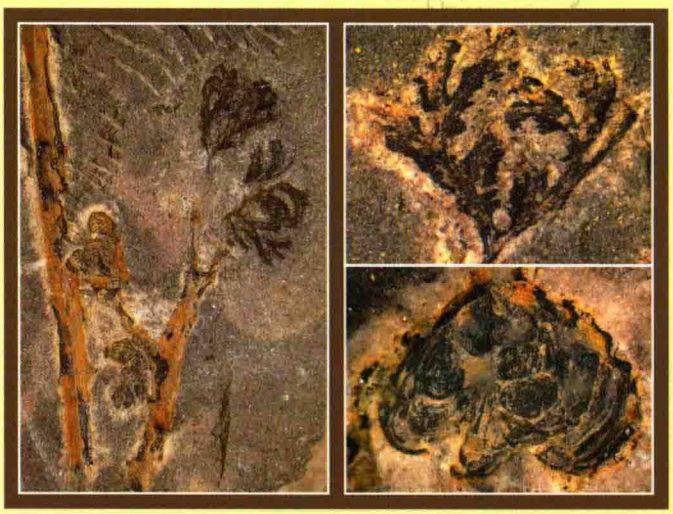
The Early Devonian Posongchong Flora of Yunnan

— A Contribution to an Understanding of the

Evolution and Early Diversification of Vascular Plants

Hao Shougang
Xue Jinzhuang



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To Professor Charles B. Beck, as a friend, who has a sincere desire to help others, and as a distinguished paleobotanist, who has made very significant contributions to our knowledge about Devonian plants.

Foreword

During the past several decades, outcrops of the Posongchong Formation in Yunnan Province, southwestern China, have yielded a remarkable array of well-preserved plant fossils. Professor Hao Shougang and his students, among others, have worked extensively in several highly fossiliferous, Lower Devonian horizons and have collected innumerable specimens, primarily preserved as compressions, but some with well-preserved internal structure. Professor Hao's studies of this material have revealed the presence of many taxa, some known from elsewhere in the world, and many others, including new genera, indigenous to southern China. This flora is clearly the most morphologically and taxonomically diverse Lower Devonian flora known, and includes some taxa of surprising complexity such as *Celatheca*, characterized by complex fertile units composed of clusters of four sporangia enclosed by bract-like structures, one of which is associated with each sporangium; *Eophyllophyton* which has multiveined leaves, and fertile structures consisting of two leaves curved toward each other enclosing numerous small ovoid sporangia; and *Estinnophyton*, the strobili of which consist of irregular whorls of once or twice bifurcate sporophylls each bearing two stalked, recurved, adaxial sporangia. Currently, there are at least 28 recognized genera in the Posongchong flora including representatives, or possible ancestors, of evolutionary lineages among zosterophyllopsids, lycopsids, sphenopsids, progymnospermopsids, and pteridospermopsids. Several genera cannot, with certainty, be associated with any previously recognized clade or even a major taxon. It is clear that this flora provides an unusually important contribution to our knowledge of plant life in the Devonian, and a wealth of information for biologists and geologists who seek to understand the myriad pathways of plant evolution.

Dawson's early discovery (1859, 1871) of specimens he named *Psilophyton*, and the Rhynie chert plants described by Kidston and Lang (1917–1921), provided conclusive evidence of the existence of vascular plants in the Devonian; and subsequently, taxa of similar morphology were described from Upper Silurian strata. For another fifty years or more, Silurian and Devonian taxa characterized by leafless, dichotomous branches bearing terminal sporangia, as well as some with laterally borne sporangia and others with more complex branching systems, were placed in the order Psilophytales. Banks (1968, 1975), recognizing the diversity of genera in this group, segregated them into three, more natural taxa, Rhyniophytina,

Zosterophyllophytina and Trimerophytina. Subsequently, other researchers raised these groups to higher taxonomic levels; and with the advent of cladistic methods and the establishment of many new genera, several evolutionary lineages have been recognized within these and other major taxa.

This progress in our knowledge of early vascular plants and their taxonomic significance has been possible only because of the diligence of many paleobotanists who have collected and studied the morphology and anatomy of fossil plants in many parts of the world. This book, a major and very important contribution, represents many years of field work and research by professor Hao, his students, and others on the Early Devonian plants of the Posongchong flora. Professor Hao's extensive collecting, his detailed anatomical and morphological studies and his comprehensive cladistic analysis in this book, which combines data from the Posongchong taxa with that of taxa from other parts of the world, add significantly to the continuing increase in our understanding of the nature of Early Devonian plants and their role in the evolution of Earth's flora.

Charles B. Beck
Professor Emeritus of Botany
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Contents

1. Introduction

During the Silurian–Devonian period, when vascular plants first invaded the land, basal groups of these vascular plants began to diversify. The origin and evolution of these plants are vitally important events that have had a profound impact on terrestrial floras and their ecosystems. During this period, plants underwent rapid radiation and evolution, and the ancestral types of the extant vascular plants, such as lycopsids, sphenopsids, ferns, and seed plants, appeared. The questions of how these plants originated and evolved, how and when their fertile and vegetative organs appeared and diversified, and how the evolution of early plants related to paleogeography and paleoenvironment have constituted profound aspects of scientific researches. The present study provides a basis upon which one can further observe the coevolution between the biota and geological processes, especially the evolution of terrestrial ecosystems. It relies on previous studies of early vascular plants that lived during the late Silurian and Early Devonian, which was the crucial period of early evolution and diversification of vascular plants.

Since the 1850s, most studies of early vascular land plants have been based on fossils collected in Laurussia, and theories of plant evolution, ecology and systematics were established on the basis of this evidence. The South China Block where the Posongchong flora developed was far away from Laurussia during the Early Devonian and thus both geographically and ecologically isolated from other blocks. The components and nature of the Posongchong flora are apparently different from those of the traditional Euramerican flora. Probing into the origin, evolution, and diversification of the Posongchong taxa may eventually enrich our knowledge of the diversity of early vascular plants and provide new insights about plant evolution.

Fossil material is crucial to the study of the diversification and evolution of plants. After several decades of continued, in-depth field examination (including at least 30 visits to the Zhichang section over the past 30 years), we obtained many valuable fossil specimens. The improvement of laboratory techniques has provided us with the accurate knowledge and high quality studies. Through effective collaborations with colleagues (particularly Professors Charles B. Beck and Patricia G. Gensel), we have benefited from their ideas and techniques. We have used and improved some of these techniques (such as peels, sediment removal, maceration, and serial sectioning of permineralized material). Typical results of studies incorporating these techniques are illustrated in this book. For example, the reconstruction and sectioning of the tiny leaves of *Eophyllophyton bellum* Hao showed dichotomous venation, and transverse views showed tracheids of the leaf veins. Fusainized tracheids and limonitic permineralized tracheid molds of *Adoketophyton subverticillatum* (Li X.X. et Cai) Li C.S. et Edwards were observed

with scanning electron microscopy (SEM) after chemical treatment.

The scientific process takes place through the gradual increase of knowledge by new discoveries. In paleobotany, this kind of progress centers around the description and classification of fossil plants and the determination of their temporal and spatial relationships, and ecological environment. New discoveries also provide an opportunity to test current hypotheses. Continued research into the Posongchong flora has been performed based on gradually accumulated data. This research prompted us to consider certain questions, such as those related to the phylogenetic affinities, ecological diversity and evolutionary patterns of the Posongchong plants. The exact geological age provides a time framework for the calibration of the plant evolutionary scale. This biostratigraphic correlation is very important in studies of plant evolutionary history. The Pragian age of the Posongchong flora has been well documented, according to strata sequence and invertebrate fossil assemblages (brachiopod, corals, and conodonts). We have tried to undertake a study of the sedimentology and taphonomy of specific plant assemblages and associated facies in order to reconstruct the environment in which they lived. A total of 28 genera and 37 species of the Posongchong flora have been presented in this book, with brief descriptions and comparisons with related taxa. The Posongchong flora is compared to coeval floras (particularly those of the Laurussian continent). Significantly, some plants were found to be endemic and quite different from the Early Devonian plants in Laurussia. These plants are difficult to classify using existing classification systems. Herein, an amended classification system is presented. This system contains some new categories that suggest a connection with their immediate Middle–Late Devonian descendants. We examined the phylogenetic relationships of the Posongchong plants using cladistic analyses based on the parsimony method and Bayesian inference that shows potential significance. These analyses were prepared by reviewing and elucidating selected characters and character states. The taxonomic diversity of the Posongchong plants strongly indicates that almost all of the basic types of vascular plants known today as well as extinct groups may have appeared suddenly. We attempted to conduct a synthetic analysis and addressed general questions about the floristic comparison and macroevolutionary patterns in terms of influence of paleophytogeographic differentiation, latitudinal trends, sedimentary facies, and habitat heterogeneity. The macroevolutionary pattern of early vascular plants in the Early Devonian could be compared to the Cambrian explosion of metazoans in that both show a great rapid evolution of morphologically diverse higher taxa. This indicates that the initial evolution of animals and plants is probably comparable.

We suggest that the Posongchong localities reflect a truer plant landscape than other localities because of the rich components found in them and the distinct diversification that took place because of diversified taphocoenoses. We propose that South China might represent one of the most important centers of the origin and diversification of vascular plants. However, the study is still insufficient because of incomplete material and limited information about some described fossils, thus a complete understanding of these plants and phylogenetic analyses are hampered. There are still some fossil clues (fragmentary specimens with unusual fertile and vegetative organs) that we have not fully studied in our laboratory. In this book, the classification and phylogenetic consideration of the Posongchong plants rely mainly on a phyletic perspective. We are also trying to reach a compromise between traditional methods and cladistic analyses, although the utility of cladistic approaches to the classification of early plants is weakened by the limited number of taxa, uncertain and missing data, and controversial assessments of homology. Further continued field collection and lab work are still absolutely

necessary to the study of the Posongchong flora.

Acknowledgments

by Hao Shougang

Fortunately I could do the domain I want to do. And I was fortunate to be both a student, and subsequently, a member of faculty of Peking University. There, An Taixiang supervised my thesis research, He Guoqi, Bai Shunliang, Jin Shanyu, Yang Shouren, Wang Xinping, Zhang Yun, Wang Xianzeng and Li Shuluan provided me with opportunities and intellectual help, and I am very grateful to them. I have also benefited greatly from colleagues in Earth Sciences and Biology in the accumulation and integration of knowledge. I thank all the students I have supervised during my professional career, including undergraduates, graduate students, and postdoctoral fellows, who have assisted me in field work and research, provided me with inspiration, and continue to contribute to my education. They are Ph.D. students: Wang Deming, Wang Qi, Liu Yu, Liu Zhenfeng, Xue Jinzhuang and Masters Degree students: Jin Haiyue, Li Min and Zhu Xiao. They have contributed to the continuing discovery and intellectual advances, and many of them are co-authors in the publication of our research studies. I also thank Xue Jia, Zhou Chunyuan, Xu Yun, Ni Debao, Geng Jinda and Jia Qiuyue for their help with photography and preparation of specimens.

I keep in the depths of my memory the departed Professors Xu Ren (Hsü Jen), Li Xingxue (Lee Hsinghsüeh), Li Zhengli, and Tian Baolin, and I am particularly grateful to them for their support and concern during the initial state of my research. I also extend my thanks to Zhu Weiqing, Li Chengsen, Gen Baoyin, Cai Chongyang, Wang Yi, Mei Meitang, and Li Daiyun for friendship and intellectual exchanges. I would like to express special thanks to Zhang Miman (Chang Meemann) and Zhou Zhiyan (Chow Tseyen) for encouragement and support.

Our knowledge of the early vascular plants has evolved by accumulation of data, analyses and comparisons of taxa from different continents. The most significant studies were on taxa from the Laurussian paleocontinent (i.e., the present Euramerican countries) and are part of a long research history. Through collaboration and exchange of ideas I have learned a great deal and benefited enormously from the very experienced colleagues and researchers who have studied plants in this region. I am grateful to them, particularly, to Charles B. Beck and Patricia G. Gensel, with whom I have collaborated on studies of the Posongchong plants. Others are Dianne Edwards, William G. Chaloner, David L. Dilcher, Thomas N. Taylor, Andrew H. Knoll, Fancis M. Hueber, Paul Kenrick, Muriel Fairon-Demaret, Christopher M. Berry, Philippe Gerrienne, Brigitte Meyer-Berthaud, Jean Galtier, James F. Basinger, and Richard C. Fox, and departed Harlan P. Banks and Hans-Joachim Schweitzer. The ideas and experiences related in the following pages owe much to their works. Their data and explanation provided the intellectual substance and inspiration for much in this summarization of my work.

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attending the IOPC-5 conference and conducting collaborative research with Patricia G. Gensel.

I am particularly grateful to Charles B. Beck for reading and reviewing the fourth and sixth chapters of the draft manuscript, to Ma Xueping for reading and reviewing the third and fifth chapters, to Qiu Yinglong for reviewing part of the sixth chapter, and to Wang Qi for reading part of the seventh chapter, for their making careful corrections and giving many suggestions for improvement. I also appreciate very much the help of James F. Basinger and Zhou Zhiyan, who have made many careful corrections throughout the manuscript. Several colleagues have generously donated their time to review various chapters of the manuscript including Dianne Edwards, William G. Chaloner and Rong Jiayu, and their suggestions have greatly improved this book. Xue Jinzhuang, as a coauthor, made contributions in each chapter of the writing process, and particularly in preparation of photographs, drawings and computer procedures in this monograph. He is a diligent young colleague, good at thinking and cooperating with others.

Finally I thank my wife Li Cong and my daughters Hao Peng and Hao Qin for their understanding and much attention to me for a long time.

2. Localities and Research History of Early Vascular Plants in Yunnan Province

2.1. Localities

There are many extensive continental fossiliferous outcrops of Early–Middle Devonian age in Yunnan Province, China. The Early Devonian fossiliferous outcrops in Yunnan that have been investigated previously are mainly distributed in two areas, Qujing and Wenshan. Qujing City is located in northeastern Yunnan Province, 130 km northeast of Kunming, and Wenshan Zhuang-Miao Autonomous Prefecture is in southeastern Yunnan, 320 km southeast of Kunming (Figure 2.1).

The Qujing area is the only place in southern China where well-exposed strata show a

Figure 2.1. Maps showing areas of the main outcrops of Lower Devonian deposits of Yunnan Province. The main outcrops of the Lower Devonian Xujiachong Formation can be found near Qujing, and southeastern counties of Yunnan Province yield major outcrops of the Lower Devonian Posongchong Formation.

successive transition from shallow marine facies of the upper Silurian Yulongsi Formation to non-marine (or continental) facies of the Lower Devonian Cuifengshan Group. The sections are distributed at Longhuashan (Mt. Longhua) to Cuifengshan (Mt. Cuifeng) from northeast to southwest, about 13 km northwest of Qujing. The Lower Devonian strata in this area represent the only complete non-marine sequence in South China (Li and Cai, 1978; Fang *et al.*, 1985; Cai, 2000; Wang, Hao and Liu, 2002; Ma, Liao and Wang, 2009) (Figure 2.2).

The Early Devonian fossil plants in Wenshan are best studied from two separate sections

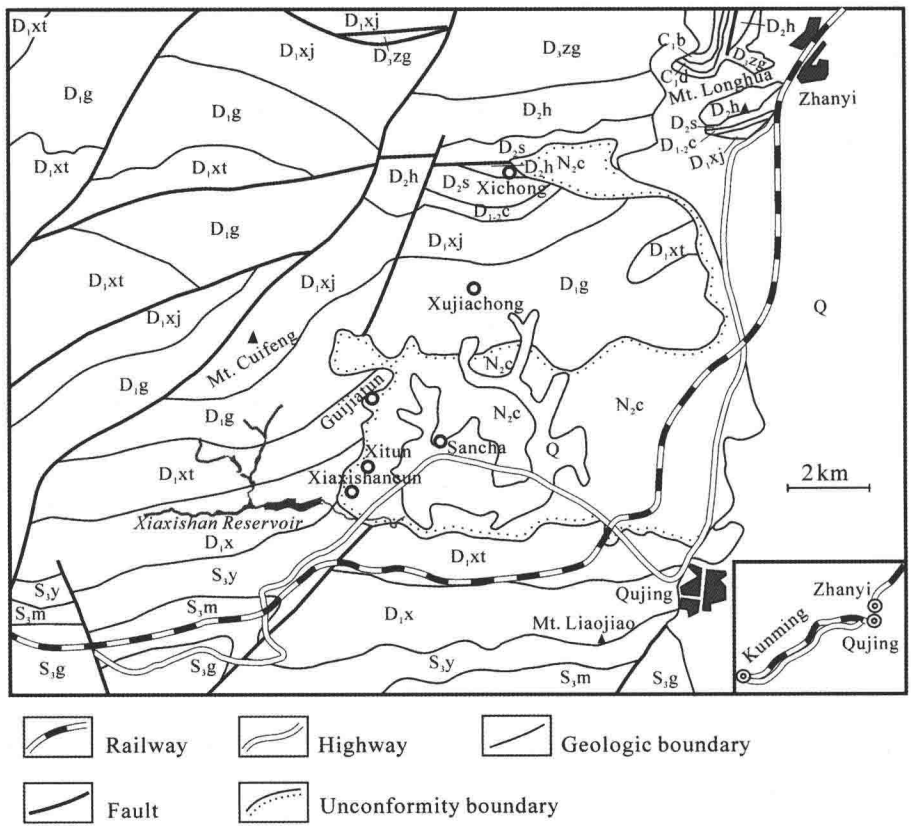

Figure 2.2. General geological map of the Qujing area in northeastern Yunnan Province, China (modified from 1:200000 Geologic Map Sheet of Qujing[①], also see Li and Ge (2001), and Hao *et al.* (2007)).

Abbreviations: Q–Quaternary; N_2c–Neogene Ciying Formation; C_1b–Lower Carboniferous Baizuo Formation; C_1d–Lower Carboniferous Datang Formation; D_3zg–Upper Devonian Zaige Formation; D_2h–Middle Devonian Haikou Formation; D_2s–Middle Devonian Shangshuanghe Formation; $D_{1\text{-}2}c$–Lower–Middle Devonian Chuandong Formation; D_1xj–Lower Devonian Xujiachong Formation; D_1g–Lower Devonian Guijiatun Formation; D_1xt–Lower Devonian Xitun Formation; D_1x–Lower Devonian Xiaxishancun Formation; S_3y–Upper Silurian Yulongsi Formation; S_3m–Upper Silurian Miaogao Formation; S_3g–Upper Silurian Guandi Formation. The Silurian System in South China was divided into Lower, Middle, and Upper Silurian when 1:200000 Geologic Map Sheet of Qujing was finished in 1978, and here the original formation labels, S_3y, S_3m and S_3g, were retained. The Guandi, Miaogao and Yulongsi formations were correlated to Ludlow to early Pridoli by Wang (2011).

① The Second Regional Survey Brigade, Geologic Bureau of Yunnan Province. 1978. Geologic Report of Regional Geologic Survey of People's Republic of China—1:200000 Geologic Map Sheet of Qujing.

located on the mountain slopes near Zhichang Village of Gumu Town and Changputang Village of Lianhuatang Town. The Zhichang Village, about 12 km south of Wenshan (Figure 2.3), is adjacent to a highway leading from Wenshan to Maguan County. Because of the well-preserved fossil material, well-exposed outcrops, and convenient travel conditions, the Zhichang section has become increasingly important to the study of the Early Devonian Posongchong flora. The Changputang Village, 16 km west of the Zhichang Village, has poor transport facilities.

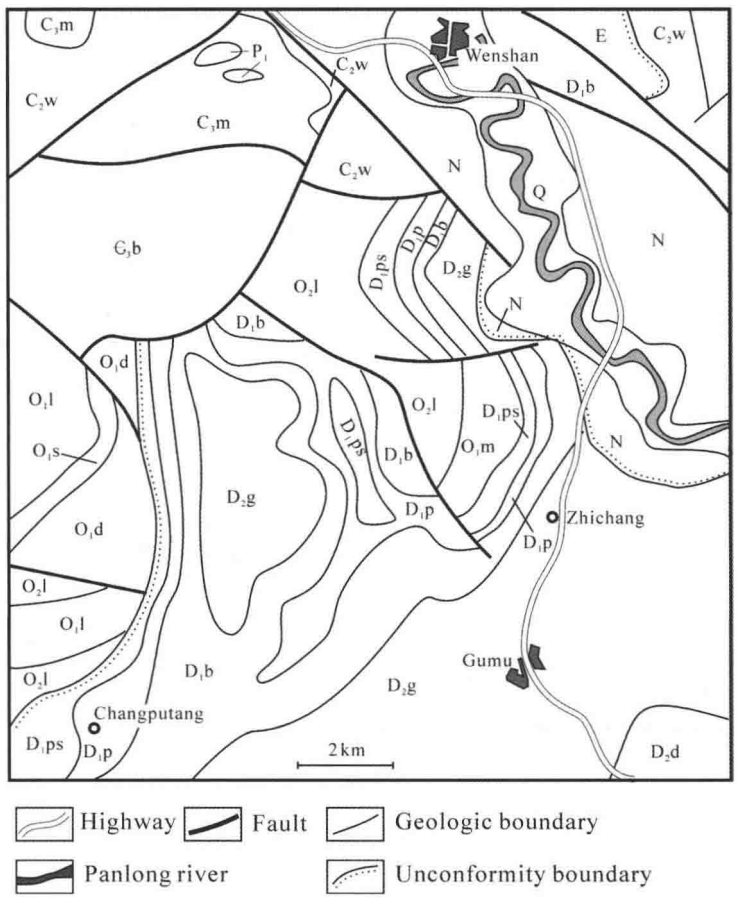

Figure 2.3. General geological map of the Wenshan area in southeastern Yunnan Province, China (modified from 1:200000 Geologic Map Sheets of Wenshan and Maguan[①], also see Li and Ge (2001), and Hao and Xue (2011)).

Abbreviations: Q—Quaternary; E—Paleogene; N—Neogene; P_1—Lower Permian; C_3m—Upper Carboniferous Maguan Formation; C_2w—Middle Carboniferous Weining Formation; D_2d—Middle Devonian Donggangling Formation; D_2g—Middle Devonian Gumu Formation; D_1b —Lower Devonian Bajiaoqing Formation; D_1p—Lower Devonian Pojiao Formation; D_1ps—Lower Devonian Posongchong Formation; O_2l—Middle Ordovician Lengshuigou Formation; O_1l—Lower Ordovician Laozhai Formation; O_1s—Lower Ordovician Shanpianshan Formation; O_1d—Lower Ordovician Dushuke Formation; O_1m—Lower Ordovician Meitan Formation; ϵ_3b—Upper Cambrian Bocaitian Formation. The Cambrian and Carboniferous systems in South China used to be divided into three series, which was retained here, and the correlation of the formations of these periods to the new chronostratigraphic divisions is still in progress.

① The Second Regional Survey Brigade, Geologic Bureau of Yunnan Province. 1978. Geologic Report of Regional Geologic Survey of People's Republic of China—1:200000 Geologic Map Sheets of Wenshan and Maguan.

2.2. Previous studies and main achievements

In China, the first study of putative Early Devonian plant fossils was performed in 1919 by M. Colani of France, slightly after the discovery of *Rhynia* Kidston et Lang in 1917. Colani recorded some significant specimens from Ta-nong-pou in southern Yunnan. However, these specimens were too fragmentary to be identified and their exact location and horizon remain unknown. During the first half of the 20th century, studies of the Devonian stratigraphy and fossil plants concentrated on northeastern and central Yunnan (such as the Qujing-Zhanyi zone). After his field work near Cuifengshan (Mt. Cuifeng) in 1914, Ding Wenjiang (Ting Wenchiang) created the Cuifengshan System to include a suite of deposits of non-marine Lower Devonian of eastern Yunnan. This name was later adopted by Grabau (1923–1924). Halle (1927) reported *Arthrostigma gracile* Dawson from a Lower Devonian or possibly Middle Devonian bed at Zhanyi County in the Qujing area. Later he described *Drepanophycus spinaeformis* Göeppert (=*Arthrostigma gracile* Dawson), *Protopteridium minutum* Halle (=*Eocladoxylon minutum*) and one lycopsid plant *Protolepidodendron scharyanum* Krejči from the Lower and Middle Devonian beds at Longhuashan (Mt. Longhua) of Zhanyi (Halle, 1936; Berry and Wang, 2006a). Subsequently Sze (1941) reported *Psilophyton princeps* Dawson and ?*Hostinella* sp. at Zhaotong in northeastern Yunnan. Hsü (1947) described some Lower–Middle Devonian plants based on fragmentary specimens collected from Qujing and other districts in eastern and central Yunnan. These were *Protolepidodendron scharyanum*, *Taneocrada* cf. *T. dubia* Kräusel et Weyland, *Asteroxylon* cf. *A. elberfeldense* Kräusel et Weyland, etc. It is interesting that, cf. *Zosterophyllum* from Qujing, which has characteristic K-shaped branchings, was the first such plant to be reported in China (Hsü, 1947, Text-figure 5). Other geologists and paleontologists have made foundational but scattered studies on the biostratigraphy and on invertebrates. Generally speaking, studies of the fossil plants were sparse at that time. In the atlas of *Palaeozoic Plants of China* (Gu and Zhi, 1974), only three Early Devonian fossil plants, i.e., *Zosterophyllum yunnanicum* Hsü, *Taeniocrada* cf. *T. dubia* and *Drepanophycus spinaeformis* were recorded and illustrated, which reflects the scattered, unsystematic character of the works of the time.

Major advances were made through large-scale geological survey during the 1960s, when many geological and paleontological workers from both research institutions and industry took part in the studies on the biostratigraphy and different fossil groups of the area. In the following years, paleontological atlases and stratigraphic charts of various provinces were also published, including works on fossil plants and regional stratigraphic charts of the Devonian non-marine or marine-continental transitional facies in Yunnan Province (Hou, 1978). Li Xingxue and Cai Chongyang (1978, 1979) preliminarily established the assemblage sequence of the Devonian floras of South China and presented six floral assemblages. A number of other significant studies focused on different plant groups of the Devonian period. These achievements were summarized in the monograph *Fossil Floras of China Through the Geological Ages*, edited by Li Xingxue (1995).

2.2.1. The Xujiachong flora in Qujing

Since the 1960s, studies on the stratigraphy and fossil plants of the Xujiachong Formation in the Qujing area have been performed continuously. Stratigraphically, the Cuifengshan Group has been divided into, in ascending order, the Xiaxishancun (or Xishancun) Formation,