

Vertebrate assemblages of the Jehol Biota in western Liaoning, China

by

Xiaolin Wang,^{1,2} Yuanqing Wang,¹ Fan Jin,¹ XingXu,¹ and Yuan Wang¹

1 Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing 100044
2 Natural History Museum, Changchun University of Science and Technology Changchun 130026

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Northern Arizona University
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Abstract

The Jehol Biota of western Liaoning Province is represented by four vertebrate complexes: the lower Yixian Fm. *Confuciusornis-Sinosauroptryx-Zhangheotherium* Complex; the middle Yixian Fm. *Monjurosuchus-Hyphalosaurus-Liaoxiornis* Complex; the upper Yixian Fm. *Lycoptera muroii-Manchurochelys manchouensis* Complex, and the Jiufotang Fm. *Cathayornis-Chaoyangia-Psittacosaurus* Complex. These assemblages are all determined to be Early Cretaceous in age and are correlated to the Mesozoic Geologic Time Scale of Gradstein et al. on the basis of $^{40}\text{Ar}/^{39}\text{Ar}$ dates from extrusive basalts and tuffs interbedded with the fossiliferous units. Age assignments for the vertebrate fossils are recognized as middle Barremian, late Barremian, and Aptian stages. The stratigraphic range represented by the Yixian and Jiufotang formations spans the late Valanginian through Barremian and Aptian stages.

Introduction*

Ever since the distinguished geologist A. W. Grabau erected the nomenclature of the Jehol System (Grabau, 1923) and Jehol Biota (Grabau, 1928) in the 1920's, the sedimentary units comprising the Jehol Group and the fauna contained therein have constituted a focal point for Chinese and international geologists and paleontologists. The Jehol Biota is produced principally from the Yixian and Jiufotang formations in western Liaoning Province, in addition to stratigraphically equivalent sediments, and represents a prolific assemblage of plants and animals characteristic of the expansive region of northeast Asia (Chen, 1988; Wang, 1990; Hong, 1993).

In the 1940's Japanese workers recovered reptilian specimens from the Yixian and Jiufotang formations at Jingangshan, in the Yixian Basin and the Fuxin, Pingquan, and Lingyuan basins (Endo, 1940; Endo and Shikama, 1942).

Since the 1970's, paleontologists have described specimens excavated from the Jiufotang Fm. at the localities of Meigeyingzi and Boluochi in the Beipiao and Chaoyang basins including a psittacosaur dinosaur (Sereno et al., 1988) and avian specimens such as *Cathayornis* (Sereno and Rao, 1992; Zhou et al., 1991; Hou et al., 1993; Zhou, 1995, Hou, 1997). Most recently, a large quantity of exquisite archaic bird specimens typified by *Confuciusornis* (Hou, 1997; Hou et al., 1995; Hou, 1996; Hou et al., 1999) have been excavated from the lower Yixian Fm. at the localities of Jianshangou and Sihetun in the Jinlingsi and Yangshan basins (Wang et al., 1998), in addition to small "feathered" theropod dinosaurs (Chen et al., 1997, Ji et al., 1998), psittacosaur ceratopsians (Xu and Wang, 1998), pterosaurs (Ji and Ji, 1997; Ji and Ji, 1998), lizards (Ji, 1998; Ren et al., 1995), turtles (Ren et al., 1995), amphibians (Ji and Ji, 1998; Wang and Gao, 1999), and a mammal (Hu et al., 1997). In addition, at Dawangzhangzi, Lingyuan Co. the first discoveries of a long-necked aquatic reptile (Gao et al., 1999) and a small delicate bird (Hou and Chen, 1999) were documented. These vertebrates constitute the most significant members of the Jehol Biota.

Vertebrate complexes

The Jehol Biota may be generally recognized as four complexes:

Lower Yixian Fm. *Confuciusornis-Sinosauroptryx-Zhangheotherium* complex: This complex is represented by an assemblage excavated at Sihetun, Beipiao Municipality. Specimens are produced from lacustrine shales of Member 3 in the Yixian Fm. at Sihetun, Shangyuanxiang, Yangshan and Jinlingsi basins and in the surrounding regions (Wang et

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al., 1998). These localities are generally correlated to the interbedded sediments of the Yixian Fm. at Jianshangou (Chen et al., 1980). Documented fossil localities include Sihetun, Jianshangou, Zhangjiagou, Huangbanjigou, Tuanshangou, Libalanggou, Heitizigou, Wudaigou, Miaogou, Dabangou, Dabeigou, Qingshiliang, and Jiancaogou. These localities trend north northeast spanning an approximately 12-14 km latitudinal range and approximately 4-5 km longitude range. The two principle vertebrate producing horizons occur in the lower section of the sediments at Sihetun and the upper section at Huangbanjigou (Wang et al., 1998, 1999). During the 1997-98 field seasons, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) undertook extensive excavations in the lower sediments at Nangou, Sihetun, and Zhangjiagou while concurrent detailed geologic field work was undertaken at Sihetun and Jianshangou. Three sites encompassing 600 square meters at Sihetun and Zhangjiagou produced several dozen significant vertebrate bearing stratigraphic levels which produced several hundred specimens of fish, reptiles (turtles, pterosaurs, theropods, sauropods, ceratopsians), and birds, in addition to copious specimens of invertebrates and gymnosperm plant macrofossils. At Sihetun and its neighboring vicinities the stratigraphic sequence of the lower Yixian Fm. is well documented, as are vertebrate bearing fossil units and their taphonomic conditions (Wang et al., 1998, 1999). The vertebrate faunal complex may now be recognized in its entirety with the following taxa:

Pisces:

Peipiaosteus pani Liu and Zhou, *P.* sp.
Lycoptera sinensis Woodward
L. davidi(Sauvage)
L. sp.,
Sinamia sp.

Amphibia:

Liaobatrachus grabaui Ji and Ji
Callobatrachus sanyanensis Wang and Gao.

Chelonia:

Manchurochelys liaoxiensis Ji
M. sp.

Lacertilia

Dalinghesaurus longiditus Ji

Pterosauria:

Eosipterus yangi Ji and Ji
Dendrorhynchus curvidentatus, Ji and Ji
Pterodactyloidea gen. et sp. nov.

Sauropoda:

Gen. et sp. indet.

Theropoda:

Sinosauropteryx prima Ji and Ji
Protarchaeopteryx robusta Ji and Ji
Caudipteryx zoui Ji et al.
Dromaeosauridae gen. et sp. nov.
Therizinosauridae gen. et sp. nov.

Ceratopsia:

Psittacosaurus sp.

Aves:

Confuciusornis sanctus Hou et al.
C. sunae Hou
C. chuonzhous Hou
C. sp.
Liaoningornis longidigitus Hou
Eoenantiornithes buhleri Hou et al.

Mammalia:

Zhangheotherium quinquecupidens Hu et al.

The taxonomic diversity of this fauna is high, with specimens dominated by the primitive sauriurine bird *Confuciusornis* (Hou et al., 1995), occasional occurrences of more derived ornithurine birds including *Liaoningornis* (Hou, 1996), and the earliest record of an enantiornithine bird *Eoenantiornithes* (Hou et al., 1999). Also documented is a developmental phase unprecedented in paleontology of small “feathered” theropods including *Sinosauropteryx* (Chen et al., 1977), *Protarchaeopteryx* (Ji and Ji, 1997), and *Caudipteryx* (Ji et al., 1998). Additional specimens representing the Dromaeosauridae and Therizinosauridae are present, as are relatively numerous specimens of psittacosaur ornithischians (Xu and Wang, 1998). Pterosaurs are dominated by the derived short-tailed Pterodactyloidea (Wang et al., 1998; Ji and Ji, 1997; Wang et al., 1999) and the long-tailed Ramphorhynchoidea also occur (Ji and Ji, 1998).

This complex preserves plesiomorphic characters while concurrently expressing derived characters. The high taxonomic diversity reflects a rapid period of radiation and a complex synthetic nature of the fauna.

The fossil vertebrates at Sihetun are principally produced from the lower stratigraphic section represented by an approximately 12 m thick unit of gray-black tuffaceous lacustrine shales interbedded with tuffs, more specifically from the lower 7 m (cross-section units 18-37), with specimens being noticeably prolific in units 25-29. The majority of the fauna is preserved in the same units producing a large quantity of *Confuciusornis* specimens which is a mere 5 mm thick tuffaceous shale (Wang et al., 1998; 1999). This represents both a phase of rapid radiation and evolution, in addition to a mass mortality event.

Middle Yixian Fm. *Monjurosuchus-Hyphalosaurus-Liaoxiornis* Complex:

This is produced from the interbedded sediments of the Yixian Fm. from the Daxinfangzi Unit in the Pingquan and Lingyuan basins (Chen et al., 1980) in addition to equivalent sediments bearing this complex. Localities include Daxinfangzi, Songzhangzi, Ershilipu, Dawangzhangzi, Fanzhangzi, and Shanzui in Yiyuan Co. Taxa within this complex include the following:

Pisces

Peipiaosteus pani Liu and Zhou

Protopsephurus liui Lu,

Lycoptera davidi (Sauvage)

Sphenacodontidae

Monjurosuchus splendens Endo

Diapsida - family insertae sedis

Hyphalosaurus lingyuanensis, Gao, Tang, and Wang

Lacertidae

Yabeinosaurus tenuis Endo and Shikama

Sauropoda indet.

Theropoda indet.

Aves

Liaoxiornis delicatus Hou and Chen

The notable characteristics of this complex include the extreme abundance of fish. In addition to the genera *Lycoptera* and *Peipiaosteus* (Lu, 1994) there is the first occurrence of *Protopsephurus* (Jin et al., 1995). Fresh water lacustrine reptiles are prolific with a relatively large quantity of *Monjurosuchus* (Endo, 1940) and the first documentation of the long necked aquatic reptile *Hyphalosaurus lingyuanensis* (Gao et al., 1999). Although avian quantity and diversity has decreased, there is an extremely tiny and delicate bird represented with a mosaic of primitive and

derived characters described as *Liaoxiornis delicatus* (Hou and Chen, 1999). This complex is extremely characteristic in its expression of primitive and derived taxa.

The Upper Yixian Fm. *Lycoptera muroii*-*Manchurochelys manchouensis* Complex: This is produced from the interbedded vertebrate bearing sediments of the Yixian Fm. at Jingangshi in the Fuxin and Yixian basins (Chen et al., 1980; Wang, et al., 1989). The predominant fossil locality is at Zaocishan, Yixian Co. Taxa include:

Pisces:

Lycoptera muroii (Takai)

Chelonia:

Manchurochelys manchouensis Endo and Shikama

Lacertilia:

Yabeinosaurus tenuis Endo and Shikama

This complex is relatively simple in character with only the single fish *Lycoptera muroii* (Lu, 1994). *Yabeinosaurus* and *Manchurochelys* are relatively abundant (Endo, 1942).

The Jiufotang Fm. *Cathayornis*-*Chaoyangia*-*Psittacosaurus* Complex: This is produced from the vertebrate bearing sediments at Meigeyingzi and Boluochi in the Beipiao and Chaoyang basins. Taxa include:

Pisces:

Peipiaosteus pani Liu and Zhou

Protopsephurus liui Lu

Sinamia zdanskyi Stensio

Lycoptera davidi (Sauvage)

Jinanichthys longicephalus (Liu et al.)

Longdeichthys luojiaxiaensis Su

Huashia sp.

Sauropoda indet.

Ceratopsia:

Psittacosaurus meileyingensis Sereno et al.

P. mongoliensis Osborn

Aves:

Sinornis santensis Sereno and Rao

Boluochia zhengi Zhou

Cathayornis yandica Zhou, Jin, and Zhang

C. caudatus Hou

Longchengornis sanyanensis Hou

Cuspirostrisornis houi Hou

Largirostrornis sexdentornis Hou

Chaoyangia beishanensis Hou and Zhang

Songlingornis linghensis Hou

Notable characteristics of this complex include the sharp decline of the fish genus *Lycoptera* which was so prolific in the Yixian Fm. and the continued abundance of *Peipiaosteus* and *Protopsephurus*, in addition to a large quantity of *Sinamia*, *Jinanichthys*, and *Longdeichthys* (Lu, 1994). Psittacosaurid ceratopsians are also abundant with the two species *P. mongoliensis* and *P. meileyingensis* (Sereno et al., 1988). Avian diversity is extremely high with a large quantity of remnant Sauriurae as represented by *Cathayornis* (Zhou et al., 1992; Hou, 1997) in addition to the derived Ornithurae such as *Chaoyangia* (Hou et al., 1993).

Discussion of chronology and correlation of vertebrate bearing units

There is definite controversy regarding the Jehol Biota and its age assignment. Geologists and paleontologists have applied different chronological methods and perspectives in their interpretations, resulting in three principle conclusions: some believe the age to be Late Jurassic (Chen, 1988; Wang, 1990; Hou et al., 1995; Chen et al., 1980; Wang, 1998; Wang et al., 1985, 1989; Gu, 1962, 1983; Liu and Zhou, 1965; Liu et al., 1963, 1986, 1987; Li et al., 1982; Sun et al., 1998), others regard the age as Late Jurassic to Early Cretaceous (Chen et al., 1997; Ji et al., 1998; Ren et al., 1995, 1997; Jin, 1996), and still others as solely Early Cretaceous (Grabau, 1923, 1928; Xu and Wang, 1998; Hao et al. 1986, 1982; Wang and Diao, 1984; Dong, 1980, 1993; Yabumoto, 1994; Li et al., 1993; Gu, 1995; Smith et al., 1995; Chen and Chen, 1997; Swisher et al., 1998). This text will address an age interpretation through the perspective of the vertebrate complexes. Previous literature recognizes the *Lycoptera* Ichthyofauna (Jin, 1996), the *Psittacosaurus* Herpetofauna (Wang and Diao, 1984; Swisher et al., 1998; Dong, 1980), and the two distinct *Confuciusornis* and *Cathayornis* avifaunas.

***Lycoptera* Ichthyofauna:** This fauna is produced from the lower lacustrine sediments of the Jehol Group in North China, typically represented by the genera *Peipiaosteus*, *Sinamia*, and *Lycoptera* (Jin, 1996). *P. pani* is extremely morphologically close to *Stichopterus* from Russia and Mongolia. Also within this fauna is *Protopsephurus liui* which most closely resembles *Paleopsephurus* from the Late Cretaceous of Montana, North America, but the latter is more derived. *Jinanichthys longicephalus* is extremely close to *Kuyangichthys* from the Early Cretaceous Guyang Fm., at Guyang, Inner Mongolia. *Londeichthys luojiaxiaensis* is closest to *Leptolepides sprattiformis* from the Kimmeridgian-Tithonian stages of Germany and France.

A comprehensive perspective of the *Lycoptera* Ichthyofauna indicates a general complexion that resembles the Late Jurassic-Early Cretaceous Purbeckian-Wealden stages of western Europe. In recent years an Early Cretaceous fish fauna has been discovered in the northern part of Kyushu, western Japan, from the Wakino Subgroup (Kwanmon Group) (Dong, 1992) which provides further evidence for determining the age of Chinese ichthyofaunas. The Japanese fauna is basically consistent with those from the Guantou Fm. and other related lithologies in the southeast coastal regions of China. The principal taxa of the coastal faunas have each been identified as resembling the North China *Lycoptera* Ichthyofauna (Jin, 1996). The Xieye Subgroup is recognized as Hauterivian-early Aptian based upon interbedded marine units (Dong, 1995). Thus the Jehol Ichthyofauna can be assigned to the Early Cretaceous with relative certainty.

***Psittacosaurus* Herpetofauna:** The reptiles within the four vertebrate complexes produced from the western Liaoning Basins may be unified into a single *Psittacosaurus* Fauna. Biogeographically, this fauna is represented in the extensive region of northeast Asia within sediments equivalent to the Jehol Group (Dong, 1980, 1993; Kimura et al., 1991; Sereno, 1990; Weishampel, 1990, Matsukawa, 1994). More recently, the fauna has also been documented in the Early Cretaceous of Thailand (Buffetaut and Suteethorn, 1992). Additional taxa representing the Jehol Biota have also migrated to neighboring regions (Chen, 1998, Buffetaut and Suteethorn, 1992).

The following reptilian taxa are recorded from the *Psittacosaurus* Fauna of western Liaoning: *Manchurochelys manchouensis*, *M. liaoxiensis*, *M. sp.*, *Monjurosuchus splendens*, *Yabeinosaurus tenuis*, *Hyphalosaurus lingyuanensis*, *Dalinghosaurus longidigitus*, *Eosipterus yangi*, *Dendrorhynchoides curvidentatus*, Pterodactyloidea gen. et sp. nov., Sauropoda indet. *Sinosauropteryx prima*, *Protarchaeopteryx robusta*, *Caudipteryx zoui*, Dromaeosauridae gen et sp. nov. Therizinosauridae gen et sp. nov., Theropoda indet. *Psittacosaurus mongoliensis*, *P. meileyingensis*, and *P. sp.*

There is a relatively close phylogenetic relationship between the turtles *Manchurochelys* from the Yixian Fm. of western Liaoning, *Dracochelys* from the Shengjinkou Fm., Tugulu Group, in the Xinjiang Autonomous Region, and *Sinemys* from the Luohandong Fm., Zhidan Group, in Inner Mongolia (Gaffney, 1992).

Yabeinosaurus is a member of the Ardeosauridae, a family commonly found in the Upper Jurassic of Europe.

Two most recently described genera from the Xixian Fm. of Beipiao, *Dalinghosaurus* (Ji, 1998) and *Hyphalosaurus* (Gao et al., 1999), both maintain an extremely long caudal series and the latter also maintains a long cervical series with 19 vertebrae, but their phylogenetic status is still under study.

The pterosaurs are dominated by the Pterodactyloidea, such as *Eosipterus* produced from the lower Yixian Fm. at Sihetun (Ji and Ji, 1997) which most closely resembles *Huanhoipterus* (Dong, 1982), a member of the Ctenochasmatidae from the Huachihuanhe Fm., Zhidan Group, Ordos Basin. *Eosipterus* and other recently recovered specimens compare well with the European Late Jurassic *Pterodactylus*, *Ctenochasma*, *Gnathosaurus*, and *Ornithodesmus* which generally retain a mosaic of plesiomorphic Late Jurassic characters in addition to derived Cretaceous characters. The newly described *Dendrorhynchus* (Ji and Ji, 1998) maintains a relatively long tail in addition to other plesiomorphic characters attributed to Late Jurassic pterosaurs.

The lower Xixian Fm. vertebrate complex displays both primitive and derived characteristics, and thus the entire faunal complex indicates it would be more appropriately assigned to the Early Cretaceous.

The prolific occurrence of psittacosaurid ornithischian and theropod dinosaurs is characteristic of the fauna. To date there are nine species of Psittacosauridae recorded from the Jehol Group of North China, a large quantity of which are produced from the lacustrine sediments in the lower Yixian Fm. at Sihetun (Wang et al., 1998, 1999; Xu and Wang, 1998) which represents the oldest record for the family. *P. mongoliensis* represents a higher stratigraphic position in the Jiufotang Fm. of China and the Aptian-Albian of Mongolia.

At least three genera and species of theropods are present in the Yixian Fm. (Chen et al., 1997; Ji et al., 1998) two of which are currently under study and assigned to the Dromaeosauridae and Therizinosauroidae. These small theropods are all "feathered," appear to be evolving toward an avian morphology, and are phylogenetically more primitive than *Archaeopteryx* from the early Tithonian, Late Jurassic, of Germany (Ji et al., 1998). *Sinosauropteryx* is assigned to the Compsognathidae (Chen et al., 1997), a family which was previously only documented in the Late Jurassic Solnhofen Limestone of Germany. Further analysis is required to determine the accurate taxonomic assignment of *Protarchaeopteryx* and *Caudipteryx*. Other dromaeosaurs are principally known from the middle to Late Cretaceous of Asia and North America (Weishampel, 1990; Jerzykiewicz and Russell, 1991; Ostrom, 1990; Barsbold and Maryanska, 1990), including *Phaedrolosaurus* and *Tugulusaurus* from the Early Cretaceous Tugulu Group of Xinjiang (Barsbold and Maryanska, 1990), *Velocipraptor* (Osborn, 1924), *Adasaurus* (Barsbold, 1983) from the Late Cretaceous Campanian-Maastrichtian of Mongolia, and *Dromaeosaurus* (Matthew, 1922) and *Deinonychus* (Ostrom, 1969) from the Aptian-Albian of North America. The Therizinosauroidae is only documented from the Cretaceous of Central Asia with the majority of specimens being produced from the Late Cretaceous (Jerzykiewicz and Russell, 1991; Barsbold and Maryanska, 1990; Dong, 1979; Dong and You, 1997; Clark et al., 1994), including *Nanshiungosaurus* (Dong, 1979, Dong and You, 1997) from the Early Cretaceous Xinminbao Fm. of Mazongshan, Gansu, and *Alxasaurus* (Russell and Dong, 1993) from the Alashan Desert of Inner Mongolia. Late Cretaceous Cenomanian-Turonian segnosaurs are represented by

Segnosaurus (Perle, 1979), *Enigmosaurus* (Barsbold, 1980), and *Erlikosaurus* (Clark et al., 1994; Barsbold, 1980).

The *Confuciusornis* and *Cathayornis* avifaunas: Two distinct avian faunas are produced from the Yixian Fm. and Jiufotang Fm. respectively. The *Confuciusornis* Fauna contains four genera and six species represented by the Sauriurae *Confuciusornis sanctus*, *C. chuonzhous*, *C. sunae*, *C. sp.*, and *Liaoxiornis delicatus*, in addition to the Ornithurae *Liaoningornis longidigitus*, and the enantiornithine *Eoenantiornithes buhleri*. The fauna is produced from the Yixian Fm. at Heitizigou and Sihetun, Beipiao Municipality, and Lingyuan Co.

The global paleontological record of archaic birds is extremely restricted, and as such the only remotely close comparison of *Confuciusornis* that can be made is to *Archaeopteryx* from the Late Jurassic Tithonian Stage of Germany. There are numerous characters shared between *Archaeopteryx* and *Confuciusornis* (Hou, 1995; Hou et al., 1995a, 1995b; Martin et al. 1998), although *Confuciusornis* also maintains apomorphic characters quite distinct from *Archaeopteryx*, including the loss of maxillary and mandibular dentition, the presence of a cutaneous beak, a relatively well developed sternum, proximal humerus with a pneumatic fenestra, and an extremely reduced tail with fused caudals (Hou, 1995). To date, *Liaoningornis* represents the oldest record of the Ornithurae, with characters more primitive than *Chaoyangia* from the Jiufotang Fm., western Liaoning, and *Ambiortus* from the Early Cretaceous of Mongolia, but it also maintains numerous apomorphic characters (Hou, 1996). *Eoenantiornithes* is the earliest record of the family which does not survive beyond the Cretaceous. The derived faunal characteristics, diversity, and extreme quantity of specimens expresses a strong degree of diversity and radiation. From a general perspective, its age should represent the Early Cretaceous.

The *Cathayornis* Avifauna is represented by eight genera and nine species including the Sauriurae *Sinornis santensis*, *Boluochia zhengi*, *Cathayornis yendica*, *C. caudatus*, *Lonchengornis sanyanensis*, *Cuspirorsrisornis houi*, and *Largirostrornis sexdentornis*, in addition to the Ornithurae *Chaoyangia beishanensis*, and *Songlingornis linghensis*. The entire assemblage is produced from the Jiufotang Fm. at Boluochi and neighboring regions of Chaoyang Co. in Liaoning, and is much more taxonomically diverse than the *Confuciusornis* Fauna.

Outside of China, Cretaceous birds are also recovered from Mongolia, Spain, Australia, North America, and Argentina. The abundance of Enantiornithidae is characteristic for the Cretaceous, and the majority of the six genera and seven species of Sauriurae in the *Cathayornis* Fauna represent this family, among which, *Sinornis* and *Cathayornis* appear extremely close to *Iberomesornis*, *Concornis*, and *Noguerornis* from the Early Cretaceous Barremian Stage of Spain. The *Cathayornis* Fauna ornithurines *Chaoyangia* and *Songlingornis* also maintain several derived characters approaching extant forms. The general complexion of this fauna and its comparison to other derived faunas indicate its age should be Early Cretaceous.

In summary, the Jehol Biota is a composition of several vertebrate faunas: The *Lycoptera* Ichthyofauna, the *Psittacosaurus* Herpetofauna, the *Confuciusornis* Avifauna, and the *Cathayornis* Avifauna. The Biota is both more derived and prolific than the assemblages from the Late Jurassic Solnhofen Limestone of Germany represented by *Archaeopteryx* and *Compsognathus*. This implies that after the Late Jurassic extinctions, the Early Cretaceous represented a significant evolutionary and radiation event.

Stratigraphic sequence and isotopic dating

The Jehol Biota is distributed within grabens of western Liaoning Province which represent a segment of the Late Mesozoic northeast Asian graben basin system (Li et al., 1987), during which time igneous activity was abnormally intense and widespread. The Yixian Fm. is composed predominantly of basalts interbedded with three to four sedimentary units (Chen et al., 1980; Wu et

al., 1989). Intense igneous and orogenic activity subsequent to the deposition of the Cretaceous deposits have provided increasing difficulties in the correlation of stratigraphic sequences between basins, the establishment of stratigraphic sections, and the sampling and diagnosis of radiometric dates. Numerous workers have conducted chronological studies of these lithologies (Wang and Diao, 1984; Gu, 1995; Smith et al., 1995; and Chen et al., 1997). $^{40}\text{Ar}/^{39}\text{Ar}$ Argon dating on the basalts and tuffs in the Yixian Fm., in combination with new discoveries of fossil vertebrates, allow a preliminary establishment of a biochronologic and stratigraphic sequence for the vertebrates of the Jehol Biota.

Smith et al. (1995) and Swisher et al., (1998) conducted $^{40}\text{Ar}/^{39}\text{Ar}$ Argon dating on volcanic and other pyroclastic deposits in the Yixian Fm. at Sihetun and Jianshangou, Beipiao; Jingangshan, Yixian Co.; and Ershilipu and Daxin角度zi, Lingyuan Co. The samples from the Yixian Fm. at Beipiao were selected from a unit 230 m above the base of the Formation. and yielded a date of 121.4 ± 0.6 Ma (Smith et al., 1995). In the third vertebrate bearing unit of the lower Yixian Fm. at Sihetun (Wang et al., 1998), a date of 125.42 ± 0.08 Ma was obtained from 18 samples of euhedral sanidine feldspars in the tephra from unit P1T-2, (3.4 m above Unit 18, the *Confuciusornis sanctus* bed). A date of 125.52 ± 0.07 Ma was obtained from 24 samples of euhedral sanidine feldspars from the tephra of P4T-1 (50 cm above the unit that produced *Zhangheotherium quinquecupidens*) in the Jianshangou section (Swisher et. al., 1998). Further refinement of these samples is currently being conducted although it is not expected there will be a significant adjustment to the age (Swisher, pers. com. 1998). These dates thus constrain the age of the *Confuciusornis-Sinosauroptryx-Zhangheotherium* Complex.

A radiometric date of 122.9 ± 0.03 Ma was obtained at Anshanyan, Daxin角度zi, Lingyuan Co. (Smith et al., 1995) and dates of 122.2 ± 0.2 Ma and 122.5 ± 0.3 Ma were obtained from the interbedded lacustrine sediments basically equivalent to Daxin角度zi but from a unit slightly higher than at Anshanyan (Smith et al., 1995), providing an age for the *Monjurosuchus-Hyphalosaurus-Liaoxiornis* Complex at Daxin角度zi and Dawangzhang, Lingyuan Co.

Dates of 121.4 ± 1.1 Ma and 121.6 ± 0.4 Ma were obtained from biotite and plagioclase sampled from an interbedded pyroclastic angular conglomerate at Jingangshan, Yixian Co., providing an age for the *Lycoptera muroii-Manchurochelys manchouensis* Complex (Smith et al., 1995). The Jingangshan diabase date of 120.9 ± 0.4 - 120.8 ± 0.4 (Smith et al., 1995) closely approaches the ages of the interbedded sediments and thus the unit represents a distinct but nearly contemporaneous facies.

The basalts approximately 10 m above the third interbedded deposit (equivalent to the Dakangbao Unit [Chen et al., 1980]) in the Zoujiagou section provide dates of 121.3 ± 2.3 - 121.4 ± 0.7 Ma. This approaches that of the lacustrine sediments at Ershilipu, Lingyuan Co., and is consistent with the sediments at Jingangshan.

Currently, there is no accurate radiometric date from the Jiufotang Fm., however, there is an $^{40}\text{Ar}/^{39}\text{Ar}$ Argon date of 110 ± 0.52 from basalts overlying sediments correlated to the Jiufotang Fm. which produce a Jehol Biota at Tebch, Inner Mongolia (Eberth et al., 1993). This date provides an upper constraint for the Jiufotang Fm. and the *Cathayornis-Chaoyangia-Psittacosaurus* Complex contained therein.

Chen and Chen (1997) conducted a systematic study of the Yixian Co. region in which they dated pyroclastic deposits using K-Ar, Rb-Sr, and Ar-Ar dating techniques. They obtained dates of 133 ± 5.0 Ma at Shangdijiagou, 129 ± 0.3 Ma at Zhuanchengzi, 125.5 ± 0.1 Ma at Sanbailong, 124.5 ± 4.9 Ma at Zhujiagou, and 119.9 ± 10.0 Ma Hejiagou. Thus the Yixian Fm. is generally bracketed between 120-133 Ma, which is basically consistent with Smith et al. (1995), and Swisher et al. (1998).

The Yixian Fm. is dominated by basalts interbedded with three to four lacustrine facies which produce the prolific Jehol Biota (Chen et al., 1980; Wu et al., 1989). Chen et al. (1980), identified four sedimentary units in ascending order as the Jianshangou Unit, the Shanyuan Unit, the Dakangbao Unit, and the Jingangshan Unit. Wu et al. (1989) later recognized three sedimentary units they identified as the Daobazi Unit, Zhuanchengzi Unit and the Jingangshan Unit,. They correlated the lower Daobazi to the Jianshangou of Chen et al. (1980), the upper Jingangshan they retained as such, but the stratigraphic relationships of the middle Shanyuan and Dakangbao to the Zhuanchengzi unit were left unclear. Furthermore, Chen (1988) and Chen et al. (1980) recognized a Daxin角度zi Unit which they correlated to the Jianshangou Unit and recognized it as the most basal sediments of the Yixian Fm. Large quantities of fossil vertebrates are produced from the Jianshangou, Daxin角度zi, and Jingangshan beds which represent three vertebrate complexes. From the perspective of the vertebrates, the Jianshangou Unit is the most prolific, is characterized by its *Confuciusornis* Fauna and associated small theropods, and is associated with radiometric dates. Stratigraphically, this should represent the most basal portion of the Yixian Fm. The vertebrates from the Daxin角度zi Fm. include several taxa retained from the underlying Jianshangou beds in addition to first occurrences of *Protopsephurus*, *Monjurosuchus*, *Hyphalosaur*, and *Liaoxiornis*. The fish *Protopsephurus* is extremely abundant in the Jiufotang Fm. and its associated radiometric date clearly indicates it is younger than the Jianshangou beds. Vertebrates from the Jingangshan unit are few, however, they include the first occurrence of the characteristic species *Lycoptera muroii* which may be correlated to the upper Jiufotang Fm., and thus this unit undoubtedly represents the uppermost unit of the Yixian Fm. as its associated radiometric date indicates.

The remaining sedimentary units have yet to produce fossil vertebrates and thus cannot be correlated, although radiometric data provides a foundation to arrange the stratigraphic sequence as follows: Although it is unclear where the samples were taken that provided the 120.0 ± 0.3 Ma date for the Zhuanchengzi volcanics, the date still reflects a generally archaic age for the sediments and as such they should be correlated to the Jianshangou beds. Basalts 10 m above the Dakangbao beds provide a Ar/Ar date of 121.3 ± 2.3 - 121.4 ± 0.7 Ma (Smith et al. 1995). This postdates the Daxin角度zi beds in Lingyan Co. and more closely correlates to the Jingangshan beds, however, further field work is required to substantiate this interpretation.

It is undisputed that the Jiufotang Fm. extends into later stages than the Yixian Fm. and the vertebrate complexes contained therein are quite distinct. The Jiufotang Fm. is characterized by the first occurrences of the fishes *Jianichthys*, *Longdeichthys*, *Sinamia zdanskyi*, *Huashia* and the *Cathayornis* Avifauna. This is quite distinct from the three complexes produced from the Yixian Fm.

Gradstein et al. (1995) applied radiometric dating and vertebrate complexes to calibrate their Mesozoic Geologic Time scale, in which they recognize the Jurassic-Cretaceous boundary at 144.2 Ma. In the Jehol Biota, the sequence of vertebrate complexes, the stratigraphic sequence, and associated radiometric dates provide the following correlations: the Lower Yixian Fm. *Confuciusornis-Sinosauroptryx-Zhangheotherium* Complex from Jianshangou and Sihetun are middle Barremian in age. The middle Yixian Fm. *Monjurosuchus-Hyphalosaur-Liaoxiornis* Complex from Daxin角度zi and Dawangzhang and the upper Yixian Fm. *Lycoptera muroii-Manchurochelys manchouensis* Complex from Jingangshan are late Barremian in age. The Jiufotang Fm. *Cathayornis-Chaoyangia-Psittacosaurus* Complex is Aptian in Age. As such, the Yixian and Jiufotang fms. span the late Valanginian to Aptian.

Conclusions

1. Four complexes are recognized in the vertebrates of the Jehol Biota: the lower Yixian Fm. *Confuciusornis-Sinosauroptryx-Zhangheotherium* Complex from the Sihetun-Jianshangou units, the middle Yixian Fm. *Monjurosuchus-Hyphalosaurus-Liaoxiornis* Complex from the Daxinfangzi-Dawangzhang units, the upper Yixian Fm. *Lycoptera muroii-Manchurochelys manchouensis* Complex from the Jingangshan unit, and the Jiufotang Fm. *Cathayornis-Chaoyangia-Psittacosaurus* Complex.
2. The fish and reptiles in the vertebrate complexes of western Liaoning Province represent the *Lycoptera* Ichthyofauna and the *Psittacosaurus* Herpetofauna. There are two distinct avian faunas: the Yixian Fm. *Confuciusornis* Avifauna and the Jiufotang Fm. *Cathayornis* Avifauna. These vertebrate faunas are all Early Cretaceous.
3. The Yixian Fm. pyroclastics and marls provide $^{40}\text{Ar}/^{39}\text{Ar}$ Argon dates of 125.42 ± 0.08 - 125.52 ± 0.07 Ma for the *Confuciusornis-Sinosauroptryx-Zhangheotherium* Complex assigning it to the middle Barremian Stage. The *Monjurosuchus-Hyphalosaurus-Liaoxiornis* Complex is 122.2 ± 0.2 - 122.5 ± 0.3 Ma assigning it to the late Barremian Stage. The *Lycoptera Muroii-Manchurochelys manchouensis* Complex is 121.4 ± 1.1 - 121.6 ± 0.4 Ma assigning it to the late Barremian Stage. The *Cathayornis-Chaoyangia-Psittacosaurus* Complex predates 110 ± 0.52 Ma assigning it to the Aptian Age.
4. The ages of the Yixian and Jiufotang fms. are Early Cretaceous late Valanginian through Barremian and Aptian respectively.

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Bibliography

- Barsbold, R. and Maryanska, T. 1990; Segnosauria. In Weishampel D. et al., eds. The Dinosauria, University of California Press, Berkeley, 408-415.
- Barsbold, R., 1983; Carnivorous dinosaurs from the Cretaceous of Mongolia. *Sov. Mong. Paleont. Eksp. Trudy*, (19), 117 pp.
- Barsbold, R. and Perle, A., 1980; Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta Palaeont. Pol.*, **377**, 616-619.
- Buffetaut, E., and Suteethorn, V.A., 1992; A new species of the ornithischian dinosaur *Psittacosaurus* from the Early Cretaceous of Thailand. *Palaeontology* **35**, 801-812.
- Chen, P.J., Dong, Z.M., and Zhen, S.N. 1997; An exceptionally well-preserved theropod dinosaur from the Xixian Fm. of China. *Nature* **393**, 753-761.
- Chen, P.J., 1988; Distribution and migration of the Jehol Fauna. *Act. Paleo. Sin.* **27**(6), 659-683 (in Chinese).
- Chen, P.J., Wen, S.Y., and Zhou, Z.Y., 1980; A study of the Late Mesozoic terrestrial sediments of Western Liaoning Province. *Nanjing Inst. Paleo. Ser. (1)*, 22-55 (in Chinese).
- Chen, Y.X. and Chen, W.J., et al. 1997; Chronological studies on the Mesozoic volcanics in Western Liaoning and neighboring regions. Geochemistry and tectonic background. Seismology Press, Beijing, 279 pp. (in Chinese).
- Clark, J.M., Perle, A., and Norell, M.A., 1994; The skull of *Erlicosaurus andrewsi*, a Late Cretaceous "segnosaur" (Theropoda: Therizinosauridae) from Mongolia. *Am. Mus. Novit.* (3115), 39 pp.
- Dong, Z.M., 1997; Early Cretaceous dinosaur faunas in China: an introduction. *Can. J. Earth Sci.* **30**(10-11), 2096-2100.
- Dong, Z.M. and You, H.L., 1997; A new segnosaur from Mazongshan area, Gansu province, China, In Dong, Z.M. ed. The Sino-Japanese Silk Road Dinosaur Expedition. China Ocean Press, Beijing, 90-95.
- Dong, Z.M., 1995; The dinosaur complexes of China and their biochronology. In Sun and Wang eds., Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers, China Ocean Press, Beijing, 91-96.
- Dong, Z.M., 1992; Dinosaurian Faunas of China. China Ocean Press, Beijing, 198 pp.
- Dong, Z.M., 1982; A pterosaur from the Ordos Basin. *Vert. PalAs.* **20**(2), 115-121 (in Chinese).
- Dong, Z.M., 1980; Chinese dinosaur faunas and their stratigraphic position *Jour. Strat.* **4**(4), 256-263 (in Chinese).
- Dong, Z.M., 1979; Cretaceous dinosaurs of South China. In. IVPP and Nanjing Institute of Paleontology eds., Mesozoic and Cenozoic Red Beds of South China. Science Press, 342-350 (in Chinese).
- Dong, Z.M., 1973; Pterosaurian Fauna from Wuerho, Sinkiang, Reports of the Paleontological Expedition to Sinkiang (II). *Mem. Inst. Vert. Paleo. Paleoanthro.* **11**, 45-52 (in Chinese).
- Eberth, D.A., Russell, D.A., Braman, D.R., and Deino, A.L., 1993; The age of the dinosaur-bearing sediments at Tebch, Inner Mongolia, P.R. China. *Can. J. Earth Sci.*, **30**(10-11), 2101-2112.
- Endo, R., and Shikama, T., 1942; Mesozoic reptilian fauna in the Jehol mountainland, Manchoukuo. *Bull. C Natl. Mus. Manchoukuo* (3), 1-20.
- Endo, R. 1940; A new genus of Thecodontia from the *Lycoptera* beds in Manchoukuo. *Bull. C Natl. Mus. Manchoukuo*, (2), 1-14.
- Gaffney, E.S. and Ye, X.K., 1992; *Dracochelys*, a new cryptodiran turtle from the Early Cretaceous of China. *Am. Mus. Novit.* (3048), 1-13.
- Gao, K.Q., Tang, Z.L., and Wang, X.L., 1999; A long-necked diapsid reptile from the Upper Jurassic/Lower Cretaceous of Liaoning Province, northeastern China. *Vert. PalAs.* **37**(1), 1-8.
- Grabau, A.W., 1928, Stratigraphy of China, Part II: Mesozoic. Geologic Survey. China, Peking, 774 pp.
- Grabau, A.W., 1923; Mollusca from North China. *Bull. Geol. Surv. China*, **5**(2), 183-197.

- Gradstein, F.M., Agterberg, F.P., Ogg, J.G., et al., 1995; A Triassic, Jurassic, and Cretaceous time Scale, Geochronology Time Scale and Global Stratigraphic Correlation, *SEPM Special Publ.* (54), 95-126.
- Gu, Z.W., 1995; A study of the age of the Jehol Fauna. In: Wang, ed. Problems Concerning the Development of Geological Disciplines - Collected Papers Commemorating the 100th Birthday of Professor Yun Sun. Chinese University of Geology Press, Wuhan, 93-99 (in Chinese).
- Gu, Z.W., 1983; A discussion of the Jurassic-Cretaceous boundary in the non-marine sediments of China. In Nanjing Institute of Paleontology ed. Research upon period boundaries in China. Science Press, Beijing, 65-82 (in Chinese).
- Gu, Z.W., 1962; The Jurassic and Cretaceous of China. Science Press, Beijing, 84 pp. (in Chinese).
- Hao, Y.C. ed., 1986; The Cretaceous of China. Geological Press, Beijing, 301 pp. (in Chinese).
- Hao, Y.C., Su, D.Y., Li, Y.G. et al., 1982; Subdivision of the non-marine Cretaceous in China and the Jurassic-Cretaceous boundary. *Acta Geo. Sin.* **56**(3), 187-199 (in Chinese).
- Hong, Y.C., 1993; The origin, development, splendor, and decline of the Jehol Fauna. *Modern Geo.* **7**(4), 373-383 (in Chinese).
- Hou, L.H. and Chen, P.J., 1999; The smallest archaic bird - *Liaoxiornis delicatus*. *Sci. Bull.* **44**(3), 311-314 (in Chinese).
- Hou, L.H., Martin, L.D., Zhou, Z.H., and Feduccia, A., 1999; *Archaeopteryx* to opposite birds - missing link from the Mesozoic of China. *Vert. PalAs.* **37**(2)
- Hou, L.H., 1997; Mesozoic Birds of China. Phoenix Valley Provincial Aviary, Taiwan, 143 pp. (in Chinese).
- Hou, L.H., 1996; The discovery of a Jurassic carinate bird in China. *Sci. Bull.* **41**(20) (in Chinese).
- Hou, L.H., 1995; Morphological comparison between *Confuciusornis* and *Archaeopteryx*. In: Sun et al., eds. Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers, China Ocean Press, Beijing, 193-201.
- Hou, L.H., Zhou, Z.H., Martin, L.D. and Feduccia, A., 1995; A beaked bird from the Jurassic of China. *Nature*, **377**, 616-619.
- Hou, L.H., Zhou, Z.H., and Gu, Y.C., 1995; First discovery of Jurassic birds from China. *Sci. Bull.* **40**(8) (in Chinese).
- Hou, L.H. and Jiang, J.Y., 1993; An early Early Cretaceous fossil bird from Liaoning. *Vert. PalAs.* **31**(3), 217-224 (in Chinese).
- Hu, Y.M., Wang, Y.Q., Luo, Z.X., and Li, C.K., 1997; A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature*, **390**, 137-142.
- Hu, H.G., Hu, S.L., Wang, S.S. et al., 1982; A discussion of sedimentary ages based upon radiometric dating of Jurassic-Cretaceous volcanics. *Acta Geo. Sin.* (4), 315-323 (in Chinese)
- Jerzykiewicz, T. and Russell, D.A., 1991; Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cret. Res.* **12**, 345-377.
- Ji, Q., Currie, P.J., Norell, M.A., and Ji, S.A., 1998; Two feathered dinosaurs from northeastern China. *Nature*, **393**, 753-761.
- Ji, Q. and Ji, S.A., 1997; A Chinese archaeopterygian. *Geo. Sci. and Tech.* (238), 38-41 (in Chinese).
- Ji, S.A., 1998; A new long-tailed lizard from the Upper Jurassic of Liaoning, China. In Dept. of Geology, Peking University Ed. Collected Works from International Symposium on Geological Sciences, Beijing, Seism. Publ. House, 496-504.
- Ji, S.A., and Ji, Q., 1998; A new pterosaur (Ramphoryhnochoidea) from Liaoning. *Jiangsu Geo.* **22**(4), 199-206 (in Chinese).
- Ji, S.A., and Ji, Q., 1998; First discovery of a Mesozoic frog (Amphibia: Anura) from China. *Chinese Geo.* (3), 39-42 (in Chinese).
- Ji, S.A. and Ji, Q., 1997; First discovery of Pterosauria from western Liaoning. *Acta Geo. Sin.* **71**(1), 1-6 (in Chinese).

- Jin, F., 1996; Remaining problems concerning the study of the development of Late Mesozoic stratigraphy in Western Liaoning. *Vert. PalAs.* **34**(2), 102-122 (in Chinese).
- Jin, F., Zhang, J.Y., and Zhou, Z.H., 1995; Late Mesozoic fishes from western Liaoning. *Vert. PalAs.* **33**(3), 169-193 (in Chinese).
- Kimura, T. Hayami, I, Yoshida, S., 1991; Geology of Japan, University of Tokyo Press, 101-137.
- Li, P.X., Su, D.Y., Li, Y.G. et al., 1993; The age of the *Lycoptera* beds. *Acta Geo. Sin.* **68**(1), 87-100 (in Chinese).
- Li, S.T., Yang, S.G., Wu, C.L. et al., 1987; The affects of Late Mesozoic subsidence in northeast China and the graben basin network of northeast Asia. *Sientia Sinica*, Vol. B, (2), 185-195 (in Chinese).
- Li, Z.W., Wang, S.E., Yu, J.S., 1982; Subdivision of the Late Jurassic of North China and the Jurassic-Cretaceous boundary. *Acta. Geo. Sin.* **56**(4), 347-363 (in Chinese).
- Liu, B.P., Chen, F., and Wang, W.L., 1986; A discussion of the Jurassic-Cretaceous boundary in East Asian terrestrial sediments through the perspective of event stratigraphy. *Seismology - Journal of the Wuhan Academy of Geology* **11**(5), 465-472 (in Chinese).
- Liu, X.T., Ma, F.C., and Wang, W.L., 1987; Late Mesozoic fish from Western Liaoning. In Yu et al. eds. Mesozoic Biostratigraphy of Western Liaoning (3), Geological Press, Beijing, 223-238 (in Chinese).
- Liu, X.T. and Zhou, J.J., 1965; A new family of sturgeon from the Upper Jurassic of Beipiao, Liaoning. *Vert. PalAs.* **9**(3), 237-247 (in Chinese).
- Liu, X.T. Su, D.Z., Huang, W.L., and Zhang, G.J., 1963; Lycoperid fishes from North China. *Mem. Inst. Vert. Paleo. Paleoanthro.* (6), 53 pp. (in Chinese).
- Lu, L.W., 1992; A Late Jurassic Acipenseriformes from Lingyuan, Liaoning. *Vert. PalAs.* **32**(2), 134-142 (in Chinese with English summary).
- Martin, L.D., Zhou, Z.H., Hou, L.H., et al., 1998; *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften*, **85**, 286-289.
- Matsukawa, M. and Obata, I., 1994; Dinosaurs and the sedimentary environment in the Japanese Cretaceous: A contribution to dinosaurfacies in Asia based on molluscan palaeontology and stratigraphy. *Cret. Res.* **15**, 101-125.
- Matthew, W.D., and Brown, B., 1922; The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.* B46, 367-385.
- Osborn, H.F., 1924; Sauropoda and Theropoda of the Lower Cretaceous of Mongolia. *Am. Mus. Novit.* (128), 1-7.
- Ostrom, J.H., 1990; Dromaeosauridae. In Weishampel, D. et al., eds. Dinosauria, University of California Press, 269-279.
- Ostrom, J.H., 1969; Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* **30**, 165 pp.
- Perle, A. 1979; Segnosauridae - a new family of theropods from the Late Cretaceous of Mongolia. *Sov-Mong. Paleont. Eksp. Trudy*, (8), 45-55.
- Ren, D., Guo, Z.G., Lu, L.W. et al., 1997; New developments in the study of the Jurassic Yixian Fm., Western Liaoning. *Geo. Rev.* **43**(5), 449-459 (in Chinese).
- Ren, D., Lu, L.W., Guo, Z.G. et al., 1995; Jurassic and Cretaceous faunas and the stratigraphy of Beijing and its neighboring regions. Seismology Press, Beijing, 222 pp. (in Chinese).
- Russell, D. and Dong, Z.M., 1993; The affinities of a new theropod from the Alax Desert, Inner Mongolia, People's Republic of China. *Can. J. Earth Sci.*, **30**(10-11), 2107-2127.
- Sereno, P.C. and Rao, C.G., 1992; Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science*, **255**, 845-848.
- Sereno, P.C., 1990; Psittacosauridae. In Weishampel et al., eds. The Dinosauria, University of California Press, Berkeley, 579-592.
- Sereno, P.C., Chao, S.C., Cheng, Z.W, and Rao, C.G., 1988; *Psittacosaurus meileyingensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northeastern China. *Jour. Vert. Paleo.* **8**(4), 366-377.

- Smith, P.E., Evensen, N.M., York, D., Chang, M.M., Jin, F., Li, J.L., Cumbaa, S., and Russell, D., 1995; Dates and rates in ancient lakes $^{40}\text{Ar}/^{39}\text{Ar}$ evidence for a Early Cretaceous age for the Jehol Group, Northeast China. *Can. J. Earth Sci.* **32**, 1246-1431.
- Sun, G., Dilcher, D.L., Zheng, S.L., and Zhou, Z.K., 1998; In search of the first flower: A Jurassic angiosperm, *Archaeofructus* from northeast China. *Science*, **282**, 1693-1695.
- Swisher, C.C., Wang, Y.Q., Wang, X.L., Xu, X. and Wang, Y., 1998; $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Lower Yixian Fm. Liaoning Province, northeastern China. *Chinese Sci. Bull.* **43**(Supp): 125.
- Wang, D.F. and Diao, N.C., 1984; Radiometric ages of Jurassic-Cretaceous volcanic deposits in western Liaoning. In Collected Papers on the International Exchange of Geological Techniques (1), Geological Press, Beijing, 1-12 (in Chinese).
- Wang, S.E., 1998; A comparative study of the Jurassic terrestrial sediments of eastern China to the interfingering marine-terrestrial Jurassic sediments of England and their bearing toward the subdivision and correlation of Jurassic sediments in North China. *Acta Geo. Sin.* **42**(4), 11-21 (in Chinese).
- Wang, S.E., 1990; The origin, evolution, and mechanism of the Jehol Fauna. *Acta Geo. Sin.* **64**(4), 350-360 (in Chinese).
- Wang, S.E. ed., 1985; The Jurassic of China. Geological Press, Beijing, 350 pp. (in Chinese).
- Wang, X.L., Wang, Y.Q., Jin, F. et al., 1999; Background of Sihetun stratigraphy and its vertebrate fauna, western Liaoning. In Ren and Jin eds. Collected Papers on Research into the Jehol Fauna, Western Liaoning. (in press).
- Wang, X.L., Wang, Y.Q., Wang, Y., Xu, X., Tang, Z.L., Zhang, F.C., Hu, Y.M., Gu, G., and Hao, Z.L., 1998; Stratigraphic sequence and vertebrate-bearing beds of the lower part of the Yixian Fm. in Sihetun and neighboring areas, western Liaoning. *Vert. PalAs.* **36**(2), 96-101 (in Chinese).
- Wang, W.L., Zheng, S.L., Zhang, L.J. et al., 1989; Mesozoic Biostratigraphy of Western Liaoning. Geological Press, Beijing, 168 pp. (in Chinese).
- Wang, Y. and Gao, K.Q., 1999; The oldest discoglossid in Asia. *Sci. Bull.* **41**(4), 407-422 (in Chinese).
- Weishampel, D.B., 1990; Dinosaurian distribution. In Weishampel et al., eds., The Dinosauria, University of California Press, Berkeley, 63-139.
- Wu, W.L., Zheng, S.L., Zhang, L.J. et al., 1989; Mesozoic biostratigraphy of western Liaoning (1), Geological Publishing House, Beijing, 168 pp. (in Chinese).
- Xu, X. and Wang, X.L., 1998; New specimens of *Psittacosaurus* from western Liaoning and their stratigraphic significance. *Vert. PalAs.* **36**(2), 147-158 (in Chinese).
- Yabumoto, Y., 1994; Early Cretaceous freshwater fish fauna in Kyushu, Japan, *Bull. Kitakyushu Mus. Nt. Hist.* **13**, 107-254.
- Zhou, Z.H., 1995; A new enantiornithine bird from the Early Cretaceous of Liaoning. *Vert. PalAs.* **33**(2) (in Chinese).
- Zhou, Z.H., Jin, F., and Zhang, J.Y., 1992; Preliminary investigation of early fossil birds from the Mesozoic of Liaoning. *Sci. Bull.* **37**(5), 435-437 (in Chinese).