GEOLOGICAL JOURNAL
Geol. J. **41**: 419–437 (2006)

Non-Avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China

XU XING [1,2]* **and MARK A. NORELL** [2]

[1] *Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China*
[2] *American Museum of Natural History, New York, NY, USA*

Over the past 10 years, numerous dinosaur specimens covering several major dinosaurian clades have been recovered from the Lower Cretaceous Jehol Group of western Liaoning. Among ornithischians from the Jehol Group, ornithopod fossils shed new light on the evolution of this largest ornithischian group; ankylosaurian discoveries add morphological diversity relevant to the highly specialized ankylosaurian body-plan and ceratopsian occurrences offer a chance to study patterns of morphological change at the base of the Ceratopsia. The most significant discoveries are exceptionally well-preserved theropod specimens covering most major coelurosaurian groups. Most theropod taxa from the Jehol Biota are the earliest, most basal members of coelurosaurian sub-clades and provide substantial new information important for the reconstruction of coelurosaurian phylogeny and understanding the character evolution. The examination of character distributions along the coelurosaurian lineages reveals that the major structural modifications seen in birds were acquired sequentially and hierarchically early in coelurosaurian evolution. Most significantly, the Liaoning theropod discoveries advanced our understanding of two long-debated evolutionary issues: the origin and early evolution of feathers and the origin of avian flight. The known distribution of the feather-like integumentary structures and true feathers along the coelurosaurian lineages suggests that: (1) simple, filamentous integuments represent a primitive morph in feather evolution; (2) pennaceous feathers evolved early in maniraptoran evolution; and (3) feathers with aerodynamic features originated before the origin of birds. The presence of flight feathers on the metatarsus represents a new morph that is not known previously, but it has implications for understanding the origin of avian flight. The discovery of four-winged dinosaurs was suggested to provide strong evidence supporting the 'tree-down' hypothesis for the origin of avian flight, though in-depth analysis and more data are needed to confirm this. A brief analysis of the fossil preservation and faunal composition reveals several interesting characteristics: (1) Volcanic activity might have contributed to the exceptional preservation of dinosaurian skeletons and in particular their soft tissues; (2) Different from most other dinosaur faunas, the Jehol dinosaur fauna has a low ornithischian specific diversity relative to a high theropod specific diversity; and (3) the Liaoning theropods show a strong tendency toward secondary herbivory. The faunal composition suggests a complex biogeographic history for this fauna and provides negative evidence for the hypothesis that eastern Asia was isolated from the Middle Jurassic through late Early Cretaceous times. Copyright © 2006 John Wiley & Sons, Ltd.

Received 13 June 2005; revised version received 12 February 2006; accepted 2 March 2006

KEY WORDS dinosaurs; bird origin; phylogeny; character evolution; Early Cretaceous; Jehol Group; Liaoning

1. INTRODUCTION

Until recently, dinosaur fossils were unknown from the Lower Cretaceous Jehol Group of western Liaoning, China (Figure 1). In 1988, Sereno and co-workers reported the discovery of the basal ceratopsian *Psittacosaurus meileyingensis* from the Jiufotang Formation, the upper section of the Jehol Group, which represents the first named dinosaur species from western Liaoning (Sereno *et al*. 1988). In 1996, Ji and Ji announced the discovery of

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* Correspondence to: Xu Xing, Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, 100044, China.
E-mail: xingxu@vip.sina.com or xu@amnh.org

Figure 1. Distribution of major dinosaur localities in western Liaoning, China.

Sinosauropteryx prima, the first known feathered dinosaur (Ji and Ji 1996). This discovery was a major event in dinosaurian research and marked the beginning of a series of significant discoveries from this region. To date, 25 species in 21 genera of non-avian dinosaurs have been named and described from the Jehol Group of western Liaoning (Table 1). These discoveries include members of most dinosaurian clades, and have significantly advanced our understanding of the early evolution of these groups. Foremost among these discoveries have been animals closely related to modern birds, many of which preserve feathers. These finds weigh heavily on the origin of birds and the acquisition of character systems like feathers and flight (Zhou *et al*. 2003; Norell and Xu 2005). The present paper briefly reviews these discoveries, comments on their major features and evolutionary implications, discusses several aspects of this Lower Cretaceous dinosaur fauna and their biogeographic implications.

It should be noted that many dinosaur specimens from the Jehol Group have been removed from China illegally. Unfortunately, some of these have been acquired by foreign museums and, even more unfortunately, descriptions or reference to some of these have appeared in the scientific literature (see Dalton 2001, 2004). We ignore all of these discoveries here, in deference to recommendations made by the Chinese Academy of Sciences (unpublished documents) in regard to these smuggled specimens.

There are five main dinosaur-fossil-bearing beds in the Jehol Group of western Liaoning (Figure 2; Wang *et al*. 2000; Zhou *et al*. 2003). The Lujiatun Beds (older than 128.2 years) are the oldest fossil-bearing units in the Jehol Group. They are mainly composed of structure-less tuffaceous sandstones and tuffs. The Jianshangou Beds are dated as younger than 125 years but older than 122.5 years. They are mainly inter-bedded shales and tuffs. The Dawangzhangzi Beds are slightly younger than 122.5 years. They are also composed of shales and intercalated tuffs. These three beds belong to the Yixian Formation. There are two dinosaur-fossil-bearing beds in the overlapping Jiufotang Formation. They are the lower Shangheshou Beds that are shales with intercalated tuffs and the upper Meileyingzi Beds that are thick sand beds. The Jiufotang Formation may have been formed from 120

Table 1. Dinosaur fossils from Jehol Group

Taxonomy	Locality	Horizon and age
Saurischia		
Theropoda		
Coelurosauria		
Compsognathidae		
Sinosauropteryx prima Ji and Ji, 1996	Sihetun, Beipiao; Dawangzhangzi, Linyuan	Jianshangou Beds (about 125 Mya); Dawangzhangzi Beds (about 122 Mya)
Huaxiagnathus orientalis Hwang, Norell, Ji and Gao, 2004	Dabangou, Beipiao	Jianshangou Beds (about 125 Mya)
Tyrannosauroidea		
Dilong paradoxus Xu, Norell, Kuang, Wang, Zhao and Jia, 2004a	Lujiatun, Beipiao; Zhangjiugou, Beipiao	Lujiatun Beds (about 128 Mya); Jianshangou Beds (about 125 Mya)
Dilong Sp.		
Ornithomimosauria		
Shenzhousaurus orientalis Ji, Norell, Makovicky, Gao, Ji and Yuan, 2003	?Sihetun, Beipiao	Lujiatun Beds (about 128 Mya)
Oviraptorosauria		
Caudipteryx zoui Ji, Currie, Norell and Ji, 1998	?Sihetun, Beipiao	Jianshangou Beds (about 125 Mya)
Caudipteryx dongi Zhou and Wang, 2000	Zhangjiagou, Beipiao	Jianshangou Beds (about 125 Mya)
Incisivosaurus gauthieri Xu, Cheng, Wang and Zhang, 2002a	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Therizinosauroidea		
Beipiaosaurus inexpectus Xu, Tang and Wang, 1999a	Sihetun, Beipiao	Jianshangou Beds (about 125 Mya)
Dromaeosauridae		
Sinornithosaurus millenii Xu, Wang and Wu, 1999b	Sihetun, Beipiao	Jianshangou Beds (about 125 Mya)
Microraptor zhaoianus Xu, Zhou and Wang, 2000b	Langshan, Chaoyang	Jiufotang Formation (120-110 Mya)
Microraptor gui Xu, Zhou, Kuang, Wang, Zhang and Du, 2003b	Dapingfang, Chaoyang	Jiufotang Formation (120-110 Mya)
Graciliraptor lujiatunensis Xu and Wang, 2004a	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Troodontidae		
Sinovenator changii Xu, Norell, Wang and Makovicky, 2002c	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Sinucerasaurus magodens Xu and Wang, 2004b	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Mei long Xu and Norell, 2004	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Family indet.		
Protarchaeopteryx robusta Ji and Ji, 1997	Sihetun, Beipiao	Jianshangou Beds (about 125 Mya)
Yixianosaurus longimanus Xu and Wang, 2003	Baicaigou, Yixian	Dawangzhangzi Beds (about 122 Mya)
Sauropoda indet.		
Ornithischia		
Ornithopoda		
Jeholosaurus shangyuanensis Xu, Wang and You, 2000a	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Jinzhousaurus yangi Wang and Xu, 2001	Baicaigou, Yixian	Dawangzhangzi Beds (about 122 Mya)
Ceratopsia		
Psittacosauridae		
Psittacosaurus meileyingensis Sereno, Chao, Cheng and Rao, 1988	Meileyingzi, Chaoyang	Jiufotang Formation (120-110 Mya)
Psittacosaurus mongoliensis Osborn, 1923	Meileyingzi, Chaoyang	Jiufotang Formation (120-110 Mya)
Psittacosaurus sp.	Lujiatun, Beipiao; Sihetun, Beipiao	Lujiatun Beds (about 128 Mya); Jianshangou Beds (about 125 Mya)
Hongshanosaurus houi You, Xu and Wang, 2003	Lujiatun, Beipiao	Lujiatun Beds (about 128 Mya)
Neoceratopsia		
Liaoceratops yanzigouensis Xu, Makovicky, Wang, Norell and You, 2002b	Yanzigou, Beipiao	Lujiatun Beds (about 128 Mya)
Ankylosauria		
Liaoningosaurus paradoxus Xu, Wang and You, 2001a	Baicaigou, Yixian	Dawangzhangzi Beds (about 122 Mya)

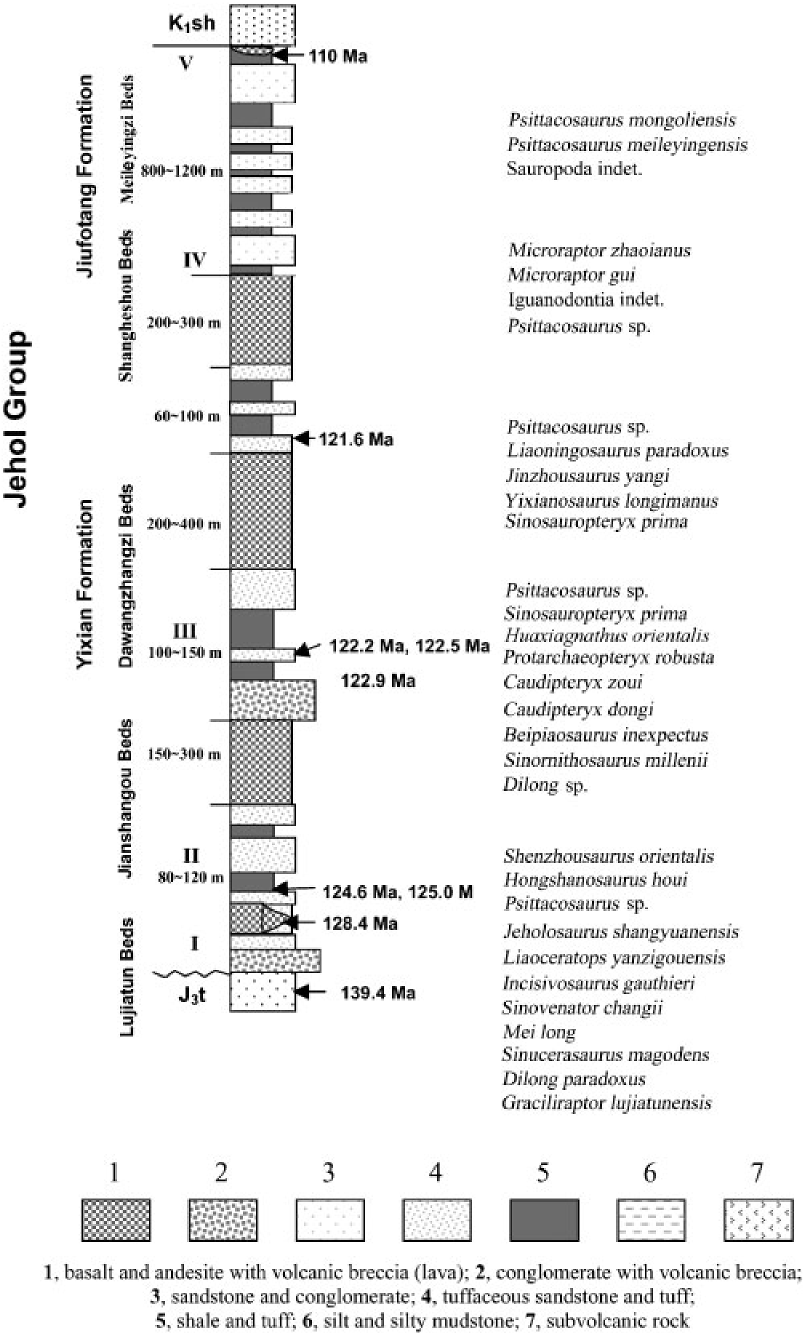

Figure 2. A stratigraphic column of the Jehol Group showing the five main dinosaur-fossil-bearing beds (I–V).

years through to 110 years based on a radiometric analysis on the lateral equivalent beds in Inner Mongolia (Smith *et al*. 1995). The reader is referred to Wang *et al*. (2000) and Ji *et al*. (2004) for more detailed information on the geological, palaeontological and preservational setting of these beds, and to Gauthier (1986), Sereno (1998) and Padian *et al*. (1999) for taxonomy used in the present paper.

2. DINOSAUR REMAINS FROM THE JEHOL GROUP

2.1. Saurischia

Theropoda

Non-avian theropods are represented by two taxa of Compsognathidae, one taxon each of Tyrannosauroidea, Ornithomimosauria and Therizinosauroidea, three taxa of Oviraptorosauria, four taxa of Dromaeosauridae, three taxa of Troodontidae and two taxa of Coelurosauria with uncertain affinities (Table 1; Figure 3). Additionally, several unnamed taxa are awaiting description.

Compsognathidae

Sinosauropteryx prima is known from four specimens (Ji and Ji 1996; Chen *et al*. 1998), all preserving nearly complete, fully articulated skeletons. These specimens are preserved on slabs, largely in two-dimensions (Figure 4A).

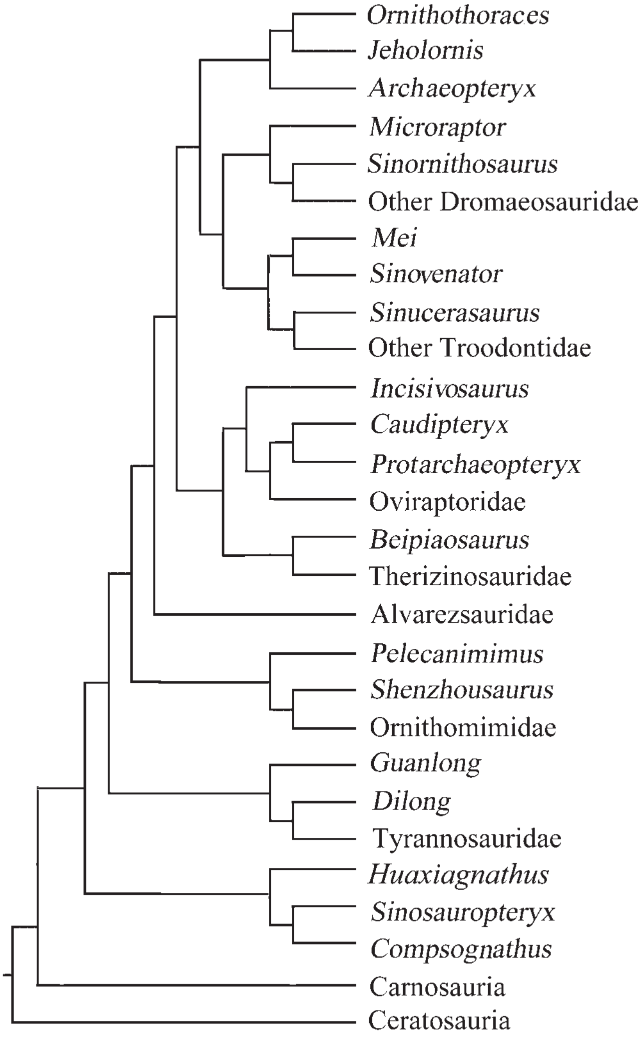

Figure 3. A simplified cladogram (based on Norell *et al*. 2001 and also referring to Sereno 1999) showing the systematic positions of Liaoning coelurosaurians.

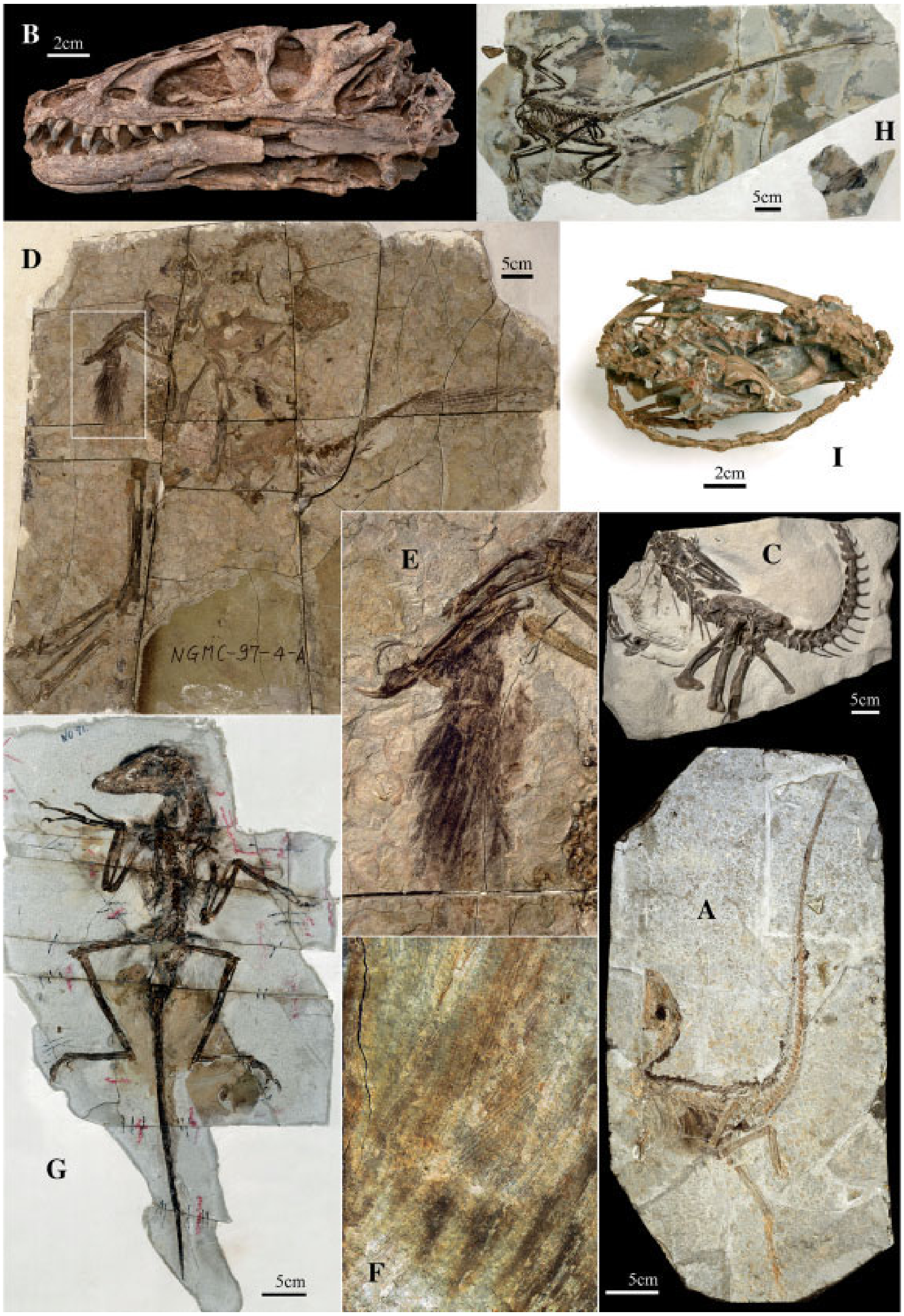

Figure 4. Selected coelurosaurians from the Jehol Biota. **A**: Compsognathid *Sinosauropteryx prima* (GMV2123; Jianshangou Beds, Sihetun, Beipiao); **B**: Ornithomimosauria *Shenzhousaurus orientalis* (NGMC 97-04-002; Lujiatun Beds, ?Lujiatun, Beipiao); **C**: Tyrannosauroid *Dilong paradoxus* (IVPP V14243; Lujiatun Beds, Lujiatun, Beipiao); **D**: Oviraptorosaurian *Caudipteryx zoui* (NGMC-97-4-A; Jianshangou Beds, Zhangjiagou, Beipiao). **E**: Remiges of *Caudipteryx zoui* (NGMC-97-4-A); **F**: Rectrices of *Caudipteryx zoui* (NGMC-97-4-A); **G**: Troodontid *Mei long* (IVPP V12733; Lujiatun Beds, Lujiatun, Beipiao); **H**: Dromaeosaurid *Sinornithosaurus millenii* (IVPP V12811; Jianshangou Beds, Sihetun, Beipiao); **I**: Dromaeosaurid *Microraptor gui* (IVPP V13352; Shangheshou Beds, Dapingfang, Chaoyang). Abbreviations: GMV, National Geological Museum of China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; NGMC, National Geological Museum of China.

Sinosauropteryx prima shares several unique features with the Late Jurassic *Compsognathus*, but also possesses several features suggesting a more derived position within the Compsognathidae. These features include proportionally shorter but more robust forelimbs (Currie and Chen 2001). All known specimens preserve filamentous integumentary structures, which are best represented dorsal to the vertebral column. However, close inspection has revealed that these structures covered the entire body and can be observed on the side of the abdomen as well as elsewhere on the body (Currie and Chen 2001). Detailed structure of the integumentary structures is difficult to identify, however, branching structures (Currie and Chen 2001), and possibly distal branching (Prum and Brush 2002), may be present.

The compsognathid *Huaxiagnathus orientalis* is represented only by two specimens, which are nearly complete, fully articulated skeletons (Hwang *et al*. 2004). The detailed morphology is unknown, as poor preparation even extends to the repositioning of several elements in the skeleton and the addition of extraneous pieces of bone. The *Huaxiagnathus orientalis* holotype is much larger than *Sinosauropteryx*. Hwang *et al*. (2004) posited this taxon within the Compsognathidae based on a numerical phylogenetic analysis. *Huaxiagnathus orientalis*, however, lacks unique compsognathid features (Currie and Chen 2001; Hwang *et al*. 2004). Furthermore, it displays several significant differences from other compsognathids (Hwang *et al*. 2004). Consequently, its suggested systematic position is tentative and needs confirmation when, and if, the specimen is fully prepared. The holotype specimen lacks preservation of integumentary structures.

Tyrannosauroidea

Dilong paradoxus is known from four specimens. The holotype (Figure 4B), a subadult individual, is estimated to be about 1.6–1.8 m in body length. While possessing several tyrannosauroid synapomorphies, such as fused nasals and small, D-shaped premaxillary teeth (Holtz 2001; Brochu 2003; Currie *et al*. 2003), it is similar to typical basal coelurosaurian dinosaurs in many features. *Dilong paradoxus* displays several derived features similar to more derived coelurosaurians, such as the size and relative position of the external naris, and a few features related to the palatine, pterygoid and manus (Brochu 2003). Inclusion in a global analysis is likely to have implications in reordering some taxa at the base of Coelurosauria. Three specimens are known from the Lujiatun Beds, however a fourth is known from the Jianshangou Beds. This specimen preserves filamentous integumentary structures close to the mandible and along the caudal vertebrae. These structures are branched and appear to even show distal branching (Xu *et al*. 2004a).

Ornithomimosauria

Shenzhousaurus orientalis is known only from the holotype (Figure 4C). It is an ornithomimosaur that is more primitive than all other known species except *Pelecanimimus polyodon* (Perez-Moreno *et al*. 1994; Ji *et al*. 2003). The plesiomorphic features of this species include unserrated, leaf-shaped dentary teeth, a short metacarpal I, a straight ischium, and a curved postacetabular process of the ilium. Gastroliths are preserved, a feature also seen in some other ornithomimosaurian specimens (Kobayashi *et al*. 1999). The presence of gastroliths has been suggested to indicate a herbivorous diet (Kobayashi *et al*. 1999). Like all other dinosaur fossils from the Lujiatun Beds, the *Shenzhousaurus orientalis* holotype preserves no integumentary structures.

Therizinosauroidea

Beipiaosaurus inexpectus is represented by one published specimen, which may be immature based on the fusion degree of the preserved elements of the skeleton. Another specimen awaits description. The holotype is about 2.2 m in body length. Different from more derived therizinosauroids but similar to typical coelurosaurians, *Beipiaosaurus inexpectus* has a tridactyl foot with a proximally tapering metatarsal I. This indicates that derived therizinosauroids re-evolved a robust first digit in which the proximal end of metatarsal I articulates with the tarsals (Xu *et al*. 1999a). Interestingly, its last five caudal vertebrae are fused into a pygostyle-like structure (Xu *et al*. 2003a), a feature only seen in oviraptorosaurian dinosaurs among non-avian theropods (Barsbold *et al*. 2000). The holotype specimen preserves filamentous structures along the limb bones and near the vertebrae, some of which appear to be distally branched.

Oviraptorosauria

Four specimens of *Caudipteryx zoui* have been collected (Ji *et al*. 1998; Zhou *et al*. 2000), which preserve nearly complete, articulated skeletons. *Caudipteryx dongi* is represented by a single partial postcranial skeleton (Zhou and Wang 2000). *Caudipteryx* shares numerous derived similarities with other oviraptorosaurians on the skull, mandible, and pelvis (Currie *et al*. 1998; Sereno 1999; Zhou *et al*. 2000), but also displays several features convergent with relatively derived avians, such as a reduction in the number of dorsal vertebrae and a reduced third manual digit (Zhou *et al*. 2000). All specimens preserve pennaceous feathers (Figures 4D–F) with symmetrical vanes associated with the arms and the tail, and plumulaceous feathers on the leg and other parts of the body (Ji *et al*. 1998; Zhou *et al*. 2000).

Incisivosaurus gauthieri is represented by one specimen, preserving a nearly complete skull, incomplete mandible, and a partial vertebra. It is an unusual animal in that it has large procumbent rodent-like teeth in its upper jaw and small posterior teeth in both the maxilla and dentary. It shares numerous derived cranial similarities with other oviraptorosaurians (Maryanska *et al*. 2002), but also differs from the latter in many features, several of which are less avian-like, suggesting that these advanced characters are independently evolved in derived oviraptorosaurians (Xu *et al*. 2002a) and avians. Most interestingly, unlike any other theropod dinosaur, it has heavy wear facets on all teeth, strong evidence that this animal was herbivorous. Recently, Senter *et al*. (2004) suggested *Incisivosaurus gauthieri* is the junior name of *Protarchaeopteryx robusta*, but the latter differs in the presence of serrations on all teeth, strong labialingual compression of the premaxillary tooth crown, and probable absence of a pair of extremely large front teeth (inferred from the size of the tooth sockets).

Dromaeosauridae

Two specimens can be referred to *Sinornithosaurus millenii* (Xu *et al*. 1999b; Ji *et al*. 2001) and a few more might be also referable (Figure 4G). *Sinornithosaurus millenii* possesses several salient dromaeosaurid features, such as the highly modified tail and hypertrophied second pedal digit, and also shares many derived similarities to basal birds as do other dromaeosaurids (Norell and Makovicky 2004). For example, its shoulder girdle is nearly identical to that of *Archaeopteryx* (Ostrom 1976). Both *Sinornithosaurus* specimens preserve extensive filamentous integumentary structures around their skeletons, which are diverse in morphology. Although no clearly pennaceous feathers are preserved, the preserved integumentary structures display salient features of modern feathers, including branching structures and differentiations of the rachis and barbs (Ji *et al*. 2001). It should be noted that many bird specimens (e.g. *Confuciusornis*) from the Sihetun locality also lack the preservation of clearly pennaceous feathers (Xu *et al*. 1999b, 2001c). Notably long filamentous integumentary structures are also preserved attached to the tibia (Ji *et al*. 2001; Xu 2002).

Microraptor zhaoianus is known from four specimens, ranging in size from less than 40–55 cm in body length (Xu *et al*. 2000b; Hwang *et al*. 2002; Xu 2002). It is similar to *Sinornithosaurus millenii* in morphology, but has a dentition similar to basal avians and some troodontids (Norell *et al*. 2000; Norell and Hwang 2004) and a more robust forelimb. The discovery of *Microraptor zhaoianus* is especially important in terms of its small size and several pedal features comparable to arboreal birds. Two of the *Microraptor zhaoianus* specimens preserve filamentous integumentary structures, some of which may be pennaceous, though details are not completely clear due to preservation. Some large feathers are clearly preserved close to the distal end of the tibia on some specimens.

Three specimens of *Microraptor gui* have been described (Xu *et al*. 2003b; Ji *et al*. 2004) and many more have been discovered. The holotype is an old individual as indicated by the fused condition of many of its elements. Slightly larger than the known *Microraptor zhaoianus* specimens, the *Microraptor gui* holotype preserves exceptionally clear integumentary structures (Figure 4H). Plumulaceous feathers are preserved around the skeleton and pennaceous feathers are attached to the skull roof, forelimbs, hindlimbs, and tail. As a non-avian theropod, *Microraptor gui* displays two unexpected integumentary features. One is the presence of asymmetrical vanes on either side of the rachis, a feature suggesting flight capability (Feduccia and Tordoff 1979); the other feature is the attachment of large flight feathers to the metatarsals (Xu 2002; Xu *et al*. 2003b), an unusual feature also reported in an unnamed dromaeosaur (Ji *et al*. 2004).

Graciliraptor lujiatunensis is based on one specimen (Xu and Wang 2004a), represented by some cranial and postcranial elements. It has several unique features that are not seen in other dromaeosaurid species, such as relatively small manual ungual I and distally-wide metatarsal II; otherwise it is similar to *Sinornithosaurus millenii*.

Troodontidae

Sinovenator changii is known from two specimens (Xu *et al*. 2002c) and numerous undescribed specimens may also belong to this species. *Sinovenator changii* lacks a bulbous parasphenoid capsule and an arctometatarsalian foot, features shared by derived troodontids (Makovicky and Norell 2004). The pectoral and pelvic girdles are similar to dromaeosaurids and basal avians. The discovery of *Sinovenator changii* significantly shortens the morphological gaps between the three eumaniraptoran groups and has implications for coelurosaurian phylogeny (Xu 2002; Xu *et al*. 2002c).

Mei long is represented by a single specimen (Figure 4I; Xu and Norell 2004). Similar in size to *Microraptor* and *Archaeopteryx*, *Mei* is among the smallest non-avian theropods. It has several avian-like features, which were previously unknown in troodontids. It seems to lack a complete postorbital bar, the quadratojugal and squamosal do not contact, and the nasal-frontal articulation may be flexible. *Mei long* presents the first known furcula reported in troodontids. Remarkably, the holotype specimen is preserved in the stereotypical sleeping posture found in extant Aves, which demonstrates that this behaviour occurred early in dinosaurian evolution. Because this behaviour has been considered an adaptation associated with homeothermy, this has anecdotal implications for the presence of an advanced metabolism in *Mei long*.

Sinucerasaurus magodens is a relatively derived troodontid from the Jehol Biota (Xu and Wang 2004b). It shares a number of features with later, more derived troodontids, such as an anteroventrally oriented pubis, a large triangular obturator process positioned at mid-shaft of the ischium, absence of posterodorsal and posteroventral processes of the ischium, the presence of fully arctometatarsalian metatarsus, and abbreviation of pedal phalanx II-2 which has a developed proximoventral heel (Osmólska and Barsbold 1990).

Integumentary structures are unknown for the troodontids from the Lujiatun Beds. One possible troodontid specimen from the Dawangzhangzi shale beds preserves murky integumentary structures, the details of which are unclear. Another specimen, the *Jinfengopteryx elegans* holotype may represent another possible troodontid from the Qiaotou Formation of neighbouring Hebei Province (Ji *et al*. 2005). Although *Jinfengopteryx* was described as the most basal bird known to date, its general body-plan and several dental features (Ji *et al*. 2005) suggest that it is a troodontid. Interestingly, the holotype, the only known specimen, preserves large pennaceous feathers for most of the length of the tail, a feature that is similar to the tail plumage in *Archaeopteryx*.

Coelurosauria incertae sedis

Protarchaeopteryx robusta is an enigmatic coelurosaurian, represented by one specimen (Ji and Ji 1997; Ji *et al*. 1998). It has large premaxillary teeth and comparatively tiny maxillary and dentary teeth, a feature not known in other theropods except for *Incisivosaurus gauthieri* (Xu *et al*. 2002a), it is therefore possible to be closely related to the latter (Figure 3). The holotype specimen preserves 12 rectrices attached to the distal caudal vertebrae and also some plumulaceous feathers around the skeleton (Ji *et al*. 1998).

Yixianosaurus longimanus is known from a partial postcranial skeleton (Xu and Wang 2003). It has several maniraptoran features, such as scapula shorter than the humerus, small coracoidal portion of the glenoid fossa, large rectangular coracoid, bowed ulna and thin radius. *Yixianosaurus* has an elongate manus and proportionally long penultimate manual phalanges (Xu and Wang 2003). Filamentous integumentary structures are preserved adjacent to the forelimbs, but the details of these are unknown.

Nearly all major coelurosaurian clades except Alvarezsauridae are recovered from the Jehol Group of western Liaoning (Figure 3). Although current phylogenetic hypotheses predict that the major coelurosaurian divergences occurred in Jurassic times (Sereno 1999; Clark *et al*. 2001; Xu *et al*. 2001b), the Liaoning discoveries in most cases are the earliest known representatives of coelurosaurian clades such as Dromaeosauridae, Troodontidae and Oviraptorosauria. Consequently, it is not surprising that most Liaoning taxa are also the most basal known taxa of their respective clades (Figure 3). Their morphologies may not be the most plesiomorphic conditions for each clade, but in general are closer to the basal condition than those of later members of each clade.

The Liaoning taxa provide significant new insight into coelurosaurian phylogeny and also patterns of morphological change. For example, the inclusion of the basal troodontid *Sinovenator* in an analysis could result in moving the whole of Troodontidae to a different lineage (Xu *et al*. 2002c); the discovery of *Incisivosaurus* suggests that derived oviraptorosaurians independently evolved many bird-like features (Xu *et al*. 2002a) that have been used as evidence to support an avian status for the group (Maryanska *et al*. 2002).

The examination of character distributions along the coelurosaurian lineages reveals that the major structural modifications seen in birds were acquired sequentially and hierarchically in coelurosaurian evolution (Figure 3; Ostrom 1976; Norell and Makovicky 1997, 1999; Novas and Puerta 1997; Norell *et al*. 2001; Xu 2002). For example, a bird-like dentition, pelvis and shoulder girdle might have evolved in the early stages of coelurosaurian, maniraptoran and eumaniraptoran evolution, respectively (Xu 2002; Norell and Makovicky 2004).

The small size of many of the Liaoning taxa that are also basal in their groups is significant when considering the origin of birds. There is an evolutionary trend of size-decrease along the line to birds within Coelurosauria (Sereno 1999), but the pattern is complicated. The Liaoning discoveries suggest that the basal representatives of most coelurosaurian clades are small in size, especially the Dromaeosauridae, Troodontidae and Oviraptorosauria, basal members of which are similar in size to basal avians. This miniaturization might have played an important role in the evolution of some avian features, as small members of each clade tend to display more bird-like conditions than large ones (Xu and Norell 2004). Noteworthy, is that the sub-*Archaeopteryx*-size is stable at the base of the Eumaniraptora, which is present in basal members of the Dromaeosauridae and Troodontidae and several basal birds. This size seems to be an optimal size for the origin and early evolution of flight and thus deserves special consideration from a biomechanical view. However, many clades, especially the Tyrannosauroidea, display a trend of secondary size-increase and derived members of which are large in size. The size change is closely correlated to the development of many features within Coelurosauria, and accounts for the distribution of both homoplastic reversals in derived, secondarily large-sized members of many clades (such as the propubic pelvis in derived troodontids and dromaeosaurids) and homoplastic developments of avian conditions in some secondarily small-sized representatives of some clades (such as the prokinetic skull in mononykines) in some key characters.

The origin and early evolution of feathers was poorly understood until feathered dinosaur specimens were discovered in western Liaoning. Feather-like filamentous integumentary structures or feathers of modern aspect have been found in all major coelurosaurian clades recovered from the Jehol shale beds (Norell and Xu 2005), including compsognathids, tyrannosauroids, therizinosauroids, oviraptorosaurians, dromaeosaurids and possibly troodontids. They are diverse in morphology, including single filaments, compound structures composed of either multiple filaments joined at the base into a tuft, or multiple filaments joined in series along a central filament, plumulaceous feathers and pennaceous feathers with both symmetrical and asymmetrical vanes (Chen *et al*. 1998; Ji *et al*. 1998, 2001; Xu *et al*. 1999a,b, 2000b, 2003b; Norell *et al*. 2002; Xu and Zhang 2005). It should be noted, however, that some morphologies cannot be unquestionably confirmed due to the preservation. For example, there is evidence suggesting the presence of single filaments and multiple filaments joined into a basal tuft (Ji *et al*. 2001; Xu *et al*. 2001c; Xu 2002), but these two morphs are rare in the recovered specimens and might be preservational artifacts. The filaments are usually clustered together, making them open to different interpretations: a pseudo-branching resulted from the preservation of the clustered single filaments, or a true morph that has multiple filaments joined basally. No barbule has been observed directly, though it is assumed to be present, based on the general features of organization preserved on large feathers (Norell *et al*. 2002). In other cases, some contradictory information is present. For example, the absence of pennaceous feathers in known specimens of *Beipiaosaurus* and *Sinornithosaurus* contradicts their phylogenetic positions; however, this absence could have resulted from preservational, ontogenetical, moulting factors or even size-change, among others. Nevertheless, it is without any doubt that some feather morphologies, including some of modern aspect, are present in some non-avian coelurosaurian specimens recovered from western Liaoning, thus undeniably suggesting that non-avian coelurosaurians evolved feathers.

In general, the feather morphologies of the Liaoning taxa display an evolutionary trend of increasing complexity and a distinctive distribution pattern as one approaches the base of Aves. The basal coelurosaurian compsognathids and tyrannosauroids have relatively simple, filamentous structures; the more derived coelurosaurian oviraptorosaurians have pennaceous feathers with symmetrical vanes; and the most bird-like dromaeosaurids have flight feathers with asymmetrical vanes. The available evidence suggests that relatively simple filamentous structures evolved phylogenetically earlier than the planar, pennaceous feathers; pennaceous feathers with asymmetrical vanes evolved later than the ones with symmetrical vanes; flight feathers and their homologues first appeared on the tail and arms, and later on the legs. Based on developmental data, Prum (1999) proposed a model of the origin and early evolution of feathers, which is largely congruent with the fossil evidence. Xu (2006) revised Prum's model, suggesting the following evolutionary scenario of feathers: (1) the first feathers represented by single tubular filaments; then (2) distal branching of the filament appeared; (3) rachis and planar form of feathers evolved, which might be correlated with the appearance of a feather follicle; (4) feathers with fully closed symmetrical vanes evolved, followed by ones with asymmetrical vanes; finally, (5) feathers of modern type are degenerated from the flight feathers and their homologues while most other morphs might have reduced and lost from the avian body. This scenario suggests some distinctive feather features, such as their tubular nature and branching, evolved before the appearance of the feather follicle, emphasizes the significance of planar form in feather evolution, and underscores that the flight feather homologue might have evolved before other various feathers of modern birds. In general, this evolutionary scenario features both transformational and innovative processes, different from Prum's that is characteristic of a total innovative process (Prum 1999). These evolutionary models could be tested by further discoveries of integumentary details on non-avian dinosaurs, particularly of more plesiomorphic morphologies on more basal taxa than the known feathered coelurosaurian species.

The origin of avian flight has long been debated (Chatterjee 1997; Shipman 1998). New discoveries and analyses show that the major modifications necessary for flight were acquired sequentially in coelurosaurian evolution before the origin of birds (Ostrom 1974; Novas and Puerta 1997; Xu *et al*. 2003b), yet there is no consensus on the evolutionary processes required for flight. Classically, there are two opposing hypotheses of how the first dinosaurs started to fly: the 'trees-down' hypothesis and the 'ground-up' hypothesis (Chatterjee 1997). The former emphasizes that the first birds took advantage of gravity and that gliding played a key role in the early evolution of flight; the latter hypothesis underscores the ground effect during the evolution of flight and suggests an active process without taking advantage of gravity. The ground-up hypothesis is supported by the fact that non-avian coelurosaurians are clearly terrestrial cursors and the most basal birds lack highly specialized features for an arboreal life (Chiappe 1997). Several studies suggested an arboreal habit for some coelurosaurians, but the evidence is often speculative (Paul 1988; Chatterjee 1997).

Recent discoveries of some basal dromaeosaurids from Liaoning provide critical information on this issue. The Liaoning dromaeosaurids are small in size, display some pedal features comparable to those in arboreal birds, and most surprisingly, have flight feathers with asymmetrical vanes on the hindlimbs as well as the forelimbs and tail, a morph not known in any birds. Xu (2002) suggested that an arboreal life-style might have contributed to the final steps of the evolution of the flight capability, though most flight-related characters, such as furcula and pennaceous feathers, obviously evolved in a terrestrial context. Some modifications for an arboreal lifestyle occurred in the early evolution of the Eumaniraptora and highly specialized arboreal structures evolved later. Xu and co-workers have proposed that basal eumaniraptorans evolved large and highly specialized pennaceous feathers on the leg and these leg feathers were later reduced and lost in birds (Xu *et al*. 2003b, Xu *et al*. 2004b; Xu and Zhang 2005). The long leg feathers, particularly the metatarsal feathers, might be significant in the origin of avian flight (but see Padian and Dial 2005). Recent discoveries suggest this morph might represent a common adaptation close to the Aves node as all basal dromaeosaurids from Liaoning and several basal taxa on the avian lineage appear all to have long leg feathers and metatarsal feathers (Xu and Zhang 2005; Xu *et al*. 2005). Further work on the four-winged basal dromaeosaurids is ongoing, including biomechanical analyses, CT scanning to reveal flight-related braincase features, and wind tunnel tests of models. This work promises to shed new light into the origin of avian flight.

Sauropoda
Sauropod remains are rare from the Jehol Group. Some fragmentary postcranial bones and several isolated teeth have been recovered from the Jianshangou shale beds, Lujiatun sandstone and tuff beds, and thick sandstone beds of the Jiufotang Formation (Figure 2). Some elements display titanosaurian features (personal observation), but detailed research has yet to be published.

2.2. *Ornithischia*

Ornithischian dinosaurs are much less diverse than theropod dinosaurs from the Jehol Biota, although they are dominant in terms of their abundance. Currently, they are represented by three major groups: Ankylosauria, Ornithopoda and Ceratopsia (Figure 5). Stegosaurian and pachycephalosaurian dinosaurs have yet to be found from the Jehol Biota.

Ornithopoda
Jeholosaurus shangyuanensis is a small-size bipedal ornithischian (Figure 6A; Xu *et al*. 2000a). It has several ornithopod and euornithopod synapomorphies, such as a small antorbital fenestra, a large quadrate foramen located on the lateral face of the quadratojugal, a crescent-shaped paroccipital process, and the absence of an external mandibular fenestra (Sereno 1999). It also displays several primitive features, such as six premaxillary teeth (Sereno 1986), a short edentulous anterior portion of the premaxilla, a short diastema between its premaxillary and maxillary teeth, and a relatively dorsally positioned premaxillary tooth row and jaw articulation. Although it is similar to ornithopods, its exact phylogenetic placement awaits confirmation by more detailed phylogenetic analysis.

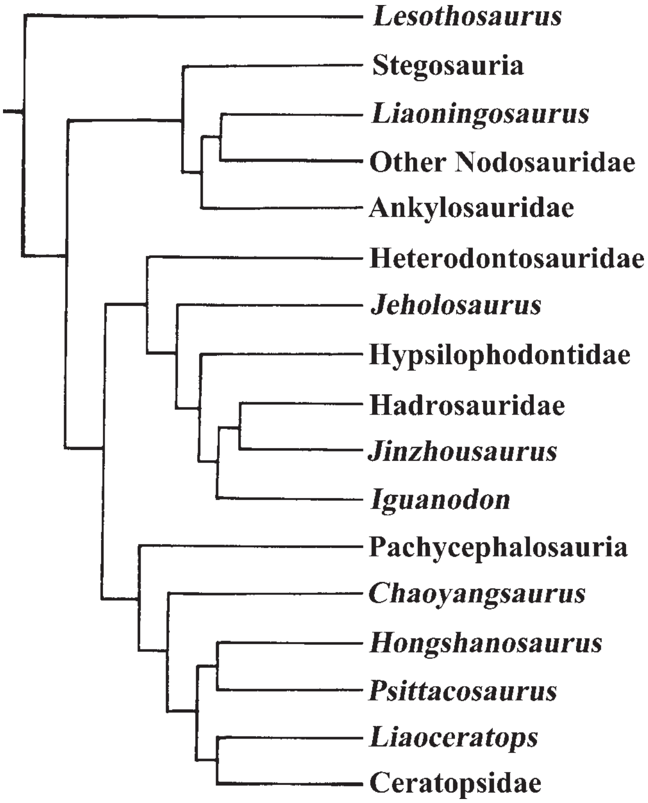

Figure 5. A simplified cladogram (from Sereno 1999) showing the systematic positions of Liaoning ornithischians.

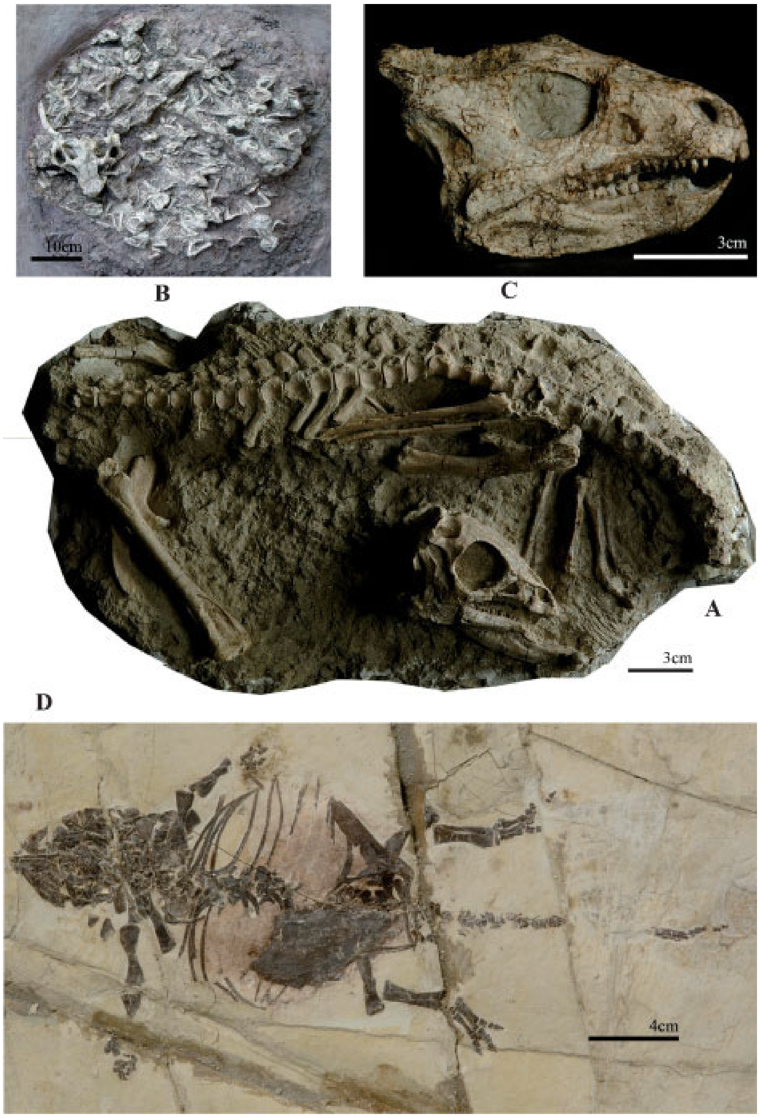

Figure 6. Selected ornithischians from the Jehol Biota. **A**: Ceratopsian *Psittacosaurus* nest (Dalian Natural History Museum D2156; Lujiatun Beds, Lujiatun, Beipiao); **B**: Neoceratopsia *Liaoceratops yanzigouensis* (IVPP V12738; Lujiatun Beds, Yanzigou, Beipiao); **C**: Ornithopod *Jeholosaurus shangyuanensis* (IVPP V12542; Lujiatun Beds, Lujiatun, Beipiao); **D**: Ankylosaurian *Liaoningosaurus paradoxus* (IVPP V12560; Dawangzhangzi Beds, Wangjiagou, Yixian).

Jinzhousaurus yangi (Wang and Xu 2001) is a large ornithopod about 7 m long. It has a combination of primitive and derived character states, including a relatively small number of dentary teeth, a weakly bifurcated ventral process of the predentary, an anteriorly extended frontal, exclusion of the frontal from participation in the orbital border, antorbital fenestra absent, squamosals in contact, and well-developed primary ridges on the lateral surface of each maxillary tooth crown.

Ceratopsia

Psittacosaurus meileyingensis was the first dinosaur species named from the Jehol Biota (Sereno *et al*. 1988). The skull has a relatively tall and round lateral profile. Some material from the same beds is referable to *Psittacosaurus* *mongoliensis*, which is widely distributed in central Asia and northern China. Numerous other *Psittacosaurus* skeletons have been recovered from the Jehol Group but have yet to be described (Xu and Wang 1998). One particularly interesting specimen is a *Psittacosaurus* nest preserving an adult and 34 juveniles (Figure 6B), providing strong evidence for the extensive parental care in ornithischian dinosaurs (Meng *et al*. 2004). *Psittacosaurus* remains have even been found as stomach contents of the mammal *Repenomamus*, suggesting that at least the young were important prey items (Hu *et al*. 2005). *Hongshanosaurus*, the second genus within the Psittacosauridae, was erected based on a juvenile individual (You *et al*. 2003) and recently an adult specimen was assigned to this genus. *Hongshanosaurus houi* is different from the known *Psittacosaurus* species in having proportionally longer snout and elliptical external naris (You and Xu 2005). The numerous well-preserved psittacosaurid specimens needs to be examined and compared carefully with other *Psittacosaurus* material throughout Asia in order to make precise taxonomic divisions and incorporate them within a phylogeny.

Liaoceratops yanzigouensis is a basal neoceratopsian dinosaur (Figure 6C). It is similar to *Psittacosaurus* in size, has intermediate morphology between that of psittacosaurids and higher neoceratopsians, and documents incremental evolution for some typical neoceratopsian diagnostic characters (Xu *et al*. 2002b). Also, it exhibits characters traditionally used to diagnose psittacosaurids, such as a weak ventral flange on the dentary and an infratemporal fenestra that is wider ventrally, and thus brings more homoplasies into the basal ceratopsian phylogeny.

Ankylosauria

Liaoningosaurus is based only on a juvenile specimen (Figure 6D), which is only about 50 cm in total body length (Xu *et al.* 2001a). Several unique features, however, distinguish this taxon from all known ankylosaurians. For example, it has a shell-like ventral armour, a feature that is not seen in any ankylosaurian specimen, juvenile or adult. Although *Liaoningosaurus* is tentatively placed in Nodosauridae, it could turn out to be a basal ankylosaurian.

The Jehol ornithischian fauna provides significant information on the evolution of several ornithischian clades. Possessing both ornithopod and euornithopod features, *Jeholosaurus* also has several features suggesting a more basal position than known ornithopods; furthermore, it shares several derived similarities with the basal ornithischian *Lesothosaurus*. Consequently, a full understanding of *Jeholosaurus* promises to shed light on the early evolution of ornithischian dinosaurs. Similarly, *Liaoningosaurus*, *Psittacosaurus* and *Liaoceratops* all have implications for the reconstruction of early evolution patterns of their respective groups.

3. PRESERVATION, FAUNAL COMPOSITION AND PALAEOBIOGEOGRAPHY

3.1. Preservation

The preservation of dinosaur fossils in the Jehol Group is unique in terms of completeness, the sheer number of recovered specimens, and the unprecedented incidence of soft tissue preservation. Most recovered specimens are nearly complete and fully articulated, with little indication of long subaerial exposure before burial. Some well-preserved specimens even indicate instantaneous burial without transport. For example, the *Psittacosaurus* nest and the sleeping *Mei* specimens preserve the life posture for the animals and behavioural information is thus recoverable (Meng *et al*. 2004; Xu and Norell 2004).

Even more unique is the superb preservation of the soft tissues on the Liaoning dinosaur fossils found in the shale beds. Recovered soft tissues include protofeathers, fully developed feathers and scales, horny claw sheathes, and even internal organs. Notable are the ‘feather-like’ or actual feather remains, rare in fossils. The fossilization of feathers requires special conditions that are different from the fossilization of hard tissue. Liaoning is a unique place for feather fossilization. However, even in Liaoning, different localities show different modes of feather preservation. In some localities, hard tissues are better fossilized and soft tissue impressions are rare; in other localities or even different layers at the same locality, the soft tissue are well preserved but the hard tissue may not be well fossilized. In several cases, the skeletons are only represented by traces of the elements although the feather-like structures, or feathers, are well preserved in a halo around the skeletal profile. It is difficult to explain the taphonomic circumstances accounting for soft tissue preservation, although current consensus is that volcanic activity may have contributed directly to death of the animals (perhaps through noxious gas) and their subsequent quick burial allowed preservation of the soft tissue.

3.2. Faunal composition

The Liaoning dinosaur fauna displays both local provinciality and stratigraphic differences (Figures 1, 2). These differences are probably preservational artifacts, but might be also partially due to ecological, chronological and geographical factors.

The *Lujiatun Beds* are the richest in dinosaurian fossils in terms of both taxonomy and specimen numbers. To date, 10 identified species are known from Lujiatun Beds (Table 1), making up about 45% of the total known species from the Jehol Group, and these beds have produced many more specimens than other beds. In the Lujiatun Beds, the most common element of dinosaurian fauna is the herbivore *Psittacosaurus*, which is represented by thousands of complete skeletons. Troodontids are the next most common group and the most common theropod dinosaurs from the Lujiatun Beds. Similar to *Psittacosaurus*, hundreds of skeletons were recovered, most of which are complete and fully articulated. Surprisingly, three troodontid genera have been identified from these beds and more species might exist, indicating a relatively high diversity. Dromaeosaurids, which are the dominant predatory dinosaurs in the shale beds, are rare in the Lujiatun Beds. The herbivorous *Jeholosaurus shangyuanenis* represents the third most common element in the Lujiatun Beds in terms of number of known specimens. Unlike *Psittacosaurus* and troodontids which have wide geographic distribution in western Liaoning, most *Jeholosaurus shangyuanenis* specimens were recovered from a small area near Lujiatun village. At other end of the scale, the ceratopsian *Liaoceratops*, the tyrannosauroid *Dilong*, the dromaeosaurid *Graciliraptor* and the oviraptorosaurian *Incisivosaurus* are the rarest elements in the Lujiatun Beds. Interestingly, there is no report of any avian fossil from the Lujiatun Beds, which is surprising, considering that avian fossils are among the dominant elements in other beds of the Jehol Group.

The *Jianshangou Beds* are also rich in species, though not as rich in terms of recovered specimens as the Lujiatun Beds. The most common taxon is the herbivore *Psittacosaurus*, although the specimen numbers are much fewer than in the Lujiatun Beds. The second commonest species might be *Caudipteryx*, a possible herbivorous theropod. Most *Caudipteryx* specimens were recovered from a small area near Zhangjiagou village, where a feathered *Dilong* and a *Sinornithosaurus* specimen were also found. The Jianshangou Beds near Sihetun village produced *Sinosauropteryx*, *Sinornithosaurus* and *Beipiaosaurus* fossil remains, only one or two specimens of each. This locality is rich for avians—several hundreds of nearly complete, articulated *Confuciusornis* specimens have been recovered.

The *Dawangzhangzi Beds* have produced a similar fauna to the Jianshangou Beds, but are less productive in terms of numbers of recovered specimens and species diversity. *Jinzhousaurus*, the largest known dinosaur species from this region is from these beds, a taxon up to 7 m in total body length.

The *Meileyingzi Beds* (Jiufotang Formation) have yielded some *Psittacosaurus* skeletons and several sauropod fragments.

The *Shangheshou Beds* produced numerous dinosaur specimens, and are probably richer than the Yixian shale beds, but in terms of specific diversity, the Jiufotang non-avian dinosaur fauna is low. The dominant dinosaurs are basal dromaeosaurids, most of which are probably *Microraptor*, and the next most common element is *Psittacosaurus*. These beds also have produced *Caudipteryx* specimens. Comparatively, the avian fauna is diverse, with both basal and derived taxa relatively close to the crown group.

In general, the Jehol dinosaur fauna is dominated by ornithischians in terms of numbers of specimens, but by theropods in terms of species diversity. Theropod dinosaurs contribute about 70% of known species from the fauna, but they are much fewer in specimens compared to ornithischians. Another interesting feature of the Jehol theropods is that some of these taxa might have competed with the herbivorous ornithischians for ecological niches. *Incisivosaurus gauthieri* displays strong evidence for a herbivorous diet; and *Caudipteryx zoui, Caudipteryx dongi*, *Shenzhousaurus orientalis*, and *Beipiaosaurus inexpectus* may have been herbivorous, based on some dental features and the presence of gastroliths. In addition, *Protarchaeopteryx* may also have been a herbivore, based on its dental similarities to *Incisivosaurus gauthieri*. In total, about 35% of the known theropod species display some evidence for a herbivorous diet, which is unusual for any known theropod fauna.

3.3. *Palaeobiogeography*

The palaeobiogeographic history of eastern Asia is in debate. Several studies suggest an isolation of eastern Asia from the rest of Laurasia during the Middle Jurassic to late Early Cretaceous (Russell 1993; Upchurch *et al*. 2002). The Jehol Biota provides new information to test this hypothesis (Luo 1999; Manabe *et al*. 2000; Zhou *et al*. 2003; Holtz *et al*. 2004). Luo (1999) suggested that the primitive nature of the Jehol Biota is consistent with long isolation for the region, whereas Manabe *et al*. (2000) disagree. These workers suggested that eastern Asia had connections with the rest of Laurasia in the middle-Early Cretaceous, the time period of the Jehol Biota, based on the presence of several vertebrate taxa that have a more cosmopolitan Early Cretaceous distribution. They further suggested that eastern Asia might have been a centre of diversification for some clades (Manabe *et al*. 2000). Zhou *et al*. (2003) accepted Manabe and co-workers' explanations and believed that the isolation of eastern Asia might have ended in the Berriasian, earlier than previously thought. This explains the composition of relict, endemic and cosmopolitan taxa in the Jehol Biota. Based on a phenetic dinosaurian palaeobiogeographic analysis, Holtz *et al*. (2004) suggested that the Jehol dinosaur fauna is more similar to the other Early Cretaceous Asian fauna than to non-Asian dinosaur faunas and even displays a close relationship with younger dinosaurian communities, a conclusion implying a long history of isolation for Asia from other continents.

The ornithopod taxa support an earlier end of the isolation. The basal ornithischian *Jeholosaurus* is primitive for a Cretaceous ornithischian, and comparable in morphology to several ornithischian taxa from the Middle Jurassic of China. *Jinzhousaurus* is a derived iguanodontid, a group of mainly Early Cretaceous ornithopods distributed on nearly all continents (Norman 2004). The ornithopod fossil record in western Lioaning is thus consistent with a Middle Jurassic isolation for the region, but also suggests contacts with other faunas before the late Early Cretaceous.

The ceratopsian fossils support an Asian origin and subsequent dispersal to other areas for this clade, but have no unambiguous information on isolation. The earliest and most basal ceratopsians are exclusively from Asia, including *Chaoyangsaurus*, probably the most basal ceratopsian from the Late Jurassic-Earliest Cretaceous Tuchengzi Formation in western Liaoning. However, *Stenopelix valdensis*, the basal-most and earliest known member of Pachycephalosauria, is from the Early Cretaceous in Europe. It thus requires either a before-Middle Jurassic Ceratopsia-Pachylocephalosauria split or minimally one dispersal event between eastern Asia and Europe during the Middle Jurassic-late Early Cretaceous times.

The Ankylosaurian *Liaoningosaurus* is uncertain in its phylogenetic positions. If nodosaurid affinities are corroborated, it could be evidence to support that western Liaoning contacted other regions before late Early Cretaceous as nodosaurids are widely distributed in other Early Cretaceous localities. If a basal ankylosaurian position is determined for *Liaoningosaurus*, it might be more consistent with an isolation pattern.

The Liaoning coelurosaurian taxa provide negative evidence for the isolation hypothesis. If eastern Asia had been fully isolated during Middle Jurassic-late Early Cretaceous times, the current coelurosaurian phylogeny and fossil record would predict that the major coelurosaurian clades had diverged before Middle Jurassic and most parsimoniously the Liaoning taxa forming monophyletic groups within the respective coelurosaurian clades. Several studies supported this hypothesis (Chatterjee, 1997; Xu *et al*. 2001b), but in general, the available evidence is weak. Furthermore, coelurosaurian phylogeny strongly rejects the monophyly of Liaoning taxa within their affiliated groups. Four coelurosaurian groups are represented by more than one species from Liaoning, that is the Compsognathidae, Oviraptorosauria, Troodontidae and Dromaeosauridae. None of these groups, except possibly the Dromaeosauridae, has a monophyletic Liaoning group in their basal phylogeny. Although all these Liaoning species could be explained as successively separated relict lineages from before the Middle Jurassic time, a dispersal hypothesis is more parsimonious to explain the current pattern of dinosaur fossil distribution.

In summary, a full isolation of eastern Asia from the Middle Jurassic to late Early Cretaceous times is not supported by the Liaoning dinosaur fossils. In our opinion, a long time period of full isolation of eastern Asia might never have occurred. Instead, a partial, regional isolation might contribute to the dinosaur fossil record during Middle Jurassic to late Early Cretaceous times in eastern Asia, which shows both strong endemism and close relationships with other communities.

4. CONCLUSIONS

As discussed above, the Jehol dinosaur fossils are significant in several aspects. (1), the unique mode of fossil preservation provides significant information on dinosaur palaeobiology. The *Psittacosaurus* nest specimen (Meng *et al*. 2004) and the sleeping troodontid specimen (Xu and Norell 2004) preserve behavioural information that is rare in fossilized vertebrates. In particular, the superb preservation of soft tissues makes it possible to study the origin and early evolution of feathers, an issue that has long suffered from a poor fossil record. The Liaoning theropod specimens conclusively indicate that simple, filamentous feathers evolved first and pennaceous ones of modern aspect developed later in coelurosaurian evolution and both have nothing to do with flight. Furthermore, feathers with aerodynamic features evolved before the origin of avians. (2), the relatively early age of the fauna and the completeness of the fossils provide many insights into the dinosaurian phylogeny. The discoveries of basal members of many dinosaurian sub-lineages are important for the reconstruction of the dinosaurian phylogeny. It is particularly evident in the case of the discovery of the basal troodontid *Sinovenator* and the basal oviraptorosaurian *Incisivosaurus*. (3), the Jehol dinosaur fauna is significant for understanding the Early Cretaceous ecosystem and the palaeobiogeographical relationships during this time period. The faunal composition differs significantly from that of many other dinosaur faunas, such as a high theropod specific diversity relative to a low one for ornithischian dinosaurs and a high percentage of herbivorous theropod species. Partly due to the astounding pace of discovery, many of the Liaoning dinosaurian taxa have received only preliminary description and analysis. It is expected that in-depth work will provide many more insights into the anatomy, functional morphology, systematics and palaeobiology of various dinosaurian clades in the future.

ACKNOWLEDGEMENTS

The authors thank Mick Ellison (AMNH) and Ding Xiaoqing (IVPP) for illustrations, the members of the Liaoxi expedition team of the Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences for their various help, and the Major Basic Research Project (G2000077700) of Ministry of Science and Technology of China, China Natural Science Foundation (40125006 and 40121202), the United States National Science Foundation (ATOL 0228693) and American Museum of Natural History for support.

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