Distribution, evolution and extinction of global Early Carboniferous flora

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The uniform Lepidodendropsis flora of the Early Carboniferous is uniformly and widely distributed in the Cathaysia, Laurasia, Kazakhstania and Gondwana continents. This is characterized by *Lepidodendropsis, Sublepidodendron, Archaeosigillaria, Archaeocalamites, Sphenopteridium, Cardiopteridtum, Rhodeopteridium, Rhacopteris, Triphyllopteris* and *Adiantites*, etc. The global climatic differentiation was not very obvious during the Early Carboniferous, therefore, all Early Carboniferous plant assemblages belonged to the same phytogeographic province. It is known that some typical genera of the Lepidodendropsis flora of the Early Carboniferous, such as *Leptdodendropsis, Lepidosigillaria* and *Archaeosigillaria* are recorded from the Lower Devonian in Libya, Africa (Lejal-Nicol, 1975) and some elements of this flora are also recorded from the Late Devonian in China and other parts of the world. It is considered that this Lepidodendropsis flora gradually started appearing in the Early Devonian, began to diversify in the Late Devonian and reached its maximum development in the Early Carboniferous. The flora tended to decline in the late Early Carboniferous and resulted in its extinction in the end of the Early Carboniferous.

Although some plant elements in Cathaysia, Euramerica, Angara and Gondwana had already appeared in the Early Carboniferous, especially in the late Early Carboniferous, the occurrence of the new taxa was regarded as a result of gradually increasing climatic differentiation and plant evolution. During the transition period from the Early Carboniferous to the Late Carboniferous, the differentiations of climatic conditions, tectonic movements, continental positions, oceanic currents and glaciation were quite obvious, resulting in the extinction of numerous typical elements of the Early Carboniferous flora and the appearance of some forerunners of the Late Carboniferous floras in the world. The Cathaysia, Euramerica, Angara and Gondwana floras derived from the identical Lepidodendropsis flora of the Early Carboniferous, but developed and flourished in different environmental conditions.

Key-words—Lepidodendropsis flora, Distribution, Evolution, Extinction, Early Carboniferous.

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सारांश

भूमण्डलीय प्रारम्भिक कार्बनीफेरस वनस्पतिजात का वितरण, विकास एवं विलुप्तीकरण

शैला चन्द्रा एवं सन केकिन

प्रारम्भिक कार्बनीफेरी कल्प में लेपिडोडेन्ड्राप्सिस वनस्पतिजात समान एवं बृहत रूप से कैथेसिआ, लॉरेशिया, कजाखस्तान एवं गोंडवाना महाद्वीपों में विद्यमान था। यह वनस्पतिजात *लेपिडोडेन्ड्राप्सिस, आर्कियोकैलेमाइटिस, सबलैपिडोडेन्ड्रान, आर्कियोसिजिलेरिया, स्फीनॉप्टेरीडियम, राडिआप्टेरीडियम, रैकाप्टेरिस, ट्राइफिल्लॉप्टेरीडियम, एडिआन्टाइटिस,* इत्यादि की उपस्थिति से अभिलक्षणित है। प्रारम्भिक कार्बनीफेरस कल्प में भूमण्डलीय जलवायु में कोई ऐसा विशेष अन्तर नहीं था । अतएव सभी कार्बनीफेरस पादप समुच्चय एक ही पुराभौगोलिक प्रान्त से सम्बद्ध थे। लेपिडोडेन्ड्राप्सिस वनस्पतिजात की कुछ सामान्य प्रजातियाँ *लेपिडोडेन्ड्रॉप्सिस, लेपिडोसिजिलेरिया* एवं *आर्कियोसिजिलेरिया* लीबिया में प्रारम्भिक डिवोनियन कल्प से ज्ञात हैं तथा इसी वनस्पतिजात के कुछ अवयव चीन एवं विश्व के अन्य भागों से ज्ञात हैं। ऐसा माना गया है कि यह वनस्पतिजात प्रारम्भिक डिवोनियन कल्प में धीरे-धीरे विकसित हुआ, अंतिम डिवोनी कल्प में इसमें विभिन्नता आई तथा प्रारम्भिक कार्बनीफेरस कल्प में इसका सर्वाधिक विकास हुआ । प्रारम्भिक कार्बनीफेरस कल्प के अंतिम काल में इसका ह्रास होने लगा और इसी काल के अन्त तक यह विलुप्त हो गया।

यद्यपि कैथेसिआ, यूरामेरिका, अंगारा एवं गोंडवाना के कुछ पादप अवयवों का विकास प्रारम्भिक कार्बनीफेरस कल्प में हो चुका था, नये वर्गकों का विकास निरन्तर बढ़ती विभिन्नता एवं पौधों में निरन्तर विकास के कारण हुआ है। प्रारम्भिक कार्बनीफेरस से अनंतिम कार्बनीफेरस के परिवर्तन के समय जलवायवी परिस्थितियों, विवर्तनिक गतिविधियों, महाद्वीपीय स्थितियों, समुद्री धाराओं एवं हिमनदन आदि में परिवर्तन हो रहे थे जिसके फलस्वरूप प्रारम्भिक कार्बनीफेरस वनस्पतिजात के अनेक सामान्य अवयव विलुप्त हो गये तथा कुछ नये वर्गकों ने जन्म लिया। ऐसा मत है कि प्रारम्भिक कार्बनीफेरस लेपिडोडेन्ड्रॉप्सिस वनस्पतिजात से ही कैथेसिआ, यूरामेरिका, अंगारा एवं गोंडवाना वनस्पतिजातों का विकास हुआ है परन्तु ये विभिन्न पर्यावरणीय परिस्थितियों में विकसित हुए हैं।

THE term Lepidodendropsis flora was proposed by Jongmans (1952, 1954), which dealt with a cosmopolitan flora of world-wide extent of the Early Carboniferous. Lutz (1933) established Lepidodendropsis as a new genus from the Lower Carboniferous of Geigen near Hof, Bavaria of Germany. *Lepidodendropsis* is characterized by having long narrow fusiform leaf cushions arranged in close spirals, forming pseudowhorls bearing false leaf scars, lacking leaf abscission and a ligule pit (Lutz, 1933; Lacey, 1962; Mensah & Chaloner, 1971). *Lepidodendropsis* is known as the representative genus of lycopods and is widely distributed in many parts of the world. Other important genera of the Early Carboniferous are *Sublepidodendron, Archaeosigillaria, Archaeocalamites, Sphenopteridium, Cardiopteridium, Rhodeopteridium, Triphyllopteris, Rhacopteris, Adiantites* and *Aneimites*, etc. and together constitute Lepidodendropsis flora (see Table 1).

Table 1 —Distribution of some important genera of Early Carboniferous flora

Genera	Cathaysia (China)	Euramerica	Angara	Gondwana
Sublepidodendron	+	+	+	+
Eolepidodendron	+	+	+	+
Siberiodendron	+			
Lophiodendron			+	
Pseudobumbudendron			+	+
Spondylodendron				+
Archaeosigillaria	+		+	
Lepidosigillaria				+
Lepidophlotos		+		
Cyclostigma			+	
Archaeocalamites	+	+		+
Sphenopteridium	+	+		+
Cardiopteridium	+	+		+
Rhodeopteridium	+	+		+
(= Rhodea) Triphyllopteris	+		+		+
Rhacopteris	+		+		+
Cardiopteris	+		+		
(= *Fryopsis*)					
Diplopteridium			+		
Psygmophyllum			+		
Archaeopteridium	+				
Adiantites	+		+	+	+
Aneimites	+		+		
Angaropteridium			+		

Cathaysia : Chang Shanchen (1956), Deng Bao (1978), Zhang Shanzhen *et al.* (1980), Wu Xiuyuan & Zhao Xiuhu (1981), Feng Shaonan *et al.* (1982), Wu Xiuyuan (1992), Chen Fen *et al.* (1994), Chen Fen *et al.* (1995).

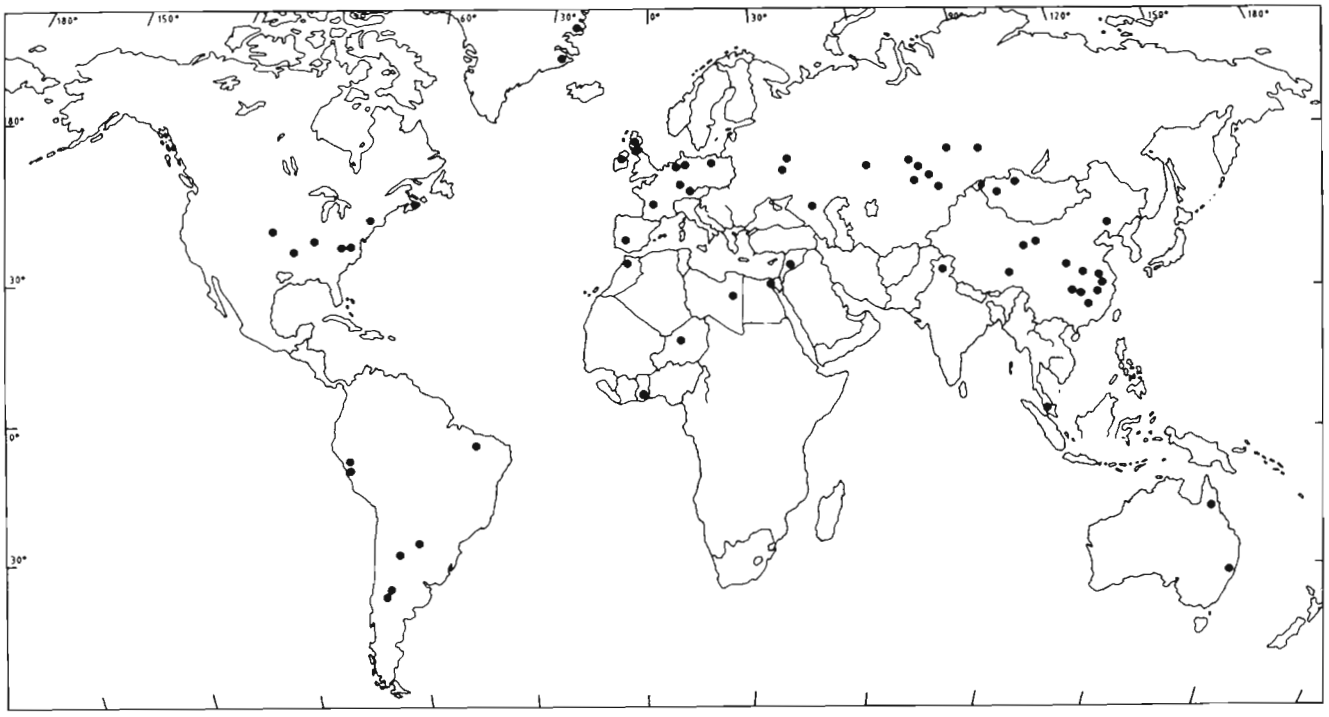
Euramerica : Lutz (1933), Jongmans *et al.* (1937), Read & Mamay (1964), Lacey (1962), Cleal & Thomas (1991).

Angara : Vakhrameev *et al.* (1970), Chaloner & Lacey (1973), Chaloner & Meyen (1973), Cleal & Thomas (1991).

Gondwana : Jongmans (1954), Hoeg *et al.* (1955), Pal & Chaloner (1979), Singh *et al.* (1982), Cleal & Thomas (1991), Pant & Srivastava (1995).

DISTRIBUTION OF GLOBAL EARLY CARBONIFEROUS FLORA

The Lepidodendropsis flora of Early Carboniferous is known from China, Malaysia, the United States of America (Arkansas, Utah, Illinois, Pennsylvania, Virginia), Nova Scotia of Canada, Bavaria of Germany, France, North Wales of Great Britain, Spain, Poland, Ireland, Greenland, Donetz, Kazakhstan, Siberia, Mangolia, Syria, Brazil, Ghana, Morocco, Niger, Libya, Sahara, Egypt, Kashmir, Peru, Australia and Argentina, etc. (Text-figure 1). The Early Carboniferous flora of the world can be recognized as belonging to four broader areas namely the Cathaysia, Angara, Euramerica and Gondwana areas on the basis of floral similarity.



The Cathaysia area

The Early Carboniferous flora has been recorded from a number of localities in China and belong to the typical Lepidodendropsis flora. Chang Shanchen (1956) described *Triphyllopteris collumbiana* Schimper, *Cardiopteridium spitsbergense* Nathorst and *Sphenopteris (Rhodea?)* sp. from the Lower Carboniferous in eastern Kansu (Gansu), China. *Triphyllopteris collumbiana* and *Cardiopteridium spitsbergense* are the characteristic elements of the Lepidodendropsis flora and the species of worldwide occurrence. Deng Bao (1978) recorded fossil plants from the Lower Carboniferous in Shanyang, southern Shanxi (Shaanxi) as *Archaeocalamites scrobiculatus*(Schlotheim) Seward, *Cardiopteridium spetsbergense* Nathorst, *Triphyllopteris collumbiana* Schimper, *Cardiopteris?* spp. and *Lepidodendron shanyangense* Wu & He, etc. Zhang Shanzhen *et al.* (1980) described the Early Carboniferous flora from the Tseshui Series in Shuangfeng of Hunan comprising *Cardiopteridium spitsbergense* Nathorst, *Triphyllopteris collumbiana* Schimper, *Adiantites gothani* (Sze), *Rhodeopteridium* cf. *hsianghsiangense* (Sze), *Archaeocalamites prolixus* Zhang, Zhao & Wu, *Lepidodendron* cf. *robertii* Nathrost, *Lepidodendron* spp., *Lepidostrobophyllum* spp. and *Lepidostrobus* sp., etc. *Lepidodendron, Lepidostrobophyllum* and *Lepidostrobus* are also common genera of the Lower Carboniferous in the Euramerica area. Zhang Shanzhen *et al.* (1980) considered that the flora showed a close relationship with the Visean or Culm flora of West Europe. Wu Xiuyuan and Zhao Xiuhu (1981) studied fossil plants from the Koalishan Formation of Lower Carboniferous in Jurong, southern Jiangsu of China, including *Sublepidodendron mirabile* (Nath.) Hirmer, *S.* cf. *mirabile* (Nath.) Hirmer, *Eolepidodendron jurongense* Wu & Zhao, *Eolepidodendron* sp., *Lepidodendron gaolishanense* Wu & Zhao, *Stigmaria ficoides* (Sternberg) Brongniart, *S. rugulosa* Gothan, *Rhodeopteridium* cf. *hsianghsiangense* (Sze), *Rhodeopteridium* sp., *Telangium* sp. and *Hamatophyton verticillatum* Gu & Zhi, etc. The flora indicates Late Tournaisian to Early Visean and represents a typical Lepidodendropsis flora. Wu Xiuyuan (1992) described fossil plants from the Yangshan Formation of Lower Carboniferous in Gushi, Henan of China, such as *Lepidodendron* aff. *aolungphyllukense*Sze, *L.* cf. *worthenii* Lesquereux, *L.* cf. *shanyangense* Wu & He, *L. dabieshanense* Wu, *L. ?gushiense* Wu, *Lepidodendron* sp., *Cathaysiodendron?* sp., *Bothrodendron yangshanense* Wu, *B. flabellatum* Wu, *Archaeocalamites scrobiculatus* (Schlotheim)

Seward, *Cardiopteridium podozamioides* (Sze), *Triphyllopteris gushiensis* Wu, *Triphyllopteris* sp., *Rhodeopteridium hsianghsiangense* (Sze), *Adiantites* cf. *gothanii* (Sze), *Eusphenopteris* cf. *scribanii* Amerom and *Neuropteris* sp., etc. The age of the flora is regarded as Visean to Early Namurian. The above mentioned elements show that some forerunners of the Cathaysia flora had already appeared in the late Early Carboniferous, belonging to a number of oriental species of lycopods. Chen Fen *et al.* (1995) studied the fossil plants from the Carboniferous strata of Ningxia and adjacent regions, China. Among the fossil plants, some elements from Early Namurian strata (Namurian A) were recorded as *Lepidodendron ninghsianense* Sze & Lee, *L. subrhombicum* Gu & Zhi, *Mesocalamites cistiformis* Stur, *Tingia trilobata* Stockmans & Mathieu, *Cardiopteris ningxiaensis* Chen, Sun & Zhou, *Rhodeopteridium* sp., *Eusphenopteris* cf. *obtusiloba* (Brongniart), *Paripteris gigantea* (Sternberg) Gothan, *P. otozamioides* (Sze & Lee) and *Linopteris simplex* Gu & Zhi, etc. The genus *Tingia* is regarded as an important element of the Cathaysia flora which first appeared in the lower part of the Namurian (Namurian A).

In China, the studies of the Early Carboniferous flora have been further developed by Feng Shaonan *et al.* (1982), Zhao Xiuhu *et al.* (1982) and Mi Jiarong *et al.* (1990).

Asama (1973) described Lower Carboniferous fossil plants from Panching, West Malaysia, namely *Lepidodendron acuminatum* Goeppert, *Lepidodendropsis vandergrchti* Jongmans, Gothan & Darrah, *Bergeria* sp., *Stigmaria* sp., *Rhodea hsianghsiangensis* Sze, *?Adiantites* sp., *?Neuropteris* sp. and *Carpolithus* sp.

The Early Carboniferous flora of the Cathaysia area is mainly distributed in China and Malaysia and consists of some typical elements of the Lepidodendropsis flora. Some forerunners of the Cathaysia flora are known to occur in late Early Carboniferous strata (Sun Keqin, 1996).

The Euramerica area

Lutz (1933) described fossil plants from the Lower Carboniferous of Geigen near Hof, Bavaria of Germany, namely *Lepidodendropsis hirmeri* Lutz, *Lepidostrobus* cf. *faudelii* Schimper, *Asterocalamites scrobiculatus* Schlotheim, *Sphenophyllum saxifragaefolioides* Leyh, *S. geigense* Lutz, *Cardiopteris frondosa* Goeppert, *Rhacopteris lindseaeformis* Bunbury, *R. semicircularis* Lutz, *Archaeopteridium dawsoni* Stur, *Sphenopteridium pachyrrhachis* Goeppert, *S. dissectum* Goeppert, *Sphenopteris foliolata* Stur, *Adiantites tenuifolius* Goeppert, *Calathiops* cf. *plauensis* Gothan, *Telangium* sp., *Rhodea patentissima* Ett., *R. lemayi* Bertrand & Broussier and *R.* cf. *hochsteteri* Stur, etc. Obviously, this flora contains some important elements of Early Carboniferous flora and hence regarded as a typical Lepidodendropsis flora. Lutz (1933) established *Lepidodendropsis* as a new genus with only one species, namely, *Lepidodendropsis hirmeri* Lutz. Later, a number of species of *Lepidodendropsis* were described from the Lower Carboniferous Pocono Formation in Pennsylvania and Virginia (Jongmans *et al.*, 1937). Lacey and Eggert (1964) described fossil plants from the Chester Series (Upper Mississippian) of southern Illinois, namely *Archaeocalamites radiatus* (Brongniart) Stur, *Lepidodendron volkmannianum* Sternberg, *L.* cf. *veltheimii* Sternberg, *Stigmaria ficoides* (Sternberg) Brongniart, *Rhynchogonium fayettevillense* White and *Trigonocarpus* sp. Read and Mamay (1964) recognized three floral zones from the Mississippian (Lower Carboniferous) in the United States, namely, zones of *Adiantites* spp., *Triphyllopteris* spp. and *Fryopsis* spp. which contain *Adiantites spectabilis* Read, *Lepidodendropsis scobiniformis* (Meek) Read, *Sphenopteridium brooksi* Read, *Rhodea vespertina* Read, *Rhacopteris latifolia* (Arnold) Read, *Triphyllopteris lescuriana* (Meek) Lesquereux, *T. varinervis* Read and *Fryopsis abdensis* (Read) Wolf, etc. This sequence is probably incomplete, because the American Mississippian is predominantly marine (Read & Mamay, 1964). They have pointed out that the Upper Devonian flora was not only mere diverse but was more similar to the Mississippian flora that follows than the Lower Devonian flora.

Lacey (1962) described Early Carboniferous fossil plants from the Lower Brown Limestone in the Vale of Clwyd, North Wales, namely *Archaeocalamites radiatus* (Brongniart) Stur, *Lepidodendron perforatum* Lacey, *Lepidostrobophyllum timbriatum* (Kidston), *Lepidodendropsis jonesi* Lacey, *L. recurvifolia* Lacey, *Stigmaria* sp., *Archaeosigillaria stobbsi* Lacey, *Clwydia decussata* Lacey, *Rhacopteris subcuneata* Kidston, *R.* cf. *subcuneata* Kidston, *R. weissii* Walton, *R.* cf. *weissii* Walton, *R.* cf. *geikiei* Kidston

and *Calathiops dyserthensis* Lacey, etc. The flora is probably of the Middle to Late Visean (Lacey, 1962).

The above mentioned fossil plants represent some of the best documented assemblages from the Lower Carboniferous in the Euramerica area and exhibit a remarkable floral uniformity.

The Angara area

The Early Carboniferous flora of the Angara area is characterized by the presence of *Lepidodendropsis, Sublepidodendron, Lophiodendron, Archaeocalamites, Chaccassopteris* and *Angaropteridium* (Chaloner & Lacey, 1973). Cleal and Thomas (1991) listed some typical genera of the Lepidodendropsis flora from Kuznetsk of the Angara area, such as *Lepidodendropsis, Archaeocalamites, Cardiopteridium* and *Adiantites*. They also listed a number of characteristic forms of the *Lepidodendropsis* flora namely, *Lepidodendropsis, Sublepidodendron, Archaeocalamites, Sphenopteridium, Cardiopteridium* and *Adiantites* from Kazakhstan. These reports show that the Lepidodendropsis flora of Early Carboniferous had already existed in the Angara area although some endemic elements of the area appeared in the late Early Carboniferous.

In addition, some genera of the Angara area were cited by Cleal and Thomas (1991), like *Lophiodendron, Siberiodendron, Chacassopteris* and *Angaropteridium*, etc. Some elements appeared in the late Early Carboniferous. Among these elements, a number of Angara genera, such as *Tomiodendron, Abacodendron, Caenodendron* and *Ursodendron* have also been found in Africa. *Tomiodendron, Abacodendron* and *Caenodendron* are described from the Lower Devonian in Libya (Lejal-Nicol, 1975) and Ursodendron and *Tomiodendron* are recorded from the Lower Carboniferous in Niger (Rouvre, 1984). In the late Early Carboniferous, the Lepidodendropsis flora was on the decline, while the Angara flora began to develop. We believe that the Angara flora later gradually separated from the Lepidodendropsis flora of the Early Carboniferous.

The Gondwana area

The Kashmir region exposes one of the best developed Lower Carboniferous sequences. The Lepidodendropsis flora of the Early Carboniferous is known from Spiti, N.W. Himalaya (Gothan & Sahni, 1937; Hoeg *et al.*, 1955) and Kashmir Himalaya (Pal, 1978; Pal & Chaloner, 1979; Singh *et al.*, 1982; Pant & Srivastava, 1995). Gothan and Sahni (1937) described fossil plants from the Po Series of Spiti, namely *Rhacopteris ovata* (McCoy) Walkom, *Sphenophyllum? furcillatum* Ludwing and *Sphenopteris* sp. Another collection of fossil plants was made from the Po Series of Spiti, northwest Himalaya (Hoeg *et al.*, 1955) and contained *Rhacopteris ovata* (McCoy) Walkom, *R. inaequilatera* Goeppert, *R.* cf. *circularis* Walton, *Rhacopteris* sp. a, *Rhacopteris* sp. b, *Sphenopteridium* sp. a, *Sphenopteridium* sp. b, *Rhodea* sp. a, *?Rhodea* sp. b, *Sphenopteris* sp., *?Asterophyllites* sp., *?Adiantites* sp. a and *?Adiantites* sp. b. Pal and Chaloner (1979) recorded fossil plants from the Gund Formation of Lower Carboniferous in Kashmir, namely, *Lepidodendropsis* cf. *sigillarioides* Jongmans, Gothan & Darrah, *L.* cf. *fenestrata* Jongmans, *Lepidodendropsis* sp., *Lepidosigillaria* cf. *quadrata* Danze-Corsin, *Archaeosigillaria* sp., *'Cyclostigma' ungeri* Jongmans, Gothan & Darrah, *Archaeocalamites radiatus* (Brongniart) Stur, *Rhodeopteridium tenuis* Gothan and *Rhacopteris* cf. *circularis* Walton. The flora contains several genera which link it with typical Early Carboniferous flora from other parts of the world and shows the close similarity with the Lepidodendropsis flora. Singh *et al.* (1982) described fossil plants from the Lower Carboniferous in Kashmir Himalaya, namely, *Archaeosigillaria minuta* Lejal, *Lepidosigillaria* cf. *quadrata* Danze-Corsin, *Lepidodendropsis fenestrata* Jongmans, *L.* cf. *peruviana* (Gothan) Jongmans, *Cyclostigma* cf. *pacifica* (Steinmann) Jongmans, *Rhacopteris ovata* (McCoy) Walkom, *Triphyllopteris lescuriana* (Meek) Lesquereux, *Rhodea* cf. *subpetiolata* (Potonié) Gothan and *Palmatopteris* cf. *furcata* Potonié. Recently, Pant and Srivastava (1995) described the Early Carboniferous fossil plants from Wallarma Spur of Panjab-Kashmir Himalaya and established two new genera, viz., *Pseudobumbudendron* Pant & Srivastava and *Spondylodendron* Pant & Srivastava and four new species. The plant elements in this flora are as follows : *Pseudobumbudendron chaloneri* Pant & Srivastava, *P. meyenii* Pant & Srivastava, *P. fenestrata* (Jongmans & Koopmans) Pant & Srivastava, *Spondylodendron wallaramensis* Pant & Srivastava, *Lepidodendropsis liddarensis* Pant & Srivastava, *Archaeosigillaria subcostata* Danze-Corsin, Knorria Sternberg, *Aspidiaria*

Presl, *Triphyllopteris lescuriana* (Meek) Lesquereux and *Nothorhacopteris argentinica* (Geinitz) Archangelsky. Early Carboniferous fossil plants from several localities in Kashmir Himalaya are now known to occur as a typical Lepidodendropsis flora.

The Lepidodendropsis flora of Early Carboniferous is also recorded from South America, Africa and Australia. Jongmans (1954) recorded a typical Lepidodendropsis flora from Peru, including *Lepidodendropsis de voogdi* Jongmans, *L.* cf. *de voogdi* Jongmans, *L. peruviana* (Gothan) Jongmans, *L. steinmanni* Jongmans, *?Lepidodendropsis (Lepidodendron) lissoni* (Steinmann) Jongmans, *?Lepidodendropsis* sp., *Cyclostigmaria pacifica* (Steinmann) Jongmans, *C.* cf. *pacifica* (Steinmann) Jongmans, *Rhacopteris ovata* (McCoy) Walkom, *R.* cf. *circularis* Walton, *R.* cf. *cuneata* (Walkom), *Triphyllopteris collombiana* Schimper, *T. lescuriana* (Meek) Lesquereux, *?T. peruviana* Jongmans and *Sphenopteris whitei* (Berry) Jongmans. Archangelsky (1990) recorded fossil plants namely, *Archaeosigillaria conferta* (Frenguelli) Menendez and *Lepidodendropsis sekondiensis* Mensah & Chaloner from the Lower Carboniferous of Argentina.

Rigby (1969) compiled coaliferous plants reported from Australia and recognized *Calamites peruvianus* Gothan, *Cyclostigma australe* Feistmantel, *Fryopsis* sp., *Lepidodendropsis* sp., *Rhacopteris septentrionalis* Feistmantel, *Rhacopteris intermedia* Feistmantel, *Rhacopteris ovata* (Mc Coy) Walkom, *Sphenopteris clarkei* Dun and *Triphyllopteris* sp. Jongmans and Heide (1955) described fossil plants from the Lower Carboniferous in Egypt, namely *Lepidodendropsis fenestrata* Jongmans, *L. schurmanni* Jongmans, *Lepidodendropsis* sp., *?Sublepidodendron fasciatum* Jongmans, *Cyclostigma sinaica* Jongmans, *'Cyclostigma' egyptiaca* Jongmans, *Asterocalamites* cf. *scrobiculatus* Schlotheim and *Sphenopteris whitei* (Berry) Jongmans, etc. Lejal (1969) described fossil plants from the Lower Carboniferous of Sahara, namely, *Protolepidodendropsis pulchra* Hoeg, *Lepidodendropsis hirmeri* Lutz, *L. scobiniformis* (Meek) Read, *L. sinaica* Jongmans & Koopmans, *L. africanum* Lejal, *Lepidodendropsis* sp. Mensah and Chaloner (1971) described two new species from the Lower Carboniferous in Ghana, namely, *Archaeosigillaria essiponensis* Mensah & Chaloner and *Lepidodendropsis sekondiensis* Mensah & Chaloner. Rouvre (1984) described fossil plants, *Lepidodendropsis rhombiformis* Rouvre, *Pseudolepidodendropsis nigeriensis* Rouvre, *Ursodendron wijkianum* (Heer) Radczenko and *Tomiodendron varium* (Radczenko) Meyen from the Lower Carboniferous of Niger. The genera *Ursodendron* and *Tomiodendron* are regarded as the representative endemic elements of the Angara area, but the two genera have also been found in Niger of Africa, therefore, they can not be regarded as the typical Angara elements.

As mentioned above, the Early Carboniferous flora of the Gondwana area contains numerous elements of the Lepidodendropsis flora (see Table 2), which is similar to those known from the other parts of the world.

Table 2—Distribution of characteristic species of Early Carboniferous in Gondwanaland

Species	Kashmir	Peru	Australia	Argentina	Brazil
Lepidodendropsis de voogdi Jongmans		+			
Lepidodendropsis fenestrata Jongmans	+				
Lepidodendropsis liddarensis Pant & Srivastava	+				
Lepidodendropsis peruviana (Gothan) Jongmans		+			
Lepidodendropsis sekondiensis Mensah & Chaloner				+	
Leptdodendropsis cf. *sigillarioides* Jongmans, Gothan & Darrah	+				
Leptdodendropsis steinmanni Jongmans		+			
Lepidodendropsis sp.	+		+		+
Pseudobumbudendron chaloneri Pant & Srivastava	+				

Pseudobumbudendron meyenii Pant & Srivastava	+					
Spondylodendron wallaramensis Pant & Srivastava	+					
Archaeosigillaria minuta Lejal						
Archaeosigillaria conferta (Frenguelli) Menendez					+	
Archaeosigillaria subcostata Danze-Corsin	+					
Lepidosigillaria cf. *quadrata* Danze-Corsin	+					
Cyclostigma australe Feistmantel				+		
Cyclostigma brasiliensis Dolianiti						
Cyclostigma pacifica (Steinmann) Jongmans			+			
Archaeocalamites radiatus (Brongniart) Stur	+					
Rhodeopteridium tenuis Gothan						
Triphyllopteris collombiana Schimper	+					
Triphyllopteris lescuriana (Meek) Lesquereux	+					
Triphyllopteris sp.						
Racopteris ovata (McCoy) Walkom	+					
Rhacopteris cf. *circularis* Walton	+					
Shphenopteridium sp.	+				+	
Sphenopteris whitei (Berry) Jongmans						
Adiantites peruianus (Berry) Read					+	
Adiantites paracasica Gothan					+	
Cardiopteridium sp.					+	+
Nothorhacopteris argentinica (Geinitz) Archangelsby	+			+	+	+
Fedekurtzia argentinica Archangelsky				+	+	

Kashmir : Hoeg *et al*. (1955), Pal & Chaloner (1979), Singh *et al*. (1982), Pant & Srivastava (1995)

Peru : Jongmans (1954)

Australia : see quotation in Rigby (1969)

EVOLUTION AND EXTINCTION OF GLOBAL EARLY CARBONIFEROUS FLORA

So far, the evolution of Early Carboniferous flora is not clear, owing to limited data and different views. According to Lejal-Nicol (1975), the elements of the earliest Lepidodendropsis flora appeared in the Lower Devonian of Libya, North Africa, namely, *Lepidodendropsis hirmeri* Lutz, *L. sinaica* Jongmans & Koopmans, *L. africanum* Lejal, *Lepidosigillaria whitei* Krausel & Weyland, *L. massae* Lejal-Nicol, *Archaeosigillaria minuta* Lejal and *Prelepidodendron mourzoukense* Lejal-Nicol, etc. It seems that Libya was the centre of origin for lycopods (Lejal-Nicol, 1975).

In China, Sze (1936) described *Protolepidodendron ?arborescens* from the Middle Devonian in Hunan Province. Later, Sze (1953) placed this species with a question mark under the genus *Lepidodendropsis*, namely *Lepidodendropsis ?arborescens* Sze (Sze). *Lepidodendropsis ? arborescens* was also recorded from the Upper Devonian in Hubei Province (Sze, 1952). Sze (1956) reported fossil plants from the Wutung Series of Kiangsu (Jiangsu), namely, *Lepidodendropsis hirmeri* Lutz and *Sublepidodendron wasibense* (Sze) Sze. Chang Chien-

shen (1965) described *Lepidodendropsis scobiniformis* (Meek) Read and *Leptophloeum suzhousenese* Chang from the Wutung Series of Kiangsu (Jiangsu). *Leptophloeum suzhousense* has been transferred to *Leptophloeum rhombicum* Dawson (Gu & Zhi, 1974). The Wutung Series (Wutung Formation) has now been regarded as the Late Devonian in age (Wu Chongzhang *et al.*, 1982; Zhao Xiuhu & Wu Xiuyuan, 1986). Zhao Xiuhu and Wu Xiuyuan (1986) listed fossil plants from the Wutung Formation, namely, *Leptophloeum rhombicum* Dawson, *Sublepidodendron mirabile* (Nathorst) Hirmer, *Lepidodendropsis hirmeri* Lutz, *Lepidostrobus grabaui* Sze, *Cyclostigma kiltorkense* Haugh, *Hamatophyton verticillatum* Gu & Zhi, *Archaeocalamites* aff. *scrobiculatus* (Schlotheim) Seward, *Sphenophyllum pseudotenerrimum* Sze, *S. lungtanense* Gothan & Sze, *Archaeopteris* spp., *Sphenopteris taihuensis* Sze and *Platyphyllum* cf. *williamsoni* (Nathorst) Hoeg, etc. Li Xingxue and Wang Hongfeng (1982) described the Late Devonian fossil plants from Mt. Longmenshan, North Sichuan, namely *Lepidodendropsis theodori* (Zal.) Jongmans, *L.* cf. *theodori* (Zal.) Jongmans, *Lepidodendropsis?* sp. (cf. *L. ?dzungariensis* Sze), *Lepidosigillaria ? sichuanensis* Li & Wang, *Archaeocalamites longinternodus* Li & Wang, *Archaeocalamites* sp., etc. Zhao Xiuhu and Wu Xiuyuan (1986) described fossil plants from the Zhongning Formation of the Upper Devonian in southern Ningxia. These are *Leptophloeum rhombicum* Dawson, *Sublepidodendron mirabile* (Nathorst) Hirmer, *Hamatophyton verticillatum* Gu & Zhi, *Archaeocalamites* sp., *Sphenopteris taiuensis* Sze, etc. The flora of the Zhongning Formation shows a striking resemblance to that of Wutung Formation in southeastern China and is probably of the Devonian age (Zhao Xiuhu *et al.*, 1986). In view of the above mentioned facts, the early Early Carboniferous flora closely relates to the Late Devonian flora, while the Late Early Carboniferous flora resembles the Namurian flora.

In the Donetz Basin, the Lepidodendropsis flora is said to occur in the Upper Devonian (Jongmans, 1954). "It is interesting to note that such plants, especially *Lepidodendropsis*, also occur in different localities and are considered as Upper Devonian" (Jongmans, 1954). "It is a well known fact that the flora of the lower part of the Lower Carboniferous has relations with that of the Upper Devonian and of the younger part with that of the Namurian" (Jongmans, 1952). So far some elements of the Lepidodendropsis flora are on record from the Upper Devonian, therefore it is possible that the Lepidodendropsis flora represents the floral appearance of the Late Devonian and the Early Carboniferous (Sun Keqin, 1996). In view of the above mentioned facts, the Lepidodendropsis flora gradually separated from the Early Devonian, started to diversify in the Late Devonian and reached its maximum development in the beginning of Early Carboniferous and caused its extinction in the end of the Early Carboniferous.

Seeing that some genera of the Angara area such as *Ursodendron, Tomiodendron* and *Lophiodendron*, etc. occurred in the South of former U.S.S.R., Tuva and Mongolia. Vakharmeev *et al.* (1970), Chaloner and Lacey (1973) and Chaloner and Meyen (1973) recognized an Angara floral province of Early Carboniferous in the region. However, the genera *Tomiodendron, Abacodendron* and *Caenodendron* have been recorded from the Lower Devonian in Libya, Africa (Lezal-Nicol, 1975) and *Ursodendron* and *Tomiodendron* were reported from the Lower Carboniferous in Niger, Africa (Rouvre, 1984). Therefore, the genera *Ursodendron, Tomiodendron, Abacodendron* and *Caenodendron* in the Angara area could not be regarded as typical Angara floral elements. In this light the Early Carboniferous flora of the Angara area also belonged to the Lepidodendropsis flora of the world.

As might be expected, a number of forerunners of the Angara flora existed in the late Early Carboniferous, which indicated that the Lepidodendropsis flora was on the decline, and the Angara flora started to develop. Sun Keqin (1996) pointed out that owing to the climatic differences, some obvious changes in floral components of the Cathaysia, Euramerica, Angara and Gondwana areas occurred during the transition from the Early Carboniferous to Late Carboniferous, which resulted in extinctions of some typical plant genera, such as *Lepidodendropsis, Sublepidodendron, Archaeocalamites, Triphyllopteris, Cardiopteridium, Rhacopteris, Fryopteris, Sphenopteridium, Rhodeopteridium* and *Adiantites*, etc. of the Early Carboniferous. Moreover, a number of forerunners of the Cathaysia, Euramerica, Angara and Gondwana floras had already appeared in their respective areas during the late Early Carboniferous. During the late Early Carboniferous, most parts of the Gondwana area were controlled by glaciation, there-

fore, the record of typical forerunners of the Gondwana flora is unclear in this age. But the genera like *Nothorhacopteris* and *Fedekurtzia* may be regarded as endemic elements to Gondwana countries (Pant & Srivastava, 1995). Global climatic differentiation was not very obvious during the Early Carboniferous. The lycopods, which were quite abundant and dominant in the Lepidodendropsis flora, indicated warm and humid climatic conditions. During the transition from the Early Carboniferous to the Late Carboniferous, the differentiation of obvious climatic conditions, tectonic movements, continental positions, oceanic currents and glaciation might have caused the extinction of the Lepidodendropsis flora. The Cathaysia, Euramerica, Angara and Gondwana floras derived from the identical Lepidodendropsis flora of the Early Carboniferous, but developed in different environments respectively (Sun Keqin, 1995, 1996). However, it is noteworthy that the origin and extinction stages 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 elements due to minor ecological variations of different vast areas, they retained the character of the original Lepidodendropsis flora.

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