

Origin, evolution and extinction of Cathaysia flora

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Abstract Recent research results showed that the Cathaysia flora originated and developed from the global uniform *Lepidodendropsis* flora of the Early Carboniferous, which had already become an independent flora in the early Late Carboniferous (Namurian B to C). The center of origin of the Cathaysia flora is restricted to the North China Plate. On the basis of the successional characteristics of the Cathaysia flora in different geological ages, it may be divided into seven evolutionary stages. The evolutionary trend of the Cathaysia flora, as a whole, was characterized by the gradual increase of the typical Cathaysian elements in the sequence from the early Late Carboniferous to the early Late Permian, which began to decline during the late Late Permian. The climatic differentiation, tectonic movement, oceanic circulation, palaeogeographical environment, extraterrestrial event and plant evolution caused the mass extinction of the Cathaysia flora on a large scale by the end of the Permian.

Keywords: Asia, Cathaysia flora, origin, evolution, extinction, Late Carboniferous, Permian.

THE Cathaysia flora is one of the four famous floras of the Late Carboniferous and Permian in the world. The term Cathaysia flora was first proposed by Halle^[1], which originated from Cathaysia. In fact, Cathaysia is the name used on Grabau's palaeogeographical maps for the Palaeozoic landmass in East Asia. Halle gave the term Cathaysia flora for the entire Carboniferous and Permian plant succession in

East Asia. The Cathaysia flora is characterized by *Cathaysiodendron*, *Lobatannularia*, *Tingia*, *Tingiostachya*, *Conchophyllum*, *Yuania*, *Rajahia*, *Fascipteris*, *Emplectopteris*, *Emplectopteridium*, *Cathaysiopteris*, *Gigantonoclea*, *Gigantopteris*, *Otofolium* and a considerable number of endemic species, including *Lepidodendron oculus-felis*, *Plagiozamites oblongifolius*, *Pecopteris taiyuanensis*, *Alethopteris norinii*, *Callipteridium koraiense*, *Taeniopteris mucronata*, *Pterophyllum daihoense*, etc. The Cathaysia flora is mainly distributed in present-day China, Korea, Japan, Laos, Thailand, Indonesia and Malaysia. In addition, some Cathaysian elements are reported in Iraq and Saudi Arabia. The mixed Cathaysia and Gondwana flora is known in South Tibet, Kashmir, Turkey and New Guinea. The mixed Cathaysia and Angara flora is recorded in Yichun of Heilongjiang and Sunan of Gansu, China. The distribution of the Cathaysia flora and its mixed floras of the Late Carboniferous and Permian is shown in fig. 1. China is one of the most important localities of the Cathaysia flora and it is also the center of origin of the Cathaysia flora. Some important advances of studies on the Cathaysia flora have been made for more than a century^[2-12], but so far its origin, evolution and extinction are still an outstanding issue. Therefore, the research on the significant subject is one of the major issues that palaeobotanists are paying close attention to.

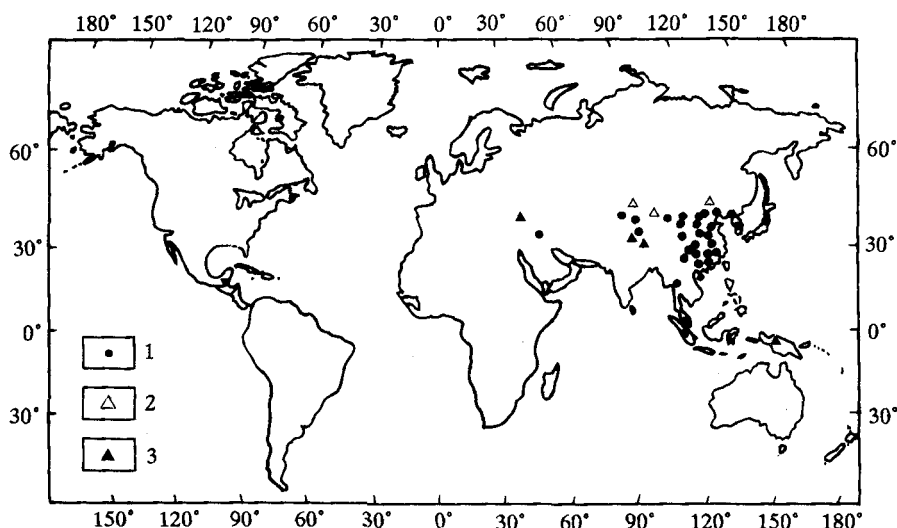


Fig. 1. Distribution of the Cathaysia flora and its mixed floras of the Late Carboniferous and Permian. 1, Cathaysia flora; 2, Mixed Cathaysia-Angara flora; 3, mixed Cathaysia-Gondwana flora.

1 Origin of the Cathaysia flora

Chinese and foreign palaeobotanists have put forward some different viewpoints on the origin of the Cathaysia flora. The controversial issue is the origin time and formative mechanism of the Cathaysia flora.

Lee^[13] suggested that the Cathaysia flora originated in Taiyuanian time (Stephanian), and this flora, known as the Early Cathaysia flora, was represented by the flora of the Taiyuan Series in North China. Li and Yao^[14] indicated that the Cathaysia flora was developed entirely out of Middle Carboniferous Euramerican flora of East Asia on the formative mechanism of the flora. At the same time, they considered that this flora reached its development climax during the early Late Permian and got largely extinct by the beginning of the Triassic.

Chaloner and Meyen^[15] pointed out that the Cathaysian area could already be recognized as a distinct floral province in Westphalian time. Their viewpoint is based on the records of the Cathaysian elements, such as *Tingia*, *Conchophyllum*, *Kaipingia* and *Lepidodendron oculus-felis* from China in Westphalian time.

Sun¹⁾ proposed that the Cathaysia flora derived and developed from the global uniform *Lepidodendropsis* flora, which had already become an initial distinct flora with *Lepidodendron* and *Bothrodendron* of the oriental type. The opinion is based on some characteristic elements of the oriental Lepidophytes and a considerable number of endemic elements of ferns and pteridosperms characterized by *Lopinopteris intercalate* Sze, etc. from the Narmurian strata of China. Sun¹⁾ [16] dealt with the formative mechanism of the Cathaysia flora and further pointed out that the flora did not originate from the Euramerica flora, while it derived from the *Lepidodendropsis* flora. The *Lepidodendropsis* flora is a cosmopolitan flora with a worldwide extent, which could not be confused with the Euramerica flora. Sun¹⁾ [16] considered that the *Lepidodendropsis* flora mainly flourished in the Tournasian and Visean of the Early Carboniferous, and it began to decline and was on the verge of extinction in the Late Visean and Namurian A of the Early Carboniferous. When the *Lepidodendropsis* flora tended towards the extinction, some forerunners and endemic elements began to appear. By the Late Namurian (Namurian C), it had already become an independent flora, namely, the Early Cathaysia flora. In addition, Sun²⁾, Mi and Sun^[17] and Sun^[18] dealt with the origin and formative mechanism of the Cathaysia flora and further emphasized that it could be recognized as an independent flora in the early Late Carboniferous (Namurian B to C). The Cathaysia flora ranged from the beginning of the early Late Carboniferous to the end of the Permian in age.

The term Procathaysian flora was first proposed by Li *et al.* [19] for the Early Carboniferous plant succession in China. The Cathaysia flora might have originated from the Procathaysian flora which perhaps existed mainly in China in the Early Carboniferous^[19,20]. During the Early Carboniferous, the global climatic differentiations were not obvious and all plants belonged to the same phytogeographical province; therefore, a uniform flora was widely distributed all over the world, namely, the *Lepidodendropsis* flora^[21]. In the late Early Carboniferous, the climatic differentiation and floral evolution led to the appearance of some forerunners of the Cathaysia, Euramerica, Angara and Gondwana floras^[18,22]. Chandra and Sun^[23] dealt with the distribution, evolution and extinction of global Early Carboniferous flora and they considered that in the Early Carboniferous, although the Cathaysia, Euramerica, Angara and Gondwana areas contained their respective endemic elements due to minor ecological variations of different vast areas. These areas retained the character of the original *Lepidodendropsis* flora. Vijaya *et al.* [24] considered that the *Lepidodendropsis* flora had provided the parent source for four floras of the Late Carboniferous and Late Permian: the Cathaysia, Euramerica, Angara and Gondwana floras. Li and Wu^[25] also considered that the *Lepidodendropsis* flora had a wide distribution on the various continents in both the Northern and the Southern Hemispheres during the Tournasian. At the same time, they proposed that the Visean floras of the Early Carboniferous dominated by *Cardiopteridium spetsbergense*, *Archaeocalamites scrobiculatus* and *Triphyllopteris collombiana* in South China and Northwest China were identical to contemporaneous floras in western Europe. As is known to all, *Cardiopteridium spetsbergense*, *Archaeocalamites scrobiculatus* and *Triphyllopteris collombiana* are typical elements of the *Lepidodendropsis* flora with a cosmopolitan distribution. Seeing that the Early Carboniferous of China contains numerous characteristic genera *Lepidodendropsis*, *Sublepidodendron*, *Archaeocalamites*, *Cardiopteridium*, *Rhodopteridium*, *Triphyllopteris*, *Adiantites*, etc.; therefore, the author regards the Early Carboniferous flora of China as an important component part of the global Early Carboniferous *Lepidodendropsis* flora, that is to say, "the Procathaysian flora" is obviously the synonym of the *Lepidodendropsis* flora. Therefore, the Procathaysian flora ought to be rejected. Although a few forerunners and a number of endemic elements of the Cathaysia flora occurred in China during the Early Carboniferous, the flora was mainly composed of the elements of the *Lepidodendropsis* flora and its character was not changed at this time. In view of the occurrence of some Cathaysian elements in the Penchi Formation, Wu^[26] considered that the Cathaysia flora originated in Penchian time (Westphalian). Obviously, Wu was unanimous in support of Chaloner and Meyen's viewpoint^[15] which the origin of the Cathaysia was in Westphalian time. From Li's paper

1) Sun Keqin, Late Carboniferous-Early Permian flora from Zibo area of Shandong and its palaeoecological study, *Doctoral Dissertation* (in Chinese with English abstract), Changchun College of Geology, 1990, 1-191.

2) Sun Keqin, Origin of the Cathaysia flora, *Abstracts of International Conference of Diversification and Evolution of Terrestrial Plants in Geological Time* (ICTPG), Nanjing, 1995, 18, 19.

tables^[27,20], he held a positive opinion that the origin of the Cathaysia flora was in the early Late Carboniferous (Namurian B to C). Tian and Wang^[28] studied fossil plants in coal balls of China and they considered that the Cathaysia flora gradually emerged after the Namurian C. Hu^[29] put forward that the Cathaysia flora did not originate from the Euramerica flora, whereas it derived from the Late Devonian flora with local colour in Northwest China, and the North Qilian Corridor was the path of the flora. In view of these opinions, although the origin time of the Cathaysia flora remains unsolved, the viewpoint that it originates from the Euramerica flora has fully been negated. However, with the continuous development of this research, the opinions that the Cathaysia flora originate in the early Late Carboniferous (Namurian B to C), and this flora, known as an independent flora at this time, are gradually being accepted by most palaeobotanists.

In recent years, we have got new knowledge on the origin of the Cathaysia flora with research advances of late Early Carboniferous (Late Visean to Namurian A) and early Late Carboniferous (Namurian B to C) floras. On the basis of the research results of recent years, a few forerunners and a number of endemic elements of the Cathaysia flora have been found in the late Early Carboniferous strata in North China Plate (see table 1).

Table 1 Occurrence of the Early Cathaysian and endemic elements of North China in the late Early Carboniferous

Species	Age	Locality	Reference
<i>Lepidodendron</i> cf. <i>aolungpylukense</i> Sze	Late Visean to Namurian A	Southeast Henan	[30]
<i>L. dabieshanense</i> Wu	Late Visean to Namurian A	Gushi, Henan	[31]
<i>L. ninghsiaense</i> Sze et Lee	Late Visean to Namurian A	Benxi, Liaoning and Wuda, Inner Mongolia	[32] [33]
<i>L. shanyangense</i> Wu et He	Late Visean to Namurian A	Southeast Henan	[30]
<i>L. subrhombicum</i> Gu et Zhi	Namurian A	Wuda, Inner Mongolia	[33]
<i>L. cf. subrhombicum</i> Gu et Zhi	Late Visean to Namurian A	Southeast Henan	[30]
<i>Cathaysiodendron</i> ? sp.	Late Visean to Namurian A	Gushi, Henan	[31]
<i>Bothrodendron flabellatum</i> Wu	Late Visean to Namurian A	Gushi, Henan	[31]
<i>Tingia trilobata</i> Stockmans et Mathieu	Namurian A	Zhongning, Ningxia	[33]
<i>Conchophyllum richthofenii</i> Schenk	Late Visean to Namurian A	Benxi, Liaoning	[32]
<i>Paripteris otozamioides</i> (Sze et Lee)	Namurian A	Zhongning, Ningxia	[33]
<i>Linopteris simplex</i> Gu et Zhi	Namurian A	Zhongning, Ningxia	[33]

In addition, Wu and Zhao^[34] studied *Lepidodendron* cf. *aolungpylukense* Sze, *Paripteris cardiopteroides* (Bohlin) and *Linopteris densissima* Gu et Zhi from the Namurian strata in Zhongning of Ningxia and *Lepidodendron ninghsiaense* Sze et Lee, *L. cf. subrhombicum* Gu et Zhi, *Cathaysiodendron* ? sp. and *Paripteris otozamioides* (Sze et Lee) from the Namurian strata in Hulusitai of Inner Mongolia. These elements ought to be regarded as the forerunners and endemic elements of the Cathaysia flora. On the basis of the characteristics of distribution of these elements, the author considers that the center of the origin of the Cathaysia flora is located in the North China Plate. This conclusion may fully be proved by the characteristics of distribution of the forerunners and endemic elements of the Cathaysia flora from the northwestern, eastern and southern areas of the North China Plate. In recent years, seeing that some early Cathaysian elements have been found in Zhongning and Zhongwei of Ningxia, Jingtai and Jingyuan of Gansu, Wuda and Hulusitai of Inner Mongolia, Gushi and Shangcheng of Henan, and Benxi of Liaoning, these areas can be regarded as the original range of the Cathaysia flora. From the beginning

of the early Late Carboniferous, the evolution, diffusion and migration of the forerunners and endemic elements of the Cathaysia flora, plate collision and sea level change led to the extension of the geographical distribution range of the flora so as to form the the Cathaysian floral province as the main body of East Asia. During the transition from the Early Carboniferous to the Late Carboniferous, the climatic differentiation, tectonic movement and oceanic circulation might have caused the extinction of the *Lepidodendropsis* flora and the appearance of the Cathaysia flora. The Cathaysia flora originated and developed from the global uniform *Lepidodendropsis* flora of the Early Carboniferous, which had already become an independent flora in the early Late Carboniferous (Namurian B to C).

2 Evolution of the Cathaysia flora

Lee^[13] made a systematic study on the Late Carboniferous (Stephanian) and Late Permian flora of the Yuenmenkou Series in North China and he divided the flora into the Early Cathaysia flora, Middle Cathaysia flora and Late Cathaysia flora in ascending order. In addition, Li^[35] proposed that it was not until the Late Carboniferous that the real Cathaysia flora gradually came into being and it did not flourish in East Asia until the Permian. At the same time, he considered that this flora reached its development climax during the early Late Permian and became largely extinct by the beginning of the Triassic. However, the opinion that the evolutionary range of the Cathaysia flora is from the early Late Carboniferous (Namurian B to C) to the end of the Permian is gradually being approved^[17, 18, 20, 27]. The Cathaysian floral province has been divided into two subprovinces: the subprovince of North China and the subprovince of South China^[36]. Recently, Mei *et al.*^[37] proposed the Xu-Huai-Yu subprovince of the Cathaysian floral province. Obviously, this subprovince is a character with the transition between the subprovince of North China and the subprovince of South China.

On the basis of the successional characteristics of the Cathaysia flora of different geological ages, it may be divided into seven evolutionary stages. These evolutionary stages are represented by seven plant assemblages. They are the *Lepidodendron aolungpylukense-Bothrodendron circulare* assemblage of the early Late Carboniferous (Namurian B—C), *Lepidodendron galeatum-Conchophyllum parvifolium* assemblage of the middle Late Carboniferous (Westphalian), *Lepidodendron szeianum-Cathaysiodendron nanpiaoense* assemblage of the late Late Carboniferous (Stephanian), *Lobatannularia sinensis-Taeniopteris mucronata* assemblage of the early Early Permian (Asselian and Sakmarian), *Emplectopteris triangularis-Cathaysiopteris whitei* assemblage of the late Early Permian (Artinskian and Kungurian), *Gigantonoclea hallei-Gigantopteris nicotianaefolia* assemblage of the early Late Permian (Kazanian) and *Yuania magnifolia-Annularia pingloensis* assemblage of the late Late Permian (Tatarian). The principle by the author dividing the plant assemblages of different evolutionary stages is based on the overall characteristics of the Cathaysia flora, which uses the typical Cathaysian species as the representative elements of various plant assemblages^[22].

The Cathaysia flora of the Late Carboniferous is mainly distributed in North China, which is characterized by the Cathaysian genera, such as *Cathysiodendron*, *Conchophyllum*, *Tingia*, *Reticaletopteris*, *Lopinopteris* and a considerable number of the Cathaysian and endemic species, including *Lepidodendron aolungpylukense*, *L. oculus-felis*, *L. posthumii*, *L. szeianum*, *Bothrodendron circulare*, *Sphenophyllum kawasaki*, *Paripteris kaipingiana*, *Alethopteris ascendens*, *Callipteridium tachingshanense*, etc. The Cathaysia flora of the Late Carboniferous also contains a number of elements in common with the Euramerica flora, such as *Calamites cistii* Brongniart, *Annularia pseudostellata* Potonié, *Pecopteris candolleana* Brongniart, *Paripteris gigantea* (Sternberg) Gothan, *Neuropteris ovata* Hoffmann, *Linopteris brongniartii* Gutbier, *Cordaites principalis* (Germar) Geinitz, etc. The Cathaysian and Euramerican areas were located in the equatorial region with the low-latitude in the tropical climatic zone during the Carboniferous and Permian. Therefore, some genera and species existed in the two areas and reflected their parallel evolution.

The Cathaysia flora of the Permian is mainly distributed in China, Korea, Japan, Laos, Thailand, Indonesia and Malaysia, which is characterized by the Cathaysian genera such as *Lobatannularia*, *Yuania*, *Rajahia*, *Fascipteris*, *Emplectopteris*, *Emplectopteridium*, *Cathaysiopteris*, *Gigantonoclea*, *Gigantopteris*, *Otofolium* and numerous endemic species, including *Lepidodendron asymmetricum*, *Annularia pingloensis*, *Plagiozamites oblongifolius*, *Pecopteris taiyuanensis*, *Alethopteris norinii*, *Cal-*

lipteridium koraiense, *Taeniopteris mucronata*, etc.

The above-mentioned plant assemblages represent the evolutionary stages of the Cathaysia flora of different geological ages. The characteristic species of this flora is, *Conchophyllum richthofenii* Schenk, which first appeared in the late Early Carboniferous (Namurian A), flourished in middle Late Carboniferous (Westphalian) and disappeared in the late Late Carboniferous (Stephanian). *Lopinopteris intercalata* Sze is regarded as a typical species of this flora, which is known to be from the late Early Carboniferous to the middle Late Carboniferous. The characteristic element of this flora is, *Reticaletopteris yuani* (Sze), which is known only in the early Late Carboniferous (Namurian B to C). *Tingia* is regarded as an important genus of the Cathaysia flora and its range is known to be from the late Early Carboniferous to the Late Permian. The forerunner of the genus is *Tingia trilobata* Stockmans et Mathieu, which is known to appear first in the late Early Carboniferous (Namurian A). Some typical species of *Tingia* include *Tingia carbonica* (Schenk) Halle, *T. crassinervis* Halle, *T. hamaguchii* Kon' no and *T. partita* Halle, flourished in the Permian and became extinct by the end of the Permian. The species of the Cathaysian type under the genus *Bothrodendron* such as *Bothrodendron circulare* Sze and *B. reticulatum* Sze chiefly flourished in the early Late Carboniferous and disappeared in the middle Late Carboniferous, but *Bothrodendron kuianum* Lee appeared in the late Late Carboniferous. In the Cathaysian floral province, the evolutionary range of the genus *Bothrodendron* was limited only in the Carboniferous. The genus *Lepidodendron* of the floral province first derived in the Early Carboniferous, which became extinct by the end of the Permian. *Lepidodendron aolungpylukense*, in general, was the characteristic species with a widespread distribution in the early Late Carboniferous. *Lepidodendron galeatum* Gu et Zhi, *L. ninghsiaense* Sze et Lee and *L. subrhombicum* Gu et Zhi chiefly flourished in the middle Late Carboniferous and disappeared in the late Late Carboniferous. *Lepidodendron szeianum* Lee mainly flourished in the late Late Carboniferous, which occasionally appeared in the early Early Permian. The range of *Lepidodendron posthumii* Jongmans et Gothan was from the late Late Carboniferous to the early Early Permian. *Lepidodendron oculus-felis* (Abbado) Zeiller ranged from the middle Late Carboniferous to the early Late Permian in age. *Lepidodendron asymmetricum* Gu et Zhi and *L. polygonale* Gu et Zhi reached their zenith in the early Late Permian. The characteristic genus of the Cathaysia flora is *Cathaysiodendron*, which is known to be from the late Late Carboniferous to the early Early Permian. As the typical species of the genus, *Cathaysiodendron nanpiaoense* Lee, was mainly distributed in the late Late Carboniferous. In the Permian, the Cathaysia flora was characterized by the occurrence of numerous typical genera, such as *Lobatannularia*, *Rajahia*, *Yuania*, *Fascipteris*, *Emplectopteris*, *Emplectopteridium*, *Cathaysiopteris*, *Gigantonoclea*, *Gigantopteris*, *Otofolium*, etc. The genus *Gigantopteris* is the most characteristic plant in the Cathaysia flora, which is known to be distributed mainly in South China in the Late Permian.

The Cathaysia flora is mainly composed of lycopods, sphenopsids, ferns, pteridosperms and cordaitan gymnosperms, which indicates the tropical climatic condition^[38-40]. It is noteworthy that a few cycads, ginkgoes and conifers are known to appear in the Permian. As noted by Wang^[41], the appearance and development of the Mesophytic elements related to the Palaeozoic upland, especially the expansion of the land area and the variation of the climatic condition. The evolution of the Cathaysia flora not only depended on the adaptive faculty of morphofunction of the plants to their ecological environments, but was also controlled by palaeoclimatic conditions, palaeogeographical barriers and tectonic movements. The evolutionary trend of the Cathaysia flora, as a whole, was characterized by the gradual increase of the typical Cathaysian plants in the sequence from the early Late Carboniferous to the early Late Permian, which began to decline during the late Late Permian and became extinct by the end of the Permian.

3 Extinction of the Cathaysia flora

The biotic extinction event is one of the principal problems in the field of palaeontology. How do we explain the mass extinction of the Cathaysia flora on a large scale by the end of the Permian? Obviously, this will pose a new question for palaeobotanists. The subject of the extinction on the Cathaysia flora was approached by Li^[27,35], Wang^[41] and Li^[42] from different aspects. Wang^[41] studied the palaeobotanical events of the Permian in North China and discussed the variations and extinctions of plant taxa during the transition from the Palaeozoic to the Mesozoic. Li^[42] proposed that the mass extinction event of terrestrial plants of the end of the Palaeozoic was not created by a global geological event, whereas it was caused by

various local geological events. Obviously, he emphasized that local geological events were the major factors to lead to the floral extinction. However, the problems of the extinction on the Cathaysia flora cannot hitherto be solved. The biotic extinction is a biological event in the course of biotic evolution. From the early Late Carboniferous to the end of the Permian, the Cathaysia flora underwent two extinction events: the extinction event (background extinction) of the end of the Carboniferous and the extinction event (mass extinction) of the end of the Permian. The latter represents the mass extinction of the Cathaysia flora on a large scale.

In the Cathaysian floral province, a few characteristic genera of the Cathaysia flora of the Late Carboniferous are represented by *Conchophyllum*, *Cathaysiodendron*, *Tingia*, *Lopinopteris* and *Reticallethopteris*, however, the Cathaysia flora contains a good deal in common with those of the Euramerica flora, such as *Lepidodendron*, *Lepidophloios*, *Bothrodendron*, *Sphenophyllum*, *Paripteris*, *Linopteris*, *Sphenopteris*, *Alethopteris*, *Pecopteris*, etc. Therefore, the differences between the two floras reflect the changes at the species level. By the end of the Late Carboniferous, a few Cathaysian genera had already become extinct, such as *Conchophyllum*, *Lopinopteris* and *Reticallethopteris*, but numerous characteristic and endemic species of this flora greatly disappeared, including *Lepidodendron aolungpylukense* Sze, *L. galeatum* Gu et Zhi, *L. ninghsiaense* Sze et Zhi, *L. subrhombicum* Gu et Zhi, *L. tripunctatum* Stockmans et Mathieu, *Lepidophloios orientalis* Gu et Zhi, *Bothrodendron circulare* Sze, *B. reticulatum* Sze, *B. kuianum* Lee, *Palaeostachya rhabda* Gu et Zhi, *Sphenopteris marchalii* Stockmans et Mathieu, *S. parabaemleri* Sze, *Paripteris kaipingiana* (Sze), *P. otozamoides* (Sze et Lee), *Linopteris densissima* Gu et Zhi, *L. simplex* Gu et Zhi, *Dicranophyllum latum* Schenk, etc. In addition, a number of genera in common with the Cathaysia flora and the Euramerica flora had already disappeared by the end of the Carboniferous, including *Lepidophloios*, *Bothrodendron*, *Paripteris* and *Linopteris*. Numerous Cathaysian elements appeared and flourished in the Permian, such as *Lepidodendron varium* Gu et Zhi, *Sphenophyllum rotundatum* Halle, *Annularia orientalis* Kawasaki, *Lobatanularia sinensis* (Halle) Halle, *Yuania striata* Sze, *Pecopteris taiyuanensis* Halle, *Fascipteris stena* Gu et Zhi, *Emplectopteris triangularis* Halle, *Emplectopteridium alatum* Kawasaki, *Gigantonoclea guizhouensis* Gu et Zhi, *Gigantopteris nicotianaefolia* Schenk, *Taeniopteris mucronata* Kawasaki, *Caulopteris sinensis* Lee, *Pterophyllum daihoense* Kawasaki, *Otofolium ovatum* Gu et Zhi, etc. It is noteworthy that numerous Cathaysian elements had already begun to disappear during the transition between the early Late Permian (Kazanian) and the late Late Permian (Tatarian), which reached a climax by the end of the Permian. Every species has its geographical distribution range, however, the distribution of plants is controlled by the climatic and environmental factors. From the early Late Carboniferous to the late Early Permian, the warm and humid climate prevailed in the North China Plate and plants flourished. From the beginning of the early Late Permian, the climate of the North China Plate gradually became much drier and reached the maximum during the late Late Permian. The South China Plate was at the stage of marine regression and the land area markedly expanded. Therefore, the flora represented by the gigantopterides was extraordinarily flourishing, which indicated a tropical climatic condition. During the late Late Permian, an extensive part of the South China Plate was submerged by the seawater, the land area markedly contracted and the existence environment of plants was destroyed. The climatic differentiation, tectonic movement, oceanic circulation, palaeogeographical environment, extraterrestrial event and plant evolution caused the mass extinction of the Cathaysia flora on a large scale by the end of the Permian.

4 Conclusions and prospects

During the transition from the Early Carboniferous to the Late Carboniferous, the *Lepidodendropsis* flora became extinct, whereas the Cathaysia flora began to develop. The Cathaysia flora gradually derived and developed from the cosmopolitan *Lepidodendropsis* flora of the Early Carboniferous. Although some advances on the origin of the Cathaysia flora have already been made in recent years, its formative mechanism remains to be solved, especially the relationship with the *Lepidodendropsis* flora. In view of occurrences of the early Cathaysian elements in the North China Plate, the plate may be regarded as the center of the origin of the Cathaysia flora, then, the Helan Mountain area in the northwest part of the plate ought to be regarded as the floral point of origin. Because the Namurian strata are well developed in this area, numerous Cathaysian and endemic elements have already been found here. Therefore, the Helan

Mountain area is an ideal area where palaeobotanists will study the origin of the Cathaysia flora in future.

From the early Carboniferous to the early Late Permian, the overall evolutionary trend of the flora shows that the characteristic elements of the Cathaysia type gradually increased, they began to decline in the late Late Permian and disappeared as a result of mass extinction by the end of the Permian. Seeing that the studies of plant morphology have already possessed a considerable foundation, the reproductive biology of fossil plants is one of main research areas at present. This research will provide some important clues and proofs for the systematic evolution of plants. The relationships among the Cathaysia flora with the Euramerica, Angara and Gondwana floras are also worth further studying. In addition, the research on plant palaeoecology is a key link of the relationship between plants and environments to understand because the ecological environment is a foundation on which plants depend for existence.

In the evolutionary course of the Cathaysia flora, there were two extinction events: the extinction event (background extinction) of the end of the Carboniferous and the extinction event (mass extinction) of the end of the Permian. The floral extinction event of the end of the Permian and the global biotic extinction event happened at the same time. It is obvious that they have relation to some comprehensive factors of the terrestrial event, extraterrestrial event and plant evolution.

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