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Pterosaur assemblages of the Jehol Biota and their implication for the Early Cretaceous pterosaur radiation

WANG XIAOLIN* and **ZHOU ZHONGHE**

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; Beijing 100044

The Early Cretaceous Jehol Biota from northeast China is well known for many beautifully preserved feathered dinosaurs, early birds and angiosperms. A great number of pterosaurs have also been discovered from the same deposits in recent years, representing arguably the best pterosaur assemblage from the Lower Cretaceous. Two pterosaur assemblages are recognized from the Jehol Biota, and represent two major adaptive radiations in the Early Cretaceous. The first radiation was preserved mainly in the Yixian Formation, and shows a strong resemblance to the Upper Jurassic pterosaur radiation in the Solnhofen Limestone of Germany. The second radiation was preserved in the Jiufotang Formation, with many of its taxa much similar to those of the pterosaur assemblages from the Lower Cretaceous Santana Formation of Brazil. Recent biostratigraphic work and radiometric datings of the Yixian and Jiufotang formations have provided a reliable geochronologic framework for the Jehol pterosaur radiations. The two major radiations occurred at about 125 Ma and 120 Ma, respectively. The radiations of the Jehol pterosaurs are characterized by a remarkable taxonomic diversity, great variation in body size, significant dietary differentiation, and occupancy of diverse niches. The appearance of several biological novelties was also critical in the success of the Jehol pterosaur radiations. The adaptive radiation of the Jehol pterosaurs was obviously coupled with the competition or co-evolution with many other groups of the Jehol Biota. Among the flying animals in the Jehol Biota, pterosaurs were the major competitors for niches and food with birds. Although the Jehol pterosaurs probably fed mainly on fishes, the co-evolution between plants and pterosaurs in the Jehol Biota might also have played a significant role in the pterosaur radiations, as is the case for plants and insects, birds, mammals and dinosaurs.

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KEY WORDS Jehol Biota; pterosaur; radiation; Lower Cretaceous; stratigraphy

1. INTRODUCTION

Recent fossil discoveries from the Lower Cretaceous of western Liaoning Province and neighbouring areas in China have some important implications for the origin of birds and their flight (Xu *et al*. 2003), and for the early evolutionary radiation of birds (Zhou *et al*. 2003; Zhou 2004a), mammals (YQ Wang *et al*. 2001; Luo *et al*. 2003) and angiosperms (Sun *et al*. 2002; Leng and Friis 2003). Although the Early Cretaceous Jehol Biota contains some pterosaurs that had their origin from an earlier age in Europe or other regions, the recent discoveries of fossil birds, dinosaurs, mammals and pterosaurs suggest that western Liaoning, northern Hebei and southeast Inner Mongolia, the major areas for the distribution of the Jehol Biota, should be regarded as the centre of the origin and diversification of many groups including pterosaurs (Zhou *et al*. 2003; Wang and Zhou 2006 in press), many of which had probably dispersed further to other continents in the late Early Cretaceous.

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* Correspondence to: Dr X. Wang, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, 142 Xi-Wai-Da-Jie, Beijing 100044, China. E-mail: xlinwang@263.net

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The pterosaurs from the Jehol Biota represent major radiational events (Wang *et al*. 1999a; Zhou *et al*. 2003; Zhou 2004b; Wang *et al*. 2005a; Wang and Zhou 2006 in press). Up to now, a total of 14 genera (belonging to about 10 families) have been described, including nine from the Yixian Formation and five from the Jiufotang Formation (Table 1). The Jehol pterosaur assemblages are dominated by the pterodactyloids, with only a few rhamphorhynchoids (Ji and Ji 1998; Ji *et al*. 1999; Unwin *et al*. 2000; Czerkas and Ji 2002; Wang *et al*. 2002; Wang *et al*. 2005a). Pterosaurs have also been reported from Lower Cretaceous deposits, comparable to those

Table 1. Taxonomic list of pterosaurs from the Early Cretaceous Jehol Group in western Liaoning and surrounding areas. Mb., Member; Fm., Formation

- Order Pterosauria
  - Suborder Rhamphorhynchoidea
    - Family Rhamphorhynchidae
      - Genus *Pterorhynchus* Czerkas and Ji, 2002
        - *Pterorhynchus wellnhoferi* Czerkas and Ji, 2002 (Daohugou Mb., Yixian Fm.)
    - Family Anurognathidae
      - Genus *Jeholopterus* Wang, Zhou, Zhang and Xu, 2002
        - *Jeholopterus ningchengensis* Wang, Zhou, Zhang and Xu, 2002 (Daohugou Mb., Yixian Fm.)
      - Genus *Dendrorhynchoides* (Ji and Ji, 1998)
        - *Dendrorhynchoides curvidentatus* (Ji and Ji, 1998) (Jianshangou Mb., Yixian Fm.)
  - Suborder Pterodactyloidea
    - Family Pterodactylidae
      - Genus *Eosipterus* Ji and Ji, 1997
        - *Eosipterus yangi* Ji and Ji, 1997 (Jianshangou Mb., Yixian Fm.)
      - Genus *Haopterus* Wang and Lü, 2001
        - *Haopterus gracilis* Wang and Lü, 2001 (Jianshangou Mb., Yixian Fm.)
    - Family Ctenochasmatidae
      - Genus *Beipiaopterus* Lü, 2003
        - *Beipiaopterus chenianus* Lü, 2003 (Jianshangou Mb., Yixian Fm.)
      - Genus *Cathayopterus* Wang and Zhou, 2006
        - *Cathayopterus grabaui* Wang and Zhou, 2006 (Dawangzhangzi Mb., Yixian Fm.)
    - Family Ornithocheiridae
      - Genus *Boreopterus* Lü and Ji, 2005a
        - *Boreopterus cuiae* Lü and Ji, 2005a (Jianshangou Mb., Yixian Fm.)
    - Family ?Gallodactylidae
      - Genus *Feilongus* Wang, Kellner, Zhou and Campos, 2005a
        - *Feilongus youngi* Wang, Kellner, Zhou and Campos, 2005a (Jianshangou Mb., Yixian Fm.)
    - Family Pteranodontidae
      - Genus *Chaoyangopterus* Wang and Zhou, 2003b
        - =*Jidapterus* Dong, Sun and Wu, 2003 (Jiufotang Fm.)
        - =*Eopteranodon* Lü and Zhang, 2005 (Jiufotang Fm.)
        - =*Eoazhdarcho* Lü and Ji, 2005b (Jiufotang Fm.)
        - *Chaoyangopterus zhangi* Wang and Zhou, 2003c (Jufotang Fm.)
    - Family Istiodactylidae
      - Genus *Nurhachius* Wang, Kellner, Zhou and Campos, 2005a
        - *Nurhachius ignaciobritoi* Wang, Kellner, Zhou and Campos, 2005a (Jiufotang Fm.)
      - Genus *Liaoxipterus* Dong and Lü, 2005
        - *Liaoxipterus brachyognathus* Dong and Lü, 2005 (Jiufotang Fm.)
    - Family Anhangueridae
      - Genus *Liaoningopterus* Wang and Zhou, 2003d
        - *Liaoningopterus gui* Wang and Zhou, 2003a (Jiufotang Fm.)
    - Family Tapejaridae
      - Genus *Sinopterus* Wang and Zhou, 2003a
        - =*Huaxiapterus* Lü and Yuan, 2005 (Jiufotang Fm.)
        - *Sinopterus dongi* Wang and Zhou, 2003a (Jiufotang Fm.)
        - *Sinopterus gui* Li, Lü and Zhang, 2003 (Jiufotang Fm.)

of Liaoning Province, in Gansu (Dong 1982) and Xinjiang, northwest China (Young 1964), and probably represent the dispersal of the Jehol pterosaurs from northeast China to northwest regions of China and beyond.

Generally, Jehol pterosaurs comprise two assemblages, preserved in the Yixian and Jiufotang formations, respectively (Wang and Zhou 2003a,b,c; Wang *et al*. 2005a). The Yixian assemblage shows a relatively less derived appearance, and comprises many immigrants from the Late Jurassic of Europe, such as those from the Solnhofen Limestone (Wellnhofer 1991a). Most of the pterosaurs from these assemblages are pterodactyloids, and the rhamphorhynchoids represent the latest records for their lineages. The Jiufotang assemblage is obviously more advanced and characterized by the appearance of many new members, many of which had probably dispersed to other regions and had a worldwide distribution.

2. TWO PTEROSAUR ASSEMBLAGES IN THE JEHOL BIOTA

2.1. *Pterosaur assemblage from the Yixian Formation*

Pterosaurs from the Yixian assemblage comprise nine genera and nine species in six families, including three genera and three species in two rhamphorhynchoid families. They are known from four of the five members of the Yixian Formation (Wang and Zhou 2003d; Figure 1).

Rhamphorhynchoids from the Yixian Formation can be referred to two families: Rhamphorhynchidae and Anurognathidae. The former currently comprises a single genus and species, *Pterorhynchus wellnhoferi* (Czerkas and Ji 2002). It was discovered in the Daohugou Member, the lowest part of the Jehol Group (Figure 1), in Inner Mongolia (Wang *et al*. 2000a; Wang and Zhou 2003d; Wang et al. 2005b). The earliest record of the Rhamphorhynchidae is *Dorygnathus* from the Lower Jurassic of Germany (Wellnhofer 1978, 1991a; Unwin 2003). Members of the Rhamphorhynchidae were also found in the Upper Jurassic Karatau (Oxfordian-Kimmeridgian) of Central Asia (Sharov 1971; Unwin and Bakhurina 1994, 2000) and the Solnhofen Limestone (Early Tithonian) (Wellnhofer 1975a,b, 1991a).

Epoch	Stage	Formation and location		Horizon	Age (Ma)	Rhamphorhynchidae	Anurognathidae	Pterodactylidae	Ctenochasmatidae	? Gallodactylidae	Istiodactylidae	Ornithocheiridae	Anhangueridae	Tapejaridae	Pteranodontidae
Early Cretaceous	Albian		Cambridge Greensand, England									■	■		
	Aptian		Santana Formation, Brazil									■	■	■	
		Jehol Group	Jiufotang Formation, China												
				Boluoche Member (Bed)	120^{a}						■		■	■	■
			Yixian Formation, China	Jingangshan Member (Bed)	121^{b}							■			
				Dawangzhangzi Member (Bed)	123^{c}				■				■		
	Barremian			Jianshangou Member (Bed)	$125^{d,e}$		■	■	■	■				■	
				Lujiatun Member (Bed)	123^{f}, 128^{g}										
	Hauterivian			Daohugou Member (Bed)		■	■								
			Dabeigou Formation, China		131^{h}, $130\sim134^{i}$										
			Zhangjiakou Formation, China		$135^{j,k}$										
	Valanginian														
	Berriasian		Purbeck Formation, England						■			■			
Late Jurassic	Tithonian		Solnhofen Limestone, Germany			■	■	■	■	■					
	Oxfordian-Kimmeridgian		Karabastau Formation, Kazakstan			■	■								

Figure 1. The geochronologic framework of the pterosaur adaptive radiation of the Jehol Biota (after Wang and Zhou, 2006 in press; modified). Dating based on a, He *et al*. 2004a; b,c, Smith *et al*. 1995; d, Swisher *et al*. 1999, 2001; e, Wang *et al*. 2001a; f, He *et al*. 2006a; g, Wang *et al*. 2001b; h, He *et al*. 2006b (in press); i, Liu *et al*. 2003; j, Niu *et al*. 2003, 2004; k, Chen and Zhang 2004.

The Anurognathidae is the second ‘rhamphorhynchoid’ family from the Yixian Formation. It is represented by two genera: *Jeholopterus* (Wang *et al*. 2002) and *Dendrorhynchoides* (Ji and Ji 1998; Ji *et al*. 1999; Unwin *et al*. 2000) from the Daohugou and Jianshangou members, respectively (Figure 1). Other anurognathids include *Batrachognathus volans* (Riabinin, 1948) from the Karabastau Formation in Kazakhstan and *Anurognathus ammoni* (Döderlein, 1929; Wellnhofer 1978) from the Solnhofen limestones. *Dendrorhynchoides*, which is possibly more closely related to *Batrachognathus* than to other anurognathids (Kellner 2003), represents the youngest record for the Anurognathidae.

Rhamphorhynchidae and Anurognathidae had first appeared in the Early Jurassic and early Late Jurassic, respectively. They both reached their greatest diversity by the late Late Jurassic (Wellnhofer 1978, Wellnhofer 1991a). Their occurrence in the Early Cretaceous of northeast China expands their known temporal distribution (Ji and Ji 1998; Ji *et al*. 1999; Unwin *et al*. 2000; Czerkas and Ji 2002; Wang *et al*. 2002; Unwin 2005; Wang and Zhou 2006 (in press)), indicating that Yixian ‘rhamphorhynchoids’ were immigrants from Europe as were many pterodactyloids from the same formation.

Pterodactyloids are the dominant pterosaurs in this assemblage. Among them, the Pterodactylidae is the first family reported from the Jehol Biota. This family currently comprises two genera: *Eosipterus* (Ji and Ji, 1997; Ji *et al*. 1999) and *Haopterus* (Wang and Lü, 2001), both known from the Jianshangou Member of the lower Yixian Formation. It is notable that *Eosipterus* has also been referred to the family of Ctenochasmatidae (Unwin *et al*. 2000). Many other members that were previously in the Pterodactylidae have been transferred to the Ctenochasmatidae (Unwin 2001; Jouve 2004), reflecting the current controversy over the family level classification of pterosaurs. Pterodactylids have been recorded mainly from the Late Jurassic deposits in Europe (France, England and Germany). They had probably dispersed to eastern Asia by the Early Cretaceous.

Ctenochasmatidae is the second major pterodactyloid family from the Yixian Formation, comprising two genera: *Beipiaopterus* (Lü, 2003) and *Cathayopterus* (Wang and Zhou 2006 in press) from Liaoning Province. They were discovered in the Jianshangou and Dawangzhangzi members of the lower and middle Yixian Formation, respectively (Figure 1). Members of the Ctenochasmatidae have also been reported from the Upper Jurassic of Germany and France (Taquet 1972; Buisonjé 1981; Wellnhofer 1978, 1991a; Unwin 2002; Jouve 2004) and the Lower Cretaceous of England (Howse and Milner 1995). Ctenochasmatidae is one of the major pterosaur taxa in the Solnhofen Limestone. It is noteworthy that another genus, *Huanhepterus* (Dong, 1982), from the Lower Cretaceous Huanhe Formation, equivalent to the Yixian Formation of Liaoning, in the Ordos Basin of northern China, belongs to the same family.

Ornithocheiridae is the third pterodactyloid family known from the Yixian Formation. It is currently represented by an un-named embryo from the Jingangshan Member of the upper Yixian Formation (Wang and Zhou 2004) and *Boreopterus* represented by a nearly complete and medium-sized skeleton (Lü and Ji 2005a) from the Jianshangou Member of the lower Yixian Formation. The embryo, encased in an egg, has a well-developed skeleton and membranes, showing a precocial developmental mode (Wang and Zhou 2004). This family usually comprises large pterosaurs, widely distributed in the Cretaceous deposits of Europe, Asia, Africa and South America (Wellnhofer 1987, 1991a,b; Martill and Naish 2001; Unwin 2001; Frey *et al*. 2003). Ornithocheiridae also represents one of the most common pterosaur taxa in the Yixian Formation and the Santana Formation in South America (Frey *et al*. 2003). The earliest record of this family is from the Wessex Formation and the overlying Vectis Formation of the Wealden Group in England (Martill and Naish 2001), indicating that it probably originated from Europe and dispersed to other continents in late Early Cretaceous.

A recently published pterosaur from the Yixian Formation, *Feilongus*, is closely related to the Gallodactylidae (Wang *et al*. 2005a). Currently, the earliest record of this family is *Gallodactylus canjuersensis* (Fabre, 1974; Bennett 1996) and *G. suevicus* (Wellnhofer 1991a) from the Upper Jurassic of southern France and Solnhofen, respectively. Therefore, the gallodactylid pterosaur from the Yixian Formation was probably also an immigrant from Europe.

2.2. Pterosaur assemblage from the Jiufotang Formation

A total of five genera (belonging to four families) of pterosaur have been reported from the Jiufotang Formation, all representing advanced pterodactyloids. Two of these families (Anhangueridae and Tapejaridae) are among the most important pterosaur groups in the Early Cretaceous Santana Formation.

In the Jiufotang Formation the Anhangueridae is represented by *Liaoningopterus* (Wang and Zhou, 2003b), which is also the largest known pterosaur from the Jehol Biota, with an estimated skull length of 650 mm and a wingspan of over 5 m. Members of the Anhangueridae are usually large with a well developed flight capability (Witmer *et al*. 2003), and mainly found from the late Early Cretaceous (Aptian) to early Late Cretaceous deposits (Cenomanian) (Wellnhofer 1991a; Kellner and Tomida 2000; Unwin 2001). Anhanguerids have been reported from the Dzun-Bayin Formation in Mongolia (Aptian/Albian) (Bakhurina and Unwin 1995; Kellner and Tomida 2000), the Romualdo Member of the Santana Formation (Campos and Kellner 1985; Wellnhofer 1991b), the Paw Paw Formation (Albian) of Texas (Lee 1994), the Cambridge Greensand Formation (Albian) of England (Kellner and Tomida 2000; Unwin 2001) and the basal Upper Cretaceous Kem-Kem Formation of Morocco (Mader and Kellner 1999). It is notable that fossils referable to Anhangueridae have also been found in the middle Yixian Formation, which suggests that this family probably had its origin in western Liaoning and spread to other continents later.

Tapejaridae is represented by one genus and two species in the Jehol Biota: *Sinopterus dongi* (Wang and Zhou, 2003a) and *Sinopterus gui* (Li *et al*., 2003) (Table 1). *Huaxiapterus*, also from the Jiufotang Formation (Lü and Yuan 2005) is hardly distinguishable from the holotype of *Sinopterus dongi*, and obviously represents a synonym of the same species. Recently, a fossil referable to the Tapejaridae has been recognized from the lower Yixian Formation, and represents the earliest record of the family. Members of the Tapejaridae are also known from the Santana Formation, where they are represented by at least three genera and five species, including two species of *Tapejara* (Kellner 1989; Wellnhofer and Kellner 1991; Campos and Kellner 1997), two species of *Tupuxuara* (Kellner and Campos 1988, 1994), and one species of *Thalassodromeus* (Kellner and Campos 2002). The tapejarids from the Jiufotang Formation are relatively small and show apparently less derived characteristics (such as a low sagittal crest on the skull) compared to those from the Santana Formation, which seems to be slightly younger than the Jiufotang Formation (Maisey 1991; Wang and Zhou 2003a,b). Like the Anhangueridae, the Tapejaridae probably also originated and radiated in western Liaoning, and then dispersed to South America.

The third pterodactyloid family from the Jiufotang Formation comprises *Chaoyangopterus zhangi*, which was previously referred to the Nyctosauridae (Wang and Zhou 2003b), but now proposed as the earliest record of the Pteranodontidae (Wang *et al*. 2005a). Pteranodontids were previously known mainly from the Upper Cretaceous of North America (Wellnhofer 1991a; Bennett 1994, 2001). *Chaoyangopterus* shows much similarity to *Pteranodon* in the skull shape, but has a much smaller skull (Bennett 1994, 2001). It is notable that three new genera of edentulous pterosaurs have recently been proposed from the Jiufotang Formation, including *Jidapterus* (Dong *et al*., 2003), *Eopteranodon* (Lü and Zhang, 2005) and *Eoazhdarcho* (Lü and Ji, 2005b). Although they show some proportional differences in skeleton from *Chaoyangopterus*, they are generally very similar to *Chaoyangopterus*, and probably all represent a synonym of *Chaoyangopterus*.

A recently described pterosaur from the Jiufotang Formation, *Nurhachius*, was referred to the Istiodactylidae (Wang *et al*. 2005a), which was previously only known from the middle and late Early Cretaceous Vectis Formation in England (Barremian-Aptian) (Hooley 1913; Howse and Milner 1995; Howse *et al*. 2001). *Liaoxipterus brachyognathus* is also a recently described pterosaur previously referred to the Ctenochasmatidae (Dong and Lü 2005). The holotype is only represented by poorly preserved and incomplete lower jaws, therefore its familial classification remains unclear. It is tentatively assigned to the Istiodactylidae in this paper due to its general similarity to *Nurhachius*.

3. GEOCHRONOLOGY AND BIOSTRATIGRAPHY OF THE JEHOL PTEROSAURS

3.1. *The first pterosaur radiation of the Jehol Biota*

Thanks to many recent radiometric isotope datings of the sediments of the Jehol Group, the geochronologic framework of the pterosaur radiations of the Jehol Biota can now be established (Figure 1). In particular, the ^{40}Ar/^{39}Ar and SHRIMP U-Pb dating of the tuffs embedded in the lacustrine sediments of both the Yixian and

Jiufotang formations has provided a reasonable estimate of the age of the fossils (Smith *et al*. 1995; Swisher *et al*. 1999, 2002; Wang *et al*. 2001a,b; Pan *et al*. 2001; He *et al*. 2004a, 2006a,b in press).

The earliest records of the Jehol Biota come from the Dabeigou Formation in northern Hebei Province (Chen 1988) and the Daohugou Member (Yixian Formation) in southeastern Inner Mongolia (Wang *et al*. 2000a; Wang and Zhou 2003d; Wang *et al*. 2005b). SHRIMP U-Pb dating of the Dabeigou tuffs and the underlying rhyolite of the upper Zhangjiakou Formation resulted in dates of 134–130 Ma and 135 Ma (Liu *et al*. 2003; Niu *et al*. 2003, 2004; Chen and Zhang 2004), respectively. The ^{40}Ar/^{39}Ar ages of the interbedded tuff in fossil-bearing layer from the Dabeigou Formation resulted in a weighted mean of 130.7±1.4 Ma (He *et al*. 2006b in press). Combining this with dates for other horizons of the Jehol Group (Eberth *et al*. 1993; Wang *et al*. 2001a,b; Chen and Zhang 2004; He *et al*. 2004b), we propose that the Jehol Biota existed roughly for a 20 million year interval between about 135–115 Ma (Hauterivian-Aptian).

The first Jehol pterosaur radiation is recorded in the Yixian Formation while the earliest records of the Jehol pterosaurs are found in the Daohugou Member, the lowest sequence of the Jehol Group (Wang *et al*. 2000a; Wang and Zhou 2003a,c,d; Wang *et al*. 2005b). Unfortunately, there is as yet no universally accepted age for this deposit (Ren *et al*. 2002; Ji and Yuan 2002; Zhang 2002; Shen *et al*. 2003; Chen *et al*. 2004; Liu *et al*. 2004). The ignimbrite of the Tiaojishan Formation underlying the Daohugou Member has been dated using ^{40}Ar/^{39}Ar method as 160 Ma (He *et al*. 2004b; Wang *et al*. 2005b), which indicates that the age of the Daohugou Member should be younger than this age. Recent discoveries of other vertebrates, such as salamanders (Wang 2004), the pterosaur *Jeholopterus* (Wang *et al*. 2002) and a feathered maniraptoran (Zhang *et al*. 2002; Xu and Zhang 2005) from the same deposits indicate a fossil assemblage that bears a great resemblance to those of typical Yixian deposits in Liaoning (Wang *et al*. 2005b). The insect assemblage from the Daohugou Member also contains some elements similar to those from other Yixian deposits (Zhang Junfeng, personal communication, 2004). Therefore, considering all the evidence, we propose that the Daohugou Member in Inner Mongolia is probably roughly equivalent to the Dabeigou Formation in Hebei. The Jehol pterosaurs had appeared from the beginning of the Jehol evolution, possibly around 132–130 Ma (See Figure 1).

The Lujiatun Member of the lower Yixian Formation has not yielded any pterosaurs or birds, although it has produced many other terrestrial animals such as frogs, lizards, dinosaurs and mammals (Xu *et al*. 2000; Wang and Zhou 2003d; Meng *et al*. 2004; Hu *et al*. 2005). It seems that flying animals were not preserved because the Lujiatun sediments are comprised exclusively of volcanic tuffs that were deposited very rapidly.

The Jianshangou Member of the lower Yixian Formation preserves the best record of the first Jehol pterosaur radiation. It comprises not only many pterodactyloids and a rhamphorhynchoid (Anurognathidae) that were originally from Europe, but also the earliest records of some pterodactyloids that only became successful by the time of the Jiufotang Formation. Several dates for the Jianshangou Member using both ^{40}Ar/^{39}Ar and SHRIMP U-Pb methods have resulted in a commonly accepted age of 125 Ma (Swisher *et al*. 1999, 2002; Wang *et al*. 2001a). Therefore, the first major radiation of the Jehol pterosaurs occurred at approximately 125 Ma, which is close to the boundary between the Barremian and Aptian (Gradstein *et al*. 2004).

Pterosaurs have also been discovered in the Dawangzhangzi and Jingangshan members of the middle and upper Yixian Formation (Wang and Zhou 2003d, 2004, 2006 in press; Ji *et al*. 2004), but are of relatively low diversity and abundance. Pterosaurs from the Dawangzhangzi Member include members of the Ctenochasmatidae, Ornithocheiridae and Anhangueridae. The pterosaur assemblage from the Jingangshan Member comprises several pterosaurs including an embryo referable to the Ornithocheiridae (Wang and Zhou 2004). Currently, the dates for these two sequences are 123–121 Ma (Smith *et al*. 1995). Most pterosaurs from these deposits were immigrants from Europe and there are also some large-sized pterosaurs of indigenous origin, such as the Anhangueridae.

In summary, the first pterosaur radiation from the Jehol Biota had a strong connection with the Late Jurassic pterosaur radiation in Europe. In a global view, if they are considered together as the first pterosaur radiation extending to the Early Cretaceous, then it had probably evolved approximately for 35 Ma, from 155 Ma (Oxfordian-Kimmeridgian) to 120 Ma (Aptian). If this radiation is further divided into two episodes, then the earlier one and the later one had lasted from 155 to 125 Ma, and from 125 to 121 Ma, respectively.

3.2. The second pterosaur radiation of the Jehol Biota

The second Jehol pterosaur radiation is recorded in the Jiufotang Formation and is dominated by aboriginal species, many of which made their first appearance in the time of the Yixian Formation and become fully developed by the time of the Jiufotang Formation. This radiation resulted in a pterosaur assemblage characterized by taxa with a cosmopolitan appearance, such as edentulous forms, but with few immigrants from other regions.

By the time of the Jiufotang Formation, the volcanic activity had become relatively weaker, and the lakes were larger than during the time of the Yixian Formation (Wang and Zhou 2003d). The sedimentation of the Jiufotang Formation is nearly 1000 m thick. The Jehol Biota had reached its greatest geographic distribution by this time (Chen 1988; Wang and Zhou 2006 in press).

Recently, the first precise dating of the Jiufotang Formation was obtained from the Shangheshou locality in Chaoyang City, Liaoning Province (He *et al.* 2004a). The result is based on ^{40}Ar/^{39}Ar dating of K-feldspar (sanidine and orthoclase), from tuffs interbedded within the fossil-bearing shales of the lower and middle Jiufotang Formation. A previously proposed age, of 110 Ma, for the Jiufotang Formation was based on dating of the basalt overlying the deposit in Inner Mongolia (Eberth *et al.* 1993). Because this date is only an indirect age, it cannot be used for estimating the duration of the formation or the temporal distribution of the pterosaur radiation. Therefore, our best estimate of when the second Jehol pterosaur radiation began is about 120 Ma (Aptian) in west Liaoning, followed by dispersal to other regions of northern China and further to other areas, such as the Araripe Basin in northeast Brazil. The pterosaur assemblage in the Santana Formation can be considered as evidence of a continued development of the second Early Cretaceous pterosaur radiation, which probably lasted mainly from the Aptian to the Albian (Maisey 1991).

4. ECOLOGICAL PERSPECTIVES OF THE PTEROSAUR RADIATIONS

4.1. Environmental background

In the context of this unique Early Cretaceous ecosystem, the temporal distribution of the Jehol pterosaur radiations shows some similarities to that of birds and other vertebrate groups, and is closely related to the success of the invertebrates in the biota. For instance, during the time of the Yixian Formation, the pterosaur assemblage was associated with the earliest avian radiation that comprises such birds as *Confuciusornis* and *Eoenantiornis* (Wang *et al.* 2000b; Wang and Zhou 2003d; Zhou *et al.* 2003; Zhou 2004a), and the most significant dinosaurian radiation of the Early Cretaceous that comprise such taxa as *Sinosauropteryx* and *Caudipteryx* (Wang *et al.* 2000b; Wang and Zhou 2003d; Chang *et al.* 2003; Zhou *et al.* 2003). The Jiufotang pterosaur assemblage was associated with the second avian radiation, which is characterized by the presence of abundant enantiornithine birds and many derived ornithurines (Wang and Zhou 2003d; Zhou 2004a; Zhou 2006a,b in press).

The radiations of the Jehol pterosaurs accord with several major global and regional geological events that occurred during the Early Cretaceous, i.e. sea-floor spreading, volcanic eruptions, black shale formations, sea-level fluctuations, Cretaceous Normal Superchron (CNS) and palaeogeographic changes (Barron 1983; Larson 1991; Huber *et al.* 1995; Stoll and Schrag 1996; Larson and Erba 1999; Tarduno *et al.* 2001; Renne 2002; Riisager *et al.* 2003; Zhou *et al.* 2003). Such global geological changes had a significant impact on the evolution of the Jehol Biota (Chang *et al.* 2003; Zhou *et al.* 2003; Zhou 2004b; Zhou 2006a,b in press).

Strong tectonic activity and frequent volcanic eruptions (Wang *et al.* 1999a,b, Wang *et al.* 2000a,b; Guo and Wang 2002; Guo *et al.* 2003) had resulted in a greenhouse-like climate, which led to the development of the Jehol Flora. Furthermore, the volcanic activities had brought abundant tuffs that could be conducive to the flourishing of lake and forest ecosystems, and could have positively affected the diversification and radiation of animals and plants (Wang *et al.* 1999a). The flourishing of the Jehol plants also led directly to the appearance of many arboreal and herbivorous animals, among such groups as birds, dinosaurs, pterosaurs, and mammals (Zhou 2004b; Zhou 2006a,b in press).

The geographic barrier that isolated East Asia from the Laurasia had completely disappeared by the time of the Jiufotang Formation as a result of the regression of the Turgai Sea and the formation of the Eurasian continent (Enkin *et al*. 1992; Upchurch *et al*. 2002; Chang *et al*. 2003; Zhou *et al*. 2003; Zhou 2004b), Therefore, the biological exchanges between the Jehol Biota and those of other continents had become more frequent and much easier, resulting in the presence of many cosmopolitan taxa in the Jehol Biota (Wang *et al*. 2005a; Zhou 2006a,b in press).

4.2. Size variations among the Jehol pterosaurs

The first Jehol pterosaur radiation bears much resemblance to that of the Late Jurassic. The shift from a marine environment to a lake ecosystem had provided many new niches for its development. The second Jehol pterosaur radiation comprises aboriginal taxa that had later spread to other regions due to growing competition in the region (Wang *et al*. 2005a). The taxonomic diversification of the pterosaur radiations was discussed earlier in the paper. In addition to the increase in diversity, the Jehol pterosaur radiations are also characterized by many other changes including body size, diet and niche differentiations.

The pterosaur evolution in the Mesozoic was generally characterized by a trend towards increasing body size (Kellner 2003), and this is also reflected in the evolution of the pterosaurs in the Jehol Biota. Furthermore, there was a great deal of size variation in both pterosaur radiations of the Jehol Biota.

The pterosaurs from the Yixian Formation are relatively small. Among them, the rhamphorhynchoids have a wingspan of less than 1 m (Ji and Ji 1998; Czerkas and Ji 2002; Wang *et al*. 2002). For example, the anurognathid *Jeholopterus* has a wingspan of 0.9 m (Wang *et al*. 2002). *Dendrorhynchoides* is represented by a juvenile individual and has an even smaller wingspan, of about 0.4 m (Ji and Ji 1998).

Other pterosaurs from the Yixian Formation are mostly small- to medium-sized forms. For instance, *Eosipterus* and *Haopterus* of the Pterodactylidae have a wingspan of about 1.2 m and 1.35 m, respectively. *Boreopterus* is a medium-sized ornithocheirid, with an estimated wingspan of 1.7 m. *Feilongus* has a wingspan of 2.4 m (Wang *et al*. 2005a). The Ctenochasmatidae, a predominant pterosaur taxa in the Yixian Formation, is represented by relatively large species.

The pterosaurs from the Jiufotang Formation are relatively large compared to those of the Yixian Formation (Wang and Zhou 2006 in press), but also vary significantly in size. The tapejarid *Sinopterus* (Wang and Zhou 2002) is a relatively small pterosaur with a wingspan between 1.2 m and 1.5 m, while the anhanguerid *Liaoningopterus* (Wang and Zhou 2003b) is large with a wingspan reaching 5 m. These two groups were not only the dominant pterosaur groups in the Jiufotang Formation in Liaoning Province, but also among the major pterosaur groups during the middle and late Early Cretaceous of other regions (Kellner and Tomida 2000; Unwin 2001).

Other large pterosaurs from the Jiufotang Formation include *Chaoyangopterus,* referable to the Pteranodontidae (Wang and Zhou 2003b; Wang *et al*. 2005a), with a wingspan of about 2 m, and *Nurhachius* referable to the Istiodactylidae, with a wingspan of 2.5 m (Wang *et al*. 2005a).

4.3. Diet differentiations

As in the case of the avian radiation in the Jehol Biota (Zhou 2004a,b; 2006a,b in press), the radiations of the Jehol pterosaurs are also highlighted by great diet differentiations (Figure 2). These diet differentiations are closely related to the terrestrial and lake environments in the Early Cretaceous of East Asia, in contrast with many other pterosaurs that were adapted to living in a marine habitat (Wellnhofer 1991a; Chatterjee and Templin 2004; Wang *et al*. 2005a).

Most of the Jehol pterosaurs are piscivorous, and they might also have fed upon invertebrates or small aquatic reptiles. This is obviously related to the abundant fish and invertebrate assemblages found in the Jehol lakes. The fish in the biota include a variety of teleosts, acipenseriforms and sinamids (Chang *et al*. 2003).

The piscivorous pterosaurs include the pterodactylid *Haopterus,* anhanguerid *Liaoningopterus* and the pteranodontid *Chaoyangopterus* etc. These pterosaurs usually possess elongated jaws with a dentition suitable for eating fish. They also had a well-developed flight capability.

Figure 2. Pterosaur skulls from the Jehol Biota, showing adaptation to different diets (after Wang and Zhou 2006 in press). a, *Haopterus* and b, *Liaoningopterus*, piscivorous; c, *Cathayopterus*, filter feeding; d–e, *Jeholopterus* and its skull restoration, insectivorous and (or) feeding on other aquatic invertebrates; f, *Chaoyangopterus*, piscivorous; g, *Sinopterus*, frugivorous or omnivorous; h, *Nurhachius* and i, *Feilongus*, piscivorous. Scale bar is 2 cm

Although piscivorous pterosaurs were dominant in the Jehol Biota they also exhibit many other adaptations including filter-feeding, insectivory, frugivory or omnivory etc. For instance, the anurognathid *Jeholopterus* is mainly insectivorous.

The ctenochamatid *Cathayopterus* was a filter-feeding pterosaur, and probably fed on invertebrates in the shallow water, in a way similar to a pelican (Chatterjee and Templin 2004). *Boreopterus* was tentatively referred to the family of the Ornithocheiridae, but it was most likely a filter feeder. Tapejarids are usually frugivorous (Wellnhofer and Kellner 1991). The small- to medium-sized tapejarid *Sinopterus* might be frugivorous or piscivorous and its diet might switch according to seasonal changes (Wang and Zhou 2002). A similar case of seasonal diet changes was also reported in the bird *Yanornis* from the same formation (Zhou *et al*. 2002, 2004).

4.4. Biological novelties and the pterosaur radiation

The wide variety of diets of the Jehol pterosaurs was probably related to the presence of a variety of food resources as well as diverse ecological niches. On the other hand, the success of the Jehol pterosaurs and their accompanying diet variations can also be explained by the occurrence of many biological novelties in the pterosaurs.

For instance, both the large pterosaurs *Liaoningopterus* and *Chaoyangopterus* are specialized piscivores. *Liaoningopterus* has the largest teeth known for any pterosaur, and the teeth are restricted to the anterior half of the upper and lower jaws (Wang and Zhou 2003b). *Liaoningopterus* also has a well-developed flight capability and the ability to keep stable in the air (Witmer *et al*. 2003). The protruding, arc-shaped crest on the tips of the jaws are probably adapted for the diving of the head for fish in the water (Wellnhofer 1987). The edentulous *Chaoyangopterus* had sharp, pointed, scissor-like upper and lower jaws, which could catch fish during their flight on the surface of the Jehol lakes.

The tapejarid *Sinopterus* has small size, which enabled it to move easily through the dense forest, and it had strong claws that were probably adapted for climbing. The skull was specialized with a long beak that had a pointed rostral end, and a robust lower jaw. The thin crest of the skull was probably used as a tool to separate tree branches, which facilitated seed or fruit eating (Wellnhofer and Kellner 1991). On the other hand, the long and robust cervicals of *Sinopterus* could also be an adaptation for frugivory or catching fish.

The upper and lower jaws of the filter-feeding ctenochamatid *Cathayopterus* are equipped with many laterally protruding, long and pointed teeth. Such a dentition increased its filtering area during feeding.

The anurognathids *Jeholopterus* and *Dendrorhynchoides* were insectivorous, and had teeth that were long and pointed. In addition, the former also possessed a webbed foot, showing that it could probably walk on the lakeshore and feed on insects or aquatic invertebrates or even fish (Wang *et al*. 2002).

4.5. Competition and coevolution among the pterosaurs and plants and other Jehol animals

The adaptive radiation of the Jehol pterosaurs was probably coupled with the competition or co-evolution with other groups of the Jehol Biota. Due to the flourishing forest in the Early Cretaceous of the region, many vertebrates including birds, dinosaurs, pterosaurs and mammals had become arboreal and/or herbivorous. Among the flying vertebrates, birds and pterosaurs were probably the major competitors for niches and food (Wang *et al*. 2005a). For instance, both *Sinopterus* and the long-tailed bird *Jeholornis* were probably arboreal and seed eaters. They probably occupied a similar niche. Like many piscivorous pterosaurs, most ornithurine birds as well as some enantiornithines such as *Longipteryx* were also fish eaters. These flying animals were the major competitors for the fish resources in the water.

The co-evolution between plants and animals in the Jehol Biota is as obvious as the competition among vertebrates. Recent discoveries from the Early Cretaceous of China and other regions indicate that the angiosperms had begun their first radiation by the late Early Cretaceous (Sun *et al*. 1998, 2001, 2002; Wing and Boucher 1998; Friis *et al*. 2003; Leng and Friis 2003; Leng *et al*. 2003). This includes the appearance of the first dicot angiosperm from the Jehol Biota (Leng and Friis 2003). Like insects and birds, pterosaurs might have played a significant role in the dispersal of angiosperms (Fleming and Lips 1991).

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REFERENCES

Bakhurina NN, Unwin DM. 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology* **10**: 197–245.

Barron EJ. 1983. A warm, equable Cretaceous: the nature of the problem. *Earth Science Reviews* **19**: 305–338.

Bennett SC. 1994. Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon* (Pterosauria, Pterodactyloidea). *Occasional Paper of the Natural History Museum, University of Kansas* **169**: 1–70.

Bennett SC. 1996. On the taxonomic status of *Cynorhamphus* and *Gallodactylus* (Pterosauria: Pterodactyloidea). *Journal Paleontology* **70**(2): 335–338.

Bennett SC. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. *Palaeontographica, Abteilung A* **260**: 1–112.

Buisonjé PH de. 1981. *Ctenochasma porocristata* nov. sp. From the Solnhofen limestone, with some remarks on other Ctenochasmatidae. *Proceedings of the Koninkijke Nederlandse Akademie van Wetenschappen, Serie B* **84**: 411–436.

Campos DA, Kellner AWA. 1985. Panorama of the Flying Reptiles Study in Brazil and South America (Pterosauria/Pterodactyloidea/Anhangueridae). *Anais Academia Brasileira de Ciências* **57**(4): 453–466.

Campos DA, Kellner AWA. 1997. Short Note on the first occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. *Anais Academia Brasileira de Ciências* **69**(1): 83–87.

Chang MM, Chen PJ, Wang YQ, Wang Y. 2003. *The Jehol Biota: The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*. Shanghai Scientific and Technical Publishers: Shanghai; 1–208.

Chatterjee S, Templin RJ. 2004. Posture, locomotion and paleoecology of pterosaurs. *Geological Society of America, Special Paper* **376**: 1–64.

Chen PJ. 1988. Distribution and migration of the Jehol Fauna with reference to non-marine Jurassic-Cretaceous boundary in China. *Acta Palaeontologica Sinica* **27**: 659–683 (in Chinese, summary in English).

Chen W, Zhang Y. 2004. Isotope geochronology. In *Mesozoic Jehol Biota of Western Liaoning, China*, Ji Q, *et al.* (eds). Geological Publishing House: Beijing; 95–158 (in Chinese).

Chen W, Ji Q, Liu DY, Zhang Y, Song B, Liu XY. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **23**(12): 1165–1169 (in Chinese, abstract in English).

Czerkas SA, Ji Q. 2002. A new Rhamphorhynchoid with a headcrest and complex integumentary structures. In *Feathered Dinosaurs and the Origin of Flight*. Blanding; 15–41.

Döderlein L. 1929. Über *Anurognathus ammoni* Döderlein. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, math–naturwiss, Klasse*, 47–63.

Dong ZM. 1982. On a new Pterosauria (*Huanhepterus quingyangensis* gen. et sp. nov.) from Ordos, China. *Vertebrata PalAsiatica* **20**(2): 115–121 (in Chinese, summary in English).

Dong ZM, Lü JC. 2005. A new ctenochasmatid pterosaur from the Early Cretaceous of Liaoning Province. *Acta Geologica Sinica* **79**: 164–167.

Dong ZM, Sun YW, Wu SY. 2003. On a new pterosaur from the Lower Cretaceous of Chaoyang Basin, Western Liaoning, China. *Global Geology* **22**(1): 1–7 (in Chinese, abstract in English).

Eberth DA, Russell DA, Braman DR, Deino AL. 1993. The age of the dinosaur-bearing sediments at Tebch, Inner Mongolia, People's Republic of China. Canadian *Journal of Earth Sciences* **30**(10–11): 2101–2106.

Enkin RJ, Yang Z, Chen Y, Courtillot V. 1992. Paleomagnetic constraints on the geodynamic history of the major blocks of China from the Permian to the Present. *Journal of Geophysical Research* **97**(B10): 13953–13989.

Fabre JA. 1974. Un nouveau Pterodactylidae sur le gisement 'Portlandien' de Canjuers (Var) *Gallodactylus canjuersensis* nov. gen., nov. sp. *Annales de Paléontologie (Vertébrés)* **62**(1): 35–70.

Fleming TH, Lips KR. 1991. Angiosperm enoczoochory: were pterosaurs Cretaceous seed dispersers? *American Naturalis* **138**(4): 1058–1065.

Frey E, Martill DM, Buchy M. 2003. A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur. In *Evolution and Palaeobiology of Pterosaurs*, Buffetaut E, Mazin JM (eds). *Geological Society, London, Special Publications* **217**: 55–63.

Friis EM, Doyle JA, Endress PK, Leng Q. 2003. *Archaefructus*-angiosperm precursor or specialized early angiosperm? *Trends in Plant Science* **8**(8): 369–373.

Gradstein FM, Ogg JG, Smith AG, Bleeker W, Lourens LJ. 2004. A New Geologic Time Scale, with special reference to Precambrian and Neogene. *Episodes* **27**(2): 83–100.

Guo ZF, Wang XL. 2002. A study on the relationship between volcanic activities and mass mortalities of the Jehol vertebrate Fauna from Sihetun, western Liaoning, China. *Acta Petrologica Sinica* **18**(1): 117–125 (in Chinese, abstract in English).

Guo ZF, Liu JQ, Wang XL. 2003. Effect of Mesozoic volcanic eruptions in the western Liaoning Province, China on paleoclimate and paleoenvironment. *Science in China (Series D)* **46**(12): 1261–1272.

He HY, Wang XL, Zhou ZH, Wang F, Boven A, Shi GH, Zhu RX. 2004a. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China and its implications. *Geophysical Research Letters* **31**: L12605.

He HY, Wang XL, Zhou ZH, Zhu RX, Jin F, Wang F, Ding X, Boven A. 2004b. ^{40}Ar/^{39}Ar dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed. *Geophysical Research Letters* **31**: L20609.

He HY, Wang XL, Zhou ZH, Zhu RX, Jin F, Wang F, Yang LK, Ding X, Boven, Zhu RX. 2006a. ^{40}Ar/^{39}Ar dating of Lujiatun Bed (Jehol Group) in Liaoning, northeastern China. *Geophysical Research Letters* **33**: L04303.

He HY, Wang XL, Jin F, Zhou ZH, Wang F, Ding X, Yang LK, Boven A, Zhu RX. 2006b. ^{40}Ar/^{39}Ar dating of the early Jehol Biota from Fengning, Hebei Province, northern China. *Geochemistry Geophysics Geosystems* (in press).

Hooley RW. 1913. On the skeleton of *Ornithodesmus latidens*: an ornithosaur from the Wealden Shales of Atherfield (Isle of Wight). *Quarterly Journal of the Geological Society of London* **69**: 372–422.

Howse SCB, Milner AR. 1995. The pterodactyloids from the Purbeck Limestone Formation of Dorset. *Bulletin of the Natural History Museum, London (Geology Series)* **51**(1): 73–88.

Howse SCB, Milner AR, Martill DM. 2001. Pterosaurs. In *Dinosaurs of the Isle of Wight*, Martill DM, Naish D (eds). The Palaeontological Association: London; 324–335.

Hu YM, Meng J, Wang YQ, Li CK. 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* **433**: 149–152.

Huber BT, Hodell DA, Hamilton CP. 1995. Middle-Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradient. *Geological Society of America Bulletin* **107**: 1164–1191.

Ji Q, Yuan CX. 2002. Discovery of two kinds of protofeathered pterosaurs in the Mesozoic Daohugou Biota in the Ningcheng region and its stratigraphic and biologic significances. *Geological Review* **48**(2): 221–224 (in Chinese, abstract in English).

Ji Q, Ji SA, Cheng YN, You HL, Lü JC, Liu YQ, Yuan CX. 2004. Pterosaur egg with a leathery shell. *Nature* **432**: 572.

Ji SA, Ji Q. 1997. Discovery of a new pterosaur in western Liaoning, China. *Acta Geologica Sinica* **71**(1): 1–6 (in Chinese, abstract in English).

Ji SA, Ji Q. 1998. A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. Jiangsu *Geology* **22**(4): 199–206 (in Chinese, abstract in English).

Ji SA, Ji Q, Padian K. 1999. Biostratigraphy of new pterosaurs from China. *Nature* **398**: 573–574.

Jouve S. 2004. Description of the skull of a *Ctenochasma* (Pterosauria) from the latest Jurassic of eastern France, with a taxonomic revision of European Tithonian Pterodactyloidea. *Journal of Vertebrate Paleontology* **24**: 542–554.

Kellner AWA. 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeastern Brazil. *Anais Academia Brasileira de Ciências* **1**(4): 439–446.

Kellner AWA. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. In *Evolution and Palaeobiology of Pterosaurs*, Buffetaut E, Mazin JM (eds.). *Geological Society, London, Special Publications* **217**: 105–137.

Kellner AWA, Campos DA. 1988. Sobre um Novo Pterossauro com Crista Sagital da Bacia do Araripe Cretáceo Inferior do Nordeste do Brasil. *Anais Academia Brasileira de Ciências* **60**(4): 459–469.

Kellner AWA, Campos DA. 1994. New Species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil. *Anais Academia Brasileira de Cîncias* **66**(4): 467–473.

Kellner AWA, Campos DA. 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. *Science* **297**: 389–392.

Kellner AWA, Tomida Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea): with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northern Brazil. *National Science Museum monographs* **17**: 1–135.

Lü JC. 2003. A new pterosaur: *Beipiaopterus chenianus* gen. et sp. nov. (Reptilia: Pterosauria) from western Liaoning Province of China. *Memoir of the Fukui Prefectural Dinosaur Museum* **2**: 153–160.

Lü JC, Ji Q. 2005a. A new Ornithocheirid from the Early Cretaceous of Liaoning Province, China. *Acta Geologica Sinica* **79**: 157–163.

Lü JC, Ji Q. 2005b. New azhdarchid pterosaur from the Early Cretaceous of Western Liaoning. *Acta Geologica Sinica* **79**: 301–307.

Lü JC, Yuan CX. 2005. New tapejarid pterosaur from western Liaoning, China. *Acta Geologica Sinica* **79**: 453–458.

Lü JC, Zhang BK. 2005. New pterodactyloid pterosaur from the Yixian Formation of Western Liaoning. *Geological Review* **51**: 458–462.

Larson RL. 1991. Latest pulse of the Earth: Evidence for a mid Cretaceous super plume. *Geology* **19**: 547–550.

Larson RL, Erba E. 1999. Onset of the mid-Cretaceous greenhouse in the Barremian-Aptian: igneous events and the biological, sedimentary, and geochemical responses. *Paleoceanography* **14**: 663–678.

Lee YN. 1994. The Early Cretaceous pterodactyloid pterosaur *Coloborhynchus* from North America. *Paleontology* **37**(4): 755–763.

Leng Q, Friis EM. 2003. *Sinocarpus decussatus* gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. *Plant Systematics and Evolution* **241**: 77–88.

Leng Q, Wu SQ, Friis EM. 2003. Angiosperms. In *The Jehol Biota: The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*, Chang MM, Chen PJ, Wang YQ, Wang Y (eds.). Shanghai Scientific and Technical Publishers: Shanghai; 179–185.

Li JJ, Lü JC, Zhang BK. 2003. A new sinopterid pterosaur from the Mesozoic of western Liaoning Province, China. *Acta Palaeontologica Sinica* **42**(3): 442–447 (in Chinese, summary in English).

Liu YQ, Li PX, Tian SG. 2003. SHRIMP U-Pb zircon age of Late Mesozoic tuff (lava) in Luanping basin, northern Hebei, and its implications. *Acta Petrologica et Mineralogica* **22**(3): 237–244 (in Chinese, abstract in English).

Liu YQ, Liu YX, Li PX, Zhang H, Zhang LJ, Li Y, Xia HD. 2004. Daohugou biota-bearing lithostratigraphic succession on the southeastern margin of the Ningcheng basin, Inner Mongolia, and its geochronology. *Geological Bulletin of China* **23**(12): 1180–1187 (in Chinese, abstract in English).

Luo ZX, Ji Q, Wible JR, Yuan CX. 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. *Science* **302**: 1934–1940.

Mader BJ, Kellner AWA. 1999. A new anhanguerid pterosaur from the Cretaceous of Morocco. *Boletim do Museu Nacional, Serie Geologia* **45**: 1–11.

Maisey JG. 1991. *Santana Fossils: An Illustrated Atlas*. T F H Publications: New Jersey; 1–459.

Martill DM, Naish D. 2001. *Dinosaurs of the Isle of Wight.* The Palaeontological Association: London; 1–433.

Meng QJ, Liu JY, Varricchio DJ, Huang T, Gao CL. 2004. Parental care in an ornithischian dinosaur. *Nature* **431**: 145–146.

Niu BG, He ZJ, Song B, Ren JS. 2003. The SHRIMP dating of lava from Zhangjiakou Formation and its implications. *Geological Bulletin of China* **22**(2): 140–141 (in Chinese).

Niu BG, He ZJ, Song B, Ren JS, Xiao LW. 2004. SHRIMP Geochronology of Volcanics of the Zhangjiakou and Yixian Formations, Northern Hebei Province, with a Discussion on the Age of the Xing'anling Group of the Great Hinggan Mountains and Volcanic Strata of the Southeastern Coastal Area of China. *Acta Geologica Sinica* **78**(6): 1214–1228.

Pan YX, Zhu RX, Shaw J, Zhou YX. 2001. Magnetic polarity ages of the fossil-bearing strata at the Sihetun section, west Liaoning: a preliminary result. *Chinese Science Bulletin* **46**(17): 1473–1476.

Ren D, Gao K, Guo ZG, Ji SA, Tan JJ, Song Z. 2002. Stratigraphic division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **21**(8–9): 584–588 (in Chinese, abstract in English).

Renne P. 2002. Flood basalts-bigger and badder. *Science* **296**: 1812–1813.

Riabinin AN. 1948. Remarks on a flying reptile from the Jurassic of the Kara-Tau. *Akademia Nauk, Palaeontological Institute, Trudy* **15**: 86–93.

Riisager P, Hall S, Antretter M, Zhao X. 2003. Paleomagnetic paleolatitude of Early Cretaceous Ontong Java Plateau basalts: implications for Pacific apparent and true polar wander. *Earth and Planetary Science Letters* **208**: 235–252.

Sharov AG. 1971. New flying reptiles from the Mesozoic of Kazakhstan and Kirghizia. *Akademia nauk, Palaeontological Institute, Trudy* **130**: 104–113.

Shen YB, Chen PJ, Huang DY. 2003. Age of fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia. *Journal of Stratigraphy* **27**(4): 311–313 (in Chinese, abstract in English).

Smith PE, Evensen NM, York D, Chang MM, Jin F, Li JL, Cumbaa S, Russell D. 1995. Dates and rates in ancient lakes: ^{40}Ar-^{39}Ar evidence for an Early Cretaceous age for the Jehol Group, Northeast China. *Canadian Journal of Earth Sciences* **32**(9): 1426–1431.

Stoll HM, Schrag DP. 1996. Evidence for glacial control of rapid sea level changes in the early Cretaceous. *Science* **272**: 1771–1774.

Sun G, Dilcher DL, Zheng SL, Zhou ZK. 1998. In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from northeast China. *Science* **282**: 1692–1695.

Sun G, Zheng SL, Dilcher DL, Wang YD, Mei SW. 2001. *Early Angiosperms and Their Associated Plants from Western Liaoning, China*. Shanghai Scientific and Technological Education Publishing House: Shanghai; 1–227 (in Chinese, summary in English).

Sun G, Ji Q, Dilcher DL, Zheng SL, Nixon KC, Wang XF. 2002. Archaefructaceae, a new basal angiosperm family. *Science* **296**: 899–904.

Swisher CCIII, Wang YQ, Wang XL, Xu X, Wang Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **400**: 58–61.

Swisher CCIII, Wang XL, Zhou ZH, Wang YQ, Jin F, Zhang JY, Xu X, Zhang FC, Wang Y. 2002. Further Support for a Cretaceous age for the Feathered-Dinosaur Beds of Liaoning, China: new ^{40}Ar/^{39}Ar Dating of the Yixian and Tuchengzi Formations. *Chinese Science Bulletin* **47**(2): 135–138.

Taquet P. 1972. Un crâne de *Ctenochasma* (Pterodactyloidea) du Portlandien inférieur de la Haute-Marne, dans les collections du Musée de St-Dizier. *Comptes Rendus de l'Académie des Sciences* **174**: 362–364.

Tarduno JA, Cottrell RD, Smirnov AV. 2001. High geomagnetic intensity during the mid-Cretaceous from Thellier analyses of single plagioclase crystals. *Science* **291**: 1779–1783.

Unwin DM. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaftlichen, Reihe* **4**: 189–221.

Unwin DM. 2002. On the systematic relationships of *Cearadactylus atrox*, an enigmatic Early Cretaceous pterosaur from the Santana Formation of Brazil. *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaftlichen, Reihe* **5**: 239–263.

Unwin DM. 2003. On the phylogeny and evolutionary history of pterosaurs. In *Evolution and palaeobiology of pterosaurs*, Buffetaut E, Mazin JM (eds). *Geological Society, London, Special Publications* **217**: 139–190.

Unwin DM. 2005. *The Pterosaurs.* Pi Press: New York; 1–347.

Unwin DM, Bakhurina NN. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* **371**: 62–64.

Unwin DM, Bakhurina NN. 2000. Pterosaurs from Russia, Middle Asia and Mongolia. In *The Age of Dinosaurs in Russia and Mongolia*, Benton MJ, Kurochkin E, Shiskin M, Unwin DM (eds). Cambridge University Press: Cambridge; 420–433.

Unwin DM, Lü JC, Bakhurina NN. 2000. On the systematic and stratigraphical significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. *Mitteilungen der Museum Naturkunde Berlin Geowissenschaften, Reihe* **3**: 181–206.

Upchurch P, Hunn CA, Norman DB. 2002. An analysis of dinosaurian biogeography: Evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings of the Royal Society of London, Series B* **269**: 613–621.

Wang Y. 2004. A new Mesozoic caudate (*Liaoxitriton daohugouensis* sp. nov.) from Inner Mongolia, China. *Chinese Science Bulletin* **49**(8): 858–860.

Wang XL, Lü JC. 2001. Discovery of a pterodactylid pterosaur from the Yixian Formation of western Liaoning, China. *Chinese Science Bulletin* **46**(13): 1112–1117.

Wang XL, Zhou ZH. 2003a. A new pterosaur (Pterodactyloidea: Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning and its implications for biostratigraphy. *Chinese Science Bulletin* **48**(1): 16–23.

Wang XL, Zhou ZH. 2003b. Two new pterodactyloid pterosaurs from the Early Cretaceous Jiufotang Formation of western Liaoning, China. *Vertebrata PalAsiatica* **41**(1): 34–41.

Wang XL, Zhou ZH. 2003c. Pterosaurs. In *The Jehol Biota*, Chang MM, Chen PJ, Wang YQ, Wang Y (eds). Shanghai Scientific & Technical Publishers: Shanghai; 99–108.

Wang XL, Zhou ZH. 2003d. Mesozoic Pompeii. In *The Jehol Biota*, Chang MM, Chen PJ, Wang YQ, Wang Y (eds). Shanghai Scientific & Technical Publishers: Shanghai; 19–36.

Wang XL, Zhou ZH. 2004. Pterosaur embryo from the Early Cretaceous. *Nature* **429**: 621.

Wang XL, Zhou ZH. 2006. Pterosaur adaptational radiation of the Early Cretaceous Jehol Biota. In *Originations and Radiations-Evidences from the Chinese Fossil Record*, Rong JY, *et al.* (eds). Science Press: Beijing (in press).

Wang XL, Wang YQ, Xu X, Wang Y, Zhang JY, Zhang FC, Jin F, Gu G. 1999a. Record of the Sihetun vertebrate mass mortality events western Liaoning, China: caused by volcanic eruptions. *Geological Review* **45**(Suppl.): 458–467 (in Chinese, abstract in English).

Wang XL, Wang YQ, Jin F, Xu X, Wang Y, Zhang JY, Zhang FC, Tang ZL, Li C, Gu G. 1999b. The Sihetun fossil vertebrate assemblage and its geological setting of western Liaoning, China. *Palaeoworld* (11): 310–327 (in Chinese, summary in English).

Wang XL, Wang YQ, Zhang FC, Zhang JY, Zhou ZH, Jin F, Hu YM, Gu G, Zhang HC. 2000a. Vertebrate biostratigraphy of the Lower Cretaceous Yixian Formation in Lingyuan, western Liaoning and its neighboring southern Nei Mongol (Inner Mongolia), China. *Vertebrata PalAsiatica* **38**(2): 81–99 (in Chinese, summary in English).

Wang XL, Wang YQ, Zhou ZH, Jin F, Zhang JY, Zhang FC. 2000b. Vertebrate faunas and Biostratigraphy of the Jehol Group in western Liaoning, China. *Vertebrata PalAsiatica* **38**(Suppl.): 39–63.

Wang YQ, Hu YM, Meng J, Li CK. 2001. An ossified Meckel's Cartilage in two Cretaceous mammals and origin of the Mammalian Middle Ear. *Science* **294**: 357–361.

Wang SS, Wang YQ, Hu HG, Li HM. 2001a. The existing time of Sihetun vertebrate in western Liaoning—evidence from U-Pb dating of zircon. *Chinese Science Bulletin* **46**(9): 779–782.

Wang SS, Hu HG, Li PX, Wang YQ. 2001b. Further discussion on geologic age of Sihetun vertebrate assemblage in western Liaoning, China: evidence from Ar-Ar dating. *Acta Petrologica Sinica* **17**(4): 663–668 (in Chinese, abstract in English).

Wang XL, Zhou ZH, Zhang FC, Xu X. 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and 'hairs' from Inner Mongolia, northeast China. *Chinese Science Bulletin* **47**(3): 226–230.

Wang XL, Kellner AWA, Zhou ZH, Campos DA. 2005a. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature* **437**: 875–879.

Wang XL, Zhou ZH, He HY, Jin F, Wang YQ, Zhang JY, Wang Y, Xu X, Zhang FC. 2005b. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chinese Science Bulletin* **50**(20): 2369–2376.

Wellnhofer P. 1975a. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Teil I: Allgemeine Skelettmorphologie. *Palaeontographica Abteilung A* **148**: 1–33.

Wellnhofer P. 1975b. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Teil II: Systematische Beschreibung. *Palaeontographica Abteilung A* **148**: 132–186.

Wellnhofer P. 1978. Handbuch der Paläoherpetologie. Teil 19. *Pterosauria*. Gustav Fischer Verlag: Stuttgart; 1–82.

Wellnhofer P. 1987. New Crested Pterosaurs from the Lower Cretaceous of Brasil. *Mitteilungen der Bayerischen Statssammlung für Paläontologie und historische Geologie* **27**: 175–186.

Wellnhofer P. 1991a. *The Illustrated Encyclopedia of Pterosaurs.* Salamander Books Limited: London; 1–191.

Wellnhofer P. 1991b. Weitere Pterosaurier funde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica Abteilung A* **215**(1–3): 43–101.

Wellnhofer P, Kellner AWA. 1991. The Skull of *Tapejara Wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, Northeastern Brazil. *Mitteilungen der bayerischen Staatssammlungfür Paläontologie und historische Geologie* **31**: 89–106.

Wing SL, Boucher LD. 1998. Ecological aspects of the Cretaceous flowering plants radiation. *Annual Reviews of Earth & Planetary Sciences* **26**: 379–421.

Witmer LM, Chatterjee S, Franzosa J, Rowe T. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behavior. *Nature* **425**: 950–953.

Xu X, Zhang FC. 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* DOI:10.1007/s00114-004-0604-y.

Xu X, Wang XL, You HL. 2000. A primitive ornithopod from the Early Cretaceous Yixian Formation of Liaoning. *Vertebrata PalAsiatica* **38**(4): 318–325.

Xu X, Zhou ZH, Wang XL, Kuang XW, Zhang FC, Du XK. 2003. Four-winged dinosaurs from China. *Nature* **421**: 335–340.

Young CC. 1964. On a new Pterosaurian from Sinkiang, China. *Vertebrata PalAsiatica* **8**(3): 221–256 (in Chinese and English).

Zhang FC, Zhou ZH, Xu X, Wang XL. 2002. A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* **89**: 394–398.

Zhang JF. 2002. Discovery of Daohugou Biota (pre-Jehol Biota) with a discussion on its geological age. *Journal of Stratigraphy* **26**(3): 173–177 (in Chinese, abstract in English).

Zhou ZH. 2004a. The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften* **91**: 455–471.

Zhou ZH. 2004b. Vertebrate radiations of the Jehol Biota and their environmental background. *Chinese Science Bulletin* **49**(8): 754–756.

Zhou ZH. 2006a. Adaptive radiation of the Jehol Biota and its evolutionary ecological background. In *Originations and Radiations-Evidences from the Chinese Fossil Record*, Rong JY, *et al.* (eds). Science Press: Beijing (in press).

Zhou ZH. 2006b. Evolutional radiation of the Jehol Biota: chronological and ecological perspectives. *Geological Journal* **41**: DOI:10.1002/GJ1045.

Zhou ZH, Clarke JA, Zhang FC. 2002. *Archaeoraptor*'s better half. *Nature* **420**: 285.

Zhou ZH, Barrett PM, Hilton J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**: 807–814.

Zhou ZH, Clarke J, Zhang FC, Wings O. 2004. Gastroliths in *Yanornis*: an indication of the earliest radical diet switching and gizzard plasticity in the lineage leading to living birds? *Naturwissenschaften* **91**: 571–574.