Evolution and Ecology of the Cathaysia flora

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The Cathaysia flora, one of four famous floras of Late Carboniferous and Permian periods in the world, is mainly distributed in Asia, such as China, Korea, Japan, Laos, Thailand, Indonesia, Malaysia, etc. China is one of the most important country for the Cathaysia flora, which derived from the identical Lepidodendropsis flora of the Early Carboniferous on a global scale. From the beginning of the Namurian A, the Cathaysia flora gradually separated from the global Lepidodendropsis flora and it could be recognized as an independent flora in the early Late Carboniferous (Namurian B to C). According to the succession of the Cathaysia flora of different geological ages, the flora may be divided into seven fossil-plant assemblages from early Late Carboniferous to late Late Permian so as to reflect the characteristics of floral evolutionary stages. From the early Late Carboniferous to the early Late Permian, the typical elements of the Cathaysia flora gradually increased. The Cathaysia flora ranged from the beginning of the early Late Carboniferous to the end of the Permian in age. The most obvious changes of dry climate and tectonic movement caused the extinction of the Cathaysia flora by the end of the Late Permian. The Cathaysian floral province, located in the equatorial region under tropical climatic condition during the Carboniferous and Permian, was characterized by lycopods, ferns, pteridosperms, sphenopsids and cordaitean gymnosperms. The vertical structure of floral communities included arbores, tree ferns, shrubs and herbs.

Kay- Words — Cathaysia flora, Carboniferous, Permian, Evolution, Palaeoecology.

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साराँश

कैथेसिया वनस्पतिजात का विकास एवं पर्यावरणिकी

सन केकिन एवं शैला चन्द्रा

कैथेसिया वनस्पतिजात अन्तिम कार्बोनीफेरस एवं पर्मियन युग के चार महत्वपूर्ण वनस्पतिजातों में से एक है, जो मुख्यतः एशियाई देशों – विशेषकर चीन, कोरिया, जापान, लाओस, थाईलैण्ड, इण्डोनेशिया, मलेशिया आदि में पाया जाता है। चीन कैथेसिया वनस्पतिजात के लिए सर्वाधिक महत्वपूर्ण देशों में एक है, जहाँ यह आरम्भिक कार्बोनीफेरस युग में सार्वभौमिक स्तर पर पाए जाने वाले इसी के समरूप 'लेपिडोडेन्ड्रॉप्सिस' वनस्पतिजात से व्युत्पन्न हुआ है। नेमूरियन ए युग के आरम्भ में यह वनस्पतिजात एक अन्य विश्वव्यापी वनस्पतिजात 'लेपिडोडेन्ड्राप्सिस' से पृथक हो गया और आरंभिक उत्तर कार्बोनीफेरस युग (नेमूरियन बी से सी तक) में एक पृथक् वनस्पतिजात के रूप में इसने अपनी स्वतंत्र सत्ता स्थापित कर ली। कैथेसिया वनस्पतिजात प्रारंभिक उत्तर कार्बोनीफेरस युग केआरम्भ से पर्मियन युग के अन्त तक प्राप्त होते हैं। विभिन्न भूगर्भीय युगों के कैथेसिया वनस्पतिजातों का अध्ययन करने पर इन्हें उत्तर अन्तिम कार्बोनीफेरस युग से प्रारंभिक उत्तर पर्मियन युग के मध्य सात पादपाश्म समुच्चयों में विभक्त किया गया, ताकि इस वनस्पतिजात के विकास के विभिन्न अभिलक्षणों को यथोचित ढंग से प्रदर्शित किया जा सके। आरंभिक उत्तर कार्बोनीफेरस से आरंभिक उत्तर पर्मियन युग तक कैथेसिया वनस्पतिजातों के विशिष्ट तत्वों की क्रमिक अभिवृद्धि प्रदर्शित होती है। अन्तिम पर्मियन युग के समाप्त होने पर जलवायु में शुष्कता आ जाने तथा प्लेटों में विवर्तनिक परिवर्तन होने जैसे विशिष्ट परिवर्तनों के कारण ये वनस्पतिजात विलुप्त हो गए। कार्बोनीफेरस एवं पर्मियन युगों के दौरान भूमध्य क्षेत्र के उष्णकटिबन्धीय जलवायु में कैथेसिया वनस्पतिजातों के लक्षणों का लाइकोपोड, पर्णांग (फर्न), टेरिडोस्पर्म, स्फीनॉप्सिड्स तथा कार्डेटियन अनावृतबीजियों द्वारा अभिलक्षणित किया गया है। वनस्पतिजात समुदाय की ऊर्ध्व संरचना के अन्तर्गत वृक्षीय, वृक्ष पर्णांग (फर्न), गुल्म एवं शाक सम्मिलित हैं।

THE term Cathaysia flora was proposed by Halle (1935) and it was the name used on Grabau's palaeogeographical maps for the Palaeozoic land-mass in East Asia. Halle gave the term Cathaysia flora for the entire Carboniferous and Permian plant successions in East Asia. Previously, the Cathaysia flora could also be considered as the Gigantopteris flora. According to Halle, the Cathaysia flora is not synonymous with the Gigantopteris flora, because the latter corresponds to only the last phase of the Palaeozoic flora of Cathaysia.

The Cathaysia flora is one of the most famous floras of the Carboniferous and the Permian in the world, which is mainly distributed in present-day China, Korea, Japan, Laos, Thailand, Indonesia and Malaysia. It is characterized by the genera *Cathaysiodendron*, *Lobatannularia*, *Tingia*, *Yuania*, *Conchophyllum*, *Rajahia*, *Fascipteris*, *Emplectopteris*, *Emplectopteridium*, *Cathaysiopteris*, *Gigantopteris*, *Gigantonoclea*, *Otofolium* and a considerable number of endemic species, namely, *Lepidodendron oculusfelis*, *L. posthumii*, *L. szeianum*, *Sphenophyllum sinocoreanum*, *Annularia orientalis*, *Pecopteris taiyuanensis*, *Alethopteris norinii*, *Callipteridium koraiense*, *Psaronium sinensis*, *Taeniopteris mucronata*, *Pterophyllum daihoense*, *Psygmophyllum multipartitum*, etc. China is the most important locality for the Cathaysia flora in Asia. The Cathaysian floral province can be divided into the northern and southern floral sub provinces in China (Li Xingxue & Yao Zhaoqi, 1985). The northern floral subprovince is located in northern China. The Carboniferous and Permian strata are well developed in northern China, which are characterized by marine-terrestrial transitional facies and terrestrial facies including a number of major coalfields, such as those of Hebei, Shanxi, Inner Mongolia, Shandong, Liaoning, Ningxia, Gansu, etc. The southern floral subprovince occupies a vast area in southern China. The Upper Carboniferous sequences in southern China are almost completely marine and no evidences of reliable fossil plants are recorded. The Permian sequences of the subprovince are characterized by marine and non-marine alternating coal-bearing deposits, which are mainly distributed in Hunan, Fujian, Jiangxi, Guangdong, Jiangsu, Yunnan, Guizhou, Hunan, Sichuan, etc. The northern subpovince and southern subporvince were located in the equatorial region under a tropical climate during the Carboniferous and Permian. Therefore, their similarity is reflected by a number of identical Cathaysian genera, such as *Cathaysiodendron*, *Lobatannularia*, *Tingia*, *Yuania*, *Fascipteris*, *Cathaysiopteris*, *Gigantonoclea*, *Gigantopteris*, etc. and numerous common endemic species, viz, *Lepidodendron oculusfelis* (Abbado) Zeiller, *Sphenophyllum sino-coreanum* Yabe, *Annularia mucronata* Schenk, *Plagiozamites oblongifolius* Halle, *Pecopteris lativenosa* Halle, *Cladophlebis nystroemii* Halle, *Alethopteris norinii* Halle, *Protoblechnum wongii* Halle, *Odontopteris subcrenulata* Halle, *Cladophlebis nystroemii* Halle and *Taeniopteris nystroemii* Halle etc. The Upper Permian of the South China also contains a number of endemic form-genera, including *Rajahia* and *Otofolium* (Cleal & Thomas, 1991). The southern floral subprovince is distinguished by such special genera as *Rajahia*, *Otofolium* and some fructiferous organ genera, including *Pectinangium*, *Gigantonomia*, *Gigantotheca* and *Distchotheca*, none of which have ever been found in the northern floral subprovince. Meanwhile, some peculiar organ genera are commonly known in North China such as *Nystroemia*, *Asterocupulites* and some unique plants, including *Pseudorhipidosis*, *Procycas*, *Primocycas*, etc. which are hitherto not seen in the southern floral subprovince (Li Xingxue *et al.*, 1995). However, it is noteworthy that *Otofolium* and *Rajahia* have been recorded in the northern subprovince (Shen Guanglong, 1995). It is worth emphasizing that some typical Cathaysian genera, such as *Gigantopteris*, *Otofolium* and *Rajahia* are of very rare occurrences in the northern floral subprovince, while *Emplectopteris* and *Yuania* are restricted to rare appearances in the southern floral subprovince. So far, *Emplectopteridium* has never been recorded in the southern floral subprovince. Minor differences between the northern floral subprovince and southern floral subprovince reflect variations of floristic composition and terrestrial ecosystem in time and space. In addition, some mixed floras between the Cathaysia province and Gondwana province are also distributed in Hazro of Anatolia in Turkey, New Guinea, Kashmir and South Tibet. Thus, although the nature of the Cathaysia flora is quite different from that of the Gondwana flora, the boundary between them seems to be more closely related. The distribution of the mixed floras was controlled by climatic conditions, plate tectonics and continental positions.

EVOLUTION OF THE CATHAYSIA FLORA

Seeing that the flora of the early Late Carboniferous (Namurian B and C) of the Cathaysia area was characterized by a variety of oriental lycopods and many endemic elements of ferns and pteridosperms, Sun Keqin (1993a, 1995 1996), Mi Jiarong and Sun Keqin (1995) put forward that the Cathaysia flora derived from the Lepidodendropsis flora of Early Carboniferous in the world and pointed out that the Cathaysia flora had become 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 (Sun Keqin, 1996).

It is known that the Lepidodendropsis flora of the Early Carboniferous is widely distributed all over the world and has similarities on a global scale. Jongmans (1952, 1954) considered that all Early Carboniferous plant assemblages belonged to the same phytogeographic province on the basis of the worldwide distribution of the genera *Lepidodendropsis, Rhacopteris, Triphyllopteris,* etc. Therefore, the term Lepidodendropsis flora was proposed by Jongmans (1952, 1954), which dealt with a cosmopolitan flora of world-wide extent of Early Carboniferous. However, it is noteworthy that the stages of the origin and extinction of the Lepidodendropsis flora varied in four major areas with their different environments and ecological variations. In the Early Carboniferous although the Cathaysia, Euramerica, Angara and Gondwana areas contained some of their endemic elements due to minor ecological variations of different vast areas, they retained the character of the original Lepidodendropsis flora (Chandra and Sun Kequin, 1996). Climatic differentiation was not obvious during the Early Carboniferous. This is a basic condition on which the Lepidodendropsis flora depends for existence. The Lepidodendropsis flora provided the parent sources for the Cathaysia, Euramerica, Angara and Gondwana floras of Late Carboniferous and Permian. Owing to the climatic changes, some obvious changes in floral components of the Cathaysia, Euramerica, Angara and Gondwana areas occurred during the transition from the Early Carboniferous to the Late Carboniferous, which resulted in extinctions of some typical plant genera, such as *Lepidodendropsis, Sublepidodendron, Archaeocalamites, Triphyllopteris, Cardiopteridium, Rhacopteris, Fryopsis, Rhodeopteridium, Adiantites,* etc. of the Early Carboniferous. In addition, these extinctions also included numerous species of lycopods, ferns and pteridosperms of this age. Moreover, a number of forerunners of the Cathaysia flora had already existed in the Cathaysia area during the late Early Carboniferous (Late Visean-Namurian A), ,such as *Lepidodendron* aff. *aolungpylukense* Sze, L. *dabieshanense* Wu, L. *quadratum* Zhao et Wu, L. *ninghsiaense* Lee, L. *shanyangese* Wu et He, L. *subrhombicum* Gu et Zhi, *L.* cf. *subrhombicum* Gu et Zhi, *Cathysiodendron*? sp., *Bothrodendron flabellatum* Wu, *Tingia trilobata* Stockmans et Msthieu, *Conchophyllum richtofenii* Schenk, etc. (Zhao Xiuhu and WU Xiuyuan, 1982: Mi Jiarong *et al.*, 1990 ; Wu Xiuyuan, 1992; Chen Fen *et al.*, 1995; Chen Fen and Sun Keqin, 1996).

In the early Late Carboniferous (Namurian B and C), the Cathaysia flora became an independent flora, belonging to the Early Cathaysai flora. The flora is mainly composed of lycopods, ferns, pteridosperms, sphenopsids and cordaitean gymnosperms, which is called the *Lepidodendron aolunghylukense-Bothrodendron circulare* Assemblage. The Cathaysia flora is characterized by the gradual increase in sequence from the early Late Carboniferous to the early Late Permian. The Cathaysia flora ranged from the beginning of the early Late Carboniferous to the end of the Permian.

According to the succession of the Cathaysia flora of different geological ages, the Cathaysia flora may be divided into seven fossil plant assemblages from early Late Carboniferous to late late Permian so as to reflect the characteristics of floral evolutionary stages. The main Cathaysian species of various evolutionary stages are as follows.

The plant assemblage of early Late Carboniferous

The plant assemblage of early Late Carboniferous (Namurian B-C) is characterized by *Lepidodendron aolungpylukense-Bothrodendron circulare* assemblage, including *Lepidodendron aolungpylukense* Sze, *L.* cf. *aolungpylukense* Sze, *L. ninghsiaense* Sze et Lee, *Cathaysiodndron* ? sp., *Bothrodendron Circulare* Sze, *B. reticulatum* Sze, *Sphenopteris* cf. *parabaeumlei* Sze, *Paripteris cardiopteroides* (Bohlin), *P. kaipingiana* (Sze), P. *otozamioides* (Sze et Lee), *Linopteris densissima* Gu et Zhi, *Alethopteris shidafenensis* Huang, *Palaeoweichselia yuanii* Sze etc.

The plant assemblage of middle Late Carboniferous

The plant assemblage of middle Late Carboniferous (Westphalian) is characterized by *Lepidodendron galeatum-Conchophyllum richthofenii* assemblage, which contains *Lepidodendron galeatum* Gu et Zhi, *L. ninghsiaense* Sze et Lee, *L. subrhombicum*

Gu et Zhi, *L. tripunctatum* Stockmans et Mathieu, *Lepidophloios orientalis* Gu et Zhi, *Tingia carbonica* (Schenk) Halle, *T.* cf. *carbonica* (Schenk) Halle, *T.* ? *trilobata* Stockmans et Mathieu, *Conchophyllum richthofenii* Schenk, *C. parvifolium* Bohlin, *Sphenopteris marchalii* Stockmans et Mathieu, *Paripteris kaipingiana* (Sze), *P. otozamioides* (Sze et Lee), *Linopteris simplex* Gu et Zhi, *Dicranophyllum latum* Schenk, *Palaeoweichselia yuanii* Sze, etc.

The plant assemblage of late Late Carboniferous

The plant assemblage of late Late Carboniferous (Stephanian) is characterized by *Lepidodendron szeianum-Cathysiodendron nanpiaoense* assemblage, which includes *Lepidodeneron oculus-felis* (Abbado) Zeiller, *L. posthumii* Jongmans et Gothan, *L. szeianum* Lee, *Cathysidodendron* incertum (Sze et Lee) Lee, *C. nanpiaoense* Lee, *Bothrodendron kuianum* Lee, *Sphenophyllum kawasakii* Stockmans et Mathieu, *Palaeostachya rhobda* Gu et Zhi, *Tingia Carbonica* (Schenk) Halle, *T. hamaguchii* Kon'no, *T. trilobata* Stockmans et Mathieu, *Sphenopteris tenuis* Schenk, *Pecopteris linsiana* Stockmans et Mathieu, *Alethopteris asscendens* Halle, *A. hallei* (Jongmans et Gothan) Stockmans et Mathieu, *A. huiana* Lee, *Callipteridium tachingshanese* (Sze) Gu et Zhi, *C. koraiense* (Tok.) Kawasaki, *Caulopteris sinensis* Lee, *Cordaites schenkii* Halle, *Cardiocarpus karipingensis* Stockmans et Mathieu, *Tongshania dentata* Stockmans et Mathieu, etc.

The Cathaysia flora of Late Carboniferous is known in northern China and which contains some typical Cathaysian genera such as *Cathaysidendron, Conchopyllum, Tingia* and a considerable number of endemic species, namely, *Lepidodendron aolungpylukense, L. galeatum, L. ninghsiaense, L. oculus-felis, L. posthumii, L. szeianum, Bothrodendron circulare, Paripteris kaipingiana, Callipteridium tachingshanese, Caulopteris sinensis*, etc. The Cathaysia flora of Late Carboniferous also contains a number of genera and species in common with the Euramerica flora, such as *Sphenophyllum emarginatum, Calamites suckowii, Annularia pseudostellata, Pecopteris affinis, Paripteris gigantea, Neuropteris ovata, Linopteris brongniartii*, etc. The Cathaysian and Euramerican areas were located in the equatorial region under a tropical climatic condition. Therefore, some plants between the two areas had certain similarities and reflected parallel evolution.

The plant assemblage of early Early Permian

The plant assemblage of early Early Permian (Asselian and Sakmarian) is characterized by *Lobatannulatia sinensis-Taeniopteris mucronata* assemblage, including *Lepidodendron acutangulun* (Halle) Stockmans et Mathieu, *L. carinum* Lee, *L. oculus-felis* (Abbdo) Zeiller, *L. tachingshanense* Lee, *L. varium* Gu et Zhi, *Cathaysiodendron incertum* (Sze et Lee) Lee, *Annularia gracilescens* Halle, *A. orientalis* Kawasaki, *A. papilioformis* Kawasaki, *Lobatannularia sinensis* (Halle) Halle, *L. ensifolia* (Halle) Halle, *Plagiozamites tungweiensis* Sze et Lee, *P. oblongifolius* Halle, *Tingia carbonica* (Schenk) Halle, *T. hamaguchii* Kon'no, *T.? oblonga* Sze, *T. partita* Halle, *T. trilobata* Stockmans et Mathieu, *Sphenopteris (Oligocarpia) gothanii* Halle, *S. rotunda* Sze, *S. tenuis* Halle, *Pecopteris (Ptychocarpus)* arcuata Halle, *P: Liuiana* lee, *P. (Asterotheca ?) huichensis* Hsü, *P. (Asterotheca) orientalis* (Schenk) Potonic, *P. sahnii* Hsü, *P. wongii* Halle, *P. yunnanensis* Hsü, *Acitheca salviniaefolia* Stockmans et Mathieu, *Cladophlebis nystroemii* Halle, *Alethopteris ascendens* Halle, *A. norinii* Halle, *Odontopteris chui* Lee, *Mariopteris hallei* Stockmans et Mathieu, *Emplectopteris alatum* Kawasaki *E. triangularis* Halle, *Callipteridium koraiense* (Tokunaga) Kawasaki, *Taeniopteris nystroemii* Halle, *T. mucronata* Kawasaki, *T. serrulata* Halle, *T. yernauxii* Stockmans et Mathieu, *Caulopteris sinensis* Lee, *Pterophyllum daihoense* Kawasaki, *Cordaites schenkii* Halle, *Tobleria minor* Hsü, *Gigantosptermum wangii* Halle, *Carpolithus bullatus* Halle, etc.

The plant assemblage of late Early Permian

The plant assemblage of late Early Permian (Artinskian and Kungurian) is characterized by *Emplectopteris triangularis-Cathaysiopteris whitei* assemblage, which contains *Lepidodendron acutangulum* (Halle) Stockmans et Mathieu, *L. cervicisum* Sze, *L. oculus-felis* (Abbdo) Zeiller, *L. tripunctatum* Stockmans et Mathieu, *Sphenophyllum laterale* Sze, *S. kawasakii* Stockmans et Mathieu, *S.*

rotundatum Halle, *S. scopulatum* Sze, *S. spathulatum* Sze, *Bowmanites laxus* Halle, *Annularia gracilescens* Halle, *A. mucronota* Schenk, *A. orientalis* Kawasaki, *A. papilioformits* Kawasaki, *Lobatannularia sinensis* (Halle) Halle, *L. ensifolia* (Halle) Halle, *L. Lingulata* (Halle) Halle. *Macrostachya huttoniaeformis* Halle, *Plagiozamites oblongifolius* Halle, *Tingia carbonica* (Schenk) Halle, *T. crassinervis* Halle, *T. hamguchii* Kon'no T.? *oblonga* Sze, *T. partita* Halle, *Discinites orientalis* Gu et Zhi, *Sphenopteris firmata* Sze, *S.* (*Oligocarpia*) *gothanii* Halle, *S. grabaui* Halle, *S. nystroemii* Halle, S. *rotunda* Gu et Zhi, *S. tenuis* Halle, *Chansitheca kidstonii* Halle, *Pecopteris anderssonii* Halle, *P.* (*Ptychocarpus*) *arcuata* Halle. *P. hirta* Halle, *P.* (*Asterotheca*) *orientalis* (Schenk) Potonié, *P. taiyuanensis* Halle, *P. tenuicostata* Halle, *P. tuberculata* Halle, *P. wongii* Halle, *Acitheca salviniaefolia* Stockmans et Mathieu, *Cladophlebis nystroemii* Halle, *Alethopteris ascendens* Halle, *A. norinii* Halle, *Odontopteris chui* Lee, *Mariopteris dentata* Sze, *M. hallei* Stockmans et Mathieu, *Emplectopteris triangularis* Halle, *Emplectopteridium alatum* Kawasaki, *Callipteridum koraiense* (Tokunaga) Kawasaki, *Callipteris changii* Sze, *Cathaysiopteris whitei* (Halle) Koidzumi, *Gigantonoclea kaipingensis* Gu et Zhi, G. *lagrelii* (Halle) Koidzumi, G. *mira* Gu et Zhi, *Taeniopteris densissima* Halle, *T. latecostata* Halle, *T. Serrulata* Halle, *T. shansiensis* Halle, *T. tingii* Halle, *Psaronius sinensis* Sze, *P. hexagonus* Gu et Zhi, *Nilssonia huadeiensis* Gu et Zhi, *Pterophyllum cutelliforme* Sze, *Cordaites schenkii* Halle, *Cordaitanthus curtus* Sze, *Cornucarpus patulus* Halle, *Carpolithus taxiformis* Stockmans et Mathieu, *Astrocupulites acuminatus* Halle, *Chiropteris reniformis* Kawasaki, etc.

The plant assemblage of early Late Permian

The plant assemblage of early Late Permian (Kazanian) is characterized by *Gigantonoclea hallei-Gigantopteris nicotianaefolia* assemblage. They are *Lepidodendron acutangulum* (Halle) Stockmans et Mathieu, *L. asymmentricum* Gu et Zhi, *L. polygonale* Gu et Zhi, *L. oculus-felis* (Abbdo) Zeiller, *Sphenophyllum sinocoreanum* Yabe, *Annularia hunanensis* Gu et Zhi, *A. mucronata* Schenk, *A. pingloensis* (Sze), *A. shirakii* Kawasaki, *Lobatannularia ensifolia* (Halle) Halle, *L. multifolia* Kon'no, *Plagiozamites oblongifolius*. Halle, *Tingia carbonica* (Schenk) Halle, *T. crassinervis* Halle, *Yuania striata* Sze, *Discinites orientalis* Gu et Zhi, *Sphenopteris norinii* Halle, *S. nystroemii* Halle, *S. tingii* Halle, *S. tenuis* Halle, *Pecopteris anderssonii* Halle, *P. (Ptychocarpus) arcuata* Halle, *P. chihliensis* Stockmans et Mathieu, *P. echinata* Gu et Zhi, *P. gracilenta* Gu et Zhi, *P. lativenosa* Halle, *P.* (*Asterotheca*) *norinii* Halle, *P.* (*Asterotheca*) *orientalis* (Schenk) Potonié, *P. sahnii* Hsü, *P. sinoboutonnetii* Stockmans et Mathieu, *P. tenuisostata* Halle, *Ptychocarpus tingii* Halle, *Danaeities mirabilis* Gu et Zhi, *D. rigida* (Yabe et Oishi), *Rajahia guizhouensis* Zhang, *Fascipteris* (*Ptychocarpus*) *densata* Gu et zhi, *F. hallei* (Kawasaki), *F. sinensis* (Stockmans et Mathieu), *F. stena* Gu et Zhi, *Cladophlebis permica* Lee et Wang, *C. ozakii* Yabe et Oishi, *Neuropteridium coreanicum* Koiwai, *Protoblechnum contractum* (Gu et Zhi). *P. imparis* (Gu et Zhi), *Odontopteris orbicularis* Halle, *Cathaysiopteris whitei* (Halle) Koidzumi, *Gigantonoclea acuminatiloba* (Shimakura), *G. guizhouensis* Gu et Zhi, G. *hallei* (Asama), *G. lobata* Gu et Zhi, G. *mira* Gu et Zhi, *G. taiyuanensis* (Asama), *Gigantopteris dictyophylloides* Gu et Zhi, *G. nicotianaefolia* Schenk, *Taeniopteris angustifolia* Stockmans et Mathieu, *T. densissima* Halle, *T. hunanensis* Gu et Zhi, *T. integra* Stockmans et Mathieu, *T. norinii* Halle, *T. latecostata* Halle, *T. Serrata* Halle, *T. szei* Chow, *Pterophyllum eratum* Gu et Zhi, *Saportaea nervosa* Halle, *Psygmophyllum multipartitum* Halle, *Walchia bipinnata* Gu et Zhi, *Cornucarpus tenuicuspis* Halle, *Samaropsis sinensis* Halle, *Dadoxylon teilhardii* Sze, *Chiropteris reniformis* Kawasaki, *Otofolium ovatum* Gu et Zhi, *O. polymorphum* Gu et Zhi, *Pelourdea hallei* Sze, *P. reflexa* Halle, *Norinia crucullata* Halle, *Pectinangium lanceolatum* Gu et Zhi, *Distichotheca crossothecoides* Gu et Zhi, *Strigillotheca fasciculata* Gu et Zhi, *Nystroemia pectiniformis* Halle, etc.

The plant assemblage of late Late Permian

The plant assemblage of late Late Permian (Tatarian) is characterized by *Yuania magnifolia-Annularia pingloensis* assemblage, which contains *Annularia pingloensis* (Sze), *Yuania magnifolia* Wang et Wang, *Discinites sunjiagouensis* Wang et Wang, *Fascipteris stena* Gu et Zhi, *Neuropteridium* *coreanicum* Koiwai, *Protoblechum contracta* (Gu et Zhi), *Callipteris lobulata* Wang et Wang, *Gigantonoclea guizhouensis* Gu et Zhi, *Gigantopteris dictyophylloides* Gu et Zhi, *Taeniopteris longifolia* Wang et Wang, *T. nystroemii* Halle, *T. taiyuanensis* Halle, etc.

The Cathaysia flora of Permian is known from China, Korea, Japan, Laos, Thiland, Indonesia, Malaysia, etc., which contains many typical Cathaysian Genera such as *Cathaysiodendron, Lobatannularia, Tingia, Yuania, Fascipteris, Rajahia, Emplectopteris, Emplectopteridium, Cathaysiopteris, Gigantopteris Gigantonoclea, Otofolium*, and a considerable number of endemic species, namely, *Lepidodendron cervicisum, Sphenophyllum kawasakii, Annularia orientalis, Plagiozamites oblongifolius, Pecopteris wongii, Alethopteris norinii, Mariopteris hallei, Taeniopteris mucronata, Caulopteris sinensis, Pterophyllum daihoense*, etc. From early Late Carboniferous to early Late Permian, the typical elements of the Cathaysia flora gradually increased which reflected a unique nature. Therefore, the Cathaysia flora is different from the Euramerica, Angara and Gondwana floras. As a whole, the differentiations of obvious climatic conditions, tectonic movements and oceanic currents caused the extinction of *Lepidodendropsis* flora during the transition from the Early Carboniferous to the Late Carboniferous. The Cathaysia flora derived from the same *Lepidodendropsis* flora and it reached its flourish in the late Late Carboniferous to the early Late Permian. The most obvious changes of dry climate and tectonic movement resulted in the extinction of the Cathaysia flora by the end of the Late Permian.

ECOLOGY OF THE CATHAYSIA FLORA

In China, the study of plant palaeoecology on the Carboniferous and Permian has been put into effect by Yao Zhaoqi (1983), Wang Zigiang *et al.* (1986), Li Xingxue et al. (1991), Sun Keqin (1992a, 1992b, 1992c, 1993b) and Sun Kegin *et al.* (1996).

The fossil record of plants provides an important evidence to examine evolutionary and ecological patterns of terrestrial ecosystem so as to reconstruct vegetational life forms in geological time. Sedimentry rocks, such as mudstones which contain fossil plants may be studied by means of the scanning electron microscope technique, X-ray diffraction analysis and chemical analysis so that the relationship between fossil plants and enclossing rocks can be revealed (Sun Keqin. 199b, 1993b). The quantitative spectrum analysis is applied to various horizons of the Late Carboniferous and Permian strata so as to judge the relationship between fossil plants and enclosing rocks and determine their sedimentary environments (see Tables 1-3). Result of X-ray diffraction analysis of clay minerals in some mudstones shows that kaolinite is widely distributed in terrestrial environments with the highest content, which indicates warm and humid conditions, while montmorillonite is mainly distributed in front delta, lagoon and tidal flat and

Table 1—Content and ratio of trace elements in argillaceous rocks from the Taiyuan Formation (after Sun Keqin, 1992b)

Horizon	Content (10^{-6})						Ratio			Palaeosalinity
	B	Sr	Ba	Ga	V	Zr	B/Ga	Sr/Ba	V/Zr	
C_2^3(Bed24)*	128	105	521	28.5	160	215	4.49	0.20	0.74	saline water to semi-saline water
C_2^3(Bed16)*	52.3	109	571	15.0	97.2	104	3.49	0.19	0.93	fresh water to semi-saline water
C_2^3(Bed4)*	25.1	100	485	32.0	114	252	0.78	0.21	0.45	fresh water
C_2^3(Bed8)*	43.0	106	531	26.4	110	-	1.63	0.20	-	fresh water
C_2^3(Bed4)*	19.8	96.2	363	40.2	127	-	0.49	0.27	-	fresh water
C_2^3(Bed2)*	140	87.8	388	25.5	143	-	5.49	0.23	-	saline water semi-saline water

* Sampling locality : Fengbayu in Zibo, Shandong, ** Sampling locality : Dongwanshan in Zibo, Shandong

Table 2—Content and ratio of trace elements in argillaceous rocks from the Shansi and Lower Shihhotse Formations (after Sun Keqin, 1992b)

Horizon	Content (10^{-6})						Ratio			Palaeosalinity
	B	Sr	Ba	Ga	V	Zr	B/Ga	Sr/Ba	V/Zr	
P_1^2 (Bed 28)	17.4	94.1	632	26.0	97.2	153	0.67	0.15	0.64	fresh water
P_1^1 (Bed 19)	41.2	118	682	33.5	111	-	1.23	0.17	-	fresh water
P_1^1 (Bed 12)	23.2	92.6	402	13.0	49.6	71.0	1.78	0.23	0.70	fresh water
P_1^1 (Bed 10)	55.7	124	488	27.0	103	137	2.06	0.25	0.75	fresh water to semi-saline water
P_1^1 (Bed 4)	54.0	111	426	51.0	130	-	1.06	0.26	-	fresh water to semi-saline water

Sampling locality : Dongheishan in Zibo, Shandong

Table 3—Content and ratio of trace elements in argillaceous rocks from the Shansi and Lower Shihhotse Formations (after Sun Keqin, 1992b)

Horizon	Content (10^{-6})						Ratio			Palaeosalinity
	B	Sr	Ba	Ga	V	Zr	B/Ga	Sr/Ba	V/Zr	
P_1^2 (Bed 21)	35.1	125	415	32.2	106	205	1.09	0.30	0.52	fresh water
P_1^2 (Bed 20)	15.0	106	663	35.5	118	-	0.42	0.16	-	fresh water
P_1^2 (Bed 18)	22.6	118	561	25.5	94.2	218	0.89	0.21	0.43	fresh water
P_1^1 (Bed 14)	19.4	103	730	32.8	105	275	0.59	0.14	0.38	fresh water
P_1^1 (Bed 8)	14.3	91.4	686	24.5	105	-	0.58	0.13	-	fresh water
P_1^1 (Bed 4)	55.0	105	605	35.5	115	267	1.55	0.17	0.43	fresh water to semi-saline water

Sampling locality : Dongheishan in Zibo, Shandong

reflects a high ratio in coastal enviroments (see Table 4). Analytical results show that distribution and preservation of fossils plants in strata have relation to the characters of the enclosing rocks. The palaeoecological reconstructions of plant communities include the studies on the composition, structure, succession, distribution, diversity and life form of various plants. The reconstruction of the early Early Permian vegetation in North China is shown by figure 1. The diversity of plant communities can be calculated with the aid of a computer (Sun Kequin, 1992c). The changes between plant evolutionary and ecological patterns are apparently governed by the climatic conditions, which can be reconstructed accordingly to plant fossils, animal fossils, rock types, clay minerals and coal seams (Sun Keqin, 1992b). The analysis of sedimentary environments and facies is necessary because it facilitates the floral palaeoecological reconstructions (Sun Keqin, 1992b).

The Cathaysia flora is mainly composed of lycopods, sphenopsids, ferns, pteridosperms and corditean gymnosperms. Arborescent lycopods were the major composition of coal-swamp forests of the Cathaysia area during the Late Carboniferous and Early Permian. Numerous species of *Lepidodendron* occurred in various swamp environments, which

Table 4 : **Results of X-ray diffraction analysis of clay minerals in some mudstones (after Sun Keqin, 1992)**

Horizon	Relative Content (%)				Sedimentary Environment
	kaolinite	illite	montmorillonite	chlorite	
P_1^2 (Bed21)***	73	24	3	-	flood plain swamp
P_1^1 (Bed14)***	55	43	2	-	delta plain swamp
P_2^3 (Bed24)**	27	54	4	15	front delta
P_2^3 (Bed8)*	24	62	2	12	tidal flat (mudflat)

* Sampling locality : Dongwanshan in Zibo, Shandong; ** Sampling locality : Fengbayu in Zibo, Shandong; *** Sampling locality : Dongdingshan in Zibo, Shandong

C_2^3 Taiyuan Formation of late Late Carboniferous : P_1^1 Shansi Formation of early Early Permian; P_1^2 : Lower Shihhotse Formation of late Early Permian

indicated warm and humid climatic conditions. The arborescent *Calamites* and the ground-cover *Sphenophyllum* occurred in swamps, floodplain and other near water settings. *Lobatannularia sinensis* has a drip tip of leaf, which is similar to those of modern tropical rain forest. Filicalea ferns and pteridosperms

Text-figure—Vegetational reconstruction during Carboniferous as depicted by Cathaysia flora.

were widely distributed in almost all lowlands during the Carboniferous and Permian and they could be regarded to be dominant groups. Among them, a few species of *Pecopteris* with synangia of *Asterotheca*-type are considerd to be near the modern tropical tree fern *Marattiales*. The woody climber like *Gigantopteris* and the tree fern *Pecopteris* may be regarded as characteristic elements with ecological significance, reflecting a tropical climatic condition. Corditean gymnosperms commonly occurred in lowland and upland environments. The vertical structures of the Cathaysian floral communities included arbores, tree ferns, shrubs and herbs. Based on the study of morphofunctional analysis, the Cathaysia flora indicated a tropical climate and it was similar to the climatic condition of the modern tropical rain forest.

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