

The remarkable fossils from the Early Cretaceous Jehol Biota of China and how they have changed our knowledge of Mesozoic life

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BENTON, M. J., ZHOU Z., ORR, P. J., ZHANG, F. & KEARNS, S. L. 2008. The remarkable fossils from the Early Cretaceous Jehol Biota of China and how they have changed our knowledge. *Proceedings of the Geologists' Association*, **119**, 209–228. Palaeontologists and others have been repeatedly amazed by reports of spectacularly well-preserved fossils from China, and one of the key sources has been the Jehol Biota of Liaoning, Hebei and Inner Mongolia in NE China. The Jehol Biota consists of three main horizons, the Dabeigou, Yixian and Jiufotang formations, spanning the late Hauterivian to early Aptian (131–120 Ma) of the Early Cretaceous and, collectively, these have produced thousands of essentially complete specimens of plants, insects, aquatic invertebrates, fishes, frogs, salamanders, turtles, lizards, choristoderes, pterosaurs, dinosaurs, birds and mammals. Most of the specimens show some aspect of exceptional preservation, ranging from clear impressions of the body outlines to traces of soft tissues (liver, teleost air sac, eye spots) and external body coverings (scales, feathers, hair). The claim was made that these discoveries have revolutionized our understanding of evolution through this critical part of the Cretaceous Terrestrial Revolution. Key insights have come from the numerous specimens of dinosaurs with feathers, but numerical study shows that only the finds of birds and mammals have substantially changed our views about global diversity and patterns of evolution through the Early Cretaceous.

Key words: Cretaceous, Jehol Biota, Jehol Group, Liaoning Province, dinosaur, bird, mammal

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1. INTRODUCTION

A series of papers in leading international journals, such as *Nature* and *Science*, astonished the palaeontological world in the 1990s. In these, ever-more amazing fossils were announced from the Jehol beds in NE China: examples of early birds, feathered dinosaurs, pterosaurs, early mammals, amphibians, pollinating insects and angiosperms. The specimens came from a time interval, the Early Cretaceous, whose faunas and floras were relatively poorly known from other locations and yet these specimens tended to be complete and they were often remarkably well preserved. How have these new discoveries impacted on our understanding of the evolution of life on land?

There are two views about the quality of the fossil record: it can be assumed to reflect either a biological or a geological signal. Note that the 'fossil record', which is all the fossils we currently know about, is less than the sum total of all ancient life. The traditional

assumption has been the first of course, that the sequence of fossils in the rocks tells us more or less the true sequence of evolution (Darwin, 1859; Sepkoski *et al.*, 1981; Benton *et al.*, 2000). However, it is clear that the fossil record is governed to a greater or lesser extent by the rocks (encompassing two variables – stratigraphic completeness and preservation potential), and that the fossil record is by no means a complete and unbiased record of all species that ever existed (Raup, 1972; Smith, 2007). In particular, certain groups of organisms may be soft-bodied, very small, or may live in the wrong sorts of habitats to be preserved.

For groups of plants and animals that have a skeleton of some sort, the fossil record might, however, be more readily assumed to reflect in some way the true pattern of the evolution of the group (Valentine, 1969; Sepkoski *et al.*, 1981; Benton *et al.*, 2000). An interesting experiment is then to assess the impact of a major new discovery, or set of discoveries, on current knowledge. Such studies, in which compendia of current

knowledge are compared across a century of work (e.g. Maxwell & Benton, 1990), or a decade (e.g. Sepkoski, 1993), have tended to show that the collections expand, but in an unbiased or random manner, so our understanding of the overall pattern of evolution of a group does not change much. This seems to be the case in comparing perceptions of diversifications and extinctions (Maxwell & Benton, 1990; Sepkoski, 1993) or the shape and patterns of phylogenetic trees (Tarver *et al.*, 2007).

In other cases, however, palaeontologists have pointed out the astonishing impact a single site, or set of linked sites, of exceptional preservation may have on perceptions of evolution. There is no doubt that the Burgess Shale, Chengjiang and other Cambrian biotas, have changed our views of life in the Cambrian seas immeasurably (Gould, 1989; Morris, 1998): they have added 200–300 new genera, some of them belonging to groups that were otherwise unknown in ‘normal’ Cambrian localities that yield only skeletonized tissues. Without those exceptional biotas, Cambrian life would have been documented solely by hard-bodied archaeocyathids, brachiopods, hyolithids and trilobites. However, with the exceptional discoveries, dozens of small, medium and large arthropods and worms were added to the diversity of life. Later exceptional biotas, such as the Late Jurassic Solnhofen fauna, have not apparently added much: virtually all the groups of marine and terrestrial animals sampled in the Solnhofen lagoon are known from fossils in ‘normal’ Jurassic sediments; those, such as jellyfish and worms, which were entirely soft-bodied, are known from older and younger fossils, and so their occurrence at Solnhofen was no surprise. Further, the Solnhofen limestones do not include entire phyla that are otherwise unknown – a feature of the Cambrian Lagerstätten.

But what of the Jehol Biota? Although the first Liaoning fossils were reported in the 1920s, the true breadth and quality of the materials have only become evident in the past 15–20 years. The purpose of this paper is to explore the question of whether this one sustained and astonishing new contribution to the fossil record has truly affected our understanding of the history of life. In particular, can it be said that the Jehol localities have substantially enhanced our understanding of the Cretaceous Terrestrial Revolution (Lloyd *et al.*, 2008), the time in the Early to mid-Cretaceous when angiosperms, leaf-eating insects, social insects, squamates (lizards, snakes) and many other terrestrial groups were diversifying fast? We begin by reviewing the faunas and localities, and then apply various numerical techniques to compare the ‘before’ and ‘after’ statistics on certain groups of animals and plants.

2. HISTORY AND GEOLOGY

History

The first information about fossils from the Jehol beds were reports of the small teleost fish in the 1880s, later

assigned to *Lycoptera* by Arthur Smith Woodward. The first broad overview of the faunas was made by the German-American palaeontologist, Amadeus William Grabau (1870–1946) in the 1920s. He had begun his career in North America, and then became Professor of Geology at Peking University in 1919, one of a small number of Americans and Europeans who were brought in at that time to develop and Westernize the leading universities in China. He proceeded to write numerous papers, and seven books, about the geology of China, exploring broad aspects of regional geology and stratigraphy, as well as the palaeontology of numerous formations. Among his many studies, Grabau (1923) gave the first description of what he called the ‘Jehol fauna’, consisting of abundant examples of the conchostracan *Eosestheria*, the mayfly *Ephemeroptera* and the teleost fish *Lycoptera* (Fig. 1). These three dominant fossils gave rise to an alternative name, the ‘EEL’ fauna. Grabau (1928) reviewed the Jehol fauna, and dated it as Jurassic and Cretaceous, although predominantly Cretaceous, based on comparison of the fossils with those from elsewhere.

Through the 1930s and 1940s, additional isolated fossils were reported, including new invertebrates, fishes, plants and occasional vertebrates. The next substantial work on the Jehol fossils was by the Chinese geologist and palaeontologist Gu Zhi-wei (born 1918). Because the Jehol fauna included plants, Gu (1962) renamed it the Jehol Biota. Gu (1962, 1983) also named the Jehol Group as a major stratigraphic unit to encompass the Jehol Coal-bearing Beds, the Jehol Oil Shale Beds and the Jehol Volcanic Rocks.

Work continued at a modest level until, in the late 1980s and early 1990s, a series of papers on fossil birds (Serenio *et al.*, 1988; Serenio & Rao, 1992; Zhou *et al.*, 1992; Hou & Zhang, 1993; Hou, 1994; Hou *et al.*, 1995; Zhou, 1995), mammals (Hu *et al.*, 1997) and dinosaurs (Ji & Ji, 1996; Chen *et al.*, 1998; Ji *et al.*, 1998) began to draw enormous international attention.

Geology

The Jehol Group, comprising the Dabeigou, Yixian and Jiufotang formations, crops out in western Liaoning, northern Hebei and SE Inner Mongoli (Nei Mongol), all in NE China (Fig. 2a). Comparable deposits of similar age occur across northern China and adjacent areas of eastern and central Asia, including Kazakhstan, Mongolia, Siberia, Japan and Korea, and many of these have yielded fossils very similar to those of the Jehol Biota (Chang, 2003; Zhou *et al.*, 2003).

The Yixian and Jiufotang formations are a nearly conformable sequence of weakly laminated to finely bedded siliciclastic sediments, mainly low-energy sandstones and shales that are interpreted to have been deposited in ancient lakes. There is no evidence of other kinds of continental deposits, such as channel infills, palaeosols or aeolian dune beds. These finely

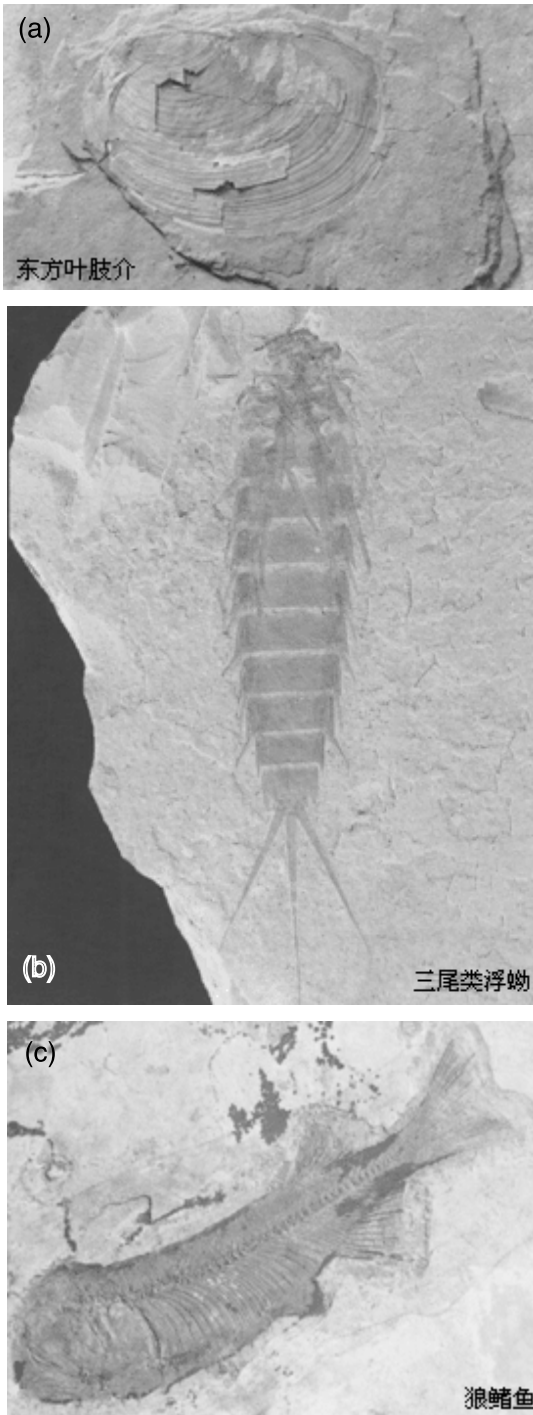


Fig. 1. The classic triumvirate of fossils that define the Jehol Biota: (a) the conchostracan *Eosestheria*, (b) the mayfly *Ephemeroptera* and (c) the teleost fish *Lycoperca*. (Photographs courtesy of IVPP.)

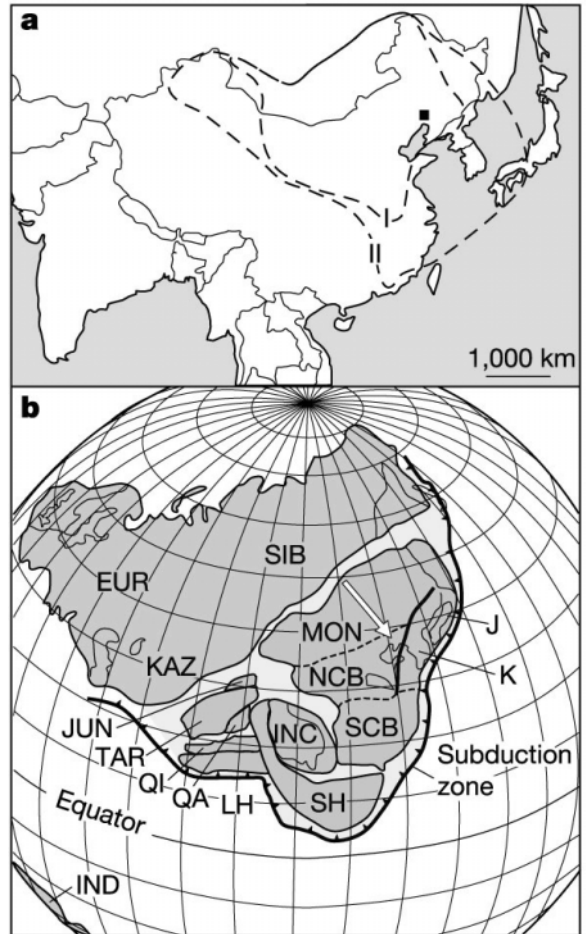


Fig. 2. (a) Modern-day map showing different geographical extents of the Jehol Biota through time. I, Yixian Formation and its lateral equivalents (late Hauterivian/ Barremian); II, Jiufotang Formation and its lateral equivalents (early Aptian). The filled square marks the position of the major vertebrate-bearing sites in Liaoning Province. (b) Palaeogeographical map of eastern Asia in the Lower Cretaceous, showing major regional tectonic features. The arrow indicates the approximate position of outcrop of the Yixian and Jiufotang Formations in northeastern China. This region would have occupied a palaeolatitude of approximately 40–45° N during the late Mesozoic. Abbreviations refer to major tectonic divisions: EUR, Europe; INC, Indo-China; IND, India; J, Japan; JUN, Junggar; K, Korea; KAZ, Kazakhstan; LH, Lhasa; MON, Mongolian; NCB, north China block; QA, Qaidan; QI, Qiangtang (North Tibet); SCB, south China block; SH, Shan Thai; SIB, Siberia; TAR, Tarim. (Based on information in Zhou *et al.*, 2003).

bedded sediments are interrupted by volcanic beds, largely conformable tuffs and basalts, as well as occasional cross-cutting dykes and sills (Zhou *et al.*, 2003).

The Jehol beds were deposited on the Eurasian landmass (Fig. 2), a large continental area that was

fully emergent from the oceans in the Early Cretaceous and composed of numerous tectonic blocks. The volcanic beds present throughout the Jehol rocks resulted from igneous activity around the then Pacific rim, and it was largely contemporaneous, as indicated by the fact that most volcanic beds are conformable with the sediments. Volcanic activity peaked at the time of deposition of the Yixian Formation and dwindled through the time of deposition of the Jiufotang Formation.

Stratigraphy

The Jehol Group (Fig. 3) consists of two major formations (Sha, 2007), the Yixian and Jiufotang, with the Dabeigou below in some regions. The Yixian Formation includes the Lujiatun bed, Jianshangou bed, Dawangzhangzi bed and Jingangshan bed; the Jiufotang Formation includes the Shahaï bed. Chiappe *et al.* (1999) argued that the lower beds of the Yixian Formation were best subdivided into a separate formation, the Chaomidianzi Formation, with a type locality at the village of Sihetun, approximately 25 km south of Beipiao City. However, this proposal has not been adopted widely and the Chaomidianzi Formation is regarded as a synonym of the Jianshangou Bed of the Yixian Formation. A further unit, the Dabeigou Formation in Fengning, northern Hebei Province, has been added as the lowest part of the Jehol Group below the Yixian Formation, although it has also been considered as equivalent to the lower part of the Yixian Formation in Liaoning Province (Zhou, 2006).

In many earlier papers (e.g. Hou & Liu, 1984; Hou *et al.*, 1995; Sun *et al.*, 1998; Ji *et al.*, 1999), the Jehol Group as a whole, or particular fossiliferous horizons, were claimed to be Late Jurassic in age. This added to the apparent significance of the fossils and would have suggested that several major groups, including angiosperms, various clades of birds, and placental mammals had had much earlier origins than otherwise understood. Subsequent work has shown that the early claims for a Late Jurassic age, based mainly on comparisons of faunas, but also on some radiometric dates, were flawed (Zhou *et al.*, 2003). For example, dates of 137 ± 7 Ma and 143 ± 4 Ma from the Yixian Formation were interpreted as Late Jurassic on the basis of an older dating that placed the Jurassic–Cretaceous boundary at 135 Ma. When this is corrected to the current boundary date (145 Ma), these Yixian dates become Cretaceous, although still rather old.

The dating has become clear and uncontroversial subsequently as a result of further comparisons of the fossils, but particularly because high-quality radiometric dates have been established throughout the succession. The radiometric dates have come from volcanic horizons, particularly throughout the Dabeigou and Yixian formations and, to a lesser extent, the Jiufotang Formation. As a result of

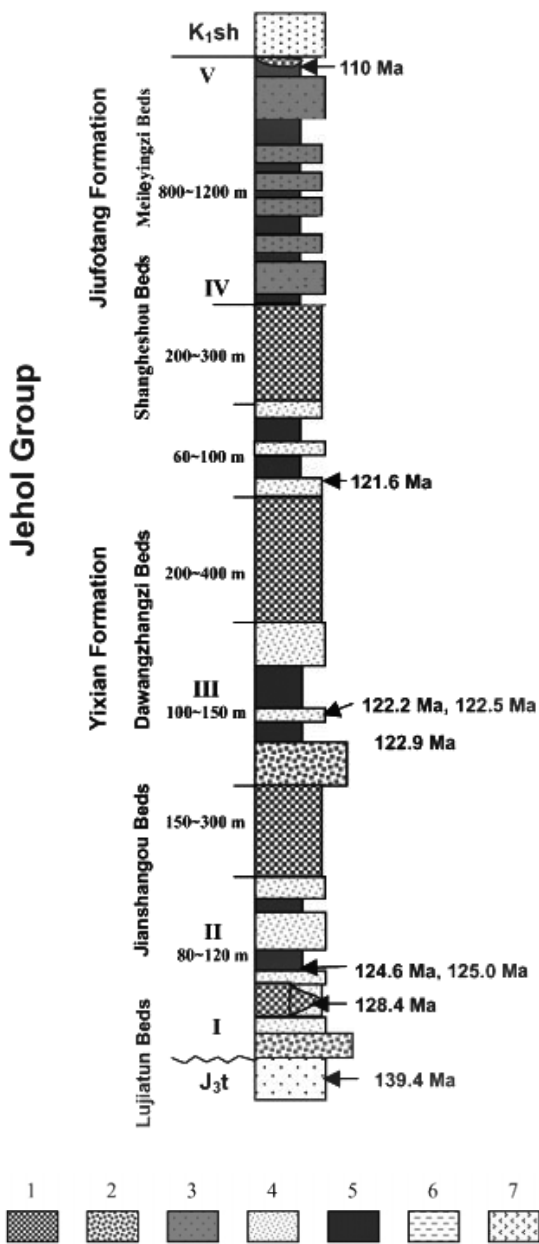


Fig. 3. A stratigraphic column of the Jehol Group showing the five main dinosaur-fossil-bearing beds (I–V). The lithological key is: 1, basalt and andesite with volcanic breccia (lava); 2, conglomerate with volcanic breccia; 3, sandstone and conglomerate; 4, tuffaceous sandstone and tuff; 5, shale and tuff; 6, silt and silty sandstone; 7, subvolcanic rock. (Based on Xu & Norell, 2006.)

sporadic eruptions throughout the time of deposition of the Jehol Group, tuffs are commonly interbedded with the shales or mudstones, even distal lacustrine sediments may contain tuffaceous horizons.



Fig. 4. Scenes of life in China. (a) The Institute for Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing, view of the front of the building, designed to represent the land animals (upper, red brick part of building) riding over the lower, white limestone-clad 'wave'. (b) Members of the expedition (from left to right, Patrick Orr, Zhang Jiangyong and Zhang Fucheng, with Zhou Zhonghe's head at front left) enjoy a lunchtime banquet in Nei Mongol.

Published dates for the Yixian Formation range from 121 Ma to 147.1 Ma (reviewed Zhou *et al.*, 2003; Zhou, 2006), but current best evidence dates the base of the formation at about 125 Ma (Swisher *et al.*, 1999, 2002) and the top at something younger than 121.6 Ma. The top of the overlying Jiufotang Formation was dated at older than 110.6 Ma, but a direct date is 120.3 Ma (He *et al.*, 2004). The Dabeigou Formation may date to 131 Ma.

Zhou *et al.* (2003) estimated that the Jehol Group spanned some 18 million years, based on a date of 128.4 Ma from a basalt overlying the Lujiatun Bed (basal Yixian Formation), and the date of 110.6 Ma from the upper part of the Jiufotang Formation. The 128.4 Ma date is now considered (Zhou, 2006) as

probably too old, and so the total duration of the Jehol Group is recalculated as 11 Ma (131–120 Ma). This implies an age span for the Jehol Group from late Hauterivian to early Aptian. The Yixian Formation (125–120 Ma) is then entirely early Aptian in age, and the overlying Jiufotang Formation also entirely early Aptian. The underlying Dabeigou Formation (131–125 Ma) then corresponds to the late Hauterivian and Barremian in age (Gradstein *et al.*, 2004).

Jehol Expedition 2007

As part of a joint-funded project between the Institute of Vertebrate Paleontology and Paleoanthropology

(IVPP; Fig. 4a), a division of the Chinese Academy of Sciences, and the Department of Earth Sciences at the University of Bristol, all five co-authors went on a one-week expedition around key Jehol Biota sites in NE China, in Liaoning and Nei Mongol ('Inner Mongolia'). The expedition involved visits to many of the fossiliferous quarries, and occasional banquets (Fig. 4b).

During the course of the expedition, we visited Yixian Formation localities in Liaoning Province, including the famous locality of Lujiatun, sometimes called the 'Chinese Pompeii' (Fig. 5a) because it preserves three-dimensional skeletons of the ceratopsian dinosaur *Psittacosaurus*, the sleeping troodontid dinosaur *Mei*, and the large mammal *Repenomamus* in ash and ignimbrite preserving a baby dinosaur in its stomach. We went on to the famous Sihetun locality (Fig. 5b), perhaps the most celebrated of all, the source of about 1000 confuciusornithid birds, as well as numerous other fossils, from the lower Yixian Formation. There is a well-established museum at this site, which shows many of the specimens *in situ*, but under glass. The third major locality we visited was Chaoyang (Fig. 5c), a key site in the Jiufotang Formation, and location of a major new museum dedicated to the palaeontology of the Jehol Biota.

3. THE JEHOI PLANTS AND ANIMALS

The Jehol Biota has produced fossils of plants, including early angiosperms and microscopic charophytes and dinocysts; aquatic snails, bivalves and hugely abundant aquatic arthropods (conchostracans, ostracods, shrimps), fishes, frogs, salamanders, turtles and choristoderes; terrestrial and flying insects, spiders, lizards, pterosaurs and dinosaurs, including feathered dinosaurs, birds and mammals.

The forests around the lakes were dominated by conifers, including members of the podocarp (*Podocarpites*), pine, araucaria (*Araucarites*) and cypress families. There were also ginkgos, czekanowskialeans, bennettitaleans, gnetaleans (*Ephedrites*, *Gurvanella*), horsetails (*Equisetites*), ferns and mosses (Zhou *et al.*, 2003). The leaves and needles of the trees show adaptations to a dry season, and these were presumably derived from plants living on higher land, while the ferns and mosses normally grow in wet habitats, presumably around the waters' edge. *Archaeofructus* was described as the earliest known angiosperm (Sun *et al.*, 1998), and it is reconstructed as a modestly-sized water plant (Friis *et al.*, 2003). Revision of the age of the deposits (see above) means that *Archaeofructus* is certainly an early angiosperm, but by no means the oldest.

Gu (1983, 1995) listed the key fossils from the Jehol Group as a whole, but Chen (1988) showed there were three phases of evolutionary radiation, defined primarily by the invertebrate fossils, corresponding to the Dabeigou, Yixian and Jiufotang formations. The

majority of the fossils come from the lower Yixian Formation and the Jiufotang Formation.

The Dabeigou Formation assemblage includes the *Nestoria*–*Keratetheria* conchostrachan assemblage, the *Luanpingella*–*Eoparacypris*–*Darwinula* ostracod assemblage, the *Arguniella* bivalve assemblage, the *Lymnaea websteri* gastropod assemblage, and the *Peipiaosteus fengningensis*–*Yanosteus longidorsalis* acipenseriform fish assemblage. Species and specimens of these fossils are rare, and the only birds known from this assemblage are *Protopteryx fengningensis*, the most primitive enantiornithine bird known (Zhang & Zhou, 2000) and *Eoconfuciusornis zhengi*, the most primitive confuciusornithid (Zhang *et al.*, 2008; Fig. 6).

The Yixian Formation has produced the classic *Eosestheria*–*Lycoptera*–*Ephemeroptera trisetalis* assemblage (Fig. 1) recognized by Grabau (1923, 1928) and Gu (1962, 1983), as well as the *Cypridea* (*Cypridea*) *liaoningensis*–*C. (Ullwellia) muriculata*–*Djungarica camarata* and *Cypridea (C.) veridica arquata*–*C. (C.) jingangshanensis*–*C. (C.) zaochishanensis* ostracod assemblages, the *Arguniella*–*Sphaerium* bivalve assemblage, the *Probaicalia vitimensis*–*Reesidella robusta* gastropod assemblage and the *Aeschnidium*–*Manlayamyia dabeigouensis* insect assemblage (Chen, 1999). These invertebrate assemblages represent the most abundant and diverse fossils of the Jehol Biota. Most are from the lower Yixian Formation (Jianshangou Bed), which has also been the source of a diverse vertebrate assemblage, including many well-known dinosaurs, birds (Fig. 7), pterosaurs and mammals. The Jehol flora was also most diverse at this time, including nearly all the typical Mesozoic plant groups, as well as some early angiosperms.

The Jiufotang Formation, and equivalent units from northern China, dated at 120 Ma or slightly younger, shows the third radiation in the Jehol Group. The invertebrate assemblages are characterized by the appearance of the *Yanjiestheria* conchostrachan assemblage, the *Mengyinaia*–*Nakamurania*–*Sphaerium* bivalve assemblage and the *Cypridea* (*Cypridea*) *veridica veridical*–*C. (C.) trispinosa*–*C. (Yumenia) acutiuscula* and *C. (Ullwellia) koskulensis*–*C. (Yumenia) casta*–*Limnocypridea abscondida*–*Djungarica* ostracod assemblages. The birds and pterosaurs from the Jiufotang Formation are distinct from those recorded in the Yixian Formation, and some of the taxa are more cosmopolitan (Zhou *et al.*, 2003; Wang & Zhou, 2006). The dinosaur *Microraptor gui* (Fig. 8), with its four 'wings', has been particularly important in confirming that birds originated from an ancestor close phylogenetically to such dromaeosaurid dinosaurs.

4. TAPHONOMY

The taphonomy of the Jehol Biota is perhaps the least resolved aspect of its palaeobiology. The exceptional preservation includes articulated skeletons, soft tissues, stomach contents, colour patterns and twigs with



leaves and flowers still attached. Critically, exceptionally preserved fossils are known from a large areal extent and stratigraphic range. It is therefore unlikely that the fossils, even just those that accumulated in lacustrine environments, are represented by a single mode of preservation. This, however, has yet to be tested. In the interim, some general observations are possible, and a preliminary taphonomic model can be erected. More detailed observations on two aspects of the taphonomy of the fossils are possible: the initial stages of the taphonomic history, including potential killing mechanisms, mode of entry to the depositional environment and, linked to these, the origin of the opisthotonic posture in fossil vertebrates, where the neck is bent back, as if in a death spasm; the mode of preservation of the feathers.

The general taphonomic history links preservation of the biota to episodes of volcanic activity (Zhou *et al.*, 2003). The most productive horizons are beneath ash tuff falls, which would have entombed most of the organisms present in the water column – the tuff layers are strongly correlated with mass mortality events. Animals and plants that lived in the water, as well as carcasses that were washed in, or fell in (insects, birds, pterosaurs) were presumably buried rapidly in the fine-grained sediments. The most productive fossil beds lie below ash-fall deposits, so these are presumably mass mortality beds where the living organisms were suffocated, and organic remains were encased instantly, in the absence of oxygen and hence of decomposers and scavengers. The tuffs also appear to have sealed the fossil-rich layers; this, or more plausibly, unfavourable bottom-water conditions, could have inhibited later burrowing or digging from above, and so the fossils remain in a highly articulated state. Leng & Yang (2003) noticed that pyrite microcrystallines and framboids occur extensively inside and on the surface of plant fossils, indicating dysoxic aqueous conditions with free oxygen levels less than $30 \mu\text{mol l}^{-1}$ for the microenvironment where these framboids were formed. They also suggested rapid tissue degradation that occurred during the earliest stages of fossilization. They further proposed a ‘fossil envelope’ model to accommodate the different

Fig. 5. The Beijing–Bristol 2007 Expedition to Liaoning, Hebei, and Nei Mongol provinces, to visit key Jehol Biota localities. (a) Members of the expedition (from left to right, Zhou Zhonghe, Patrick Orr, Stuart Kearns and Zhang Fucheng) look at tuffs and ignimbrites at the Lujiatun locality (Yixian Formation). (b) View across the floor of the Sihetun quarry, showing the interpretative board in front of a major, conformable, layer of basalt, intruding between layers of siliciclastic sediments with abundant fossils (Yixian Formation). (c) Three members of the expedition (from left to right, Michael Benton, Patrick Orr and Stuart Kearns) keenly hunting for small fossils in a pit excavated through numerous laminae of siltstone and fine-grained sandstone at the Chaoyang locality (Jiufotang Formation).

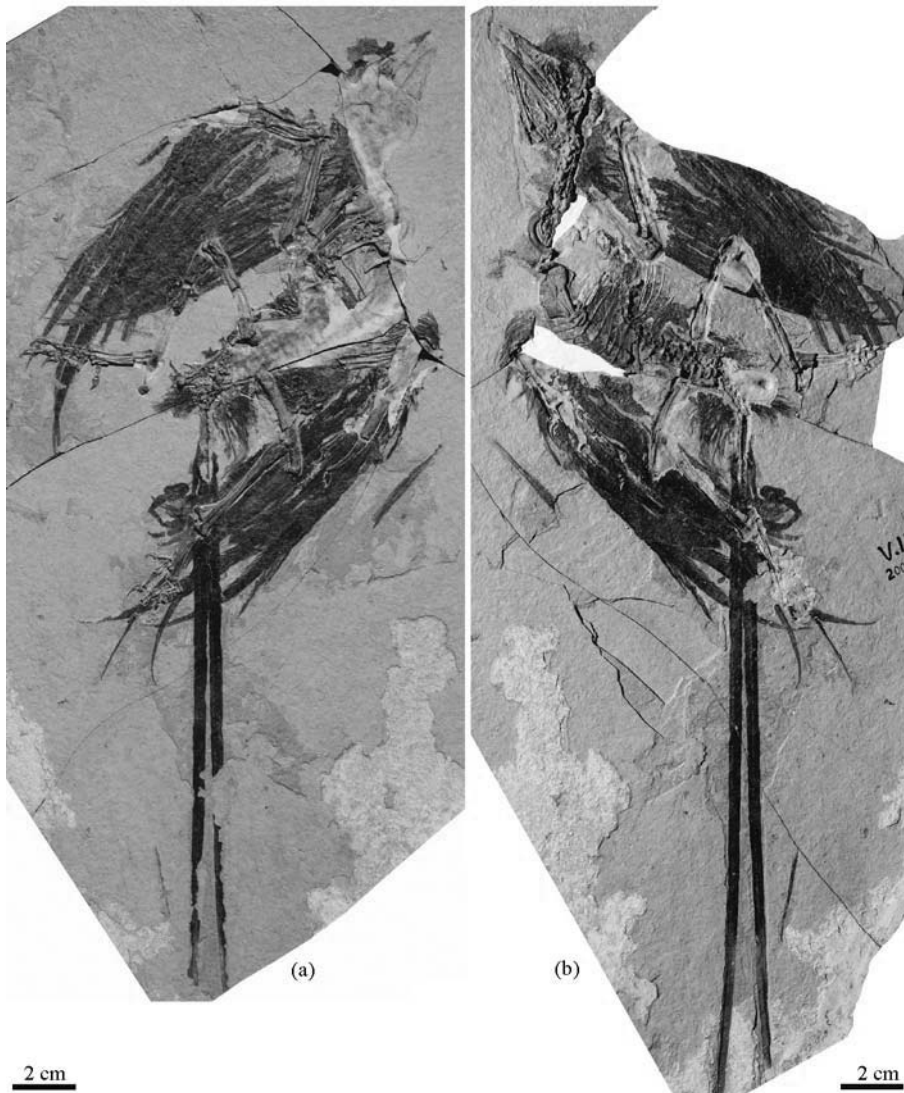


Fig. 6. The oldest confuciusornithid bird, *Eoconfuciusornis zhengi* Zhang *et al.*, 2008, from the Dabeigou Formation; skeleton and feather impression on (a) the counterslab and (b) main slab. (Courtesy of IVPP.)

geochemical conditions between the microenvironment surrounding the fossil material and the macroenvironment of the background lake bottom water. This is therefore a classic Konservat Lagerstätte.

The preservation of soft tissues includes dermal structures, such as scales, feathers and hair, sometimes showing colour banding (but probably not the original colours). In addition to dermal structures, many Jehol fossils retain a two-dimensional, dark-coloured body outline, often considered to be 'organic' or 'carbonaceous' in composition. Specimens often display a lighter-coloured periphery associated with this dark-coloured film (e.g. Wang & Evans, 2006, fig. 1A), a combination and arrangement strikingly similar to that

found in amphibians from the Miocene lacustrine Libros fauna from NE Spain (McNamara *et al.*, 2006, fig. 1A); in the latter the lighter-coloured material represents phosphatized skin preserved in histological detail. Evans & Wang (2007) reported the impressions of skin cells and square scales in a lizard specimen, and our initial analyses of Jehol material have also revealed examples of subcircular squameous skin cells between the feathers of several taxa of birds and dinosaurs. The fish *Lycoptera* shows a darkened patch corresponding possibly to the swim bladder, and black eye spots (Fig. 9).

The material examined to date comprises mainly birds held in museum collections. Two caveats should



Fig. 7. One of the most spectacular fossils of all time from the Yixian Formation, two specimens, a presumed male (with long tail plumes) and female of *Confuciusornis sanctus*, a species now known from more than 2000 specimens. (Courtesy of IVPP.)

therefore be borne in mind. The possibility of a taxonomic control on the fidelity of preservation should not, as yet, be excluded. Almost invariably, complete or nearly complete specimens are often

over-represented in datasets assembled from museum collections.

Careful examination of numerous fossils has, however, revealed little evidence for extensive preservation of tissues from the more labile end of the non-biomineralized spectrum; for example, tissues such as muscles are rarely, if ever, reported. Certain caveats apply to this observation; notably, high resolution, SEM-based, imaging of specimens reveals details that are not apparent under the optical microscope (compare Figs. 10c, d). None the less, in our experience, examples of mineralized soft tissues can be identified invariably using optical microscopy, even in hand specimen, in other, comparable, biotas (for example Cenozoic lacustrine exceptional faunas; McNamara *et al.*, 2006, 2009). The virtual absence of these tissues in the Jehol Biota is therefore considered real and in striking contrast to many other lacustrine-hosted Mesozoic and, especially, Cenozoic, exceptional faunas (see e.g. McNamara *et al.*, 2009). Similarly, unlike the latter, evidence for fossilized microbes is also absent. Some bird fossils are, however, associated with a thin structureless siliceous layer, the appearance of which is reminiscent of the exopolysaccharide matrix of biofilms.

Death and burial: the initial stages of the taphonomic history

Initial observations suggest that the entombment of carcasses within, or their burial by, depositing ash layers in the Jehol Biota does not apply in all, perhaps even the majority of, cases. Specimens tend to occur in intervals of finely laminated sediments; individual laminae are on the order of millimetres or less in thickness and, therefore, represent either small-scale events, the distal ‘signature’ of larger-scale events, or semi-continuous, possibly seasonal, hemipelagic deposits. Whatever their origin, few individual laminae/beds are thick enough that carcasses would have been entrained within them as they were deposited. Specimens of birds are invariably present with their largest surface area parallel to bedding, an orientation that suggests specimens settled vertically through the water column and came to rest on the sediment–water interface (Fig. 7). In many cases the skeletons display high values for both completeness and articulation (although collector bias may be an issue). Skeletons are not, however, always complete and fully articulated; i.e. they entered the depositional environment after some limited decay either in the water column or at the sediment–water interface. It is difficult to reconcile this with their death, deposition on the lake floor and entombment by a depositing volcanic ash having been a continuous, essentially instantaneous, process. This scenario, however, is a critical element of the model recently proposed by Marshall Faux & Padian (2007) to explain the occurrence of vertebrate fossils in an opisthotonic posture.



Fig. 8. The type specimen of *Microraptor gui* Xu *et al.*, 2003 (IVPP V13476), a remarkable small dromaeosaurid dinosaur with fully developed 'wings' of flight feathers on both arms and both hind limbs, from the Jiufotang Formation. (Courtesy of IVPP.)

Origin of the opisthotonic posture in fossil vertebrates

Articulated specimens of fossil vertebrates often exhibit opisthotonus; the condition is characterized by extreme dorsally hyperextended posture of the spine, in which the skull and neck are recurved over the back, and with strong extension of the tail (Marshall Faux & Padian, 2007). This is a recurrent feature of articulated specimens in numerous exceptional faunas; the examples cited by Marshall Faux & Padian (2007) include taxa from the Jehol fauna. Traditionally, the development of opisthotonus is attributed to *post mortem* processes; the various mechanisms that have been suggested, some more plausible than others, are reviewed by Marshall Faux & Padian (2007). These authors favour the idea that opisthotonus arose at the time of death, not afterwards, and they attribute it to poisoning of the central nervous system. Intriguingly, they posit, based in part on data from the Jehol Biota (Marshall Faux & Padian, 2007, pp. 219–220, tables 2 and 3), that clades of animals with high metabolic rates may be more susceptible. As they acknowledged, *post mortem* rigor mortis typically persists for 24–48 hours after death, after which stiffness resolves and muscles are once again flaccid. Any disturbance of the specimen after that period is likely to obliterate evidence of an opisthotonic posture acquired at the time of death. Such re-orientation could result from various processes including scavenging, current activity (this need not result in transport of the carcass), or even settling vertically through the water column.

Marshall Faux & Padian (2007) envisaged rapid burial of recently deceased carcasses as key to retaining an opisthotonic posture. They consider this likely to

have happened not only in the Jehol Biota, but also in the bird carcass from Quaternary hot spring deposits reported by Channing *et al.* (2005) ('.. after death the carcass was swiftly entombed...'; Marshall Faux & Padian, 2007, p. 222). Similarly, terrestrial taxa 'were rapidly immersed and buried in the Solnhofen lagoon' (p. 223). A key aspect of the taphonomy of allochthonous vertebrate taxa in Solnhofen, including *Archaeopteryx* is, however, that they were overgrown by a microbial mat after deposition; clearly rapid burial is inconsistent with this. Marshall Faux & Padian's (2007) case is probably strongest for the Jehol Biota, in which an association of fossiliferous horizons and event beds (volcanic ash horizons) has been noted above.

Various potential *peri mortem* causes of an opisthotonic posture are identified by Marshall Faux & Padian (2007). These include asphyxiation and environmental toxins; more specifically, gases derived from volcanic eruptions and cyanobacterial blooms are cited as possible agents, respectively. The latter is a known cause of death for individual vertebrates (e.g. Nehring, 1993), as well as populations (Briand *et al.*, 2003; Stewart *et al.*, 2008), in the latter case generating mass mortality events (Matsunaga *et al.*, 1999; Reyero *et al.*, 1999). Notably, such events may generate a biochemical signature (Romero *et al.*, 2006) that can be retained in the geological record (Braun & Pfeiffer, 2002; see also Koenigswald *et al.*, 2004). The association of fossiliferous intervals and volcanic ash layers in the Jehol Biota has prompted suggestions that volcanic emissions were the cause of mass mortality events that provided at least the majority of vertebrate



Fig. 9. Typical example of the fish *Lycoptera*, showing brownish iron-stained preservation of all the fine bones, and a black, carbonaceous impression of the rather large eyeball and the swim bladder, the elongate structure beneath the vertebral column. Scale bar in millimetres.

carcasses. For example, Guo *et al.* (2003) presented a complex model in which short- and longer-term environmental perturbation results from the injection of various volatile gases into the stratosphere. Volcanic events would also neatly couple the cause of death with rapid entombment within or beneath the depositing volcanic ash, a critical part of the model proposed by Marshall Faux & Padian (2007).

It remains uncertain how far the association of fossil material with specific beds or intervals reflects a concentration of collecting effort at certain horizons. The association with volcanic ash horizons may be significant in this respect. Thicker ash beds are potentially isochrons that allow the stratigraphic position of horizons known to be fossiliferous at one locality to be identified elsewhere.

The various models are amenable to, and require, further testing. A more detailed model of the physical taphonomy of the Jehol Biota would require analysis of the specimens themselves to be integrated into a detailed study of the sedimentology, organic chemistry and mineralogy of the host lithologies. This should be undertaken on a locality-by-locality basis, targeting, in

the first instance, those with horizons known to yield diverse assemblages in which taxa are numerous and occur at different levels.

Taphonomy of feathers

Elucidating the taphonomy of the feathers has wider implications, in particular as concerns the current debate about the integumentary structures preserved in association with certain dinosaurs from the Jehol fauna (e.g. Lingham Soliar *et al.*, 2007). Initial analysis of unequivocal feathers shows, as Zhang *et al.* (2006) described, obvious identifiable morphology at the macro scale (Fig. 10a). A notable detail is that the rachis, the central quill, one of the most distinctive features of feathers, is in almost all cases absent. The vanes of feathers are dark in colour in backscattered electron images (Fig. 10b), suggesting that they are preserved as carbon (see Orr *et al.*, 2002); energy dispersive X-ray analysis confirms this. The carbon is clearly the degraded remains of the original tissues; i.e. these have not been replicated in authigenic minerals. There

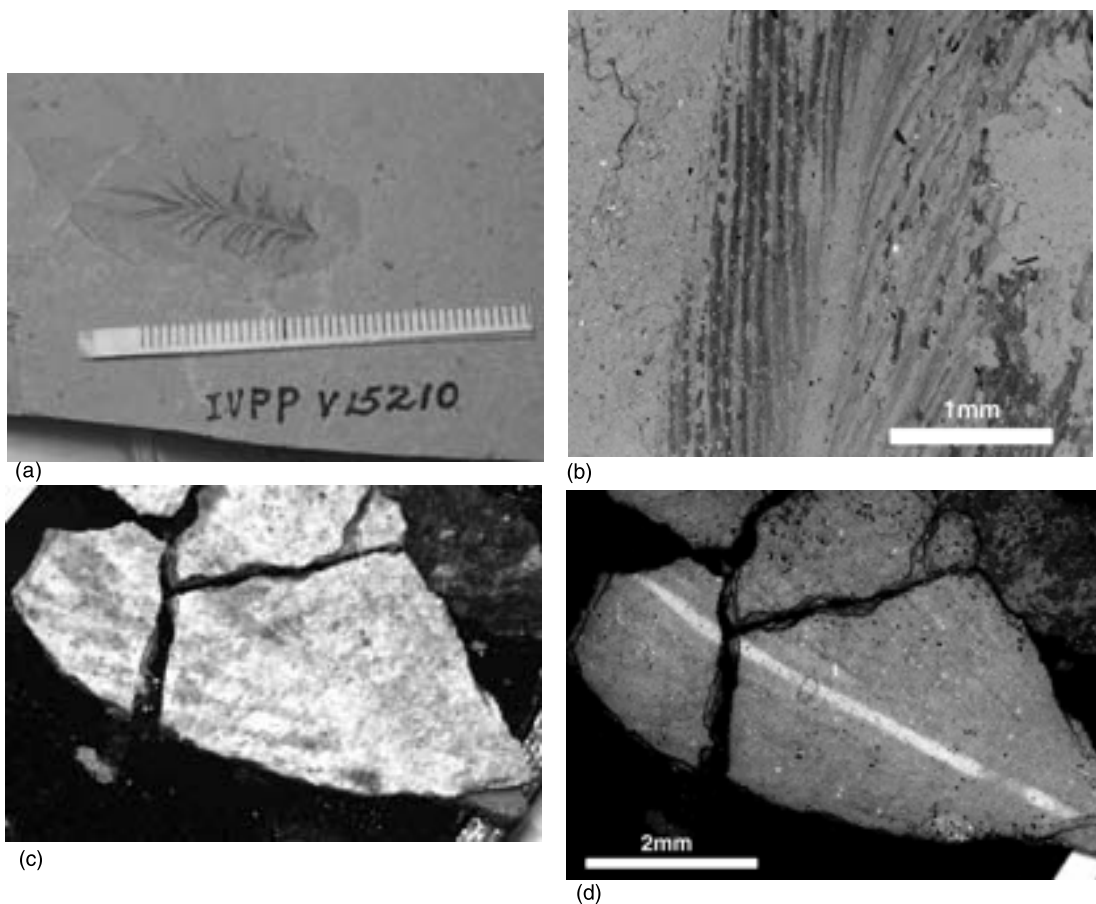


Fig. 10. Photographs illustrating aspects of the taphonomy of Liaoning feathers. (a) Typical example of an isolated feather from Liaoning (IVPP V15210); note that the rachis, the central 'quill', is not preserved. (b) Back-scatter electron SEM image of a typical feather, in which dark tones are indicative of carbon preservation (confirmed by X-ray analysis); the central rachis contains the same silicate assemblage as the rock matrix, and the small carbonaceous particles are plant fragments. (c) Light micrograph of a *Confuciusornis* feather, and (d) back-scatter electron SEM image of the same feather showing the light-coloured phosphatized rachis in a largely silicate matrix; feather barbs are less distinct than in (b), indicating less carbon. Scale bars in millimetres.

is, however, some replication of the rachis in calcium phosphate (e.g. *Confuciusornis*; Figs. 10c, d) and the claw sheath of the same sample is also phosphatized. For reasons that are not as yet understood, this mineralization is clearly restricted to the rachis; it must therefore reflect a physical or biochemical attribute possessed by this part of the feather. This unusual combination, partial preservation in authigenic minerals and as a carbonaceous residue, offers an indirect test of what other, more problematical, integumentary structures are likely to represent. The preservation of keratinous tissues, such as these in calcium phosphate, is noteworthy for another reason. Calcium phosphate offers the best potential for observing cellular and subcellular details of animal tissues (Briggs, 2003) and may well lead to further discoveries of soft tissues.

Feathers occur in various states of preservation. These range from essentially pristine, with the barbs and barbules of each vane in life position, to a more 'bedraggled' appearance, in which groups of barbs are bundled along the length of the rachis and individual bundles are separated from each other. Inside each bundle the barbs occur juxtaposed or overlapping. This condition is much more likely to be of taphonomic origin, rather than representing the feather's morphology *in vivo*. This is, however, strongly reminiscent of the structure of feathers reported from Lower Cretaceous amber by Perrichot *et al.* (2008). It is therefore possible that the structure of the latter is taphonomic in origin, not as suggested by these authors, an intermediate stage in the evolution of feathers (see Prum, 1999, Prum & Brush, 2002).

Table 1. Total numbers of species of different major groups of organisms named from the three fossiliferous divisions of the Jehol Group.

Group	Dabeigou Formation	Yixian Formation	Jiufotang Formation
Frogs and salamanders	0	7	0
Turtles	0	2	0
Lizards	0	3	0
Choristoderes	0	4	1
Pterosaurs	0	8	7
Ornithischian dinosaurs	0	7	2
Sauropod dinosaurs	0	*	*
Theropod dinosaurs	0	18	2
Birds	2	15	12
Mammals	0	12	0
Totals	2	67	35

*Present, but unnamed. Data from Zhou *et al.* (2003) and other sources.

5. IMPACT ON KNOWLEDGE

Introduction

The plants, invertebrates, fishes, amphibians and smaller reptiles from the Jehol Biota are certainly abundant and spectacularly preserved, but they are not diverse. A few species within each major group are present (Table 1), as would be expected in a balanced flora or fauna, but they do not seem to have made major impacts in changing viewpoints. Earlier claims that, for example, the plant *Archaeoartocarya* was the oldest angiosperm, have been disproved, and so it is one of several early angiosperms, whose fossils are known from numerous Early Cretaceous localities in North America, Europe, and Asia.

The totals of species from the Jehol Group are 60 species of plants, nearly 1000 species of invertebrates, and 140 species of vertebrates (fishes and tetrapods). Many of the plant, invertebrate and fish species are unique to the Jehol Biota, and yet they often belong to genera that are known from Early Cretaceous rocks elsewhere. In other words, the species are not unexpected. The same is broadly true of the frogs, salamanders, turtles, lizards and pterosaurs – many belong to genera known elsewhere in Asia, or world-wide.

The dinosaurs, birds and mammals from Liaoning have, on the other hand, caused most excitement and this is, perhaps, not simply a reflection of public interest. The Liaoning dinosaurs include some remarkable forms and the birds and mammals are much more diverse than anywhere else in the world at that time. In assessing their impact, we should review the new taxa in these three groups, look at their numerical contribution to global datasets and then assess where they have impacted on our understanding of patterns and processes of the history of life.

The Liaoning dinosaurs, birds and mammals

So far, there are 31 species of dinosaurs, 27 species of birds and 14 species of mammals from the three fossiliferous formations of the Jehol Group (Table 2). Of the dinosaurs, the sauropods (unnamed titanosaurs, based on isolated teeth) and ornithischians (a hypsilophodontid, a basal hadrosauroid, an ankylosaur, a neoceratopsian and many psittacosaurids) are typical of other Early Cretaceous localities in Asia, as well as in other parts of the world.

The theropods have attracted most attention; to date, there are some 22 species of mainly small animals, representing compsognathids, therizinosaurs, troodontids, dromaeosaurids, oviraptorosaurids, ornithomimids and tyrannosaurids. Comparative taxa are known, for example, from the Wealden of England and the Cloverly and Cedar Mountain formations of North America, but nowhere else has yet produced such a diversity of forms, nor preserved so exquisitely. These theropods from the Jehol Group include a number of earliest representatives of their groups, but none of the taxa is unexpected when compared to fossils from elsewhere.

The birds have made more impact; so far some 27 species have been named, which have collectively more than doubled the diversity of birds known from the Cretaceous. Until 1980, there was a long gap of some 70 million years in the fossil record of birds, spanning from the oldest bird, *Archaeopteryx* from the Late Jurassic, dated at some 150 Ma, and the wide appearance of the aquatic hesperornithids and ichthyornithids in the latest Cretaceous of North America, some 80 Ma. Only rather isolated and often disputed fossils of putative Cretaceous birds filled this gap. In the 1980s, *Ambiortus* from the Lower Cretaceous of Mongolia was represented by only one incomplete skeleton (Kurochkin, 1985), while *Gansus*, the first known Early Cretaceous bird from China, was represented only by an incomplete leg (Hou & Liu, 1984). Then, in the early 1990s, three important new bird fossils were reported from the Las Hoyas locality in Spain, dated at 120 Ma: *Iberomesornis*, *Concornis* and *Eoalulavis*. Further, less complete, bird fossils have also been reported from the Early Cretaceous of other regions in China and from Argentina. The addition of 27 new species of Early Cretaceous birds to a handful from other parts of the world has plugged a very large gap in bird evolution, and has turned the Mesozoic bird fossil record from one of the worst, to reasonable (Fountaine *et al.*, 2005).

The increase in knowledge of Mesozoic mammals is slightly less impressive overall: of the 300 or so genera of mammals named up to 2003 from the late Triassic, Jurassic and Cretaceous, the Jehol Group has produced 11, about 3% of the world total (Kielan-Jaworowska *et al.*, 2004). However, whereas about 100 mammal species have been recorded from over 50 localities in the Early Cretaceous (Kielan-Jaworowska *et al.*, 2004), these are all isolated

Table 2. The species of dinosaurs, birds and mammals from the three fossiliferous formations of the Jehol Group, listed according to the order of establishment.

Dabeigou Formation (? 131–125 Ma), late Hauterivian–Barremian		
Birds	<i>Protopteryx fengningensis</i> Zhang & Zhou, 2000	enantiornithine
	<i>Eoconfuciusornis zhengi</i> Zhang, Zhou, & Benton, 2008	confuciusornithid
Yixian Formation (125–120 Ma), early Aptian		
Dinosaurs (25)	<i>Sinosauropteryx prima</i> Ji Q. & Ji S., 1996	compsognathid
	<i>Protarchaeopteryx robusta</i> Ji & Ji, 1997	oviraptorosaurid
	<i>Caudipteryx zoui</i> Ji <i>et al.</i> , 1998	oviraptorosaurid
	<i>Beipiaosaurus inexpectus</i> Xu, Tang & Wang, 1999	therizinosaur
	<i>Sinornithosaurus millenii</i> Xu, Wang, & Wu, 1999	dromaeosaurid
	<i>Caudipteryx dongi</i> Zhou & Wang, 2000	oviraptorosaurid
	<i>Jeholosaurus shangyuensis</i> Xu <i>et al.</i> , 2000	hypsilophodontid
	<i>Jinzhouosaurus yangi</i> Wang & Xu, 2001	hadrosauroid
	<i>Liaoningosaurus paradoxus</i> Xu <i>et al.</i> , 2001	ankylosaur
	<i>Incisivosaurus gauthieri</i> Xu <i>et al.</i> , 2002	oviraptorosaurid
	<i>Liaoceratops yanzigouensis</i> Xu, 2002	neoceratopsian
	<i>Sinovenator changii</i> Xu <i>et al.</i> , 2002	troodontid
	<i>Hongshanosaurus houi</i> You, Xu, & Wang, 2003	psittacosaurid
	<i>Shenzhouosaurus orientalis</i> Ji <i>et al.</i> , 2003	ornithomimid
	<i>Yixianosaurus longimanus</i> Xu & Wang, 2003	maniraptoran
	<i>Dilong paradoxus</i> Xu <i>et al.</i> , 2004	tyrannosauroid
	<i>Graciliraptor lujiatunensis</i> Xu & Wang, 2004	dromaeosaurid
	<i>Huxiagnathus orientalis</i> Hwang <i>et al.</i> , 2004	compsognathid
	<i>Mei long</i> Xu & Norell, 2004	troodontid
	<i>Sinornithosaurus haoiana</i> Liu J. <i>et al.</i> , 2004	dromaeosaurid
	<i>Sinusoasus magnodens</i> Xu & Wang, 2004	troodontid
	<i>Jinfengopteryx elegans</i> Ji <i>et al.</i> , 2005	troodontid
	<i>Psittacosaurus lujiatunensis</i> Zhou <i>et al.</i> , 2006	psittacosaurid
	<i>Psittacosaurus major</i> Sereno <i>et al.</i> , 2007	psittacosaurid
	<i>Sinocalliopteryx gigas</i> Ji <i>et al.</i> , 2007	compsognathid
Birds (15)	<i>Confuciusornis sanctus</i> Hou <i>et al.</i> , 1995 ^a	confuciusornithida
	<i>Confuciusornis dui</i> Hou <i>et al.</i> , 1999	confuciusornithid
	<i>Confuciusornis suni</i> Hou <i>et al.</i> , 1998	confuciusornithid
	<i>Changchengornis hengdaoziensis</i> Ji & Chiappe 1999	confuciusornithid
	<i>Jinzhourornis yixianensis</i> Hou <i>et al.</i> , 2002 ^b	confuciusornithid ^b
	<i>Jinzhourornis zhangjyiyingia</i> Hou <i>et al.</i> , 2002 ^b	confuciusornithid ^b
	<i>Liaoningornis longidigitris</i> Hou, 1996	ornithurine
	<i>Liaoxiornis delicatus</i> Hou & Chen, 1999	enantiornithine
	<i>Eoenantiornis buhleri</i> Hou <i>et al.</i> , 1999	enantiornithine
	<i>Longirostravis hani</i> Hou <i>et al.</i> , 2004	enantiornithine
	<i>Hongshanornis longicresta</i> Zhou & Zhang, 2005	ornithurine
	<i>Archaeorhynchus spathula</i> Zhou & Zhang, 2006	ornithurine
	<i>Paraptopteryx gracilis</i> Zheng, Zhang, & Hou, 2007	enantiornithine
	<i>Vescornis hebeiensis</i> Zhang <i>et al.</i> , 2004	enantiornithine
	<i>Zhongornis haoae</i> Gao <i>et al.</i> , 2008	sister to Pygostylia
Mammals (12)	<i>Zhangtheotherium quinquecuspidens</i> Hu <i>et al.</i> , 1997	spalacotherioid
	<i>Jeholodens jenkinsi</i> Luo, 1999	triconodont
	<i>Repenomamus robustus</i> Li <i>et al.</i> , 2000	triconodont
	<i>Eomaia scansoria</i> Ji <i>et al.</i> , 2002	basal eutherian
	<i>Sinobaatar lingyuanensis</i> Hu & Wang, 2002	multituberculata
	<i>Gobiconodon zofiae</i> Li <i>et al.</i> , 2003	triconodont
	<i>Maothierium sinensis</i> Rougier <i>et al.</i> , 2003	spalacotherioid
	<i>Sinodelphys szalayi</i> Luo <i>et al.</i> , 2003	metatherian
	<i>Meemannodon lujiatunensis</i> Meng <i>et al.</i> , 2005	triconodont
	<i>Repenomamus giganticus</i> Hu <i>et al.</i> , 2005	triconodont
	<i>Akidolestes cifellii</i> Li & Luo, 2006	spalacotherioid
	<i>Yanoconodon allini</i> Luo <i>et al.</i> , 2007	triconodont
Jiufotang Formation (120–? Ma), early Aptian		
Dinosaurs (4)	<i>Psittacosaurus mongoliensis</i> Osborne, 1923 ^c	psittacosaurid
	<i>Psittacosaurus meileyingensis</i> Sereno <i>et al.</i> , 1988	psittacosaurid
	<i>Microraptor zhaoianus</i> Xu <i>et al.</i> , 2000	dromaeosaurid
	<i>Microraptor gui</i> Xu <i>et al.</i> , 2003	dromaeosaurid

Table 2. Continued.

Birds (12)	<i>Cathayornis yandica</i> Zhou <i>et al.</i> , 1992	enantiornithine
	<i>Simornis santensis</i> Sereno & Rao, 1992	enantiornithine
	<i>Otogornis genghisi</i> Hou & Zhang, 1993	enantiornithine
	<i>Boluochia zhengi</i> Zhou, 1995	enantiornithine
	<i>Confusiusornis sanctus</i> Hou <i>et al.</i> , 1995 ^a	confuciusornithid ^a
	<i>Songlingornis linghensis</i> Hou, 1997	ornithurine
	<i>Longipteryx chaoyangensis</i> Zhang <i>et al.</i> , 2001	enantiornithine
	<i>Yanornis martini</i> Zhou & Zhang, 2001	ornithurine
	<i>Yixianornis grabaui</i> Zhou & Zhang, 2001	ornithurine
	<i>Jeholornis prima</i> Ji <i>et al.</i> , 2002	jeholornithid
	<i>Sapeornis chaoyangensis</i> Zhou & Zhang, 2002	basal bird
<i>Pengornis houi</i> Zhou <i>et al.</i> , 2008	enantiornithine	

Data from Zhou *et al.* (2003) and other sources.

^aSpecies that are known from both the Yixian and Jiufotang formations.

^bSpecies that are probably not valid, mostly because they were not fully described and documented.

^cSpecies named first from Mongolia, but reported also in the Jehol Group

elements, mostly teeth. The 12 Jehol species, all of them based on more or less complete specimens, represent a significant addition to overall knowledge. These mammals include the only skeletons known of symmetrodonts and triconodonts, the oldest complete eutherian skeleton, and the largest Mesozoic mammal ever, *Repenomamus*, famed as the first Mesozoic mammal that ate a dinosaur (Li *et al.*, 2001; Hu *et al.*, 2005)!

It is hard to list the key contributions to knowledge of the Jehol Biota, but a roughly ranked list of internationally important findings may be enumerated.

- (1) At least the majority of the theropod dinosaurs possessed feathers. Maniraptoran theropods and, perhaps, all coelurosaurian theropods possessed feathers. There are debates about the fluffy filaments in the compsognathid *Sinosauropteryx*, but more derived maniraptorans, such as the dromaeosaurid *Microraptor gui* Xu *et al.*, 2003 (Fig. 8), had pennaceous flight feathers. These are bird feathers in every detail, and they confirm the long-held view, dating back to Thomas Henry Huxley in the nineteenth century, that birds evolved from theropod dinosaurs.
- (2) Some derived theropods possessed wings and so indulged in some form of flight. *Microraptor gui* Xu *et al.*, 2003 (Fig. 8) famously has four wings, arrays of flight feathers along each arm and each leg. It may have glided from tree to tree, perhaps engaging in a form of flight that was a precursor to the full flapping flight of *Archaeopteryx* and all birds.
- (3) *Eomaia scansoria* Ji *et al.*, 2002 from the Yixian Formation is the oldest known certain eutherian, and the only member of the clade from the Early Cretaceous known from fossils other than teeth or jaws. This species then provides key evidence about the origin and early evolution of placental mammals.
- (4) *Sinodelphys szalayi* Luo *et al.*, 2003 from the Yixian Formation represents the oldest known metatherian, suggesting a possible Asian origin of both eutherians and metatherians.
- (5) *Repenomamus* is the largest known Mesozoic mammal, and preserved the first evidence of a mammal eating baby dinosaur.
- (6) The diversity of complete skeletons of mammals belonging to extant and extinct clades provides a unique insight into early mammalian evolution. All previous attempts to determine the relationships and palaeobiology of many of the uniquely Mesozoic groups of mammals had been severely limited by the incompleteness of the fossil remains.
- (7) *Dilong paradoxus* Xu *et al.*, 2004 from the Yixian Formation is one of the oldest known tyrannosauroids, precursor to *Tyrannosaurus rex* and relatives from the Late Cretaceous.
- (8) *Mei long* Xu & Norell, 2004 from the Yixian Formation preserves the oldest known sleeping posture of a dinosaur, showing resemblance to birds behaviour.
- (9) *Protopteryx fengningensis* Zhang & Zhou, 2000 and *Eoconfuciusornis* Zhang *et al.*, 2008 from the Dabeigou Formation represent the oldest and most primitive enantiornithine and confuciusornithid, respectively.
- (10) The birds from both the Yixian and Jiufotang formations are much more significantly diverse and abundant than any other contemporaneous sites in the world.
- (11) *Jeholornis prima* Zhou & Zhang, 2002 from the Jiufotang Formation represents the oldest bird preserving seeds in the stomach, showing a specialized adaptation to seed eating.
- (12) The bird embryo from the Yixian Formation represents the oldest known avian embryo, providing further evidence for a precocial embryological development in early birds.
- (13) The pterosaur egg from the Yixian Formation represents the first known pterosaur egg, providing the first direct evidence for a pterosaur laying eggs (Wang & Zhou, 2004).

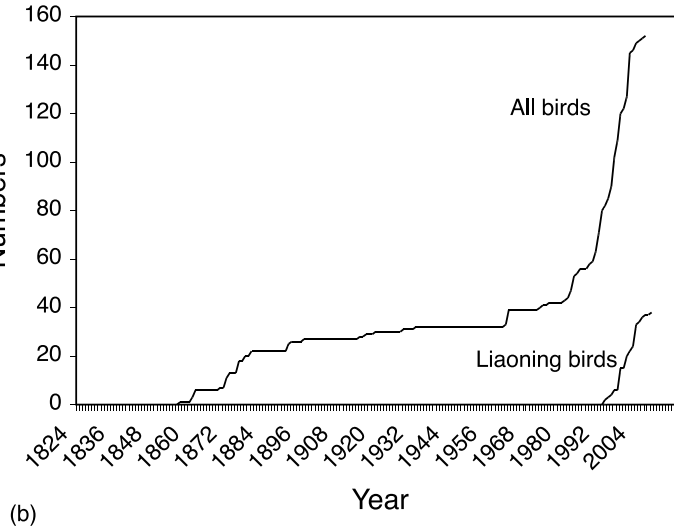
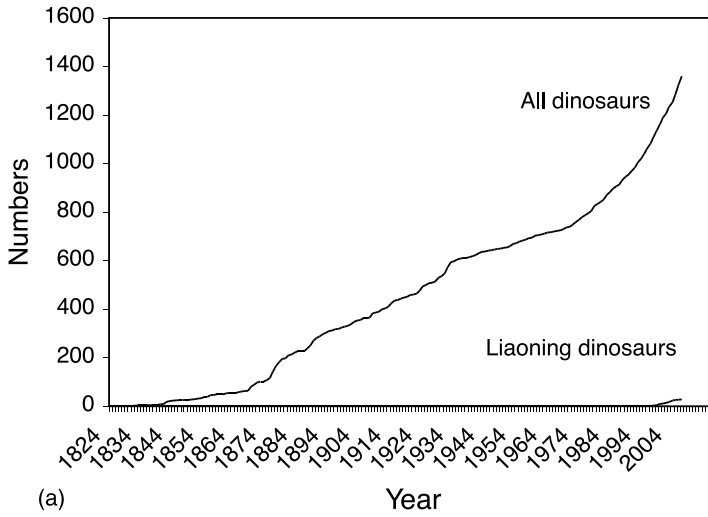


Fig. 11. Species discovery curves for (a) dinosaurs and (b) Mesozoic birds showing the accumulation of knowledge through research time for the global sample (upper curve) and for the Jehol Biota (lower curve). The Liaoning dinosaurs represent a tiny proportion of the total, whereas the Liaoning birds are a much larger proportion of the global total of species.

- (14) The pterosaur assemblages from the Jehol Biota represent the most diverse and abundant pterosaur fauna in the world (Wang *et al.*, 2005).
- (15) *Mesomyzon mengae* Chang *et al.*, 2006 represents the first Mesozoic record and the earliest freshwater lamprey in evolutionary history.

Increase in knowledge

Can these qualitative assertions of the importance of the Jehol fossils be substantiated quantitatively? A classic way to evaluate the current understanding of biodiversity, whether of living or extinct organisms, and whether at a global or local scale, is to use the

collector, or species discovery, curve. Cain (1938) showed how collectors typically acquire new species of their group of interest following a sigmoid, or logistic, curve: early collecting rates are often slow and then, with increased or better effort, the rate of recovery accelerates and the curve bends upwards sharply. Finally, as all common species have been identified, the curve bends into an asymptote towards the ultimate total.

For dinosaurs (Fig. 11a), the Liaoning discoveries have probably had a negligible effect on our understanding of overall diversity. Whereas the global species discovery curve for dinosaurs seemed to have peaked in the 1940s and had, perhaps, entered

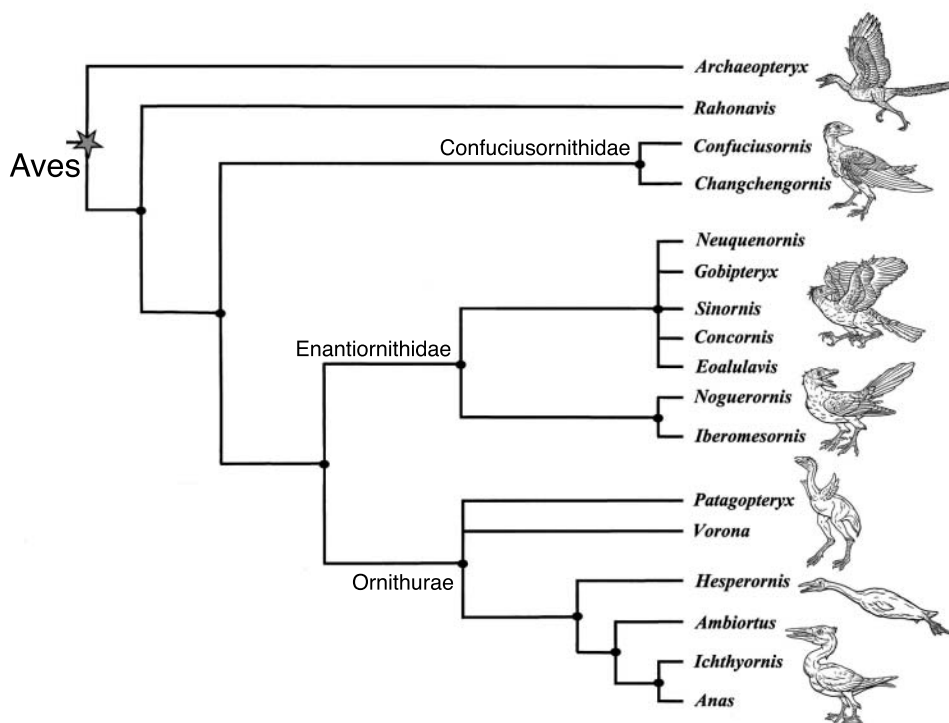


Fig. 12. Phylogeny of 17 representative Mesozoic birds, from Chiappe & Dyke (2002). The three Jehol birds are *Confuciusornis*, *Changchengornis* and *Sinornis*. (Courtesy of Luis Chiappe.)

the asymptote phase, there has been a remarkable acceleration in naming of new species from 1970. Much of this increase in naming new dinosaurs, from 5–10 per year in the 1960s to 30–40 per year in the 2000s, comes from Chinese discoveries. However, other localities in China have been more productive of new dinosaurian taxa than the Jehol Group.

The picture is quite different for Mesozoic birds (Fig. 11b). Of the 158 Mesozoic bird species named so far, 38 (24%) come from the Jehol Group. Note that these totals refer to all species ever named (Benton, 2008): the currently valid totals are closer to 100 Mesozoic bird species in all, with 27 (27%) from Liaoning. The effect on current knowledge is especially marked, when it can be seen that Jehol birds make up 38 (39%) of the 99 species named world-wide since 1990, and nearly all new species from China were represented by nearly complete skeletons, while most other species are more often known from only isolated limb bones or incomplete skeletons.

Change in knowledge

Change in knowledge may be assessed from a phylogenetic context: how does the evolutionary tree of a clade change if particular taxa are excised? This approach is assessed here for the Jehol birds and mammals.

There is no complete phylogeny of all 100 or so valid species of Mesozoic birds, but Chiappe & Dyke (2002) published perhaps the most substantial analysis (Fig. 12). In this, they represent a cross-section of Mesozoic birds, including materials known up to 2001 from Jehol. If the Jehol birds are removed, the number of taxa falls by 18%, from 17 to 14. More importantly, the tree balance changes slightly. Tree balance is assessed by the Colless imbalance index (as corrected by Heard, 1992): for every interior node in a tree of n taxa, count the number of terminal taxa subtended by the right-hand branch (T_R) and the number subtended by the left-hand branch (T_L), and calculate

$$I_m = \frac{\sum |T_R - T_L|}{(n-1)(n-2)/2} \quad (1)$$

A perfectly balanced tree has $I_m=0$ (equal number of nodes on either side), whereas a perfectly imbalanced tree, a so-called ‘Hennigian comb’, has $I_C=1$ (all nodes on one side; none on the other). In the case of Chiappe & Dyke’s (2002) tree, the tree imbalance changes from 0.42 to 0.38 with removal of the three Jehol taxa (out of 17 taxa in all), only a modest change in tree balance.

A similar analysis on the current and comprehensive cladogram of Mesozoic mammals by Luo et al. (2002, fig. 2), shows uniform values of 0.53 for the full tree

($n=46$) and the tree with the two Jehol taxa (*Jeholodens*, *Zhangotherium*) removed.

These studies are inconclusive because the sample trees are not *complete*; that is, they do not contain all species. If the tree is incomplete, measures of tree balance can be meaningless. The only justification for including the analyses here is that the trees (Chiappe & Dyke, 2002; Luo *et al.*, 2002) were constructed to represent a comprehensive array of Mesozoic birds and mammals, and so presumably neither over- nor under-sampled the Jehol Biota. Until complete trees of Mesozoic birds and mammals are available, the overall effect of the addition of the Jehol birds and mammals to knowledge from all other parts of the world cannot be assessed definitively.

6. CONCLUSION

The discovery and presentation of the Jehol Biota in the past twenty years has been one of the most exciting episodes in palaeontology in recent years. It might be tempting to claim that these discoveries have revolutionized all areas of palaeontology, but that is not so. For most groups (plants, insects, aquatic invertebrates, fishes, amphibians, turtles, lizards, choriostoderes and

pterosaurs), the taxa may be new in some cases and, in others, they replicate species known from elsewhere, but most are the forms that would be expected in lacustrine rocks of this age. The Jehol Biota documents a number of key stages through the Cretaceous Terrestrial Revolution (Lloyd *et al.*, 2008), but does not materially change views based on other localities around the world. However, the dinosaurs, birds and mammals from Jehol have not only impressed the public, they have also materially affected our understanding of the evolution of those groups. This is especially true of the birds and mammals. Numerical studies here emphasize changes not only to the numbers of taxa known world-wide, but also to our perception of the shape of the evolutionary tree.

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