The Early Devonian Posongchong Flora of Yunnan

—— A Contribution to an Understanding of the

Evolution and Early Diversification of Vascular Plants

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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

Charles B. Beck
Professor Emeritus of Botany
University of Michigan

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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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

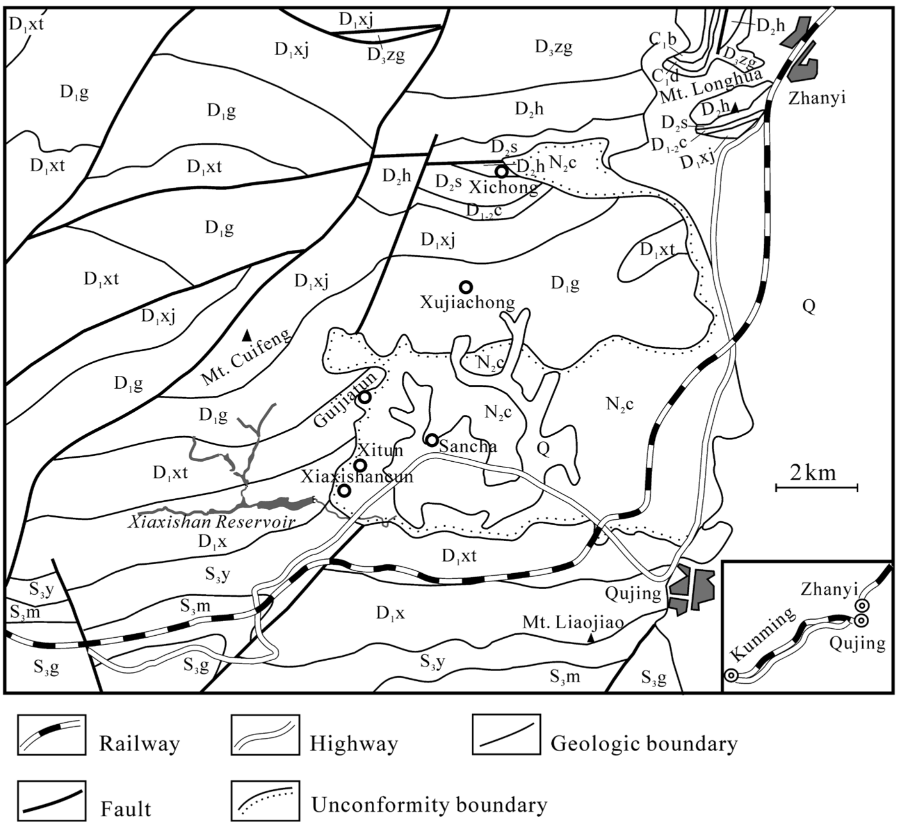

Figure 2.2. General geological map of the Qujing area in northeastern Yunnan Province, China (modified from 1:200000 Geologic Map Sheet of Qujing[1], also see Li and Ge (2001), and Hao *et al.* (2007)).

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.

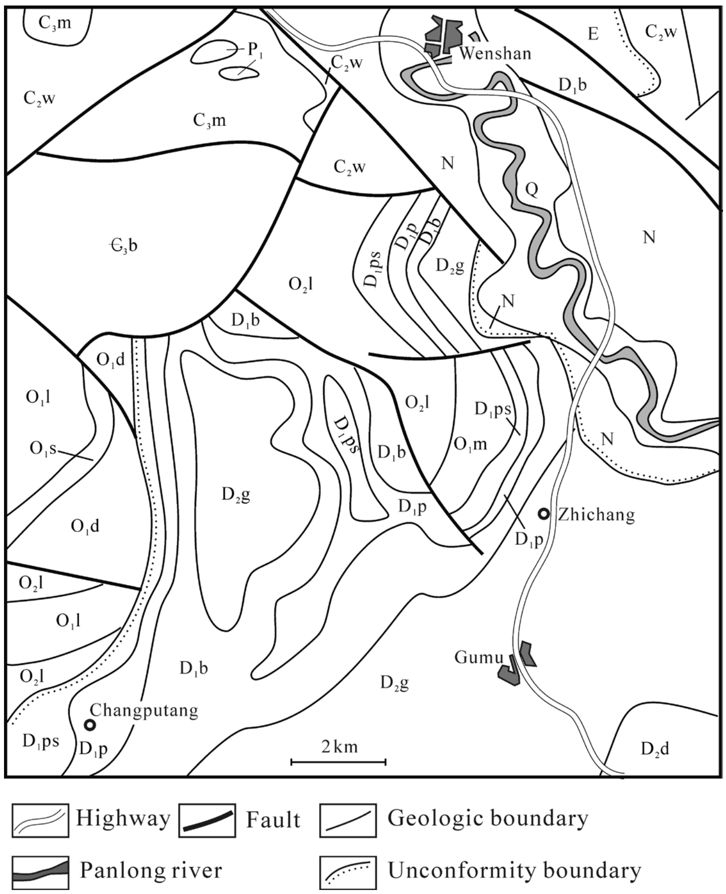

Figure 2.3. General geological map of the Wenshan area in southeastern Yunnan Province, China (modified from 1:200000 Geologic Map Sheets of Wenshan and Maguan①, also see Li and Ge (2001), and Hao and Xue (2011)).

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; $Є_3b$—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, the Xitun Formation, the Guijiatun Formation, and the Xujiachong Formation (Liu *et al*., 2004 and references therein). The Xujiachong Formation was also called the Cuifengshan Formation by the Second Regional Survey Brigade, Geologic Bureau of Yunnan Province① and the Longhuashan Formation by Li and Cai (1978, 1979). These four formations are generally considered Early Devonian in age, but their exact age is still a matter of controversy (Rong and Chen, 2000; Tian *et al*., 2011; Xue, 2012). Li Xingxue and Cai Chongyang (1978) suggested that the Xiaxishancun Formation and the Xitun Formation are Gedinnian (Lochkovian) in age, that the Guijiatun Formation is roughly Siegenian (Pragian), and that the Xujiachong Formation is roughly Emsian (Table 2.1). These suggestions should be considered tentative, and may be revised when further evidence is obtained (Cai, 2000). Currently, regarding the Xujiachong Formation, comprehensive analyses of spore assemblages (Gao, 1981), stratigraphic sequences, floras and faunas (fish and bivalves), and biostratigraphic correlations indicate that this formation could be considered to be late Pragian to early Emsian in age (Wang, Hao and Liu, 2002; Wang, 2007). However, based on palynological evidence, Tian *et al*. (2011) suggested a late Lochkovian to Pragian age for the Xujiachong Formation. Detailed investigation of the spore assemblages from the upper part of the Xujiachong Formation indicates an early Pragian to ?earliest Emsian age (Wellman *et al*., 2012). The Siluro-Devonian boundary, which was once placed at the base of the Xiaxishancun Formation (Fang *et al*., 1994; Cai, 2000; Hao *et al*., 2007), was suggested to occur in the middle part of the Xitun Formation (Tian *et al*., 2011).

Table 2.1. Division and dating of the Early Devonian deposits in Qujing and Wenshan districts of Yunnan Province and area of Zhuang Autonomous Region of Guangxi

Age		Li and Cai, 1978			Bureau of Geology and Mineral Resources of Yunnan Province, 1990			Zhu, Wang and Fan, 1994			Cai, 2000		This book	
Middle Devonian	Eifelian				Chuandong Fm.	Gumu Fm.	Yingtang Fm.		Gumu Fm.	Yingtang Fm.	Chuandong Fm.	Gumu Fm. / Daliantang Fm.	Chuandong Fm.	Gumu Fm.
Early Devonian	Emsian	Longhuashan Fm. / Guijiatun Fm.	Dalian-tang Fm. / Pojiao Fm.	Tangding Fm. / Yujiang Fm.	Cuifengshan Fm.	Gumu Fm. / Daliantang Fm.	Sipai Fm. / Yujiang Fm.	Xujiachong Fm.	Pojiao Fm.	Sipai Fm. / Yujiang Fm.	Chuandong Fm. / Longhuashan Fm.	Daliantang Fm. / Pojiao Fm.	Chuandong Fm. / Xujiachong Fm.	Gumu Fm. / Bajiaoqing Fm. / Pojiao Fm.
	Pragian	Guijiatun Fm.	Posongchong Fm.	Nagaoling Fm.	Guijiatun Fm. / Xitun Fm.	Pojiao Fm.	Yujiang Fm. / Nagaoling Fm.	Xujiachong Fm. / Guijiatun Fm.	Posong-chong Fm.	Nagao-ling Fm. / Lianhuashan Fm.	Longhuashan Fm. / Guijiatun Fm.	Posongchong Fm.	Xujiachong Fm. / Guijiatun Fm.	Posong-chong Fm.
	Lochkovian	Xitun Fm. / Xiaxishan-cun Fm.		Lianhua-shan Fm.	Xitun Fm. / Xiaxishan-cun Fm.	Posongchong Fm.	Lianhuashan Fm.	Xitun Fm. / Xiaxishan-cun Fm.		Lianhuashan Fm.	Guijiatun Fm. / Xitun Fm. / Xiaxishan-cun Fm.		Xitun Fm. / Xiaxishan-cun Fm.	

Notes: Under the first three references, left column represents formations of Qujing area, middle column to those of Wenshan area, and right column to those of Guangxi. Modified from Table 1 of Liu *et al*. (2004).

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.

The first detailed description of *Zosterophyllum yunnanicum* Hsü was from the Xujiachong Formation (Hsü, 1966). Li Xingxue and Cai Chongyang (1977) published their preliminary article on the Early Devonian *Zosterophyllum* remains, and demonstrated distinct diversification of zosterophyllopsids in southwestern China. They described 29 species of *Zosterophyllum*, including seven new species, such as *Z. longhuashanense* Li X.X. et Cai, *Z. spathulatum* Li X.X. et Cai, *Z. bifurcatum* Li X.X. et Cai from the Cuifengshan Group and others from the Posongchong Formation in Yunnan (see section 2.2.2) and the equivalent strata in adjacent provinces. Among them, however, *Z.* cf. *Z. yunnanicum* and *Z.* spp. have been identified as *Z. yunnanicum* (Cai and Schweitzer, 1983; Hao, 1985), and "*Z. subverticillatum*" and "*Z. contiguum*" were assigned to two new genera by Li C.S. and Edwards (1992, 1996) (see section 2.2.2). Li Daiyun (in Fang *et al.*, 1985) described a new genus *Scopulaphyton*, and up to ten new plant species including those of *Asteroxylon*, *Taeniocrada*, *Dawsonites*, as well as two species of *Drepanophycus* and one species of *Zosterophyllum* from the Xujiachong Formation. Most of the specimens lacked fertile organs and were too fragmentary for an unequivocal identification and for comparison with other plants (Cai and Wang, 1995). *Hsüa robusta* (Li X.X. et Cai) Li C.S. was established from the Xujiachong Formation at the Longhuashan section (Li C.S., 1982, 1992a). Its vegetative and fertile specimens were considered separate species, *Taeniocrada robusta* and *Cooksonia zhanyiensis*, by Li X.X. and Cai (1977). Li Chengsen studied in detail the anatomy of *Hsüa robusta*, which shows a centrarch primary xylem strand.

Li Chengsen and Edwards (1995) described a new species of *Drepanophycus*, *D. qujingensis*. It differs from *D. spinaeformis* in its predominantly recurved leaves and anomocytic stomata. Further observation on the tracheid structure of *Hsüa deflexa* Wang D.M., Hao et Wang Q., which strikingly resembles *Hsüa robusta*, indicates that the tracheid structures once regarded as simple pits in the walls may be artificial due to preservation (Wang D.M., Hao and Wang Q., 2003a, b). Studies on *Zosterophyllum australianum*, *Huia gracilis* Wang et Hao, *Guangnania cuneata* Wang et Hao, *Hedeia sinica* Hao et Gensel and *Bracteophyton variatum* Wang et Hao added the members of the Xujiachong flora (Hao, 1992; Wang and Hao, 2001, 2002, 2004). In the Lower Devonian deposits of the Qujing area, there are a few plants with possible algal affinities, such as *Emplectophycus yunnanensis* Li X.X. et Cai (Fang *et al.*, 1985; Cai and Wang, 1995). Li Daiyun and Ge (2001) made a preliminary survey of these plants. The plant components of the Xujiachong Formation have been enriched by all these studies, which contribute to a deeper understanding of the diversification of early vascular plants. Common plant members offer direct evidence for a close relationship between the Xujiachong flora and Posongchong flora (Wang, Hao and Liu, 2002). There have also been some significant advances in relation to palaeogeography, stratigraphic correlation, and sedimentary environmental study (Lu and Ouyang, 1976; Gao, 1981, 1984; Pan and Wang, 1981; Fang *et al.*, 1994; Zhu, Wang and Fan, 1994; Li D.Y. and Ge, 2001; Wang D.M., Hao and Liu, 2002; Liu *et al.*, 2004). Currently, workers have begun to pay more attention to the floras of early Early Devonian (Lochkovian) and Middle Devonian (e.g., Wang Y. and Berry, 2001a, 2006; Berry and Wang Y., 2006a, b; Hao *et al.*, 2007, 2010; Xue, 2009, 2012).

2.2.2. The Posongchong flora in Wenshan

The Posongchong Formation of the Lower Devonian was established by Liao *et al.* (1978). The type section is found along a valley near the Posongchong Village in Guangnan County. The Zhichang section of the Posongchong Formation was discovered through a geological survey performed by the Second Regional Survey Brigade, Geologic Bureau of Yunnan Province in the 1960s (Bureau of Geology and Mineral Resources of Yunnan Province, 1990). In the 1980s, Professor Jin Shanyu and some students from Peking University made a detailed stratigraphic measurement and performed a systematic collection of invertebrate fossils from the marine Pojiao Formation of the Lower Devonian through all the rest of the Devonian (Jin *et al*., 2005). During that time, the Changputang section of the Posongchong Formation was discovered by Hao Shougang (Hao and Beck, 1991a). Since the 1970s, along with the discoveries of many unique plants, interest in the Posongchong flora has been increasing, some new fossil genera and species have been established, and others have been discussed and clarified. Many paleobotanists participated in these studies. The Chinese workers included Li Xingxue, Cai Chongyang, and Wang Yi (Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences); Li Chengsen, Geng Baoyin, Zhu Weiqing, and Yang Nan (Institute of Botany, Chinese Academy of Sciences); Li Daiyun (Geological Institute of Yunnan); Hao Shougang, Wang Deming, Wang Qi, Xue Jinzhuang, and Zhu Xiao (Department of Geology, Peking University). Foreign paleobotanists included Charles B. Beck (The University of Michigan, U.S.A), Dianne Edwards (Cardiff University, U.K.), Patricia G. Gensel (University of North Carolina, U.S.A), Francis M. Hueber (National Museum of Natural History, Washington, D.C., U.S.A), Paul Kenrick (The Natural History Museum, U.K.), and Philippe Gerrienne (Université de Liège, Belgium). The collaboration and academic exchange undoubtedly improved the laboratory techniques and enhanced the quality of studies.

Li Xingxue and Cai (1977) made the first investigation involving megafossil plants of the Posongchong flora and illustrated four species under the genus *Zosterophyllum*. They are *Zosterophyllum australianum* Lang et Cookson, Z.? sp., "*Z. contiguum*" and "*Z. subverticillatum*", which were separately described from different sections of the Posongchong Formation at Daliantang in Guangnan and Zhichang in Wenshan. The latter two species were assigned separately to *Adoketophyton subverticillatum* and *Demersatheca contigua* by Li Chengsen and Edwards (1992, 1996). Cai and Wang (1995) reported *Taeniocrada* cf. *T. decheniana* (Göeppert) Kräusel et Weyland and *Drepanophycus*? *gaspinanus* (Dawson) Kräusel et Weyland from this formation, but these plants were not illustrated.

Researchers from the Institute of Botany, Chinese Academy of Sciences have made some important findings regarding the Posongchong flora. Geng (1983, 1985) described two new plants, *Stachyophyton yunnanense* Geng and *Huia recurvata* Geng from the Zhichang section. The former possesses planate leaf-like branches and strobili at the tips of fertile branchlets. Wang Yi and Cai (1996) supplemented the anatomic information of *Stachyophyton*, which has an exarch primary xylem strand. *Huia* has terminal spikes consisting of long-ovate sporangia recurved adaxially downwards, and a centrarch protostele. These works showed for the first time a unique combination of morphological and anatomical characteristics among the Posongchong plants. *Adoketophyton subverticillatum* and *Demersatheca contigua* also have novel morphology and architecture (Li C.S. and Edwards, 1992, 1996). *A. subverticillatum* bears terminal strobili composed of fan-shaped sporophylls with stalked sporangia (Li C.S. and Edwards, 1992) and centrarch primary xylem (Hao, Wang and Beck, 2003). Li Chengsen and Edwards (1997) described a new lycopsid, *Halleophyton zhichangense*. Li Chengsen and Hueber (2000) described a questionable sphenopsid plant, *Cervicornus wenshanensis*. Zhu and Kenrick (1999) described a zosterophyllopsid, *Wenshania zhichangensis*. More recently, *Hueberia zhichangensis* was established based on vegetative axes with closely helically arranged enations (Yang, Li and Edwards, 2009). It superficially resembles the Early Devonian primitive lycopsids such as *Asteroxylon* and *Drepanophycus*.

Hao Shougang first came to the Zhichang slope in the 1980s, where he began his preliminary collection of fossil plants, starting with the interesting megaphyllous plant *Eophyllophyton bellum*, which Hao (1988) described mainly based on morphological characteristics of the compression and impression material. Based on more additional collections and anatomically preserved material from other new outcrops, Hao and Beck (1993) supplemented the significant anatomical information of this plant, and revised the generic diagnosis of *Eophyllophyton*.

During the past 30 years, the paleobotanical team of the Department of Geology, Peking University, explored numerous other localities in southeastern Yunnan, including the Guangnan, Mengzi, Xichou, and Yanshan districts. Some beautiful fossil plants have been studied. Among them, the less complex zosterophyllopsids include four new taxa: *Discalis longistipa* Hao; *Gumuia zyzzata* Hao; *Ramoferis amalia* Hao et Xue; possible zosterophyllopsid *Guangnania cuneata* Wang D.M. et Hao; and two *Zosterophyllum* species, *Z. australianum* and *Z. ramosum* Hao et Wang (Hao, 1989a, b; Hao and Wang, 2000; Wang D.M. and Hao, 2002; Hao and Xue, 2011). The trimerophytes include *Psilophyton primitivum* Hao et Gensel and *Pauthecophyton gracile* Xue *et al*. (Hao and Gensel, 1998; Xue *et al*., 2012). Some other plants showed unusual or more advanced combination of morphological and structural features which had never been seen in other coeval floras. They include: *Catenalis digitata* Hao et Beck, which is probably a primitive vascular plant of algal derivation (Hao and Beck, 1991a); *Yunia dichotoma* Hao et Beck, a genus whose centrarch protostele has protoxylem area consisting of parenchyma cells and small tracheids (Hao and Beck, 1991b; new material offers definitive evidence of a connection between the sporangia and fertile axes in this book; see section 4.2.13); *Celatheca beckii* Hao et Gensel, an unusual plant with synangium-like fertile structure (Hao and Gensel, 1995); *Polythecophyton demissum* Hao, Gensel et Wang, a plant with more or less adaxially borne fusiform sporangia forming clusters (Hao, Gensel and Wang, 2001); *Estinnophyton yunnanense* Hao, Wang D.M. et Wang Q., showing the probably primitive sporangiophore-like structure of the sphenopsids (Hao, Wang D.M. and Wang Q., 2004); and *Zhenglia radiata* Hao *et al*., a typical herbaceous lycopsid with microphylls and sporophylls (Hao *et al*., 2006). Recently, two unusual plants have been described. *Dibracophyton acrovatum* Hao *et al*. has terminal strobili of fertile units, each of which consists of a stalked long-elliptical sporangium covered by two discrete bracts (Hao *et al*., 2012). *Pauthecophyton gracile*, a newly discovered trimerophyte, has pseudomonopodial branches and lateral dichotomous branches terminating in clustered sporangia (Xue *et al*., 2012). It is difficult to classify some of these plants into the traditional taxonomic categories of the Early Devonian plants. The affinities of many of these plants were once regarded as uncertain, and, as stated by Edwards (1997), "their classification and phylogeny certainly present a significant challenge to future researches".

In the meantime, there have been several advances in relation to the studies of phytogeography and paleoenvironment. The concept of the northeastern Gondwanan phytogeographical unit during the Early Devonian was first proposed by Hao and Gensel (1998). In a preliminary summary study, the remarkable diversification of the Posongchong flora has been discussed through a comprehensive comparison between the Posongchong flora and coeval floras, and possible reasons for this have been discussed (Hao and Gensel, 2001). South China was reasonably suggested to represent one of the centers of radiation and evolution of early vascular land plants (Hao and Wang, 2003). In addition, based on morphological and anatomical evidence of the megaphylls of *Eophyllophyton*, adaptation of these rudimentary true leaves to an environment with high concentration of atmospheric CO_2 have been suggested (Hao, Beck and Wang, 2003).

Previous advances mainly involved the recognition of different types of plants and the discussion of their evolutionary relationships. There are still many important questions regarding the phylogeny, classification, evolution, and paleoenvironments. The available information produced by comparative morphology studies is still incomplete, when viewed with the concept of whole fossil plants (Crane, Herendeen and Friis, 2004). Most plants lack sufficiently detailed anatomical descriptions, except for only a few completely known plants, such as *Eophyllophyton* and *Adoketophyton*. Some taxa remain poorly understood, and further field collection and laboratory work are needed. For example, *Polythecophyton* lacks vegetative morphology and anatomy, and *Zhenglia* lacks a complete morphology and anatomy, and more data would allow a complete reconstruction of these two important plants. A steady accumulation of morphological and anatomical data is contributing significantly great depth in the analyses of the diversification and evolution of early vascular plants.

3. Stratigraphy and Sedimentary Environments

3.1. Geological setting

3.1.1. Geological setting of Yunnan Province

During the Devonian, the present China consisted of up to 11 variously sized palaeoplates, including all or part of the Siberia, Kazakhstan, Songhua River-Bureja, Tarim, Qilian-Qaidam, North China, Hoh Xil-Bayan, Xizang (Tibet), Yangtze (South China), Shan Thai-Malaya (Sibumasu), and India plates (Scotese and McKerrow, 1990; Liao and Ruan, 2003; Boucot *et al*., 2009; Wan and Zhu, 2011). The Tarim, Qaidam and North China plates were regarded as a vast northern continent by Wang H.Z. *et al*. (1990). The Yangtze plate (South China plate) comprised at least three subregions: Cathaysia, Longmenshan, and Guangxi-Hunan (including eastern Yunnan and southern Guizhou). In Yunnan Province, the Lancangjiang (Lancang River) rift zone is a boundary dividing eastern and western Yunnan, which are traditionally considered part of the Guangxi-Hunan subregion of the Yangtze plate and part of the Shan Thai-Malaya paleoplate (Figure 3.1). In both eastern and western Yunnan, there are some localities with Early Devonian plant fossils. Plant fossils are particularly abundant and diverse in eastern Yunnan. The presence of the North Vietnam platform has been suggested, which was adjacent to, and located on south of Wenshan-Mengzi during the Palaeozoic. It has been suggested that the North Vietnam platform was an isolated tectonic element from the Yangtze platform, because of the absence of the Sinian System (Neoproterozoic) and difference in geologic setting (Wu, 2003). Perhaps deposits of the Posongchong Formation were also related with geologic setting of the North Vietnam platform. Other Lower Devonian plant-bearing localities can be found in Sichuan, Guizhou, and Guangxi, all of which are part of the Yangtze platform. A Silurian plant assemblage has been reported from the Junggar region of northwestern Xinjiang in northwestern China, which was probably part of the Kazakhstan paleoplate (Cai, Dou and Edwards, 1993; Li X.X. and Wu, 1996). No irrefutable Lower Devonian plant localities have yet been found in the North China paleoplate (Hao and Gensel, 2001).

Due to the influence of the Caledonian orogeny, the paleogeographic pattern of South China was changed in the Early Devonian and became distinct from that of pre-Devonian time (Wu, 2001; Rong *et al*., 2003; Liao and Ruan, 2003). Eastern Yunnan was subsiding, and transgression occurred from south to north and gradually began to widen during the middle–late Early Devonian. In the meantime, large rift faults also developed and cut the epicontinental sea into isolated platforms, forming a network of rift valleys and carbonate platforms (Ma, Liao and Wang, 2009). The northwestern part of the Dian-Qian-Gui (short for Yunnan-Guizhou-Guangxi regions) Oldland of the late Silurian, and all southeastern Yunnan were occupied largely by sea, which extended through Wuding-Dongchuang zone into the middle part of eastern Yunnan. The formerly united oldland was divided by marine water into isolated small Chuan-Dian (short for Sichuan-Yunnan Provinces) Oldland, Huize Uplift, and Niutoushan (Niutou Mountain) Paleoisland, with the Wuding and Qujing bays in between. In this way, the palaeogeographic framework of Yunnan contained, from northeast to southwest, a series

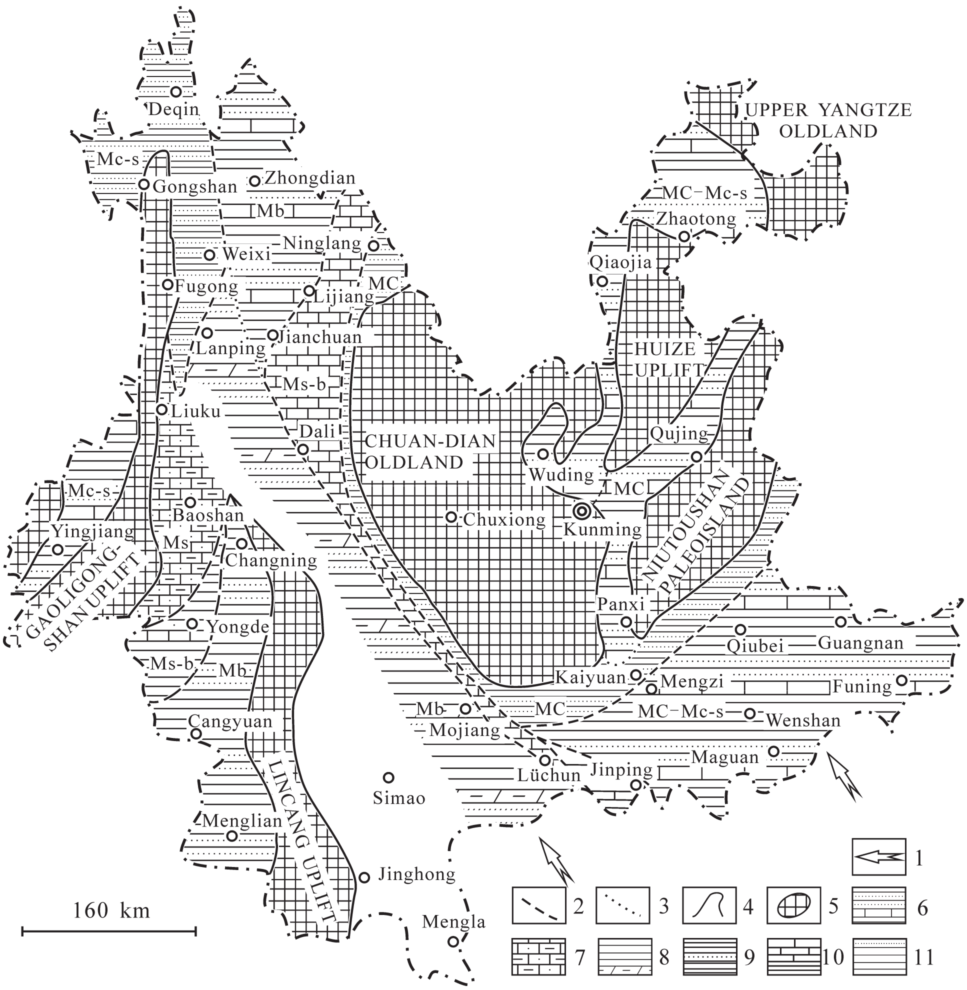

Figure 3.1. Early Devonian lithofacies palaeogeography of Yunnan Province (modified from Bureau of Geology and Mineral Resources of Yunnan Province, 1990)

Abbreviations: 1—Direction of transgression; 2—Lithofacies boundary; 3—Formation boundary; 4—Possible transgressive zone; 5—Oldland or uplift; 6—Shale-Sandstone-Limestone group; 7—Sandy argillaceous limestone group; 8—Sandstone-Shale-Argillaceous limestone interbedded with chert group; 9—Shale-Sandstone-Chert group; 10—Limestone-Shale group; 11—Sandstone-Shale group; MC—Paralic; Mc-s—Littoral facies-Shallow marine facies; Mb—Bathyal facies; Ms—Shallow marine facies; Ms-b—Shallow marine facies-bathyal facies; MC-Mc-s—Paralic-Littoral facies-Shallow marine facies.

of oldlands or islands, specifically the Upper Yangtze Oldland (i.e., the Guangxi-Hunnan subregion), Huize Uplift, Niutoushan Paleoisland, Chuan-Dian Oldland, Lingcang Uplift and Gaoligongshan (Gaoligong Mountain) Uplift, and the intramontane zone, where it changed into shoals or estuaries suitable for sedimentation (Figure 3.1). These complex water-land settings may have created many different topographic areas and habitats for early land plants (also see section 3.3).

Devonian strata in the Yangtze platform may be divided into four facies types based on lithologies, marine faunal and floral compositions: Qujing type non-marine sediments, Xiangzhou type shallow marine facies, transitional type (platform marginal facies) and Nandan type deep water facies (Liao *et al*., 1978; Hou and Wang, 1985; Jin *et al*., 2005; Ma, Liao and Wang, 2009). This division reflects characteristics of sedimentary facies of the Devonian as a whole. However, in Yunnan, except the Qujing type, the Xiangzhou and transitional types have common non-marine deposits (i.e. the Posongchong Formation of late Pragian age) below the Lower Devonian Emsian, such as the Zhichang section (Xiangzhou type) and the Changputang section (transitional type) in Wenshan (Jin *et al*., 2005; Ma, Liao and Wang, 2009).

The non-marine Lower–Middle Devonian strata and fossil plants of Yunnan have become major objectives for Devonian paleobotanists, particularly the Early Devonian Xujiachong Formation of Qujing and Posongchong Formation of Wenshan. The major Devonian plant localities were summarized by Li X.X. and Wu (1996) and Li D.Y. and Ge (2001), and the major plant types at that time, by Cai and Wang (1995). Here, the stratigraphy and related sedimentary environments of the Posongchong Formation, as well as the plant assemblages, as a particular interest of this book, are discussed as follows.

3.1.2. Lower Devonian strata in the Wenshan area

Southeastern Yunnan refers to the area located east of the Lancangjiang rift zone and south of Huize Uplift, Niutoushan Paleoisland and Chuan-Dian Oldland. In this area, two sections i.e. the Zhichang section and the Changputang section of Devonian were examined in detail in the 1980s (Jin *et al*., 2005). They both show marine strata from the Lower Devonian Pojiao Formation up to the top of the Devonian. The underlying non-marine strata (i.e. the Posongchong Formation) of these two sections were examined by Hao (1989a) and Hao and Gensel (1998). Lower Devonian strata at the Zhichang section are well exposed extending from the west to the east, as described in Table 3.1. These Lower Devonian sediments unconformably overlie the quartzose sandstones of the Lower Ordovician Meitan Formation. The four formations, from the base upwards, are as follows: the Posongchong Formation, Pojiao Formation, Bajiaoqing Formation, and the lower member of the Gumu Formation. The marine fauna of the latter three formations indicate an Emsian age (Jin *et al*., 2005) (Table 3.1).

3.1.3. Lower Devonian Posongchong Formation

The Lower Devonian terrestrial-marine deposits of southeastern Yunnan are best developed and most widely distributed in the Wenshan, Guangnan, Mengzi, Xichou, and Yanshan districts (Bureau of Geology and Mineral Resources of Yunnan Province, 1990; Li and Ge, 2001; Liu *et al*., 2004). The Posongchong Formation unconformably overlies Cambrian or Ordovician

Table 3.1. Brief descriptions of the Lower Devonian formations at the Zhichang section

Lithologic unit	Age	Descriptions of the lithology	Fossils
Gumu Formation (lower member)	late Emsian	limestone with dolostone	corals: *Siphonophrentis acheensis* Jing *et al*., etc.; conodonts: *Neopanderodus aequabilis* Telford and *Polygnathus pseudoserotinus* Mawson
Bajiaoqing Formation	early−middle Emsian	limestone and thick-bedded dolostone	corals: *Thamnopora* sp., *Cystiphylloides mirable* (Wedekind et Vollbrecht) and *Siphonophrentis angusta* (Yu); conodonts: *Neopanderodus aequabilis* Telford, *Polygnathus dehiscens abyssus* Mawson and *P. perbonus* (Philip)
Pojiao Formation	early Emsian	gray-green mudstone and shale	brachiopods: *Dicoelostrophia annamitica* (Mansuy), *D. punctata* Wang and *Acrospirifer tonkinensis* (Mansuy); corals: *Calceola sandalina sinensis* Mansuy and *Xystriphylloides nobilis* Yu, Liao et Deng
Posongchong Formation	late Pragian	gray sandstone and gray-black mudstone and shale	plants: *Zosterophyllum australianum*, *Gumuia zyzzata*, *Discalis longistipa*, *Adoketophyton subverticillatum*, *Eophyllophyton bellum*, etc.

Notes: Data from Ruan *et al*. (1979), Zhong *et al*. (1992), Hao and Gensel (2001) and Jin *et al*. (2005).

deposits in different areas, and conformably underlies the early Emsian Pojiao Formation. These deposits are generally composed of fine sandstone, siltstone, and mudstone, but vary in thickness at different sections. In the northwestern part of the Wenshan-Bozhushang zone, there is a layer of basal purplish red conglomerate and sandy conglomerate with feldspar sandstone. In the Wenshan area, this formation has multiple layers of carbonaceous shale and mudstone yielding rich plants; in Xichou of southeastern Wenshan, it has many quartz sandstone layers yielding plants and bivalves, with a thickness of over 1300 m. The Posongchong sandstone at Guangnan yields cross-bedding and scouring structures with marine invertebrates (Li D.Y. and Ge, 2001). During the past three decades, we have examined the Posongchong Formation of these areas and have measured four sections. The Zhichang section is the best one, because of its clear stratigraphic sequence, very rich and well-preserved fossil materials, and ease of access. A more detailed introduction of the Zhichang section is given in the following pages. We would like to thank Liu Zhenfeng, who performed most of the measurement fieldwork during 2002−2003. Other workers included Liu Jianbo, Wang Deming, Xue Jinzhuang, and Hao Shougang. For analyses of the sedimentary and plant living environments, numerous thin rock layers were divided based on the sedimentary cycles. Each rock layer was described for grain size, color variation, and primary sedimentary structure. Samples of critical rock types and some plant-bearing strata were prepared for petrologic examination (Liu *et al*., 2004). The sedimentary facies were compared to the classic models, particularly with those concerning the Early Devonian depositional conditions, some of which were directly associated with plant habitats and burial settings (Wellman *et al*., 2000; Hotton *et al*., 2001; Edwards and Richardson, 2004; Wellman, 2004; Richardson, 2007).

Four sections of the Posongchong Formation in southeastern Yunnan

1. Zhichang section in Wenshan district

The Zhichang section is on the southeast slope of a mountain called Zhichang slope

(Figures 3.2, 3.3). The Posongchong Formation unconformably overlies the quartzose sandstones of the Lower Ordovician Meitan Formation yielding the brachiopod *Sinorthis* sp. A conformable contact is present between the non-marine Posongchong Formation and the overlying marine Pojiao Formation, which consists of neritic or paralic mudstone and siltstone yielding coral and brachiopod fossils (Table 3.1; also see Hao, 1989a). The sequence is basically continuous, although in the lower-middle part of the formation it is in disorder because of faulting and displacement. The strata dip to the south at an angle of 15°−30°. Based on recent survey of the section and studies of sedimentary environment, the Posongchong Formation, 178.32 m in thickness, was divided into 43 sedimentary units, which can be combined into

Figure 3.2. (a) Zhichang Village (viewed from the Zhichang slope). (b) Zhichang slope (viewed from southwest). Photographs by Xue Jia in 2007.

Figure 3.3. Topography of upper part of Posongchong Formation at the Zhichang slope. Photograph by Xue Jia in 2007.

nine stratigraphical layers (see section 3.2). Measurements were made along two southeast trends, monoclinal mountain slopes and in the intervening valley. The final lithological column is synthetic in that the outcrops are intermittently exposed and some parts are covered by vegetation. This section was first measured in 1983; at that time the measurement was made at a road cut along the south slope. Results were published by Hao (1989a, Figure 2). Two formations (i.e., the Posongchong Formation and Pojiao Formation), including their lithology, main fossils and position of collections were demonstrated. The Posongchong Formation of the first measurement is about 158 m in thickness, which is about 20 m less than the recent measurement. It was divided into seven stratigraphical units at that time. Based on the general lithologic features and occurrence of the plant fossils, the present stratigraphic division can be roughly compared to that of Hao (1989a, see Figure 3.4).

Most of the plant megafossils were collected from the scattered sites just west of Zhichang Village. The outcrops occur along the mountain slopes (mostly farmland) and in the intervening valley. Some plant fossils were collected from the measured section. Sites outside the section or at the tilled farmland were generally correlated with the corresponding units at the section as far as possible. A total of over 20 fossil sites containing at least 32 fossil plants have been discovered (Figure 3.4; Table 3.2). Generally, we visited some fossil sites many times, and large blocks were quarried, but in some cases only relatively small hand samples could be gathered. The GPS locations of the main fossil sites are listed in Table 3.2, but some early sites are now difficult to locate because of the covering of farmland or vegetation.

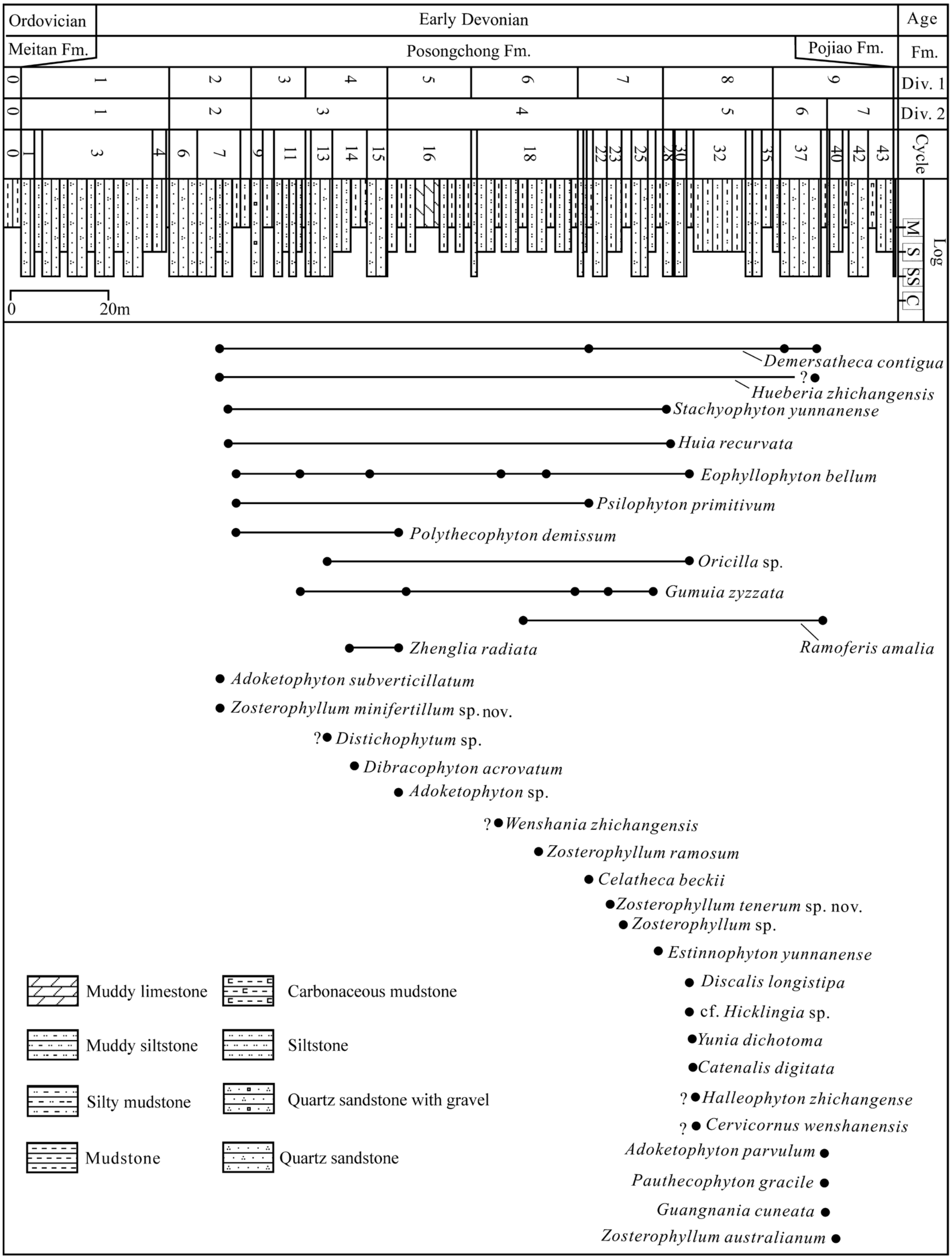

Figure 3.4. Stratigraphic column of Posongchong Formation at the Zhichang section shows distribution of fossil plants. Positions of fossil plants are indicated by black circles; question marks indicate uncertain positions. Div. 1, the new stratigraphic division in this book; Div. 2, the stratigraphic division in Figure 2 of Hao (1989a). M, mudstone; S, siltstone; SS, sandstone; C, conglomerate.

Table 3.2. GPS locations of plant fossils at the Zhichang section

Fossil site	GPS location	Altitude	Plant fossils
1*	23° 17. 53' N, 104° 15. 22' E	1506 m	*Eophyllophyton bellum*, *Psilophyton primitivum*, *Polythecophyton demissum*
2*	23° 17. 52' N, 104° 15. 23' E	1497 m	*Stachyophyton yunnanense*, *Huia recurvata*
3*	23° 17. 51' N, 104° 15. 22' E	1496 m	*Adoketophyton subverticillatum*, *Hueberia zhichangensis*, *Demersatheca contigua*, *Zosterophyllum minifertillum* sp. nov.
4*	23° 17. 50' N, 104° 15. 28' E	1475 m	*Eophyllophyton bellum*, *Zosterophyllum ramosum*, *Dibracophyton acrovatum*
5	23° 17. 51' N, 104° 15. 29' E	1474 m	*Zhenglia radiata*
6	23° 17. 50' N, 104° 15. 30' E	1468 m	*Eophyllophyton bellum*
7	23° 17. 52' N, 104° 15. 30' E	1457 m	*Polythecophyton demissum*
8*	23° 17. 51' N, 104° 15. 33' E	1443 m	*Gumuia zyzzata*, zosterophyllopsids
9	23° 17. 54' N, 104° 15. 29' E	1445 m	*Adoketophyton* sp.
10	23° 17. 48' N, 104° 15. 31' E	1456 m	*Gumuia zyzzata*, *Wenshania zhichangensis*
11*	23° 17. 45' N, 104° 15. 31' E	1415 m	*Zosterophyllum tenerum* sp. nov.
12	23° 17. 43' N, 104° 15. 31' E	1402 m	*Zosterophyllum tenerum* sp. nov.
13*	23° 17. 44' N, 104° 15. 32' E	1401 m	*Estinnophyton yunnanense*
14*	23° 17. 44' N, 104° 15. 32' E	1406 m	*Eophyllophyton bellum*, *Discalis longistipa*, *Catenalis digitata*, *Yunia dichotoma*, *Oricilla* sp., cf. *Hicklingia* sp., *Taneocrada*-like axes
15*	23° 17. 41' N, 104° 15. 33' E	1422 m	*Eophyllophyton bellum*
16*	23° 17. 43' N, 104° 15. 33' E	1398 m	*Adoketophyton parvulum*, *Pauthecophyton gracile*
17*	23° 17. 43' N, 104° 15. 34' E	1403 m	*Guangnania cuneata*, *Demersatheca contigua*, *Ramoferis amalia*
18	23° 17. 58' N, 104° 15. 25' E	1484 m	*Stachyophyton yunnanense*, *Adoketophyton subverticillatum*, *Distichophytum* sp.
19*	23° 17. 58' N, 104° 15. 32' E	1455 m	*Demersatheca contigua*, plant fragments
20*	23° 17. 58' N, 104° 15. 33' E	1449 m	*Eophyllophyton bellum*

Notes: The GPS data were taken in December, 2006 by Hao Shougang and Xue Jinzhuang. The definite GPS locations are marked by *. Others are less certain because the original fossil outcrops either can not be undoubtedly located or are covered by farmlands or vegetations.

2. Changputang section in Wenshan district

The Changputang section is a roadside exposure on the Tiechan slope, about 400 m northwest of Changputang Village (Figure 3.5). Here the Posongchong Formation has a total thickness of about 197 m, and the stratigraphic and lithologic characteristics are similar to those of the Zhichang section (Hao and Gensel, 1998). A thin basal layer of conglomerate disconformably separates it from the quartzose sandstone with glauconite of the Middle Ordovician Shizipu Formation (the age is based on lithologic correlation, no direct fossil evidence). It is conformably overlain by marine mudstone of the Pojiao Formation containing abundant marine invertebrate fossils. We have reported for the first time the following plants from the Posongchong Formation of this section: *Catenalis digitata* (Hao and Beck, 1991a), *Celatheca beckii* (Hao and Gensel, 1995), *Zosterophyllum australianum* (Hao and Gensel, 1998), *Ramoferis amalia* (Hao and Xue, 2011) and *Hedeia sinica* (Hao and Gensel, 1998). Several taxa found from the Zhichang section are also documented at this section: *Gumuia*