Vol. 92 No. 5 pp. 2004–2025 ACTA GEOLOGICA SINICA (English Edition) Oct. 2018

Reviews

Mid-Cretaceous Hothouse Climate and the Expansion of Early Angiosperms

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Abstract: The remarkable transition of early angiosperms from a small to a dominant group characterized the terrestrial ecosystem of the Cretaceous. This transition was instigated and promoted by environmental changes. Mid-Cretaceous is characterized by major geological events that affected the global environment. $\delta^{18}O$, palaeothermometer TEX_{86}, and other climatic indices from marine sediments suggest rapid temperature increase during mid-Cretaceous despite occasional short cooling events. Simultaneously, terrestrial deposits in East Asia changed from coal-bearing to shale, then to red beds and evaporites. Plant assemblages and other paleoclimate indicators point to rapid aridification for mid-Cretaceous terrestrial environments. In addition, the wildfires were frequently spread all over the earth by the numerous charcoal evidence during the Mid-Cretaceous. Thus, we speculate that the seasonally dry and hot conditions of mid-Cretaceous created a fiery hothouse world. Early angiosperms increased in abundance and diversity and evolved from a few aquatic species to terrestrial herbaceous and then to the diversified flora of today. Angiosperms showed rapid physiological evolution in vein density and leaf area that improved photosynthesis and water absorption. These ecophysiological changes made early angiosperms well adapted to the hot and dry environment in mid-Cretaceous. Moreover, these physiological changes facilitated the fire–angiosperm cycles in mid-Cretaceous that likely further stimulated the early angiosperm evolution.

Key words: Mid-Cretaceous, hothouse, wildfire, early angiosperm, diversification

1 Introduction

Mid-Cretaceous (125–90 Ma, i.e., Aptian to early Turonian) is the interval with the strongest tectonic activity in the Mesozoic era. The high rate of oceanic crust production, normal magnetic superchron and complete opening of southern Atlantic seaway probably changed the global carbon cycle and affected marine ecosystems (Bralower et al., 1994, 1999; Jenkyns, 2003; Erba, 2004). Especially, frequent oceanic anoxic events (OAEs) greatly affected the marine biology and caused extinction events in the marine realm (Kaiho et al., 2014). In addition to the impact on marine life, terrestrial ecosystems were affected because of the extremely high temperatures, i.e., hothouse conditions (Ludvigson et al., 2010; Li et al., 2013). Early mammal and bird fossils from the mid-Cretaceous suggest an important early evolutionary stage for contemporary zoocoenosis (e.g., Zhou et al., 2003). Plants serve as the bridge between the animals and the environment and shifted from the Early Cretaceous gymnosperm-dominated plant biomes to angiosperm-dominated ones in Late Cretaceous (Lidgard and Crane, 1988). Many studies have proposed that the most critical expansion of early angiosperms occurred in mid-Cretaceous (Bond, 1989; Feild et al., 2011; Doyle et al., 2012).

The environmental conditions of terrestrial ecosystems during the mid-Cretaceous provide context for the evolution of early angiosperms. The hothouse conditions

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of mid-Cretaceous and geological events strongly affected terrestrial environments (Ludvigson et al., 2010; Li et al., 2013). For example, precipitation patterns and regional climate were affected by the reorganization of the continental plates (Chaboureau et al., 2014). However, unlike the marine records, the terrestrial record is discontinuous, which makes chronostratigraphic correlations difficult. Therefore, an assessment of the mid-Cretaceous terrestrial record is needed to understand the evolution of early angiosperms in mid-Cretaceous.

To better understand the evolution of early angiosperms, we first review the global environmental changes in mid-Cretaceous that triggered the terrestrial climatic fluctuations. Based on the existing records of terrestrial environments, with particular emphasis on East Asia, and early angiosperm evolution, we discuss the mid-Cretaceous continental climate–ecology pattern. The critical question is what environmental factors made significant impact on the rapid early angiosperm expansion during mid-Cretaceous.

2 General Framework and Research Methods

The mid-Cretaceous environmental changes and early angiosperm evolution are the focus of this study. Below, we analyze the driving forces behind the rapid evolution of early angiosperms.

2.1 Environmental conditions in mid-Cretaceous

Temperature and humidity directly control plant growth. However, it is very difficult to reconstruct the terrestrial temperature variations of the past. To date, reliable marine paleotemperature estimates are obtained by using proxies. The ocean temperatures are relatively steady and the variability reflect the global temperature trends (e.g., O'Brien et al., 2017). Common paleotemperature proxies include the TEX_{86} of Archaebacteria and oxygen isotopes obtained from calcareous nannofossils. TEX_{86} paleothermometry is mainly used to derive sea surface temperatures (SSTs). $\delta^{18}O$ paleotemperature data are more complex and reflect the complexities of incorporation in the calcareous fauna (e.g., belemnites, planktonic, or benthic foraminifera) (Mutterlose et al., 2012). Furthermore, sporopollen, and clay minerals can be used to obtain paleotemperature variability in non-marine depositional setting.

Humidity data are needed to reconstruct the climate fluctuations relevant to plants. Quan et al. (2014) discussed the significance of humidity variations to various rock types. For example, coal deposits form mainly in regions with either perennial or seasonal rainfall (Ziegler et al., 1987; Cecil, 1990; Tabor and Poulsen, 2008). Oil shales form in large either fresh or brackish water bodies. Microstratigraphy studies have shown that environmental conditions were not always stable but alternated annually, seasonally, or irregularly between dry and wet (see Quan et al., 2014). Terrestrial red beds comprise sandstone, mudstone, conglomerate, etc. These rocks form under arid conditions or tropical to subtropical humid conditions (see Quan et al., 2014). Aridity and high temperature are critical to the formation of these rock types. In addition, evaporites are good indicators of arid conditions (Quan et al., 2014).

Plant physiognomy is another important indicator of paleoclimatic conditions for terrestrial realm. The spore-pollen assemblages are typically consistent with the plant macrofossil record; for example, the *Classopollis* pollen and its parent plant Cheirolepidiaceae are abundant in arid mid to mid-low latitudes (Vakhrameyev et al., 1982). In addition, the macroscopic (e.g., leaf thickness and blade tip) and microscopic structures (e.g., cutinite thickness and stoma forms) of plant macrofossils (Cheirolepidiaceae) correlate with paleoenvironmental conditions. In this study, we use plant macrofossil and palynological data to evaluate the climatic conditions of mid-Cretaceous.

2.2 Mid-Cretaceous wildfires

Fires can affect the distribution of vegetation, the carbon cycle, and ultimately the climate (Bowman et al., 2009). Charcoal, soot, and pyrolitic polycyclic aromatic hydrocarbons (PAHs) are generated through wildfires and preserved in sediments. Charcoal assemblages can be divided into microscopic (<125um), mesoscopic (125um to 1mm), and macroscopic (>1 mm) (Glasspool and Scott, 2013) components. The microscopic and mesoscopic components can be difficult to distinguish from inertinite. Macroscopic charcoal is preserved in sedimentary rocks and enables taxonomic identification and better understanding of past fires (Scott, 2010). Moreover, the size, shape, and abundance of charcoal fossils provide information regarding wildfires, such as fire temperature, scale, and post-fire erosion (Scott, 2010; Brown et al., 2012; Glasspool and Scott, 2013). The evidence for wildfires in East Asia is limited compared with the evidence for a high-fire Cretaceous world (Brown et al., 2012). To clarify this, we discuss charcoal-based evidence by using microscopic observations and field data.

2.3 Early angiosperm evolution in mid-Cretaceous

Diversity and abundance are treated as two critical indices to assess the evolution of early angiosperms in this study. Early angiosperm fossils comprise pollen, flowers, fruits, seeds and stamens (mesofossils), and leaves and stems (macrofossils). Pollen data can be used to

reconstruct local changes through time when obtained from stratigraphic sections. The Potomac group in America (Doyle and Robbins, 1977), the Iberian Peninsula in Europe (Heimhofer et al., 2007), and North China (Hua Ruhong, 1991) have continuous angiosperm pollen sequences for mid-Cretaceous. The early angiosperm pollen grains comprise inaperturate, monosulcate, tetrachotomocolpate, tricolpate, and polyaperturate which represent different groups of flowering plants. Shifts in their relative importance through time reflect ecological and/or evolutionary phases. The geographical distribution, timespan, and abundance of these four pollen types are summarized in this review. The available evolutionary information regarding the reproductive organs is based primarily on angiosperm mesofossils. The phylogenetic relationships of these mesofossils are also examined in this review. Early Cretaceous macrofossils (leaves and stems) are very rare but there are abundant morphological and structural data to place them on the phylogenetic tree. In addition, habitat (hydrophilous, xerophytic, etc.) and plant community structure (herbaceous, tree, shrub, etc.) are suggested. There are key links between early angiosperm evolution and the environment. In this study, we use these three fossil types to reconstruct the early angiosperm chronological order. In addition, we look into the flora composition and the emergence of eudicots based on tricolpate pollen.

2.4 Research methods

Paleoenvironmental reconstruction of marine and continental realms during mid-Cretaceous were respectively evaluated by different research methods. Geochemical approaches for the marine deposits allows quantitative reconstruction of the sea temperature, such as the TEX_{86}, $\delta^{18}O$. Long-term greenhouse climatic trends was mainly reconstructed by the connection of many short -time climatic records and comparison of many regions. Nevertheless, the humidity of the continent was relatively independent from the global temperature variations. Here, we mainly presented some lithological evidence to reflect the humidity changes. Though non-quantitative, these lithological evidences are very visual for the moisture variation. For example, evaporites and terrestrial red beds are good indicators of arid conditions. In addition, the wildfires were mainly indicated by the structural characters and bearing frequency of charcoal in the sedimentary rock.

The expansion process of the early angiosperm were mainly evaluated by the fossil records of pollen (microfossils), flowers, fruits, seeds and stamens (mesofossils), and leaves and stems (macrofossils). For the mid-Cretaceous early angiosperm evolution process, mainly four time part divided, pre-Aptian, Aptian, Albian and Cenomanian. They were discussed respectively for the abundance and diversity of the early angiosperm.

3 Mid-Cretaceous Environmental Abnormalities

3.1 Tectonic activity and environmental fluctuations

3.1.1 Tectonic activity

Mid-Cretaceous is marked by intensive tectonic activity, as suggested by the high production rate of oceanic crust and superplumes. The South Atlantic Ocean entered a fast opening stage. South America and Africa were finally separated (Granot and Dyment, 2015). The growth of oceanic crust peaked at about $30\times10^6 km^3/Ma$ (Larson, 1991). The strontium isotope ratio ($^{87}Sr/^{86}Sr$=0.70725) decreased to the lowest level at the late Aptian (Jones and Jenkyns, 2001), probably suggesting intensive oceanic crust formation. Consequently, hot buoyant rocks rose through the mantle, forming anomalously thick and extensive oceanic plateaus, i.e., large igneous provinces (LIPs) (Fig. 1). The Ontong–Java–Manihiki Plateau and the Nova Canton Trough formed in early Aptian (about 125–118 Ma) (Tejada et al., 1996; Larson, 1997; Larson and Erba, 1999). The intensity and duration of this submarine volcanic eruption peaked in mid-Cretaceous. LIPs formed at about 116–110 Ma in the Rajmahal and the adjacent southern Kerguelen Plateau (Wallace et al., 2002; Kent et al., 2002; Frey et al., 2000). Subsequently, LIP intensity was low and the duration was short, e.g., in Elan Bank (110–108 Ma), central Kerguelen Plateau (95–85 Ma), and Caribbean Plate (94–87 Ma) (Sinton et al., 1998). Submarine volcanism became more frequent. The breakup of the southern Atlantic Ocean at the end of mid-Cretaceous may be related to the end of the hothouse conditions owing to the mixing of polar and warm sea water (Granot and Dyment, 2015). In addition, giant explosive continent volcanic eruptions occurred. Multi-layer volcanic sedimentary rocks occurred in the successive Mid-Cretaceous deposits of the Songliao Basin, the largest sedimentary basin with roughly 260,000 km^2 in northeast Asia (Wang, 2016). Southeastern China also has records of volcano sedimentary deposits (Chen et al., 2008; Shu et al., 2009). Submarine volcanism increased the hydrothermal activity and changed the ocean chemistry (Leckia, 2002; Bralower et al., 1997; Jones and Jenkyns, 2001). Furthermore, the greenhouse gases released into the atmosphere likely changed the global environment. Atmospheric CO_2 just increased in mid-Cretaceous (Fig. 1) in contrast to the decreasing trend noted in the entire Cretaceous (e.g., Wang et al., 2014). The highest atmospheric CO_2 concentration was 1900ppm

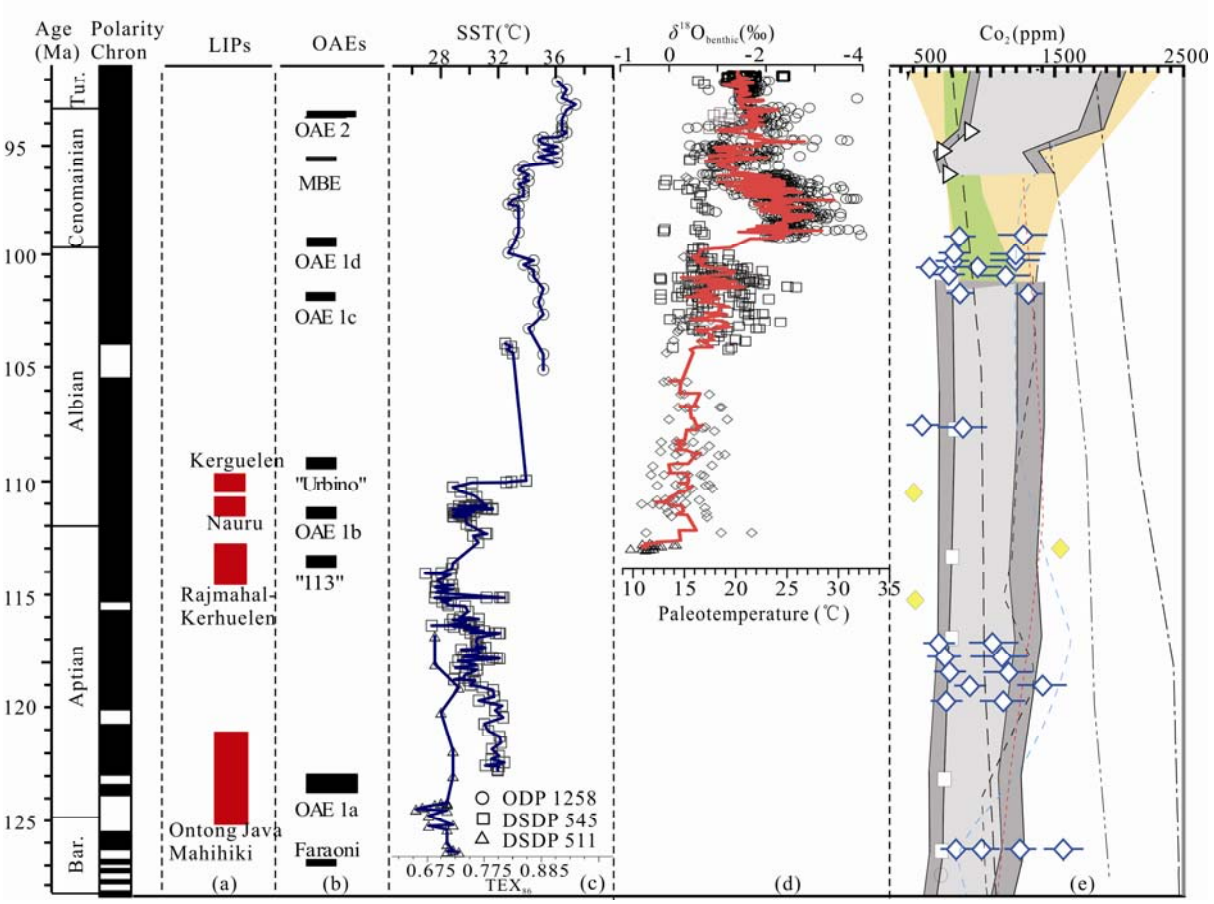


Fig. 1. Tectonic and palaeoenvironmental trends in mid-Cretaceous.
(a), large igneous provinces; (b), oceanic anoxic events; (c), TEX_{86} SSTs, (DSDP 545: McAnena et al., 2013; ODP1258: Forster et al., 2007; DSDP 511: Jenkyns et al., 2012); (d), paleotemperatures based on stable oxygen isotopes of benthic foraminifera (Friedrich et al., 2012);(e), mid-Cretaceous paleo-CO_2 reconstruction from Wang et al. (2014).

at the end of mid-Cretaceous; thus, it is speculated that the intensive tectonic activities triggered a series of global environmental events.

3.1.2 Rapid warming

A roughly rapid warming trends during mid-Cretaceous time was better displayed most comprehensive compilation of available planktonic foraminiferal $\delta^{18}O$ ($\delta^{18}O_{pl}$) and TEX_{86}-SST proxy data in the reviews by O'Brien et al. (2017). The two paleothermometry proxies shows many similarities in the Cretaceous climate change. Actually, the mid-Cretaceous warming process was also interluded by many complex climatic fluctuations, coupled with abnormal deposition and intensive tectonic activities events.

The late Barremian to early Aptian is characterized by remarkable environment fluctuations that mark the onset of the mid-Cretaceous hothouse conditions (Fig. 1). The Tethys Ocean was better oxygenated and demonstrated a low preservation rate of organic matter. Urgonian-type carbonate platforms characterized by an carbonate-producing ecosystems reemerged on the shelves bordering the Tethys Ocean, (Föllmi, 2012; Stein et al., 2012). Phosphorus-burial rates decreased during this period and kaolinite in sections of southeastern France increased, suggesting relatively warm and humid conditions on the adjacent continent (Bodin et al., 2006; Godet et al., 2008; Stein et al., 2012). Belemnite (Ruffell and Batten, 1990) and bulk carbonate (Sprovieri et al., 2006; Stein et al., 2011) $\delta^{18}O$ data move towards larger values during late Barremian, reflecting cooler conditions, and agree with the TEX_{86} paleotemperatures (SST 28–32°C) (Mutterlose et al., 2010).

Thick organic-rich shales were deposited in the shelves, slopes, and basins during late Barremian to early Aptian and are associated with marine life extinctions owing to OAEs (Schlanger and Jenkyns, 1976; Jenkyns, 2010). Carbon isotope curves all show negative excursion when these organic-rich shales were deposited. The paleoenvironmental changes during this period have been called the Taxy episode (Föllmi, 2012) and coincide with the onset of the Ontong Java LIP at about 126 Ma (Tejada

et al., 2004, 2009).

Positive $\delta^{18}O$ stages were firstly show from the Early Aptian $\delta^{18}O$ (Sprovieri et al., 2006; Stein et al., 2011; Ando et al., 2008; Menegatti et al., 1998) likely suggesting greenhouse pulses. The sea level also rose (Haq, 2014) and the Ontong Java submarine volcanism entered the most active stage that most likely triggered OAE1a (Tarduno et al., 1991, Larson and Erba, 1999; Tejada et al., 2009). TEX_{86} data from the Early Aptian Fischschiefer unit in northern Germany suggest very warm surface-water temperatures (34–39°C, Mutterlose et al., 2010). Similar warm temperatures (30–36°C) were reported from equivalent sediments at the Hess Rise (Pacific, DSDP Site 463) (Schouten et al., 2003) and Shatsky Rise (western Pacific) (Dumitrescu et al., 2006). The warm periods were interrupted by frequent short cooling periods. Late Aptian (121–112 Ma) is characterized by relatively stable climatic conditions. The whole-rock $\delta^{18}O$ and $\delta^{13}C$ data are approximately flat curves and ended at the Aptian–Albian boundary (Herrle et al., 2004). Furthermore, temperatures were less variable and moderate. TEX_{86} data from the DSDP Site 511 on the Falkland Plateau suggest a phase of slight warming (26–30°C, Jenkyns et al., 2012). TEX_{86} data from the DSDP Site 545, Mazagan Plateau (McAnena et al., 2013) suggest that North Atlantic Ocean probably experienced warm periods with temperatures between 29–33°C at middle to low latitudes.

The warm climate conditions of the mid-Cretaceous were interrupted by short cool intervals represented by the cold events of the Aptian–Albian transition. SST values from TEX_{86} data in the Mazagan Plateau of the North Atlantic Ocean suggest that surface waters cooled by about 5°C within two million years, affecting marine ecosystems and biogeochemical cycles (McAnena et al., 2013; Mutterlose et al., 2009; Leckie et al., 2002; Herrle et al., 2003). Glendonite and ice-draft sediments are found in high-latitude areas (e.g., Herrle et al., 2015).

The most typical hothouse conditions of mid-Cretaceous begin in the Albian and culminate in the Cenomanian–Turonian thermal maximum. TEX_{86}-based temperatures from the Mazagan Plateau, offshore Morocco are 29–33°C (Hofmann et al., 2008), 30–33°C for Blake Nose (Wagner et al., 2008), and 32–34°C for the Demerara Rise in the tropical Atlantic Ocean (Forster et al., 2007). Oxygen isotope data from benthic foraminifera suggest rapidly decreasing temperatures, bottoming at mid-Cenomanian and suggesting a dramatic increase from 10 to 28°C for bottom waters (Friedrich et al., 2012). The meridional temperature gradient was lower than that today during this interval, when the polar areas were mostly ice-free. In this interval, there are three OAEs, respectively early Albian (OAE1b), Late Albian (OAE1d), and Cenomanian–Turonian (OAE2). High-resolution paleothermometry data suggest rapid warming in the corresponding deposits (Hofmann et al., 2008; Wagner et al., 2008). Apparently, the mid-Cretaceous warming correlates with geological events. The frequent episodes of intense volcanism during mid-Cretaceous triggered changes in the climate and oceans (e.g., Arthur, 2000, Jahren et al., 2001; Van Breugel et al., 2007). Especially, rapid atmospheric CO_2 increases in geologically short-time scales are considered responsible for episodic warming pulses (e.g., Larson and Erba, 1999, Méhay et al., 2009 and Tejada et al., 2009).

3.2 Terrestrial environment

Generally, sedimentary sequences from terrestrial basins well record the climatic changes. East Asia has many thick Cretaceous sedimentary deposits. For example, the Songliao Basin in northeastern China has the most thick and continuous Cretaceous terrestrial sediments in the world. There are also mid-Cretaceous outcrops in northwestern China and central East Asia. In this study, we review lithological, palynological, and megafossil plant data and paleoenvironmental indices from mid-Cretaceous deposits in China to synthetically understand the mid-Cretaceous terrestrial environment.

3.2.1 Late Barremian–Albian climate in western China, central East Asia

Thick Lower Cretaceous sedimentary sequences are common in central western China and are represented by the deposits of the Liupanshan and Jiuquan Basins. The Liupanshan Basin is at the border of the Gansu and Ningxia provinces, China and is filled with 1500-m thick fluvial and lacustrine sediments that are upward divided into the Sanqiao, Heshangpu, Liwaxia, Madongshan, and Naijiahe formations. To date, abundant palynomorphs, ostracoda, and plant megafossils have been found in the basin covering Barremian to Albian (Qi Hua, 1987; Li Zuwang, 1995; Li Jianguo and Du Baoan, 2006; Du et al., 2014). In addition, Dai Shuang et al. (2009) reported high-resolution magnetostratigraphic data that suggest a long normal polarity zone for the Liwaxia to Naijiahe formations. This was interpreted to correlate with the Cretaceous normal superchron of the Aptian–Albian section. The Sanqiao and Heshangpu formations are likely Late Barremian. The Jiuquan Basin in the northern Qilian Mountains is at higher latitude than the Liupanshan Basin. The Chijinbao, Xiagou, and Zhonggou formations are part of the Jiuquan Basin. Abundant fossils include palynomorphs and Ostracoda that suggest Barremian to Albian ages (Hu Yanxia, and Xu Donglai, 2005; Zhang et al., 2015). It is crucial that volcanic rocks are found at the

boundary of the Xiagou and the Zhonggou formations. Radiometric ages for the volcanism are in the range of 110 –125 Ma (Li et al., 2013; Li Haibing and Yang Jingsui, 2004).

In the Liupanshan Basin, the Sanqiao and Heshangpu formations represent fan alluvialand fluvial coarse-grained sedimentary deposits that become fine-grained upward. The Aptian Liwaxia Formation comprises grayish green to gray-black mudstone, siltstone, and carbonaceous siltstone, and red mudstone and siltstone at the top. Obviously, the stratigraphically lower lithologies reflect a relatively humid climate. Based on Quan et al. (2015), the upper lithologies of the Liwaxia Formation suggest high temperatures and dry climate. The calcareous component in the early Albian Madongshan Formation (Figs. 2a, 3b) is higher than that in the Liwaxia Formation, suggesting drier conditions. In the late Albian Naijiahe Formation, gypsum deposits are interlayered with the red beds (Figs. 2b, 3b), likely reflecting dry weathering. The above lithologies suggest that dry climatic conditions prevailed in the middle latitudes of continental interiors; furthermore, the palynological data from the Liupanshan Basin are rich in *Classopollis* (Li Jianguo and Du Baoan, 2006). To improve the palynological resolution, we specially collected samples from the successive Sikouzi section spanning the Aptian to Albian. Besides the high *Classopollis* content, xerophilous Ephedripites increase upward in the section, suggesting aridification. To date, the plant megafossils discovered in the basin are xerophilous Pseudofrenelopsis (Cheirolepidiaceae) (Du et al., 2014). Their papilliform and thick cuticles suggests arid environment. Dry environment is also suggested by the low magnetic susceptibility during the Lower Cretaceous of the Liupanshan Basin (Dai Shuang et al., 2010).

Similarly, the lithological changes in the Jiuquan Basin record upward evaporite deposition. The Late Barremian to the Aptian Chijinbao and Xiagou formations mainly constitute black oil shale, carbonaceous shale, gray mudstone, and other coarse-grained sedimentary rocks (Fig. 3a). The thick organic-rich mudstone beds are the main source rocks in the Yumen oilfield, the first one in China. Megafossil plants are represented by Solenitesluanpingensis Wang, Pityocladus cf. iwaianus

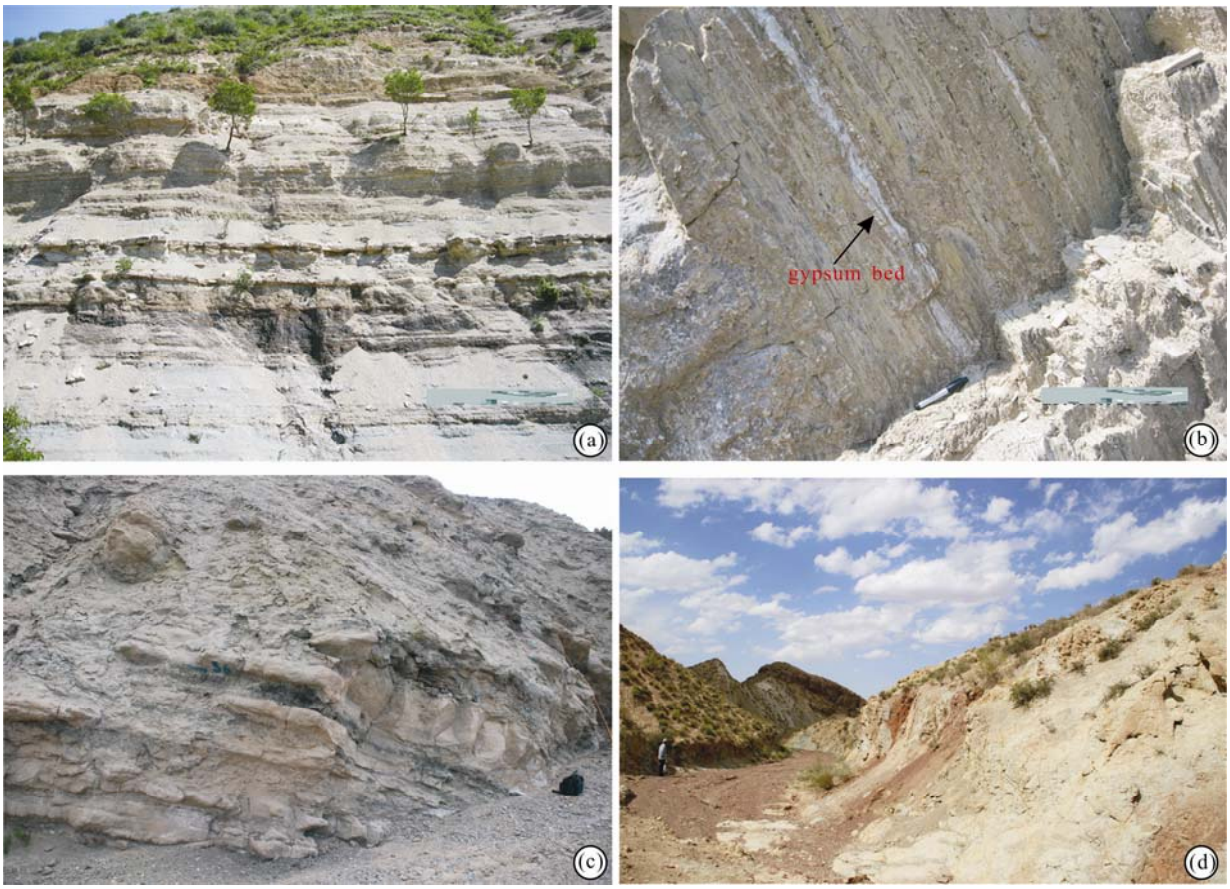


Fig. 2. Field photo showing mid-Cretaceous sediments in central East Asia.
(a), ray oilshale and light gray carbonaceous mudstone and limestone in the Aptian Liwaxia Formation, Liupanshan Basin; (b), light-gray carbonaceous mudstone and thin gypsum beds in the Albian Naijiahe Formation, Liupanshan Basin; (c), gray-black oilshale and gray carbonaceous mudstone in the Aptian Xiagou Formation, Jiuquan Basin; (d), reddish calcareous mudstone and gray-green mudstone in the Albian Zhonggou Formation, Jiuquan Basin.

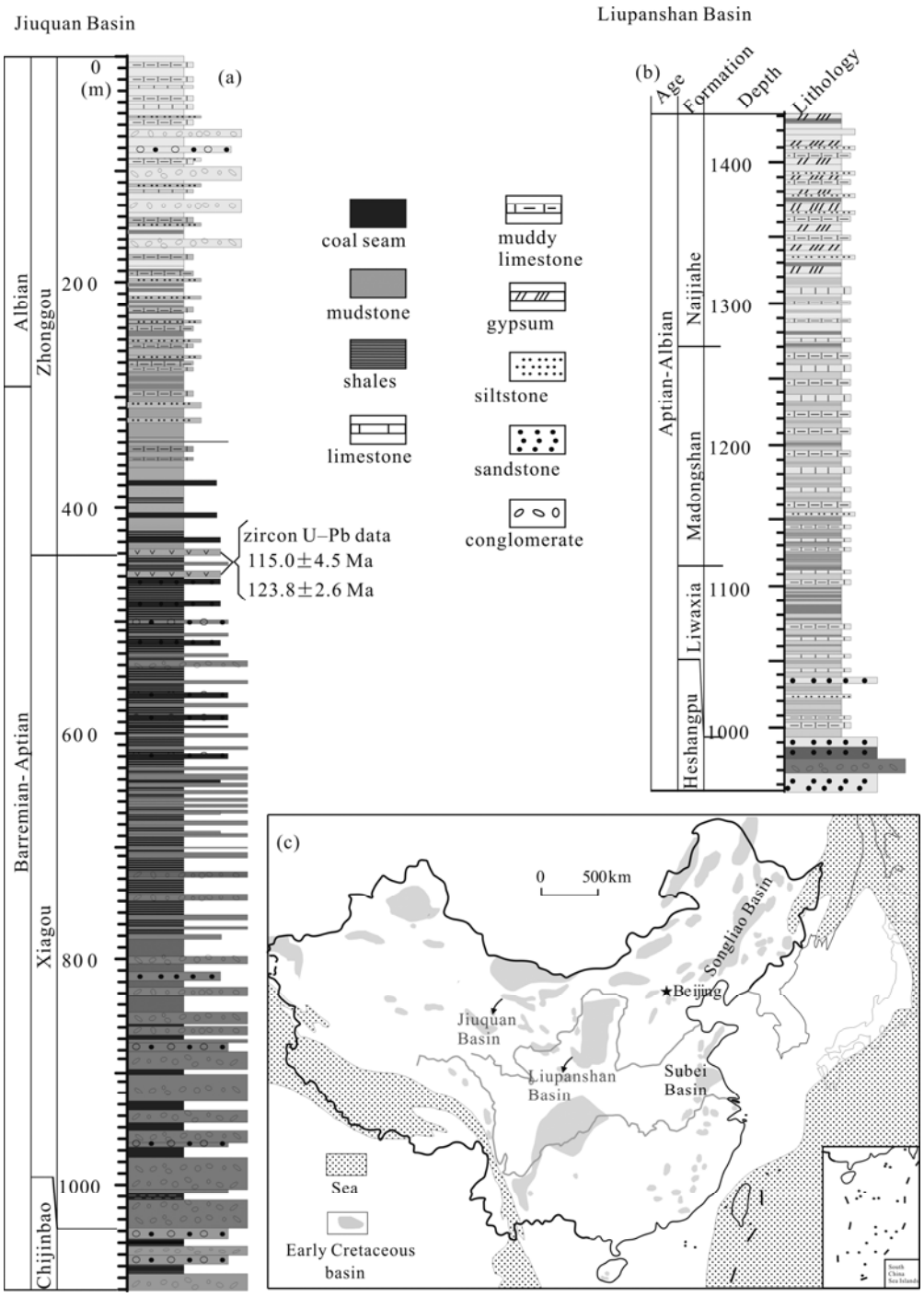


Fig. 3. Correlation of sedimentary sequences between Liupanshan and Jiuquan Basin in the central East Asia.

(a), sedimentary logs of Jiuquan Basin; (b), sedimentary logs of Liupanshan Basin; (c), paleogeographic map of China during late Early Cretaceous (China basemap after China National Bureau of Surveying and Mapping Geographical Information) .

(Oishi) Chow, Pityocladus sp., and Athrotaxites berryi Bell, which reflects humid to semihumid climate (Deng Shenghui and Lu Yuanzheng, 2008). Similar climatic conditions are suggested by the sporopollen assemblages of Perinopollenites, bisaccate pollen, and minor spores (Liu Zhaosheng, 2000). In addition, a latest study of quantitative temperature estimation for the Xiagou Formation (mean annual air temperatures 20.2 ^{o}C) indicated relatively warming paleoenvironment (Suarez et al., 2017). The Albian Zhonggou Formation is characterized by calcareous and grayish green clastic sedimentary rocks that differ from those in the underlying Chijinbao and Xiagou formations. In the middle of this formation, the reddish calcareous mudstones merge to

Table 1 Some representativefossil records of early angiosperm during Mid-Cretaceous

Angiosperm pollen			
Ages	Location	Fossil types	Reference
late Barremian-Aptian	Inner Mongolia, China	Monocolpate and tetrachotomocolpate	Zhang et al., 2014
Barremian- Cenomanian	Inner Mongolia, China	Monocolpate, tetrachotomocolpate and Tricolpate	Hua, 1991
Albian	Jiuquan Basin, China	Tricolpate	Zhang et al., 2015
late Barremian- Albian	Portugal	Monocolpate, tetrachotomocolpate and Tricolpate	Heimhofer et al., 2007
Late Aptian to early Albian	Northeast Brazil	Monocolpate and Tricolpate	Heimhofer and Hochuli, 2010
Albian	Portugal	Tricolpate	Horikx et al., 2016
Late Albian	Spain	Tricolpate	Villanueva-Amadoz et al., 2010
late Barremian	Argentina, South America	Monocolpate	Quattrocchio et al., 2006
Late Aptian	Patagonia, South America	Monocolpate and tetrachotomocolpate	Llorens and Loinaze, 2016
Late Aptian	Patagonia, South America	Monocolpate and tetrachotomocolpate	Limarino et al., 2012
Late Albian	Argentina, South America	Tricolpate	Archangelsky et al., 2008.
Barremian- Cenomanian	Potomac Group, eastern North America	Monocolpate, tetrachotomocolpate and Tricolpate	Doyle and Robbins, 1977
Albian	southeast Australia	Tricolpate	Korasidis et al., 2016
Barremian- Albian	Eastern Australia	Monocolpate, tetrachotomocolpate and Tricolpate	Burger, 1993
Barremian- Cenomanian	Northern Egypt	Monocolpate, tetrachotomocolpate and Tricolpate	Mahmoud and Deaf, 2007
Barremian- Cenomanian	southern South America	Monocolpate, tetrachotomocolpate and Tricolpate	Summarized by Archangelsky et al., 2012
Angiosperm mesofossils			
Late Albian and Cenomanian	Czech Republic and France	stamens	Kvaček and Gomez, 2012
	Portugal	Stamens and flower	Eriksson et al., 2000
early-middle Albian	(Potomac Group) Maryland, USA	flower	Friis et al., 2017
Barremian–Aptian	Portugal	Stamens and flower	Friis et al., 2004
Barremian- Cenomanian	Iberian Peninsula	Stamens and flower	Summarized by Friis et al., 2010
Angiosperm megafossils			
Albian	Austral Basin, Argentina	leaves	Cunéo, and Gandolfo, 2005
Aptian- Cenomanian	Virginia, U.S.A	leaves	Hickey and Doyle, 1977
Late Albian	Northeastern Spain	leaves	Gomez et al., 2009
Late Aptian	Crato Formation, Brazil	roots, cordate, leaves, flowers and seeds	Mohr et al., 2008
Albian	Jordan	leaves	Taylor et al., 2008
Late Albian	Spain	leaves	Sender et al., 2010
Early Aptian	Northeastern China	Roots, leaves, flowers	Dilcher et al., 2007
Early Aptian	Northeastern China	leaves, flowers	Sun et al., 2011
Early Aptian	Northeastern China	leaves, flowers	Sun et al., 1998
Early Aptian	Northeastern China	leaves, flowers	Sun et al., 2002
Late Albian	Alexander Island, Antarctica	leaves	Cantrilland Nichols, 1996
Albian—Cenomanian	Czech Republic and France	leaves	Kvaček et al., 2012
Barremian- Cenomanian	southern South America	leaves	Summarized by Archangelsky et al., 2012
Barremian- Cenomanian	Potomac Group, eastern North America	leaves	Summarized by Hickey and Doyle, 1977

form 20–30 cm thick layers (Fig. 2c, 2d). Xerophytic Cherirolepidiaceae, such as Pseudofrenolopsis and Brachyphyllum, are abundant in the megafossil plant assemblages (Deng Shenghui and Lu Yuanzheng, 2008; Du et al., 2013; Lei et al., 2018; Jin et al., 2017). *Classopollis* with Cherirolepidiaceae affinity distinctly increase in the Albian Zhonggou Formation (Zhang et al., 2015). Therefore, relatively dry climate is suggested to have prevailed during Albian in the Jiuquan Basin.

Based on the above mentioned paleoclimatic data from terrestrial basins in central China, a gradual change from warm and humid to dry and hot conditions is suggested for late Barremian to Albian.

3.2.2 Mid-Cretaceous climatic conditions in eastern China

Mid-Cretaceous terrestrial sedimentary sequence were widely distributed in eastern China, on the west shore of the Pacific. They were characterized by continuous sediments and large thickness. In this study, we select two representative sedimentary sequences, respectively in Songliao and Subei basins, to recognize paleoenvironmental information during Mid-Cretaceous.

The best preserved terrestrial sedimentary sequence of Cretaceous is in northeastern China (Fig. 3). The SK-I Well of the International Continental Drilling Program (ICDP) established Late Cretaceous strata from the Quantou to Mingshui formations (Wan et al., 2013). Presently, the SK-II Well is being drilled to constrain the Lower Cretaceous. The multiple types of fossils and

volcaniclastic layers provide reliable chronological evidence for the various formations (Gao et al., 1999; Wang et al., 2013; Deng et al., 2013; Li et al., 2011). Generally, it is accepted that the Upper Yingcheng (Yc) Formation is Later Barremian, the Denglouku (Dlk) Formation is Aptian to Early Albian, the lower Quantou (Qt) Formation is Middle to Late Albian, the upper Qt Formation is Cenomanian, and the Lower Qingshankou (QSK) Formation is Turonian (Wang et al., 2013; Deng et al., 2013; Li et al., 2011).

Coal beds are common in the Valanginian to Late Barremian Shahezi and Yc formations (Fig. 4), suggesting humid environment for early to middle Early Cretaceous. The first and second members of the Dlk Formation are Early Aptian and characterized by thick mudstone and coarse-grained sandstone or conglomerate layers, pointing to semihumid climate. The Late Aptian third member of the Dlk Formation constitutes red beds and gypsum deposits (Fig. 4) that formed under dry climatic conditions. However, thin coal seams occasionally occur and suggest alternating humid and arid conditions. The Albian to Cenomanian Qt Formation is characterized by red beds and thin gypsum layers, interbeded with gray-green and gray mudstone and sandstone (Fig. 4). The Qt Formation red beds are the most prominent ones among the four large-scale Cretaceous red beds in the Songliao Basin (Wang et al., 2013) and likely represent aridification during Albian to Cenomanian. This long sequence of red beds was then replaced by the black gray mudstone of the Turonian Qingshankou Formation.

This gradual change to dry climate during mid-Cretaceous in the Songliao Basin is well recorded by palynology (Gao et al., 1999) (Fig. 4). Cheirolepidiaceae generally grow in the middle–low latitudes, and the *Classopollis* content in the Cretaceous of the Songliao Basin is low and probably insensitive to climate fluctuations. Nevertheless, the pteridophyte spores are abundant and are more sensitive to the dry and wet climate changes. The spores content is high (55%–85%) in the Yc Formation and the third member of the Dlk Formation during Late Barremian to Aptian, suggesting a humid environment (Fig. 4). Simultaneously, the xerophilous *Ephedra* pollen content is less than1.2%. The spores content decrease (35%–48%) (Fig. 4) in the Albian–Cenomanian fourth member of the Dlk and Qt Formations. Moreover, the xerophytic *Ephedra* pollen increase from 6.1% to 21% (Fig. 4) from the YC to the QT Formation. In similar deposits in southern China, *Ephedripites* are more abundant and diverse than in the Songliao Basin. Apparently, dry climatic conditions prevailed in the Songliao Basin, northeastern China during Albian to Cenomanian.

Another representative terrestrial sedimentary sequence of Mid-Cretaceous is in Subei Basin, eastern China (Fig. 3). About at least 3000 m thick deposits were upwardly divided into Dawangshan (DW) Formation, Gecun (GC)

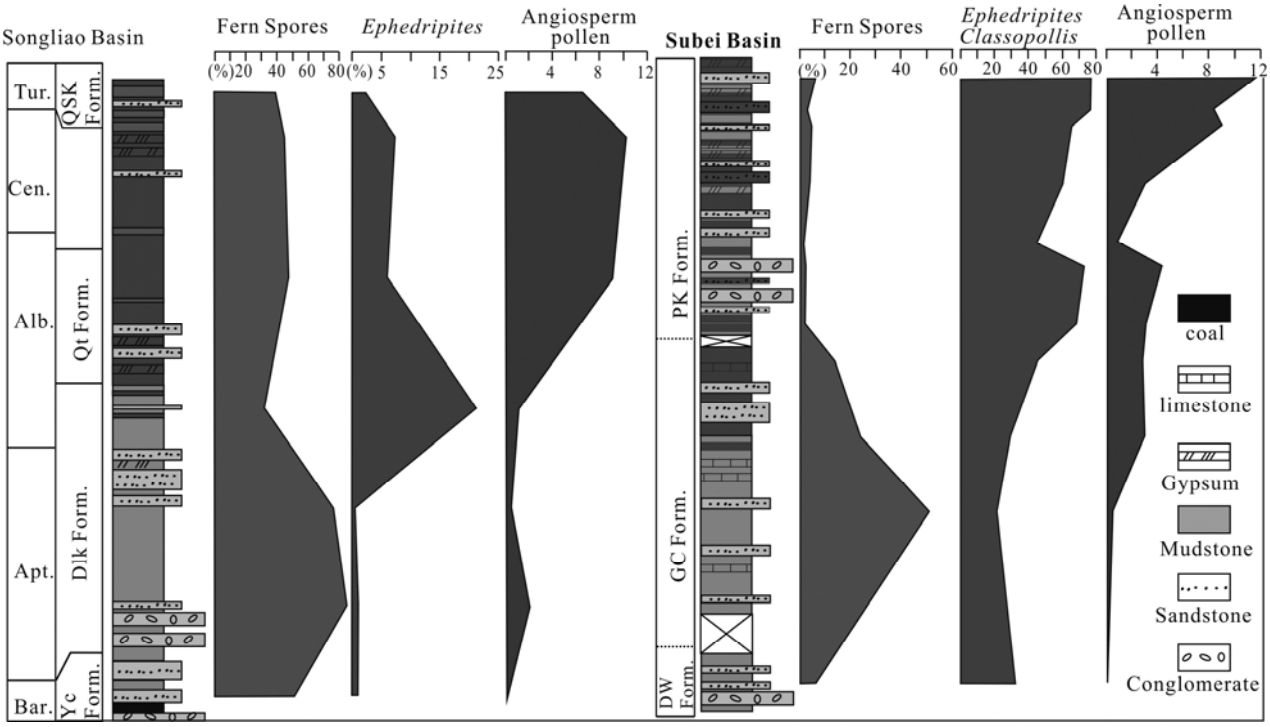


Fig. 4. Mid-Cretaceous lithologies and changes in hygrophilous spore and xerophilous pollen contents, Songliao and Subei basins, eastern China.

Formation and Pukou (PK) Formation with unconformable contact. The chronostratigraphic system was relatively reliable based on palynostratigraphy and radioactive age of volcaniclastic layers (Zhou Shanfu et al., 2009; Zhang Ni, 2009). It is generally accepted that the Dawangshan (DW) Formation is Barremian, the Gecun (GC) Formation is Aptian to Albian, the Pukou (PK) Formation is Cenomanian to Turonian (Zhou Shanfu et al., 2009; Zhang Ni, 2009).

The lithologic sequence of Subei Basin was very similar to Songliao Basin. The red beds were gradually increased from DW to PK formations (Fig. 4). Especially, amount of halites and gypsum deposits were extremely developed in the PK Formation (Fig. 4), which as the target stratum of salt mine in Jiangsu Province. Thus, dry climatic conditions were indicated by these lithologic evidences. In addition, palynomorph assemblage were dominated by the xerophilous *Ephedripites* and *Classopollis* pollen which also show remarked increased trend from DW to PK formation (Fig. 4). The hygrophilous fern spores present obviously decreased trend. Simultaneously, angiosperm pollen content rapidly increased during Mid-Cretaceous in the Subei Basin (Fig. 4).

3.2.3 Mid-Cretaceous warming and aridification

Based on global and regional climate data, four climate stages can be recognized. The first is the cold and humid stage of Late Barremian to Early Aptian. The onset of the Ontong LIP, the powerful meridional temperature gradients, the frequent small glacial events, and extensive coal-bearing deposits are the characteristics of this stage. The second is the Aptian warming and semihumid stage. Oilshales were deposited in middle–high latitudes. Atmospheric CO_2 concentration were firstly increased. The global environment was disturbed by multiple LIPs and OAEs. Albian greenhouse conditions further intensified in third stage, in which extensive gypsum-bearing sediments and red beds were deposited, following significant increases in temperature. Besides East Asia, low latitudes (Martill et al., 2007) and the High Arctic (Herrle et al., 2015; Schröder-Adams et al., 2016) contain dry-climate deposits. The fourth climate stage is the extreme hothouse conditions during the Cenomanian, as recorded via the ice-free poles and weak meridional temperature gradients.

3.3 Wildfires

3.3.1 Evidence

Fires significantly regulate terrestrial ecosystems. For example, many major biomes, grasslands, Mediterranean shrublands, and boreal forests are controlled by fires (Bond et al., 2005). Fires are not only widespread today (Chuvieco et al., 2008; Krawchuk et al., 2009) but also frequent on the earth in the past time (Harris, 1958; Chaloner, 1989; Scott, 2000; Scott and Glasspool, 2006). Cretaceous has always been considered a very fire-intensive period. Brown et al. (2012) have reviewed the Cretaceous wildfire records on global in which roughly show fires were scarce in the Early Cretaceous but increased in Barremian. Charred fossils are abundant in the Aptian to Albian; however, they are rare in East Asia.

In this study, we review the wildfire evidence in mid-Cretaceous deposits from several basins in the interior of East Asia. Charcoal and charred mesofossils or macrofossils offer direct evidence for fires. Preliminary investigations suggest that charcoal is abundant in all mid-Cretaceous sediments of the Jiuquan, Liupanshan, and Yin-E basins (Fig. 5). Charcoal has very clear microstructure with well-preserved tracheids (Fig. 6). The walls of the tracheids are 1–2 um thick, without intercellular layers. The homogenized cell walls suggest fire temperatures exceeding 350°C (Scott, 2000, 2010).The tracheids are often filled with calcite (Fig. 6d). The shape of charcoal varies in the sediments. In coarse-grained deposits (e.g., sandstones), charcoal typically forms thin layers parallel to the bedding. Charcoal sizes do not exceed 1 cm and are slightly longilineal, which suggests short transport distances. Occasionally, round charcoal is also seen, which points to long-distance transport. The different charcoal sizes likely denote fires of variable scales. In fine-grained sediments, charcoal is also occurred, especially in gray-black mudstone or calcareous fine-grained deep or semideep lacustrine deposits. Apparently, charcoal or charred plants floated on lake surfaces or were water- or wind-transported (Scott, 2010).

We have found charred wood in the upper Xiagou Formation of the Jiuquan Basin and the Bayingobi Formation of the Yin-E Basin (Fig. 5c, 5d). The surfaces of these fossils were wrapped by thick charcoal tissue different from conventional wood fossils. Some of them also had tree holes. The layout of the fossilized wood followed the sedimentary bedding, suggesting transport from the source. Lastly, the organic extract from the charcoals in the Bayingobi Formation of the Yin-E Basin yielded pyrolitic polycyclic aromatic hydrocarbons (PAHs) that are typically attributed to high-temperature fires (Scott, 2010). In addition, organic compounds associated with wildfires, such as phenanthrene, pyrene, fluoranthene, and benzo[*e*]pyrene, were discovered (Zhang Rui et al., 2014).

Clearly, wildfires were frequent in the interior of East Asia during mid-Cretaceous. The era was an one of many fires, as the entire Cretaceous (Brown et al., 2012).

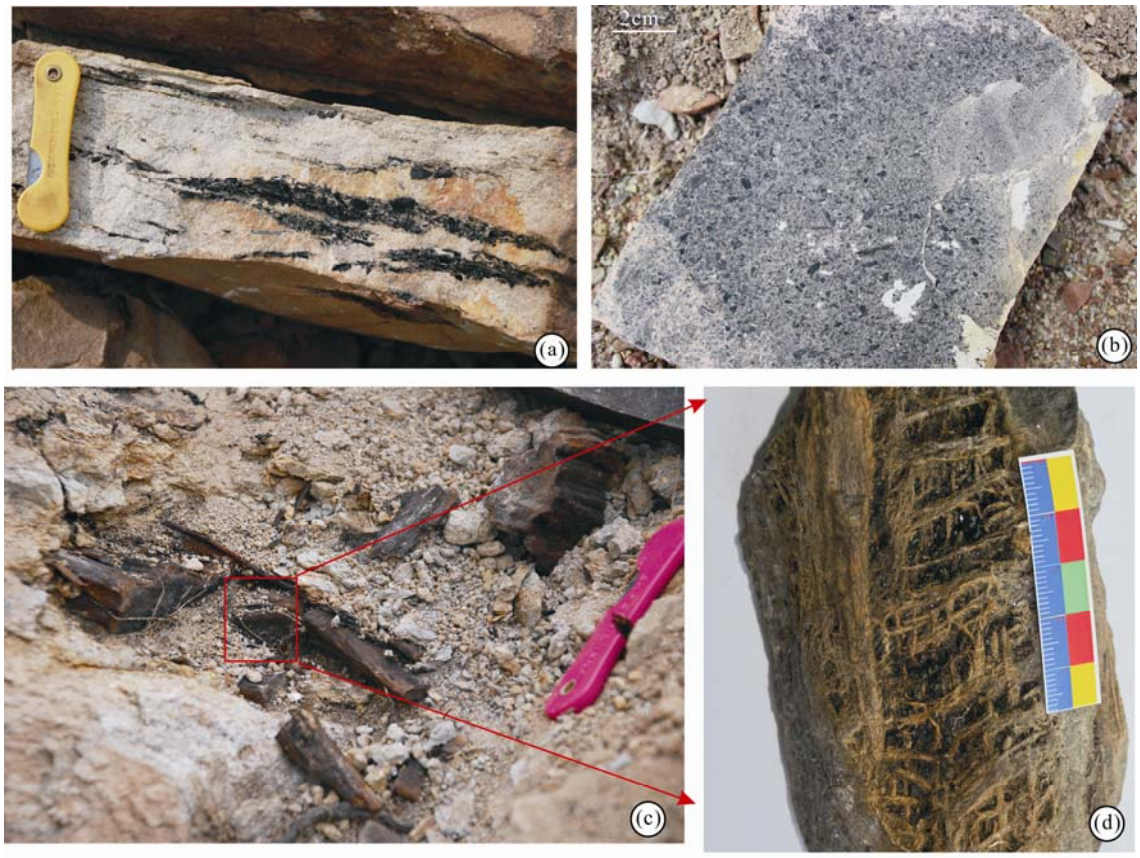


Fig. 5. Field photo of charcoal (a, b) and charred wood (c, d).

3.3.2 Dry hothouse climate and wildfires

The fire activity in mid-Cretaceous was not random. The fire frequency and severity (Keeley, 2009) are generally controlled by physical factors and vegetation (Bond and Scott, 2010). The atmospheric O_2 levels required to allow combustion, which show obvious increasing from the Aptian, and reach peak at the Cenomanian (Berner, 2009; Bergman et al., 2004; Glasspool and Scott, 2010). However, many studies revealed that even the highest level of atmospheric O_2 in the Cretaceous just roughly equal to present day levels (Falkowski et al., 2005; Berner, 2006, 2009). Therefore, we speculate the increasing trends in atmospheric O_2 during mid-Cretaceous interval might conductive to the fire spreading on the earth, but which is not the primary factor for the high-fire world. Vegetation provides the fuel and controls the flammability. In mid-Cretaceous, plant abundances apparently decreased because of the dry and hot climate; however, this did not affect the fire regime. Hence, external physical factors, such as climate (dry or humid and cool or warm), lightning, and volcanic activity, might have been critical. Modern meteorological and fire data show the primacy of climate in driving large regional fires (Bowman et al., 2009). For example, fire occurrence increases during the La Niña phase of the Southern Oscillation (Werf et al., 2004, 2008; Kitzberger et al., 2001) and there is tight coupling between high fire activity and interannual- and decadal-scale climate oscillations (Swetnam, 1993; Kitzberger et al., 2007). Furthermore, the majority of the data suggest that drought and warming favor fires (Westerling et al., 2006; Bowman et al., 2009). Under prolonged and severe droughts associated with the El Niño Southern Oscillation and Arctic Oscillation, large fires become common in North American boreal forests (Macias Fauria and Johnson, 2008). Modern meteorological observations suggest that large fires typically occur during the breakdown of persistent mid-tropospheric ridges and are associated with the occurrence of troughs (short waves) that generate strong surface winds, enhance lightning, and do not produce sufficient rain to moisten the vegetation (Street and Birch 1986; Macias Fauria and Johnson 2006). Therefore, warmer and drier weather dries the vegetation over large areas quickly and increases the fire frequency. In mid-Cretaceous, a hot Earth would require massive energy movement between the equator and the poles. In addition to energy transported by oceanic currents, most energy transport depends on atmospheric exchange (Vonder Haar and Oort, 1973; Trenberth, 1979; Carissimo et al., 1985). This increases air currents and the transport of warm vapor (William, 2008).

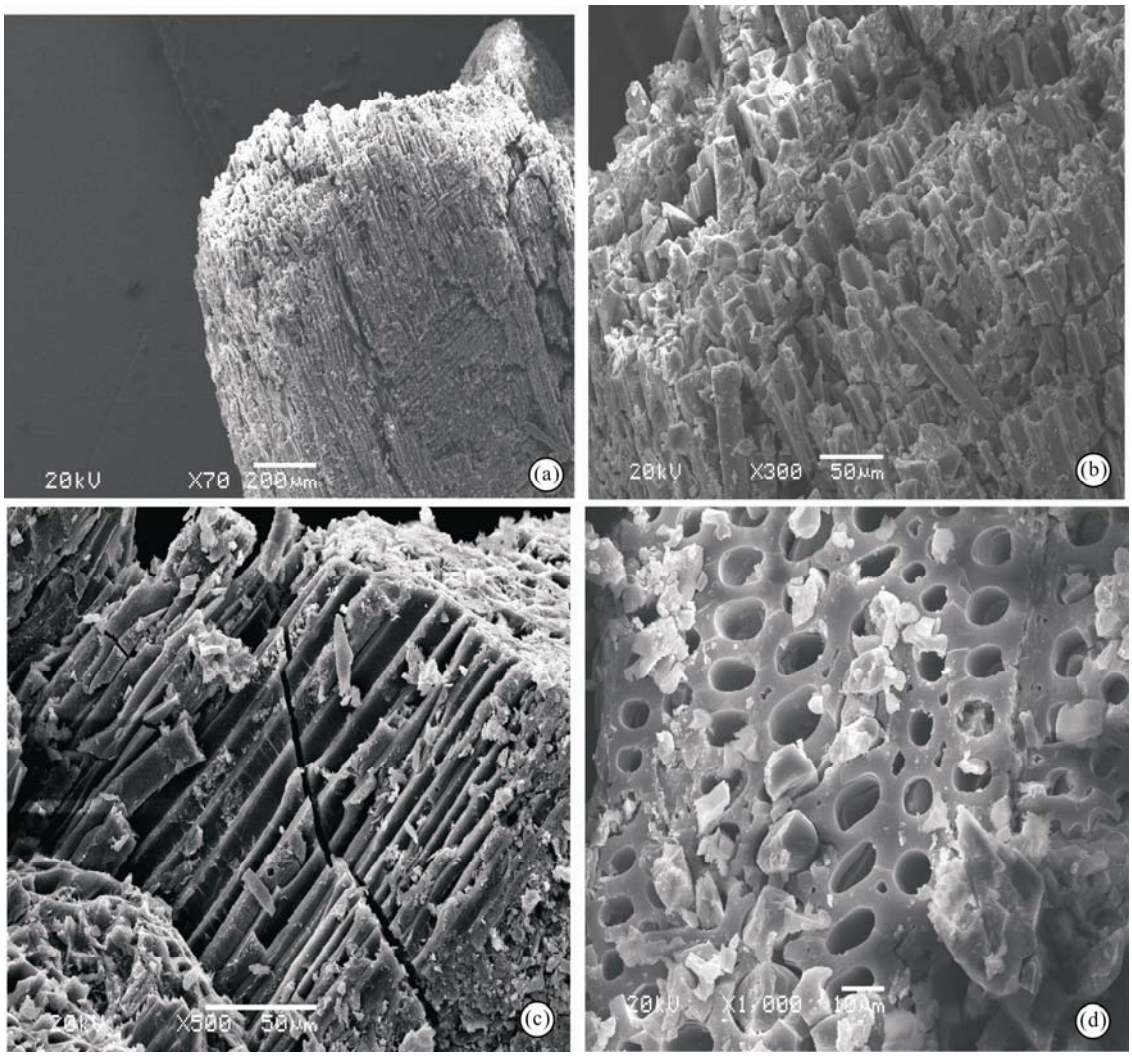


Fig. 6. SEMs of wood charcoal.
(a), charcoal particle; (b, c, and d), Charred conifer wood charcoal. (b and c), tangential longitudinal section. (d), detail of tracheids showing homogenized and thick cell walls.

The intensive air convection enhances lightning, which can then easily cause forest fires. Thus, the mid-Cretaceous hot and dry climate was conducive to high fire regimes.

4 Mid-Cretaceous Early Angiosperm Evolution

Systematic molecular analysis and fossils suggest that early angiosperms appeared before Cretaceous, possibly even before Permian (Hochuli and Feist-burkhardt, 2013; Doyle, 2012; Clarke et al., 2011; Smith et al., 2010). However, the general consensus is that the expansion of angiosperms occurred during the Cretaceous. Furthermore, mid-Cretaceous is the critical transitional period for floras dominated by ferns, conifers, and cycads to angiosperm-dominated ecosystems (e.g., Lidgard and Crane, 1988; Crane et al., 1995). In this section, megafossils, mesofossils, and pollen fossils are discussed to understand the evolution of early angiosperms in mid-Cretaceous (Fig. 7).

4.1 Mid-Cretaceous angiosperm megafossils

Angiosperm megafossils from mid-Cretaceous are rare, especially early, but nonetheless provide useful ecological information.

Pre-Aptian angiosperm megafossils are very rare. Recent work has corrected the affinities of *Montsechia* based on fossils recovered more than 100 years ago by various institutions in England, France, Germany, and Spain (Gomez et al., 2015). The morphology and anatomy of the plant suggest that *Montsechia*has aquatic *Ceratophyllum* affinities. *Archaefructus* from northeastern China has a simple root system and delicate stems with highly dissected leaves, suggesting an aquatic environment (Sun et al., 1998). The aquatic plants were

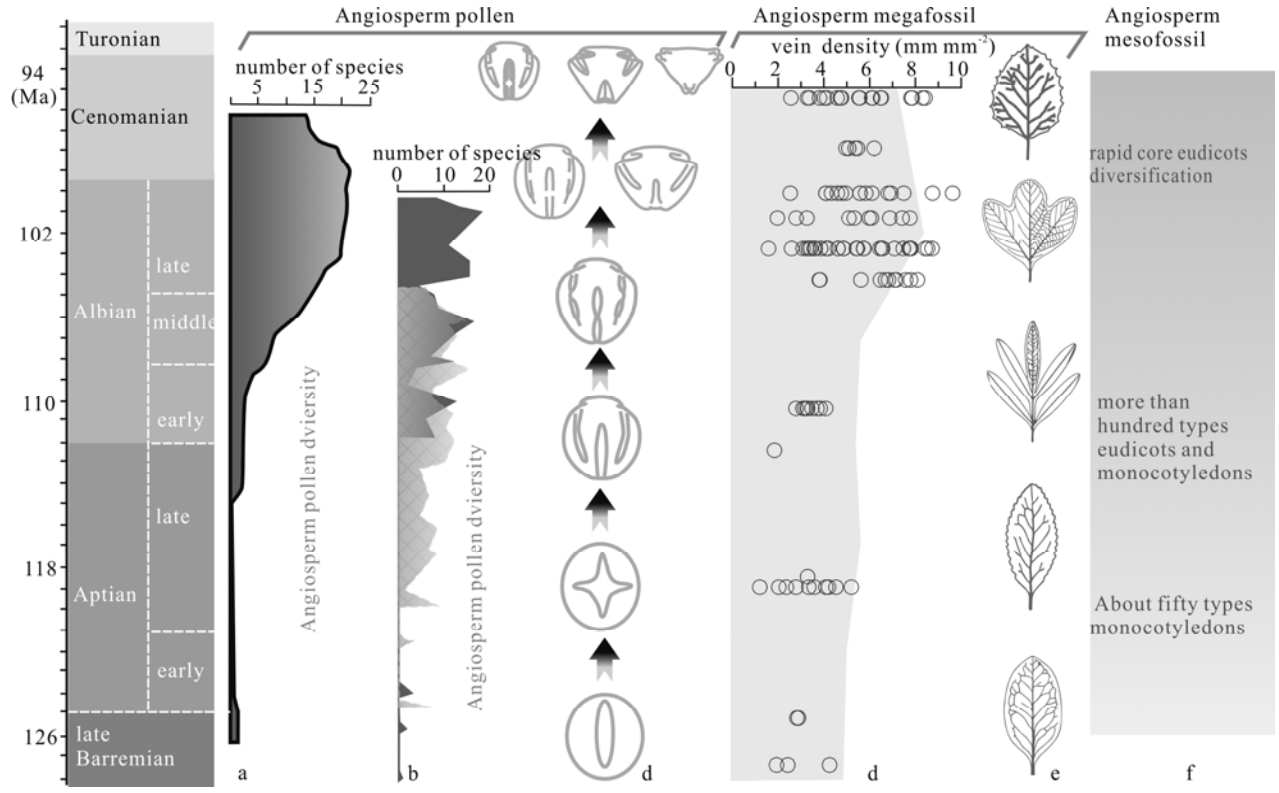


Fig. 7. Synthesis of the early angiosperm expansion in mid-Cretaceous based on angiosperm pollen (a: Burger, 1993; b: Heimhofer et al., 2007; c: after Doyle, 2012), angiosperm megafossil (d: Feild et al., 2011; e: after Doyle, 2012), and angiosperm mesofossil (f: Friis et al., 2010).

locally common at the very-early stage of angiosperm evolution and apparently aquatic habitats have played a major role in the diversification of some early angiosperm lineages.

More morphologically diverse early angiosperm megafossils became common after Aptian. Angiosperm leaf fossils are rare, simple, and usually pinnate, with unusually irregular venation. In addition to the aquatic types, herbaceous angiosperm, such as *Hyrcantha decussata* (Dilcher et al., 2007) and *Sinocarpus decussatus* (Leng and Friis, 2006), began to emerge based on their morphological characteristics. The eudicot *Leefructusgen*. nov. (Sun et al., 2011) is slightly younger than *Archaefructus* and both were found in the Yixian Formation, northeastern China. The morphological characteristics suggest plant affinities with Ranunculaceae, a basal eudicot family. The leaf architecture of *Potomacapnos apeleutheron* from Aptian sediments of the Potomac Group also support the relation with crown-group Ranunculales, with herbaceous habits (Jud and Hickey, 2013; Jud, 2015). Though a rarity, the herbaceous habit for early angiosperms in the Aptian was probably an early diversification phase. Herbaceous plants are recognized as colonizers of disturbed microsites in wet riparian habitats (e.g. Jud, 2015); The morphology and anatomy of the fossil plant in the Aptian, such as upright stems, lobed leaves, pinnate venation, all indicated a terrestrial ecological habits. This imply early angiosperm had firstly break away from aquatic environments in the Pre-Aptian move to inland in the Aptian time. From Albian to Cenomanian, the herbaceous angiosperms were already well diversified and common. The megafossils record points to complex morphological characteristics in leaves, roots, wood, etc. (e.g., Iglesias et al., 2007; Upchurch et al., 1990; Oakley and Falconlang, 2009). Especially, the same types occurred in equivalent deposits at different locations, e.g., leaves of *Sapindopsis* genus were simultaneously discovered by the Potomac Group in the United States (Fontaine, 1889) and in western Canada (Bell, 1956), the Middle East and Asia (Krassilov and Bacchia, 2000; Tao Junru, and Zhang Chuanbo, 1990), the Russian Far East (Golovneva, 2007), and northeastern Spain (Sender et al., 2015). This suggests that early angiosperms may have had long distance migration from the originated area. The angiosperm leaves exhibit high diversity in the margins (toothed and smooth), leaf shape (reniform, cordate, and peltate), and well-defined venation (palmate, pinnately, and others) (e.g., Doyle, 2012; Passalia et al., 2015) (Fig. 7e). The vein density of early angiosperms increased threefold (Fig. 7d) (Brodribb and

Feild, 2010).These leaves have high systematic value. For example, palmately lobed "platanoids" can be compared with *Platanus* (sycamore), and pinnately dissected and compound leaves (*Sapindopsis*) are now known to be related to *Platanus* (Crane et al., 1993). Therefore, the Albian to Cenomanian megafossils exhibit high diversity and abundance; especially, under shrubs and tree angiosperms began to emerge. This evolutionary progress implies that early angiosperms completely broke away from the aquatic environment and gradually dominated terrestrial ecosystems.

4.2 Mid-Cretaceous angiosperm mesofossils

Rich mesofossil flora is more informative about the systematic relations and ecological traits, such as herbaceous and insect-pollinated forms. Angiosperm mesofossils often include small plant fragments of well-preserved flowers, fruits, seeds, and stamens of angiosperms (e.g., Friis et al., 1992, 1997, 1999, 2000b, 2006a; Pedersen et al., 2007; Friis et al., 2009b). The most representative area for early angiosperms is the western Iberian Peninsula (Friis et al., 2010). To date, abundant well-preserved angiosperm reproductive structures have provided a new understanding of the systematic relations and biology of angiosperms at several stratigraphic levels throughout Cretaceous (Friis et al., 2010).

The oldest mesofossil assemblages are angiosperm remains from Late Barremian–Early Aptian deposits in the Lusitanian Basin. Fifty different kinds of angiosperm fossils with uncommonly complete and unequivocally unisexual and bisexual flowers were found (Fig. 7f). The unisexual flowers are very similar to those of the extant *Hedyosmum* Sw. The bisexual flowers are trimerous, hypogynous, and have a distinct perianth. The in situ pollen grains are monocolpate and reticulate and are assigned to the pollen genus *Retimonocolpites*. Other mesofossil assemblages also include seeds and fruit structures. Based on the probable extant relatives and the general appearance of the plant remains, early angiosperms were probably monocotyledons and aquatic in the entire area.

Late Aptian–early Albian mesofossils include hundreds of different kinds of angiosperm reproductive structures (Fig. 7f), e.g., fruits and seeds, flowers, and stamens. The major difference in these mesofossils from the Late Barremian–Early Aptian mesofossil flora is the higher species diversity of angiosperms and the generally larger size of the angiosperm seeds. The earliest seeds range from about 0.4 to 3.9 mm in length, whereas seeds from this interval range from about 0.5 to 1.1 mm. Unlike the few eudicots reported in Portugal and Spain from Late Barremian–Early Aptian, the Late Aptian–Early Albian eudicots are more diverse. These eudicots have been placed reliably in the extant basal angiosperm tree and resemble extant herbaceous or shrubby taxa of extant Buxale and Ranunculales.

Since Cenomanian, the rapid diversification of core eudicots characterised the Late Cretaceous flora from Portugal. The core eudicots types seemly completely dominated the fossil flora during this period. There are clear similarities, in terms of the general floral structure and the broad systematic affinities, among the mesofossil flora from around the globe. The floral assemblages are well represented by rosids, including many species belonging to the diverse and widespread *Normapolles* group that is related to the core Fagales (Friis et al., 2006b). These fossils are thought to come from small trees growing in open habitats where frequent forest fires occurred because of the seasonally dry climate (Friis et al., 2010).

4.3 Mid-Cretaceous angiosperm pollen

The pollen record offers the best evidence for the abundance and diversity of early angiosperms (Fig. 7). The characteristic columellar exine structure, with radial rods connecting the inner and outer wall layers (nexine and tectum, respectively), is distinctly different from the gymnosperm pollen. To date, there are many areas with well-established early angiosperm pollen succession in terms of stratigraphy. These areas include the Songliao Basin of northeastern China (Gao et al., 1999), the Potomac Group of eastern United States (Doyle and Robbins, 1977), and Queensland of eastern Australia (Burger, 1993). Recent discoveries of angiosperm pollen also filled the gaps in the interiors of continents (Zhang Rui et al., 2014; 2015). Nearly four successive angiosperm pollen zones from Late Barremian to Cenomanian are established.

In Late Barremian, the angiosperm pollen are monosulcate types with monocotyledon affinities (Fig. 7c). The most common taxa are *Clavatipollenites* genes, which have been reported in pre-Aptian sediments around the globe. A comparison with extant forms and *in situ* palynological records suggests that the most common *Clavatipollenites* have extant Chloranthaceae affinities (Couper, 1953; Pedersen et al., 1991). The abundance of these pollen types is very low in all regions (Fig. 7a, b).

The Aptian angiosperm pollen increased in abundance and diversity. Morphologically, new forms of tri- or tetrachotomocolpate apertures represented by *Asteropollis* emerged and are probably transitional from monosulcate to tricolpate (Fig. 7c). The extant genus *Hedyosmum* of the Chloranthaceae family has the highest affinity with them (Walker and Walker, 1984). *Asteropollis* genes are not

only widespread globally but also slightly increased during Aptian (Zhang Rui et al., 2014). Monosulcate types are common in this period but new pollen forms also emerge, such as *Pennipollis*, *Stellatopollis*, and *Retimonocolpites*. In this period, the percentage of early angiosperm pollen has reached the statistical significance at a 5% confidence level of the total. By Albian, besides the monosulcate and multi-chotomocolpate early angiosperm pollen, the tricolpate types became common in the various regions globally. These pollen types are characterized by three longitudinal furrows and were succeeded by tricolporate pollen since Late Albian with a pore in the middle of each furrow. Tricolporate pollen is the most common among living eudicots. The presence of three apertures likely provided an advantage because of the increase in the number of available sites for germination (Archangelsky et al., 2009). The tricolpate pollen have affinities with eudicots, in agreement with megafossils. Actually, the tricolpate pollen constitutes various morphological types, such as the reticulated or ribbed exine, fusiform, and oval and subsphaeroidal forms, that resemble pollen from "dicots" (see Zhang et al., 2015; Heimhofer et al., 2007; James and Robbins, 1977). Therefore, the early angiosperm pollen assemblages in Albian are remarkably diverse. In addition, their abundance increased, reaching 10–50% of the total (see Heimhofer et al., 2007) (Fig. 7a, 6b).

More new forms emerged during Cenomanian, and the angiosperm pollen diversified and became more common (Fig. 7a, 7b, 7c). Several pollen species, such as *Asteropollis asteroides* and *Stellatopollis* spp., became extinct during this time (Archangelsky et al., 2009; Zhang Rui et al., 2014). The tricolpate increased in abundance and developed a small short axis, e.g., *Nyssapollenites*, *Cupanieidites*, *Retitricolporites oblaus,* and *Talisiipites* (Zhang Yiyong, 1999). The most representative taxa aretriporate pollen of the *Normapolles* group, and their relation to Fagales is well established based on fossil flowers (see Friis et al. 2006). Therefore, pollen with tree affinities appeared in Cenomanian. Angiosperm pollen accounts for more than 10% in the palynological assemblages on Earth. Thus, angiosperm became the third group of land plants, followed by gymnosperm and ferns.

4.4 Early angiosperm evolution in mid-Cretaceous

Based on megafossils, mesofossils, and pollen records, the diversity and abundance of early angiosperms increased during mid-Cretaceous. Especially, the pollen, leaves, and flowers suggest that the early flowering plants were essentially weedy plants, generally small and herbaceous or shrubby with little wood (Taylor and Hickey, 1996; Royer et al., 2010). Early angiosperm fossils from Late Barremian are very rare and probably aquatic. The abundance of Aptian angiosperms slightly increased and new species emerged. Herbaceous flora began to invade the terrestrial vegetation while maintaining their presence in wet riparian habitats. This transition is a key ecological jump from water to land habitats for the early angiosperms. The universally emerging evidence for eudicots around the world since Albian suggests the growth of herbaceous plants and trees. Angiosperms of this period were apparently more suitable to arid land environments. In addition, the proportion of angiosperms rapidly increased from about 5 to 10%. In Cenomanian, angiosperms comprised trees and herbaceous plants and a few aquatic species. Furthermore, the wide distribution of early angiosperms on Earth, even at the very arid mid-latitude regions, suggests a large range of habitats, either dry or wet.

5 Hot, Dry and Fiery Climate and Angiosperm Expansion

5.1 Hot and dry environment and early angiosperm diversification

The gradual aridification of continents and the extreme greenhouse conditions characterize mid-Cretaceous. Palynological data and plant fossils point to decreasing diversity and abundance of gymnosperms and ferns. Cheirolepidiaceae were the most representative tree plants in Late Mesozoic, despite their preference for dry and hot habitats. With the intensification of aridification and hot climate, we assume that high plants far from rivers or lakes would have been destroyed first. Soil moisture loss and erosion because of the vegetation decrease and the frequent wildfires (see preceding discussion) would favor intermittent flooding, which would also destroy the native vegetation. The plants in pre-angiosperm times were mainly high trees, such as Coniferae, Cheirolepidiaceae, Cupressaceae, and ferns (Lidgard and Crane, 1988). Once these perennial trees died, long recovery periods were needed to achieve full growth. Herbaceous or shrub angiosperms might have been less affected by the floods and dry conditions. First, most of them were likely annual plants that could easily revive. They also had high reproductive capacity near water, and the wind and insects carried their pollen or seeds (Friis et al., 2010; Hu et al., 2008). Second, herbaceous and tree shrubs were probably better adapted to dry conditions. For example, present-day arid and semi-arid areas of Africa and northwestern China have steppe and savanna vegetation. In addition, early angiosperms' habitats ranged from the equator to the poles in mid-Cretaceous. Their strong adaptability to various environments, like present-day dicotyledonous plants,

allowed them to grow and expand globally. In addition, shrub gymnosperms were common. For example, *Ephedra* is occasionally found in pre-Barremian strata and are more common since Aptian, peaking (*Ephedripites*account for about 50%) in the Cenomanian of southern China (Song et al., 2000). Obviously, the gradual dry and hot climate in continents during mid-Cretaceous probably accelerated the diversification of early angiosperms.

The rapid temperature increase and aridification perfectly match the expansion of early angiosperms in mid-Cretaceous. The ecological traits and physical structures of early angiosperms also comply with this co-evolutionary path. The invasion of early angiosperms first from aquatic to wet and then to terrestrial environments implies a climatic driving mechanism. Second, mid-Cretaceous early angiosperms showed increased leaf venation density and areas (Feild et al., 2011; Boer et al., 2012; Royer et al., 2010; Brodribb and Field, 2010). The high venation density and large leaf area form efficient hydraulic systems that facilitate water absorption and temperature dissipation under hot and dry conditions, especially important during mid-Cretaceous, and promote photosynthesis (Fig. 8).

5.2 Wildfire frequency and early angiosperm expansion

The high temperatures and dry conditions on land during mid-Cretaceous probably caused frequent wildfires that profoundly affected the vegetation. Bond and Scott (2010) proposed an angiosperm–fire cycle for Cretaceous that promoted diversification and angiosperm expansion. The fossil record suggests that early flowering plants were essentially weedy plants, generally small and herbaceous or shrubby with little wood (Taylor and Hickey, 1996; Royer et al., 2010). Similar to present-day steppe vegetation, these early angiosperms had short life cycles but strong reproductive and regenerative capacity. Thus, they could use the released rich inorganic nutrients resulting from wildfires. The high vein densities in Late mid-Cretaceous are linearly related to photosynthetic rate, and thus the plants may have coped better with droughts owing to the low atmospheric CO_2 (Bond and Scott, 2010). Additionally, phosphorous, nitrogen, and other elements beneficial to plant growth would have been washed away by floods and the subsequent-to-fires erosion, leading to poorer soils and droughts (e.g., Moody and Martin, 2009; Cannon et al., 2010; Brown et al., 2012). In these conditions, the high photosynthetic rate and efficient hydraulic systems of these early weedy angiosperms probably were more capable of growing than the high gymnosperm forests. Therefore, with the high gymnosperm flora destroyed by fires (Fig. 8), the early weedy angiosperms would have space to grow.

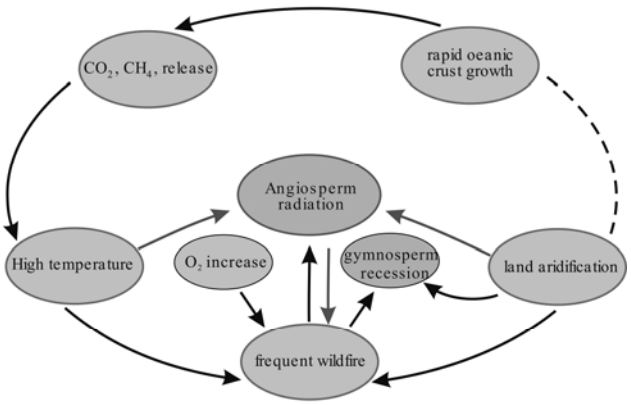


Fig. 8. Angiosperm expansion and environmental factors.

Chaloner (1989) proposed that sufficient biomass to fuel fires is a precondition for wildfires. The rapid increase in venation densities during mid-Cretaceous would have accelerated the photosynthetic rates of early angiosperms (Brodribb and Field, 2010; Feild et al., 2011 and biomass would have accumulated quickly in mid-Cretaceous (Bond and Scott, 2010; Brown et al., 2012). In addition, the weedy early angiosperms were usually thin with large leaf blades and flexible stems and were presumably more flammable than the acicular or scale-like leaves of conifer plants. As Bond and Scott (2010) proposed, the angiosperm–fire cycle would have created fire regimes with positive feedback, leading to frequent fires that would have promoted their expansion in Cretaceous (Fig. 8).

6 Conclusions

Mid-Cretaceous is characterized by major geological events such as OAEs, LIPs, and marine extinctions. These events favored and controlled the rapid temperature increases documented by $\delta^{18}O$, TEX_{86}, and other indices from marine sediments. The high temperatures were occasionally interrupted by short cooling periods. During mid-Cretaceous, the changes in the terrestrial environments were also profound. The sedimentary record and climatic indices from Late Barremian to Cenomanian deposits of terrestrial basins in East Asia suggest several climatic stages. First, coal-bearing sediments and moisture-loving plants developed in various basins in late Barremian, suggesting humid conditions. Second, organic-rich shale interlayered with calcareous mudstone characterizes Aptian sediments. The obvious increase in xerophytic plants and other climatic indices suggest aridification. Since Albian, the red beds and evaporates

increased in terrestrial basins, and the xerophytic *Classopollis* pollen peaked, suggesting extremely dry conditions. Finally, even high latitudes had red beds in the Cenomanian, and the vegetation changes owing to climate fluctuations suggest dry climatic conditions around the globe.

Modern forest fires occur in dry and hot environments. Mid-Cretaceous fire charcoal is well preserved globally, but there are few reports for East Asia. We identified charcoal and charred wood in mid-Cretaceous sediments in the Jiuquan, Liupanshan, and Yin-E basins of inner East Asia. Thus, we speculate that dry and hot conditions prevailed in mid-Cretaceous.

A literature review of megafossils, mesofossils, and pollen occurrences suggests that early angiosperms increased in abundance and diversity globally. Angiosperm fossils from pre-Aptian are rare and mostly aquatic. Monocotyledon angiosperms and herbaceous eudicots began to flourish in Aptian. From Albian, herbaceous eudicots rapidly increased based on the high pollen content, complex leaf types, and abundant mesofossils. Their habitats became more diverse than before. In addition to the herbaceous angiosperms in the Cenomanian, shrub and tree angiosperms were abundant and widely distributed globally. Early angiosperms, gymnosperms, and ferns dominated the terrestrial ecosystems of mid-Cretaceous.

The dry and hot conditions in mid-Cretaceous were lethal to the preexisting vegetation of mainly tall conifer plants. In the contrast, early angiosperms increased and evolved physiologically; the increased vein densities and leaf area improved photosynthesis and water absorption. Moreover, the physiological changes responded to the fire –angiosperm cycle in mid-Cretaceous, which likely further stimulated early angiosperm evolution.

Acknowledgments

This work is supported by the National Natural Science Foundation of China (No. 41602023, 41402007), and the Key Laboratory Project of Gansu Province (Grant No.1309RTSA041). We thank Prof. Heimhofer Ulrich (Leibniz University Hannover, Germany) for his kind support and helpful comments on the manuscript.

Manuscript received Sept. 3, 2018
accepted Sept. 23, 2018
edited by Liu Lian

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