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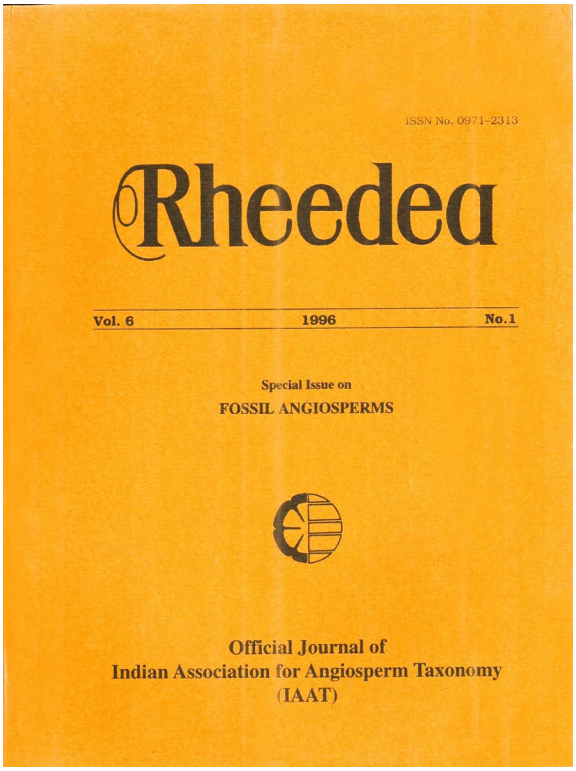

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Cretaceous Angiosperm evolution and floral succession in China

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Abstract

In Early Cretaceous, the Pteridophytes, Gymnosperms and Angiosperms were all composed of their extinct genera. The pteridophytes and gymnosperms were predominant. The angiosperms were not over 40% in the floras and were mostly represented by microphyllous woody dicotyledons with weakly developed venations. Since Late Cretaceous, the extinct genera of the pteriodophytes and gymnosperms decreased, and their modern genera have appeared and developed and gradually replaced their extinct genera. The angiosperms developed and flourished well for the first time and became the predominant component of the plant kingdom.

INTRODUCTION

The Cretaceous angiosperm–bearing floras have already been reported in the world. The Cretaceous angiosperms have greatly attracted botanists and palaeobotanists who paid special attention to discover them which are a reliable evidence to understand the origin, development and evolution of angiosperms. The pre-Cretaceous angiosperms have not been extensively approved of by botanists and palaeobotanists.

During Cretaceous, extreme changes in the plant kingdom took place. One of these changes was the disappearance of the ancient taxa of pteridophytes and gymnosperms. They were replaced by their modern genera and species. The most important change was that angiosperms appeared, flourished, and spread all over the world.

The Cretaceous terrestrial sedementary strata in China were extensively distributed, well developed and widely exposed. During the past, the pteridophytes and gymnosperms were discovered from there. In the last 30 years, the angiosperms were successively collected from the Cretaceous strata. These angiosperms are of important botanical significance, especially those found in the Early Cretaceous strata. They help us to recognize the early morphological characters and evolutionary trends of angiosperms.

The Early Cretaceous floras in China could be divided in to those belonging to two major regions, i.e., Northern China and Southern China based on the floristic characters and climatic environments. The boundary of both the major regions is approximately situated in 40°N latitude in China (Wu Xiangwu, 1995). The fossil plants in northern China region

consisted chiefly of macrophyllous pteriodophytes, minor cycadophytes, abundant ginkgophytes, and well flourished broad-leaved and flat-leaved conifers. Angiosperms appeared in some areas in northern China region, though they were very rare. These fossil plants in northern China region grew in a subtropical and humid climate prevailed during that time. The fossil plants in Southern China region are mainly composed of dominant pteridophytes, abundant cycadophytes, few ginkgophytes and many conifers with scaly leaves. These plants grew under the tropical to subtropical and arid climates. In southern China region, angiosperms were hardly discovered, but a few fossil fragments were found from the southern valley of the Yangtze River. The pteridophytes, gymnosperms and angiosperms were mostly composed of their extinct taxa in Early Cretaceous in China.

The fossil localities of the Late Cretaceous floras were poorer than those of the Early Cretaceous ones. However, the fossil localities of angiosperms were much more than that of Early Cretaceous. So far as we know, they were mainly distributed in northern and southern China. Fossil localities were not found in central China. Based upon the floral characters, the Late Cretaceous floras could be divided into that belonging to the two regions, i. e., northern and southern China. The central China was a blank region. In Late Cretaceous, a few taxa of pteridophytes and gymnosperms were still in existence, which were survivals of the Early Cretaceous, but the number of taxa got diminished. However, angiospermous taxa increased and became dominant in floras. This paper is a study of the evolutionary trends in angiosperms on the basis of leaf architecture and floral succession during Cretaceous in China. The leaf classification by Webb (1959) and leaf architecture by Hickey (1979) are adopted in the present study.

The determinations of geological ages in the plant-bearing strata are based on the upper and lower relations of stratigraphical sequences and other palaeontological and palynological evidences. The ages of the stratigraphic formations have not been determined yet by radioisotope applications. So the plant-bearing strata are represented in relative geological ages.

MEGAFOSSIL LOCALITIES OF THE ANGIOSPERM-BEARING FLORAS

This paper is only concerned with the Cretaceous angiosperm-bearing floras of China. The fossil localities of the Early Cretaceous floras were found from the Chengzihe Formation in Jixi Basin in eastern Helongjiang and from the Dalazi Formation in Yanji Basin in Jilin of northern China. The fossil localities of the Late Cretaceous floras were found from the Quantou, Qingshankuo, Yaojia and Nenjiang Formations in Songhuajiang-Liaohe Basin in western Helongjiang, from the Yongantun, Taiping-Linchang and Furao Formations in Jiayin Basin in eastern Helongjiang, from the Hunchun Formation in Hunchun Basin in Jilin in Northeast China, from the Bali Formation in Yongning Basin in Guangxi Autonomous Region in South China and from the Xigaze Geoup in Xigaze area in Xizang (Tibet) Autonomous Region in Southwest China. Except the above fossil localities, fossil angiosperm fragments were not identified in other areas. This paper is on the basis of the stratigraphical sequences in ascending order to describe these floras.

Table 1. The correlation of Cretaceous angiosperm-bearing formations in China (compliled after Luo et al., 1983; Zhang, 1984, 1985)

Geological age		N E China Helongjiang		Jilin	S China Guangxi	SW China Xizang
Cretaceous	Maastrichtian		Furao Fm.			Xigazi Fm.
	Campanian					
	Santonian		Taiping–Linchang Fm. Yongantun Fm.			
	Coniacian	Nenjiang Fm. Yaojia Fm.		Hunchun		
	Turonian	Qingshankou Fm.				
	Cenomanian	Quantou Fm.			Bali Fm.	
	Albian			Dalazi Fm.		
	Aptian					
	Barremian		Chengzihe Fm.			
	Hauterivian					
	Valanginian					
	Berriasian					

EARLY CRETACEOUS FLORAS IN NORTHEAST CHINA

Chengzihe flora :

The Chengzihe flora was small, composed of 15 species belonging to 156 genera and were found from the Chenzihe Formation in Jixi Basin (long. 130°32' E, lat. 45°12'N) in the Province of Helongjiang, Northeast China. This flora consisted of pteridophytes *(Equisetites, Coniopteris, Acanthopteris)*, gymnosperms *(Nilssonia, Ginkgo, Elatocladus, Pityocladus, Rhipidicladus, Schizolepis)* and angiosperms *(Asiatifloium elegans, Chengzihella obovata, Jixia pinnatipartita, Shenkuoa caloneura, Rogersia lanceolata* and *Dicotylophyllum* sp.)· (Sun Ge et al., 1993). The fossil angiosperms were all referred to woody dicotyledons. The leaf architectures of the dicotyledons were characterized by simple microphyllous leaves and sometimes lobed leaves, both with entire margins. Their leaf blades were elliptical, obovate,

and elongate-oval in shape. The leaves were 1.9–4.8 cm in length; mostly coriaceous and less papyraceous. The petioles were thick and somewhat flat. The venation was pinnate and camptodromous. Midveins were rather thick at base, thin upwards. The secondary veins were very slender and weakly developed. They diverged at narrow-acute and irregular angles from midveins, and formed weakly developed loops at margins. The tertiary veins were very fine, radom, and forming irregular areoles. The quarternary veins were little distinct and nearly equal to the tertiary ones in thickness, forming obscurely rhomboidal webs. The higher-order veins were not observed, and perhaps absent. The lobes of pinnatipartite leaves were irregular and asymmetrical. The leaf architecture seemed to show the primitive characters of angiosperms and were similar to those of the Potomac Group (Hickey & Doyle, 1977).

The affinity between these fossil and the modern dicotyledons is indistinct. The leaf architectures of *Asiatifolium* and *Shenkuoa* seems to be common in Magnoliidae; and that of *Jixia* common in Hamamelidae or Dillendiidae (Cronquist, 1981, 1988). Anyhow, the leaf architectures of these dicotyledons were of rather primitive angiosperms. The age of the flora was determined to be around Late Hauterivian or Early Barremian of Early Cretaceous, indicated by dinoflagellates. These fossil angiosperms might be the earliest ones in the world. This flora represented a northern subtropical or warm temperate and subarid climate.

Dalazi flora : The Dalazi flora was composed of 26 taxa consisting of 4 pteridophytes, 12 gymnosperms and 10 angiosperms. These plants occured from the Dalazi Formation in Yanji Basin (long. 129-130°E, Lat. 42°40' –43°N) in the Province of Jilin, Northeast China. They contained pteroidophytes *(Acrostichopteris, Gleichenites, Onychiopsis,* and *Ruffordia),* gymnosperms *(Brachyphyllum, Czekanowskia, Dicotyozamites, Elatides, Elatocladus, Frenelopsis, Otozamites, Pagiophyllum, Pityophyllum, Pseudofrenelopsis, Suterovagina, Williamsonia* and *Zamiophyllum)* (Chow & Tsao, 1977) and angiosperms *(Clematites lanceolata, Ficophyllum* sp., *Ranunculophyllum pinnatisectum, Rogersia angustifolia, Saliciphyllum longifolium, Sapindopsis magnifolia, Sassafras* sp., *Sterculiphyllum eleganum, Yanjiphyllum ellipticum* and *Carpolithus)* (Guo Shuang-xing, 1986; Zhang Zhichang, 1985; Tao & Zhang 1990).

This flora was represented by woody dicotyledons excepting one herb. The dicotyledons were represented by the simple microphyllous leaves, or occassionally lobed leaves *(Ranunculophyllum),* and compound leaves *(Sapindopsis).* However, it should be pointed out that the leaf blades of these woody dicotyledons in this flora were larger in average size than those of the Chengzihe flora. The leaves including lobed and compound ones were all having entire margins. The leaf texture was mostly papyraceous and less coriaceous in contrast to that of the Chengzihe flora. The type, structure and organization of the veins in this flora were quite similar to those in the previous flora. The leaf architectures of this flora were generally close to those of the Chengzihe flora and seems to show the primeval angiospermous characters.

Three genera viz., *Ficophyllum, Rogersia* and *Sapindopsis,* were common in this flora and the Potomac flora. The leaf architectures of dicotyledons are quite similar to those of the

zones I–II in Potomac flora in the United States (Hickey & Doyle, 1977). Compared to the Chengzihe flora, the number of genera and species in this flora is more. The compound leaf has appeared in *Sapindopsis*. The venations were more obvious and regular than those of the above flora. The age of this flora was generally considered as Aptian to Albian. The flora consisted of all extinct taxa of pteriodophytes, gymnosperms and angiosperms except the modern angiospermous genera like *Clematis* and *Sassafras*. This flora was represented by a mixed gymnospermous and angiospermous forests, reflecting a northern subtropical or warm temperate and subhumid climate.

LATE CRETACEOUS FLORAS IN NORTHEAST CHINA

Quantao and Qingchaguan assemblages

The fossil plants which contained 16 taxa were found from the Quantou Formation in the Songhua–Jiang and Liao–he Basin (ca. long. 124°20'–126°10'E, lat. 45°40'–47°30'N) in Helongjiang, Northeast China. These fossil plants were mainly composed of three pteridophytes, viz., *Selaginella suniana, Cladophlebis* sp., *Onychiopsis psilotoides,* and twelve angiosperms, viz., *Dicotylophyllum rhomboidale, Platanus appendiculata, P. cuneifolia, P. septentrionalis, Platanophyllum* sp., *Protophyllum* sp., *Quercus* sp., *Tilia* cf. *jacksoniana, Trapa angulata, Viburnum* cf. *maginatum* and *Viburniphyllum serrulatum* from the Quantou Formation (Guo Shuang–xing, 1984; Tao Junron et al., 1980; Zheng Shaolin et al., 1994). In the same area was found one pteridophyte–*Onychiopsis* sp., two gymnosperms–*Pterophyllum nudulatum, Sphenolepis* sp., and seven angiosperms–*Celastrophyllum* sp., *Diospyros rotundifolia, Dryophyllum subfalcatum, Saliciphyllum* sp., *Schisandra durbudensis, Carpitis* sp. and *Monocotylophyllum* sp. (Tao Junron et al., 1980; Guo Shuang–xing, 1984; Zheng Shaolin et al., 1994). These fossil plants were found from the Qingshankou Formation which overlies the Quantou Formation.

From these fossil plants of both the Quantou and Qingshankou Formations, we could learn that there was one modern genus among the four pteridophytic genera. This showed that the modern pteridophytes have begun to appear. Both the gymnosperms have become extinct. Among 18 species of angiosperms, the modern and extinct genera are represented alike. It meant that angiosperms increased in member of taxa since the beginning of Late Cretaceous. Besides this, the modern angiosperm genera have appeared, and primeval form genera decreased. The numbers of the form and modern genera of angiosperms were 7 and 4 in the Quantou assemblages, and 5 and 2 in the Qingshankuo assemblage respectively. Angiosperms occupying over 70 percent exceeded the sum of pteridophytes and Gymnosperms in both the assemblages.

The leaf architectures of angiosperms in both assemblages compared with that of Early Cretaceous floras were more various and diverse especially in shapes of leaf blades. The leaf sizes of angiosperms were larger. The venations were distinct and well developed. The higher orders of veins i. e., above quarternary veins, were in existence. The monocotyledons

appeared in the Qingshankou Formation. Based on the stratigraphic sequence and other considerations both Quantou and Qingshankou Formations are considered to be of the Cenomanian and Turonian ages respectively. (Cao Zhengyao et al., 1983; Zheng Shaolin et al., 1994). These fossil plants might represent a broad–leaved forest. The climate might be a little warmer than before owing to existence of *Platanus*. But it still was subtropical and of humid climatic conditions.

Yaojia and Nenjiang fossil plants

In the above area, the only aquatic dycotyledon, *Trapa angulata,* was found from the Yaojia Formation which overlies the Qingshankou Formation. Besides that, other fossil plants such as the extinct genus *Coniopteris* of pteriodophytes; the extant *Thuja* of conifers and the aquatic *Trapa angulata* were found from the Nenjiang Formation which overlies the Yaojia Formation in the same area (Zheng & Zhang, 1994). The fossils in both the Formations were very poor in number of taxa, with only one ancient pteriodophyte and one modern gymnosperm. *Trapa angulata* was common in both Yaojia and Nenjiang Formations. This aquatic dicotylydon was found from the Quantou Formation to Nenjiang Formation. It is widely distributed and most common fossil species in Northeast China in Late Cretaceous. It should be pointed out that the leaf architecture of *Trapa* is quite different from that of modern representatives. Some workers doubted whether this fossil species could be referred to the modern genus *Trapa.* It was called *Quereuxia angulata* (Kryshtofovich, 1957, p. 415–416). However, its leaves were very similar to those of the modern *Trapa.* The occurrence of the aquatic herbaceous dicotyledon might indicate that the lake which contained it was widely extended in this area. The two Formations might be of Coniacian and Santonian ages respectively.

Hunchun flora

This flora was found from the Hunchun Formation in Hunchun county (ca. lat. 42°52' N, long. 130°22' E) in Jilin, Northeast China (Guo Shuang–xing et al., 1979). It contained pteridophytes *(Equisetum* and *Salvinia),* gymnosperms (*Glyptostrobus, Sequoia* and *Metasequoia)* and angiosperms *(Arthollia* sp., *Betulites* sp., *Ceratophyllum* sp., *Cercidiphyllum* sp., *Corylites* sp., *Hamamelites* sp., *Juqlandites poliophyllum, Leguminosites* sp., *Mytophyllum* sp., *Populites* cf. *litigiosus, Protophyllum cordifolium, P. haydenii, P. microphyllum, P. multinerve, P. ovatifolium, P. renifolium, P. rotundum, Trochodendroides vassilenkoi, Stephaniophyllum ovatiphyllum* and *Graminophyllum* sp.). In this flora, there were two genera of pteridophytes and three genera of conifers which are modern ones. The angiosperms had 19 species belonging to 14 genera, almost all of which were form genera, except the modern genera *Ceratophyllum* and *Cercidiphyllum.* The angiosperm elements occupy 80% of the total species. The *Protophyllum* was dominant with 7 species. These angiosperms were almost woody dicotyledens except the two aquatic herbaceous *Ceratophyllum* and the monocotyledon *Graminophyllum.* The woody dicotyledons were both microphyllous and nothophyllous leaves with various leaf shapes. The venation was well developed, but not in *Protophyllum.* These woody dicotyledons were almost composed of the deciduous trees and

shrubs, but *Myrtophyllum* probably was represented by everygreen trees. The Hunchun Formation might be of Turonian to Santonian age. This flora represented a mixed coniferous and broad–leaved deciduous florest, reflecting a very warm temperate or northern subtropical and humid climate.

Yongantun flora

A number of fossil plants were found from the Yongantun Formations of Jiayin Group in Jiayin county (ca. long. 130°37' E, lat. 48°48' N) in Hellongjiang, Northeast China. They were composed of a modern pteridophyte genus *Asplenium,* two extant genera viz., *Taxodium* and *Metasequoia* of gymnosperms, and five species of angiosperms viz., *Platanus densinerva, Pterospermites* sp., *Trapa angulata, Trochodendroides arctica, T. smilacifolia* (Zhang Zhicheng, 1984). Among these fossils, the ancient pteridophytes and gymnosperms were not yet found. However, a modern fern and two modern conifers came into existence. Among angiosperms, the modern and form genera were equally represented. There were two form genera viz., *Pterospermites* and *Trochodendroides* which were commonly distributed in Northeast China and in high latitudes of Northern Hemisphere in Late Cretaceous, i. e., especially *Trochodendroides* was very common than *Pterospermites* in the Late Cretaceous and Palaeocene. The leaf architectures of woody dicotyledons were well developed. The Yongantun Formation might be of Turonian age or a little younger. These fossil plants were represented by a mixed conifeous and broad-leaved deciduous forest, reflecting a warm temperate or northern subtropical and humid climate.

Taiping–Linchang flora

In the same area, there were more fossil plants found from the Taiping–Linchang Formation which overlies the Yongantun Formation. They consisted of pteridophytes *(Equisetum, Asplenium, Arctopteris, Cladophlebis),* gymnosperms *(Ginkgo, Taxodium, Podocarpus, Pityophyllum, Cupressinocladus)* and angiosperms *(Dicotylophyllum* sp., *Laurophyllum* sp., *Nordenskioldia borealis, Platanus raynoldsi, Platanus* sp., *Pterospermites orientalis, Pterospermites* sp., *Trapa angulata, Tiliaphyllum tsagajanensis, Trochodendroides arctica, T. smilacifolia* and *Viburnum contornum)* (Zhang Zhicheng, 1984). In these fossils, there were four genera of pteridophytes occupying one half each of both modern and form genera, and 5 genera of gymnosperms of which three were modern genera and two were form genera, and 12 species of angiosperms belonging to nine genera. The form genera of angiosperms still occupied high proportion in this flora. Four genera viz., *Platanus, Pterospermites, Trapa* and *Trochodendoides* were dominant in the number of species and specimens. The leaf architectures of angiosperms were more advanced than previous floras. The leaf blades were more various in shapes. The leaf sizes were larger. However, the venations were better developed than before. The Taiping–Linchang Formation seemed to be of Coniacian to Santonian age, as evidenced by findings of conchostracans, gastropods and ostracods. These fossils seem to represent a mixed coniferous and broad-leaved deciduous forest. The climate was near to that of the Yongantun flora.

Furao flora

Recently, there were new collections from the Furao Formation in Jiayin county (ca. lat. 40°20' N, long. 130°22' E) in Helongjiang, Northeast China. After preliminary study, two modern genera of gymnosperms *(Gingko* and *Sequoia*), and 10 genera of angiosperms *(Acer* sp., *Ampelopsis* sp., *Cercidiphyllum* sp., *Cissus* sp., *Corylus* sp., *Platanus* sp., *Protophyllum* sp., *Ribis* sp., *Trochodendoides* sp. and *Vitis* sp.) were found. No pteridophyte was found yet. Among angiosperms, there were only two form genera; others were modern ones. The angiosperms were nearly composed of woody dicotyledons with notophyllous leaves. The leaf artchitectures were well developed. This flora in the Furao Formation seems to be of Campanian to Maastrichtian age. It represented a mixed coniferous and broad-leaved deciduous forest, reflecting a warm temperate and humid climate.

LATE CRETACEOUS FLORA IN SOUTHERN CHINA

Bali flora

Some fossil plants were found from the Bali Formation in Yongning (long. 108°38' E, lat. 22°45' N) in Guangxi, South China. They contained one extinct species of gymnosperm *(Brachyphyllum rhombimamiferum)* and four species of two modern genera of angiosperms *(Cinnamomum hesperium, C. newberryi, Nectandra prolifica, N. quangxiensis).* These angiosperms belong to Lauraceae of dicotyledons. The fossil species of *Cinnamomum* and *Nectandra* represented the microphyllous evergreen trees. Their leaf textures were coriaceously sclerophyllous with entire margins. The leaves were not over 5 cm in length. The venations were fo moderate development. The Bali Formation might be of the Early Cenomanian age. These fossils represented an evergreen broad-leaved forest, reflecting a tropical or southern subtropical and arid climate (Guo Shuang–xing, 1979).

Xigaze flora

The small flora was found from the Xigaze Group in Xigaze region (ca. lat. 29°18' N, long. 89°15' E) in Xizang (Tibet) Autonomous Region, Southwest China. This flora was composed entirely of angiosperms *(Aralia firma, Salix* cf. *meeki, Juglandites sinuatus, Ficus daphnogenoides, Laurophyllum* sp., *Leguminosites* sp., *Rhamnites eminense* and *Dicotylophyllum* sp.) (Guo Shuang-xing, 1979). In this flora, any pteridophyte and gymnosperm species have not been found till now. The angiosperms are all woody dicotyledons. *Ficus* and *Laurophyllum* might be evergreen trees, and others were deciduous. Among them, there are five form genera and three modern ones. The leaves of angiosperms were all simple, except *Jugladites* and *Legumniosites* which were with compound leaves. The leaf architectures were very well developed. The Xigaze Group was assigned to Late Cretaceous based on findings of marine foraminiferas. This small flora seemed to be of a mixed deciduous and evergreen broad-leaved forest, representing a southern subtropical and subarid climate.

EVOLUTION OF LEAF ARCHITECTURE IN ANGIOSPERMS

The Early Cretaceous angiosperms in China were represented by abundant leaf impressions. However, their reproductive organs were hardly found. So we have just to recognize their evolutionary trends based on the leaf architectures. Although there has been a long history of study of the leaf fossils of angiosperms based on their foliar physiognomy, the evolutionary trends of the leaf architectures have not ban fully recognized for long time. Recently, after further research of the Potomac flora, the evolutionary trends of leaf architectures of early angiosperms in Early Cretaceous had a relatively clear comprehension (Hockey and Doyle, 1977). The characteristics of leaf architecture of early angiosperms in China in Early Cretaceous were generally similar to those of the Potomac flora. The angiosperms were dominated by woody dicotyledons with most simple and occasionally lobed leaves as in *Jixia* and *Ranunculophyllum.* The compound leaves as in *Sapindopsis* appeared till Albian. Their leaf blades were with entire and rarely nonentire margins, and were microphyllous, generally not more than 5 cm in length; and just a few leaves were over 5 cm. Naturally, the variations in leaf size and textures depended upon the ecological factors. Their types of venation were commonly pinnate and comptodromous, viz., closed venation. The craspedodromous (open) venation had scarcely been discovered in China in Early Cretaceous. According to the characteristics of leaf architecture in these early angiosperms, it seemed to indicate that the plants with the open venation might be more advanced taxa. Therefore, they appeared late. The higher-order veins, i. e., higher than quarternary veins might not have been developed, or even absent in Early Cretaceous. Among Early Cretaceous angiosperms, there were just a few species with open venations, e. g., *Nelumbites, Ulmophyllum, Vitiphyllum* in the Potomac flora in the United States, and only one species *Nelumbites* found in Siberia in Russia (Samylina, 1968). In fact, the characteristics of early angiosperms in Early Cretaceous are represented by microphyllous plants with irregular and weakly-developed venations which were noted and recognized by many palaeobotanists (Vakhrameev, 1976; Crabtree, 1990; Taylor & Hickey, 1990).

The early Late Cretaceous plants were rarely discovered in Northeast China as they were all collected from the cores. The leaf blades were mainly oblong, ovate, elliptic, lanceolate, and sometimes lobed with major microphylls and minor notophylls (Webb, 1959). Till middle Late Cretaceous, numerous angiosperms were collected from outcrops in Northeast China. Their leaf sizes were larger than those of earlier period, as seen in common *Platanus* and *Trochodendroides.* In late Late Cretaceous, the angiosperm leaves were of further large size. Their shapes were of more diverse. It was because the temperature dropped and humidity increased from Cenomanian to Maastrichtian of Late Cretaceous in Northeast China. The venations were weakly development in early Late Cretaceous plants such as in both *Trapa* and *Protophyllum.* Since middle Late Cretaceous, the higher-order venations were fairly well-developed in leaves of the Furao Formation.

In South China, the leaves of Cenomanian angiosperms were coriaceously microphyllous with entire margins. Their venations were of moderate development. The climate in

South China at that time was torrid and arid. In Southwest China, the Maastrichtian angiosperms were microphyllous and notophyllous with leaf margins both entire and nonentire. Their venations were fairly well-development. The climate was subtropical and subarid.

FLORAL SUCCESSION IN COMPOSITIONS

After extensive comprehension of Cretaceous floras in China, a distinct sequence of floral succession and the proportional changes of pteridophytes, gymnosperms and angiosperms (PGA) from Early to Late Cretaceous were clearly recognized (Table 2).

Table 2. The number of species of different groups in Cretaceous floras of China

Age		Formations	Pteridophytes Extant	Pteridophytes Extinct	Gymnosperms Extant	Gymnosperms Extinct	Angiosperms Extant	Angiosperms Extinct	%
Cretaceous	Upper	Xigaze					3	5	100
		Furao			2		9	1	83.3
		Taiping–Linchang	2	2	3	2	4	8	57.1
		Yongantun	1		2		2	3	62.5
		Hunchun	2		3		2	18	80
		Nenjiang	1		1		1		33.3
		Yaojia					1		100
		Qingshankou		1		2	2	5	70
		Quantou	1	2			4	7	78.5
		Bali				1	4		80
	Lower	Dalazi		4		13	2	8	37
		Chengzihe		3		6		6	40

From the Table 2, we could learn that in early Early Cretaceous, the Pteridophytes, Gymnosperms and Angiosperms (PGA) were all composed of extinct genera and species. The angiosperms were not over 40% of the total species in number. In late Early Cretaceous, though the number of taxa of PGA increased, the proportion of angiosperms did not increase in any flora. Angiosperms were still composed of extinct genera and species except two modern genera. It means that angiosperms were not still well developed in late Early Cretaceous. Anyhow, a herbaceous plant *Ranuculophyllun* and a compound leaved *Sapindopsis* appeared. It showed that the morphology of angiosperms have undergone reformation.

Since the beginning of the Late Cretaceous, those extinct genera and species of PGA gradually declined. Afterwards, those ancient genera of PGA were gradually replaced by the modern genera. The proportion of angiosperms was greater in floras. In early Late Cretaceous, the extinct genera and species of angiosperms were still preponderant. In middle Late Cretaceous, those extinct species of both form and modern genera of angiosperms were still of high proportions. *Protophyllum, Trochodendroides, Platanus* and *Trapa* were commonly distributed in Northeast China. From Campanian onwards, the extinct genera of both pteridophytes and gymnosperms have been replaced by modern ones step by step. The extinct genera of both pteridophytes and gymnosperms almost vanished in late Late Cretaceous. However, the extinct and modern genera of angiosperms were in existence contemporaneously in late Late Cretaceous.

DISCUSSION AND CONCLUSIONS

The conclusions just depend upon the fossil records of Cretaceous angiosperms and floras in China, and can understand the following:

The early angiosperms might be small microphyllous woody dicotyledons with weakly-developed venation. The herbs would also have appeared very early since fossil herbs were recorded in late Early Cretaceous in China. The monocotyledons came into being in middle Late Cretaceous. The modern genera of angiosperms started to develop from the beginning of Late Cretaceous. The modern genera of pteridophytes and gymnosperms appeared in middle Late Cretaceous.

In Early Cretaceous, the floras consisted almost entirely of extinct genera and species of pteridophytes, gymnosperms and angiosperms. The modern genera of angiosperms appeared earlier than those of modern pteridophytes and gymnosperms. The extinct genera of pteridophytes and gymnosperms almost vanished in late Late Cretaceous. However, the extinct and modern genera of angiosperms were still in existence contemporaneously in late Late Cretaceous.

During Early Cretaceous, the climate in Northeast China was hot and dry. In Late Cretaceous the temperature slightly decreased and the humidityslightly increased. The decline of temperature and increase of humidity became more obvious in late Late Cretaceous. The

climatic changes have affected the evolution of angiosperms and the succession of floras and the percentage of pteridophytes, gymnosperms and angiosperms in floras of Cretaceous in China.

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