formation and can be correlated with the beds of the upper Itoshiro Subgroup of the Tetori Group in Japan. The latter beds of Japan have been recently dated, based on ammonites and marine bivalves, as Hauterivian (Early Cretaceous). Therefore, the present assemblage is regarded to be around Valanginian in age.

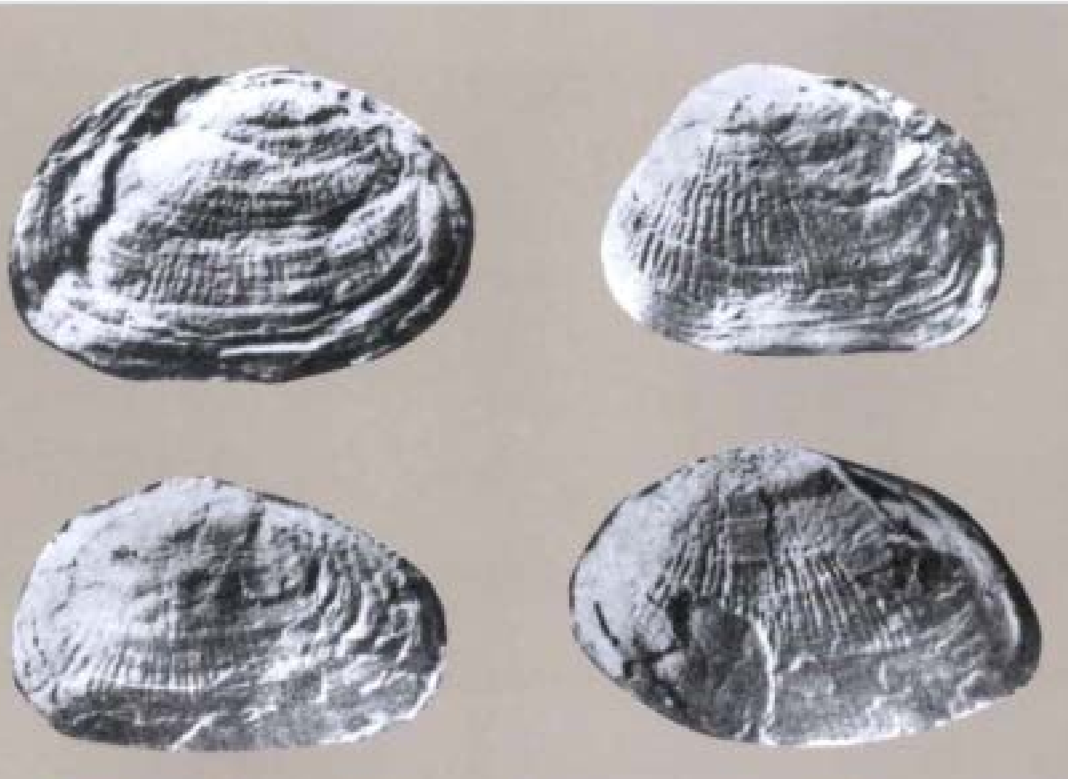


Fig. 39 Shells of *Weichangella qingquanensis* (29~34 mm long), a plicatounionid bivalve, from Shalingou locality (Jiufotang Formation) in Weichang, Hebei. (Photo: Pu Wang/ GPH)

Eosestheria lingyuanensis
Photo: Da-jian CHEN

CONCHOSTRACANS

Pei-ji Chen

Conchostracans, or clam shrimps, are small, bivalved branchiopod crustaceans (Fig. 40). They have a short laterally compressed body enclosed between two lateral valves that constitute the chitinous carapace with an interior membranous lining. The head is located anteriorly and bears sessile, paired compound eyes with well-developed ocelli. Posteriorly, the telson is distinguished by two flattened, upwardly curved processes or claws. The antennules are small and simple, but the antennae are modified into powerful biramous swimming organs. During mating, males use them to aid in seizing the female carapace. Trunk legs (swimming legs) vary from 10 to 32 pairs.

These animals occur in non-marine facies sporadically, but often abundantly from the Devonian to the present day. Many paleontologists still refer to them informally using the pre-occupied generic name "*Estheria*", originally used for a fly.

The clam shrimps flourished twice in the Late Paleozoic of Europe and in the Mesozoic of Asia with about 200 genera in 27 families, but rapidly declined in the Cenozoic with only 14 genera in 5 families still living today.

The living conchostracans reside in small and temporary inland ponds, flood-plain pools, rice fields, roadside ditches, and almost any shallow depressions filled with water. They have also been reported from spring water, along margins of large lake and on coastal salt flats. They appear in the Yangtze River drainage area during spring or in North China, Northwest China, Northeast China, and Inner Mongolia during summer and early autumn. The most favorable temperature for the majority of living forms is 13 to 34℃.

There are two kinds of conchostracan eggs: the thin-shell eggs can hatch after several days of ovulation by females; the thick-shell dormant eggs could withstand long desiccation or frozen of the pools, so as subsequently to become dispersed by wind, water or birds and hatch even a number of years later. This may explain the worldwide distribution of fossil clam shrimps, which has great potential in biostratigraphical research, especially for the non-marine Jurassic and Cretaceous in eastern Asia.

40 *Eocyzicus mongolianus*, a recent conchostracan arthropod from Zhenglanqi, Inner Mongolia. (Photo: Ji-liang Mao/ NIGP)

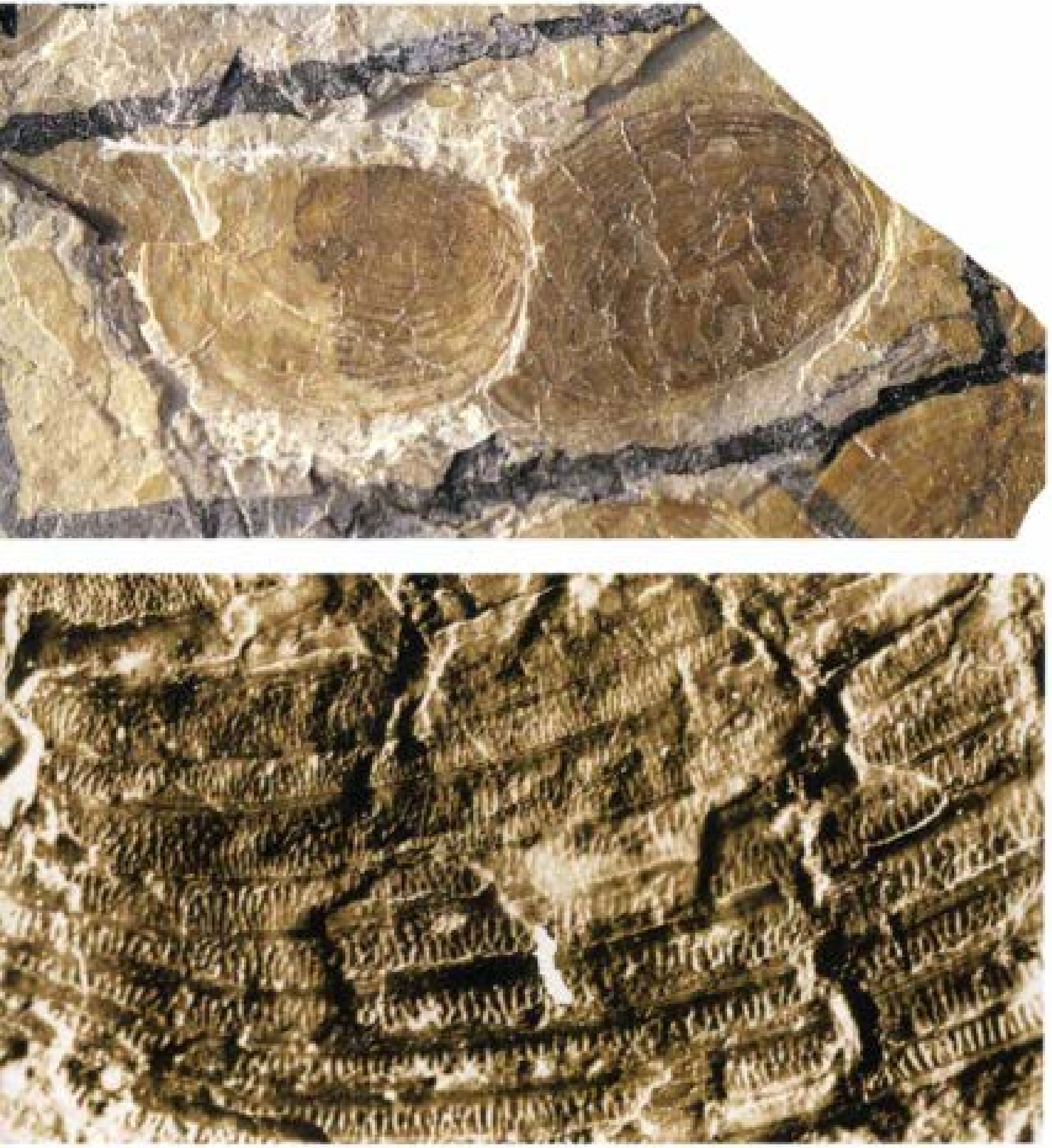
The taxonomy of living conchostracans is based on the structures of soft body, which is seldom preserved as fossils. Thus, we have to pay more attention to the variation of carapace and the minute ornamentation of growth bands of valve in fossil clam shrimps. For example, the euestheriids and loxomegaglyptids bear reticulate sculpture and the orthestheriids radial lirae, whereas the eosestheriids have the mixed sculpture of reticulation and radial lirae. From the Jehol Biota, three conchostracan assemblages can be clearly identified chronologically as follows.

Nestoria-Keratestheria assemblage: Besides its namesake forms, the assemblage includes *Sentestheria*, *Abrestheria*, *Ambonella*, and *Jibeilimnadia*. Generally, they have a large carapace with several brawny growth lines sometimes bearing spines or nodes. Growth bands are broad and flatted with big reticulate sculpture (Fig. 41). These fossils were found from the Dabeigou Formation of northern Hebei Province, the Baoshi, Murei, or Baiyingaolao Formations of Inner Mongolia of China and the Argun and Ust'kal Formations of eastern Transbaikalia.

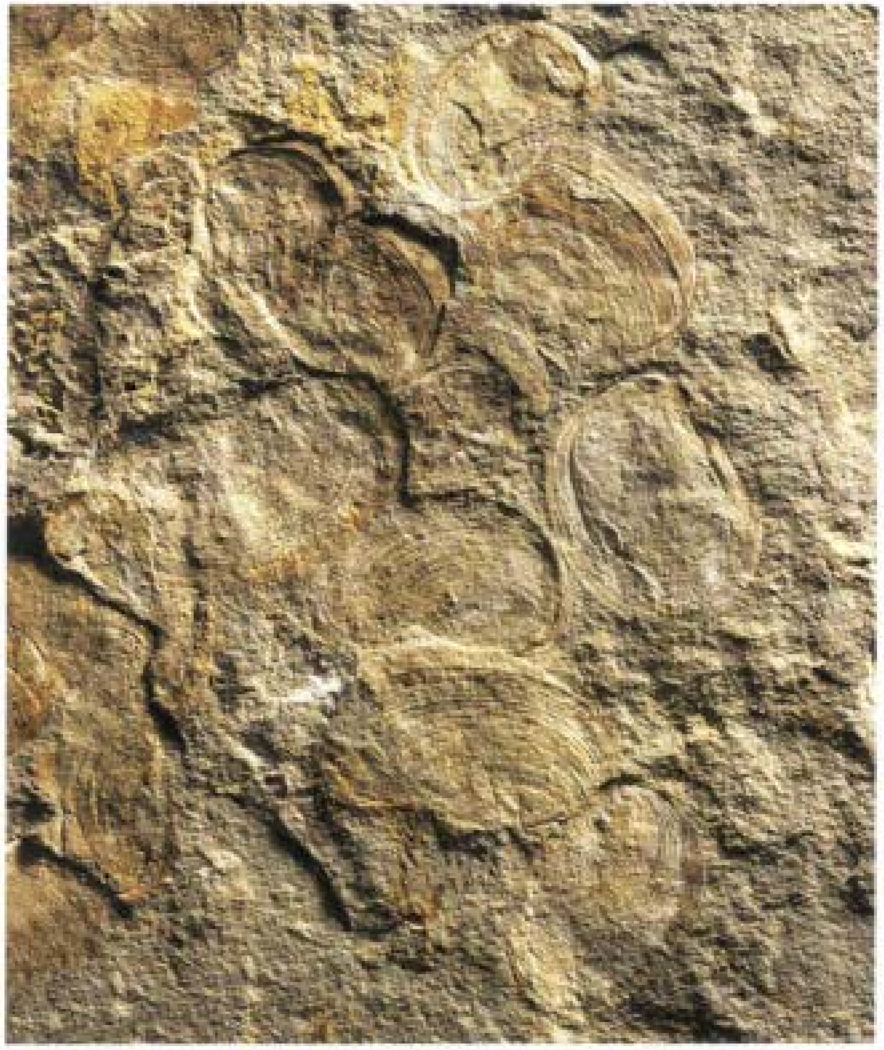
41 Carapace valves of *Nestoria pissovi* (14 mm long), a loxomegaglyptid conchostracan with several brawny growth lines ornamented by large reticulations in between, from Dadianzi locality (Dabeigou Formation) in Luanping, Hebei. (Photo: Da-jian Li/ CAS)

Eosestheria-Diestheria assemblage: These two genera were absolutely predominant in quantity among this assemblage when they lived in the Paleo-Amur River valley including Inner Mongolia, Northeast and North China, Mongolia and Transbaikalia. Their fossils are collected from the Yixian Formation of western Liaoning Province, NE China and the relevant horizons in other regions. The well-known forms of this assemblage are *Eosestheria* aff. *middendorfii* (Fig. 42), *E. lingyuanensis* (Fig. 43), *E. ovata* (Fig. 44), *E. jingangshanensis*, *Diestheria yixianensis* (Fig. 45) and *D. jeholensis*. In addition, some other species of *Eosestheriopsis* has been recognized recently from the Jehol Fauna, but in the past were found only from the Upper Jurassic deposits such as the Penglaizhen and Tuodian Formations of southwestern China.

Eosestheria has a relative large carapace with moderate growth lines but without spines or nodes. Growth bands are ornamented with irregular



42 Carapace valves of *Eosestheria* aff. *middendorfii* (13—14 mm long), an eosestheriid conchostracan with mixed sculpture of reticulation and radial lirae on growth bands (enlarged detail), from Zaocishan locality (Jingangshan Bed of the upper Yixian Formation) in Yixian, Liaoning. (Photo: Da-jian Li/ CAS, Mao-fang Pang/ NIGP)



43 Carapace valves of *Eosestheria lingyuanensis* (11 mm long), an eosestheriid conchostracan, from Sihetun locality (Jianshangou Bed of the lower Yixian Formation) in Beipiao, Liaoning. (Photo: Da-jian Li/ CAS)

medium reticulations transferring gradually into the radial lirae near ventral and posterior margins of the valve. The ornamentation of *Diestheria* is similar to that of *Eosestheria*, with additional overlapped big reticulations near the posteroventral margin of the valve. The impressions of these overlapped reticulations are large and flattened tubercles in the mould fossils.

Eosestheria-Yanjiestheria assemblage: It includes *Allestheria*, *Yumenestheria*, *Diestheria*, in addition to its namesake forms. During this period, *Eosestheria* was bearing numerous growth lines and the corresponding growth bands changed into narrow ornamentation with relatively small reticulate sculpture only near the dorsal side but fine and crowded radial lirae in the rest parts of the valve. The genus *Yanjiestheria* was evolved from *Eosestheria*. It has smaller reticulate sculpture near the dorsal side and finer and more crowded radial lirae near ventral and posterior parts of the valve. The conchostracan fossils of this assemblage were collected from the Jiufotang Formation in lacustrine facies of western Liaoning or similar rocks of other regions of China, Mongolia, Transbaikalia, Korea peninsula, and southwestern Japan.

44 Carapace valve of *Eosestheria ovata* (19 mm long), an eosestheriid conchostracan with mixed sculpture of reticulation and radial lirae on the chitinous growth bands and corresponding small and polygonal platforms and radial grooves in the external mould, from Sihetun locality (Jianshangou Bed of the lower Yixian Formation) in Beipiao, Liaoning. (Photo: Da-jian Li/ CAS)

45 Carapace valve of *Diestheria yixianensis* (21 mm long), a diestheriid conchostracan, from Zhoujiatun locality (Dakangpu Bed of the middle Yixian Formation) in Yixian, Liaoning. (Photo:Da-jian Li/CAS)

Fossil ostracods
Photo: Zhou-qing Chen/ NIGP

OSTRACODA

Mei-zhen Cao, Yan-xia Hu

Ostracods are tiny crustaceans of the phylum Arthropoda. They are important microfossils and useful in geological prospecting. The most conspicuous feature of these animals is the bearing of a bivalved carapace in which the soft body is enclosed (Fig. 46). The two valves are not symmetrical, and are constituted by calcareous layer and chitinous coating. The left valve is normally somewhat larger and overlapping the right one. The exterior surface of valves may be ornamented or smooth. The ostracod carapace is generally between 0.5 and 1.5 mm in length, with a few either less than 0.5 mm or more than 1.5 mm, and very few reaching 70 mm such as *Paramoelleritia* from the Devonian carbonate rocks of Guangxi Province, China.

Ostracods have a long history and a worldwide distribution. They first appeared in the Cambrian of 500 million years ago and are still flourishing today. They have a high salinity and temperature tolerance and can live in seawater, freshwater, and brackish water, but they are especially common in shallow-sea and lakes. They even live in hot or sulfur springs. Most ostracods are crawling benthos, but some are plankton, and still others swim or burrow into mud. Ostracods are gonochoristic and can reproduce all year round. In suitable environmental conditions, they reproduce bisexually, whereas in the unsuitable environments they are parthenogenetic. Ostracods are oviparous animals. Their eggs, round or oval in shape, can withstand desiccation and cold, spreading for long distance and hatching in a suitable condition. The ontogeny of ostracods is discontinuous. As is in other arthropods, after the larva hatched out from the egg, with the growth of the soft body the hard carapace shed when the new carapaces are formed. There are approximately eight molts during their ontogeny. And the shape and ornament of the carapace change with the growth. The chitin layers of the carapace are very thin and rarely preserved and the soft body is prone to decay. Therefore, only the calcareous layers are usually preserved as fossils.

The fossil ostracods of the Jehol Biota from the northern Hebei and western Liaoning are very abundant and all of freshwater types. Fossil ostracods usually occur in great abundance on the rock surface of the Dabeigou, Yixian, and Jiufotang Formations, like a "sesame bread" (Fig. 47). Up to now, more than 130 species belonging to 25 genera of fossil ostracods have been found in the Jehol Biota, of which 5 species in 5 genera were collected from the Dabeigou Formation, over 80 species of 11 genera from the Yixian Formation, and more than 80 species of 19 genera from the Jiufotang Formation.

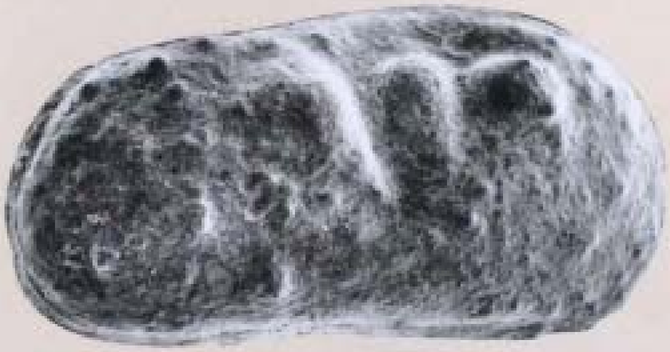
46 *Cyprinotus* sp., a recent ostracod arthropod in lateral view, from Wuhan, Hubei.

47 Fossil ostracods, on the rock surface like a "sesame bread" (× 4), from Senjitu locality (Yixian Formation) in Fengning, Hebei. (Photo: Hai-chun Zhang/ NIGP)

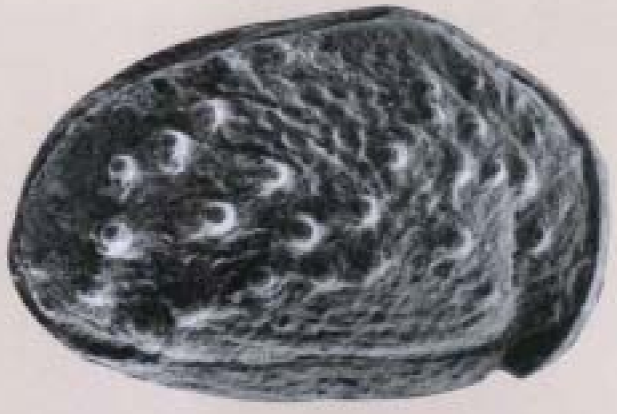
The fossil ostracods from the Dabeigou Formation are so far only known from Dabeigou, Jingshang and Zhangjiegou areas, Luanping County, Hebei Province. They are dominated by the large-sized (about 2 mm in length) and smooth-surfaced *Luanpingella* (Fig. 48) and *Torinina* (Fig. 49), associated with small-sized (less than 1 mm) *Rhinocypris* with small spines and tubercles on the surface (Fig. 50) as well as the smooth-surfaced *Darwinula* . *Torinina* first appeared in the Late Jurassic Turga Formation in the Argun River valley of East Transbaikalia. In the past, some ostracod specialists identified *Torinina* from the Dabeigou Formation as *Eoparacypris*. Because both of the Dabeigou and Turga Formations share the *Torinina*, they may be closely

48 Left valve of *Luanpingella postacuta* (× 27), external lateral view, from Jingshang locality (Dabeigou Formation) in Luanping, Hebei.

49 Right internal mould of *Torinina tersa* (× 30), external lateral view, from Jingshang locality (Dabeigou Formation) in Luanping, Hebei.

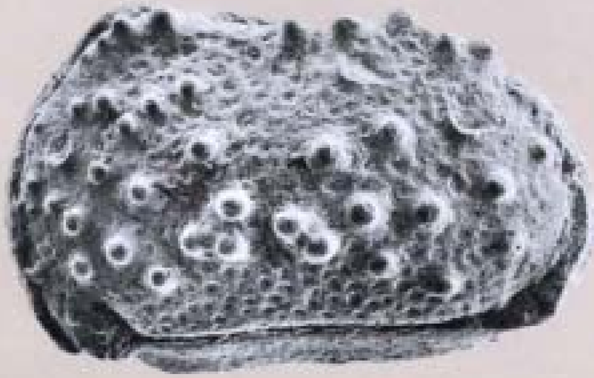


50 Carapace of *Rhinocypris jurassica* (× 80), external lateral view, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning.

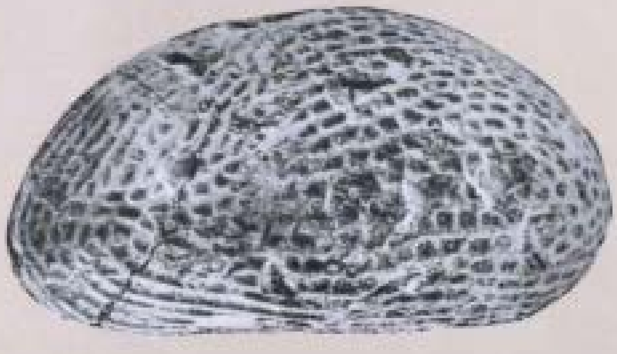


51 Carapace of *Cypridea (Cypridea) sihetunensis* (× 50), external lateral view, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning.

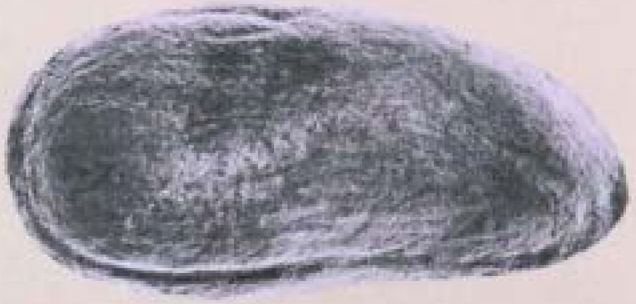
52 Carapace of *Cypridea (Cypridea) dabeigouensis* (× 50), external lateral view, from Dabeigou locality (lower part of Yixian Formation) in Luanping, Hebei.



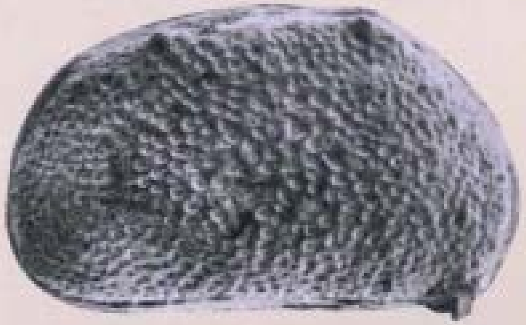
53 Carapace of *Cypridea (Ulwellia) beipiaoensis* (× 50), external lateral view, from Libalanggou locality (lower part of Yixian Formation) in Beipiao, Liaoning.



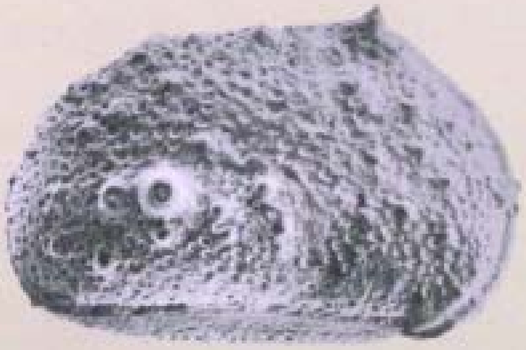
54 Carapace of *Timiriasevia jianshangouensis* (× 80), external lateral view, from Jianshangou locality (lower part of Yixian Formation) in Beipiao, Liaoning.



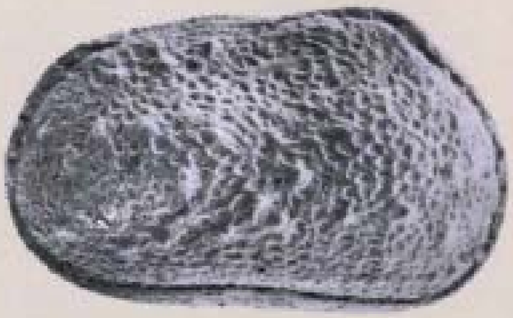
55 Carapace of *Darwinula leguminella* (× 70), external lateral view, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning.



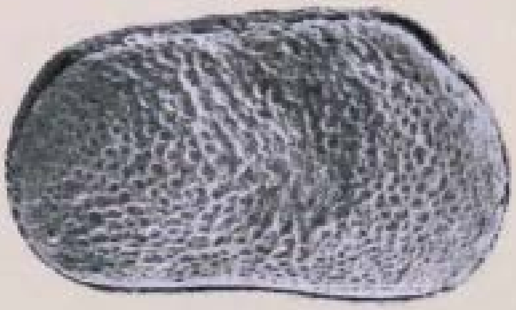
56 Carapace of *Cypridea (Cypridea) jingangshanensis* (× 45), external lateral view, from Zaocishan locality (upper part of Yixian Formation) in Yixian, Liaoning.



57 Carapace of *Cypridea (Cypridea) zaocishanensis* (× 45), external lateral view, from Zaocishan locality (upper part of Yixian Formation) in Yixian, Liaoning.



58 Carapace of *Yumenia casta* (× 40), external lateral view, from Pijiagou locality (upper part of Jiufotang Formation) in Yixian, Liaoning.



59 Carapace of *Yumenia jianchangensis* (× 40), external lateral view, from Pijiagou locality (upper part of Jiufotang Formation) in Yixian, Liaoning.

60 Carapace of *Yixianella marginulata* (× 40), external lateral view, from Pijiagou locality (upper part of Jiufotang Formation) in Yixian, Liaoning.

correlated. Their age is Late Jurassic.

Ostracods from the Yixian Formation are very rich in quantity and more diverse than those from the Dabeigou Formation. *Cypridea* is the predominant form. These ostracods may be grouped into two assemblages. The lower assemblage, in addition to *Cypridea* (Figs. 51 ~ 53), includes abundant large-sized and smooth-surfaced forms such as *Yanshanina*, *Djungarica* and small-sized forms *Timiriasevia* (Fig. 54), *Darwinula* (Fig. 55), etc.; The upper assemblage consists chiefly of species of genus *Cypridea* in which the subgenus *Cypridea (Cypridea)* (Figs. 56, 57), with left valve larger than the right, occupied a dominant position. The ostracods from the lower part of the Yixian Formation are similar to the two ostracod assemblages in the lower part of the Purbeck Group of England and may be correlated with the ostracod assemblage from the Bulum Member of the Kuti Formation in the Argun River valley of the eastern Transbaikalia. Judging from the above-mentioned facts, the lower part of the Yixian Formation should be late Tithonian or late Tithonian to Berriasian in age.

Ostracods from the Jiufotang Formation are extremely abundant and highly diverse. They may be grouped also into two assemblages. The lower assemblage is comparatively similar to that from the upper part of the Yixian Formation predominant with forms of *Cypridea (Cypridea)*. The fossil ostracods from the upper part of the Jiufotang Formation are abundantly represented with rapidly evolved and widely distributed forms such as *Yumenia* (Figs. 58, 59), *Limnocypridea* and a lot of *Cheilocypridea*, *Yixianella* (Fig. 60) and *Cypridea (Ulwellia)* with the right valve larger than the left one. This assemblage is characteristically identical to the Early Cretaceous Valanginian-Barremian ostracods in and outside China.

(Except where indicated, all photos in this chapter were taken by Yong-qiang Mao/ NIGP)

Dawangzhangzi locality
Photo: IVPP

SHRIMPS

Yan-bin Shen

The highly sporadic fossil record of freshwater shrimps is improved by the discovery of abundant specimens of astacids and spelaeogriphids from the Jehol Group. The former are a large well-known crayfish (Decapoda, Astacidea) and the latter a new member of the family Spelaeogriphidae (Hemicaridea), *Liaoningogriphus*.

Crayfish Astacids are commonly referred to as "crayfish", and are also known by many other common names in the different parts of the world: crawfish, paper-shell crabs, ecrevisse, yabbies, mud-bugs, flusskrebs, raks, ditch bugs and koonacs. With over 500 known species, they are almost distributed worldwide.

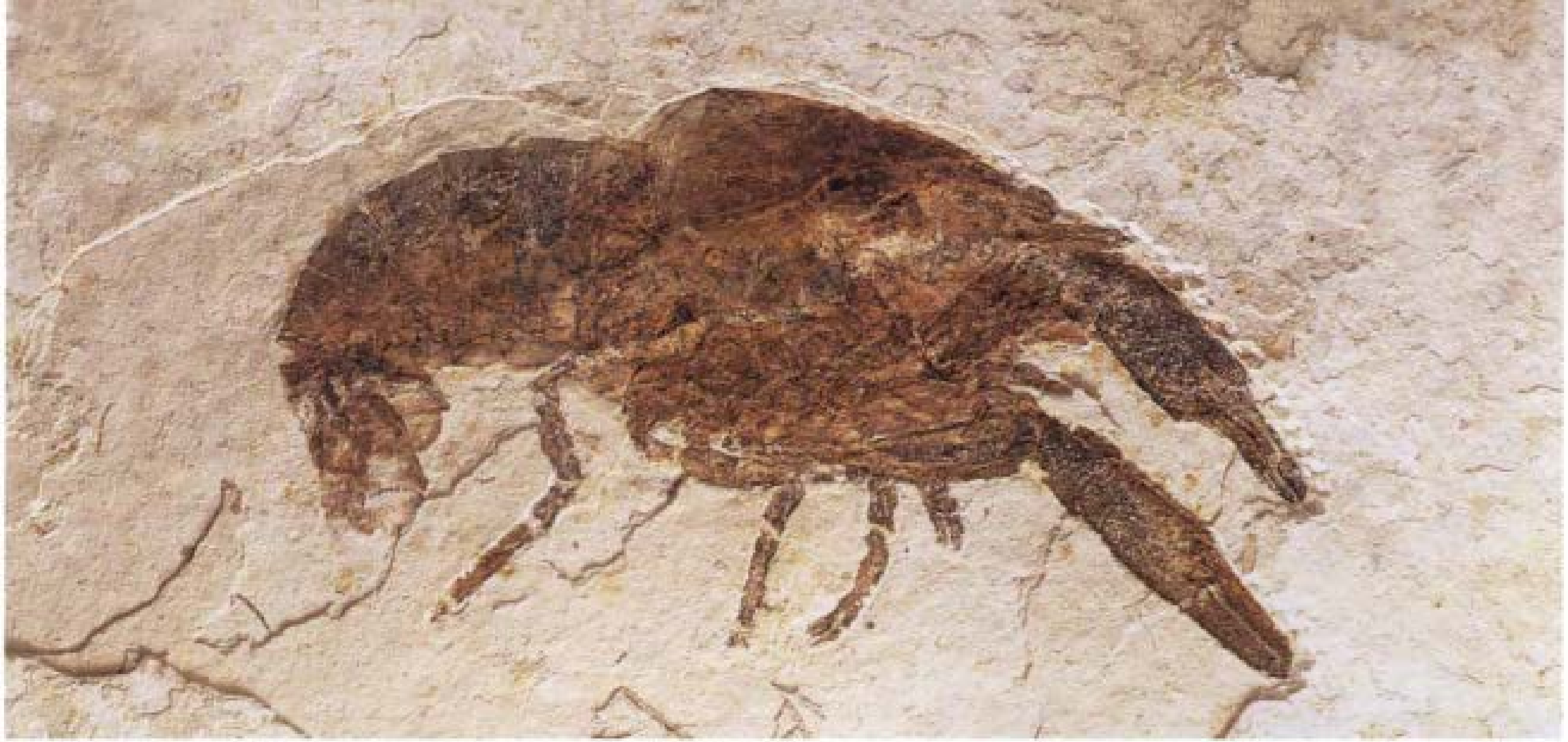
Traditionally, two large groups of freshwater crayfish are recognized, the superfamilies Astacoidea and Parastacoidea. The astacoids live in the Northern Hemisphere. They are divided into the family Astacidae (Europe, western North America) and the family Cambaridae (North America and East Asia). The parastacoids are restricted to the Southern Hemisphere.

The Astacidea is characterized by subcylindrical cephalothorax, well-developed rostrum and abdomen, simple cervical groove, chelate first three pereiopods with the first of them the largest, well-developed abdominal pleura, telson with transverse suture, and uropods with diaeresis.

Males of the superfamily Astacoidea are typically with the first and second pleopods modified into a rather elongated, styliform blade to assist in the transfer of the spermatophore. Females of the family Cambaridae bear an

61 Recent crayfish *Procambarus clarkii*. Dorsal view of a male (**Left**). Ventral view of a male, showing the tubular form of pleopods 1 and 2 (**Middle**). ventral view of female, showing the annulus ventralis and pleopods 1–5 (**Right**). (Photo: Shi-wei Zhao/ NIGP)

62 A male *Cricoidoscelosus aethus* in ventral view, 87 mm long from rostrum to distal telson, from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Da-jian Li/ CAS)



63 A female *Cricoidoscelosus aethus* in lateral view, 99 mm long from top of cheliped to the last pleomere, from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Da-jian Li/ CAS)

64 Tail fan in ventral view (27 mm wide) of a female *Cricoidoscelosus aethus*, from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Dong-xing Deng/ NIGP)

65 A molted crayfish exoskeleton (115 mm long) of a female *Cricoidoscelosus aethus*, from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Da-jian Li/ CAS)

annulus ventralis, a specific form of spermatheca, in the areas between the fourth and fifth pereiopods (Fig. 61). The males of the Cambaridae sometimes have a robust set of directed processes, or ischial hooks, on the second through fourth pereiopods. However, the members of the Astacidae lack ischial hooks in the males and annulus ventralis structure in the females.

The crayfish specimens of the Jehol Biota were obtained from the Yixian Formation in Dawangzhangzi, Daxinfangzi, Songzhangzi, and Niuyingzi areas, Lingyuan City, and Houshuangshanzi village of Yixian County, Jinzhou City, Liaoning Province. The excellently preserved specimens include molted exoskeleton, juveniles, adults, males and females, as well as dorsal, ventral and lateral remains of the thorax. They were named as *Cricoidoscelosus aethus* (Figs. 62~65) and *Palaeocambarus licenti* by Taylor, Schram and Shen (Family Cricoidoscelosidae) (Figs. 66, 67). The former is distinguished from the latter in its flagellate or crenulate pleopods, whereas the latter bears paddle pleopods. Both of them are very similar to recent cambarideans in their modified first pleopod in the males and annulus ventralis in the females.

Living crayfish mostly inhabits freshwater habitats. Some species can tolerate high salinity, e.g., in the Caspian Sea and Black Sea, but they were never found in real marine environments. More than 500 species of freshwater crayfish are found in the temperate zones of the Northern Hemisphere, and the temperate and tropical zones of the Southern Hemisphere.

Crayfish is polygraphist and feeds on a variety of living and dead animal and plant materials. A few species of the family Astacidae are also adapted to the cold-water habitats. Typically, molting is restricted to the warmer summer months, when feeding can take place. In contrast, the members of the family Cambaridae show greater variations and reflect their ability to adapt to a wider range of habitats than the Astacidae. A number of species of the Cambaridae have the ability to make burrows or burrow systems, which enable them to inhabit water bodies that are periodically dried out. Other species occur in both lotic and lentic habitats under rocks, in vegetation, among the roots of riparian trees, in leaf litter and they also burrow into the gravel beds of streams.

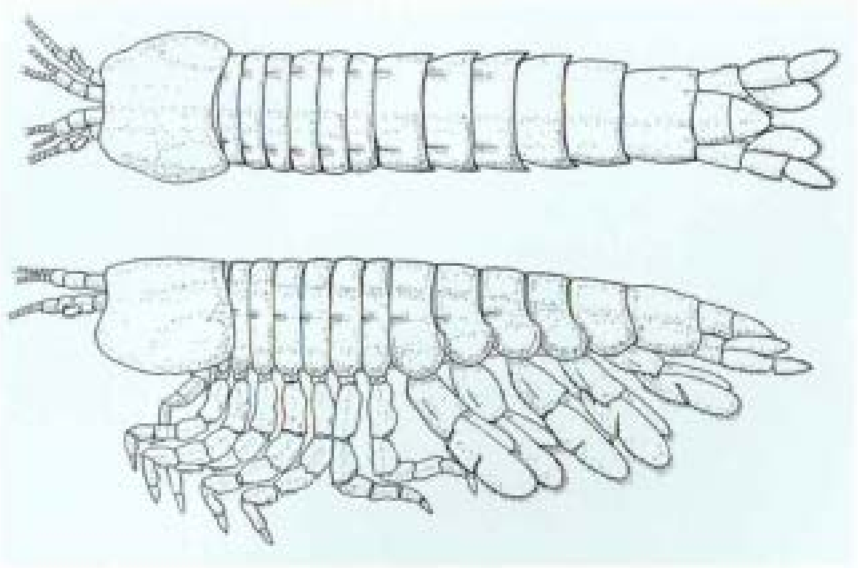
Liaoningogriphus The family Spelaeogriphidae possesses a typically peracaridan brood pouch with five pairs of oostegites, and was thus placed within the Superorder Peracarida (Order Hemicaridea). The living *Spelaeogriphus* was first found from underground cave pools in the Table Mountain, South Africa. *Acadicaris novascotica*, the only known fossil species, was reported from the Lower Carboniferous black shale in the Maritime Province of Canada. Recently, some other fossil spelaeogriphaceans from the Lower Cretaceous

66 A female *Palaeocambarus licenti* in lateral view, 47.5 mm long from top of chelate to the last pleomere, from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Da-jian Li/ CAS)

67 A male *Palaeocambarus licenti*, showing (by a red arrow) the first pleopods as styliform blade (× 2), from Dawangzhangzi locality (Yixian Formation) in Linyuan, Liaoning. (Photo: Dong-xing Deng/ NIGP)

68 A nearly complete individual (ventral view, 16 mm long) of *Liaoningogriphus quadripartitus* from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning, showing thorax, abdomen and tail. (Photo: Hai-chun Zhang/ NIGP)

69 A nearly complete individual (16 mm long) of *Liaoningogriphus quadripartitus* in lateral view, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: Da-jian Li/ CAS)



70 Reconstruction of *Liaoningogriphus quadripartitus* in dorsal (a) and lateral (b) aspects. (Courtesy: F. R. Schram/ ZMUA)

deposits of Las Hoyas, Spain are under description.

A new spelaeogriphacean, *Liaoningogriphus quadripartitus*, was recently described by Shen, Taylor and Schram (Figs. 68—70) from the Yixian Formation in Sihetun, Jianshangou, and Huangbanjigou areas of Beipiao City, and near Dakangpu village of Yixian County, Liaoning Province. Its body is elongated and cylindrical in outline with a maximum observed length about 20 mm. Thinly sclerotized carapace covers the head and most of the first two thoracomeres. *Liaoningogriphus* possesses a very short, broadly rounded rostrum. The antennules are biramous and the antennae uniramous. Thoracopods 2~8 are well developed with endopods. The last six thoracomeres are freely exposed. Very well developed, elongate, biramous pleopods are equally present on the pleomeres 1~5. The distal protopod margin is sigmoidally curved, with two-segmented exopods and an endopod. The telson possesses two pairs of short, robust median terminal spines and a fine transversal line in its lower middle part. The uropods are more than twice as long as the telson. The exopod has two ovoid segments.

The living spelaeogriphaceans are restricted to the Southern Hemisphere. Conversely, all known fossil taxa are found from the Northern Hemisphere. There is a trend of size reduction: the recent taxa appear to be considerably smaller (about 7 mm long) than the fossil forms (9.4—20 mm long).

Liaoningogriphus is extremely abundant but completely lack of diversity. They are usually preserved in yellowish-gray tuffaceous shales and siltstones with fine laminated structure and often associated with terrestrial freshwater organisms, such as conchostracans, ostracods, bivalves, gastropods, insects and plants. Three living spelaeogriphacean forms, *Spelaeogriphus lepidops*, *Potiicora brasilensis* and *Mangkutu mityula*, are swiftly swimming animals with rapidly undulating body. They are found in caverned freshwater pools and underground aquifer. However, based on associated conchostracan habits and the shrimp-bearing beds with abundant tuffaceous materials, *Liaoningogriphus* must have lived in ground-water lakes and pools instead of cave pools or underground water. It was warm temperate-subtropical climatic environments during the late Mesozoic in eastern Asia.

71 Mayfly nymph *Ephemeropsis trisetalis*, about 60 mm long.

INSECTS AND SPIDERS

Jun-feng Zhang, Hai-chun Zhang

As they had been and continued to be, insects were undoubtedly the most successful animals in the Jehol Biota. This has been confirmed by the extremely high diversity of at least 500 species referable to over 100 families within 17 orders based on over 10,000 specimens collected from the non-marine rocks in northern Hebei and western Liaoning provinces. This extremely high diversity and superb preservation of imprints are quite rare in the geological history throughout the world. These fossil insects have provided a vivid picture of the late Mesozoic, in which some of them flew in the sky, some crawled on the ground, and some swam in the water; some fed on plant leaves, seeds or fruits, some were saprophagous, and some preyed on other insects or sucked blood of birds or beasts. Among these fossil insects, some are familiar to us, such as wasps (Order Hymenoptera), mosquitoes and flies (Order Dipera), beetles (Order Coleoptera), cockroaches (Order Blattaria), dragonflies (Order Odonata) and grasshoppers (Order Orthoptera). These insects open a window through which we have caught a glimpse of the late Mesozoic entomofauna in East Asia. Comparing them with modern insect faunas, we also know more about insect phylogeny and evolution. Moreover, many components had special forms and ecological characteristics, which enable us to reconstruct the paleogeography, paleoclimate and paleoecology. One of the most interesting aspects is many kinds of flower-visiting insects found from this entomofauna, such as flower bugs, tumbling flower beetles, brachyceran flies, digger wasps and cockroaches. From the same locality and the same rocks, the flowering plants have also been recovered. These wonderful discoveries have provided important data in the discussion of the origin of flower-visiting insects and flowering plants as well as their coevolutionary relationships.

In the Jehol Biota, certain geographically widespread and dominant insect species have been found in almost every terrestrial basins in northern Hebei and western Liaoning provinces. They usually had abundant individuals and are easy to collect, with some important and familiar representatives as follows.

Ephemeropsis trisetalis (Figs. 71, 72), a giant mayfly assigned to the family Hexagenitidae of the order Ephemeroptera, is very important in the correlation of non-marine strata in East Asia. Its nymphs, with abundant individuals, lived in the warm, shallow and stagnant waters near the shore, crawling on the bottom or swimming in the waters and preying on other aquatic insects. The adults lived on land and were short-lived and poor fliers. This mayfly is distinguished from other components of Hexagenitidae by its large size, and is a cecal branch in the evolution of this family in the late Mesozoic.

Aeschnidium heishankowense (Fig. 73) is a kind of large dragonfly referred to Aeschnidiidae of Odonata. Its larvae are numerous, and lived in a similar environment to that of *Ephemeropsis trisetalis*. They preyed on other aquatic insects dominated by wigglers of mosquitoes and flies or small, young aquatic insects and fishes. The adults lived upon land as long-lived and excellent fliers.

72 Adult mayfly *Ephemeropsis trisetalis*, about 60 mm long.

73 Adult, female dragonfly *Aeschnidium heishankowense*, about 130 mm wide when wings stretched. Red arrow denoting the long ovipositor.

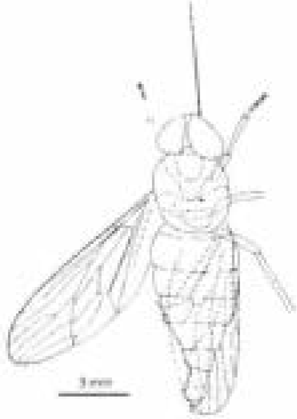
This large species influences, directly or indirectly, on the quantity variation of almost all other insects, or even on their rise and fall, for both larvae and adults of this species are the largest carnivorous insects of the Jehol entomofauna. Its con-generic relative has been found from the lower Tithonian in Solnhofen, Germany, and thus it plays an important role in ascertaining the age of the Jehol insect fauna. The family Aeschnidiidae was an interesting group in the Late Jurassic—Early Cretaceous, and as the typically early-staged representative of this group. This Chinese species shows some primitive characteristics such as the dense veins and much small cells on fore- and hind-wings.

Mesolygaeus laiyangensis (Fig. 74), a medium or small-sized aquatic bug belonging to an extinct family Mesolygaeidae referable to Heteroptera within Hemiptera, plays an important role in the correlation of non-marine strata in East Asia. Both juveniles and adults, with abundant individuals, lived in the warm, shallow and stagnant waters near the shore, crawling and swimming in the waters, but sometimes they also disembarked. The adults could fly off the waters, preying on other small aquatic insects, such as the wigglers of mosquitoes and flies. This species only lived in the late Mesozoic but was closely related to extant shore bugs (the family Saldidae), and both of them

74 Saldoid bug *Mesolygaeus laiyangensis*, about 7 mm long, from Nanligezhuang locality (Laiyang Formation) in Laiyang, Shandong.

75 Chaoborid mosquito *Chironomaptera gregaria*, about 6 mm long, from Nanligezhuang locality (Laiyang Formation) in Laiyang, Shandong.

76 Brachyceran fly *Protonemestrius jurassicus*, about 13 mm long, red arrow denoting the proboscis. (Courtesy: Dong Ren/ CNU)



77 Sketch drawing of *Protonemestrius jurassicus*. (Courtesy: Dong Ren/ CNU)

78 Flower bug, about 10 mm long.

79 Echinosomatid earwig, about 20 mm long.

80 Katydid, about 25 mm long.

81 Mesoblattinid cockroach, about 35 mm long.

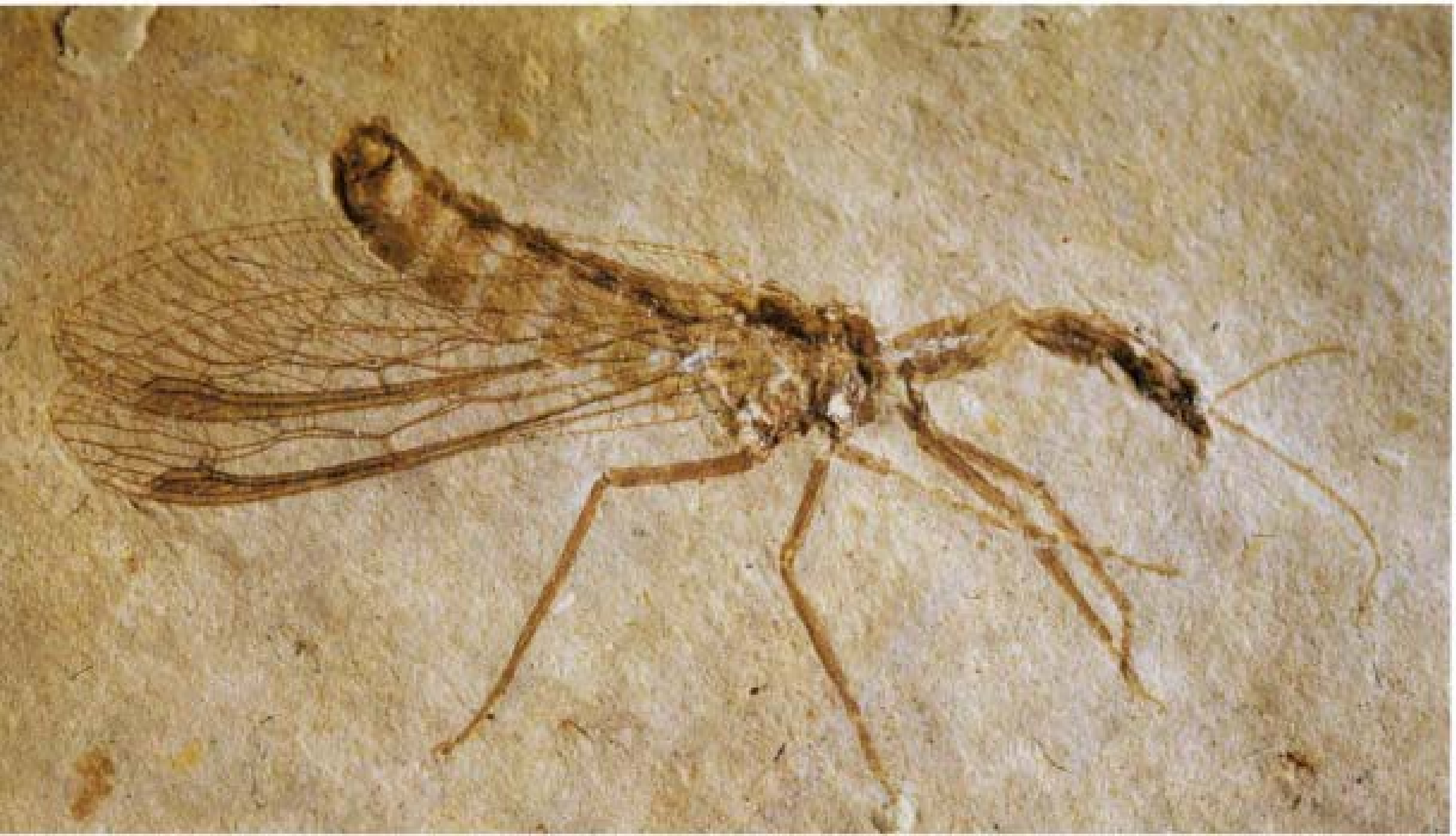
82 Froghopper, about 15 mm long.

83 Elater (elaterid beetle), about 15 mm long.

84 Cupedid beetle *Notocupes laetus*, about 15 mm long.

85 Dung beetle, about 20 mm long.

86 Snakefly *Alloraphidia longistigmosa*, about 20 mm long.



87 Chaoborid mosquitos *Chironomaptera vesca*, about 10 mm long.

belong to the same superfamily Saldoidea. As for lifestyle, however, the former could live in water and is regarded more primitive than the latter that are often seen along shores of ponds or lakes.

Chironomaptera gregaria (Fig. 75), belonging to phantom midges (the extant family Chaoboridae), is a small mosquito. It is also an important component in the correlation of non-marine strata in East Asia. Their wrigglers, with abundant individuals, lived in the warm, shallow and stagnant waters near the shore, wriggling in the waters. The adults were terrestrial, flying over the marshes where plants were prosperous. The species belongs to the Chironomapterinae, a Mesozoic extinct subfamily, the phylogenic position of which in the family Chaoboridae remains unclear. As the food of other medium-sized and small predatory insects, these wrigglers were important in the ecological chains of the lacustrine systems in the period they lived.

Though not large in quantity, the Jehol probably flower-associated insects are of great importance to the Biota, giving an example of co-evolution between these ancient probable pollinators and earliest representatives of angiosperms (flowering plants). The identification of the flower-related

88 Brachyceran fly *Protonemestrius* sp., about 15 mm long.

90 Ephialtitid wasp *Crephanogaster rara*, about 10 mm long.

89 Sawfly, about 10 mm long.

91 Ichneumon fly *Tanychora beipiaoensis*, about 7 mm long.

92 Pelecinid wasp *Scorpiopelecinus versatilis*, about 15 mm long.

93 Digger wasp *Pompiloperus sp*., about 15 mm long.

insects gives further proofs that the flowering plants were possibly present, though not dominant, in the Biota from the Late Jurassic—Early Cretaceous in the northeastern part of China. Some of the probably pollinating insects of the Jehol Biota are referred to the order Diptera, e.g., *Protonemestrius jurassicus* (Figs. 76, 77), *Protonemestrius beipiaoensis*, *Florinemestrius pulcherrimus*, and flowering bug (Fig.78), etc. The characteristic feature of these insects is with special nectaring mouthparts (proboscis) that are similar to modern con-familial pollinating taxa. However, the probability that these insects fed, in fact, on juice of plants or blood of other animals could not be excluded. Besides the aforementioned taxa, materials of other Jehol insects (Figs. 79~93) were also intensively collected.

In the Jehol Biota, spiders were low in diversity and not rich in abundance, with representatives in some species of the family Araneidae referable to the order Araneida within the class Arachnida (Fig. 94). They usually lived amongst wood branches or leaves in the forests, spinning orb webs that were vertical or horizontal or inclined depending on the spatial relationships of the supporting objects. Usually, the spider sat on the center of the web from dusk to dawn, and hid between plant stems or leaves near its web during the day, preying on many kinds of small and medium-sized winged insects.

(Except where indicated, all fossils in this chapter were collected from the Huangbanjigou locality of the lower part of the Yixian Formation in Beipiao, Liaoning)

94 Orb-web spider, about 10 mm long.

Lycoptera

Photo: IVPP

FISHES

Jiang-yong Zhang, Fan Jin

Fishes are the most abundant fossils in the Jehol Biota. They are counted tens of thousands. The scientific study on fossil fishes of Jehol Biota in western Liaoning started in the second half of the 19th century when H. E. Sauvage, a French anatomist, named the specimens from northern China as a new species, *Prolebias davidi*, of Cyprinodontidae. Nearly half a century later, Amadeus W. Grabau, an American paleontologist, described *Lycoptera jobolensis* and *L. jobolensis* var. *minor* in his book *Stratigraphy of China* in 1928. Subsequently, Kazuo Saito and Fuyuji Takai, from Japan, also studied fossil fishes from the area. The first work published by Chinese scholars is the monograph *Lycopterid Fishes from North China* by Hsien-ting Liu and others. In recent years, many new fossil fishes were found in the area. To date, seven genera of the fossil fishes of Jehol Biota have been published, including *Peipiaosteus*, *Yanosteus*, *Protopsephurus*, *Sinamia*, *Longdeichthys*, *Lycoptera*, and *Jinanichthys*.

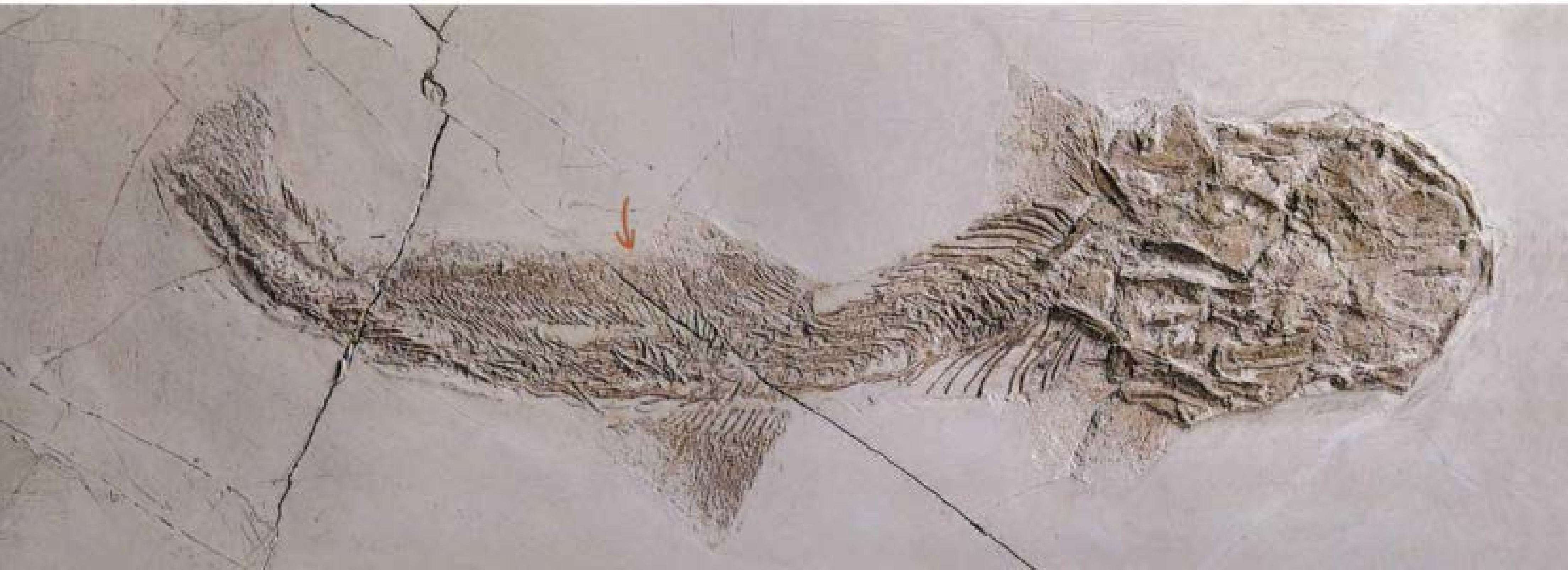
Peipiaosteus, *Yanosteus*, and *Protopsephurus* are fishes belonging to Acipenseriformes (sturgeons), Chondrostei, Actinopterygii. The earliest acipenseriform fishes were found from the Early Jurassic of Britain and Germany. But the Late Jurassic-Early Cretaceous ones were only found in Central Asia and the north of East Asia. Both fossil and extant acipenseriforms appear only in Holarctic and live in fresh waters or in anadromous migration style since Early Jurassic. Acipenseriforms are predators and prey on planktonic animals in juvenile and soon after acquire a benthic life. Adapting themselves to this lifestyle, they develop an elongated jaw and an inferior mouth. The preys are primarily shellfishes, mollusks and small fishes, including certain kinds of their own. *Acipenser sinensis* (Fig. 95) is an endemic species of China and is a national treasure. It is a large anadromous migration fish, with an individual weighing up to 550 kg. The juveniles live in the littoral of the Eastern China Sea and then migrate up the rivers to spawn. The spawning areas are mainly in the Yangtze and Pearl Rivers.

Peipiaosteus and *Yanosteus* are referred to a newly erected fossil family

95 *Acipenser sinensis*, a large anadromous migration fish, with juveniles living in the littoral of eastern China and adults migrating mainly to the Yangtze and Pearl rivers to spawn. (Courtesy: IHB)

96 *Peipiaosteus pani*, the first fossil acipenseriform fish found in China, usually less than one meter. A very well preserved specimen (**Left**), with impressions of muscles and roes, from Huangbanjigou locality (lower part of Yixian Formation) in Beipiao, Liaoning, and a close-up view of its digestive tract impression (**Right**, denoted by a red arrow). (Photo: IVPP)

97 *Yanosteus longidorsalis*, characterized by an extremely long dorsal fin (denoted by a red arrow) nearly up to one third of its total body length. The fish may reach one meter in standard length. (Photo: IVPP)



Peipiaosteidae. *Peipiaosteus* (Fig. 96) from Yixian and Jiufotang Formations of Beipiao, Liaoning and Fengning, Hebei, is the first fossil acipenseriform found in China, with a relatively small body size usually not exceeding one meter. Judging from the specimens preserved with nests, the fish probably became mature when its body reached 50 cm long. *Peipiaosteus* differs from other acipenseriforms in the absence of the caudal fulcra on its caudal fin.

Yanosteus (Fig. 97) was discovered in Lingyuan, Liaoning and Fengning, Hebei. The remarkable feature of the fish is its extremely long dorsal fin, nearly up to one third of its total body length. Although approximately fusiform in its body shape, *Yanosteus* has a relatively straight dorsal margin of the body. The length of the smallest individual is about 20 cm whereas a large specimen may reach one meter long. No specific information such as nests can be used to determine the adult size.

Protopsephurus (Fig. 98) is a member of a recent family Polyodontidae (paddlefish). It was collected from Lingyuan, Liaoning, with a length of approximately 10 cm in smallest individuals and over one meter in large specimens. Judging from the matured skeletons, *Protopsephurus* could be the smallest in body size among the genera of Polyodontidae. This genus is the earliest fossil record of the family. An extremely long rostrum, a series of rostral splints and spine-fringed scales are the most prominent features of the family. *Psephurus* is the only extant polyodontid in China who lives in the drainage of the Yangtze River and littoral region of the East China Sea whereas *Protopsephurus* is a stem-polyodontid closely related to *Paleopsephurus*, a Late Cretaceous sturgeon from North America. The living paddlefish is commercially an important freshwater fish. It has naked body surface and spoon-like rostrum and is thus also called duck-mouthed sturgeon. The paddlefish eats mainly zooplankton, and is adapted to a wide range of temperature ([illegible]°C). A native in the drainage of the Mississippi in the United States, the paddlefish has been growing very well in China since it was introduced here.

Sinamia (Fig. 99) is supposed to belong to a fossil family of its own, Sinamiidae (Amiiformes). The genus was named by E. A. Stensiö, a Swedish paleontologist, based on the materials from Mengyin, Shandong, China collected by Xi-chou Tan from China and O. A. Zdansky from Austria in 1923. *Sinamia* was found in the Yixian and Jiufotang Formations in Yixian, Chaoyang, Liaoning and also in Shaanxi, Gansu, Ningxia, Inner Mongolia, Anhui and Zhejiang. The wide distribution of *Sinamia* implies the possible connections between the drainages of the aforementioned places.

Sinamia is very similar to, but more primitive than, the living bowfin *Amia*. Fossil bowfins were usually found in marine deposits in many parts of the world, in contrast, they have occurred only in freshwater deposits of the Early Cretaceous of both North and South China and early Tertiary of North America. The only surviving species of bowfin (*Amia calva*) lives in fresh waters of eastern part of North America and is called a "living fossil". Normally, *Amia* inhabits sluggish, clear, lowland fresh waters preferably rich in vegetation. It can withstand high temperature, gulp and expel air at the surface, and is even known to aestivate. With its strong and sharp teeth, *Amia* is a voracious predator. The juvenile *Amia* feeds on smaller animals such as insects, insect larvae, ostracods, other zooplankton and phytoplankton, but after reaching 10 cm long, it begins to feed on other fishes. Adults also eat crayfish. The teeth of *Sinamia* are similar to those of *Amia*. Their food sources might be also similar.

Lycoptera (Fig. 100) is the most frequently met fish from the Jehol group. It is a small fish referred to a group called teleosts that reach the greatest diversity among the recent vertebrates. The fish was found mainly in the Yixian Formation in west Liaoning. Endemic to East Asian, *Lycoptera* was discovered only in Siberia, Mongolia, Korea and northern China from the late Mesozoic. The genus was named by a German anatomist, J. Müller, based on the materials from Transbaikalia of Siberia. The study of *Lycoptera* in China began with the work of Henri E. Sauvage on the fossil teleosts collected from North China (probably Daxinfangzi, Lingyuan, Liaoning). The fish was named by Sauvage as *Prolebias davidi* and was referred to *Lycoptera* by A. S. Woodward (a British paleontologist) afterwards. From then on, many scientists of both China and foreign countries have worked on the genus and named about 20 species. Most species of *Lycoptera* had tiny teeth and ate plankton, but *L. sinensis*, *L. gansuensis* and *L. muroii* bore relatively large teeth and were capable of preying on small insects and their larvae. *Lycoptera* is usually well-preserved, possibly because they were buried in situ. Entombed in great density, the fish seems to have a habit of swimming in shoals (Fig. 101).

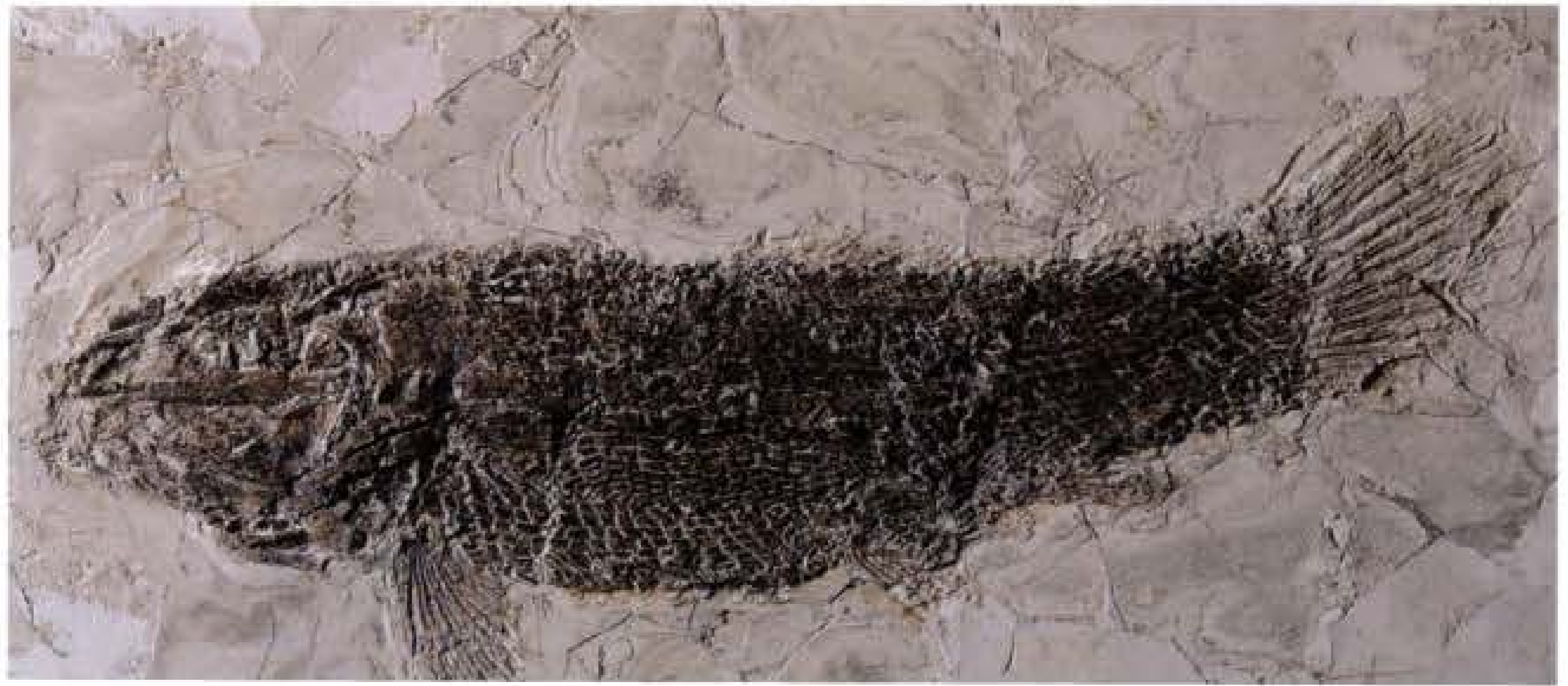
Lycoptera is also the earliest fossil teleosts discovered in China. The strata bearing *Lycoptera* were previously considered the Late Jurassic. The vanishing of *Lycoptera* was regarded as the indicator of the boundary between the Jurassic and Cretaceous. But workers studying ostracods, fossil plant and some other invertebrates have long regarded the strata as the Early Cretaceous. The debate has lasted for decades and drawn much attention of geologists and paleontologists. From in-depth studies on *Lycoptera* in recent years, many paleoichthyologists considered that the fish existed in the Late Jurassic to Early Cretaceous.

Lycoptera became the earliest known osteoglossomorph fish after the British ichthyologist P. H. Greenwood suggested a close relationship between the genus and the superorder Osteoglossomorpha. Fossils of the superorder were found from the Early Cretaceous to Oligocene in nearly all the main continents except Antarctica, but early osteoglossomorphs were mostly recovered from China. Fossil fishes similar to *Lycoptera* found from the Mesozoic terrestrial deposits of China were frequently referred to the superorder. Up to now, about 25 genera and 50 species of them were reported from China.

The superorder Osteoglossomorpha (bonytongues) is a very early branch of teleosts. The number of its fossil genera far exceeds the extant ones; however, the reverse is the case with most other teleost groups. Living bonytongues are exclusively fresh-water. The Southeast Asian *Scleropages* (Fig. 102) is the most prized and expensive osteoglossomorphs. Because of the two

98 *Protopsephurus liui*, the earliest fossil polyodontid found to date and more than one meter long in large specimens, is a distinct relative of *Psephurus* living in the drainage of the Yangtze River and littoral region of China. This is a well-preserved specimen from Dawangzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning, showing distinct scales and caudal skeleton. (Photo: IVPP)

99 *Sinamia*, found from freshwater deposits of both North and South China, is a distinct relative of living bowfin with strong and sharp teeth, and a voracious predator. This specimen is about 50 cm long. (Photo: IVPP)



100 *Lycoptera*, the most common fossil vertebrate in western Liaoning and the earliest teleost found in China, is an important member of the Jehol Biota and only distributed in East Asia. This specimen is about 12 cm long. (Photo: IVPP)

101 *Lycoptera* is usually preserved in great density. The specimen was found in Daxinfangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning. (Photo: IVPP)

102 *Scleropages formosus* ("fortune fish"), a living osteoglossoid fish, is the most prized and expensive osteoglossomorphs, a group also includes *Lycoptera* and *Jinanichthys* as primitive members. (From: http://www.arowana.com.tw)

103 *Jinanichthys*, very similar to *Lycoptera*, was found mainly from the *Jiufotang* Formation in western Liaoning. This specimen is about 9 cm long. (Photo: IVPP)

barbels, glorious large scales and old history of the fish, it was called "dragon fish" in China and was believed to have the power to ward off evil and to bring luck and fortune.

Jinanichthys (Fig. 103) was mainly found from the Jiufotang Formation and was described by Feng-zhen Ma and Jia-ru Sun based on the fossils from southern Jilin Province. The authors believed that the specimens from Jilin were similar to *Lycoptera longicephalus* but different from other species of the genus. Therefore, they gave a new generic name, *Jinanichthys*, to both *Lycoptera longicephalus* and the specimens from Jilin.

Extant osteoglossomorphs survived in the tropical or subtropical fresh waters of North America, South America, Australia, Southeast Asia, India, and Africa. No consensus has been reached by ichthyologists up to now about the interpretations of the transoceanic distribution of these freshwater fishes. Lycoptera, Jinanichthys and other fossils of the superorder found in China are the earliest known osteoglossomorphs. Therefore, some paleoichthyologists suggested that East Asia might be the ancestral origin center of osteoglossomorphs. An African origin was also suggested. In recent years, some researchers argued that the transoceanic distribution was resulted from the split of an ancestral land block according to vicariance principle. That is to say, the early evolution of osteoglossomorphs had already finished before the last break of the supercontinent Pangea.

Longdeichthys was another teleost found in western Liaoning. It was collected from Jiufotang Formation of Yixian and Heishan. Its total body length may reach 25 cm. The original name was given by Zhi-cheng Liu, based on the specimens from Longde, Ningxia and Yikezhaomeng, Inner Mongolia.

104 Holotype of *Callobatrachus sanyanensis* (snout-pelvis length 94 mm), a discoglossid frog, from Sihetun locality (lower part of Yixian Formation, Early Cretaceous) in Beipiao, Liaoning. (Photo: IVPP)

AMPHIBIANS

Yuan Wang, Ke-qin Gao

Amphibians ("double life" in Greek) are a class of primitive tetrapods (vertebrates with four limbs) that spend at least part of their lives in water and part on land, although some are entirely aquatic or terrestrial. Amphibians provide a biological link between fishes and the true land-living vertebrates, as they are the first group of tetrapods that invaded the land some 370 million years ago. Living amphibians are classified in the Subclass Lissamphibia (with their closely related ancestors in fossil forms). They include not only the familiar forms such as the frogs and toads (Order Anura), salamanders and newts (Order Urodela), but also the less familiar forms such as the limbless caecilians (Order Gymnophiona). Extinct archaic amphibians include labyrinthodonts and lepospondyls that flourished in the Late Paleozoic, from either of which the ancestral stocks of the living amphibians may have evolved.

Compared with other vertebrate groups, amphibians, especially the lissamphibians (having thin and fragile bones unfitted for fossilization), are generally less well documented in the fossil record. This is especially, and painfully, true of the Mesozoic Era, during which important events of origin and early diversification of modern amphibians took place. Therefore, discoveries of any lissamphibian fossils of this time are usually newsworthy, if not outright sensational. In the past few years, many well-preserved specimens of lissamphibians were recovered from the Mesozoic beds in western Liaoning, northern Hebei and southeastern Inner Mongolia in China. Most of the fossils are important components of the Jehol Biota that flourished in East Asia about 130—110 million years ago. The recovered fossils constitute a diverse lissamphibian fauna in the late Mesozoic of Asia, and provide crucial information on understanding the biogeographic evolution of early salamanders and frogs of modern amphibian affinities.

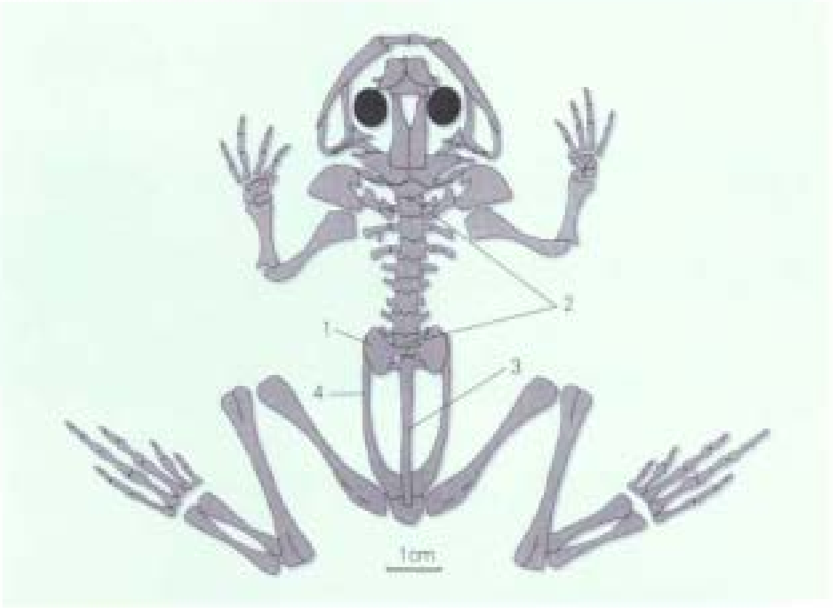
Before these discoveries, fossil amphibians from China were rather limited in both quantity and taxonomic diversity. Prior to 1998, all the known fossils were the Cenozoic in age (early Miocene to middle Pleistocene), totaling ten species of five genera from five major localities in northern China. Since then, new findings from northeastern China have added nearly as many species of the rare Mesozoic lissamphibians to the Chinese record. The fossils include several hundred well-preserved skeletons, some with clear impressions of soft parts such as eyes, gills, and skins. They also include the earliest known record of several taxonomic groups. These incredible finds have not only rejuvenated amphibian paleontology but also drawn a worldwide attention beyond the scientific community.

Frogs Frogs are tailless amphibians classified in the order Anura (belonging to the superorder Salientia, which also includes the primitive proanurans). They have unusual body structures that are specialized for jumping. Such structures include a rodlike urostyle formed by fusion of tail vertebrae and the greatly elongated hind limbs with highly modified tarsal elements. The earliest fossil representatives of Salientia were from the Early Triassic of Madagascar and Poland. After a long time evolution, now the order Anura includes some 4,800 living species with a global distribution except for extreme northern latitudes, Antarctica, and most oceanic islands.

The fossil frogs known from the Liaoning beds include several archaic forms that documented an important diversification of anurans during the Early Cretaceous time in the area. One of the frogs known from Liaoning is *Callobatrachus sanyanensis* (Fig. 104, 105), named and described on the basis of a nearly complete skeleton from the Sihetun site. The fossil beds yielded a radiometric date of 125 million years BP, indicating the Early Cretaceous age of the fossil. Taxonomic studies have revealed that *Callobatrachus sanyanensis* is a primitive member of the Discoglossidae, a basal family group of the living anurans. *Callobatrachus* is basal (or primitive) in having nine opisthocoelous presacral vertebrae, differing from eight in other discoglossids. It further differs from other members of the family in the combination of the following characters: lacking a dorsal protuberance but having a weak dorsal crest on ilium; having bicondylar sacro-urostylar articulation; lacking dermal sculptures on skull roof, and having anteriorly expanded sacral diapophysis.

Living discoglossids in China include five species in a single genus *Bombina*, with *Bombina orientalis* popularly known as the "oriental fire-bellied toad" (Fig. 106). Before the discovery of *Callobatrachus*, no discoglossid fossils were known in the same range of the extant group in East Asia. Consequently, *Callobatrachus* represents the first discoglossid frog known from China, and the earliest fossil record of the group from Asia.

Mesophryne beipiaoensis (Fig. 107) is another Mesozoic frog reported from



105 Skeletal reconstruction of *Callobatrachus sanyanensis*. 1, sacrum; 2, presacral vertebrae; 3, urostyle; 4, ilium. (Art: Yuan Wang/ IVPP)

106 *Bombina orientalis*, a living discoglossid frog mainly distributed in East Asia, and an extant relative of *Callobatrachus*. (Courtesy: Er-mi Zhao/ CIB)

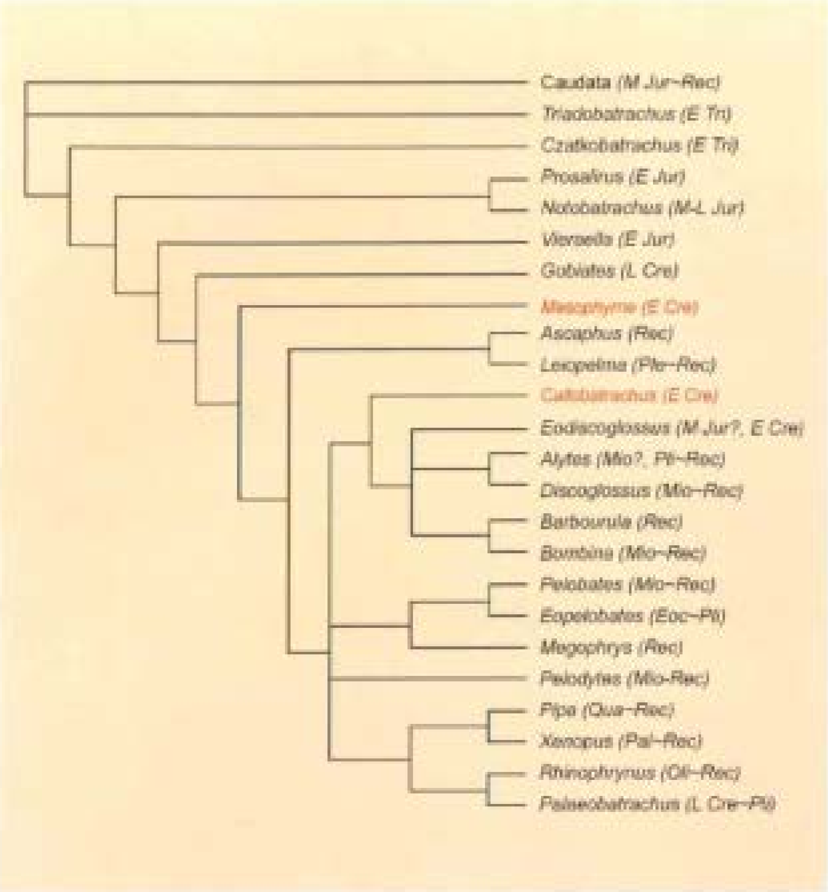
the Liaoning beds. It is represented by a nearly complete skeleton split on part and counterpart of a shale slab. It has obviously different osteological structures from *Callobatrachus*, including the presence of procoelous presacrals and greatly shortened vertebral column. It is worth noting here that *Mesophryne* also has nine presacrals, albeit having a short vertebral column. The number of presacral vertebrae is among the few crucially significant anatomical features in the evolution of frogs. In the earliest known frog, *Triadobatrachus* (a proanuran) of the Early Triassic of Madagascar, this number is as many as 14; *Vieraella*, an Early Jurassic frog from Argentina, has ten presacrals. Nine presacrals can be found in the Middle to Late Jurassic Argentine frog *Notobatrachus*, as well as in the aforementioned two Early Cretaceous Chinese taxa. This number is eight or fewer in all living frogs, except for two very primitive forms, *Ascaphus* (North American tailed frogs) and *Leiopelma* (New Zealand frogs), both having nine presacrals. Thus, the decrease in presacral number has been recognized as an obvious trend in the frog evolution.

In addition to its large presacral number, *Mesophryne* also has primitive features such as the presence of free ribs on anterior three presacrals, and the retaining of an intermedium bone in the carpal region. Thus, it is not surprising that a recent phylogenetic study has recognized it as a distinct clade of basal anurans (Fig. 108).

Liaobatrachus grabaui is the first Mesozoic frog described from the Liaoning beds; however, its systematic position is still questionable at present. *Liaobatrachus grabaui* was named and briefly described in early 1998 based on an incomplete skeleton with a disarticulated and poorly preserved skull. It has a snout-pelvic length of about 75 mm, intermediate between *Callobatrachus sanyanensis* (94 mm) and *Mesophryne beipiaoensis* (71.3 mm). The taxonomic status of this animal remains to be investigated, as the referral of it to the family Pelobatidae (by the original researchers) was based on several characters in question, such as the presence of procoelous presacrals and the lack of free ribs, which cannot be confirmed due to poor preservation.

Salamanders Salamanders are tailed amphibians classified in the order Urodela (belonging to the superorder Caudata, which also includes some primitive non-urodeles). In the past few years, several hundred of salamander fossils have been found from the fossil beds in northern China. Some were recovered from the Fengshan fossil bed in northern Hebei Province, and the Jiufotang Formation in western Liaoning. These strata can

107 Holotype of *Mesophryne beipiaoensis* (Slab A, dorsal view, snout-pelvis length about 71 mm), a primitive frog representing a distinct basal anuran clade, from Heitizigou locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)



108 Cladogram showing the hypothesized phylogenetic relationships of major lineages of archaic anurans and the relationships within the Discoglossidae, with two Jehol frogs included (in red).

110 Holotype of *Sinerpeton fengshanensis* (dorsal view, snout-pelvis length 47 mm), a primitive salamander with neotenic features indicated by the ossified ceratobranchial (denoted by a red arrow) and ossified carpals (denoted by yellow arrows), from Fengshan locality in Fengning, Hebei. (Photo: Mick Ellison/ AMNH)

109 A specimen of *Laccotriton subsolanus* (dorsal view, snout-pelvis length about 40 mm), a small, primitive metamorphic salamander, from Fengshan locality in Fengning, Hebei. (Photo: Mick Ellison/ AMNH)

111 Holotype of *Jeholotriton paradoxus* (Slab A, ventral view, body length about 140 mm), a primitive neotenic salamander similar to living cryptobranchoids in some skeletal structures, from Daohugou locality in Ningcheng, Inner Mongolia. (Photo: IVPP)

112 One of the three paratypes of *Jeholotriton paradoxus* (Slab A, lateral view, body length about 120 mm). Note aquatic adaptation as shown by the presence of external gills (denoted by a red arrow), laterally compressed tail, unossified carpals and tarsals, and some other osteological features. (Photo: IVPP)

be included in the Jehol Group (*sensu lato*) that has yielded the Jehol Biota. Some other fossils were recovered from the Daohugou locality of southeastern Inner Mongolia, the strata older in age (refer to Chapter 2 for stratigraphic information). The discovery of Mesozoic salamanders from China has special implications, as they are the earliest known representatives of modern salamander groups, and thus, provide important insights into the early evolution of some anatomical structures and the biogeographic history of these tailed amphibians.

Living salamanders form China have been grouped in three families: the Hynobiidae, the Cryptobranchidae, and the Salamandridae. None of the fossil salamanders reported from northern China can be assigned to any of these families except for one taxon, *Chunerpeton*, which is referred to the Cryptobranchidae.

Laccotriton subsolanus (Fig. 109) is the first Mesozoic salamander reported from China. It is a small-sized metamorphosed salamander, represented by a large number of articulated skeletons from a small quarry in Fengshan Basin of northern Hebei Province. *Laccotriton subsolanus* is characterized by having 16 presacrals and unicapitate ribs with a broadened base (most living salamanders have bicapitate ribs, except for hynobiids and cryptobranchids). It primitively retains lacrimal and prefrontal bones on the skull, and has five separate bones in the lower jaw. The phalangeal formula (number of phalanges in hand and foot) is 2-2-3-2 in the hands, and 2-2-3-4-2 in the feet.

Sinerpeton fengshanensis (Fig. 110) is another salamander from the Fengshan

113 Holotype of *Chunerpeton tianyiensis* (part and counterpart of a slab of shale, body length about 180 mm), a basal cryptobranchid salamander and the only Mesozoic member of the group found to date, from Daohugou locality in Ningcheng, Inner Mongolia. (Photo: Mick Ellison/ AMNH)

114 *Andrias davidianus* (**Upper**) and *Batrachuperus pinchonii* (**Lower**), a living representative of the Cryptobranchidae and Hynobiidae, respectively; the two families are widely accepted as the most basal groups of living salamanders. (Courtesy: Er-mi Zhao/ CIB)

site, and the fossils were collected from the same quarry as that of *Laccotriton*. Different from the metamorphosed *Laccotriton*, this salamander has ossified ceratobranchials (as bony support for external gill filaments in life) and ossified carpals and tarsals (ossification of these bones only seen in adulthood). The combination of these features suggests a mature individual with larval external gills, a condition called neoteny in modern biology. *Sinerpeton* also differs from *Laccotriton* in having the phalangeal formula of 1-2-3-2 in the hands and 1-2-3-4-2 in the feet.

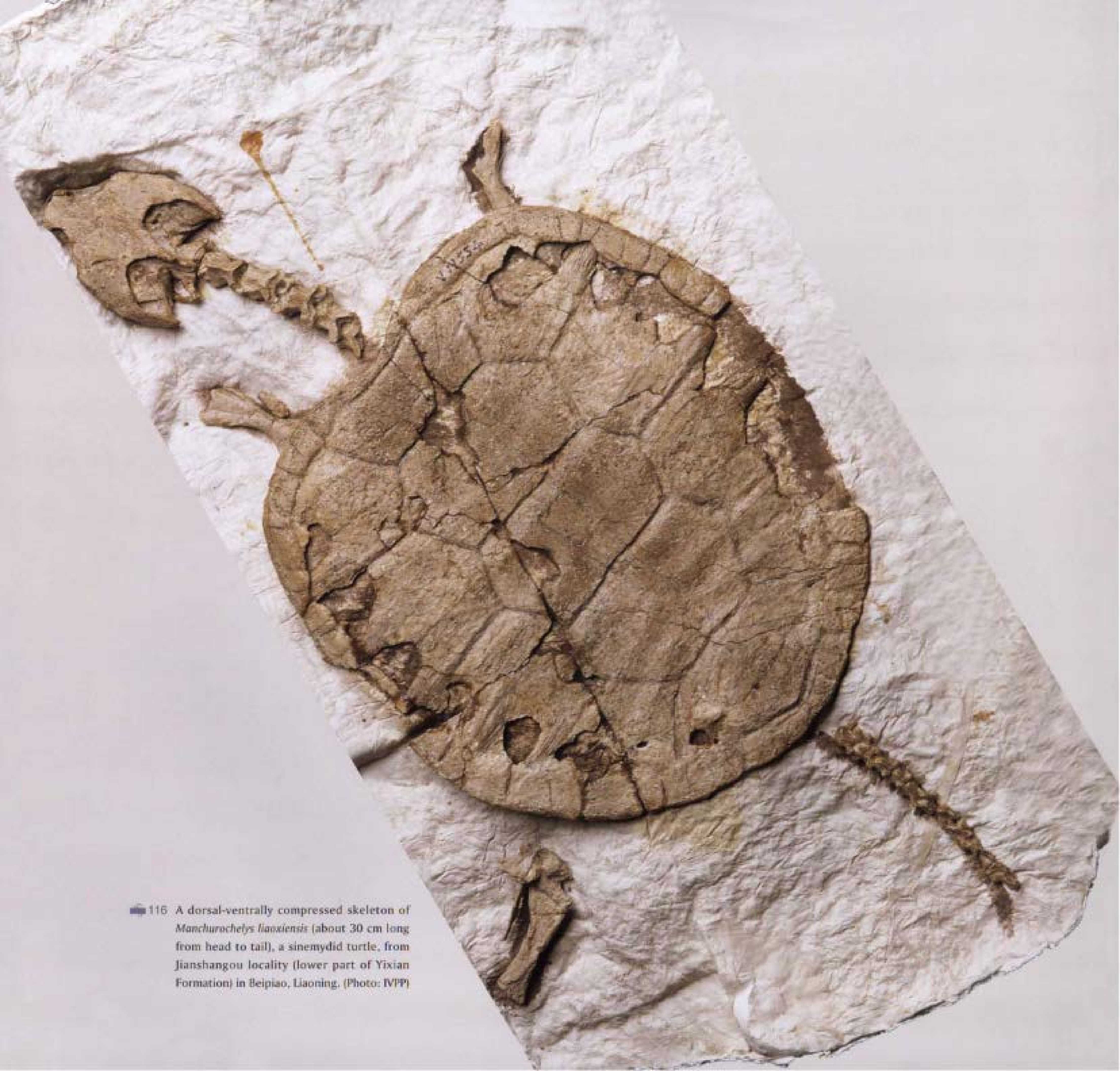
Jeholotriton paradoxus (Figs. 111, 112) is reported from the Daohugou locality, Ningcheng County, Inner Mongolia. This apparently is an aquatic salamander as indicated by its external gills, laterally compressed tail, presence of well-developed haemal arches on caudal vertebrae, and the lack of ossified carpal and tarsal elements. *Jeholotriton* is a special Mesozoic salamander showing a combination of larval and adult features that indicate neoteny. The larval features include the presence of external gills, a tooth-bearing coronoid bone on the lower jaw, the larval shaped pterygoids and a short maxillary arcade with underdeveloped maxilla in the cranial part. The adult features include extensive medial contact of the two nasals and the presence of a posteriorly directed tooth row in the palate. *Jeholotriton* is characterized by having 17 presacrals, the vertebrae with short transverse processes, and a prominent dorsal process on the premaxillae. Its ribs are like those of Fengshan salamanders as unicapitate and proximally expanded. The phalangeal formula is 2-2-3-2 for the hands and 2-2-3-3-2 for the feet.

Chunerpeton tianyiensis (Fig. 113) is another salamander from the Daohugou site. This salamander represents a basal member of the Cryptobranchidae, the family including the endangered Asian giant salamander *Andrias* (Fig. 114, Upper) and the North American hellbender *Cryptobranchus*. Morphologically, *Chunerpeton* shares with extant cryptobranchids several derived characters, such as the nasals being much narrower than the interorbital width; nasal-prefrontal contact absent; and the anterolateral process of parietal extending along the lateral border of the frontal. It primarily differs from extant cryptobranchids, however, in lacking the frontal-maxillary contact; retention of a palatal fenestra between vomers; presence of a distinct medial process of pterygoid; and ossification of basibranchial II as a trident-shaped structure. Because no pre-Paleocene fossils were known for the family, the *Chunerpeton* fossils from the Daohugou site document the first Mesozoic and the earliest known record of the Cryptobranchidae. The fossils also provide evidence supporting the hypothesis that the divergence of the Cryptobranchidae from the Hynobiidae had taken place during the Jurassic in Asia.

Liaoxitriton zhongjiani (Fig. 115) is the only salamander taxon of the Jehol Biota that is known from the Jiufotang Formation. Fossils of this salamander were recovered from a site near Huludao City of western Liaoning. As the formation is dated as about 110 million years BP, *Liaoxitriton* documents so far the youngest stratigraphic occurrence of salamander fossils in the Jehol Group. The species is represented by dozens of articulated skeletons in various preservation conditions, and was the first Chinese Mesozoic lissamphibian to be reported with well-preserved soft tissue impressions (e.g., the skin & eye impressions). The diagnostic features of this animal include the presence of 16 presacral vertebrae and transverse processes of vertebra about half-length of the centrum. It also has the cryptobranchoid type unicapitate ribs with an expanded proximal end. The phalangeal formula is 2-2-3-2 in the hands and 1-2-3-4-3 in the feet. This salamander is similar to some living hynobiids (Fig. 114, Lower) in several osteological features. It is noted that the species is represented by a series of fossils showing different developmental stages, which allows a possible ontogenetic study of the animal in the near future.

In general, the amphibian fossils (especially those of salamanders) from the Mesozoic beds in northern China are important for their superb preservation, large quantity, and considerable taxonomic diversity. The discoveries of these wonderful fossils provide solid paleontological evidence to answer some major questions on the evolution of amphibians; and the studies of these fossils have opened a new window to view the evolutionary history, including the origins, taxonomic diversification and geographic radiation, of modern amphibians.

115 Holotype of *Liaoxitriton zhongjiani* (Slab A, ventral view, body length about 120 mm), a primitive salamander similar to living hynobiids in some skeletal structures, from Shuikouzi locality (Jiufotang Formation) in Huludao, Liaoning. (Photo: IVPP)



116 A dorsal-ventrally compressed skeleton of *Manchurochelys liaoxiensis* (about 30 cm long from head to tail), a sinemydid turtle, from Jianshangou locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)

TURTLES

Jun Liu

"Because they are still living, turtles are commonplace objects to us; were they entirely extinct, their shells — the most remarkable defensive armor ever assumed by a tetrapod—would be a cause for wonder." — A. S. Romer, 1945.

Turtles are unique among living animals. Their trunk is embedded in the bony shell. The shell can be divided into dorsal and ventral parts (carapace and plastron), and usually includes inner and outer layer: the outer one is horny, made up by many scutes; the inner one is bony, made up by many plates. Not only do the vertebrae grow together with shell, but also the carapace bony plates are fused with ribs. They differ from all other terrestrial vertebrates by the ribs outside the shoulder and pelvic bones, which enables them to retract their heads and limbs into shells for protection and self-defense.

The turtles are one kind of specialized reptiles; they also are one branch of ancient reptiles. They used to be classified as primitive anapsids (i.e. reptiles with no temporal opening on the skull), but also regarded as diapsids (i.e. reptiles with two temporal openings) by other people. The turtles primarily can be divided into two groups: the Pleurodira and the Cryptodira. These names refer to the manner in which the living members of these groups retract their necks. The pleurodires do so by lateral flexure of the cervical vertebrae and the cryptodires by vertical flexure. All the living pleurodires inhabit fresh water of the southern continents (Africa, Australian and South America), but extinct ones may have lived in a marine environment. This group has a worldwide distribution in the Cretaceous and Paleogene. Cryptodires are much more diverse in the modern fauna than are the pleurodires. Modern cryptodires may be classified into three groups: the Testudinoidea, including the tortoise and most freshwater turtles; the Chelonioidea, the sea turtles, with the limbs specialized as flippers and the shell reduced; and the Trionychoidea, the soft-shelled turtles.

Where did the turtles come from? How the shell and the strange structure were formed? The most primitive turtle known by now, *Proganochelys*, which was found in the Upper Triassic of Germany, had a completely "normal" shell. The Jurassic turtles almost had the structure of modern turtles. *Eunotosaurus* from the Permian of South Africa was once thought to be the ancestor of the turtles, but in fact it is not related to turtles at all. Among reptiles preceded the turtles, pareisaurs, procolophonoids, captorhinids had once been regarded as the ancestor group of the turtles, but none of these animals has convincing derived characters shared with turtles. Some paleontologists think the turtles may be closest to the marine reptile sauropterygian, but current evidence is not strong enough to support this view. The origin of turtles still is an unsolved puzzle.

Many well-preserved turtle specimens have been found in western Liaoning. Most of them can be referred to *Manchurochelys* belonging to the family Sinemydidae. Three species have been described so far of the genus: *Manchurochelys manchoukuoensis*, *M. donghai* and *M. liaoxiensis* (Fig. 116). *M. manchoukuoensis* was named by Riuji Endo and Tokio Shikama in 1942, the holotype of which was lost during WWII. *M. donghai* was from the coalmine in Jixi (possibly from a higher horizon than the Jehol Group), Heilongjiang Province, named by Shao-liang Ma in 1986. *M. liaoxiensis* was established on a specimen from Jianshangou village, Beipiao, Liaoning Province by Shu-an Ji in 1995. Some smaller-sized turtles were also collected from the Yixian and Jiufotang Formations of the Jehol Group, whereas their systematic position remains to be studied (Fig. 117).

Characteristic features of *Manchurochelys* include: skull very low, nasal small, prefrontal in contact with vomer, a paired pit present on ventral surface of basisphenoid, the supramarginal scales absent, shell very flat, plastron cruciform, mesoplastra absent. Based on these characters, *Manchurochelys* could be classified into Sinemydidae, Cryptodira. And it is the closest to *Dracochelys*, a group of turtles from the Early Cretaceous of Xinjiang, China.

Turtles are cold-blooded like most other reptiles; their modern groups are mainly distributed in the temporal, torrid zones. Most turtles live in terrestrial environment, normally in river, lake or swamp. Only a few groups are completely terraneous. There were many lakes in western Liaoning during the time of *Manchurochelys*, and this kind of turtle may have lived in the lake areas. Perhaps its lifestyle is similar to that of modern freshwater turtles.

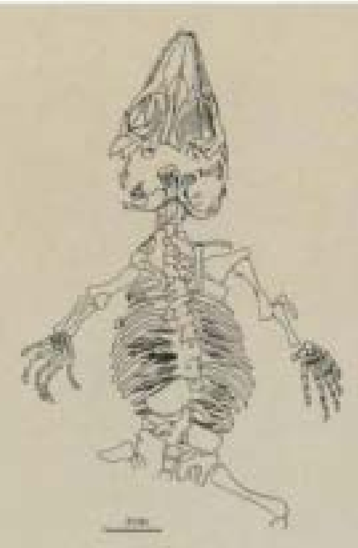
117 A small turtle (about 7 cm long) from Shangheshou locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

CHORISTODERES

Jun Liu, Xiao-lin Wang

The Choristodera is a clade of distinctive but poorly known aquatic reptiles. For more than one century, knowledge of this group was limited to two highly specialized genera: *Champsosaurus* and *Simoedosaurus* from North America and Europe. Over the last two decades, additional nine genera have been referred to the Choristodera. Thus, we now have a better understanding of these animals. They had a temporal range spanning at least 190 million years from the Late Triassic to the late Oligocene and a geographical distribution from western North America to Japan via Eurasia.

The Jehol Biota is famous for its fossil vertebrates found in recent years, especially birds and feathered dinosaurs. The earliest reported tetrapod of the Jehol Biota was a small reptile — *Monjurosuchus splendens* (Fig. 118). It was named in 1940 by R. Endo, and was classified as a primitive archosaur (Thecodontia). The holotype of the taxon was reportedly lost during the WWII. R. Endo and T. Shikama named another taxon, *Rhynchosaurus orientalis*, in 1942 based on a specimen from the same locality and horizon where the holotype of *Monjurosuchus splendens* was found. This taxon was classified into Rhynchocephalia, a group related to lizards and represented today by the isolated New Zealand Tuatara, *Sphenodon*. These two kinds of reptiles were compared by F. F. von Huene (1942), who believed that they are the same taxon and should be classified into Rhynchocephalia. *Monjurosuchus* was finally referred to Choristodera by Ke-qin Gao and others in 2000 based on the neotype specimen (Fig. 119) that they newly selected. They diagnosed the taxon by the following combination of characters: dorsoventrally flattened skull; a deeply incised posterior skull margin; parietal foramen absent; conical subthecodont teeth, with striae; three sacral vertebrae; fibula with wide distal but narrow proximal head; fifth metatarsal with expanded proximal end but no plantar tubercles. *Monjurosuchus* can be distinguished from all other choristoderes by the combination of the small supratemporal fossa and closed subtemporal fossa.



118 Line drawing of the lost holotype of *Monjurosuchus splendens* (skull length 92 mm), recently identified as a choristodere, from Danangou (Tanankou) locality (middle part of Yixian) in Lingyuan, Liaoning. (Art: Mick Ellison/ AMNH; Courtesy: Ke-qin Gao/ PKU)

Many specimens of *Monjurosuchus* have been discovered in western Liaoning in recent years, some of which bear exquisite integumentary impressions (Fig. 120). Gao and others suggested that the overall appearance of the integument may be like that of the living Chinese crocodile lizard, *Shinisaurus crocodilurus* (Fig. 121), a semi-aquatic lizard that feeds on small fish, amphibians and invertebrates, and *Monjurosuchus* may have had a similar lifestyle.

There also is one kind of "long-necked" choristoderes, the hyphalosaurs, in the Jehol Biota. The specimens of *Hyphalosaurus* were excavated from Dawangzhangzi Bed of the Yixian Formation (ca. 123 Ma). It is referred to choristoderes based on the following characteristics: vertebral centrum platycoelus; three sacral vertebrae; dorsal ribs pachyostotic; epipodial segments (radius, ulna, tibia, fibula) greatly shorter than the humerus and femur. But its neck is greatly elongated.

There are mainly two fossil localities for *Hyphalosaurus*, one of them lies in the north of Fanzhangzi of Lingyuan City, Liaoning Province. A nearly complete fossil skeleton was found here in August, 1998. Then it was studied by Gao and his collaborators from the IVPP, CAS, and was named as *Hyphalosaurus lingyuanensis* (Figs. 122, 123). The paper was published in the journal *Vertebrata PalAsiatica* of January, 1999. However, its counterpart was named as "*Sinohydrosaurus lingyuanensis*" by Jian-jun Li and others from the Beijing Natural History Museum. J. B. Smith and J. D. Harris published a paper in *Journal of Vertebrate Paleontology* to discuss the validity of two names in 2001; he pointed out that the two names are actually a synonymy, and he chose *Hyphalosaurus lingyuanensis* as the valid name.

119 Neotype of *Monjurosuchus splendens* (skull length 58 mm) from Niuyingzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning. (Photo: Mick Ellison/ AMNH; Courtesy: Ke-qin Gao/ PKU)

120 Skin impressions on a specimen of *Monjurosuchus splendens*. (Photo: IVPP)

The holotype of *Hyphalosaurus lingyuanensis* is a 116 cm long specimen exposed in ventral view. It has a small skull, several needle-like teeth lying in the anterior part of the skull. There are at least 13 rows of ribs and more than 20 rows of gastralia ("abdomen ribs"). The vertebral column consists of 19 cervicals, 16~17 dorsals, three sacrals, and more than 55 caudals. Therefore, the most striking feature on this specimen is the presence of greatly elongated neck (about 20 cm long) and a long tail.

The proportionally small head, pointed snout, needle-like teeth and greatly elongated neck of *Hyphalosaurus* strongly indicate its fish-eating diet in life. The dorsal ribs are pachyostotic and thickened distally. Functionally, this thickening appears to increase the specific gravity of the body, enabling the animal to remain submerged with a minimum of effort. It also shows other morphological features that reflect an aquatic lifestyle, including platycoelous vertebrae, poor ossification of the distal ends of the limb bones, reduced ossification of the carpals and tarsals and short epipodials.

It is interesting to note that at least six fossil fish of the genus *Lycoptera* were preserved on the same slab with the holotype of *Hyphalosaurus*. One of them is so close to the mouth of *Hyphalosaurus* (Fig. 123) as if it could not escape from being preyed on when *Hyphalosaurus* opened its mouth.

Many complete skeletons of *Hyphalosaurus* were found in Wangjiagou, Wanfotang and Hejiaxin of Yixian County in fall, 1999. This area became the second fossil locality of *Hyphalosaurus*.

All known specimens of *Hyphalosaurus* were excavated from tuffaceous shales deposited in lacustrine environment. These rocks recorded the frequent volcanic eruptions. One can imagine the scenery during that time: the volcanoes threw masses of ashes into the atmosphere, and as the ashes fell down, they spread out and buried everything. Volumes of greenhouse gases and toxic gases came along with volcanic eruptions; the habitat was devastated, and hundreds of thousands of animals died together. Some individuals of *Hyphalosaurus* were buried together, as seen in many specimens (Fig. 124).

The first specimen mentioned as choristodere in China was a snout fragment from the Otog Qi District in the Ordos Basin, Inner Mongolia studied by E. Buffetaut. It was revised by D. Sigogneau-Russell in 1981, and a new taxon, *Ikechosaurus sunailinae* was named based on that specimen. A few years later, many well-preserved, articulated specimens of *Ikechosaurus* were discovered in Luohandong Formation, Zhidan Group (Early Cretaceous) during the fieldwork of China-Canada Dinosaur Project. Sigogneau-Russell had noted that in the presence of a broad snout and closely packed teeth with rectangular bases, *Ikechosaurus* was most similar to the Paleocene genus *Simoedosaurus*, a view also held by several other researchers. However, still others thought *Ikechosaurus* is more closely related to *Champsosaurus* than to *Simoedosaurus*. A new species, *Ikechosaurus gaoi* (Fig. 125) was erected based on a fragmentary skeleton from the Jiufotang Formation of Chifeng, Inner Mongolia by Jun-chang Lü and others. This is the third choristodere reported from the Jehol Biota.

Many well-preserved skeletons have been found in Yixian and Chaoyang, Liaoning Province recently, which could be referred to *Ikechosaurus*. Their skull is flat, having elongated snout and large temporal openings, with a skull length of 30 cm. The total length of these reptiles can be up to 2 m, and the length of the tail is more than half of the total length.

121 *Shinisaurus crocodilurus*, Chinese crocodile lizard, a living semi-aquatic lizard, to which *Monjurosuchus* may have a similar integumental overall appearance. (Photo: Chun-xuan Chen)

122 Holotype of *Hyphalosaurus lingyuanensis* (total body length 116 cm), a long-necked choristodere, from Fanzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning Province. (Photo: IVPP)

123 A close-up view of the skull of the holotype of *Hyphalosaurus lingyuanensis*, showing a fossil fish near its mouth. (Photo: IVPP)

124 Four individuals of *Hyphalosaurus* on one slab, with two adults and two young, as if one family died in a single accident. (Photo: IVPP)

图 125 A crushed skull of the holotype of *Ikechosaurus gaoi* (skull about 19 cm long), a gavial-like choristodere, from a locality of Jiufotang Formation in Chifeng, Inner Mongolia. (Photo: IVPP)

126 An incomplete skeleton of *Yabeinosaurus* from Gezidong locality (Jiulongxhan Formation), Lingyuan, Liaoning. (Photo: IVPP)

127 An undescribed fossil skeleton of *Yabeinosaurus* from Dawangzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning, red arrow denoting a possible condition of autotomy in the tail. (Photo: IVPP)

SQUAMATES

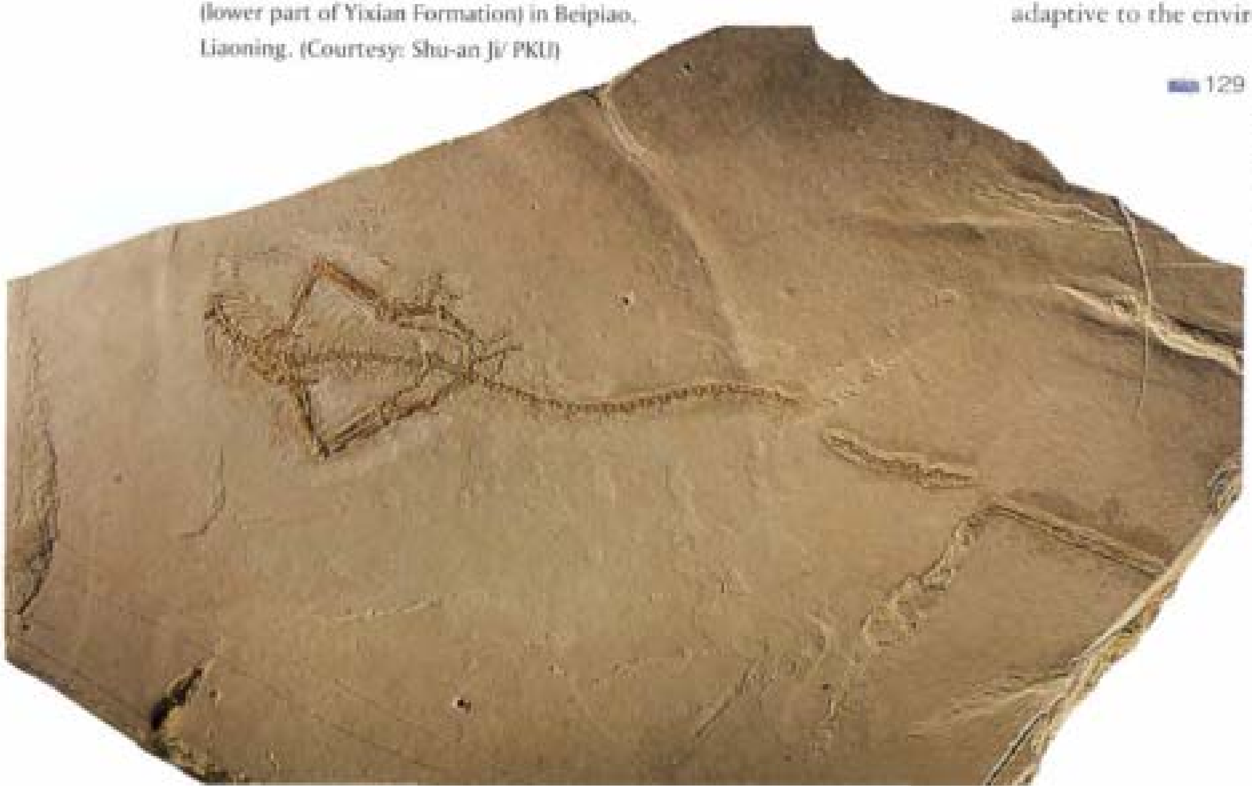
Jun Liu

The Squamata (lizards and snakes) is the most successful group of modern reptiles. Squamates usually are slender animals with scutella covering their bodies. This group can be identified by skull characteristics: a high degree of skull mobility and an incomplete lower temporal bar. The Order Squamata is divided into six infraorders: Iguania, Gekkota, Amphisbaenia, Scincomorpha, Anguimorph and Serpentes. Serpentes are snakes, and the other five groups are generally called lizards.

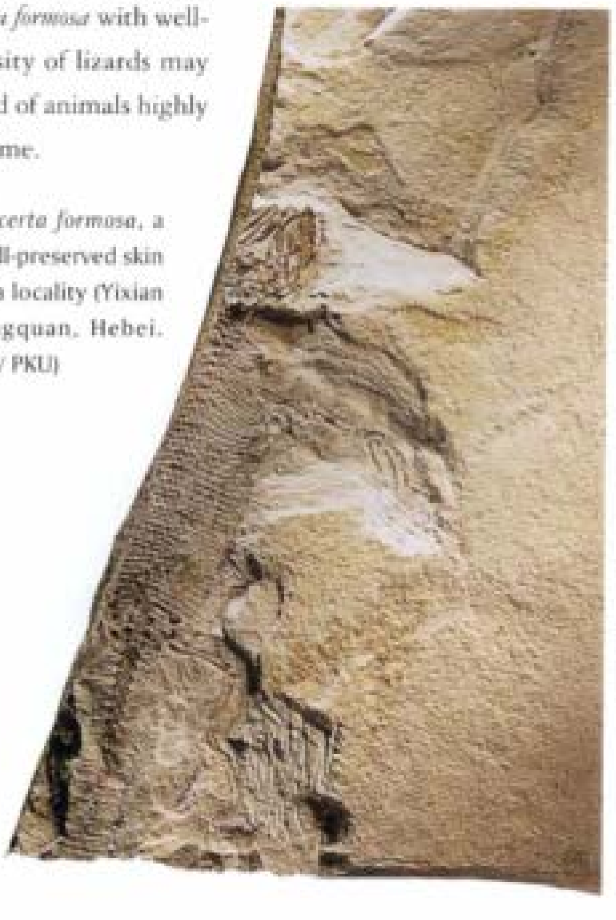
The undoubted oldest-known lizards were found in the Middle Jurassic. They are represented by several genera of about three infraorders. Thus, lizards must have originated earlier than this time, and the earliest lizard should have appeared on earth at least from the Triassic, in view of the date of the origin of the sphenodontians. *Santaisaurus*, found near the Permian-Triassic boundary in Xinjiang, northwestern China, was referred to lizards by some paleontologists. Squamates increased rapidly from the Middle Jurassic, then they had another evolutionary radiation in the Early Cretaceous along with the emergence of the first snake.

Yabeinosaurus tenuis is one of the earliest found tetrapods in the Jehol Biota and the earliest studied fossil lizard in China. This species was named in 1942 based on the material from Zaocishan, Yixian County of Liaoning Province by R. Endo and T. Shikama, who erected a new family for this genus, but it was later classified into the family Ardeosauridae by R. Hoffstetter in 1964. Another specimen from Lingyuan, Liaoning Province was referred to this species by C.-c. Young in 1958 (Fig. 126). The specimen of Lingyuan was regarded as from the Late Jurassic originally, but it more probably is from Jiulongshan Formation of the Middle Jurassic, and perhaps represents a different species. The holotype of *Yabeinosaurus tenuis* was lost in World War II. Shu-an Ji and his collaborators recently proposed a new specimen from Jingangshan, Yixian County as the neotype of this species, and some newly discovered materials may also be referred to the genus (Fig. 127).

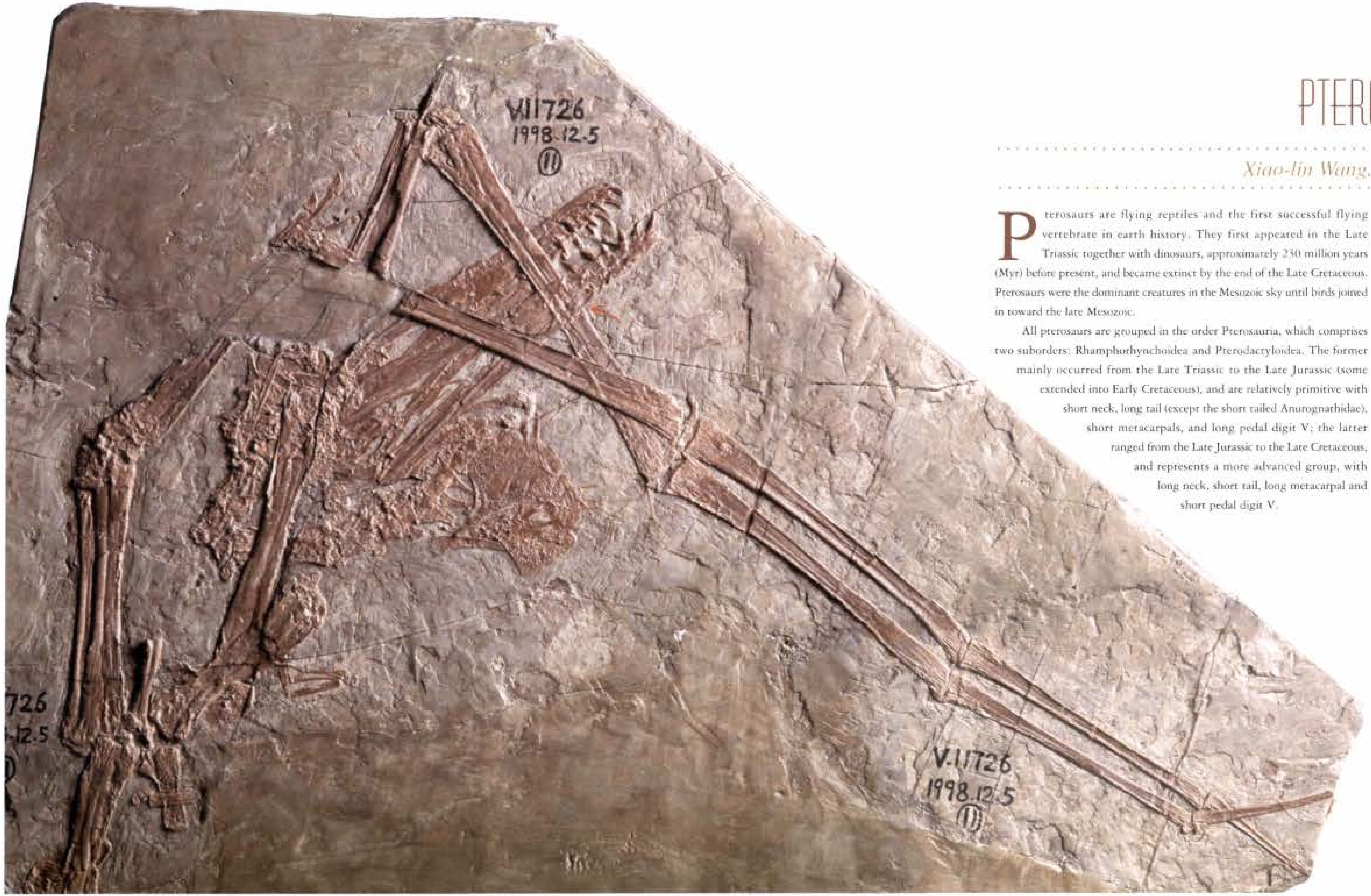
Two other lizard species were also added to the Jehol Biota by Shu-an Ji and others in recent years: *Dalinghosaurus longidigitus* with a long tail (Fig. 128), and *Jeholacerta formosa* with well-preserved scales (Fig. 129). The diversity of lizards may indicate that the Squamata was one kind of animals highly adaptive to the environments of that time.



128 Holotype of *Dalinghosaurus longidigitus*, a long-tailed lizard, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Courtesy: Shu-an Ji/ PKU)



129 Holotype of *Jeholacerta formosa*, a Jehol lizard with well-preserved skin impressions, from a locality (Yixian Formation) in Pingquan, Hebei. (Courtesy: Shu-an Ji/ PKU)



PTEROSAURS

Xiao-lin Wang, Zhong-he Zhou

Pterosaurs are flying reptiles and the first successful flying vertebrate in earth history. They first appeared in the Late Triassic together with dinosaurs, approximately 230 million years (Myr) before present, and became extinct by the end of the Late Cretaceous. Pterosaurs were the dominant creatures in the Mesozoic sky until birds joined in toward the late Mesozoic.

All pterosaurs are grouped in the order Pterosauria, which comprises two suborders: Rhamphorhynchoidea and Pterodactyloidea. The former mainly occurred from the Late Triassic to the Late Jurassic (some extended into Early Cretaceous), and are relatively primitive with short neck, long tail (except the short tailed Anurognathidae), short metacarpals, and long pedal digit V; the latter ranged from the Late Jurassic to the Late Cretaceous, and represents a more advanced group, with long neck, short tail, long metacarpal and short pedal digit V.

Many pterosaurs have been discovered from the Mesozoic deposits and most of them were preserved in the marine deposits. The Solnhofen is among the most notable pterosaur localities in the world, and the Solnhofen limestone has produced the fossils of both Rhamphorhynchoidea and Pterodactyloidea. These pterosaurs lived in the Late Jurassic of approximately 145 ~ 150 Myr ago (Tithonian). The Santana Formation in the northeastern Brazil has produced only pterodactyloid pterosaurs, which lived in the Early Cretaceous (Aptian-Albian, about 100 ~ 110 Myr before present). The Late Cretaceous Niobrara Formation (Santonian, around 85 Myr ago) in western Kansas, USA is famous for producing thousands of large-sized pterodactyloids. Recently, several dozens of pterosaurs have been discovered from the lacustrine deposits of the Lower Cretaceous Jehol Group in western Liaoning Province.

Many pterodactyloid pterosaurs have been reported from the Lower Cretaceous terrestrial deposits in other parts of northern China comparable to the Jehol Group. Among them are *Dsungaripterus weii* and *Noripterus complicidens* from the Tugulu Group of the Dsungar (Junggar) Basin of Xinjiang, and *Huanhepterus quingyangensis* from the Zhidan Group of the Ordos Basin, Gansu Province.

Lots of pterosaur skeletons have been discovered from both the Yixian and Jiufotang Formations of the Jehol Group. These fossils comprise mostly pterodactyloids and a few rhamphorhynchoids. Among the known pterodactyloids are *Eosipterus yangi* and *Haopterus gracilis* from the Jianshangou Bed of the Yixian Formation at the Hengdaozi locality and Sihetun locality of Beipiao, Liaoning respectively, and *Sinopterus dongi*, *Chaoyangopterus zhangi* and *Liaoningopterus gui* from the Jiufotang Formation at the Dongdadao and Dapingfang localities in Chaoyang, Liaoning. Rhamphorhynchoids comprise

130 Holotype of *Haopterus gracilis* (subadult, wingspan about 1.35 m), a pterodactylid pterosaur, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. The wing digit appears to be in the mouth (denoted by a red arrow), possibly reflecting the struggle of the animal shortly before being killed by the poisonous gases from volcanic eruption. (Photo: IVPP)

Dendrorhynchoides curvidentatus from the Zhangjiagou locality in Beipiao, Liaoning and *Jeholopterus ningchengensis* from the Daohugou locality in Ningcheng, Inner Mongolia.

Shu-an Ji and his colleague (1997, 1998) first reported two pterosaurs from the Yixian Formation: *Eosipterus yangi* and *Dendrorhynchoides curvidentatus*. *Eosipterus* is represented only by fragmentary postcranial materials, and *Dendrorhynchoides*, an incomplete skeleton. The former is a small to medium sized pterodactyloid with a wingspan about 1.2 m long, referable to the Pterodactylidae. It has a relatively robust forelimb, with the ulna and radius approximately 1.3 times as long as wing metacarpal. The femur is slightly smaller than 2/3 of the length of the tibia. The ulna, the first wing digital phalanx and the tibia are approximately of equal length. *Dendrorhynchoides* is represented by a small juvenile individual, with a wingspan of about 40 cm. This pterosaur was initially referred to the Rhamphorhynchoidae, and is now generally agreed to be a member of the Anurognathidae ("frog-jawed" pterosaurs). Its characteristics include robust cervical vertebrae, short metacarpals only about 1/4 of the length of the radius, tibia shorter than humerus, metatarsals I~IV of approximately equal length, and pedal digit V comprising two long phalanges.

Since 1998, the field crews of the IVPP, CAS have excavated abundant pterosaurs specimens. We have described five specimens (including four nearly complete skeletons and one skull), each representing a new genus and species: *Haopterus gracilis*, *Jeholopterus ningchengensis*, *Sinopterus chaoyangensis*, *Chaoyangopterus zhangi*, and *Liaoningopterus gui*.

Haopterus (Fig. 130) was named in 2001 after the late Prof. Yi-chun Hao in memory of her contribution to the study of the Jehol Biota. It is a nearly complete skeleton, and probably represents a subadult with a wingspan of about 1.35 m. The skull is long and low, lacking any sagittal crest, and the rostrum is relatively pointed. The upper and lower jaws are each equipped with 12 posteriorly curved and sharp teeth, mainly distributed in the anterior part of the jaws. The forelimb is extremely robust with a long wing metacarpal. The metatarsals are slender and very small. Metatarsals I~III are less than 1/5 of the length of the wing metacarpal. The sternum is large and fan-shaped with well-developed keel, and its length and width are about the same.

Haopterus has a large skull and a pointed rostrum. The front teeth are sharp and slender, suggesting a piscivorous feeding habit. Its extremely reduced foot suggests that it probably has strong flight capability and the body was suspended by the hind limb in resting position.

Jeholopterus (Figs. 131 ~ 133) was named in 2002, and represents a nearly completely articulated pterosaur with excellently preserved fibers in the wing membrane and "hairs" in the body. The new species can be further referred to the "strange" short-tailed rhamphorhynchoid family Anurognathidae. It is the most complete and largest known individual of the family, with a wingspan of about 90 cm. Its characteristics include: a skull wider than long, resembling that of a frog; a short neck; metacarpal short and less than 1/4 of the length of the radius; extremely long pedal digit V (about 1.5 times the length of the third pedal digit) comprising two long phalanges; and a short tail.

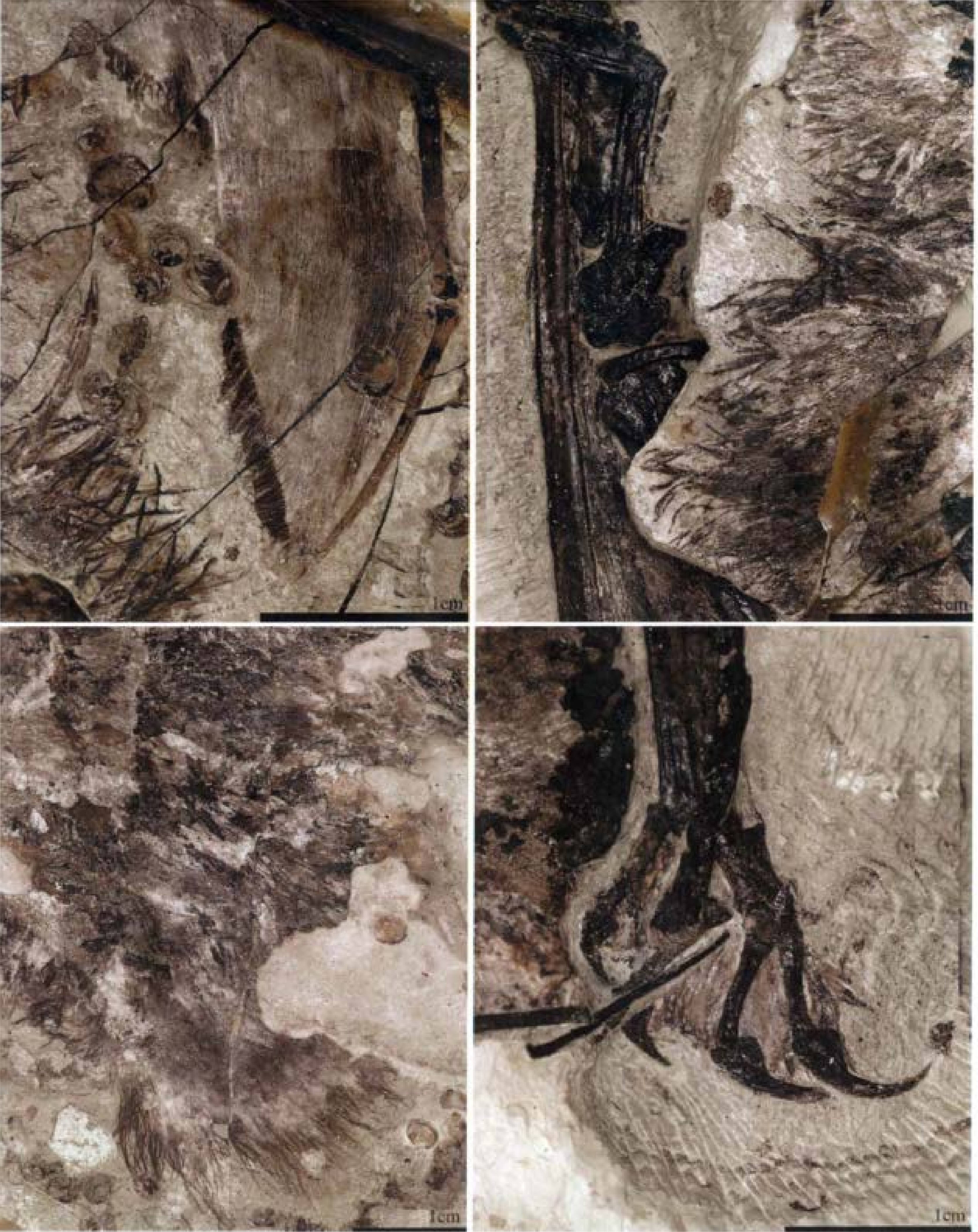
The wing membrane and "hair"-like structures represent one of the most distinctive features of the new pterosaur. The propatagium, cheiropatagium and the uropatagium of the wing membrane can be well recognized. The cheiropatagium clearly attaches to both sides of the legs as far as the ankle. The uropatagium is between the two legs and composed of fibers that are shorter than those of the cheiropatagium. Short fibers were also preserved associated with the pedal digits, including the fifth digit, indicating that the foot was webbed and that the medially curved robust fifth digit provided both attachment and control for the uropatagium.

The purported webbed foot in *Jeholopterus* may indicate that this pterosaur probably lived near the water, and could even swim. This pterosaur may eat insects or other animals such as fishes. Its extremely long wings suggest strong flying capability.

It is a controversial issue as to whether pterosaurs are warm-blooded and "haired" vertebrates. In *Jeholopterus*, "hairs" are short, thick and curved; they also taper from the base to the tip; and they are associated with the whole body from the neck to the tail region (Figs. 131 ~ 133). Functionally, the "hairs" of pterosaurs could be used for thermoregulation, flight or reducing noises during flight. The "hairs" in *Jeholopterus* may also indicate that some pterosaurs might be warm-blooded. The "hairs" of *Jeholopterus* bear some resemblance to the hairlike integumental structures of the feathered dinosaur *Sinosauropteryx* and *Beipiaosaurus*, which might suggest that the "hairs" of pterosaurs and the fiber-like protofeathers in *Sinosauropteryx* are homologous structures.

Sinopterus (Figs. 134, 135) is a recently described pterodactyloid from

131 Holotype of *Jeholopterus ningchengensis* (Slab A, adult or subadult with wingspan about 90 cm), a short tailed pterosaur belonging to the Anurognathidae ("frog-jawed" pterosaurs), from Daohugou locality (lowest part of Yixian Formation) in Ningcheng, Inner Mongolia. (Photo: IVPP)



132 Wing membrane and the "hairs" on *Jeholopterus ningchengensis*, representing the most complete wing membrane and "hairs" found to date in pterosaurs. The wing membrane is relatively long and straight fibers. "hairs" are generally short, wavy and curved and present all over the body. The "hairs" of this pterosaur resembles the hairlike integuments of the dinosaur *Sinosauropteryx*, suggesting a possible homology of these structures. (Photo: IVPP)

133 Reconstruction of *Jeholopterus ningchengensis*. (Artwork by: Rong-shan Li/ IVPP)

the Jehol Biota. It is referred to the family Tapejaridae, representing its first record outside Brazil. It also represents the earliest occurrence as well as the most complete skeleton of the family.

Sinopterus has a wingspan of about 1.2 m, with the skull length about 170 mm. It is characterized by an edentulous low and long skull, with long and pointed rostrum and a horny beak. The sagittal crest of the premaxilla and dentary are low and small. The posterior process of the premaxilla is curved upward, separate from the skull, and parallel to the sagittal crest of the parietal. The nasopreorbital fenestra is large and long (length about 2.5 times of the height), exceeding 1/3 of the total length of the skull. The tibia is about 1.4 times of the length of the femur. Metatarsal III is about 22.1% of the length of the wing metacarpal, and metatarsal V is less than the 1/5 of the length of metatarsal I.

Chaoyangopterus (Fig. 136) is a medium to large-sized pterodactyloid with a wingspan about 1.85 m long. The skull is long and low, with a pointed rostrum; it is edentulous. Its manual digits I~III are robust, and wing claws large and curved. The wing digit comprises four phalanges, progressively shorter toward the distal end. Wing metacarpal and first phalanx of the wing digit are relatively short compared to *Nyctosaurus gracilis* from the Upper Cretaceous of western Kansas. Ratios of tibia to femur and tibia to humerus are 1.5 and 2.2, respectively, and the ratio of forelimb (humerus + ulna + wing metacarpal) to hind limb (femur + tibia + metacarpal III) is 1.1. *Chaoyangopterus* not only represents the first such record in Asia but also the earliest record and most complete skeleton of the family Nyctosauridae. Some revisions of the family are made, such as having four wing digits and well-developed manual digits I—III.

Liaoningopterus (Fig. 137) is referred to the family Anhangureidae. It is the largest pterosaur ever discovered in China; its teeth also represent the largest known from any pterosaurs. *Liaoningopterus* is a large-sized pterodactyloid, with an estimated skull length of 610 mm and wingspan about 5 m. The skull is low and long. Premaxilla and dentary are equipped with sagittal crest. The teeth are only restricted to the proximal part of the upper and lower jaws. Toothed portion of the jaws, about half the length of the skull, does not extend posteriorly to 1/3 of the nasopreorbital. Teeth near the rostral end of the jaws are huge. The fourth tooth of the premaxilla is the largest; the first and third are much smaller than the second and the fourth ones.

Members of the Pterodactylidae were previously known only in European and African Late Jurassic deposits. The discovery of the *Haopterus* represents the first record of the family in Asia; it also extends the distribution of the family to the Early Cretaceous. Members of the Anurognathidae were rarely known in the past; they are mainly known from the Solnhofen in Germany and Karatau in Kazakhstan. The discovery of members of this family in Liaoning represents the first record of the family in the Early Cretaceous. *Sinopterus* represents the first fossil record of the family Tapejaridae outside Brazil.

Two pterosaur assemblages appear to have existed in the Jehol Group, represented by the Yixian Formation and Jiufotang Formation. Among the several dozens of pterosaur specimens known from these assemblages, most are pterodactyloids, and only a few of them are rhamphorhynchoids. The assemblage from the Yixian Formation, the lower assemblage, comprises *Eosipterus* and *Haopterus* belonging to Pterodactyloidea, and *Dendrorhynchoides* and *Jeholopterus* belonging to the rhamphorhynchoid Anurognathidae. This assemblage shows some resemblance to that of the Late Jurassic in Solnhofen (Tithonian) by the sharing of members of the Pterodactylidae and Anurognathidae. The assemblage is associated with the *Confuciusornis* avian fauna. Associated dinosaurs are also abundant, including feathered theropods *Sinosauropteryx*, *Beipiaosaurus*, *Sinornithosaurus*, *Protarchaeopteryx* and *Caudipteryx*, the iguanodontid *Jinzhousaurus*, and the ankylosaurid *Liaoningosaurus*, etc. They are mainly from the Jianshangou Bed, Dawangzhangzi Bed and Jingangshan Bed of the Yixian Formation, with isotope dates ranging between 121—125 Ma.

The Daohugou bed of the lowest Yixian Formation (note: it is still debatable as to whether this bed should be referred to the Yixian Formation) produced *Jeholopterus*. Although currently there is no precise age for the fossil bed, we estimate that it cannot be older than 139 Ma, a recent ^{40}Ar/^{39}Ar age of the upper part of the Tuchengzi Formation, which is underlying the Daohugou bed. Our conclusion on the stratigraphic relationship between the Daohugou bed and the Tuchengzi Formation is based on the field observation of their contact at the Daohugou locality.

The upper pterosaur assemblage comprises pterosaurs from the Jiufotang Formation. All pterosaurs collected so far from this formation are pterodactyloids. Among them *Sinopterus*, *Chaoyangopterus* and *Liaoningopterus* have been described. No rhamphorhynchoid has been discovered among over

134 Holotype of *Sinopterus dongi* (subadult, wingspan about 1.2 m), a tapejarid pterosaur, from Lamagou locality (Jiufotang Formation), Chaoyang, Liaoning. (Photo: IVPP)

135 Close-up view of the skull of *Sinopterus dongi* (about 17 cm long). (Photo: IVPP)

a dozen specimens known from the Jiufotang Formation. The upper assemblage shows more resemblance to that of the Early Cretaceous Santana Formation (Aptian/Albian) in comprising only pterodactyloids such as the Tapejaridae and the Anhangueridae. The age of the Jiufotang Formation is slightly older than the Santana Formation. This pterosaur assemblage is associated with the *Cathayornis* avian fauna that includes birds such as *Sinornis*, *Yanornis*, *Sapeornis* and *Jeholornis*. Associated dinosaurs include the feathered dromaeosaurids *Microraptor zhaoianus* and *M. gui*. Although no radiometric date has been obtained directly from the beds in which the pterosaurs were collected, the basalt overlying the Jiufotang Formation was dated as 110 Ma in Inner Mongolia, and therefore, the temporal distribution of this formation is estimated as 110—120 Ma.

136 Holotype of *Chaoyangopterus zhangi* (wingspan about 1.85 m), a nyctosaurid pterosaur, from Gonggao locality (Jiufotang Formation), in Chaoyang, Liaoning. (Photo: IVPP)

137 Holotype of *Liaoningopterus gui* (estimated wingspan about 5 m, skull length 61 cm), a large pterodactyloid with the largest tooth known from any pterosaurs, from Xiaoyugou locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

139 Close-up view of the integuments of *Sinosauropteryx prima*. The filamentous integuments represent primitive feathers and this discovery gives us a glimpse at the origin and early evolution of feathers. (Photo: Da-jian Li/ CAS)

138 Holotype of *Sinosauropteryx prima*, a rooster-sized theropod dinosaur, from Sihetun locality (lower part of Yixian Formation), Beipiao, Liaoning. (Photo: Da-jian Li/ CAS)

DINOSAURS

Xing Xu

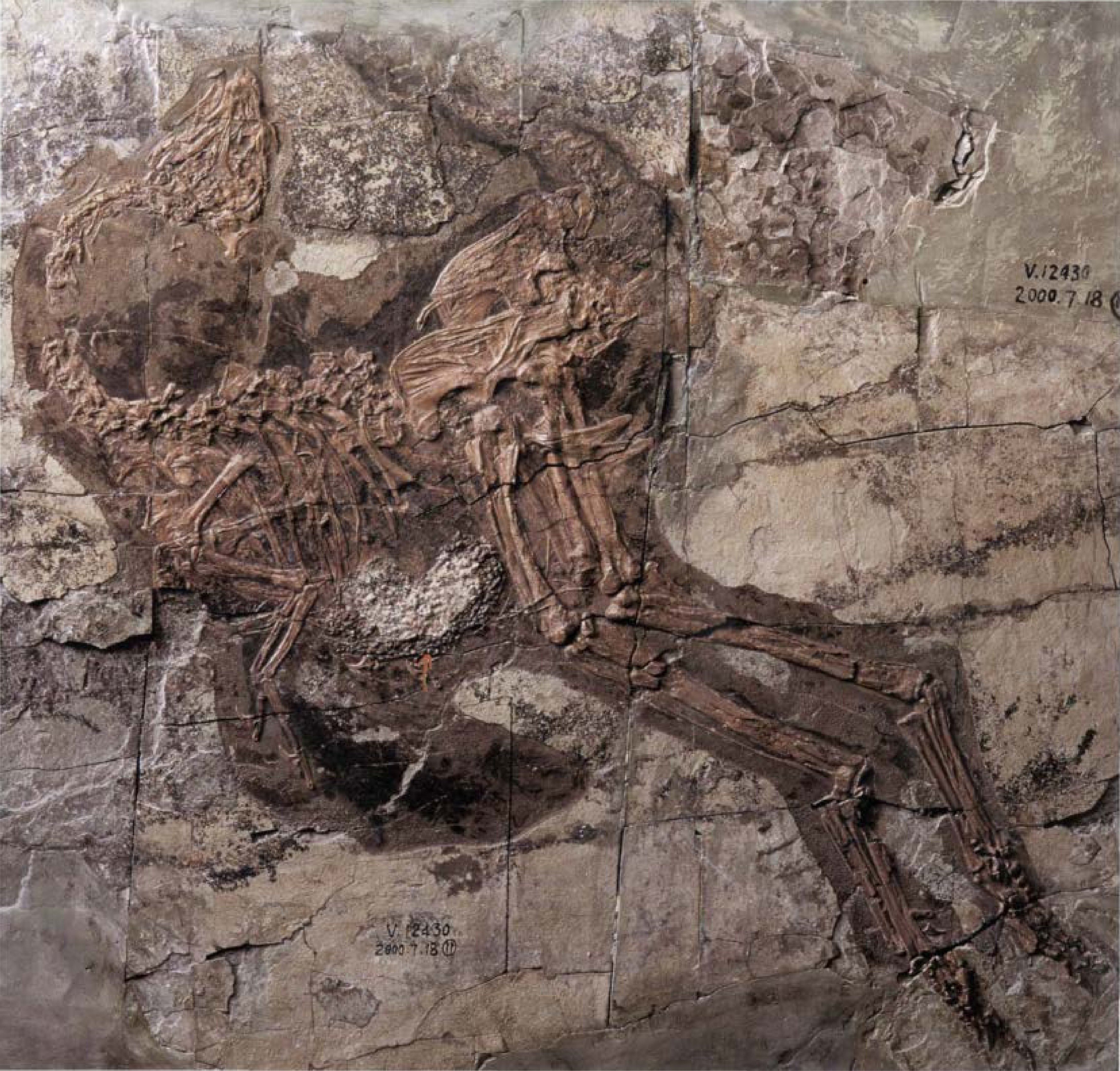
Dinosaurs are among the best known prehistorical animals. They were the world's conquerors during the Mesozoic, representing one of the most successful vertebrate groups. That is why the Mesozoic Era is also called the "Age of Dinosaurs". China is extraordinarily rich in dinosaur fossils, the record of which spans almost the entire age of dinosaurs. Recently, the dinosaur remains from the Lower Cretaceous Jehol Group have aroused worldwide attention. The feathered dinosaurs, in particular, have challenged the conventional idea on both dinosaurs' appearance and their life history.

Most major dinosaur groups are represented in the Jehol Group, including sauropods, theropods, ornithopods, ceratopsians and ankylosaurs. The following paragraphs briefly describe some important dinosaur taxa from the Jehol Biota with comments on their evolutionary implications.

Coelurosaurs are a group of derived theropod dinosaurs, including the giant tyrannosaurids, the long-clawed therizinosauroids, the deep-skulled oviraptorosaurs, and the volant birds and their close relatives — the agile dromaeosaurs and the large-brained troodontids. In the Jehol Biota the non-avian coelurosaurians are represented by 12 species in 10 genera.

Sinosauropteryx prima (Figs. 138 — 140), the first named coelurosaurian from the Jehol Biota, was found in western Liaoning in 1996. It is about the

140 Reconstruction of *Sinosauropteryx prima*. Although a few artists restored some non-avian dinosaurs with feathers or featherlike integuments as early as 1970s, the discovery of *Sinosauropteryx prima* provides the first fossil evidence for such a restoration. (Art: Xiao-lian Zeng/ KIB)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141 A complete skeleton of *Caudipteryx zoui*, an emu-sized theropod dinosaur, from Zhangjiagou locality (lower part of Yixian Formation), Beipiao, Liaoning, red arrow denoting the gizzard stones. (Photo: IVPP)

142 Reconstruction of *Caudipteryx zoui*. Similar to its oviraptorid relatives, *Caudipteryx* is a cursorial animal, with feathers but could not fly. (Art: Anderson Yang)

size of a rooster, with a large skull and sharp teeth, very short arms and an unusually long tail. Although it is a primitive coelurosaurian, osteologically quite different from birds compared to advanced non-avian coelurosaurians, *Sinosauropteryx* occupies an important position in understanding the origin of birds because of the presence of a hairlike covering on its body. Many paleontologists regarded the hairlike structures as primitive feathers used for insulation, but others disagreed and believed they are unrelated to feathers.

The following year, two other feathered dinosaurs were found from the same area. One was named as *Protarchaeopteryx robusta* and the other *Caudipteryx zoui* (Figs. 141, 142). These two dinosaurs are comparatively more similar to birds in terms of bony structure than is *Sinosauropteryx prima*; yet both were unable to fly. *Protarchaeopteryx* has sharp teeth and long arms, and is similar to, but does not belong to, the dromaeosaurids. Dromaeosaurids are one of the most birdlike dinosaur groups that also include the small-sized *Velociraptor*, figured in the movie "Jurassic Park". *Caudipteryx* has short arms like *Compsognathus* but other features suggest it is an oviraptorosaurian dinosaur. It has a tall and short skull atypical of that in theropod dinosaurs, long legs, and short tail. The gizzard stones (Fig. 141) indicate that *Caudipteryx zoui* is likely a herbivore. Both *Protarchaeopteryx* and *Caudipteryx* have unquestionable true feathers that are composed of a prominent shaft and flat vanes. Unlike flight feathers of birds, the long feathers on the arms and tails of *Protarchaeopteryx* and *Caudipteryx* have symmetrical vanes, suggesting that

143 Holotype of *Beipiaosaurus inexpectus*, the largest feathered dinosaur found from the Jehol Biota to date with estimated total length more than 2 m, from Sihetun locality (lower part of Yixian Formation), Beipiao, Liaoning. Different from the typical theropods, *Beipiaosaurus* has numerous tiny teeth, and broad feet suggestive of a slow lifestyle. (Photo: IVPP)

144 Close-up view of integuments of *Beipiaosaurus inexpectus*. These filamentous structures probably represent the primitive feathers and may have wider distribution among non-avian theropods. (Photo: IVPP)

they are not suitable for flight.

This was the first time in history that feathers had been discovered on non-avian animals — living or extinct, but it was not the last time, fortunately. In 1999, two other feathered dinosaurs were again reported from western Liaoning. *Beipiaosaurus inexpectus* (Figs. 143, 144) is the biggest theropod yet discovered from Liaoning. It is more than 2 meters long, with tiny teeth, a bulky body, and a short tail. Although some features of *Beipiaosaurus* suggest it perhaps a plant eater, *Beipiaosaurus* has unusually long, curved, sharp claws on its hands as in meat-eating dinosaurs. *Sinornithosaurus millenii* (Figs. 145 – 149), the second species, is a close relative of *Velociraptor* but much smaller. It has dagger-like teeth, long arms that could flap, and a rodlike, stiff tail. Actually *Sinornithosaurus* represents one of the most birdlike dinosaurs, and is more closely related to birds than the other species mentioned above. Although no vaned feathers were found on either *Beipiaosaurus* or *Sinornithosaurus* specimens, the featherlike structures on the two dinosaurs are apparently more complex than those of *Sinosauropteryx* in having a branched structure.

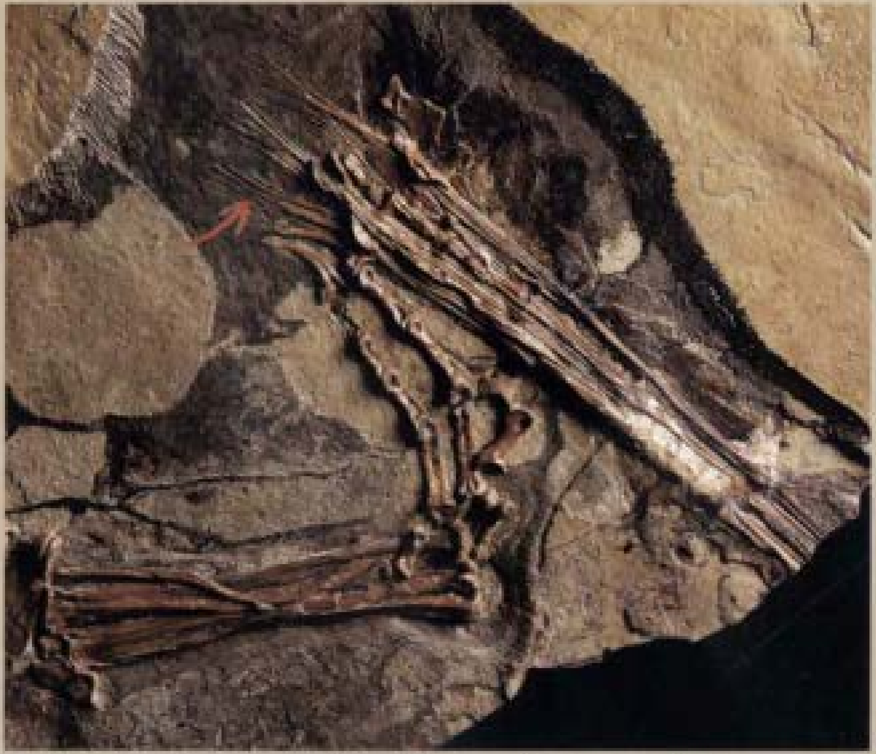
In 2000, the sixth and seventh feathered dinosaur species were reported from western Liaoning. One is a new species of an established genus — *Caudipteryx dongi* (Figs. 150, 151), which helps clarify some morphological features of the genus. The other one is a tiny dinosaur, less than 40 cm long. This dinosaur, named as *Microraptor zhaoianus* (Figs. 152 – 154), represents the smallest adult dinosaur found to date. Like *Sinornithosaurus*, it is also a dromaeosaurid. *Microraptor* is the most birdlike among all known dinosaurs. It is small and has an expanded braincase like birds, long arms that could flap, and feet that show adaptations to dwelling in trees. This finding suggests that some small-sized non-avian dinosaurs moved into the trees in order to escape larger hunters or chase small prey, and gradually evolved flight capability living in the trees. A halo of featherlike structures surrounds the fossil skeleton of *Microraptor zhaoianus*, some of which bear the central shaft. Although the preservation does not allow us to draw a conclusion that *Microraptor zhaoianus* had vaned feathers, it is most likely that it did.

In 2002, three new coelurosaurian theropods have been reported from western Liaoning and adjacent Inner Mongolia. Two of them, namely *Sinovenator changii* (Figs. 155, 156) and *Incisivosaurus gauthieri* (Figs. 157, 158) were from the same fossil bed, the Lujiatun Bed of the lowest Yixian Formation (refer to Chapter 1 for stratigraphic information). Although no feathers were found on these specimens, maybe due to the nature of the deposits — coarse sandstone, they most probably had feathers on their body during life. *Sinovenator* is a troodontid, one of the most birdlike dinosaur groups and very similar in some features to the dromaeosaurids. Again, *Sinovenator* is a small animal less than one meter long. Its braincase is very similar to early birds, indicating a relatively high level of intelligence. Despite being a theropod dinosaur usually regarded as carnivores, *Incisivosaurus* is unusual in having teeth similar to those of the plant-eaters.

The third theropod reported in 2002 was a small arboreal dinosaur, *Epidendrosaurus ningchengensis* (Figs. 159, 160), and its holotype was collected from southeastern Inner Mongolia. It has an extremely long third manual digit, indicating a type of adaptation previously unreported from the Mesozoic. *Epidendrosaurus* has some features previously unknown in non-avian dinosaurs, including a fully reversed hallux. Its precise phylogenetic position is not yet clear though *Epidendrosaurus* is tentatively regarded as the closest relative of

145 Holotype of *Sinornithosaurus millenii*, a small theropod dinosaur (estimated length 1.1 m), from Sihetun locality (lower part of Yixian Formation), Beipiao, Liaoning. It has feathered forelimbs that can move the way birds' wings do, indicating that non-avian theropods were pre-adapted for evolving flying capacity. (Photo: IVPP)

146 Skull of *Sinornithosaurus millenii*, showing the sharp and serrated teeth of a seemingly ferocious animal. (Photo: IVPP)



147 The rodlike tail bones of *Sinornithosaurus millenii*, unique to the dromaeosaurids, indicating a stiff tail. (Photo: IVPP)

148 Wishbone of *Sinornithosaurus millenii*, a structure previously thought to be present only in birds, but recently found to be widespread among dinosaurs. It is morphologically identical to that of *Archaeopteryx*, the most primitive bird. (Photo: IVPP)

149 Close-up view of the integuments of *Sinornithosaurus millenii*, showing the branched filamentous integuments, a unique feature in feathers. (Photo: IVPP)

150 Holotype of *Caudipteryx dongi*, similar in size to *C. zoui*, from Zhangjiagou locality (lower part of Yixian Formation), Beipiao, Liaoning. (Photo: IVPP)

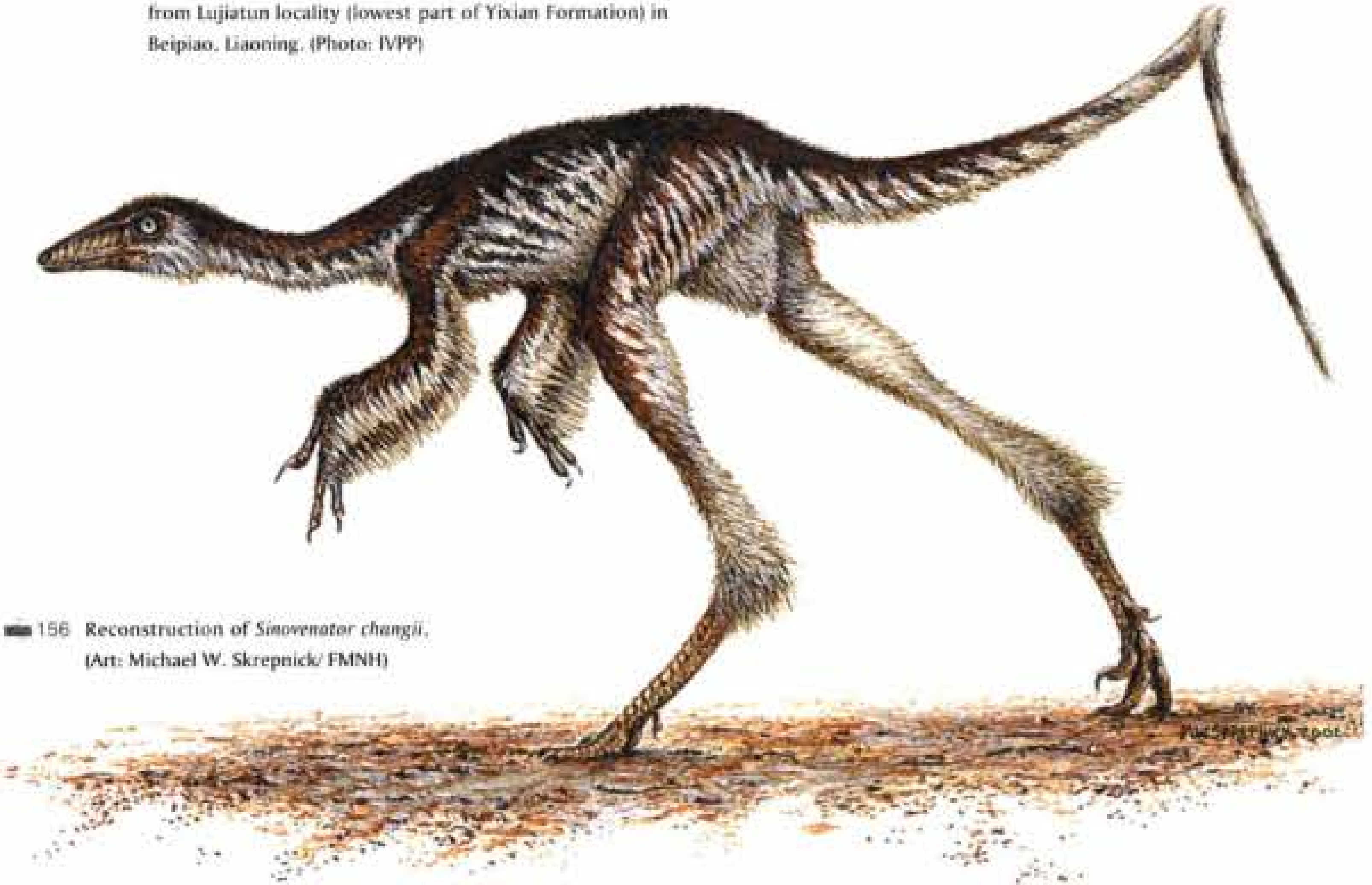
151 The remiges preserved on the *Caudipteryx dongi* specimen. Different from the flight feathers in volant birds, the remiges on the forelimbs of *Caudipteryx dongi* have symmetrical vanes, indicating a lack of aerodynamic function. (Photo: IVPP)

152 Holotype of *Microraptor zhaoianus*, the smallest known adult non-avian dinosaur (estimated total length less than 40 cm), from Langshan locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

153 The pes of *Microraptor zhaoianus*, some of its pedal features suggestive of an arboreal habit, indicating that the theropod ancestors of birds might have passed through an arboreal phase. (Photo: IVPP)

154 Reconstruction of *Microraptor zhaoianus*. (Art: Rong-shan Li/ IVPP)

155 Partial skull of the holotype of *Sinovenator changii*, a small theropod dinosaur with estimated body length less than 1 m, from Lujiatun locality (lowest part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)



156 Reconstruction of *Sinovenator changii*. (Art: Michael W. Skrepnick/ FMNH)

157 Holotype of *Incisivosaurus gauthieri* (skull length about 11 cm), a small oviraptorosaur with peculiar tooth morphology, from Lujiatun locality (lowest part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)

158 Reconstruction of *Incisivosaurus gauthieri*. (Art: Portia Sloan).

the birds.

A new feathered dinosaur, *Microraptor gui* (Figs. 161, 162), was described early in 2003. It is the second species of *Microraptor*, and a small lightweight animal of 77 cm long, with a rodlike long tail. This dinosaur probably lived in the trees. Surprisingly it has long pennaceous feathers not only on its forelimbs and tail, but also on its hind limbs (the so-called "four-winged dinosaur"). Furthermore, the feathers were almost identical to those of living birds, with asymmetrical vanes, a feature associated with flight or gliding in extant birds. It is very likely that *Microraptor gui* is a gliding animal, representing an intermediate stage between the flightless dinosaurs and the volant birds.

Amazingly, as many as 12 coelurosaurian theropod species have been reported from a small area in western Liaoning and the adjacent Inner Mongolia in last a few years. More surprisingly, these discoveries have provided us with much-needed information on important issues such as the origin of feathers and bird flight that was unavailable from all other known dinosaur specimens collected worldwide over the last century and a half.

Before these discoveries from western Liaoning, there was little fossil evidence for studying the origin of feathers. Due to their structural complexity, feathers are very distinctive from all other integumentary structures, and their abrupt appearance in the fossil record has been perplexing. Now that the hypothesis of dinosaurian origin of bird has been well established, it theoretically follows that feathers should be present on some birdlike theropods. However, no intermediate structures that could be feather precursors were preserved in the related theropods. On the contrary, most evidence suggested that dinosaurs were scaled animals, including some theropod dinosaurs. For example, some psittacosaurid specimens from the same localities as the feathered theropod specimens preserved beautiful skin impressions, showing that these animals had scaly skin. The feathered dinosaurs from Liaoning are just what many paleontologists were anticipating, and thus provide direct fossil evidence for the hypothesis that feathers are not unique to birds and can be traced back into the dinosaurian ancestors of birds. The featherlike structures on these different dinosaurs are diverse in morphology, but display an evolutionary trend in complexity approaching the origin of birds. *Sinosauropteryx* has simple feathers; *Beipiaosaurus* and *Sinornithosaurus* have branched feathers but bear no vanes; *Protarchaeopteryx* and *Caudipteryx* have developed vaned feathers. The lack of vaned feathers on *Beipiaosaurus* and

159 Holotype of *Epidendrosaurus ningchengensis*, a small theropod with the size of a house sparrow, from Daohugou locality in Ningcheng, Inner Mongolia. (Photo: IVPP)

160 Reconstruction of *Epidendrosaurus ningchengensis*, showing its arboreal features. (Art: Rong-shan Li/ IVPP).

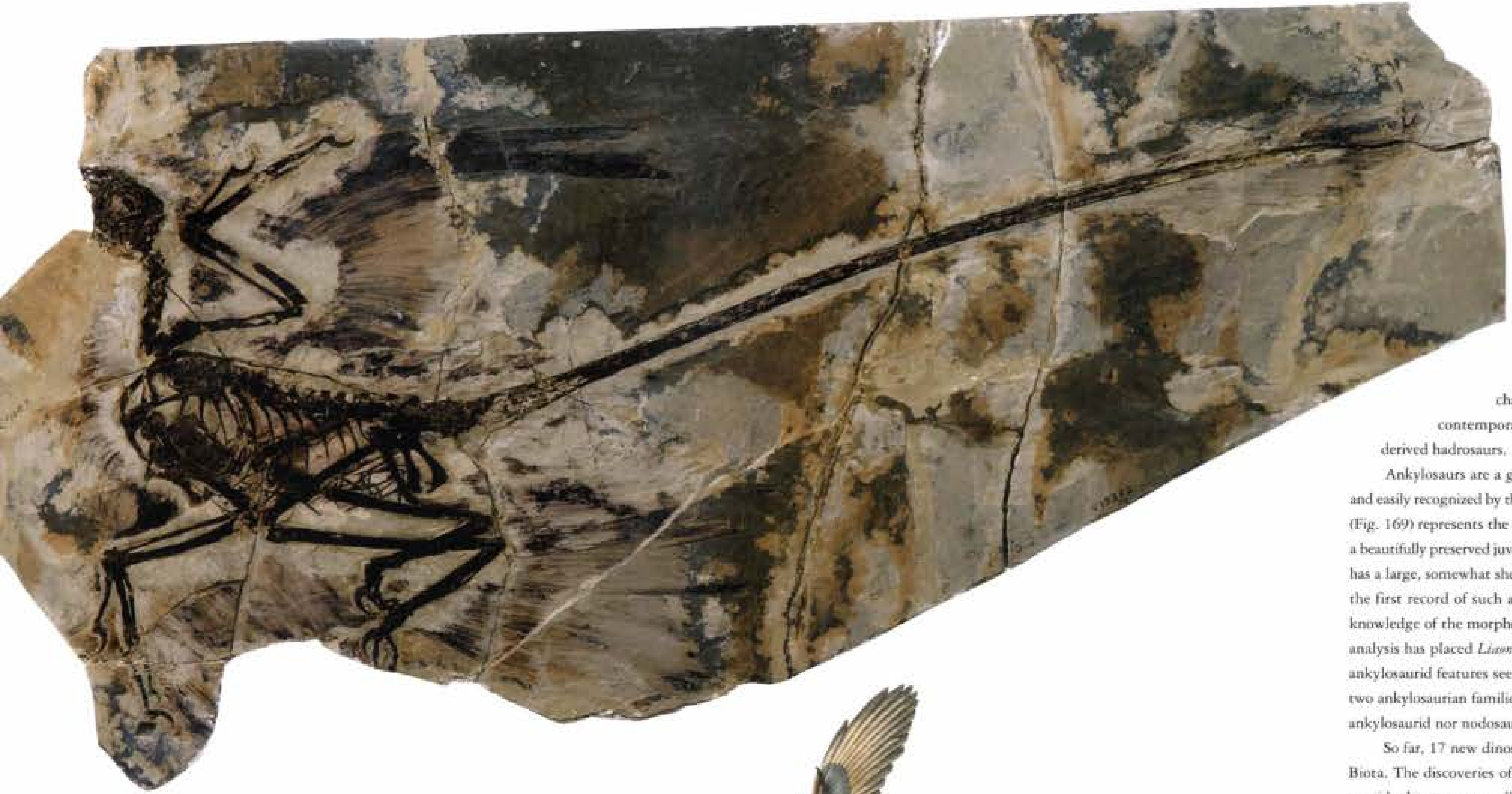
Sinornithosaurus are most likely due to preservations. In fact, the most recent discovery suggests that *Sinornithosaurus* and *Microraptor* have vaned feathers as *Protarchaeopteryx* and *Caudipteryx* do.

Here is the current picture of feather evolution: most dinosaurs, including all ornithischian ("bird-hipped" dinosaurs), all prosauropods and sauropods, and some primitive theropods, are similar to typical reptiles in that their bodies are covered with scales or tubercles; the first feather evolved in the early stages of coelurosaurian dinosaurs, and was a simple, hairlike structure, probably used to keep the animal warm; more complex feathers evolved later, and display a branching structure; long, vaned feathers evolved in some maniraptoran dinosaurs, probably including therizinosauroids, oviraptorosaurs, troodontids and dromaeosaurids, and these complex feathers were likely for display; finally, asymmetrical flight feathers evolved and are used to generate lift during flight. Therefore, feathers appeared before the origin of birds (Fig. 163) and early feathers functionally had nothing to do with flight. In the future, if we find a feathered fossil animal, we need to be careful when determining what kind of animal it is — it could be a bird, but it could also be a flightless dinosaur.

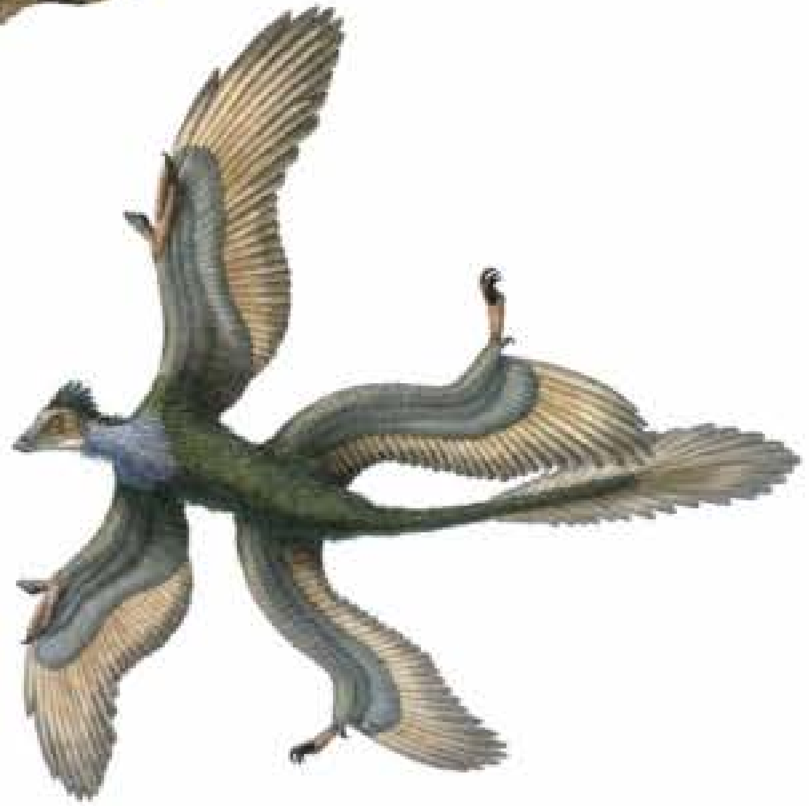
Compared to the highly publicized theropod dinosaurs from the Jehol Fauna, the ornithischian dinosaurs remain little known, despite the fact that the first dinosaurian discovery from the Jehol Fauna was an ornithischian. To date, three major ornithischian groups have been reported from the Jehol Biota, i.e., ankylosaurs, ornithopods, and ceratopsians.

The ceratopsians are a late group of herbivorous dinosaurs, mostly restricted to the Cretaceous period. They are characterized by some cranial modifications, including the unique rostral bone that is otherwise unknown in any other dinosaurs. In 1970s some ceratopsian dinosaur specimens were collected from the Jiufotang Formation of western Liaoning. Identified later as a new species of psittacosaurid dinosaur, *Psittacosaurus meileyingensis* has a relatively tall and rounded skull (Fig. 164). Psittacosaurids, known only from the Early Cretaceous of Asia, are a basal lineage of the ceratopsian dinosaurs. They are facultative biped, different from the more derived, quadrupedal neoceratopsians. The other ceratopsian from the Jehol Fauna is the goat-sized *Liaoceratops yanzigouensis* (Figs. 165, 166), a neoceratopsian, which belongs to the second major lineage of the ceratopsians. It has only rudimentary horns and a frill, different from the more derived neoceratops that usually weigh much heavier and have massive horns and a wide frill. *Liaoceratops yanzigouensis* is the smallest, oldest and most primitive neoceratopsian ever found.

The ornithopods represent the most diverse group of ornithischian dinosaurs, including the primitive small-bodied forms such as Heterodontosauridae, the intermediate representatives such as the famous *Iguanodon*, and the derived large-bodied forms such as duck-billed dinosaurs. The first ornithopod found from the Jehol Fauna is *Jeholosaurus shangyuanensis* (Fig. 167). It is a small dinosaur less than one meter long, and appears to be very primitive in a number of features despite being a Cretaceous ornithopod. *Jeholosaurus* is placed in the Ornithopoda, but displays a few features similar to those of ceratopsian dinosaurs. It is a potentially important taxon for understanding the early evolution of the ornithischian dinosaurs. *Jinzhousaurus yangi* (Fig. 168) represents the second



161 Holotype of *Microraptor gui* (total length 77 cm), a small dromaeosaurid and the so-called "four-winged dinosaur" characterized by feathers on all its limbs, from Dapingfang locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

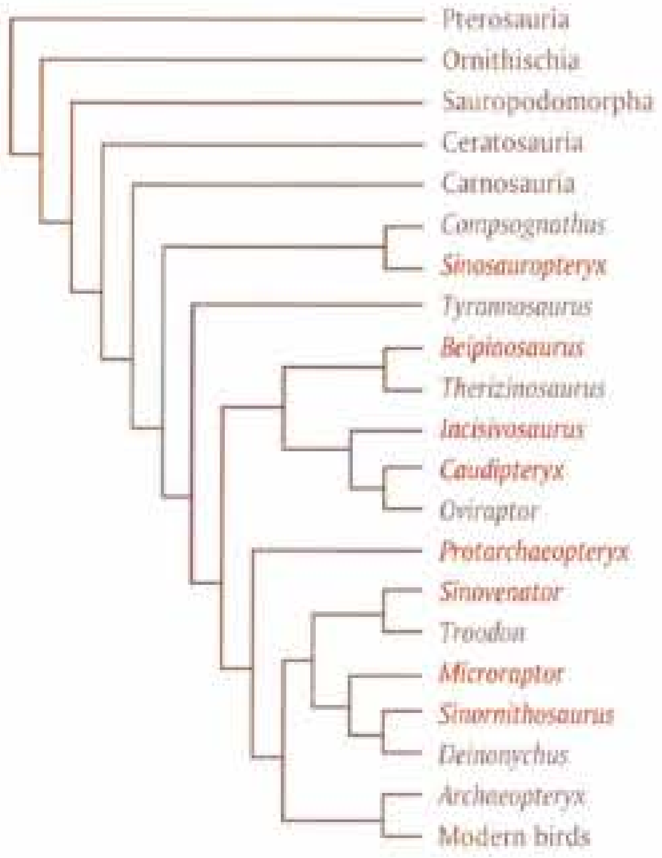


162 Reconstruction of *Microraptor gui*. (Art: Portia Sloan)

ornithopod species found from the Yixian Formation of western Liaoning. About seven to eight meters long, it represents the largest named dinosaur from the Jehol Group. *Jinzhousaurus* is similar to *Iguanodon*, one of the earliest named dinosaurs in the world, in many features, such as the spike-like pollex. Interestingly, it has a combination of primitive and derived characters, some features more primitive than the contemporary iguanodontids but others similar to those of derived hadrosaurs.

Ankylosaurs are a group of highly specialized ornithischian dinosaurs and easily recognized by their extensive body armor. *Liaoningosaurus paradoxus* (Fig. 169) represents the only known ankylosaur from the Jehol Biota. It is a beautifully preserved juvenile specimen less than 40 cm long. *Liaoningosaurus* has a large, somewhat shell-like bony plate under its belly. This discovery is the first record of such a structure among dinosaurs, thus adding to our knowledge of the morphological diversity of dinosaurs. Though a cladistic analysis has placed *Liaoningosaurus* in Nodosauridae, a number of distinct ankylosaurid features seem to bridge the morphological gaps between the two ankylosaurian families. It is also possible that *Liaoningosaurus* is neither ankylosaurid nor nodosaurid, but rather a basal ankylosaur.

So far, 17 new dinosaurian species have been reported from the Jehol Biota. The discoveries of feathered dinosaurs are significant because they provide the most compelling evidence supporting the hypothesis that birds were descended from dinosaurs, and also improve our understanding of the origin and early evolution of feathers and the origin of bird flight by indicating that feathers evolved before powered flight, and that flight probably evolved through a gliding stage. Other discoveries of non-feathered dinosaurs from western Liaoning are also very important because they have changed dinosaurian phylogenetic patterns proposed by previous studies and significantly advanced the study on character evolution for many dinosaurian lineages. The recent dinosaurian discoveries from the Jehol Group have provided the most comprehensive evidence yet of dinosaurian soft tissues, and will undoubtedly produce many more insights in the future.



163 The phylogenetic positions of the Jehol non-avian theropods (in red) among the related groups.

164 Skull of the holotype of *Psittacosaurus meileyingensis* (estimated body length 1–2 m) from Meileyingzi locality (Jiufotang Formation), Chaoyang, Liaoning. Psittacosaurs are a group of herbivorous dinosaur living in the Early Cretaceous of Asia and a distant relative of *Triceratops*.

165 Complete skull of a juvenile *Liaoceratops yanzigouensis* (total body length less than 1m), a small primitive ceratopsian, from Yanzigou locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)

167 A skull of *Jeholosaurus shangyuanensis* (estimated body length less than 1 m), a small ornithopod dinosaur, from Lujiatun locality (lower part of Yixian Formation), Beipiao, Liaoning. (Photo: IVPP)

166 Reconstruction of *Liaoceratops yanzigouensis*. (Art: Michael W. Skrepnick/ FMNH)

168 Skull of the holotype of *Jinzhousaurus yangi* (skull about 50 cm long and 28 cm high), an iguanodont, from Baicaigou locality (middle part of Yixian Formation), Jinzhou, Liaoning. (Photo: IVPP)

169 Holotype of *Liaoningosaurus paradoxus* (body length less than 40 cm), the smallest ankylosaur found to date, from Wangjiagou locality (middle part of Yixian Formation), Jinzhou, Liaoning. (Photo: IVPP)

BIRDS

Fu-cheng Zhang, Zhong-he Zhou, Lian-hai Hou

Probably more than any other animals, birds have immensely enriched our lives with their colorful plumages and beautiful songs, which always evoke man's artistic inspirations. Side by side with flowers, birds have been the favorite subjects of the Chinese painters over the centuries. It is not surprising to find both "The Hundred Birds Sing to a Phoenix" in the Cantonese music repertoire and Ottorino Respighi's symphonic poem "The Bird" offer equally unblemished musical enjoyment to the people all over the world.

Largely imitating avian flight, we have seen our dream of flying come true through the inventions of airplane and spacecraft. Consequently, these inventions have made not only our global village ever more accessible but also our outspace travel increasingly feasible. Birds are also our friends, some as pets to accompany and amuse us, and some as foes to rats, helping eliminate such natural disasters as rat calamity and thus maintain a balanced ecosystem to which we also belong. In addition, birds also attract hundreds of thousands bird-watching fans annually worldwide to outdoors to admire their beauty, and as a result, keep the birdwatchers themselves fit.

Birds, with a global distribution of over 9,000 known living species, are the most flourishing land vertebrate group on earth today. The issue of the origin of birds dates back to the old days. The discovery of the *Archaeopteryx* (Fig. 170) fossil from Bavaria of Germany in 1861, for the first time, linked birds with reptiles. Against the backdrop of the classic work Origin of Species published by Charles Darwin two years earlier, the first *Archaeopteryx* specimen, with a combination of feathers of modern birds and a long skeletal tail typical of reptiles, stirred an outright public sensation and convinced people that birds evolved from reptilian ancestors. Evolutionism has since prevailed over Creationism.

Birds have light skeleton due to flight adaptation. Compared to other animals, they are usually more difficult to be preserved as fossils. This can probably explain why only 7 skeletons and one feather specimen of *Archae-*

170 Model of *Archaeopteryx*, the oldest bird, which linked reptile to bird, suggesting a reptile-bird relationship. (Courtesy: Larry D. Martin/ KU)

171 A complete skeleton of *Confuciusornis* sp., a primitive beaked bird, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning, showing well preserved impression of two long central tail feathers. Note the two special features of this bird: jaws beaked (toothless, **Upper**); humerus triangular with elliptic fenestra at its expanded proximal end (**Lower**). (Photo: IVPP)

172 A *Confuciusornis* "couple" buried together. The one on the left with a long tail feather is assumed as a male. (Photo: Da-jian Li/ CAS)

173 Two *Confuciusornis*, buried in one slab, from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. The number of *Confuciusornis* specimens has surpassed the total number of other Mesozoic birds combined. (Photo: IVPP)

opteryx have been found over the past 140 years. Although some other Mesozoic birds were also discovered in other regions of the world, they are all much younger than *Archaeopteryx*, with little diversity.

This situation has significantly changed since the 1990s with the discoveries of abundant Mesozoic birds from Liaoning, Hebei, Inner Mongolia, Shandong, Ningxia and other areas of China. These new fossils have revolutionarized our view of the early evolution and radiation of birds.

The first Mesozoic bird from Liaoning was actually collected by a farmer from the Meileyingzi locality in Chaoyang in 1987 and then sent to the Beijing Natural History Museum for study; this bird was later named *Sinornis*. In September of 1990, we discovered three fossil bird skeletons from the Boluochi locality in Chaoyang, Liaoning Province (one of them was later

174 The distal ends of central tail feather of *Confuciusornis*. (Photo: IVPP)

175 Reconstruction of *Confuciusornis*, the earliest beaked bird from about 125 million years ago. The upper one, bigger and long-tailed, was assumed as a male. (Art: Xiao-Dan Zeng & Jin-Feng Hou).

named *Cathayornis*). These fossils were all from the Early Cretaceous Jiufotang Formation, and fit right in the transition form the Late Jurassic *Archaeopteryx* to the Late Cretaceous birds. However, their discovery was only the beginning of a series of exciting fossil findings in the area that have lasted to this day. For instance, over two dozens of bird skeletons were discovered from this locality alone during the following field seasons in the early 1990s.

In 1993, the first skeleton of *Confuciusornis* in a fossil collector's home drew the attention of some colleagues from the IVPP. It was later named after a renowned Chinese saint, Confucius, who lived more than 2,500 years ago, and recognized as the earliest known bird with a horny beak. A large number of *Confuciusornis* specimens have since been excavated from the Yixian Formation at several localities in Beipiao and Chaoyang, western Liaoning. Many fossil birds have also been collected from a younger formation, the Jiufotang Formation in that area. Hundreds of specimens of Mesozoic birds have been discovered from the Jehol Biota since *Sinornis* was described, and western Liaoning has increasingly become the hottest area for the study of the origin and early evolution of birds.

Confuciusornis *Confuciusornis* (Figs. 171 ~ 175) is the earliest known bird without teeth. Unlike most other early birds, *Confuciusornis* had a horny beak, just like the birds in your backyard. The loss of teeth and the appearance of horny beak may also indicate the reduction of the cutting function of jaws, and the shifting of the masticatory process mainly to its gizzard, for which, however, we have not had any direct fossil evidence.

Confuciusornis is about the size of *Archaeopteryx*. The postorbital of *Confuciusornis* is large, and ventrally connected with the jugal, suggesting that *Archaeopteryx* may also have a postorbital, thus a typical diapsid skull.

The pectoral girdle bones, scapula and coracoid, are firmly connected, and appear more primitive than in *Archaeopteryx*. *Confuciusornis* also has a primitive hand similar to that of *Archaeopteryx*. Except for the pectoral girdle and forelimb, most of other features of *Confuciusornis* are, however, more derived, suggesting a more powerful flight capability. For example, the distal tail vertebrae of *Confuciusornis* are fused into one solid bone, pygostyle, which is remarkably distinguishable from that of *Archaeopteryx* that has a long caudal tails with 22 unfused vertebrae. A short and steady body of *Confuciusornis* is,

176 A specimen of *Sapeornis chaoyangensis*, the largest known Early Cretaceous bird (about twice as large as *Archaeopteryx*), from Shangheshou locality (Jiufotang Formation) in Chaoyang, Liaoning. Its elongated forelimbs are longer than those of *Longipteryx* in proportion; however, its short and robust coracoids are comparable to those of *Archaeopteryx* and theropod dinosaurs. (Photo: IVPP)

178 Seeds in *Jeholornis*, suggesting its seed-eating diet. (Photo: IVPP)

177 Holotype of *Jeholornis prima*, a primitive bird only slightly more derived than *Archaeopteryx*, from Dapingfang locality (Jiufotang Formation) in Chaoyang, Liaoning, representing the only bird with a complete long skeletal tail after *Archaeopteryx*. (Photo: IVPP)

Fig 179 Reconstruction of *Jeholornis*. (Art: Yong Xu/ IVPP)

180 Holotype of *Cathayornis yandica*, an opposite bird (size about a domestic sparrow) and the first complete fossil bird skeleton collected by a Chinese scientist, from Boluochi locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

181 Holotype of *Boluochia zhengi*, an opposite bird (slight larger than *Cathayornis*), from Boluochi locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

182 Reconstruction of *Boluochia*, with a raptorlike lifestyle. (Art: Xiao-lian Zeng)

like modern birds, more adapted for flight than a long and incompact body of *Archaeopteryx*.

One of the most distinctive features of *Confuciusornis* is the fenestra at the proximal end of the humerus (Fig. 171), though we are not yet sure about its exact function.

Up to now, probably over one thousand *Confuciusornis* specimens have been discovered. In many cases, many individuals were preserved in close proximity, indicating mass mortality (Figs. 172, 173). Other birds are relatively less abundant than *Confuciusornis*. *Confuciusornis* is not only characteristic of complete skeletal preservation, but it usually contains beautiful feather impressions in areas such as the skull, neck, wing, and tail. These feathers are comparable to those of *Archaeopteryx* and modern birds, with rachis and barbs; some of them even with barbules. Some *Confuciusornis* specimens also preserve a pair of long tail feather, suggesting that they may be male individuals (Figs. 171, 172, 175). It is rather often to find male and female lying next to each other preserved on one slab (Fig. 172). We may further conclude that at least by the time of the Early Cretaceous, the sexual dimorphism of feathers in early birds are much like that of modern birds (Fig. 175).

The name of *Sapeornis* was derived from the SAPE, the abbreviation of the Society of Avian Paleontology and Evolution; this bird's holotype was discovered shortly after the SAPE's 5th symposium meeting, which was held in Beijing in June 2000. *Sapeornis* (Fig. 176) was collected from a new locality only a few kilometers northwest from the downtown of the Chaoyang City. It is the largest known Early Cretaceous bird. It is not only larger than *Archaeopteryx* but also larger than many dromaeosaurs from the same region such as *Microraptor*.

Its elongated forelimbs, relatively short hind limbs, fused carpometacarpus and short pygostyle indicate powerful flight capability. On the other hand, this bird retains some primitive features such as a short and robust coracoid, similar to that of *Archaeopteryx* and theropod dinosaurs. The coexistence of such a large sized bird with many small to medium sized birds from the same age suggests that by the Early Cretaceous the differentiation of early birds is greater than previously assumed.

Jeholornis *Jeholornis* (Figs. 177 — 179) is a very primitive bird, and phylogenetically only slightly more derived than *Archaeopteryx*. It is the third bird known to have a long skeletal tail. Its long bony tail contains about 24～25 caudal vertebrae. Its tail is even more primitive than that of *Archaeopteryx*. In fact, the tail bears a lot more resemblance to dromaeosaurids dinosaurs than any other known birds. For instance, the elongated prezygapophysis and chevron of the caudal vertebrae are characteristic of dromaeosaur dinosaurs, providing further evidence for the link between birds and theropod dinosaurs, in particular, the dromaeosaurid dinosaurs.

The holotype of *Jeholornis* preserved more than 50 seeds as imprint in the belly (Fig. 178). It is the first direct evidence for seed-eating adaptation in the Mesozoic. This bird is clearly a seedeater. There are also other lines of evidence for this conclusion, such as the short, deep and robust jaws, which have only very reduced teeth on the lower jaw. Many intact seeds also indicate that this bird probably has a well-developed crop.

The combination of a much derived pectoral girdles and forelimbs with very primitive tails and hind limbs indicates the mosaic pattern of characters in early evolution of birds. In other words, early birds first developed flight capability and then became modern in the features of the hind limbs and the tail.

Cathayornis *Cathayornis* (Fig. 180) is a small-sized enantiornithine bird, slightly larger than a sparrow in size. Enantiornithine birds ("opposite birds") are the dominant Mesozoic avian group, characterized by its unique articulation between the scapula and coracoid that is "opposite" to that of modern birds. *Cathayornis* is the very first avian specimen collected by professional paleontologists in Liaoning, China. Its discovery in 1990 has boosted the study of early birds in China and trigged a series of discoveries of feathered dinosaurs and early birds such as *Confuciusornis* in that region.

Cathayornis was from the Jiufotang Formation, which overlies the Yixian Formation (see Chapter 2). Although *Cathayornis* is much younger than *Archaeopteryx* in age, they share similarities in the skull structure such as toothed jaws. However, it has a more expanded braincase than *Archaeopteryx*. It has many advanced features in the pectoral girdle and wing than in *Archaeopteryx* and *Confuciusornis*. Compared to the most primitive enantiornithine *Protopteryx* (see below), *Cathayornis* has more reduced and shortened digits in the hand.

Boluochia *Boluochia* (Figs. 181, 182) is another enantiornithine bird from the Jiufotang Formation. It was discovered from the same horizon and locality as *Cathayornis*. This bird was named after the locality Boluochi, a village near Chaoyang City, western Liaoning. The most distinctive feature

183 Holotype of *Liaoxiornis delicates*, a juvenile or subadult opposite bird (size about a Great Tit), from Dawangzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning. (Photo: IVPP)

184 Reconstruction of *Liaoxiornis delicates*. (Art: Anderson Yang)

185 Holotype of *Eoenantiornis buhleri*, a primitive opposite bird (size about a cuckoo) with a relatively short rostrum (denoted by a red arrow) and deep skull, from Heitizigou locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)

186 Holotype of *Protopteryx fengningensis* (size about a gray starling), the most primitive opposite bird to date, from Sichakou locality (Yixian Formation) in Fengning, Hebei. (Photo: IVPP)

of *Bolunchia* is that the most anterior end of premaxilla is curved into a hook as in some extant raptorial and passerine birds. No tooth has been discovered from the premaxilla. It was therefore proposed that *Bolunchia* probably had a similar lifestyle as some extant raptorial and passerine birds.

Another significant feature of *Bolunchia* is its long and curved foot claws, suggesting climbing and perching ability. At the distal end of the tarsometatarsus the trochleae for the digits are nearly on the same level, further proving that it is a bird with strong perching capability.

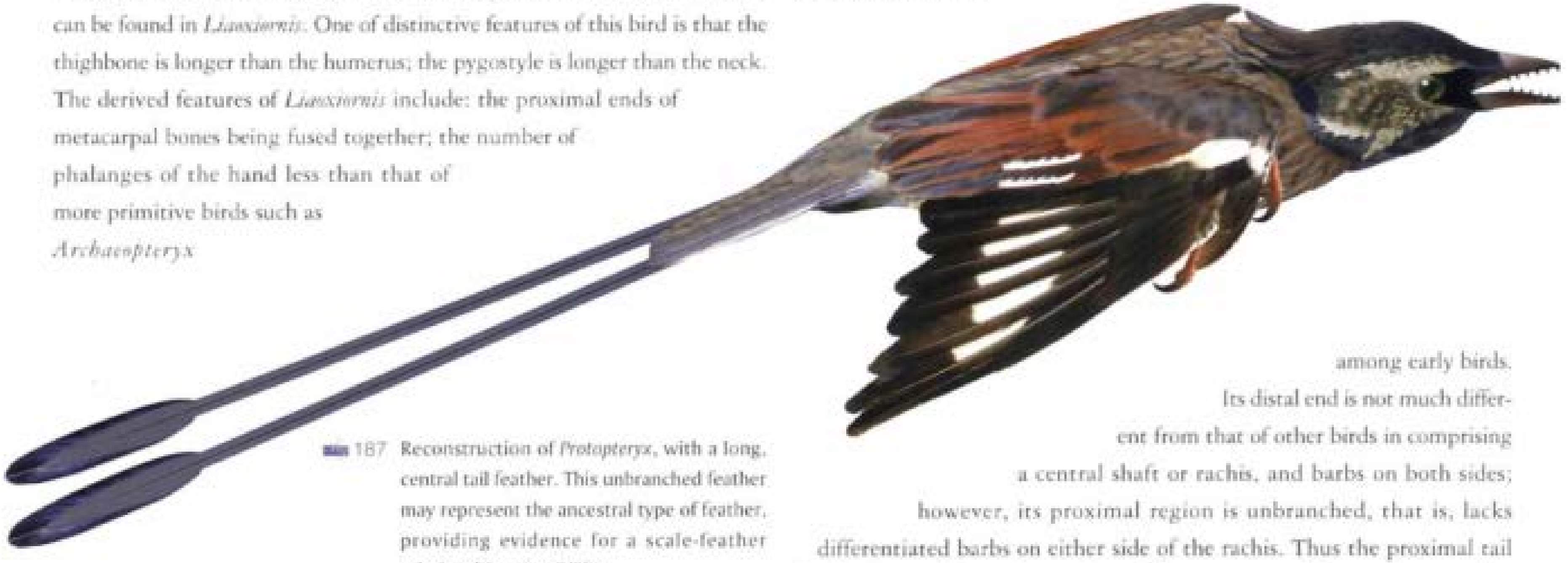
Liaoxiornis *Liaoxiornis* (Figs. 183, 184) is the smallest known Mesozoic bird reported from the Yixian Formation in Lingyuan, western Liaoning in 1999. It is about the size of a sparrow.

Liaoxiornis has a large and deep skull. Both upper and lower jaws are toothed as in most other Mesozoic birds. Both primitive and derived features can be found in *Liaoxiornis*. One of distinctive features of this bird is that the thighbone is longer than the humerus; the pygostyle is longer than the neck. The derived features of *Liaoxiornis* include: the proximal ends of metacarpal bones being fused together; the number of phalanges of the hand less than that of more primitive birds such as *Archaeopteryx* and *Confuciusornis*; the wishbone having a long hypocleideum; and the coracoid elongated.

The juvenile and enantiornithine features of *Liaoxiornis* indicate that it is a juvenile enantiornithine bird, yet more materials are needed to clarify its phylogenetic position in early avian evolution.

Eoenantiornis *Eoenantiornis* (Fig. 185) was so named because when it was published in 1999 it represented the most primitive enantiornithine bird at that time. It is distinguishable from other birds by its relatively short rostrum and deep skull. *Eoenantiornis* is smaller than *Confuciusornis*, but larger than other enantiornithine birds, consistent with the tendency of body size reduction in the evolution of early birds. The teeth of *Eoenantiornis* are characteristic of all known toothed birds in having a constriction at the base of the crown. Another notable feature of *Eoenantiornis* is the preservation of bastard wing as in *Protopteryx*. The bastard wing was not present in *Archaeopteryx* and *Confuciusornis*. It is probably present in all other enantiornithines and ornithurines (all extant birds are ornithurine birds).

Protopteryx *Protopteryx* (Figs. 186, 187) is about the size of a gray starling. As its name implies it is "A bird with primitive feathers". The two central tail feathers of *Protopteryx* are most distinctive among early birds. Its distal end is not much different from that of other birds in comprising a central shaft or rachis, and barbs on both sides; however, its proximal region is unbranched, that is, lacks differentiated barbs on either side of the rachis. Thus the proximal tail feather is more like an elongated scalelike structure, which was interpreted as an intermediate stage between reptilian scale and avian feather. After the discovery of *Protopteryx*, similar primitive tail feathers have also been recognized in the specimens of *Confuciusornis* and some other enantiornithine birds.



187 Reconstruction of *Protopteryx*, with a long, central tail feather. This unbranched feather may represent the ancestral type of feather, providing evidence for a scale-feather relationship. (Art: IVPP)

Protopteryx also represents the most primitive of the known enantiornithine birds. Some of its hand bones are longer than those of other enantiornithine birds. On the other hand, it develops the initial procoracoid on the coracoid, indicative of the presence of triosseal canal, which is a derived and key structure adapted for flapping flight of modern birds.

168 Holotype of *Longipteryx chaoyangensis*, an opposite bird (size about a dove) with long wings, from Shangheshou locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

Protopteryx also preserves bastard wing or alula, which is important for balance during the slow flight and take-off of birds. It again is a derived feature of birds, suggesting the capacity of more skillful flight in this early bird than in *Archaeopteryx* and *Confuciusornis*.

Longipteryx *Longipteryx* (Fig. 188) is a long-winged bird, which was discovered from the same locality of *Sapeornis* in Chaoyang. Its forelimb is markedly longer than the hind limb; the ratio of forelimb to hind limb is about 1.4. About nine cervical vertebrae show developed saddle-shaped vertebral body. This is an indicator of high agility of the head and neck.

Longipteryx has at least four uncinate processes on each side; this is the first evidence of such structure in enantiornithine birds. In some modern birds the uncinate processes are attached to the caudal border of the ribs, providing connection between neighboring ribs. The reinforced ribs provide effective attachment for some muscles responsible for flight and respiration.

Longipteryx has long thoracic limb and beak, and it also has strong perching capability. Therefore, it is suggested that the bird probably had a lifestyle comparable to kingfisher. The discovery of *Longipteryx* also suggests that early enantiornithine birds had undergone a significant radiation in the Early Cretaceous.

Liaoningornis *Liaoningornis* (Fig. 189) was collected from the Sihetun locality, a site famous for producing the bird *Confuciusornis*, the feathered dinosaur *Sinornithosaurus* and many other important vertebrates. *Liaoningornis* is the only ornithurine bird known from the Yixian Formation. Among ornithurine birds, *Liaoningornis* is a small-sized bird, comparable to the gray starling. It has a nearly completely fused tarsometatarsus. It also has sharp and curved pedal claws, indicating strong perching capability.

Another distinctive feature of this bird is the well-developed keel of the sternum, suggesting that *Liaoningornis* has more power of flight than enantiornithines and other basal birds. It is also notable that *Liaoningornis'* sternum is thicker than that of *Yanornis* and *Yixianornis*, both of which are more advanced and younger ornithurine birds also found in western Liaoning (see bellow). The sternum of *Liaoningornis* also lacks lateral processes.

Yanornis *Yanornis* (Fig. 190) was derived from "Yan", name of an ancient country with Chaoyang the capital. It is a largesized bird, comparable to the ring-necked pheasant. This is an ornithurine bird from the Jiufotang Formation. Long beak, elongated snout and densely distributed teeth are three of the most marked features of *Yanornis*. The neck vertebrae are long and saddle-shaped, suggesting that *Yanornis* has head and neck maneuverability comparable to modern birds. The pedal digits are relatively long, but the claws are relatively short. Like modern plover, *Yanornis* might have spent most of their time on the waterside, catching mollusks, fishes or arthropods as food. The long mouth and flexible long neck are well adapted to this lifestyle.

Yixianornis *Yixianornis* (Figs. 191, 192) was collected from the Jiufotang Formation in Yixian County, Jinzhou City, Liaoning Province. Compared with *Yanornis*, *Yixianornis* has a relatively short head, less teeth in the jaws, and thinner long bones. Like *Yanornis*, it is an ornithurine bird with a well-developed sternal keel. *Yixianornis* also preserved well-

189 Holotype of *Liaoningornis longidigitus* (Slab A), the only ornithurine bird (size about a sparrow) found in Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)

190 Holotype of *Yanornis martini*, a large ornithurine bird (size about a ring-necked pheasant), from Dapingfang locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

developed uncinate processes, indicating the presence of a strong ribcage.

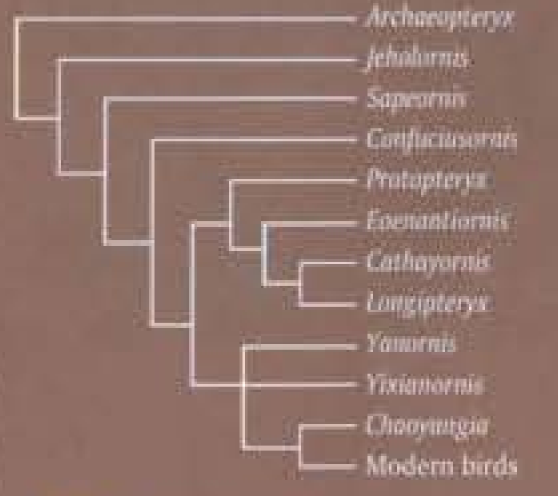
Chaoyangia *Chaoyangia* (Fig. 193) was the first ornithurine bird described from the Jehol Biota. It was collected from the same locality of *Boluochia* and *Cathayornis*, the Boluochi site of Chaoyang. It is an incomplete specimen, with only partial postcranial bones preserved. Uncinate processes are well preserved in the holotype of *Chaoyangia*. It has at least nine sacral vertebrae compared to eight in enantiornithines and seven in *Confuciusornis*. It also has a well-developed cnemial crest at the proximal tibiotarsus. On the other hand, it also retains a long pubic symphysis comparable to more primitive birds.

With numerous well-preserved fossils, as well as a high taxonomic diversity represented by both very primitive and quite advanced forms, the Jehol birds have provided important information on the phylogeny and evolution of early birds (Fig. 194). Though still debatable concerning various hypotheses, some consensus has been reached.

191 Holotype of *Yixianornis grabaui*, an ornithurine bird (slightly smaller than *Yanornis*) with well-preserved skeleton and feather imprints, from Qianyang locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)

192 Wing feather of *Yixianornis grabaui*, same as to those of extant flying birds. (Photo: IVPP)

193 Holotype of *Chaoyangia beishanensis*, an ornithurine bird with uncinate processes (denoted by a red arrow) on ribs and developed cnemial crest (denoted by a blue arrow) at the proximal tibiotarsus, from Beishan locality (Jiufotang Formation) in Chaoyang, Liaoning. (Photo: IVPP)



194 Cladogram showing the phylogenetic relationship of the Jehol birds and to *Archaeopteryx* and modern birds.

Zhangheotherium quinquecuspidens
Photo: IVPP

MAMMALS

Yuan-qing Wang, Yao-ming Hu, Chuan-kui Li

Mammalia is biologically the most differentiated group of vertebrates, consisting of all the living mammals, their common ancestor, and their extinct allies. Mammals have predominated the modern terrestrial ecosystems throughout the Cenozoic Era since some 65 million years (Myr) ago, which is thus often referred to as the "Age of Mammals". However, the first two-thirds of mammalian history occurred in the preceding Mesozoic Era that extended from roughly 250 to about 65 Myr before present. After their first appearance in the Late Triassic (about 220 Myr ago) and throughout the remainder of the Mesozoic, mammals shared the earth with some great reptiles such as dinosaurs. During all that time, mammals were small and scarce, and lived in the shadow of dinosaurs. Mammals, however, outsmarted dinosaurs by surviving through the mass extinction at the end of the Cretaceous and became dominant on the earth's landmasses afterwards.

Mammals lived in the Mesozoic Era for about 155 Myr, but their fossil record is rather poor and fragmentary. Unlike the uniform teeth of reptiles, mammalian teeth differentiated into four kinds: incisor, canine, premolar, and molar, with each kind performing a different function. Based mainly on the dental morphology, Mesozoic mammals are grouped as Triconodonta, Docodonta, Multituberculata, Symmetrodonta, Eupantotheria, Monotremata, Marsupialia, and Eutheria. Among them, only the last three groups are still living on earth today. Before the recovery of mammals from the Jehol Biota, ten localities had been reported to yield Mesozoic mammal fossils in China. Of them, only the Early Jurassic Lufeng of Yunnan Province in southwestern China produced some well-preserved specimens, including a number of skulls of triconodonts, such as *Sinoconodon* and *Morganucodon*. Fossils from the other sites were generally represented by fragmentary jaws. From the Middle Jurassic coal-bed of northeastern China was reported the first Chinese Mesozoic mammal, *Manchurodon*. Later, two other mammals, *Endotherium* and *Liaotherium*, were discovered in that area.

In 1992, the first mammal of the Jehol Biota was unearthed near a small village, Jianshangou of western Liaoning Province. It was named *Zhangheotherium quinquecuspidens* in 1997. Since then, six other mammalian species have been reported from the Jehol Biota. Compared to many other kinds of animals in the fauna, especially to the feathered dinosaur-bird lineage and a variety of invertebrates, mammals were not at all that rich. Despite this, fossil mammals of the Jehol Biota are an important and integrative part of the Mesozoic mammalian history. The exceptionally well-preserved materials provide critical evidence for understanding the transition of mammalian characteristics and reconstructing the phylogeny of early mammals. These fossils have shown a fairly high diversity of Mammalia in eastern Asia during the Early Cretaceous and represent four major mammalian groups: triconodonts, multituberculates, symmetrodonts, and eutherians. In the following paragraphs, they will be briefly introduced in systematical sequence.

Triconodonts Triconodonts consist of the most primitive known mammals and some of their derived relatives. As their name implies, their basic dental structure comprises three major cusps anteroposteriorly aligned, whereas some advanced forms have an enlarged fourth cusp on the distal margin. The triconodont lineage spans the entire Mesozoic mammalian history from the Late Triassic to Late Cretaceous. Although abundantly represented by teeth and some cranial and postcranial materials, fully articulated skeleton of triconodonts was yet unknown until the discovery of triconodonts in the Jehol Biota.

The first triconodont reported from the Jehol Biota is *Jeholodens jenkinsi* (Figs. 195, 196). It was represented by a nearly complete skeleton consisting of a partial skull and the whole postcranial skeleton preserved as two counterparts and was described by Q. Ji and others in 1999. *Jeholodens* is distinctive from the other primitive mammals in having diagnostic features: dental formula (i.e., number of incisors, canine, premolars, molars on each side of the upper/lower jaw) 4·1·2·3/4·1·2·4; buccolingually compressed molars with three main cusps in a straight alignment, and possessing spoon-shaped incisors that is uniquely derived among triconodonts.

The articulated type specimen of *Jeholodens jenkinsi* shows a mosaic of derived, therian-like characters for most parts of the shoulder girdle and the

195 Holotype of *Jeholodens jenkinsi*, a triconodont (skull length about 2 cm), from Sihetun locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: CMNH)

196 Reconstruction of *Jeholodens jenkinsi*. (Art: Mark A. Klingler/ CMNH)

humeri, but very primitive characters for the vertebral column, pelvic girdle, hind limbs and pedes. Q. Ji and others interpreted the mosaic of derived and primitive features in *Jeholodens* as either the derived shoulder girdle and forelimbs representing convergence with those of multituberculates-therian clade, or the primitive shoulder girdle and forelimbs in monotremes being atavistic reversals to the ancestral conditions in the more distantly related non-mammalian cynodonts.

One year after the report of *Jeholodens*, J.-L. Li and her colleagues described another triconodont, *Repenomamus robustus*, based on a fairly well-preserved skull and some associated postcranial bones (Figs. 197, 198). Several additional specimens were collected from the same locality after the first report of this animal. It is the largest mammal known from the Mesozoic Era in the world. The skull is 108 mm long in the holotype and 114 mm in another specimen. The dental formula of *Repenomamus robustus* is 3·1·2·4/3·1·2·5 (Figs. 198). On its upper molars, the middle one of three main cusps is large and the other two are weak, without distinct ectocingulum (a girdle-like structure on labial margin of the tooth). Besides the large size and the dental features, *Repenomamus* further differs from other Mesozoic mammals in the following character combination: short dorsal process of premaxilla not contacting the nasals; retainment of a large septomaxilla; short and low sagittal crest; well-developed lambdoid crest; and the sloping occipital surface exposed in dorsal view of the skull.

The most striking feature of these *Repenomamus* specimens is the presence of a separate bone attached to the medial side of dentary. The dentary is the single lower-jaw bone of all the living and most extinct mammals. In the mammallike repetiles and most primitive mammals, however, the dentary, together with postdentary bones (usually include articular, prearticular, angular, and surangular), constituted the lower jaw. During the early evolutionary stage of mammals, the postdentary bones greatly reduced and either shifted into the ear region (becoming the ear ossicles and part of bulla) or fused to the dentary. The peculiar bone on the lower jaw of *Repenomamus* is rodlike, with a pointed anterior tip and a flared posterior end (Fig. 197). Its anterior portion is lodged in a depression that appears to be an expanded posterior portion of the meckelian groove. Because there is no other scar on the dentary, it can be inferred that all postdentary bones in *Repenomamus* have been detached from the dentary. Structures of the ear region and their small dimensions indicate that in relation to the sizes of the skull and mandible, the ear ossicles in *Repenomamus* must have been reduced in size.

197 Skull (108 mm long) of the holotype of *Repenomamus robustus*, the largest Mesozoic mammal to date, in dorsal (**Left**) and ventral (**Right**) views, from Lujiatun locality (lowest Yixian Formation) in Beipiao, Liaoning, red arrow denoting the ossified Meckel s cartilage on the lower jaw. (Photo: Jin Meng/AMNH)

198 Skull of *Repenomamus robustus* in anterior (**Upper**) and lateral views (**Lower**), showing the tooth morphology. (Photo: Jin Meng/ AMNH)

Therefore, it is reasonable to conclude that the rodlike bone attached to the dentary is not any of the postdentary bones. Embryological studies of living mammals have demonstrated the whole process from the posterior part of the Meckel's cartilage to the ear ossicles, and anatomical research reveals the Meckel's cartilage lying in an internal groove of the dentary in prenatal and some postnatal extant marsupials, monotremes, and eutherians. The shape of the separate bone and its relation to the skull in *Repenomamus* are closely comparable to those of the Meckel's cartilage in the aforementioned living mammals. We identified this peculiar bone as the ossified middle portion of the Meckel's cartilage in 2001. This finding, for the first time, documented the Meckel's cartilage ossified in fossil record and provided direct evidence for its persistence in adults of the common ancestor of living mammals.

This has been strengthened yet by another partial skull with both lower jaws from the same locality that also preserves the ossified Meckel's cartilage. The specimen represents a new species of *Gobiconodon*, also a triconodont (Fig. 199). This genus is phylogenetically closely related to *Repenomamus* and has been previously known from the Early Cretaceous of both North America and Asia. Its dental formula is 2·1·4·4/1·1·4·5. In 2003, C.-k. Li and his colleagues named it *Gobiconodon zofiae*.

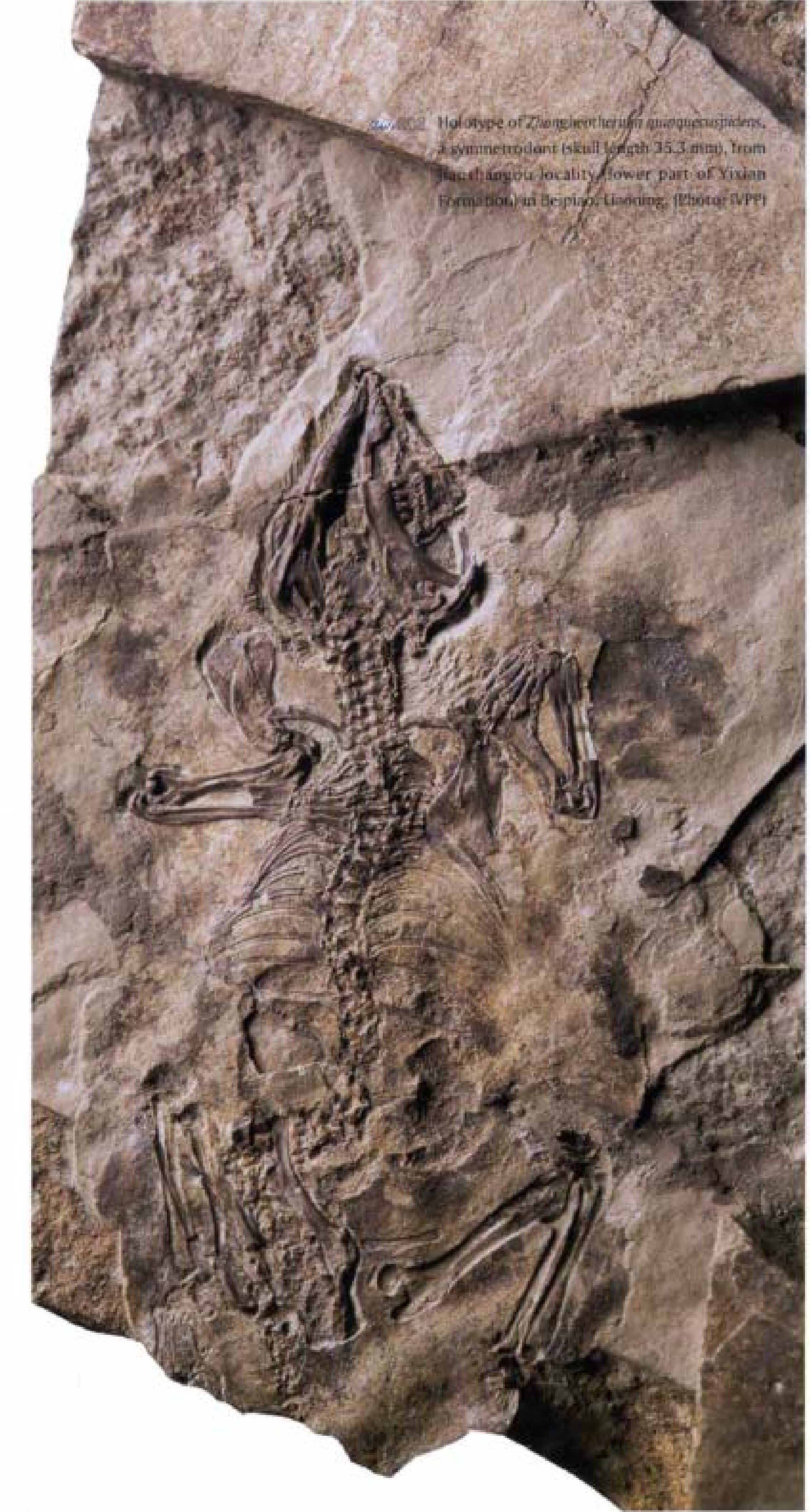
Discovery of the ossified Meckel's cartilage helps interpret the function of the internal groove on dentaries of many early mammals. The groove has been variably considered as holding dental nerves and/or arteries, or the Meckel's cartilage, or even as facets for the postdentary bones. Because of the presence of such a groove in a number of phylogenetically derived mammalian forms, the interpretation for the persistence of the postdentary bones in these taxa argues for multiple origins of the definitive triossicular mammalian middle ear. The discovery of the ossified Meckel's cartilage from the internal groove of the dentary in *Repenomamus* and *Gobiconodon* clearly shows the function of the groove as holding the cartilage. This in turn suggests that in early mammals a Meckel's cartilage, whether ossified or not, should be considered as a potential, or even primary, occupant for the internal groove. Thus, this extrapolation no longer calls for multiple origins of the triossicular mammalian middle ear.

Multituberculates Multituberculates first appeared in the latest Triassic and became extinct in the late Eocene of the Cenozoic Era. They are frequently called "rodents of the Mesozoic", due to their superficially rodentlike features, such as the pair of enlarged and procumbent lower incisors. In later forms, the first pair of lower incisors is chisellike and only the ventral side is covered by enamel, which is especially similar to those of rodents. But, unlike rodents, multituberculates usually have more than one pair of incisors. In the mid-portion of the lower dentitions of most multituberculates, premolars are modified into bladelike structure. Their molars have varying number (from several to more than a dozen) of

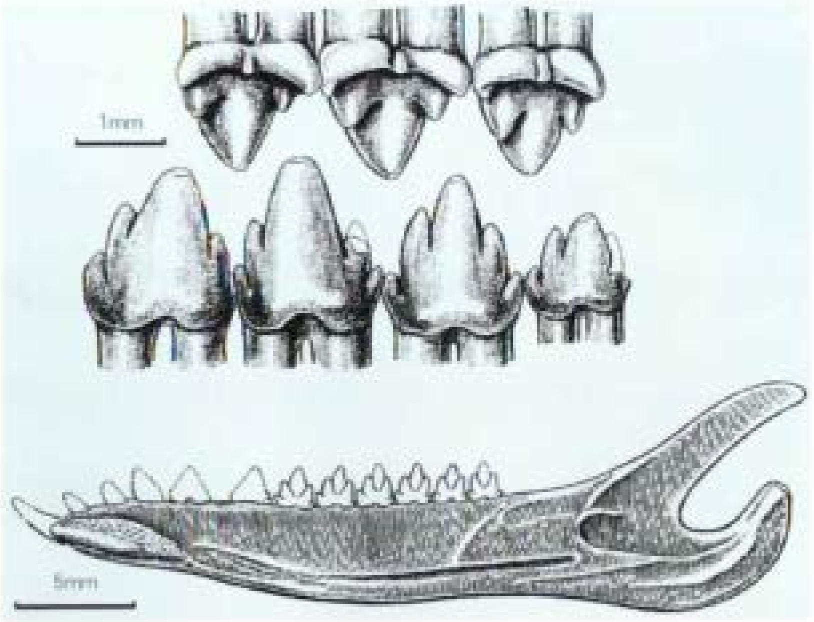
199 Holotype of *Gobiconodon zofiae* (skull length 45 mm), showing cranium in lateral (**Upper**) and ventral (**Middle**) views and lower jaw in labial and lingual views (**Lower**), from Lujiatun locality (lowest Yixian Formation) in Beipiao, Liaoning, red arrow denoting the ossified Meckel's cartilage. (Photo: IVPP)

200 Holotype of *Sinobaatar lingyuanensis* (Slab A, skull length 26.6 mm), a multituberculate from Dawangzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning. (Photo: IVPP)

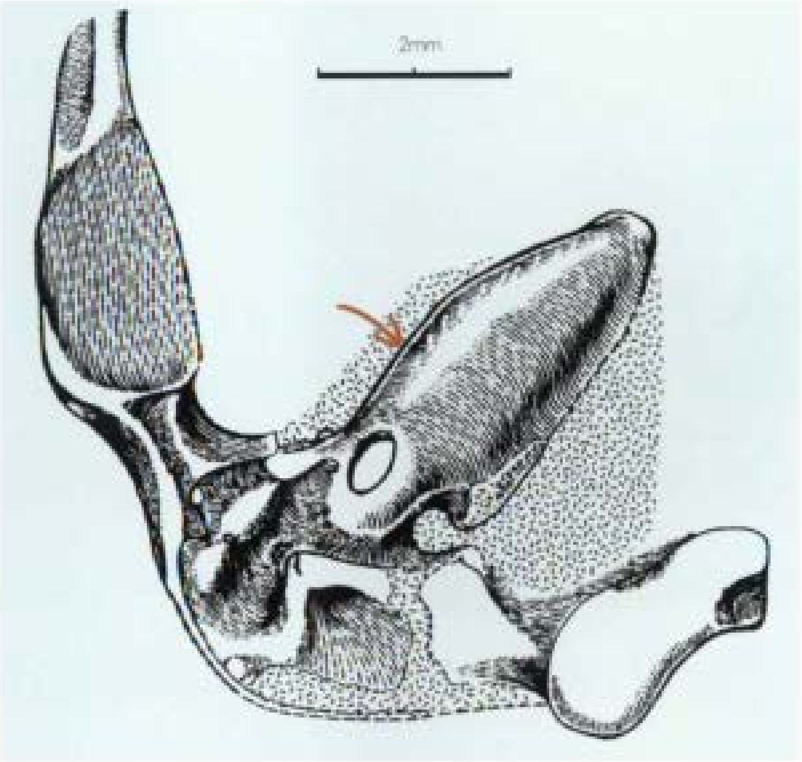
201 A bladelike premolar on the lower jaw of *Sinobaatar lingyuanensis* (cast). (Photo: Jin Meng/ AMNH)



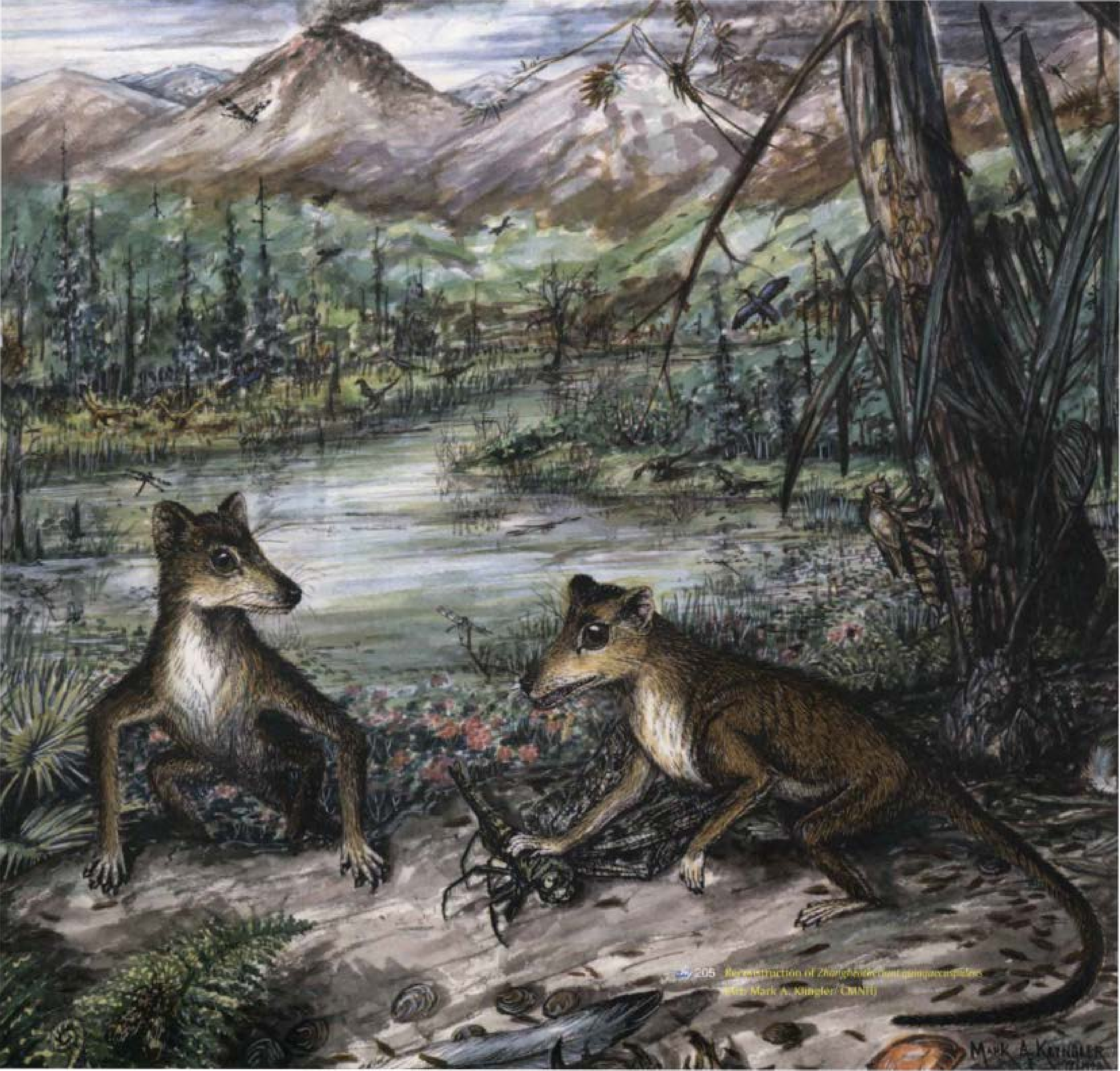
202 Holotype of *Zhangheotherium quinquecuspidens*, a symmetrodont (skull length 35.3 mm), from Jianshangou locality (lower part of Yixian Formation) in Beipiao, Liaoning. (Photo: IVPP)



203 The upper and lower tooth rows and the lower jaw of *Zhangheotherium quinquecuspidens*.



204 Reconstruction of the ear region of *Zhangheotherium quinquecuspidens*, showing the finger-shaped promontorium (denoted by a red arrow) that houses the cochlea, implying its auditory system not very sensitive to high frequency sound.



205 Reconstruction of *Zhangheotherium quinquecuspidens*
(Art: Mark A. Klingler/ CMNH)

tuberclelike low cusps, from which they derived their name. Distinct changes in their dental morphology through time are characterized by the decrease in the number of premolars, the increase in the number of serrations and ridges on the bladelike last lower premolar and in the number of molar cusps.

To date, only one species of multituberculates has been recovered from the Jehol Biota. Y.-m. Hu and Y.-q. Wang, in 2002, named it *Sinobaatar lingyuanensis* (Fig. 200). The type specimen represents a subadult. Its body length, from the tip of rostrum to the hip, is about 10.3 cm. Its dental formula is 3·?·5·2/1·0·3·2. Differing from later multituberculates, the first lower incisor of *Sinobaatar* is conical and completely covered by enamel. The bladelike middle portion of the lower dentition involves three premolars (Fig. 201). *Sinobaatar* has the same dental formula as and similar dental morphology, especially of the cheek teeth, to that of some Early Cretaceous multituberculates from Mongolia.

The holotype of *Sinobaatar lingyuanensis* is the most complete pre-Late Cretaceous multituberculate specimen. It also provides new morphological information of postcranial skeleton previously unknown for early multituberculates. In contrast to the significant changes of their dental features, the available information shows little change in the postcranial morphology of multituberculates during their history. This may suggest that the locomotory patterns in different multituberculates did not change much during evolution. Their morphologically generalized postcranial skeletons indicate that they lived on a variety of substrata.

The specimen of *Sinobaatar* by far reveals most morphological information on multituberculate hand. The wrist structure of *Sinobaatar* is very similar to that of *Kryptobaatar*, a Late Cretaceous multituberculate of Mongolia, and that of *Zhangheotherium*, a symmetrodont from the Jehol Biota. *Sinobaatar* has well-preserved feet and resembles *Ptilodus*, a Paleocene multituberculate of North America, in having a large tibial condyle, and asymmetrical but widely movable astragalotibial joint, etc. Based on the foot and ankle structure, plus the long and prehensile tails, F. A. Jenkins, Jr. and D. W. Krause reconstructed *Ptilodus* as an arboreal animal, a lifestyle that may also be shared by *Sinobaatar*.

Symmetrodonts Symmetrodonts were shrew-sized mammals, characterized by the triangular, imperfectly symmetrical cusp arrangement of both upper and lower molars. The orientation of the triangles on the upper and lower molars is reversed — the central cusp is at the lingual side on the uppers, while at the buccal side on the lowers. The earliest symmetrodonts were found in the latest Triassic to earliest Jurassic of Wales, while their latest record was from the Late Cretaceous of North America.

Y.-m. Hu and his colleagues reported a symmetrodont mammal, *Zhangheotherium quinquecuspidens*, from the Jehol Biota in 1997 (Figs. 202~205). It is the first mammal known from the Biota and is represented by a well-preserved skeleton consisting of a partial skull and most of the postcranial skeleton, including all cervical and thoracic vertebrae, forelimbs and pectoral girdle, as well as excellent impressions of the hind limbs, pelvic girdle, and ribs. The dental formula of *Zhangheotherium* is 3·1·2·5/3·1·2·6 (Fig. 203). This animal is diagnosed by having blunt trigonid cusps, weak cristids, large cingulid cuspules, and no labial and lingual cingulids. Before the discovery of *Zhangheotherium*, symmetrodonts were only known from the fragments of upper and lower jaws. The nearly complete skeleton of *Zhangheotherium* reveals some valuable morphological information for this group.

One of the most interesting cranial features is related to auditory apparatus. Although fractured and distorted in preservation, the petrosal bone of *Zhangheotherium* is complete. Its promontorium, in which the cochlea is housed, has a cylindrical and fingerlike shape (Fig. 204), similar to those of triconodonts and multituberculates. This kind of promontorium is closely correlated with either a straight or slightly curved (but uncoiled) cochlea, a spiral-shaped cavity of the inner ear. An uncoiled cochlea was, therefore, inferred for *Zhangheotherium*. This means that the hearing function of *Zhangheotherium* was not as well-developed as in most of more derived mammals.

The shoulder girdle and forelimbs of *Zhangheotherium* are the best-preserved and most informative parts in its postcranial skeleton. The clavicle of *Zhangheotherium* is rodlike and in similar shape to that of marsupials and placentals. But, unlike marsupials and placentals, a separate interclavicle is present anterior to the sternum (breastbone) and between two clavicles. In marsupials and placentals, interclavicle does not exist as a separate bone, whereas it is very large in monotremes (e.g. platypus and echidnas) and acts as primary supporting structure. Unlike monotremes where the clavicle-interclavicle joint is fixed, *Zhangheotherium* has a mobile clavicle-interclavicle joint, which allows the clavicle to move in a wider range and further results in free movement of forelimbs.

206 Holotype of *Eomaia scansoria* (Slab A, skull length about 3 cm), an eutherian, from Dawangzhangzi locality (middle part of Yixian Formation) in Lingyuan, Liaoning. (Photo: CMNH)

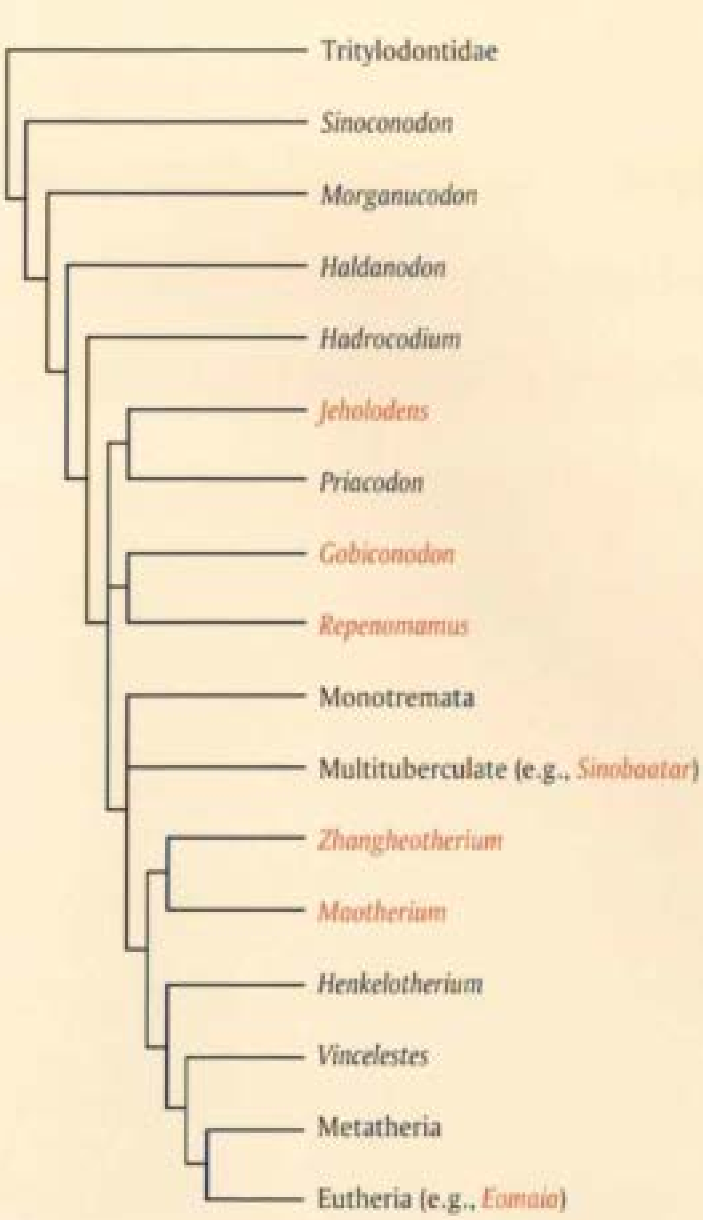
In extant land mammals, marsupials and placentals move in a parasagittal posture, i.e., the fore and hind limbs straight under the body during movement, while monotremes in a sprawling posture with legs extending laterally in certain extent. Comparative anatomical study shows that different postures are related to morphology of limb bones. The forelimbs of *Zhangheotherium* have some features similar to those of therian mammals with parasagittal posture. However, they also retained some primitive characters that are common in the known non-therian mammals having a sprawling posture. The combination of both primitive and derived features of forelimbs probably suggests that *Zhangheotherium* has a forelimb posture intermediate between that of the sprawling monotremes and that of the parasagittal therians.

Early in 2003, G. W. Rougier and others reported another symmetrodont, *Maotherium sinensis*, from the Jehol Biota. It is represented by a fully articulated skeleton and closely related to *Zhangheotherium*. Although differing in some details, they share many morphological features of cranium, dentition, and postcranial skeleton, and thus are grouped into the same family.

207 Reconstruction of *Eomaia scansoria*. (Art: Mark A. Klinglet/ CMNH).

Eutherians Eutherians are a group of mammals consisting of extant placentals and their extinct close relatives. They share the most recent common ancestor with marsupials. The number of molars distinguishes eutherians (three molars on each side for both upper and lower dentitions) from marsupials (four upper and four lower molars). The earliest record was previously documented in the late Early Cretaceous (ca. 110 Myr ago). In 2002, Q. Ji and his collaborators reported an eutherian mammal, *Eomaia scansoria*, from the Jehol Biota (Figs. 206, 207). It is the earliest representative of eutherians so far known in the world. The animal has specialized limb and foot features that are only known from scansorial (climbing) and arboreal (tree-dwelling) extant mammals, quite different from the terrestrial or cursorial (running) features of other Cretaceous eutherians. This suggests that the earliest eutherian lineages developed different locomotory adaptations, facilitating their spread to diverse ecological niches in the Cretaceous.

The phylogenetic relationships of early mammals are of great interest to paleomammalogists. Mammalian fossils from the Jehol Biota are either the best-preserved or the earliest occurred specimens within their respective group. Therefore, they provide a new insight into the relationships of the major lineages of mammals and the evolution of the mammalian skeleton. Different phylogenetic analysis shows some uncertainties, but the results are not strongly conflicted with each other and show the evolutionary trends of some major mammalian characters. Given the framework of these results (Fig. 208), it seems safe to make the following conclusions: (1) The absence of a coiled cochlea in *Zhangheotherium* is best considered primitive, i.e., a coiled cochlea yet to be evolved. (2) The parasagittal forelimb posture of living therians was not present in monotremes, multituberculates, and many Mesozoic mammals such as *Zhangheotherium*, *Henkelotherium* and *Vincelestes*. It probably arose in later stage of mammalian evolution. (3) The presence of definitive triossicular mammalian middle ear in *Repenomamus* and *Gobiconodon* provides evidence for its wide distribution in the mammals.

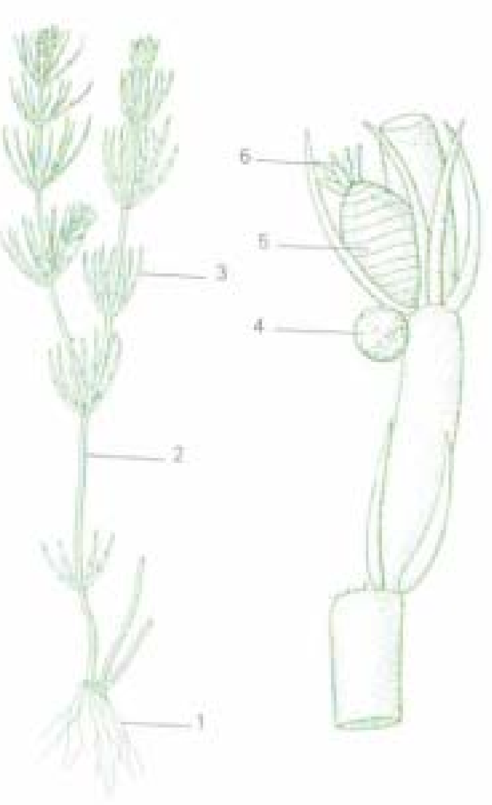


208 **Cladogram showing mammalian phylogenetic relationships, combining results of different analyses related to the Jehol mammals (in red).**

CHAROPHYTES

Qi-fei Wang, Hui-nan Lu, Jing-lin Yang

The charophytes (or stoneworts), a kind of algae, grow in fresh or brackish waters including streams, ponds, lakes, lagoons, fjords and have a wide geographical distribution on all continents except Antarctica. Most of them live in the waters that are clear, transparent and rich in calcium, mostly with pH ranging from 7.0 to 8.0, e.g., alkaline, high-calcium lakes. Charophytes are present in running water only where movement is slight. They grow submerged in the water from shorewards to a depth of 18 m, compact or bushy. The structure of charophytes is relatively simple in vegetative organs, with no vascular bundles. However, their reproductive organs are rather complex. People usually place them in a separate division of the plant kingdom, the Charophyta.



209 Sketch map showing a living charophyte plant (**Left**, × 1; 1, rhizoid; 2, axis; 3, branch) and its reproductive organs (**Right**, × 40; 4, antheridium; 5, oogonium; 6, coronular cells). (After Nordstedt, 1891; redrawn by Yu-gao Ren/ NIGP)

The charophyte thallus is green, ranging from 0.5 to 200 cm in height (15—25 cm in average), and usually has an erect, central axis or stalk, regularly whorled branches arising from the very short nodal cells and rhizoids at the base to attach to the muddy or sandy substrate (Fig. 209). The plant cells contain small and elliptic chloroplasts that carry out photosynthesis and convert inorganic compounds to organic nutrients. The plants commonly are monoecoius, i.e., a single plant producing both types of gametes. Both male gametes (antheridia) and female gametes (oogonia) occur on the branches. Oogonia in living charophytes are elliptic to spherical, covered with five sinistral enveloping cells, whereas antheridia are spherical, protected with four to eight shield cells. Charophytes reproduce both vegetatively and sexually. Vegetative reproduction may occur by means of bulbils or fragments from mature plant. Greater or lesser degree of calcification takes places in the plant during the growth of charophytes, especially within the enveloping cells of oogonia, which enables the good preservation of the lime shells. The term gyrogonite is commonly used to designate the fossilized oogonium.

Most charophyte fossils are remains of gyrogonites as shown in the figures (Figs. 210~223). The geological occurrence of fossil charophytes may trace back to the Late Silurian, nearly 400 million years ago. Quite a few species have wide geographic but limited geologic range, which allow their use as stratigraphic indices for freshwater and brackish sediments as well as tools in environment reconstruction. The diagnoses in fossil charophytes' classification and identification include the size and shape of gyrogonites, characters of calcification and utricle, apical structures and depressions, rosettes and coronular cells, etc.

The Jurassic charophytes are absent in Northeast China. No charophytes have been reported from the upper part of the Yixian Formation and the lower part of the Jiufotang Formation at present. The fossil charophytes obtained

from the lower part of the Yixian Formation of northern Hebei and western Liaoning are predominant with *Mesochara*, *Peckisphaera* and *Minhechara*.

The upper part of the Jiufotang Formation to the Fuxin Formation yields rich charophytes, including mainly *Flabellochara hebeiensis*, *F. harrisi*, *Atopochara trivolvis triquetra*, *Aclistochara mundula*, *A. huihuibaoensis*, *Mesochara stipitata*, *M. voluta*, *Peckisphaera verticillata*. These species are common in the middle part of the Lower Cretaceous deposits in northern China. Among them, *Flabellochara hebeiensis* and *Atopochara trivolvis triquetra* have special stratigraphic significance, i.e., both are typical to the Barremian in the world. Charophytes from the Jiufotang, Shahai and Fuxin Formations can be included in the third Clavatoraceae Biozone of China, namely the late Barremian *Atopochara trivolvis triquetra-Flabellochara hebeiensis* Biozone.

According to the charophyte distribution, the geological age of the lower part of the Yixian Formation can be attributed to the early Early Cretaceous; the upper part of the Jiufotang Formation as well as the Shahai and Fuxin Formations are regarded as the late Barremian.

The figures show some fossil charophytes from Inner Mongolia, Hebei and Liaoning provinces. Their diagnoses are briefly stated as follows.

Aclistochara huihuibaoensis (Fig. 210): gyrogonites oval to prolate, 400~550 μm long, 350~500 μm wide, 8~9 convolutions visible in lateral view, spiral cells concave, intercellular ridges narrow and sharp; found from the Lower Cretaceous of China.

Aclistochara mundula (Fig. 211): gyrogonites urn-shaped, 370~600 μm long, 250~400 μm wide, 10~12 convolutions visible in lateral view; found from the Lower Cretaceous over the world.

Peckisphaera verticillata (Figs. 212, 213): gyrogonites spheroidal, apex broadly round and base narrowly round, 450~750 μm long, 400~600 μm wide, 10~12 convolutions visible in lateral view; found in the Lower Cretaceous over the world.

Mesochara xuanziensis (Fig. 214): gyrogonites very small, ovoidal to subovoidal, 230~350 μm long, 200~250 μm wide, 6~8 convolutions visible in lateral view; found in the Lower Cretaceous of Hebei, Shaanxi, Anhui, Henan, Gansu and Xinjiang, China; northern Spain and northwestern Germany in Europe.

Mesochara voluta (Fig. 215): gyrogonites small, conically ovoidal, 300~400 μm long, 210~330 μm wide, 8~9 convolutions visible in lateral view; having a worldwide distribution during the Late Jurassic and Early Cretaceous.

Mesochara producta (Fig. 216): gyrogonites ovoidal, apex broadly round, base contracted and forming a stalklike projection, 250~380 μm long, 200~250 μm wide, 8~9 convolutions visible in lateral view; found in the Lower Cretaceous of northern China.

Peckisphaera multispira (Fig. 217): gyrogonites broadly ovoidal, apex round, base narrowly round or contracted to a stalk, 300~400 μm long, 200~300 μm wide, 10~11 convolutions visible in lateral view; found in the Lower Cretaceous of Inner Mongolia and Hebei.

Peckisphaera paragranulifera (Fig. 218): gyrogonites ovoidal or subspheroidal, apex round, base round and protruding, basal end flat, 450~600 μm long, 350~465 μm wide, 11~12 convolutions visible in lateral view; found in the Lower Cretaceous of China.

Atopochara trivolvis triquetra (Figs. 219~221): utricles 820~1080 μm long, 750~1000 μm wide, formed with 36 units, which are divided into three groups, basal view triangular; distributed in the Barremian over the world.

Flabellochara hebeiensis (Fig. 222): utricles ovoidal, 620~800 μm long, 520~700 μm wide, lateral units consist of 5 or 6 cells; found in the Barremian over the world.

Minhechara sp. (Fig. 223): gyrogonites subspheroidal, apex and base round, apical center projected, forming a columella, 750~1050 μm long, 450~610 μm wide, 10~11 convolutions visible in lateral view; found in the Lower Cretaceous of Liaoning and Qinghai provinces.

(All fossils shown in this chapter are the fossilized oogonia, i.e. gyrogonites, of the plants. Photos were taken by Yong-qiang Mao and Zhou-qing Chen of the NIGP)

210 *Aclistochara huihuibaoensis*, lateral view (550 µm long, 440 µm wide), from Halawusu drilling sample (Shahai Formation) in Horqin Zuoyi Houqi, Inner Mongolia.

211 *Aclistochara mundula*, lateral view (550 µm long, 250 µm wide), from Pijiagou locality (Jiufotang Formation) in Yixian, Liaoning.

212 *Peckisphaera verticillata*, apical view (550 µm wide), from Dongliang drilling sample (Fuxin Formation) in Fuxin, Liaoning.

213 *Peckisphaera verticillata*, lateral view (575 µm long, 525 µm wide), from Dongliang drilling sample (Fuxin Formation) in Fuxin, Liaoning.

214 *Mesochara xuanziensis*, lateral view (290 µm long, 230 µm wide), from Dadianzi locality (lower part of Yixian Formation) in Luanping, Hebei.

215 *Mesochara voluta*, lateral view (390 µm long, 300 µm wide), from Sanguanmiao locality (lower part of Yixian Formation) in Kazuo, Liaoning.

216 *Mesochara producta*, lateral view (360 µm long, 200 µm wide), from Dadianzi locality (lower part of Yixian Formation) in Luanping, Hebei.

217 *Peckisphaera multispira*, lateral view (370 µm long, 300 µm wide) , from Dadianzi locality (lower part of Yixian Formation) in Luanping, Hebei.

218 *Peckisphaera paragranulifera*, lateral view (450 µm long, 350 µm wide), from Pijiagou locality (Jiufotang Formation) in Yixian, Liaoning.

219 *Atopochara trivolvis triquetra*, apical view (860 µm wide), from Halawusu drilling sample (Shahai Formation) in Horqin Zuoyi Houqi, Inner Mongolia.

220 *Atopochara trivolvis triquetra*, lateral view of the same fossil in Fig. 219 (900 µm long, 860 µm wide), from Halawusu drilling sample (Shahai Formation) in Horqin Zuoyi Houqi, Inner Mongolia.

221 *Atopochara trivolvis triquetra*, basal view of the same fossil in Fig. 219 (860 µm wide), from Halawusu drilling sample (Shahai Formation) in Horqin Zuoyi Houqi, Inner Mongolia.

222 *Flabellochara hebeiensis*, lateral view (750 µm long, 660 µm wide), from Qijiawopeng drilling sample (Shahai Formation) in Kangping, Liaoning.

223 *Minhechara* sp., lateral view (1030 µm long, 610 µm wide), from Sanguanmiao locality (lower part of Yixian Formation) in Kazuo, Liaoning.

Rehezamites anisolobus

224 *Muscites tenellus*, a bryophyte, 3.15 cm long.

LAND PLANTS

Shun-qing Wu

Land plants constitute an important component of the Jehol Biota. They are recorded mainly from the Yixian Formation of West Liaoning, and represent almost all major groups of land plants known from the Mesozoic Era including free-sporing plants (Bryophyta, Lycopsida, Sphenopsida, Filicopsida) and seed plants (Ginkgoales, Czekanowskiales, Coniferales, Bennettitales, Gnetales and Angiospermae). This presentation is based mainly on the study of plant fossils from the Jianshangou Bed of the lower part of the Yixian Formation at Huangbanjigou, Beipiao City, western Liaoning. A total of 54 species in 34 genera have been identified. Among these, 28 species and nine genera are new taxa. Below is a brief characterization of the major plants groups and where possible, their inferred paleoecological conditions will be also discussed.

Bryophytes Bryophytes (Bryophyta) are the most basal group among the land plants. They include small green plants of simple construction with unlignified conducting tissue and without roots. They are distinguishable from all other land plants in having a dominant gametophyte and a very simple sporophyte that is born on the gametophyte (in other land plants the sporophyte is the dominant and the conducting tissue is lignified). The gametophyte is typically upright with dichotomous branching and small leaf-like appendages, or in liverworts it may be flattened and thalloid. The unbranched sporophyte is born on the gametophyte and produces a single terminal sporangium. Bryophytes mostly inhabit shady and humid environments. In the Jehol Biota they are represented by four species in two genera. Both leafy and thalloid types are present (Figs. 224, 225).

Lycopods Lycopsids (Lycopsida) have a basal position among the vascular plants. Extant lycopods are all herbaceous plants. They are characterized by having upright dichotomously branching stems growing from horizontal rhizomes and bearing densely spaced leaves. The plants are heterosporous or homosporous and sporangia either grouped in small cones or scattered along the axes, born on the adaxial surface of leaf-like sporangiophylls. Lycopods have a wide ecological range with representatives in wet and humid environment as well as in arid regions. The three extant lycopod families, Lycopodiaceae, Selaginellaceae and Isoetaceae, were also

225 *Thallites riccioites*, a bryophyte, 1.1 cm long, round print probably representing the vegetative-reproductive organ gemma cups.

present in the Cretaceous, but so far only members of the Lycopodiaceae were recorded from the Jehol Biota, such as *Lycopodites faustus*, a homosporous plant with sporangia arranged in a strobilus (Figs. 226, 227).

Sphenopsids Sphenopsids or horsetails (Sphenopsida) are characterized by upright and distinctly articulate and typically hollow stems arising from horizontal rhizomes. Branches and leaves are born in whorls at the nodes. The plants are heterosporous or homosporous with terminal, mostly abaxial sporangia, born on peltate, scaly sporophylls that are arranged in terminal, ellipsoid cones. The only extant genus, *Equisetum* (Equisetaceae) is herbaceous and homosporous. It has very small leaves that are more or less fused to form a dentiform leaf sheath at the node. The surface of the internodes shows distinct longitudinal ridges from the vascular bundles. *Equisetum* predominately occurs in wet environments, and the hollow stems, characteristic also of many extinct sphenopsids, indicate that it was adapted to growth in moist areas. Remnants of *Equisetum*-like plants, described as

226 *Lycopodites faustus*, a lycopod, 5.95 cm long.

227 Enlargements of the tip of the specimen shown in Fig. 226, showing the strobili with two rows of round sporangia.

Equisetites, are very common in the fossil-bearing strata of the Yixian Formation. The most abundant sphenopsid in the Biota is *Equisetites longevaginatus* (Fig. 228), characterized by very small stem and rather long leaf sheath.

Filicopsids Filicopsids or ferns (Filicopsida) are the largest group of the free-sporing vascular plants. The plants have distinctly differentiated root, stem and leaves. They are woody or herbaceous and some attain tree habit, characterized by having an upright growth with a crown of large leaves. The leaves, often referred to as fronds, are simple or more commonly pinnately or dichotomously compound. Most ferns are homosporous whereas a few are heterosporous. Sporangia are terminal born on the abaxial surface of normal or specialized leaves. Their position on the leaves is highly variable. They may be scattered over the surface of the lamina or variously aggregated in circular, elongate or linear sori. Ferns mainly grow in humid and moist areas, but some are adapted to more arid conditions. Ferns are very common in the Yixian Formation and so far more than 5 species have been recognized. Particularly, species of the extinct genera *Botrychites* (Figs. 229, 230), *Eboracia* (Fig. 231), and *Coniopteris* are conspicuous in the Jehol plant assemblages.

Ginkgos Ginkgos (Ginkgoales) comprise large trees characterized by long shoots and short shoots. They have wood with small pith, proliferate helical branching and leaves born in a helical arrangement. Leaves on long shoots are typically widely spaced while those on the short shoots are clustered around the apical part. They are unique, fan-shaped with dichotomously branching veins, bilobed or sometime strongly dissected. The only extant species, *Ginkgo biloba*, is dioecious with female and male trees. The ovules and microsporophylls are terminal and born on the short shoots. The ovules are borne in small cups on a ovulate axis. Of typically two ovules in extant *Ginkgo*, only one reaches maturity. In some ancestral ginkgos ovules were more numerous on the ovulate axis. The ovules and mature seeds are relatively large with an outer fleshy layer. Ginkgos were much more abundant and diverse in the Mesozoic, particularly in the Late Jurassic and Early Cretaceous. Ginkgos declined drastically both in diversity and geographic distribution during the Late Cretaceous and Tertiary. During the Quaternary it became restricted to small areas in eastern China. The only known wild population of *Ginkgo biloba* is in a temperate moist forest of Zhejiang. *Ginkgo biloba* is

228 *Equisetites longevaginatus*, a sphenopsid, 3.7 cm long.

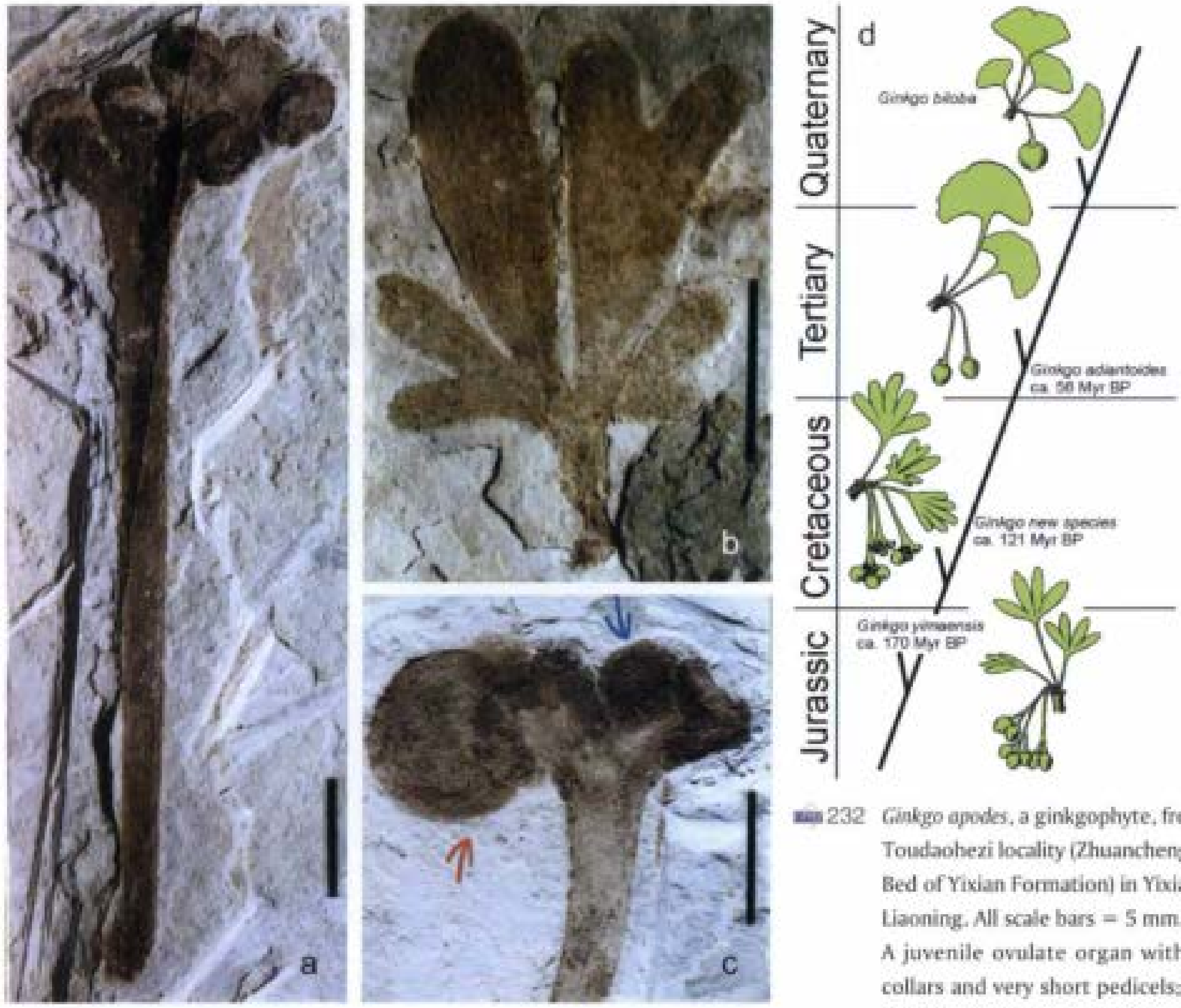
229 *Botrychites reheensis*, a filicale, 6.8 cm long, showing the heteromorphic sterile and fertile pinna.

deciduous and the abundant occurrence of leaves in certain geological horizons indicates that at least some extinct ginkgos were also deciduous. In the Yixian Formation a single species of *Ginkgo* was reported recently by Z.-y. Zhou and S.-l. Zheng (2003) (Fig. 232). It is intermediate in the ovulate structure between modern *Ginkgo* and Jurassic ginkgos with many ovules. The flora also comprises several taxa belonging to extinct ginkgoalean genera such as *Baiera* (Fig. 233), *Ginkgoites*, and *Sphenobaiera*.

Czekanowskialeans Czekanowskialeans (Czekanowskiales) represent an extinct group of seed plants of unknown systematic affinity. It was

230 Pinna of *Botrychites reheensis*, a filicale, 4 cm long.

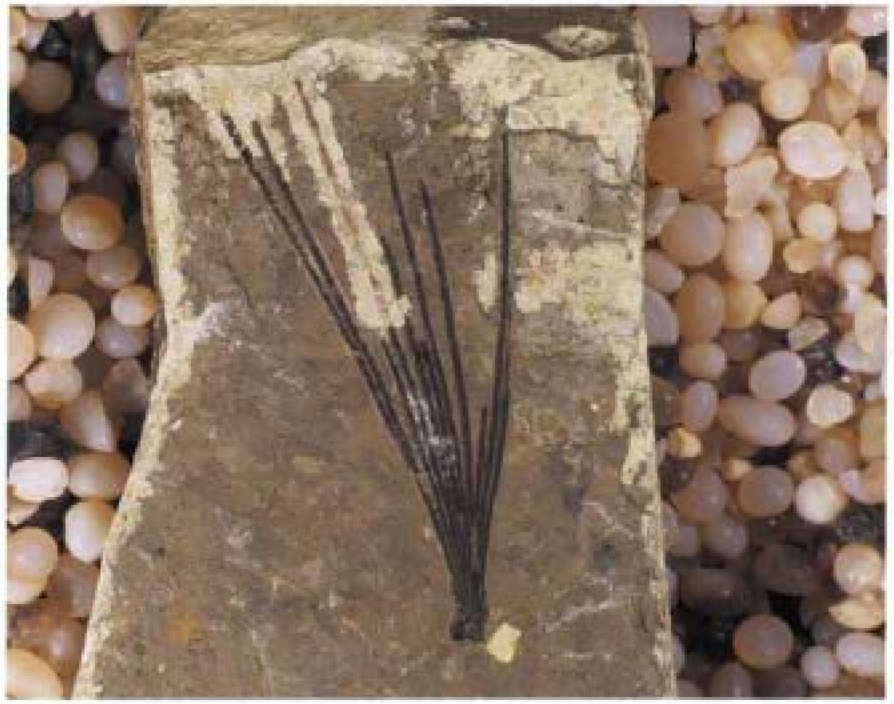
231 Sterile pinna of *Eboracia lobifolia*, a filicale, 1.8 cm long. Note the shape of the variant pinnule at the right of the base of pinna. (Photo: Shi-wei Zhao/ NIGP)



232 *Ginkgo apodes*, a ginkgophyte, from Toudaohezi locality (Zhuanchengzi Bed of Yixian Formation) in Yixian, Liaoning. All scale bars = 5 mm. a, A juvenile ovulate organ with 6 collars and very short pedicels; b, Associated leaf; c, An ovulate organ bearing one nearly mature (red arrow) and probably one aborted ovule (blue arrow) and 1～2(?) empty collars; d, Sketch reconstruction of the species and some other *Ginkgo* taxa, showing evolution of this group in geological history. (Courtesy: Zhi-yan Zhou/ NIGP)

233 *Baiera borealis*, a ginkgophyte, 7.1 cm long. (Photo: Shi-wei Zhao/ NIGP)

234 *Solenites murrayana*, a ginkgophyte, 4.55 cm long.



235 Cone of *Schizolepis beipiaoensis*, a conifer, 9.15 cm long.

236 Samara of *Schizolepis beipiaoensis*, a conifer, 1.15 cm long.

237 *Elatocladus leptophyllus*, a conifer, 4.45 cm long.

included in the Ginkgoales, but their leaves and their reproductive structures, particularly the ovulate structures, are distinct from those of *Ginkgo*, and they are now usually placed in a separate order. The leaves are borne in clusters on short shoots. They are very narrow and supplied by only a single vein, in contrast to the two veins that enter the leaves of *Ginkgo*. The leaves are typically dichotomized into several sections, each with a single vein. The ovulate structure called *Leptostrobus* is characterized by having elongated axes with bivalved ovule bearing units in a spiral arrangement. Each bivalved unit, often referred to as a capsule, contains several ovules. The microsporangiate structure, *Ixostrobus*, is a simple axis with pairs of pollen sacs also arranged in a spiral pattern. The Czekanowskiales were widespread and abundant during the Jurassic and Cretaceous, particularly in floras of the Northern Hemisphere. In the Jehol Biota species of *Solenites* (Fig. 234) and *Sphenarion* are common Czekanowskialean elements.

Conifers Conifers (Coniferales) comprise trees or more rarely shrubs characterized by long shoots and short shoots. Wood is massive with small pith. Branching is proliferating and phyllotaxis is helical or decussate. Leaves are homomorphic or heteromorphic, typically small needlelike, scaly or conical, supplied by a single vein or more rarely two veins. Most conifers are monoecious. The ovules and microsporangia are terminal borne in cones. Ovulate cones are compound with ovules born on seed scale that is fused to the supporting cone scale. Mature seeds are usually rather small with a hard seed wall. Microsporangiate cones are simple and the pollen sacs are born on the abaxial surface of the microsporophylls. Conifers were abundant in the Mesozoic with many extinct forms occurring well into the Cretaceous. In the Yixian Formation all conifers so far recorded appear to belong to extinct genera and families. The most abundant conifer is *Schizolepis* (Figs. 235, 236), but *Elatocladus* (Fig. 237) and *Brachyphyllum* also constitute an important part of the Jehol plant assemblage.

Bennettites Bennettites (Bennettitales) are extinct seed plants with a habit resembling that of the cycads both in the stature and in the morphology of leaves. Bennettites are reconstructed as small, sparsely branched or unbranched trees or small shrubs. The trunk is slender or in some bennettites barrel-shaped. Leaves are large, simple (entire) or pinnately divided, very similar in gross morphology to some cycad leaves. The two groups can, however, easily be distinguished by their epidermal features when present. The ovules and microsporophylls are crowded in rather large flowerlike structures that may be unisexual or bisexual. The ovules and mature seeds are minute and terminal densely spaced on a conical or spherical receptacle together with small interseminal scales. The microsporangia are borne on simple or branched (pinnate, bipinnate) microsporophylls. The bennettites were common in Triassic, Jurassic and Early Cretaceous strata but became extinct by the end of the Cretaceous. In the Yixian Formation four forms have been reported (Figs. 238—240).

Gnetales Gnetales comprise three extant genera (*Ephedra*, *Gnetum*, *Welwitschia*) that are morphologically very distinct. The phylogenetic posi-

238 *Williamsonia bella*, a bennettite, 10.1 cm long.

tion of the group is uncertain. It was sometimes placed close to the angiosperms, but has recently been associated with the conifers. *Ephedra* and *Gnetum* include trees, shrubs, vines and climbers with proliferate branching and decussate or whorled phyllotaxis. *Welwitschia* is unusual in having a very condensed, unbranched stem and two persistent leaves that grow for the entire life of the plant. The plants are mostly dioecious, rarely monoecious. The ovules and microsporophylls are terminal borne in small compound, unisexual cones. The mature seeds are small to large. The microsporangia are borne in synangia. *Ephedra* is xerophytic and *Welwitschia* extreme xerophytic, while *Gnetum* is tropical genus with a wider ecological range inhabiting moist to rather dry environments. The fossil history of Gnetales is poorly known but Gnetales pollen occurs abundantly in Early Cretaceous sediments. In the Yixian Formation remnants of Gnetales are relatively common and several taxa have been described. Among these are *Eragrosites changii* and *Liaoxia chenii* (Fig. 241) that was assigned to the extinct genus *Ephedrites* (Guo and Wu, 2000), and *Chaoyangia liangii* (Fig. 242) assigned to the extinct genus *Gurvanella* (Sun et al., 2001). They are all closely similar to Ephedra in their vegetative morphology, but some (e.g., *Gurvanella*) are distinguishable from *Ephedra* in the ovulate structures.

Angiosperms Angiosperms (Angiospermae) are the most diverse of all plant groups and exhibit an enormous range in vegetative and reproductive features. Probably the most distinct feature that distinguishes angiosperms from other plants is the enclosure of the ovules in carpellary tissue and pollen tube growth via the carpellary tissue to the ovules. Several angiosperms have been described from the Yixian formation but most of them are dubious (Figs. 243～250). Some have already been placed in the Gnetales, while the features of others such as *Archaefructus* is still debated (see the Chapter "Angiosperms"). A more distinct angiosperm was described recently by Qin Leng and Else M. Friis and will be treated in the next chapter together with a discussion on the Jehol angiosperms.

(Unless otherwise stated, fossils shown in this chapter are collected from the Jianshangou Bed of the lower part of the Yixian Formation at Huangbanjigou, Beipiao, Liaoning, photo by Da-jian Li/ CAS)

239 *Rehezamites anisolobus*, a possible bennettite, 10.1 cm long (**Left**).

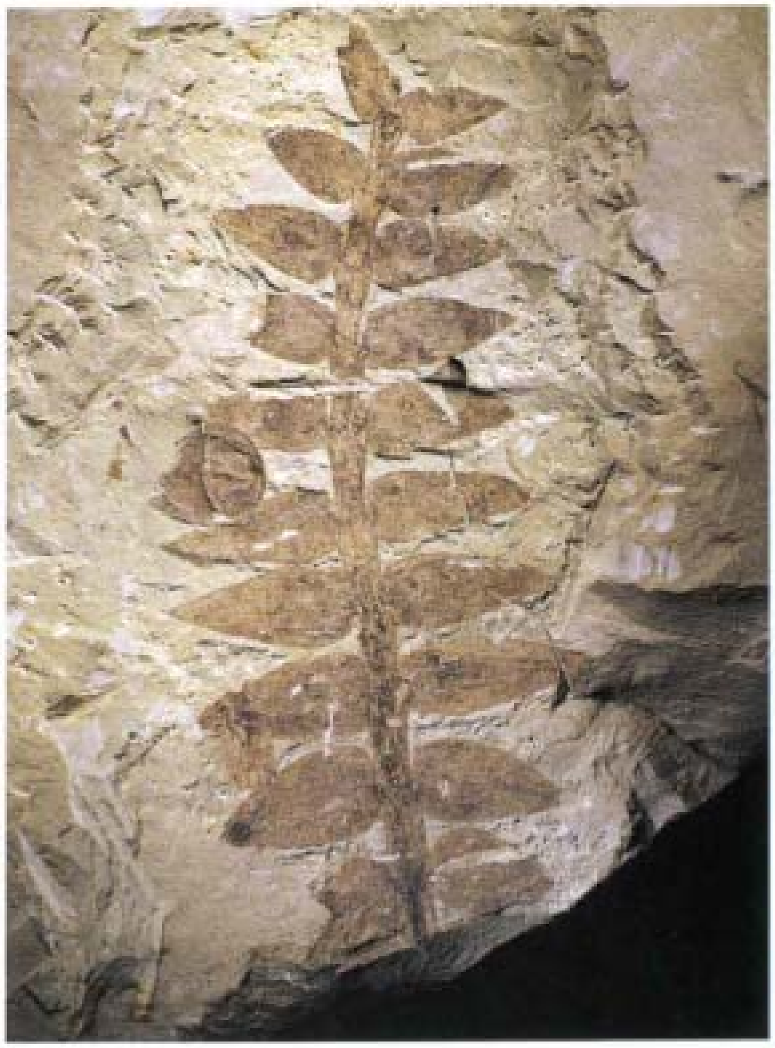
240 *Tyrmia acrodonta*, a bennettite, 6.9 cm long (**Right**).

241 *Liaoxia chenii*, a gnetale, 8.9 cm long. (Photo: Dong-xing Deng/ NIGP)

242 *Chaoyangia liangii*, a gnetale, 0.85 cm long.

243 *Erenia stenoptera*, Plantae incertae sedis, 0.5 cm long. (Photo: Dong-xing Deng/ NIGP)

244 *Typhaera fusiformis*, Plantae incertae sedis, 1.8 cm long. (Photo: Shi-wei Zhao/ NIGP)



245 Leaf shoot of *Lilites reheensis*, Plantae incertae sedis, 9.8 cm long, showing opposite and amplexicaul leaves, and arching veins.

246 Fruit spur of *Lilites reheensis*, Plantae incertae sedis, 4.5 cm long, showing terminal fruit and opposite leaves.

247 *Carpolithus* sp., Plantae incertae sedis, 0.6 cm long. (Photo: Dong-xing Deng/ NIGP)

248 *Antholithus ovatus*, Plantae incertae sedis, 1.9 cm long.

249 *Antholithus* sp. 1, Plantae incertae sedis, 3.1 cm long. (Photo: Dong-xing Deng/ NIGP)

250 *Antholithus* sp. 2, Plantae incertae sedis, 3.5 cm long. (Photo: Shi-wei Zhao/ NIGP)

Sinocarpus decussatus
Photo: Yvonne Arremo/ NRM

ANGIOSPERMS

Qin Leng,
Shun-qing Wu,
Else Marie Friis

Angiosperms (flowering plants) are ecologically dominant in most terrestrial vegetation today, accounting for the bulk of the primary productivity on land. They constitute the most species-rich group of land plants that ever existed, with an overwhelming morphological diversity of flowers and growth forms ranging from the tiniest duckweed to the tallest trees. They also occur in most ecosystems on land from deserts to coastal swamps and even have representatives living in the oceans. Despite their prominent position in the modern world, the angiosperms diversified very late in the history of land plants and their rise to ecological dominance took place over a relatively short time interval during the Cretaceous, more than 300 million years after plants' first invasion onto the land.

The earliest unequivocal angiosperm fossils are pollen grains from Valanginian–Hauterivian strata of Israel (Brenner, 1996) and southern England (Hughes, 1994), about 130~135 million years old. Angiosperms are rare in these earliest Cretaceous strata but by the Barremian–Aptian, 10~15 million years after their first occurrence, they were already widely established, and the transition from the ancient Mesozoic vegetation, dominated by gymnosperms (cycads, ginkgos, seed ferns, bennettitaleans, conifers) and pteridophytes (lycopods, horsetails, ferns), to the modern ecosystems was well under way.

Plum trees, tea bushes, walnut trees, sunflowers, rice, and the crops that give us our breakfast cereals are among the familiar angiosperms essential to our everyday lives. The first angiosperms shared many features with their present-day descendants, but they were also different. How different, we do not fully know. The origin and early diversification of angiosperms have been intensively studied for more than 100 years, but many questions remain unresolved regarding the time of their origin, their

251 *Archaefructus sinensis*, an aquatic plant (preserved main axis 15 cm long), from Dawangzhangzi locality (Dawangzhangzi Bed of Yixian Formation) in Lingyuan, Liaoning (ca. 125 or 122 Ma). The left picture shows the close-up view of a reproductive axis. (Photo: Yvonne Arremo/ NRM)

ancestral features, and their closest relatives among other plant groups. So far there are neither clear signals from molecular studies nor universally accepted theoretical models on angiosperm evolution. Therefore, information from the fossil record is crucial to our understanding of angiosperm evolution and for testing various models for their phylogenetic relationships.

The Jehol Group sediments were deposited during the early phases of this Cretaceous vegetational revolution and provide a window to study changes and innovations in Early Cretaceous floras. The deposits preserve a biota that either lived in or was trapped in a system of low-energy lakes. There is no or little indication of transportation prior to fossilization. Some of the plant fossils are preserved as whole plants with roots, stems, leaves and reproductive organs in organic connection, and some of the plants were obviously aquatic. Whole plant preservation is very rare in the fossil record and has been reported only from a few places around the world. Fossil remains of whole water plants are even more unusual because they typically have very delicate structures with low fossilization potential. The Jehol plant assemblage thus provides insight into a part of the vegetational history that is poorly known. Despite the deposition that resulted in whole plant preservation and excellent information on gross morphology, plant fossils from the Jehol sediments have experienced rapid tissue decay during the very early stage of fossilization, which destroyed most of the cell-level structures (Leng and Yang, 2003). This, along with the highly specialized features of water plants, sometimes makes interpretations and systematic inferences very difficult.

History of the search for Jehol angiosperms The first Jehol plants assigned to angiosperms were *Potamogeton jeholensis* Yabe et Endo and *Potamogeton?* sp. reported by two Japanese botanists H. Yabe and S. Endo in 1935, but an intensive search for angiosperms did not start until about 60 years later and several putative angiosperms were recently described from the Yixian Formation. The Late Jurassic age assignment of the lower Yixian Formation that was adopted by some authors gave the fossils an older age than angiosperms from other places and certainly contributed to the excitement of the search. The mid-Early Cretaceous age that is now widely accepted (Zhou

Fig. 252 An inflorescence (about 6.5 cm long) of *Archaefructus liaoningensis* with female (Upper) and male (Lower) organs, from Huangbanjigou locality (Jianshangou Bed of Yixian Formation) in Beipiao, Liaoning (ca. 125 Ma). (Photo: Yvonne Arremo/ NRM)

253 An almost complete plant (13.4 cm long) of *Archaefructus sinensis*, from Dawangzhangzi locality (Dawangzhangzi Bed of Yixian Formation) in Lingyuan, Liaoning (ca. 125 or 122 Ma). (Photo: Yvonne Arremo/ NRM)

et al., 2003) places the fossils in another context as coeval with early angiosperm floras from other regions. Among the fossil plants that have been recently related to the angiosperms are *Chaoyangia liangii* Duan (Duan, 1997); *Eragrosites changii* Cao et Wu, *Liaoxia chenii* Cao et Wu, and "Monocotyledon Leaf" (Cao et al., 1998); *Erenia stenoptera* Krassilov, *Lilites reheensis* Wu, *Orchidites linearifolius* Wu, *Orchidites lancifolius* Wu, *Trapa?* sp., and *Typhaera fusiformis* Krassilov (Wu, 1999); *Archaefructus liaoningensis* Sun, Dilcher, Zheng et Zhou (Sun et al., 1998) and *A. sinensis* Sun, Dilcher, Ji et Nixon (Sun et al., 2002); *Beipiaoa parva* Dilcher, Sun et Zheng, *B. rotunda* Dilcher, Sun et Zheng, and *B. spinosa* Dilcher, Sun et Zheng (Sun et al., 2001); and *Sinocarpus decussatus* Leng et Friis (Leng and Friis, 2003). Other putative angiosperms were described based on very fragmentary or poorly preserved material (e.g. several taxa described under the heading "Problematic Angiosperms" by Wu, 1999) and are not discussed further here.

The rapid decay prior to fossilization and possible morphological specialization of some of the plants to an aquatic environment make it difficult to interpret the morphology and structures. Interpretation and systematic assignment have subsequently been questioned for many of these fossils. *Chaoyangia liangii*, *Eragrosites changii*, *Liaoxia chenii* and *Potamogeton jeholensis* (later reassigned to *Ranunculus jeholensis* by Miki, 1964) show distinct affinity with members of the relict seed plant group Gnetales and two of them, *Eragrosites changii* and *Liaoxia chenii* were transferred to the extinct genus *Ephedrites* (Guo and Wu, 2000). *Potamogeton?* sp., the "Monocotyledon Leaf", *Lilites*, and the two species of *Orchidites* were re-interpreted as conifers (Sun et al., 2000, 2001), an assignment that is also problematic (see below). *Archaefructus* was originally described as bearing multiparted bisexual and naked flowers and was resolved as sister to all extant angiosperms (Sun et al., 1998, 2002). This interpretation has also been questioned and an alternative explanation offered (Friis et al., 2003), and the possibility that *Archaefructus* is more closely related to other seed plants was discussed by Zhou and others (2003). In the following sections we comment briefly on fossil plants that still remain of interest in the discussion on Early Cretaceous angiosperm structure and diversity.

Archaefructus—a submerged water plant The extinct genus *Archaefructus* was established by Sun and others (1998). The original description included a single species, *A. liaoningensis*, which was known

256 Reconstruction of *Sinocarpus decussatus*. (Art: Qin Leng and Yu-gao Ren/ NIGP)

254 *Sinocarpus decussatus* (5 cm long), an angiosperm with advanced features, from Dawangzhangzi locality (Dawangzhangzi Bed of Yixian Formation) in Lingyuan, Liaoning (ca. 125 or 122 Ma). (Photo: Yvonne Arremo/ NRM)

255 A close-up view of the partly united carpels of the specimen shown in Fig. 254 (Photo: Xiao-yi Fan/ NIGP)

only from fragments of reproductive axes. Later more complete specimens were found and an additional species, *A. sinensis*, was described (Sun et al., 2002). *Archaefructus* includes small herbaceous plants with axillary branching and elongated terminal reproductive axes (Figs. 251～253). Their general habit and morphology, particularly the strongly dissected leaves, indicate that the *Archaefructus* plants were aquatic. The reproductive axes have ovulate (female) organs above and microsporangiate (male) organs below (Fig. 252). The ovulate organs are often borne in pairs and the microsporangiate organs in clusters of one to four (Figs. 251, 253). The presence of critical angiosperm features of *Archaefructus* has not been fully documented, and many of the reproductive features are still poorly understood. The morphology of the reproductive organs indicates that the ovulate organs might be carpels and the microsporangiate organs stamens as in angiosperms. Their arrangement in pairs or clusters along the axis suggests that each reproductive axis is an inflorescence with many laterally arranged flowers (Friis et al., 2003), rather than a single flower as originally described. Each flower in the inflorescence is simple and unisexual with only few parts. The female flowers above consist of one or two carpels and male flowers below one to four (typically two or three) stamens. The flowers are naked, which may be interpreted as a secondary loss. This is compatible with a submerged aquatic nature inferred for the flowers, since flowers underwater do not require perianth parts for protection against desiccation or for attracting pollinators. Similar simple and naked floral structures are typical for modern angiosperms specialized for flowering under water. The position of the inflorescence axes at different levels of the plants (Figs. 251, 253) also supports the interpretation of submerged flowers as do the lax appearance of some of the reproductive

257 *Orchidites linearifolius*, an uncertain angiosperm (6.7 cm long), from Huangbanjigou locality (Jianshangou Bed of Yixian Formation) in Beipiao, Liaoning (ca. 125 Ma). (Photo: Xiao-yi Fan/ NIGP)

258 *Orchidites lancifolius*, an uncertain angiosperm (2.2 cm long), from Huangbanjigou locality (Jianshangou Bed of Yixian Formation) in Beipiao, Liaoning (ca. 125 Ma). (Photo: Xiao-yi Fan/ NIGP)

axes (Fig. 252).

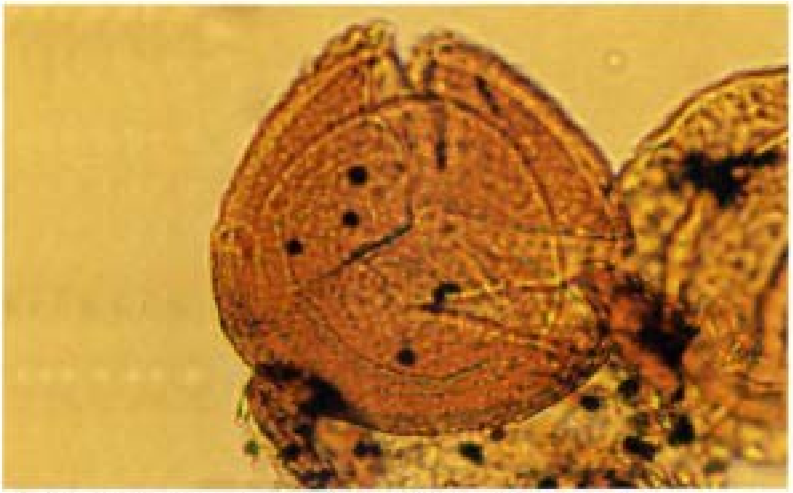
Sinocarpus — an angiosperm with advanced features *Sinocarpus decussatus* comprises a single fragment of an infructescence axis (Figs. 254–256). The specimen is fossilized in the fruiting stage with fruits born on long, slender stalks in an opposite pattern (Figs. 254, 256). The fruits are from hypogynous flowers and composed of (3–) 4 carpels that are partly united. Although the fossil is incomplete and strongly compressed, it is clearly from an angiosperm mainly because of its united carpels. United carpels are generally regarded as a more derived feature in angiosperms and characteristic for most of the "higher" flowering plants called eudicots. The systematic position of *Sinocarpus* has not been established with certainty, but the fossil shows particular similarity to living eudicot plants that have a combination of derived and more primitive features of angiosperms as seen in members of the Ranunculaceae, Buxaceae, and Myrothamnaceae.

Other possible angiosperms The affinity of other putative angiosperms in the Jehol Flora is still uncertain. Since many of them are fragmentarily preserved or lack reproductive organs, we can only speculate until more information is available. Among these uncertain angiosperms are the vegetative branches of *Potamogeton?* sp., the "Monocotyledon Leaf", and the two species of *Orchidites* (Figs. 257, 258). All of them have leaves that in size and shape, venation pattern and arrangement are very similar to each other and may be conspecific. They all display long, linear and lax leaves with parallel venation, and in general appearance they resemble some monocotyledons and also some modern aquatic plants. They were all transferred to the conifers and included in the extinct taxon *Liaoningocladus boii* Sun, Zheng et Mei (Sun et al., 2001, 2000). Features supporting the affinity with conifers are not clear and the special (syndetocheilic) type of stomata described for *Liaoningocladus* is characteristic for angiosperms but absent in conifers. It is thus possible that these fossils are indeed angiosperms as first suggested, but their systematic affinity still remains to be studied in more detail. The putative angiosperm *Lilites reheensis* was also re-interpreted as a conifer and renamed *Podocarpites reheensis* (Wu) Sun et Zheng (Sun et al., 2001). However, for a full documentation of its systematic position, more details of venation pattern, epidermal structure, and reproductive organs are needed.

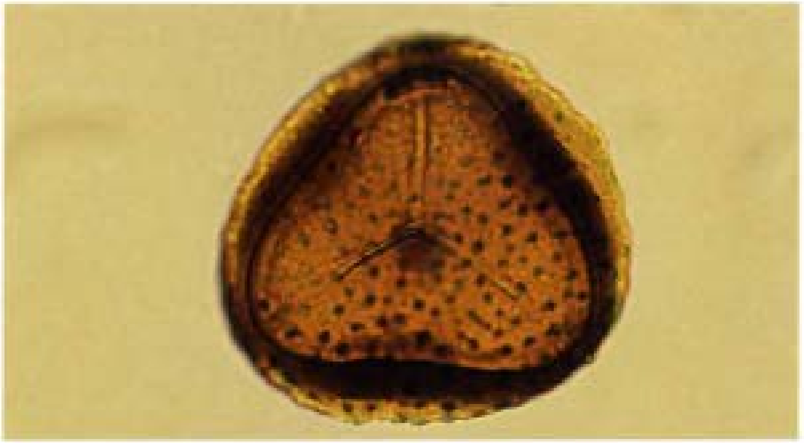
Some of the isolated reproductive organs from the Yixian Formation such as those described as *Trapa?* sp., *Beipiaoa parva*, *B. rotunda* and *B. spinosa* have sturdy spines (Fig. 259), a feature often seen in fruits and seeds of extant aquatic angiosperms, and these organs may also be produced by ancient water plants. But so far they have not been discovered in organic association with any vegetative structures and thus their full nature has yet to be clarified.

259 A spiny fruit (seed) of *Beipiaoa spinosa*, an uncertain angiosperm (1 cm long), from Huangbanjigou locality (Jianshangou Bed of Yixian Formation) in Beipiao, Liaoning (ca. 125 Ma). (Photo: Xiao-yi Fan/ NIGP)

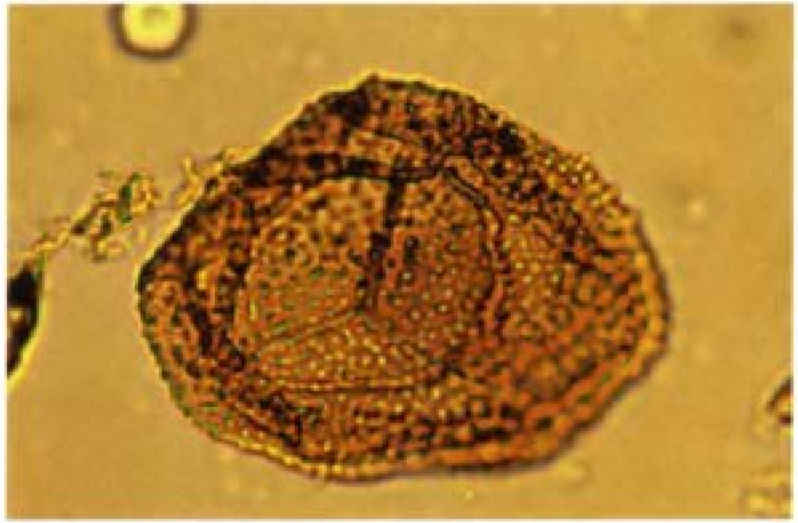
The Jehol angiosperms in a global context Although angiosperms are relatively rare in the Jehol Biota and different from plant fossils described from other regions, they are also in broader terms in good agreement with plants from other Barremian–Aptian floras. Small, simple and few parted unisexual flowers as known for *Archaefructus* are common in contemporaneous floras from Europe and North America and eudicots were established by this time at least in Africa, Europe and North America. The presence of aquatic plants early in the history of angiosperms has also been inferred based on fossils from other places, but so far whole plant evidence for an early specialization to aquatic environment has only been discovered in the Jehol Biota.



260 *Densoisporites microrugulatus*, spore of a selaginellales.



261 *Tenuangulasporis microverrucosus*, spore of a possible selaginellales.



262 *Osmundacidites wellmanii*, spore of a filicales.

SPORES AND POLLEN

Wen-ben Li

Spores and pollen are productive organs of plants. Pteridophytes and some of the more primitive plants, such as bryophytes, algae and fungi, produce spores by which new generation of plant is reproduced sexually or nonsexually. Seed plants (spermatophytes), including gymnosperms and angiosperms, produce pollen. Sperms of pollen (male spores) combine with ova of female ovule and develop into seeds. The reproduction of seed plants depends on germination of the seeds. The study of spores and pollen is called palynology. Spores and pollen are very small in size, commonly under 200 microns, but very large in quantity. Because of their organic anti-decomposition wall (exine), they can be well preserved together with mineral clastics in the sediments through the geological history. In order to extract spores and pollen from the sediments, the rock containing spores and pollen must be generally macerated in nitric and hydrofluoric solutions to separate the spores and pollen from mineral clastics. After collected from the rock residue, the spores and pollen are mounted with glycerine jelly on glass slides. We can observe and identify them under microscope at power from 600 to 1000 enlargements. Generally speaking, the spores and pollen from different plant taxa show different morphology, including that of their exinal structure and ornamentation. By means of palynological taxonomic study, we can well reconstruct the vegetation, climate and environment, and date the age when they were growing.

The Yixian Formation cropping out at Jianshangou and Huangbanjigou of Beipiao, Zaocishan of Yixian and Sunjialing, Sanguanmiao and Gujialing of Harqin Zuoyi, western Liaoning yields abundant fossil spores and pollen (Figs. 260—268), with about 70 known species assigned to 40 genera. Most species in the spore-pollen assemblage are common taxa through the whole Mesozoic era, for example, the spores of *Stereisporites antiquasporites* of bryophytes, *Lycopodiumsporites austroclavatidites*, *Leptolepidites verrucosus*, *Neoraistrickia equalis*, *Densoisporites microrugulatus* of lycopodiales, *Cyathidites minor*, *Osmundacidites wellmanii*, *Klukisporites pseudoreticulatus* and *Baculatisporites comaumensis* of filicales, and the pollen grains of *Classopollis annulatus*, *Ginkgocycadophytus nitidus*, *Ephedripites* sp., *Caytonipollenites pallidus*, *Perinopollenites elatoides*, *Pinuspollenites divulgatus*, *Abietineaepollenites pectinellus*, *Cedripites pusillus*, *Cedripites*

263 *Cicatricosisporites pacificus*, spore of a filicales.

264 *Schizaeoisporites certus*, spore of a filicales.

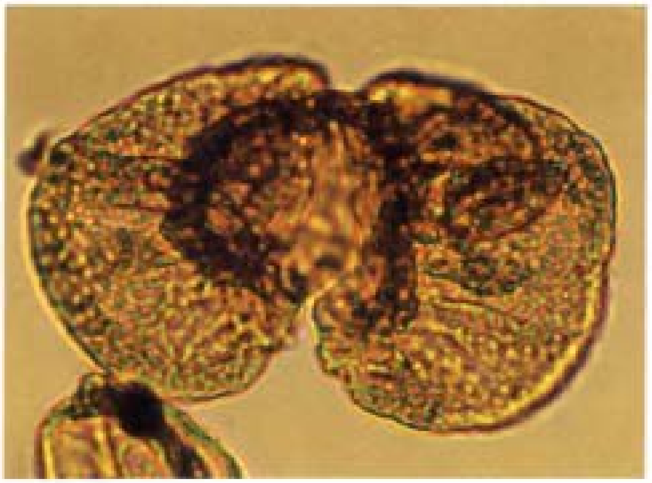
265 *Pinuspollenites divulgatus*, pollen of a gymnosperm.

microsaccoides, *Piceaepollenites* spp., *Abiespollenites* spp., *Podocarpidites multesimus*, *Podocarpidites ornatus*, *Callialasporites dampieri*, *Bicestopollis wulanensis*, *Quadraeculina limbata*, *Protoconiferus funarius*, *Protopinus sp.*, *Pseudopicea variabiliformis* and *Pseudopicea rotundiformis* of gymnosperms. But some others are species rising from the Cretaceous period, such as *Cicatricosisporites australiensis*, *Cicatricosisporites pacificus*, *Schizaeoisporites certus* of lygodiaceae, *Cyclocristella senticosa*, *Tenuangulasporis qinchengensis*, *Tenuangulasporis microverrucosus* of selaginellales and *Jugella claribaculata*, *Jiaohepollis flexuosus* and *Jiaohepollis annulatus* of gymnosperms.

Palynological study demonstrates that during the accumulation time of deposition of the Yixian Formation, the main part of the vegetation in western Liaoning Province was composed of conifers that occupies over 90 % of the whole vegetation. Under the coniferous forest some bryophytes, pteridophytes and cycadophytes grew sparsely. Angiosperm megafossil plant *Sinocarpus decussatus* and several other purported ones were recorded from different horizons of the Yixian Formation (see the Chapter "Angiosperms"), but so far we have not found a single reliable angiosperm pollen grain from the whole Yixian Formation. In consideration of the infrequent appearance of the genera *Cicatricosisporites*, *Schizaeoisporites*, *Tenuangulasporis* and *Jiaohepollis*, the age of the Yixian Formation should be of the earliest Cretaceous (Berriasian), 135—131 million years before present.

The *Classopollis* of xerophytic cheirolepidiaceae, usually amounts to 15—91% in content, dominating the spore-pollen assemblage of the latest Jurassic Houcheng Formation in Xuanhua and Wanquan, northern Hebei Province. In contrast, *Classopollis* and other arid-tolerating taxa, *Schizaeoisporites* and *Ephedripites*, are rare in the Yixian Formation, only under 2% in content. This fact indicates the climate change from the arid Late Jurassic into the relatively humid Early Cretaceous in northern Hebei and western Liaoning Provinces.

(All specimens shown in this chapter are from the upper part of the Yixian Formation in Sanguanmiao, Harqin Zuoyi Mongolian Autonomous County, Liaoning Province, and photographed by Wen-ben Li/ NIGP)



266 *Podocarpidites ornatus*, pollen of a gymnosperm.

267 *Protoconiferus funarius*, pollen of a gymnosperm.

268 *Jugella claribaculata*, pollen of a gymnosperm.

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LIST OF TAXA

Animalia

Phylum Mollusca
Class Gastropoda
Subclass Prosobranchia
Family Cyclophoridae 1847
Pseudarinia yushugouensis Zhu, 1976
Family Valvatidae Muller, 1774
Amplovalvata sp.
Family Hydrobidae Fischer, 1885
Reesidella sp.
Family Micromelaniidae Brusina, 1874
Probaicalia gerassimovi (Reis, 1910)
Probaicalia vitimensis Martinson, 1949
Subclass Pulmonata
Family Ellobiidae Bolten, 1798
Ptychostylus philippii (Dunker, 1846)
Ptychostylus harpaeformis (Koch et Dunker, 1837)
Zaptychius sp.
Family Lymnaeidae Broderip, 1839
Galba sphaira Pan, 1983
Family Planorbidae Geffroy, 1767
Gyraulus sp.
Gyraulus loryi Coquand, 1855

Class Bivalvia
Subclass Palaeoheterodonta
Order Unionoida Stoliczka
Superfamily Unionacea
Family Unionidae Fleming, 1828
Mengyinaia mengyinensis (Grabau, 1923)
Mengyinaia shifoensis Yu, Dong et Yao, 1989
Mengyinaia tugrigensis (Martinson, 1961)
Family Sibireconchidae Kolesnikov, 1977
Arguniella lingyuanensis (Gu, 1976)
Arguniella yanshanensis (Gu, 1976)
Superfamily Trigonioidacea
Family Nippononaiidae Kobayashi, 1968
Nakamuranaia chingshanensis (Grabau, 1923)
Nakamuranaia subrotunda Gu et Ma, 1976
Family Plicatounionidae Kobayashi, 1968
Weichangella angularis Wang, 1982
Weichangella qingquanensis Wang, 1982
Weichangella shalingouensis Yu et Yao, 1980
Subclass Heterodonta
Order Cyrenodonta
Superfamily Corbiculacea
Family Pisidiidae Gray, 1857
Sphaerium anderssoni (Grabau, 1923)
Sphaerium jeholense (Grabau, 1923)
Sphaerium pujiangense Gu et Ma, 1976

Phylum Arthropoda
Class Crustacea
Subclass Branchiopoda
Order Conchostraca
Family Eosestheriidae Zhang et Chen, 1976
Abrestheria rotunda Wang, 1981
Allestheria striata Shen et Chen, 1982
Eosestheria aff. *middendorfii* (Jones, 1862)
Eosestheria fuxinensis Chen, 1976
Eosestheriopsis gujialingensis (Wang, 1987)
Eosestheria jingangshanensis Chen, 1976
Eosestheria lingyuanensis Chen, 1976
Eosestheria ovata (Chen, 1976)
Eosestheria peipiaoensis (Kobayashi et Kuzumi, 1953)
Eosestheria subrotunda Chen, 1976
Yanjiestheria jinfotangensis (Chen, 1976)
Yanjiestheria beipiaoensis Chen, 1999
Yanshania xishunjingensis Wang, 1981

  - *Yumenestheria delicatula* Shen et Chen, 1982
- Family Diestheriidae Zhang et Chen, 1976
  - *Diestheria jeholensis* (Kobayashi et Kuzumi, 1953)
  - *Diestheria longinqua* Chen, 1976
  - *Diestheria yixianensis* Chen, 1976
- Family Loxomegaglyptidae Novojilov, 1950
  - *Ambonella lepida* Wang, 1981
  - *Nestoria dabeigouensis* Wang, 1981
  - *Nestoria pissovi* Krasinetz, 1962
- Family Sinoestheriidae Chen et Shen, 1982
  - *Sentestheria banjietaensis* Wang, 1981
  - *Sentestheria weichangensis* Wang, 1981
- Family Ipsiloniidae Novojilov, 1958
  - *Keratestheria gigantea* Wang, 1981
  - *Keratestheria longa* Wang, 1981
- Family Palaeolimnadiidae Tasch, 1956
  - *Jibeilimnadia ovata* Wang, 1981

- Subclass Ostracoda
  - Order Podocopida
    - Superfamily Cypridacea
      - Family Cyclocyprididae Kaufmann, 1900
        - Subfamily Cyclocypridinae Kaufmann, 1900
          - *Damonella extenda* Wu et Yang, 1980
          - *Damonella formosa* Cao, 1999
          - *Damonella subsymmetraca* Zhang, 1985
          - *Ziziphocypris cosdata* (Galeeva, 1955)
          - *Ziziphocypris linchengensis* Su et Li, 1981
          - *Ziziphocypris simacovi* (Mandelstam, 1955)
      - Family Cyprididae Baird, 1845
        - Subfamily Cyprideinae Martin, 1940
          - *Cheilocypridea trapezoidea* Zhang, 1985
          - *Cypridea (Cypridea) altidorsangulata* Pang, 1984
          - *Cypridea (Cypridea) dabeigouensis* Yang, 1981
          - *Cypridea (Cypridea) jingangshanensis* Zhang, 1985
          - *Cypridea (Cypridea) liaoningensis* Zhang, 1985
          - *Cypridea (Cypridea) luanpingensis* Pang,1984
          - *Cypridea (Cypridea) obliquoblonga* Pang, 1984
          - *Cypridea (Cypridea) prognata* Lubimova, 1956
          - *Cypridea (Cypridea) sihetunensis* Cao, 1999
          - *Cypridea (Cypridea) subgranulosa* Pang, 1984
          - *Cypridea (Cypridea) tersa* Zhang, 1985
          - *Cypridea (Cypridea) tubercularis* Pang, 1984
          - *Cypridea (Cypridea) unicostata* Galeeva, 1955
          - *Cypridea (Cypridea) vitimensis* Mandelstam, 1955
          - *Cypridea (Cypridea) zaocishanensis* Zhang, 1985
          - *Cypridea (Ulwellia) beipiaoensis* Cao, 1999
          - *Cypridea (Ulwellia) koskulensis* Mandelstam, 1958
          - *Cypridea (Ulwellia) muriculata* Zhang, 1985
          - *Cypridea (Ulwellia) regia* Lubimova, 1956
          - *Cypridea (Ulwellia) subelongata* Zhang, 1985
          - *Djungarica camarata* Zhang, 1985
          - *Djungarica circulitriangula Zhang*, 1985
          - *Djungarica procurva Zhang*, 1985
          - *Limnocypridea abscondida* Lubimova, 1956
          - *Limnocypridea grammi* Lubimova, 1956
          - *Limnocypridea posticontracta* Zhang, 1985
          - *Limnocypridea rara* Zhang, 1985
          - *Limnocypridea redunca* Zhang, 1985
          - *Limnocypridea tulongshanensis* Zhang, 1985
          - *Luanpingella postacuta* Yang, 1981
          - *Mongolianella palmosa* Mandelstam, 1955
          - *Mongolianella subtrapezoidea* Yang, 1981
          - *Yanshanina dabeigouensis* (Yang, 1981)
          - *Yumenia casta* Zhang, 1985
          - *Yumenia jianchangensis* (Su et Li, 1985)
        - Subfamily Cypridinae Baird, 1845
          - *Lycopterocypris infantinis* Lubimova, 1956
          - *Mantelliana* sp.
          - *Torinina obesa* (Pang, 1984)
          - *Torinina tersa* Sinitsa, 1992
          - *Yixianella marginulata* Zhang, 1985
      - Family Ilyocypridae Kaufmann, 1900
        - Subfamily Ilyocyprinae Kaufmann, 1900
          - *Rhinocypris jurassica* (Martin, 1940)
    - Superfamily Darwinulacea
      - Family Darwinulidae Brady et Norman, 1889
        - *Darwinula leguminella* (Forbes, 1855)
        - *Darwinula oblonga* (Roemer, 1839)
    - Superfamily Cytheracea
      - Family Limnocytheridae Klie, 1933
        - *Timiriasevia eminula* Zhang, 1985
        - *Timiriasevia jianshangouensis* Zhang, 1985
        - *Timiriasevia polymorpha* Mandelstam, 1955

Subclass Malacostraca
Order Decapoda
Superfamily Astacoidea
Family Cricoidoscelosidae Taylor, Schram et Shen, 1999 (emend.)
Cricoidoscelosus aethus Taylor, Schram et Shen, 1999
Palaeocambarus licenti (Van Straelen, 1928) Taylor, Schram et Shen, 1999
Order Hemicaridea
Family Spelaeogriphidae Gorden, 1957
Liaoningogriphus quadripartitus Shen, Taylor et Schram, 1998

Class Arachnida
Order Araneida
Family Araneidae Koch et Berendt, 1854
Araenidae indet.

Class Insecta
Order Ephemeroptera
Ephemeropsis trisetalis Eichwald, 1864
Order Odonata
Aeschnidium heishankowense (Hong, 1965)
Chrysogomphus beipiaoensis Ren, 1994
Congqingia rhora Zhang, 1992
Liogomphus yixianensis Ren et Guo, 1996
Mesocordulia boreala Ren et Guo, 1996
Rudiaeschna limnobia Ren et Guo, 1996
Stylaeschnidium rarum Zhang et Zhang, 2001
Order Blattaria
Blattula exetenuata Ren, 1995
Blattula platypa Ren, 1995
Blattula delicatula Ren, 1995
Karatauoblatta formosa Ren, 1995
Laiyangia delicatula Zhang, 1985
Nipponoblatta acerba Ren, 1995
Parablattula cretacea (Hong, 1982)
Order Dermaptera
Archaeosoma serratum Zhang, 1993
Longicerciata mesozoica Zhang, 1993
Sinostaphylina nanligezhuangensis (Hong et Wang, 1990)
Order Orthoptera
Falsirameus ravus Zhang, 1985
Habrohagla curtivenata Ren, 1995
Liaonemobius tanae Ren, 1998
Pseudacrida costata Lin, 1982
Sinohagla pleioneura Ren, 1995
Order Phasmatodea
Aethephasma megista Ren, 1997
Hagiphasma paradoxa Ren, 1997
Orephasma eumorpha Ren, 1997
Order Hemiptera
Anomoscytina anomala Ren, Yin et Dou, 1998
Anthoscytina aphthosa Ren, Yin et Dou, 1998
Caudaphis spinalis Zhang, Zhang, Hou et Ma, 1989
Clypostemma xyphiala Popov, 1964
Lapicixius decorus Ren, Yin et Dou, 1998
Liaocossus hui Ren, Yin et Dou, 1998
Liaocossus beipiaoensis Ren, Yin et Dou, 1998
Liaocossus exiguus Ren, Yin et Dou, 1998
Liaocossus fengningensis Ren, Yin et Dou, 1998
Liaocossus pingquanensis Ren, Yin et Dou, 1998
Mesanthocoris brunneus Hong et Wang, 1990
Mesolygaeus laiyangensis Ping, 1928
Miracossus ingentius Ren, Yin et Dou, 1998
Paroviparosiphum opimum Zhang, Zhang, Hou et Ma, 1989
Pauropentacoris macrurata Ren, Zhu et Lu, 1995
Schizopterax shandongensis Hong, 1984
Sinaphis epichare Zhang, Zhang, Hou et Ma, 1989
Sinojassus brevispinalis Zhang, 1985
Sinoviparosiphum lini Ren, 1995
Yanocossus guoi Ren, 1995
Order Coleoptera
Coptoclava longipoda Ping, 1928
Cretihaliplus chifengensis Ren, Zhu et Lu, 1995
Cretihaliplus sidaojingensis Ren, Zhu et Lu, 1995
Geotrupoides fortus Ren, Zhu et Lu, 1995
Glypta qingshilaensis Hong, 1984
Hesterniasca obesa Zhang, Wang et Xu, 1992
Holcoribeus evittatus Zhang, 1992
Notocupes laetus (Lin, 1982)
Notocupes tuanwangensis (Hong et Wang, 1990)
Ovidytes gaoi Ren, Zhu et Lu, 1995
Palaeoendomychus gymnus Zhang, 1992
Tetraphalerus lentus Ren, 1995
Sinosornia longiantenna Zhang, 1992

- Order Neuroptera
  - *Allopterus luianus* Zhang, 1990
  - *Choromyrmeleon othneius* Ren et Guo, 1996
  - *Drakochrysa sinica* Yang et Hong, 1990
  - *Kalligramma liaoningensis* Ren et Guo, 1996
  - *Lasiosmylus newi* Ren et Guo, 1996
  - *Lembochrysa miniscula* Ren et Guo, 1996
  - *Lembochrysa polyneura* Ren et Guo, 1996
  - *Limnogramma mira* Ren, 2003
  - *Mesascalaphus yangi* Ren, 1995
  - *Oloberotha sinica* Ren et Guo, 1996
  - *Oregramma gloriosa* Ren, 2003
  - *Siniphes delicates* Ren et Yin, 2002
  - *Sophogramma eucalla* Ren et Guo, 1996
  - *Sophogramma papilionacea* Ren et Guo, 1996
  - *Sophogramma plecophlebia* Ren et Guo, 1996
  - *Yanosmylus rarivenatus* Ren, 1995
- Order Raphidioptera
  - *Alloraphidia anomala* Ren, 1997
  - *Alloraphidia longistigmosa* Ren, 1994
  - *Baissoptera grandis* Ren, 1995
  - *Baissoptera euneura* Ren, 1997
  - *Caloraphidia glossophylla* Ren, 1997
  - *Mesoraphidia amoena* Ren, 1997
  - *Mesoraphidia heteroneura* Ren, 1997
  - *Mesoraphidia sinica* Ren, 1997
  - *Mioraphidia furcivenata* (Ren, 1995)
  - *Phiradia myrioneura* Ren, 1997
  - *Rudiraphidia liaoningensis* (Ren, 1994)
  - *Siboptera fornicata* (Ren, 1994)
  - *Xynoraphidia polyphlebia* (Ren, 1994)
  - *Xynoraphidia shangyuanensis* (Ren, 1994)
  - *Yanoraphidia gaoi* Ren, 1995
- Order Mecoptera
  - *Liaobittacus longantennatus* Ren, 1993
  - *Megabittacus colosseus* Ren, 1997
  - *Megabittacus beipiaoensis* Ren, 1997
  - *Orthophlebia liaoningensis* Ren, 1997
  - *Sibirobittacus atalus* Ren, 1997
  - *Yanorthophlebia hebeiensis* Ren, 1995
- Order Trichoptera
  - *Multimodus dissitus* Ren, 1995
  - *Multimodus stigmaeus* Ren, 1995
  - *Multimodus? elongatus* Ren, 1995
  - *Tuanwangica aethoneura* Zhang, 1985
- Order Diptera
  - *Alleremonomus xingi* Ren, 1995
  - *Alleremonomus liaoningensis* Ren, 1995
  - *Allomyia ruderalis* Ren, 1998
  - *Archisolva cupressa* Zhang, Zhang et Li, 1993
  - *Atalosciophila yanensis* Ren, 1995
  - *Basilorhagio venustus* Ren, 1995
  - *Chironomaptera gregaria* (Grabau, 1923)
  - *Chironomaptera vesca* Kalugina, 1976
  - *Eopangonius pletus* Ren, 1998
  - *Florinemestrius pulcherrimus* Ren, 1998
  - *Helempis eucalla* Ren, 1998
  - *Helempis yixianensis* Ren, 1998
  - *Lepteremochaetus lithoecius* Ren, 1998
  - *Lichnoplecia kovalevi* Ren, 1995
  - *Manlayamyia dabeigouensis* Zhang, 1991
  - *Oiobrachyceron limnogenus* Ren, 1998
  - *Opiparifungivora aliena* Ren, 1995
  - *Orsobrachyceron chinensis* Ren, 1998
  - *Palaepangonius eupterus* Ren, 1998
  - *Pauromyia oresbia* Ren, 1998
  - *Plecíomimella perbella* Zhang, Zhang, Liu et Shangguan, 1986
  - *Protapiocera megista* Ren, 1998
  - *Protapiocera ischyra* Ren, 1998
  - *Protempis minuta* Ren, 1998
  - *Protonemestrius beipiaoensis* Ren, 1998
  - *Protonemestrius jurassicus* Ren, 1998
- Order Hymenoptera
  - *Allogaster ovata* Ren, 1995
  - *Alloserphus saxosus* Zhang et Zhang, 2001
  - *Alloxyelula lingyuanensis* Ren, 1995
  - *Angaridyela endemica* Zhang et Zhang, 2000
  - *Angaridyela exculpta* Zhang et Zhang, 2000
  - *Angaridyela robusta* Zhang et Zhang, 2000
  - *Angaridyela suspecta* Zhang et Zhang, 2000
  - *Baissodes grabaui* Ren, 1995
  - *Beipiaoserphus elegans* Zhang et Zhang, 2000

Ceratoxyela decorosa Zhang et Zhang, 2000
Chengdeserphus petidatus Ren, 1995
Crephanogaster rara Zhang, Rasnitsyn et Zhang, 2002
Eopelecinus similaris Zhang, Rasnitsyn et Zhang, 2002
Eopelecinus vicinus Zhang, Rasnitsyn et Zhang, 2002
Eophelecinus shangyuanensis Zhang, Rasnitsyn et Zhang, 2002
Gurvanotrupes exiguus Zhang et Zhang, 2001
Gurvanotrupes liaoningensis Zhang et Zhang, 2000
Gurvanotrupes stolidus Zhang et Zhang, 2001
Heteroxyela ignota Zhang et Zhang, 2000
Isoxyela rudis Zhang et Zhang, 2000
Jeholoropronia pingi Ren, 1995
Lethoxyela excurva Zhang et Zhang, 2000
Lethoxyela vulgata Zhang et Zhang, 2000
Liadoxyela chengdeensis Ren,1995
Liaoropronia leonina Zhang et Zhang, 2001
Liaoropronia regia Zhang et Zhang, 2001
Liaoserphus perrarus Zhang et Zhang, 2001
Liaotoma linearis Ren, 1995
Liaoxyela antiqua Zhang et Zhang, 2000
Manlaya flexuosa (Ren, 1995)
Mesaulacinus rasnitsyni Ren, 1995
Ocnoserphus sculptus Zhang et Zhang, 2001
Palaeathalia laiyangensis Zhang, 1985
Pompiloperus sp.
Procretevania pristina Zhang et Zhang, 2000
Protocyrtus validus Zhang et Zhang, 2001
Protoscolia imperialis Zhang, Rasnitsyn et Zhang, 2002
Protoscolia normalis Zhang, Rasnitsyn et Zhang, 2002
Protoscolia sinensis Zhang, Rasnitsyn et Zhang, 2002
Saucrotrupes decorosus Zhang et Zhang, 2001
Scalprogaster fossilis Zhang et Zhang, 2001
Scolichneumon rectivenius Ren, 1995
Scorpiopelecinus versatilis Zhang, Rasnitsyn et Zhang, 2002
Shandongodes lithodes Zhang, 1985
Sinopelecinus delicatus Zhang, Rasnitsyn et Zhang, 2002
Sinopelecinus epigaeus Zhang, Rasnitsyn et Zhang, 2002
Sinopelecinus magicus Zhang, Rasnitsyn et Zhang, 2002
Sinopelecinus viriosus Zhang, Rasnitsyn et Zhang, 2002
Sinosepulca giganthoracalis Ren, 1995
Sinowestratia communicata Zhang et Zhang, 2000
Sinoxyela viriosa Zhang et Zhang, 2000
Spherogaster coronata Zhang et Zhang, 2001
Steleoserphus beipiaoensis Zhang et Zhang, 2001
Stemmogaster celata Zhang, 1985
Tanychora beipiaoensis Zhang et Rasnitsyn, 2003
Tanychora exquisita Zhang et Rasnitsyn, 2003
Tanychora sinensis Zhang, 1991
Tanychora spinata Zhang et Rasnitsyn, 2003
Tanychorella dubia Zhang et Rasnitsyn, 2003
Trematothoracoides liaoningensis Zhang, Zhang et Wei, 2001
Tuphephialtites zherikhini Zhang, Rasnitsyn et Zhang, 2002
Xyelites lingyuanensis Zhang et Zhang, 2000
Yanocleistogaster canaliculata Ren, 1995

- Phylum Chordata
  - Subphylum Vertebrata
    - Class Osteichthyes
      - Subclass Actinopterygii
        - Order Acipenseriformes
          - Family Peipiaosteidae Liu et Zhou, 1965
            - *Peipiaosteus fengningensis* Bai, 1983
            - *Peipiaosteus pani* Liu et Zhou, 1965
            - *Yanosteus longidorsalis* Jin, Tian, Yang et Deng, 1995
          - Family Polyodontidae Bonaparte, 1838
            - *Protopsephurus liui* Lu, 1994
        - Order Amiiformes
          - Family Sinamiidae Berg, 1940
            - *Sinamia zdanskyi* Stensiö, 1935
        - Superorder Osteoglossomorpha
          - Family Lycopteridae Cockerell, 1925
            - *Lycoptera davidi* (Sauvage, 1880)
            - *Lycoptera fuxinensis* Zhang, 2002
            - *Lycoptera muroii* (Takai, 1943)
            - *Lycoptera sankeyushuensis* (Ma et Sun, 1988)
            - *Lycoptera sinensis* Woodward, 1901
            - *Lycoptera tokunagai* Saito, 1936
          - Family Kuyangichthyidae Liu, Ma et Liu, 1982
            - *Jinanichthys longicephalus* (Liu, Su, Huang et Zhang, 1963)
        - Teleostei incertae sedis
            - *Longdeichthys luojiaxiaensis* Liu, 1982
    - Class Amphibia Linnaeus, 1758

Subclass Lissamphibia Haeckel, 1866
Superorder Salientia Laurenti, 1768
Order Anura Rafinesque, 1815
Family Discoglossidae Günther, 1859
Callobatrachus sanyanensis Wang et Gao, 1999
Family incertae sedis
Liaobatrachus grabaui Ji et Ji, 1998
Mesophryne beipiaoensis Gao et Wang, 2001
Superorder Caudata Scopoli, 1777
Order Urodela Duméril, 1806
Family Cryptobranchidae Fitzinger, 1826
Chunerpeton tianyiensis Gao et Shubin, 2003
Family incertae sedis
Jeholotriton paradoxus Wang, 2000
Laccotriton subsolanus Gao, Cheng et Xu, 1998
Liaoxitriton zhongjiani Dong et Wang, 1998
Sinerpeton fengshanensis Gao et Shubin, 2001

Class Reptilia
Order Chelonia
Suborder Cryptodira
Family Sinemydidae Yeh, 1963
Manchurochelys liaoxiensis Ji, 1995
Manchurochelys manchoukuoensis Endo et Shikama, 1942

Subclass Diapsida
Order Choristodera
Family incertae sedis
Hyphalosaurus lingyuanensis Gao, Tang et Wang, 1999
(=*Sinohydrosaurus lingyuanensis* Li, Zhang et Ji, 1999)
Ikechosaurus gaoi Lu, Kobayashi et Li, 1999
Monjurosuchus splendens Endo, 1940

Infraclass Lepidosauromorpha
Order Squamata
Suborder Lacertilia
Infraorder Gekkota
Family Ardeosauridae Camp, 1923
Yabeinosaurus tenuis Endo et Shikama, 1942
Infraorder Scincomorpha
Family ?Lacertidae Gray, 1825
Jeholacerta formosa Ji et Ren, 1999
Infraorder incertae sedis
Family incertae sedis
Dalinghosaurus longidigitus Ji, 1998

Subclass Archosauromorpha
Order Pterosauria
Suborder Rhamphorhynchoidea
Family Anurognathidae Kuhn, 1937
Dendrorhynchoides curvidentatus (Ji et Ji, 1998)
Jeholopterus ningchengensis Wang, Zhou, Zhang et Xu, 2002
Suborder Pterodactyloidea
Family Anhangueridae Campos et Kellner, 1985
Liaoningopterus gui Wang et Zhou, 2003
Family Nyctosauridae Nicholson et Lydekker, 1889
Chaoyangopterus zhangi Wang et Zhou, 2003
Family Pterodactylidae Bonaparte, 1838
Eosipterus yangi (Ji et Ji, 1997)
Haopterus gracilis Wang et Lüπ, 2001
Family Tapejaridae Kellner, 1989
Sinopterus dongi Wang et Zhou, 2002

Order Saurischia
Suborder Theropoda
Family Compsognathidae
Sinosauropteryx prima Ji et Ji, 1996
Family Dromaeosauridae Matthew et Brown, 1922
Sinornithosaurus milleni Xu, Wang et Wu, 1999
Microraptor gui Xu, Zhou, Wang, Kuang, Zhang et Du, 2003
Microraptor zhaoianus Xu, Zhou et Wang, 2000
Family Troodontidae Gilmore, 1924
Sinovenator changii Xu, Norell, Wang, Makovicky et Wu, 2002
Superfamily Therizinosauroidea
Family incertae sedis
Beipiaosaurus inexpectus Xu, Tang et Wang, 1999
Infraorder Oviraptorosauria
Family Caudipteridae Zhou et Wang, 2000
Caudipteryx zoui Ji, Currie, Norell et Ji, 1998
Caudipteryx dongi Zhou et Wang, 2000
Family incertae sedis
Incisivosaurus gauthieri Xu, Cheng, Wang et Chang, 2002

Theropoda, Family incertae sedis
Epidendrosaurus ningchengensis Zhang, Zhou, Xu et Wang, 2002
Protarchaeopteryx robusta Ji et Ji, 1997
Yixianosaurus longimanus Xu et Wang, 2003
Order Ornithischia
Suborder Ankylosauria
Family incertae sedis
Liaoningosaurus paradoxus Xu, Wang et You, 2001
Suborder Ceratopsia
Family Psittacosauridae Osborn, 1923
Hongshanosaurus houi You, Xu et Wang, 2003
Psittacosaurus meileyingensis Sereno, Zhao, Cheng et Rao, 1988
Psittacosaurus mongoliensis Osborn, 1923
Neoceratopsia
Liaoceratops yanzigouensis Xu, Makovicky, Wang, Norell et You, 2002
Suborder Ornithopoda
Family incertae sedis
Jeholosaurus shangyuanensis Xu, Wang et You, 2000
Infraorder Iguanodontia
Family incertae sedis
Jinzhousaurus yangi Wang et Xu, 2001

Class Aves
Subclass Sauriurae
Order and Family indet
Jeholornis prima Zhou et Zhang, 2002
Sapeornis chaoyangensis Zhou et Zhang, 2002
Order Confuciusornithiformes
Family Confuciusornithidae Hou, Zhou, Gu et Zhang, 1995
Changchengornis hengdaoziensis Ji, Chiappe et Ji, 1999
Confuciusornis chuonzhous Hou, 1997
Confuciusornis dui Hou, Martin, Zhou et Feduccia, 1999
Confuciusornis sanctus Hou, Zhou, Gu et Zhang, 1995
Confuciusornis suniae Hou, 1997
Jinzhouornis yixianensis Hou, Zhou, Zhang et Gu, 2002
Jinzhouornis zhangjiyingia Hou, Zhou, Zhang et Gu, 2002
Subclass Enantiornithes Walker, 1981
Order Eoenantiornithiformes
Family Eoenantionithidae Hou, Martin, Zhou et Feduccia, 1999
Eoenantiornis buhleri Hou, Martin, Zhou et Feduccia, 1999
Order Liaoxiornithiformes
Family Liaoxiornithidae Hou, Zhou, Zhang et Gu, 2002
Liaoxiornis delicatus Hou et Chen, 1999
Order Sinornithiformes
Family Sinornithidae Hou, 1997
Sinornis santensis Sereno et Rao, 1992
Order Cathayornithiformes
Family Cathayornithidae Zhou, Jin et Zhang, 1992
Eocathayornis walkeri Zhou, 2002
Cathayornis aberransis Hou, Zhou, Zhang et Gu, 2002
Cathayornis caudatus Hou, 1997
Cathayornis yandica Zhou, Jin et Zhang, 1992
Longchengornis sanyanensis Hou, 1997
Family Cuspirostrisornithidae Hou, 1997
Cuspirostrisornis houi Hou, 1997
Largirostrornis sexdentornis Hou, 1997
Order Longipterygiformes
Family Longipterygidae Zhang, Zhou, Hou et Gu, 2000
Longipteryx chaoyangensis Zhang, Zhou, Hou et Gu, 2000
Enantiornithes, Order and Family indet.
Boluochia zhengi Zhou, 1995
Jibeinia luanhera Hou, 1997
Otogornis genghisi Hou, 1994
Protopteryx fengningensis Zhang et Zhou, 2000
Subclass Ornithurae
Order Liaoningornithiformes
Family Liaoningornithidae Hou, 1996
Liaoningornis longiditris Hou, 1996
Order Chaoyangiformes
Family Chaoyangidae Hou, 1997
Chaoyangia beishanensis Hou et Zhang, 1993
Family Songlingornithidae Hou, 1997
Songlingornis linghensis Hou, 1997
Family incertae sedis.
Yixianornis grabaui Zhou et Zhang, 2001
Order Yanornithiformes Zhou et Zhang, 2001
Family Yanornithidae Zhou et Zhang, 2001
Yanornis martini Zhou et Zhang, 2001
Order Gansuiformes Hou et Liu, 1984
Family Gansuidae Hou et Liu, 1984
Gansus yumenensis Hou et Liu, 1984
Class Mammalia

- Order Triconodonta
  - Family incertae sedis
    - *Jeholodens jenkinsi* Ji, Luo et Ji, 1999
  - Family Repenomamidae Li, Wang, Wang et Li, 2000
    - *Repenomamus robustus* Li, Wang, Wang et Li, 2000
  - Family Gobiconodontidae Chow et Rich, 1984
    - *Gobiconodon zofiae* Li, Wang, Hu et Meng, 2003
- Order Multituberculata
  - Family Eobaataridae Kielan-Jaworowska, Dashzeveg et Trofimov, 1987
    - *Sinobaatar lingyuanensis* Hu et Wang, 2002
- Order Symmetrodonta
  - Family Spalacotheriidae Marsh, 1887
    - *Maotherium sinensis* Rougier, Ji et Novacek, 2003
    - *Zhangheotherium quinquecuspidens* Hu, Wang, Luo et Li, 1997
- Infraclass Eutheria
  - Order and Family incertae sedis
    - *Eomaia scansoria* Ji, Luo, Yuan, Wible, Zhang et Georgi, 2002

Plantae

- Division Charophyta
  - Class Charophyceae
    - Order Charales
      - Family Characeae L. Cl. Richard, 1815
        - Subfamily Aclistocharoideae Mädler, 1952
          - *Aclistochara huihuibaoensis* S. Wang, 1965
          - *Aclistochara mundula* Peck, 1941
        - Subfamily Charoideae Leonhardi, 1863
          - *Mesochara producta* Liu et Wu, 1985
          - *Mesochara voluta* (Peck, 1937)
          - *Mesochara xuanziensis* Yang, 1983
        - Subfamily Nitelloideae Al. Braun et Migula, 1890
          - *Peckisphaera multispira* (Lu et Yuan, 1991)
          - *Peckisphaera verticillata* (Peck, 1937)
          - *Peckisphaera paragranulifera* (S. Wang, 1965)
      - Family Clavatoraceae Pia, 1927
        - *Atopochara trivolvis triquetra* L. Grambast, 1968
        - *Flabellochara harrisi* (Peck, 1941)
        - *Flabellochara hebeiensis* Lu, Zhang et Zhao, 1981
      - Family Porocharaceae L. Grambast, 1962
        - Subfamily Cuneatocharoideae Z. Wang et Huang, 1978
          - *Minhechara* sp.

- Free-sporing plants
  - Bryophyta
    - *Muscites drepanophyllus* Wu, 1999
    - *Muscites tenellus* Wu, 1999
    - *Thallites dasyphyllus* Wu, 1999
    - *Thallites riccioites* Wu, 1999
  - Lycopsida
    - *Lycopodites faustus* Wu, 1999
  - Sphenopsida
    - *Equisetites longevaginatus* Wu, 1999
  - Filicopsida
    - *Botrychites reheensis* Wu, 1999
    - *Coniopteris burejensis* (Zalessky) Seward, 1904
    - *Coniopteris spectabilis* Brick, 1953
    - *Eboracia lobifolia* (Phillips) Thomas, 1829
- Seed plants
  - Ginkgoales
    - *Baiera borealis* Wu, 1999
    - *Baiera gracilis* (Been Ms) Bunbury, 1851
    - *Ginkgo apodes* Zheng et Zhou, 2003
    - *Ginkgoites* sp.
    - *Sphenobaiera* sp.
  - Czekanowskiales
    - *Czekanowskia? debilis* Wu, 1999
    - *Solenites murrayana* Lindley et Hutton, 1834
    - *Sphenarion parilis* Wu, 1999
  - Coniferales
    - *Brachyphyllum cf japonicum* (Yokoyoma) Ôishi, 1894
    - *Brachyphyllum rhombicum* Wu, 1999
    - *Cupressinocladus* sp.
    - *Cyparissidium* sp.

        - *Elatocladus leptophyllus* Wu, 1999
        - *Pityocladus densifolius* Wu, 1999
        - *Pityospermum* sp.
        - *Schizolepis beipiaoensis* Wu, 1999
        - *Schizolepis jeholensis* Yabe et Endo, 1934
    - Bennettitales
        - *Tyrmia acrodonta* Wu, 1999
        - *Williamsonia bella*, Wu, 1999
    - Bennettitales?
        - *Rehezamites anisolobus*, Wu, 1999
        - *Rehezamites* sp.
    - Gnetales
        - *Liaoxia changii* (Cao et Wu) 1997
        - *Liaoxia chenii* Cao et Wu, 1997
        - *Chaoyangia liangii* Duan, 1997
    - Angiospermae
        - *Sinocarpus decussatus* Leng et Friis, 2003
    - Angiospermae?
        - *Archaefructus liaoningensis* Sun, Dilcher, Zheng et Zhou, 1998
        - *Archaefructus sinensis* Sun, Dilcher, Ji et Nixon, 2002
        - *Beipiaoa parva* Dilcher, Sun et Zheng, 2001
        - *Beipiaoa rotunda* Dilcher, Sun et Zheng, 2001
        - *Beipiaoa spinosa* Dilcher, Sun et Zheng, 2001
        - *Liaoningocladus boii* Sun, Zheng et Mei, 2000 (*Potamogeton*? sp.; *Orchidites lancifolius* Wu, 1999; *Orchidites linearifolius* Wu, 1999)
        - *Trapa*? sp.
- Plantae Incertae Sedis
        - *Antholithus ovatus* Wu, 1999
        - *Carpolithus* sp.
        - *Erenia stenoptera* Krassilov, 1982
        - *Lilites reheensis* Wu, 1999
        - *Polygonites planus* Wu, 1999
        - *Polygonites polyclonus* Wu, 1999
        - *Rhizoma elliptica* Wu, 1999
        - *Typhaera fusiformis* Krassilov, 1982

- Spores and pollen
    - Bryophyte spores
        - *Stereisporites antiquasporites* (Welson et Webster, 1946) Dettmann, 1963
    - Pteridophyte spores
        - *Cyathidites minor* Couper, 1953
        - *Leptolepidites verrucosus* Couper, 1953
        - *Osmundacidites wellmanii* Couper, 1953
        - *Baculatisporites comaumensis* (Cookson, 1953) Potonié, 1956
        - *Neoraistrickia equalis* (Cookson et Dettmann, 1958) Pu et Wu, 1985
        - *Lycopodiumsporites austroclavatidites* (Cookson, 1953) Potonié, 1956
        - *Klukisporites pseudoreticulatus* Couper, 1958
        - *Cicatricosisporites australiensis* (Cookson, 1953) Balme, 1957
        - *Cicatricosisporites pacificus* (Bolchovitina, 1961) Zhang, 1965
        - *Schizaeoisporites certus* (Bolchovitina, 1956) Gao et Zhao, 1976
        - *Tenuangulasporis qiuchengensis* (Wang et Li, 1981) Jia, 1986
        - *Tenuangulasporis microverrucosus* (Zhang, 1984) Jia, 1986
        - *Densoisporites microrugulatus* Brenner, 1963
        - *Cyclocristella senticosa* Phillips et Felix, 1971
    - Gymnospermous pollen
        - *Perinopollenites elatoides* Couper, 1958
        - *Classopollis annulatus* (Verbitskaya, 1962) Li, 1984
        - *Ginkgocycadophytus nitidus* (Balme, 1957) de Jersey, 1962
        - *Jugella claribaculata* Mtchedlishvili et Shakhmundes, 1973
        - *Ephedripites* sp.
        - *Jiaohepollis annulatus* Yu et Miao, 1984
        - *Jiaohepollis flexuosus* (Miao, 1982) Miao et Yu, 1984
        - *Callialasporites dampieri* (Balme, 1957) Dev, 1961
        - *Bicestopollis wulanensis* Li, 1983
        - *Caytonipollenites pallidus* (Reissinger, 1950) Couper, 1958
        - *Quadraeculina anellaeformis* Maljawkina, 1949
        - *Quadraeculina limbata* Maljawkina, 1949
        - *Protoconiferus funarius* (Naumova, 1937) Bolchovitina, 1956
        - *Protopinus* sp.
        - *Pseudopicea variabiliformis* (Maljawkina, 1949) Bolchovitina, 1956
        - *Pseudopicea rotundiformis* (Maljawkina, 1949) Bolchovitina, 1956
        - *Pinuspollenites divulgatus* (Bolchovitina, 1956) Qu, 1980
        - *Abietineaepollenites pectinellus* (Maljawkina, 1949) Liu, 1982
        - *Abiespollenites* spp.
        - *Piceaepollenites* sp.
        - *Cedripites pusillus* (Zauer, 1954) Krutzsch, 1971
        - *Cedripites microsaccoides* Song et Zheng, 1981
        - *Podocarpidites multesimus* (Bolchovitina, 1956) Pocock, 1962
        - *Podocarpidites ornatus* Pocock, 1962

A COMPOSITE PICTURE OF THE JEHOL FOSSILS

Art: Anderson Yang

Fish

1. *Peipiaosteus pani*
2. *Lycoptera muroii*

Amphibian

3. *Callobatrachus sanyanensis*
4. *Jeholotriton paradoxus*

Turtle

5. *Manchurochelys liaoxiensis*

Choristodere

6. *Hyphalosaurus lingyuanensis*

Lizard

7. *Yabeinosaurus tenuis*

Pterosaur

8. *Haopterus gracilis*

Dinosaur

9. *Sinosauropteryx prima*
10. *Caudipteryx dongi*
11. *Sinornithosaurus millenii*
12. *Jinzhousaurus yangi*
13. *Beipiaosaurus inexpectus*
14. *Psittacosaurus meileyingensis*

Bird

15. *Confuciusornis sanctus*
16. *Protopteryx fengningensis*
17. *Cathayornis yandica*
18. *Longipteryx chaoyangensis*
19. *Yanornis martini*

Mammal

20. *Zhangheotherium quinquecuspidens*

Insect

21. *Ephemeropsis trisetalis*
22. *Aeschnidium heishankowense*
23. *Protonemestrius jurassicus*

Gastropod

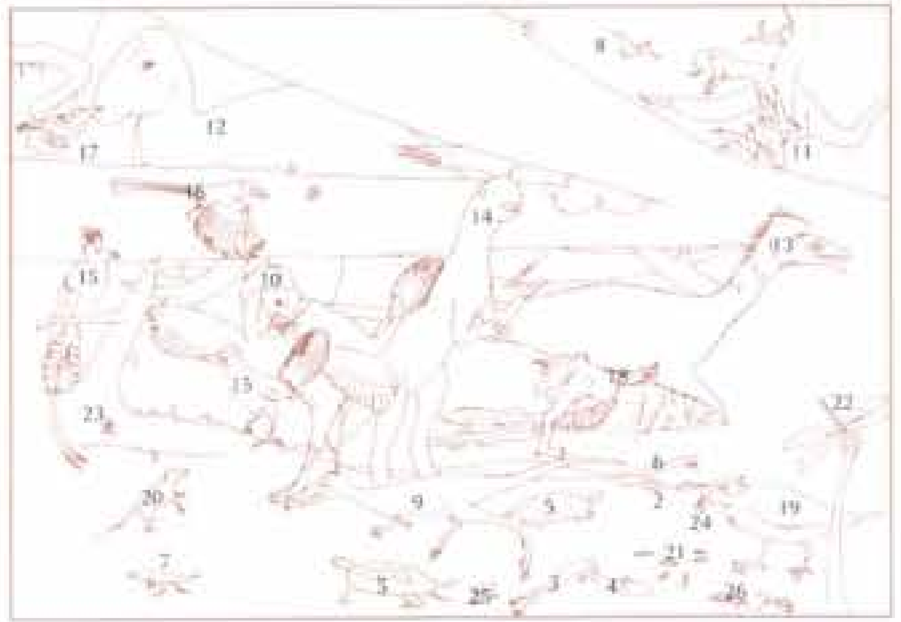
24. *Probaicalia vitimensis*

Bivalve

25. *Arguniella lingyuanensis*

Shrimp

26. *Cricoidoscelosus aethus*



ABBREVIATION OF INSTITUTIONS AND ORGANIZATIONS

AMNH	American Museum of Natural History
CAS	Chinese Academy of Sciences
CIB	Chengdu Institute of Biology, Chinese Academy of Sciences
CMNH	Carnegie Museum of Natural History
CNU	Capital Normal University (Beijing)
FMNH	The Field Museum of Natural History
GPH	Geological Publishing House (Beijing)
IHB	Institute of Hydrobiology, Chinese Academy of Sciences
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences
KIB	Kunming Institute of Botany, Chinese Academy of Sciences
KU	University of Kansas
NIGP	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
NRM	Naturhistoriska riksmuseet (Swedish Museum of Natural History)
PKU	Peking University
SAPE	Society of Avian Paleontology and Evolution
ZMUA	Zoological Museum, University of Amsterdam