Botanica Pacifica. A journal of plant science and conservation. 2015. 4(2): 87–94
DOI: 10.17581/bp.2015.04219

RESEARCH PAPER

Historical Distribution of *Metasequoia* Referenced to Paleoclimate Factors

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Manuscript received: 30.07.2015
Review completed: 18.09.2015
Accepted for publication: 21.09.2015
Published online: 31.10.2015

ABSTRACT

Metasequoia Miki 1941 was a prominent element of vegetation distributed in the high latitudes of Northern Hemisphere from the late Early Cretaceous to Miocene. However, at present this genus survived only in some mountain areas of Hubei, Hunan and Chongqing of China as a relict genus. Although the distribution of *Metasequoia* through geologic time have been studied in detail, the relationship between its distribution and paleoclimates remained unclear. In this paper, the potential migratory routes of *Metasequoia* are explained on the basis of the its fossil records plotted in the paleoclimate maps. It can be concluded that: 1) the Warm Temperate climate favored to the diffusion of *Metasequoia*, while the Arid climate curbs its migration; 2) with the global temperature decreased markedly since Pliocene, *Metasequoia* was forced to migrate to the south, and survived only in South China, under the Warm Temperate climate support.

Keywords: *Metasequoia*, distribution, paleoclimate factors

РЕЗЮМЕ

Жан Й., Ван Ж.Ж. Историческое распространение *Metasequoia* по отношению к палеоклиматическим факторам. *Metasequoia* Miki 1941 была весьма значимым элементом растительного покрова, распространенным в высоких широтах Северного полушария с конца раннего мела до миоцена. Тем не менее, представители этого рода в настоящее время сохранились только в некоторых горных районах провинций Хубэй, Хунань и Чунцин в Китае как реликтовые растения. Хотя распространение *Metasequoia* в геологическом времени было детально изучено в предыдущих исследованиях, отношения между распространением рода и факторами палеоклимата оставались не ясными. В данной статье потенциальные миграционные маршруты *Metasequoia* проясняются путем наложения местоположения найденных фоссилий *Metasequoia* на разработанные палеоклиматические карты. Полученные результаты позволяют сделать следующие выводы: 1) теплоумеренный климат благоприятствовал распространению *Metasequoia*, в то время как засушливый климат сдерживал миграции рода; 2) по мере понижения глобальных температур в плиоцене *Metasequoia* мигрировала на юг и выжила в настоящее время только в Южном Китае, в условиях теплоумеренного климата.

Ключевые слова: *Metasequoia,* распространение, палеоклиматические факторы

Переведено редколлегией

Metasequoia as a "living fossil" is now ascribed to the subfamily of Sequoioideae (Cupressaceae) (Gadek et al. 2000) and characterized as deciduous, monoecious tree; trunk is monopodial with branches irregularly whorled; leaves are linear, flat, decussate, with basic parts twisted into two columns and apical parts obtuse; petioles are absent; stomata on the lower surface of leaves are generally parallel to the midrib; male inflorescence is racemose or paniculate; male cone is ovoid with a short pedicel; female cone is generally borne singly at the end of a leafy twig with a pedicel; seed scales are decussate; seeds are flat surrounded by wings (Liu et al. 1996, Farjon 2010, Wang & Leng 2011).

Previous research results show that *Metasequoia* was probably originated from the Early Cretaceous of Northeast Asia, and diffused to Alaska and western North America through the Bering Strait, and quickly diffused to China and Japan. From Paleocene to Eocene, the genus widely distributed from western North America, Northeast Asia, Central Asia, North Japan, to eastern North America and Spitsbergen islands in Europe. In Miocene, it began to decline in the North Hemisphere except for Honshu and Hokkaido, Japan. After Pliocene, it was extinct in North America and most of areas of Northeast Asia except in Japan and China. Extant *Metasequoia* is only distributed in Shizhu, Chongqing; Lichuan, western Hubei and Longshan, Hunan of China (Yu 1995, Liu et al. 1996, Lepage et al. 2005, Liu et al. 2007).

Although many studies were focused on paleogeography of *Metasaquoia* (LePage et al. 2005, Liu et al. 2007), the analysis of its distribution based on paleoclimate reconstructions made by Boucot et al. (2013) has not been performed.

In this paper, we assume that: 1) the Warm Temperate climate has an advantage for the diffusion of *Metasequoia*, while the Arid climate curbs its migration; 2) in conditions when the global temperature decreased dramatically since Pliocene, *Metasequoia* was forced to migrate southward, and only survives in South China under the warm temperate climate.

MATERIAL AND METHODS

All known occurrences of *Metasequoia* through geological time are plotted in the paleoclimate reconstruction charts of Boucot et al. (2013), from Early Cretaceous, through Late Cretaceous, Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene to Holoene. Most of fossil records documented in this article are referenced to LePage (2005) and Liu et al. (2007). Tectonic plate information is based on Paleomap projection (Scotese 1986, Scotese & Sager 1988, Scotese & Golonka 1992, Boucot et al. 2013).

Paleoclimate information from early Late Cretaceous, Paleocene, Eocene, Oligocene and Miocene, is referenced to Boucot et al. (2013). Pileoclimate information of Pliocene and Pleistocene is given in accordance with the Pliocene (Salzmann et al. 2011) and the Pleistocene climate charts (Ray & Adams 2001), respectively. Both legends in these two charts are changed to legends used in the Paleoclimate Reconstruction from the Cambrian to Miocene (Boucot et al. 2013). Present climate information is referenced to the present climate chart (Fan & Zhou 2011).

RESULTS

Distribution of *Metasequoia* in Late Early Cretaceous (Albian)

Although Tao (1992) reported that *Metasequoia* was recorded from the Albian Lindian Formation of Heilongjiang, China, the detailed information including the description and figures of *Metasequoia* is not shown in that article. We also can not found any information about *Metasequoia* in the Lindian flora (Tao & Sun 1980). Therefore, no reliable evidence of *Metasequoia* originated from the Early Cretaceous has been shown. The earliest known *Metasequoia* record in Northeast China is from the Campanian Taipinglinchang Formation (Sun et al. 2011).

Distribution in Early Late Cretaceous (Cenomanian–Turonian)

Based on reliable evidences, the *Metasequoia* fossils are first recorded in the Cenomanian Arkagala Formation from the Arkagala River and Kolyma Rivers, Russia; the Amkinskaya Formation from the Okhotsk–Chukotka Volcanogenic Belt in the Ul'inskiy Trough near Amka, Russia; unnamed Cenomanian deposits along the Yukon River in Alaska and the Cenomanian Dunvegan Formation from western Canada (LePage 2005). The Beringian Corridor, which was established in Albian, probably gave a way for *Metasequoia* migration. The Beringian Corridor (LePage 2005), as trans-Beringian land connections (Krassilov 2009), is very important for us to understand the diffusion, derivation and differentiation of the taxon (LePage 2005, Krassilov 2009).

Although the early Late Cretaceous (Cenomanian and Turonian) distribution pattern of *Metasequoia* is shown in the paleogeographic reconstruction figure of the Northern Hemisphere suggested by Lepage (2005), the climatic zone is not plotted in this paleogeographic reconstruction. Paleoclimatic information suggested by Boucot et al. (2013) give us an opportunity to evaluate the relationship between the distribution of *Metasequoia* and corresponding climatic factors (Fig. 1). Because all of early *Metasequoia* fossil sites are located in the Warm Temperate zone, it is clearly seen that type of climate is very suitable for *Metasequoia* to live.

Distribution in Late Late Cretaceous (Maastrichtian)

Liu et al. (2007) show the distribution of *Metasequoia* for the Maastrichtian (70 Mya) in details. In order to appraise the relationship between the distribution of *Metasequoia* and corresponding climatic factor in that age, paleoclimatic information (Boucot et al. 2013) also be introduced in the paleogeographic chart (Fig. 2). On the basis of the paleogeographic reconstruction with paleoclimatic information, it can be concluded that *Metasequoia* had diffused to Boreotropical zone by the end of Late Cretaceous.

Distribution in Paleocene

On the basis of the distribution of *Metasequoia* for Paleocene (60 Mya) (Liu et al. 2007) and paleoclimatic information (Boucot et al. 2013), *Metasequoia* had an extensive distribution during the Paleocene (60 Mya) and grew under a wider range of environmental conditions. *Metasequoia* fossils are found in the Warm Temperate, Boreotropical and Arid zones (Fig. 3). Most of *Metasequoia* fossils recorded in Warm Temperate zone and few fossils found in Arid zone and Cool Temperate zone indicate that cool or dry conditions are not suitable for the growth of *Metasequoia* plants.

Distribution in Eocene

The distribution of *Metasequoia* in Eocene (Ypresian) (50 Ma) is generally similar to that of Paleocene, although the global cooling has taken place. Most of *Metasequoia* fossils are recorded in western North America under the control of Warm Temperate climate. The distribution of the genus in this area appears to have experienced considerable range expansion in the more southern area in Rocky Mountain Range and eastern North America, where it was under the control of Boreotropical climate. Some of *Metasequoia* fossils are recorded in eastern Asia under the control of Boreotropical (Subtropical) climate. Few of them are found in the Arid Zone of Eastern Asia (Fig. 4).

The distribution of *Metasequoia* in the Eocene (Bartonian) (40 Ma) is very similar to that Paleocene except many *Metasequoia* fossils that documented in the middle part of Eurasia (Liu et al. 2007).

Distribution in Oligocene

The distribution of *Metasequoia* during the Oligocene is characterized as the following: 1) the *Metasequoia* fossils recorded in Alaska are significantly decreased due to the global cooling taken place continuously; 2) the genus was diffused in the middle of Eurasia under the control of Warm Temperate and Boreotropical climates; 3) *Metasequoia* tried to migrate to the south areas in the middle of Eurasia and North America, but it was stopped by the Arid climate condition in those places. Few fossils found in the Arid zone of East Asia indicate some areas were probably suitable for the growth of *Metasequoia* plants (Liu et al. 2007) (Fig. 5).

Distribution in Miocene

The difference between the distribution of *Metasequoia* during the Miocene and the Oligocene is as follow: 1) the genus has the trend to migrate in East Asia, especially in the areas of Northeast China, southern Russian Far East and Japan; 2) the *Metasequoia* fossils recorded in the middle area of Eurasia are decreased because of the Arid climate developed in that place; 3) few of *Metasequoia* fossils found in the Europe indicate that the genus tried to migrate to western Eurasia under the control of the Warm Temperate climate; 4) the *Metasquoia* plants are dramatically decreased in the North America due to the Cool Temperate climate developed in this region (Liu et al. 2007) (Fig. 6) .

Distribution in Pliocene

The distribution of *Metasequoia* was significantly contracted resulted from the second dramatic global cooling event taken place in the Pliocene. Both *Metasequoia* populations in North America and Europe extincted. The genus can only be found in Japan, some places in China and the middle of Eurasia under the control of Warm Temperate climate (Liu et al. 2007) (Fig. 7).

Distribution in Pleistocene

With the temperature continuously decreased, the distribution was further contracted resulted from Earth entering the Quaternary ice age. The *Metasequoia* plants were extinct in Siberia. The genus can be only found in southwestern Japan, in location with coordinates 32.38°N 130.1E° (Otsuka 1966, Otsuka & Nishiinoue 1980) and in Hunan, South China, in location with coordinates 31.67°N 130°E (Qi et al. 1993) (Fig. 8).

Distribution in Holocene

There is no fossil record documented during the Holocene although several fossil sites are found from this time in southwestern Japan, in locations with coordinates 33.13°N 132.32°E (Mizuno 1980), 35.41°N 139.25°E (Group & Group 1970), 34.4°N 135.3°E (Ithihara 1987), 35.17°N 136°E (Yamasaki et al. 1996) and 35.2°N 136.5°E (Takemura 1984).

Distribution in Present period

Extant *Metasequoia* is only distributed in Shizhu, Chongqing; Lichuan, western Hubei and Longshan, Hunan, where it forms very narrow triangular distribution area (29°.55'N 108°39'E; 30°15'N 108.56'E; 29°22'N 110°19'E) within the elevation range 800–1500 m above sea level. In the region, the Qinling Mountains have been blocked the cold winds from the North in the Quaternary glacial period (Yu 1995, Liu et al. 1996; LePage et al. 2005, Liu et al. 2007) (Fig. 10).

On the basis of the analysis of the distribution of *Metasequoia* referenced on climate conditions from Cretaceous, Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene, Holocene to present period, it can be concluded that:

1. *Metasequoia* as a deciduous conifer tree is a genus of

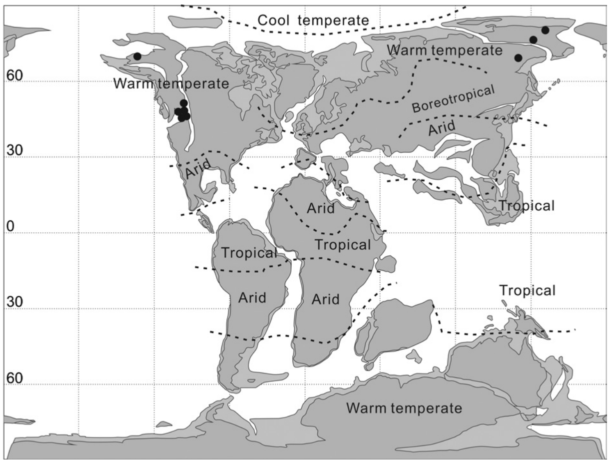

Figure 1 The distribution of *Metasequoia* in late Early Cretaceous (Cenomanian–Turonian) (100–92 Ma). Here and after, in figures 2–10, filled circles indicate the fossil sites, and tectonic plate information is based on Paleomap projection (Scotese 1986, Scotese & Sager 1988, Scotese & Golonka 1992, Boucot et al. 2013). Information concerning the distribution of *Metasequoia*, and paleoclimate is referenced to Lepage et al. (2005) and Boucot et al. (2013), respectively

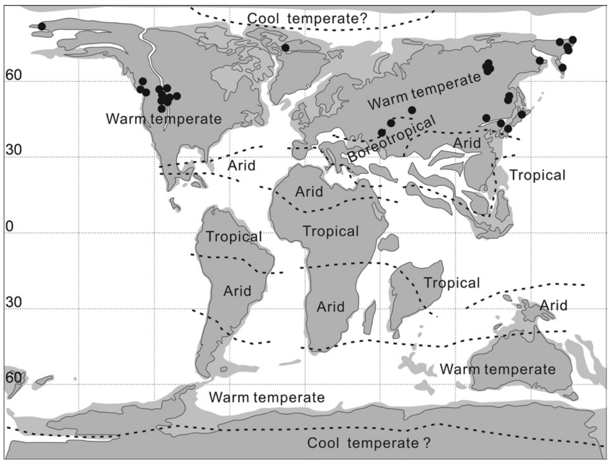

Figure 2 The distribution of *Metasequoia* and paleoclimate in the late Late Cretaceous (Maastrichtian) (70 Ma) according to Liu et al. (2007) and Boucot et al. (2013) respectively

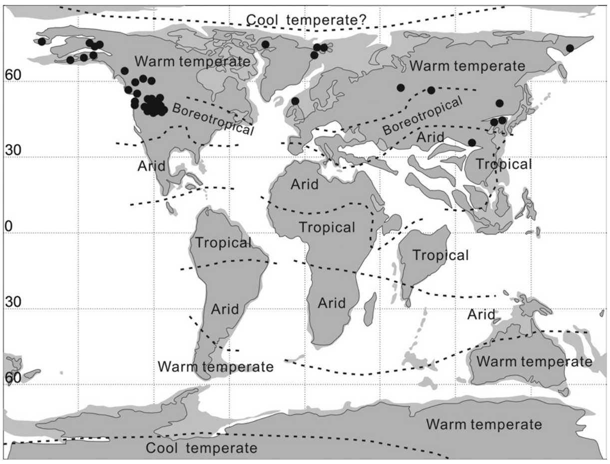

Figure 2 The distribution of *Metasequoia* paleoclimate in the Paleocene (60 Ma) according to Liu et al. (2007) and Boucot et al. (2013), respectively

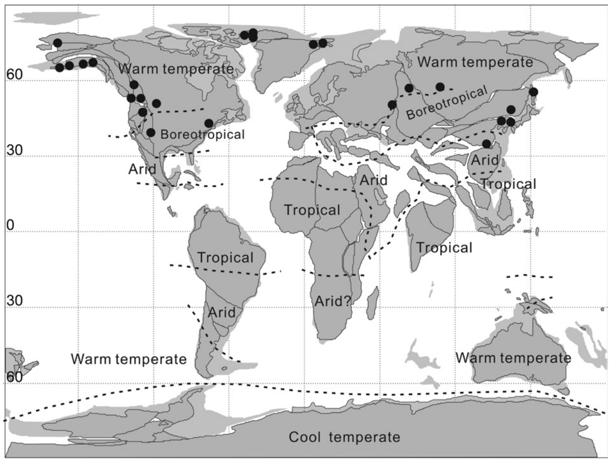

Figure 4 The distribution of *Metasequoia* and paleoclimate in the Eocene (Ypresian) (50 Ma) according to Liu et al. (2007) and Boucot et al. (2013), respectively

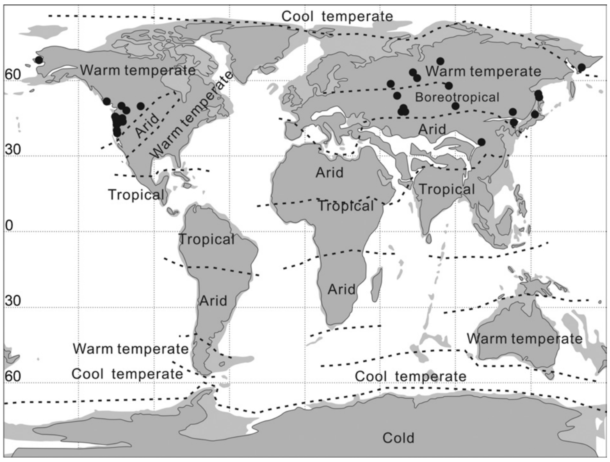

Figure 5 The distribution of *Metasequoia* and paleoclimate in the Oligocene (30 Ma) according to Liu et al. (2007) and Boucot et al. (2013), respectively

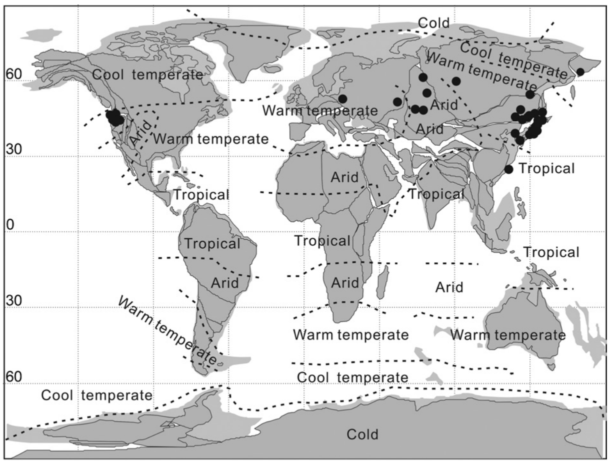

Figure 6 The distribution of *Metasequoia* and paleoclimate in the Miocene (20 Ma) according to Liu et al. (2007) and Boucot et al. (2013), respectively

Warm Temperate climate, characterized as not too hot or too cold temperatures, and not too dry or too wet moisture regimes. Subtropical and Cool Temperate climates can be tolerated by *Metasequoia* and are suitable for growth of the genus representatives. The hot and dry Arid climate makes

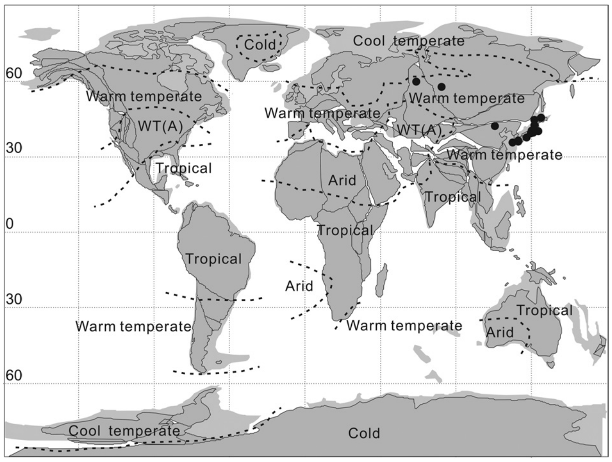

Figure 7 The distribution of *Metasequoia* in the Pliocene (5 Ma) according to Liu et al. (2007). Paleoclimate information is from the National Geophysical Data Center (Salzmann et al. 2011). The relationship between the legends in Pliocene climate chart (Salzmann et al. 2011) and those in Paleoclimate Reconstruction figure from Cambrian to Miocene (Boucot et al. 2013) is shown in Table 1. WT (A) = Warm temperate (but similar to Arid)

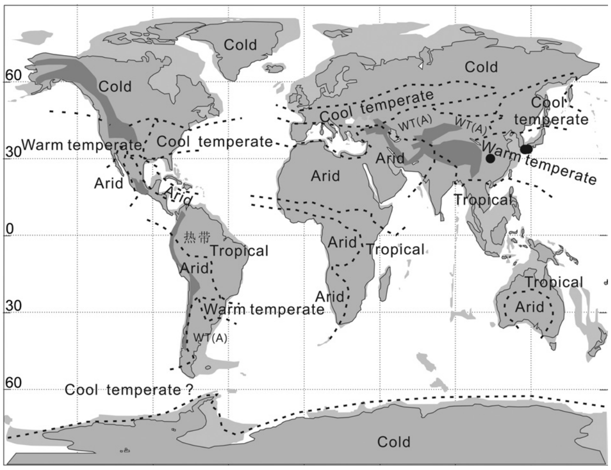

Figure 8 The distribution of *Metasequoia* in the Pleistocene (2 Ma) according to Otsuka (1966), Otsuka & Nishiinoue (1980) and Qi et al. (1993). Paleoclimate information is from the National Geophysical Data Center (Ray & Adams 2001). The relationship between the legends in Pliocene climate chart (Ray & Adams 2001) and those in Paleoclimate Reconstruction figure from Cambrian to Miocene (Boucot et al. 2013) shows in Table 2. WT(A) = Warm temperate (but similar to Arid)

genus survival impossible. Tropical and Cold climates are not suitable for the genus representatives either.

2. *Metasequoia* is probably originated from the high latitude areas of Northeast Asia under the control of Warm Temperate climate. The Warm Temperate climate has an advantage for the distribution of *Metasequoia*, while the Arid climate stops its migration.

3. With the global temperature decreased significantly since Pliocene, *Metasequoia* was forced to migrate southward. There were three routes for the genus to migrate from the north to the south areas in Northern Hemisphere: the first is from North America, the second is from the middle Eurasia and the third is from East Asia. Of these three routes, the first and second were curbed by the Arid climate, and only the third route from the higher latitude areas to lower latitude areas of East Asia was suitable for the genus migration under

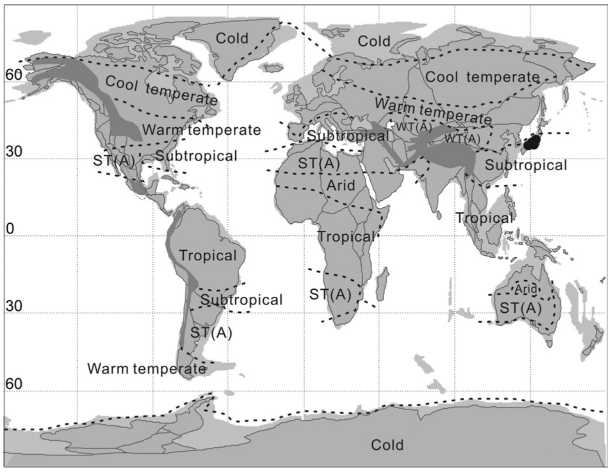

Figure 9 The distribution of *Metasequoia* in the Holocene according to Mizuno (1980), Group & Group (1970), Ithihara (1987), Yamasaki et al. (1996) and Takemura (1984). Paleoclimate information is from the National Geophysical Data Center (Fan & Zhou 2011). The relationship between the legends in Present climate chart (Fan & Zhou 2011) and those in the paleoclimate reconstruction figure from Cambrian to Miocene (Boucot et al 2013) is shown in Table 3. WT(A) = Warm temperate (but similar to Arid), ST(A) = Subtropical (but similar to Arid)

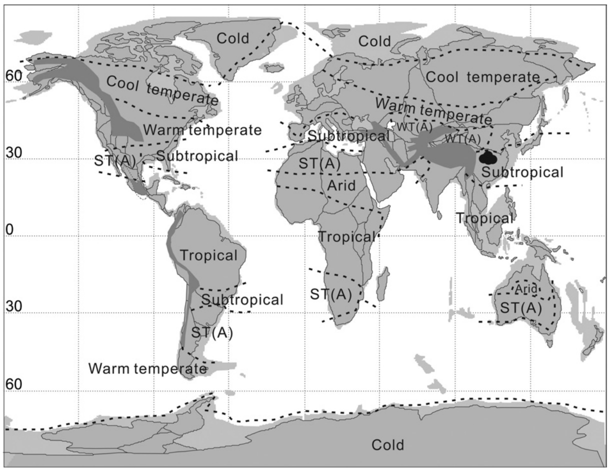

Figure 10 Present natural distribution of *Metasequoia* according to Liu et al. (2007). Climate information is from the National Geophysical Data Center (Maboshi 2011). The relationship between the legends in Present climate chart (Maboshi 2011) and those in the paleoclimate reconstruction figure from Cambrian to Miocene (Boucot et al 2013) is shown in Table 3. WT(A) = Warm temperate (but similar to Arid), ST(A) = Subtropical (but similar to Arid)

control of Warm Temperate or Subtropical climates. This is the reason why *Metasequoia* survived only in South China. The *Metasequoia* can not migrate to the Tropical zone because this conifer tree with deciduous foliage, originated from the Warm Temperate zone has not developed mechanisms to adapt the Tropical climate.

DISCUSSION

There are several ways to classify climates, including genetic methods and empiric methods. The Köppen climatic classification is based on average monthly values of temperature and precipitation. The most commonly used form of this classification has five primary climate types labeled by A through E. These are A – tropical; B – dry; C – mild mid-latitude; D – cold mid-latitude; and E – polar. The five primary climate types can be further divided into classes such as the tropical rainforest, tropical monsoon, tropical savanna, tropical desert, subtropical Mediterranean, subtropical monsoon and humid, subtropical evergreen broad-leaved forest, subtropical grassland and desert, temperate deciduous broadleaved forest, temperate marine, temperate monsoon, temperate grassland, temperate desert, taiga, tundra, and land ice (Peel et al. 2007, Fan & Zhou 2011).

Because the most important factors influencing the distribution of plants are temperature and moisture, the Köppen classification is a very useful tool to understand the global climate zones. Boucot et al. (2013) selected the similar way to classify climates through geological time from Cambrian to Miocene. In paleoclimitic reconstruction (Boucot et al. 2013), the temperatures (warm and cool), and moisture regime (wet and dry) are the basic climatic factors. Tropical zone, Arid zone, Cool Temperate zone and Cold zone are characterized by different combinations of the temperature and moisture conditions, such as warm and wet, warm and dry, cool and wet, and cool and dry climates that determine

Table 1 The relationship between the legends in Pliocene climate chart (Salzmann et al 2011) and those in Paleoclimate Reconstruction from Cambrian to Miocene (Boucot et al 2013)

Legends and their identification numbers in the Pleistocene climate chart	Legends in the paleoclimate reconstruction from Cambrian to Miocene
27. Land ice	Cold
20. Cushion-forb, lichens, moss tundra	Cold (in Antarctica)
18. Dwarf-shrub tundra	Cool temperate (in Antarctica)
19. Prostrate shrub tundra	Cool temperate (in Antarctica)
17. Shrub tundra	Cool temperate
16. Steppe tundra	Cool temperate
15. Evergreen taiga/montane forest	Cool temperate
21. Deciduous taiga/montane forest	Cool temperate
12. Cool mixed forest	Cool temperate
13. Cool conifer forest	Cool temperate
14. Cold mixed forest	Cool temperate (in Central Asia mountains)
11. Temperate conifer forest	Warm temperate
7. Open conifer woodland	Warm temperate
5. Temperate deciduous forest	Warm temperate
6. Temperate broadleaved savanna	Warm temperate
4. Warm-temperate mixed forest	Warm temperate
25. Temperate sclerophyll woodland	Warm temperate
10. Temperate grassland	Warm temperate
8. Boreal parkland	Warm temperate
1. Tropical evergreen forest	Tropical
2. Tropical semi-deciduous forest	Tropical
3. Tropical deciduous forest/woodland	Tropical
22. Tropical savanna	Tropical
9. Tropical grassland	Tropical
23. Tropical xerophytic shrubland	Arid
26. Desert-in lower latitude area	Arid
26. Desert-in higher latitude area	Warm temperate (but similar to Arid)
24. Temperate xerophytic shrubland	Warm temperate (but similar to Arid)

Table 2 The relationship between the legends in Pleistocene climate chart (Ray & Adams 2001) and those in Paleoclimate Reconstruction from Cambrian to Miocene (Boucot et al 2013)

Legends in the Pleistocene climate chart	Legends in the paleoclimate reconstruction from Cambrian to Miocene
Ice sheet or other permanent ice	Cold
Polar and alpine dsert	Cold
Alpine tundra	Cold
Tundra	Cold
Main Taiga	Cool temperate
Steppe tundra	Cool temperate
Broadleaved temperate evergreen forest	Warm temperate
Temperate steppe grassland	Warm temperate
Temperate desert	Warm temperate (but similar to Arid)
Dry steppe	Warm temperate
Forest steppe	Warm temperate
Open boreal woodlands	Warm temperate
Semi-arid temperate woodland or scrub	Warm temperate
Subalpine parkland (in Mexico)	Warm temperate
Temperate semi-desert	Warm temperate
Tropical grassland	Tropical
Tropical rainforest	Tropical
Tropical thorn scrub and scrub woodla	Tropical
Tropical woodland	Tropical
Monsoon or dry forest	Tropical
Montane tropical forest	Tropical
Savanna	Tropical
Tropical semi-desert	Arid
Tropical extreme desert	Arid

Table 3 The relationship between the legends in Present climate chart (Fan & Zhou 2011) and those in the paleoclimate reconstruction from Cambrian to Miocene (Boucot et al 2013).

Legends and their identification numbers in the Present climate chart	Legends in the paleoclimate reconstruction from Cambrian to Miocene
1. Land ice in Cold	Cold
2. Tundra in Cold	Cold
3. Taiga in Subcold	Cool Temperate
4. Temperate deciduous broad-leaved forest	Warm Temperate
5. Temperate marine	Warm temperate
6. Temperate monsoon	Warm temperate
7. Temperate grassland	Warm Temperate
8. Temperate desert	Warm temperate (but similar to Arid)
9. Subtropical Mediterranean	Subtropical
10. Subtropical monsoon and humid	Subtropical
11. Subtropical evergreen broad-leaved forest	Subtropical
12. Subtropical grassland and desert	Subtropical (but similar to Arid)
13. Tropical desert	Arid
14. Tropical savanna	Tropical
15. Tropical monsoon	Tropical
16. Tropical rainforest	Tropical

Table 4 The distribution of Metasequoia in different climate zones from Cenomanian–Turonian to Present period

Age	Ma	Cool Temperate	Warm Temperate	Boreo-tropical	Arid	Tropical
Cenomanian-Turonian	100–92		●			
Maastrichtian	70		●	●		
Paleocene	60		●	●	●	
Eocene	50		●	●	●	
Oligocene	30	●	●	●	●	
Miocene	20	●	●		●	●
Pliocene	5		●			
Pleistocene	2		●			
Holocene	0		●			
Present Period	0		●			

the expansion of each zone.

Warm temperate zone is an intermediate zone. In that climate zone, neither too warm nor too cold, neither too wet nor too dry are taken place. Boreotropical zone is similar to Subtropical zone, indicating the area in Northern Hemisphere with lower temperature and moisture than tropical zone.

In paleoclimatic reconstruction, Pliocene and Pleistocene paleoclimatic charts have not been shown by Boucot et al. (2013). In order to compare the distribution of *Metasequoia* in these two geological periods with the former periods, we select other paleoclimatic charts (Salzmann et al. 2011, Ray & Adams 2001). Although the legends in Pliocene and Pleistocene climate charts (Salzmann et al. 2011, Ray & Adams 2001) are different from those in Paleoclimate reconstruction from Cambrian to Miocene (Boucot et al. 2013), the two former legends can be changed to the later, respectively (Tables 1, 2).

Holocene and Present Period climatic charts are referenced to Fan & Zhou (2011) because its climate classification is also similar to the Köppen classification, and its climate projection can be compared with the Paleomap projection (Boucot et al. 2013). The legends in Holocene and Present Period climate charts are also different from those in Paleoclimate Reconstruction figure (Boucot et al. 2013), the former legends can also be changed to the latter (Table 3).

Origin, diffusion and migration of *Metasequoia*

On the basis of the plaeoclimate information shown in the paleogeographic charts, we can come to tentative conclusions about the origin, diffusion and migration of *Metasequoia*.

Warm Temperate climate, as the most suitable climate condition for *Metasequoia*, influence the origin, diffusion and migration of the genus (Table 4).

Based on the earliest reliable fossil records of *Metasequoia*, the genus was probably originated from the areas of Northeast Asia or Northwest America under the control of Warm Temperate climate (Fig. 1).

After the origin of *Metasequoia*, the genus diffused into the Boreotropical zone from Warm Temperate zone in Maastrichtian (Fig. 2), as well as Boreotropical zone and Arid zone in Paleocene and Eocene from Warm Temperate zone (Fig. 3, 4, Table 4). The diffusion of the genus in Arid zone and Cool Temperate zone very limited indicates that these two climate zones are unsuitable for the growth of *Metasequoia* plants.

Since early Eocene, the Earth experienced a long-term cooling (Fig. 11). The areas of Warm Temperate zones were contracted markedly, while Cool Temperate zones developed in North Hemisphere. In this situation, on the one hand, *Metasequoia* plants greatly reduced in Cool Temperate

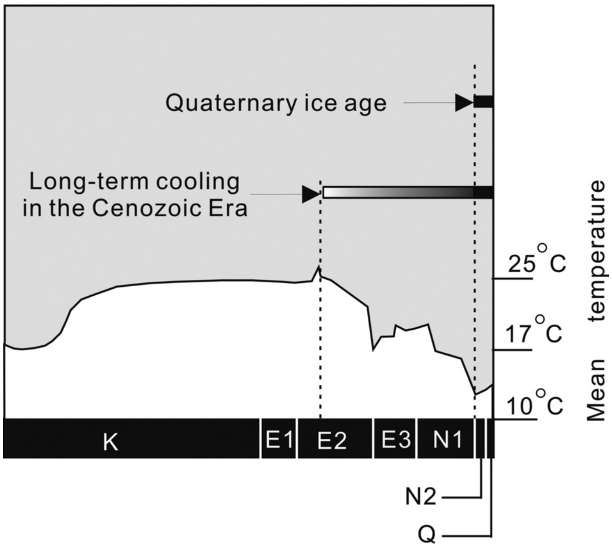

Figure 11 Global temoerature change from Cretaceous to Quaternary (modified from Scotese 2000). K: Cretaceous; E1: Paleocene; E2: Eocene; E3: Oligocene; N1: Miocene; N2: Pliocene; Q: Quaternary, including Pliestocene and Holocene

zone; on the other hand, *Metesequoia* was forced to migrate to the south areas and tried to adapt to all kinds of climate, such as Arid climate, Tropical climate (Fig. 5, 6, Table 4). This migration was stopped in the North America and in the middle of Eurasia by the expansion od the Arid zone. Furthermore, the presence of *Metasequoia* in these two areas is dramatically decreased since the Earth entered the Quaternary ice age in Pliocene. Only in East Asia, this migration appeared to be successful, and a small part of *Metasequoia* population survived from Pliocene to Present Period in China (Figs. 7, 8, 10, Table 4).

Implications of paleoclimate information

Palaeoclimate information provided by Boucot et al. (2013) gives an opportunity to analyze the relationships between the distribution of the taxon and its tolerable climate condition. In this paper, we can conclude that the most suitable climate condition for *Metasequoia* through geological time in the Warm Temperate zone. This work is very similar to that of *Protophyllocladoxylon* (Zhang et al. 2010). We also can tentatively decipher the origin, diffusion and migration of *Metasequoia* and answer the question why *Metasequoia* as a relic plant only survives in a small area of South China on the basis of Palaeclimate information. Furthermore, *Metasequoia* plants with deciduous foliage indicate that they adapt the climate characterized as warm in summer and cold in winter. This is very like *Lepidopteris* fronds with the rachis covered with small subepidermal swellings to adapt the climate of desertification (Zhang et al. 2012).

ACKNOWLEDGEMENTS

The work was supported the the project 111 of China (B06008), National Natural Science Foundation of China (31470324) and Doctoral Fund of Shenyang Normal University. We are very grateful to Prof. Valentin Krassilov, Academician of the Russian Academy of Sciences, Institute of Evolution, University of Haifa, Israel, and his wife Mrs. Sophia to encourage us to study Paleobotany referenced on Paleoclimate information; Many thanks for Prof. Ge Sun, College of Paleontology, Shenyang Normal University, and Prof. Yong-dong Wang, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, for their positive advices on this work. We are deeply indebted to Prof. Xu Chen, Academician of the Chinese Academy of Sciences, and Prof. Suhai. Xiao, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, for their supports in Paleoclimarte and Tectonic plate information. Many thanks go to Dr. Li Wang, researcher of Xishuangbanna Tropical Botanic Garden, Chinese Academy of Sciences, Ms. Yue Hong and Xue-shu Ding, librarians of Library of Shenyang Normal University, for their helps in literatures. We would like to extend our thanks to Dr. Pavel Krestov, Director of Botanical Garden-Institute, Russia, as well as two anonymous referees for their helpful comments and supports.

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Yi Zhang:

I am saddened to learn of the passing of our respectable Prof. Valentin Krassilov. Prof. Krassilov was among the greatest paleobotanists in the world – brave enough to think differently and carefully, diligent enough to make great progress, and kind enough to help young researchers, including me and other Chinese researchers, to enter the mysterious world of paleobotany.

The world has lost a visionary in paleobotany, who led us to explore the ancient world tirelessly and successfully. We also have lost an excellent research envoy from Israel and Russia to China. And there may be no greater tribute to Prof. Krassilov than the fact that more and more young Chinese paleobotanists work closely with Israelian and Russian researchers, make great progress in paleobotany and take peace and happiness to the world.