Chapter 7
Extinction Pattern and Recovery of the Permian–Triassic Flora in South China

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7.1 On Researching the Extinction Pattern and Recovery of Plants During the Permian–Triassic Transition

The end-Permian mass extinction and its subsequent survival and recovery patterns have been studied by many geologists and paleontologists in the last two decades. A number of papers involving extinction patterns and controlling factors of the mass extinctions, have been published (Peng and Shi 2009; Fielding et al. 2019; Vajda et al. 2020). To this extinction pattern, geologists made suggestions, such as catastrophe, step-wise and gradualism (Kauffman 1987); pulse pattern and press pattern (Erwin 1996); two episodes (Rong and Fang 2004; Xie et al. 2005) and so on. This great extinction event affected not only marine realm, but also the terrestrial ecosystem. The Cathaysian Flora, for example, which thrived in the Permian, became extinct as a whole. In contrast, little is known about the Early Triassic flora of South China, suggesting a desolated and impoverish environment on the ancient land. This displays the disruption of land ecosystem that led to the degradation and the delay of recovery after the mass extinction.

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In discussing terrestrial P–T vascular plants extinction, some scholars tend to put them together with the transformation from paleophyte into mesophyte. As a matter offact, the two problems are not similar though they may be related to each other (Rong and Fang 2004). It is known that the transformation of paleophyte into mesophyte should have suffered a long evolution over 40 Ma, related to the change of climate, characterized by diachronic developments in different areas (Meyen 1973; Knoll 1984; Traverse 1988). For instance, the wetland or swamps well developed in Carboniferous disappeared rapidly; the coal swamp forest dominated by woody lycopods began to vanish at the beginning of Early Permian in this Euramerican domain. This started the transformation from paleophyte into mesophyte marked by widespread development of highland flora and the large-scale occurrence of Peltaspermales represented by *Autunia* in this period. In contrast, South China only witnessed this transformation in Early Triassic though the area also lies in the ocean-island block of the equatorial zone, where the coal-forming flora maintained the basic paleophytic outlook until Changhsing stage (Ouyang 1982).

As described above, the vegetations in Euro-America and in South China all changed greatly at the end of Permian although the former had entered earlier mesophytic conditions and the latter, the Cathaysian area, still remained in paleophytic paleoenvironments, both of which are characterized in common by the occurrence of new type of lycopods and the substitution of the original plants (Fang 2004). It has been assumed that the vegetation transformation should be the result of the global sudden catastophe and should have no relation with whether they entered mesophytic time, for the characteristics of this event is different from the progressive change from paleophyte into mesophyte. Meanwhile, the palynofloras also prove that the vegetations in the world experienced sudden changes to a great extent at the turn from Permian to Triassic. It is found that the Late Permian palynomorphic assemblages in the most areas of the northern hemisphere are dominated by gymnospermae pollens, with the typical examples found in middle Euramerican flora and Angara flora (Utting and Piasecki 1995). At the traditional marine Permian–Triassic boundary, gymnospermae pollen grains from the upland floras are suddenly replaced by the coastal low diversity assemblages characterized by lycopods (Balme 1970; Utting and Piasecki 1995; Eshet et al. 1995; Visscher et al. 1996; Looy et al. 1999, 2001; Twitchett et al. 2001). However, in South China are dominated by Pteridophytic and Pteridospermous spores in Late Permian, dominated by gymnospermae pollen grains in Early Triassic.

The previous geological workers also researched the paleofloral changeovers across the Permian–Triassic boundary in non-marine depositional areas of South China (Yao et al. 1980; He et al. 1996; Li 1995; Yu et al. 2007, 2015). They considered that the paleofloral evolution is a gradual change in this period. Ouyang (1986) indicated that the evolution of plants during Late Permian and Early Triassic had a sharp continuity by analyzing the Late Permian and Early Triassic palynomorph assemblages in Fuyuan District, Yunnan Province. Wang and Yin (2001) proposed that the plants showed an obvious break, while having a shade during the break by researching the fossil plants from non-marine Permian–Triassic transitional strata in western

Guizhou and eastern Yunnan. Fang (2004) pointed out that terrestrial Permian–Triassic vascular plants presented two-episodes extinctions during the Permian–Triassic transition. Now based on the data from both macroflora and microflora studied from the non-marine PTB sections, including four non-marine PTB sections in present dissertation and several other non-marine in western Guizhou and eastern Yunnanstudied by previous workers. (Yao et al. 1980; Zhao et al. 1980; Ouyang and Li 1980; Ouyang 1982, 1986), the changing patterns of land vegetation across the non-marine PTB in South China will be discussed in the following.

7.2 Changes of Mega-Flora Fossils from the Late Permian to Early Triassic

Fossil Plants are the most common megafossils found in the non-marine PTB sections in western Guizhou and eastern Yunnan,and are usually highly concentrated in the Upper Permian associated with abundant coal beds/seams. They are composed mainly of Filicopsida, Pteridospermopsida, Sphenopsida, Lycopsida, Gigantopteridales and some members of Cycadopsida, Ginkgopsida and Cordaitopsida. In comparison, the Lower Triassic in the study area is poorly fossiliferous; until now only a few macrofloral fossils have been found from the Lower Triassic Kayitou Formation. This disparity in the diversity of early Triassic plant species clearly contrasts with the diverse flora in the Late Permian.

7.2.1 Short-Term Mega-Flora Changes Across the PTB

In western Guizhou and eastern Yunnan, the abundance and diversity of plants demonstrate profound changes across the PTB interval. Plant fossils are abundant in the Late Permian strata in the whole area, with up to 59 genera and 138 known species recorded (data after Li 1995). The most common plant genera found are those typical of the Cathaysian *Gigantopteris* flora; notable examples are *Gigantopteris, Gigantonoclea, Fascipteris, Taeniopteris, Lobatannularia* and *Tingia*, etc. In contrast, the Earliest Triassic vegetation was low in abundance and diversity, with only 15 genera and 19 known species represented (data after Zhao et al. 1980), and locally, such as in the paralic Mide and Tucheng sections, they are associated with typical Early Triassic marine bivalve species such as *Pteria ussurica variabilis* and *Pteria ussurica.* In general, the sparse and monotonous Early Triassic vegetation is mainly composed (found up to date) of *Annalepiszeilleri* Fliche, *A. latiloba* Meng*, A. brevicystis* Meng, *Peltaspermum lobulatum* Wang and Wang, cf. *Peltaspermum martinsii* sterile foliage (Germar) Poort and Kerp., *Annularia shirakii* Kawasaki, *Compsopteriscontracta* Gu and Zhi, *Cordaites principalis* Geinitz, *Gigantonoclea* sp., *Gigantopteris* sp., *Lobatannularia* sp., *Paracalamites stenocostatus* Gu and Zhi, *Pecopteris* sp., *Rajahia guizhouensis* Zhang. Most of the listed Early Triassic species are relicts of the Permian Cathaysian *Gigantopteris* flora. They extended to the early Early Triassic as the survivals, lastly gradually disappeared along with the occurrences of *Annalepis* and *Peltaspermum.* Only two genera *Annalepis and Peltaspermum*, considered to be Triassic newcomers, were found in the Lower Triassic of the Mide and Tucheng sections.Thus, the regional disappearance of plants across the PTB in the study area appears to be gradual.

7.2.2 *Long-Term Changes of Megaplants from Late Permian to Early Triassic*

As any temporal patterns of diversity changes are very much a function of time scale used, it is therefore considered important to also consider the patterns of megaplant changes across a longer timescale, which in this case refers to the interval from Wuchiapingian to the Early Triassic Griesbachian. To do this, we compiled a stratigraphic database of megaplant distributions in western Guizhou and eastern Yunnan, (mainly based on data from Zhao et al. 1980; Li 1995; collecting by the author etc.). As statistically illustrated in Table 7.1, plant genera and species gradually decreased

Table 7.1 Genus and species number of the groups of the paleofloras and percentage of species in western Guizhou and eastern Yunnan, South China

Type	Genus		Species		Percentage of species (%)	
	Changhsingian	Induan	Changhsingian	Induan	Changhsingian	Induan
Lycophyta, Lepidodendrales and Isoetales	4	3	13	6	12.4	33.3
Sphenophytes	6	2	15	2	14.3	11.1
Pteridophytes	7	1	29	1	27.6	5.6
Progymnospermophyta, Noeggerathiales	1		3		2.9	
Pteridospermophyta	7	3	18	4	17.1	22.2
Cycadophyta	2		3		2.9	
Ginkgophyta	2	1	4	1	3.8	5.6
Cordaitopsida	1		3		2.9	
Gymnospermum seeds	1		1		1.0	
Gigantopteridales	2	2	11	2	10.5	11.1
Glossopteridales	2		2		1.9	
Plantae incertae sedis	4	2	4	2	3.8	11.1
Other forms	2		2		1.9	
Total	**39**	**14**	**105**	**18**	100.0	100.0

from 47 genera and 114known species in the Wuchiapingian, to 45 genera and 87 known species in the Changhsingian, and only 15 genera and 19 known speciesin the Induan. Regionally, up to date the PTBST (Beds 66f-68 in Chahe section; Beds 47–49 in Zhejue section), has only recorded two genera and three species. In other words, about 24% of megaplant species were eliminated at the end-Wuchiapingian, and those species that survived into the Changhsingian mostly also decreased in abundance. About 90% species of the Changhsingian flora were the descendents of Wuchiapingian taxa, and only about 15% of species originated in the Changhsingian. At the end of the Changhsingian, about 80% of species vanished (Table 7.1). The surviving 12 known species in the earliest Triassic also decreased in abundance and most of them were descendents of the Late Permian Cathaysian types.

Stratigraphic distribution shows that both the macro- and microfloras from the WGEY region have suffered a dramatic change in composition, abundance and diversity (Fig. 7.1) across the PTB. The Wuchiapingian flora is characterized by abundant gigantopterids, which were rather abundant and diverse and commonly present in most of the Upper Permian successions in South China (Fig. 7.2). The coeval palynoflora was dominated by spores of the Pteridophyta and Pteridospermae. Most genera are characteristics of the Permian Cathaysian elements (i.e., *Nixispora* and *Patellisporites*). During the Changhsingian stage, the *Gigantopteris* flora markedly

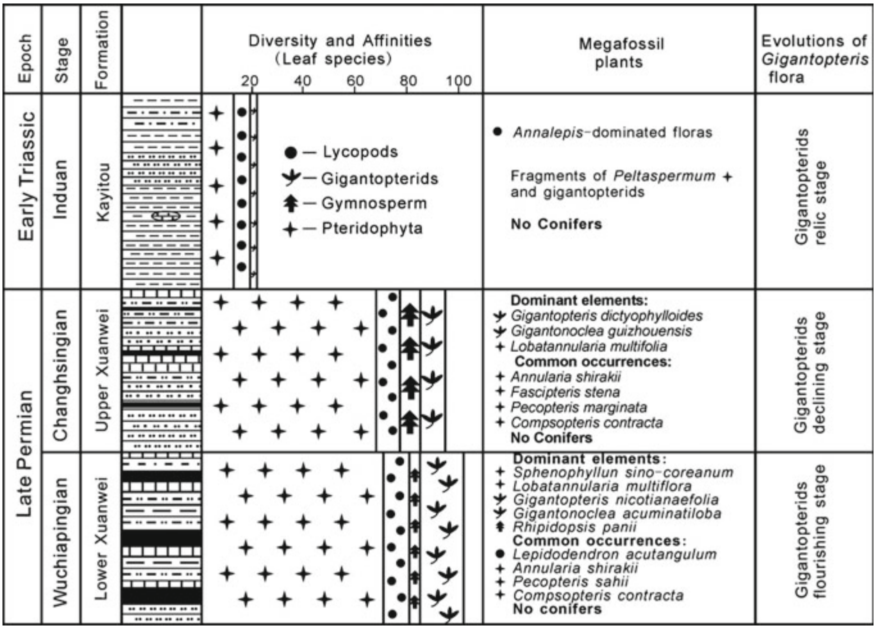

Fig. 7.1 Changes in fossil floras of non-marine facies deposits across the Permian–Triassic boundary within the Southwestern China, showing abrupt decline of the coal-forming *Gigantopteris* flora and replacement by a low-diversity lycopod flora

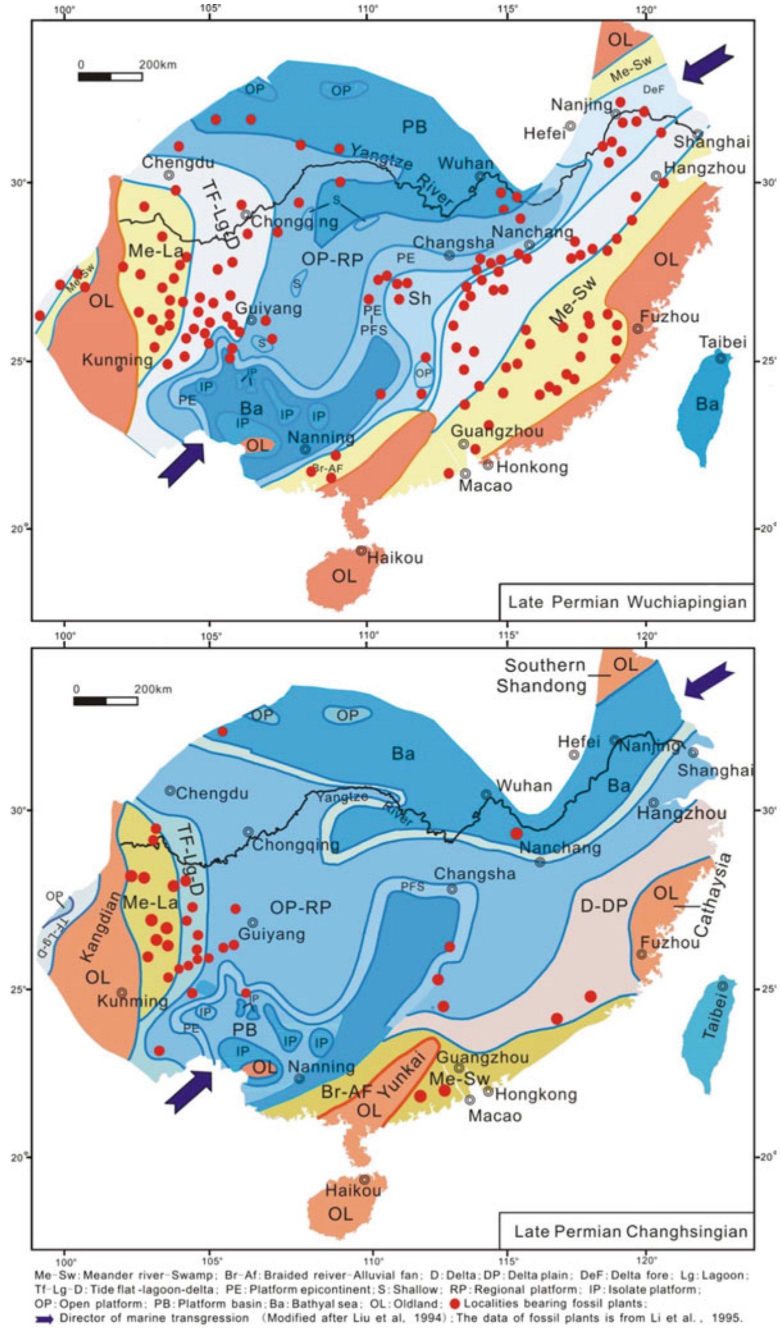

Fig. 7.2 Distribution of the Late Permian *Gigantopteris* flora localities related with marine transgressions in South China

decreased in species richness and localities (Fig. 7.2). In contrast, increasing representatives of gymnosperms occurred in the Changhsingian palaeoflora. It should be noted that the WGEY flora contains not only many taxa typical of the Late Permian *Gigantopteris* flora (such as *Lobatannularia*, *Fascipteris*, *Gigantoclea*, and *Gigantopteris*), but also many Triassic-type elements, and thus, appears a mixture nature of the Permian-type and Triassic-type floras, like the well-known mixed faunas near the PTB in marine regime in South China (Sheng et al. 1984; Chen et al. 2005).

7.3 Changes of Palynomorph Assemblages Across the PTB

Like the megaplants, the palynomorph assemblages in the study area also demonstrate significant changes across the PTB (Peng et al. 2006). In general, the palynomorphs changed from fern-dominated spores to pteridosperm and gymnosperm-dominated pollen across the PTBST, which itself contains a mixed flora with Late Permian relicts and Early Triassic elements, such as *Aratrisporites yunnanensis*, *Lundbladispora communis*, as well as abundant spores of lower organisms (e.g. fungi and/or algae). The latter is comparable with the so-called fungal event (Eshet et al. 1995; Visscher et al. 1996) or algae event.

However, the long-term, Wuchiapingian to Early Triassic Induan, temporal changes in the palynomorph assemblages in south China show a different pattern with regards to the megaplants over the same interval in that it first recorded a small increase in diversity from the Late Permian Wuchiapingian to the Changhsingian, followed by a decrease from the Changhsingian to early Early Triassic Induan (Fig. 7.3). However, from Wuchiapngian to Induan the palynomorphs decreased in abundance in a stepwise pattern, as do the mega-flora records, with most disappearing in the Induan. Therefore, again the temporal changing patterns of palynomorphs from the Late Permian to the Early Triassic do not suggest a synchronous mass extinction at the end-Permian.

Data on terrestrial floral changes across the Permian–Triassic boundary are presented separately from megaplant fossils and palynomorphs across several non-marine PTB sections in western Guizhou and eastern Yunnan. The changing trend in higher plant vegetation across the Paleozoic–Mesozoic transition is characterized by a change from fern-dominated vegetation in the Upper Permian to pteridosperm and gymnosperm-dominated vegetation in the Lower Triassic. Temporarily, the decline of land vegetation in southwest China began in the early Late Permian (Wuchiapingian) and persisted through to the Early Triassic, and the rate of decline in both species and generic diversity was accelerated at the Permian–Triassic transitional interval.

Overall, the temporal trend in the change of plants in the study area appears to be indicative of a long, protracted extinction process that may have commenced well before the Permian–Triassic boundary. Such a “drawn out” extinction process spanning the entire Late Permian and across the PTB therefore does not support a globally synchronous end-Permian catastrophic event such as meteor impacts;

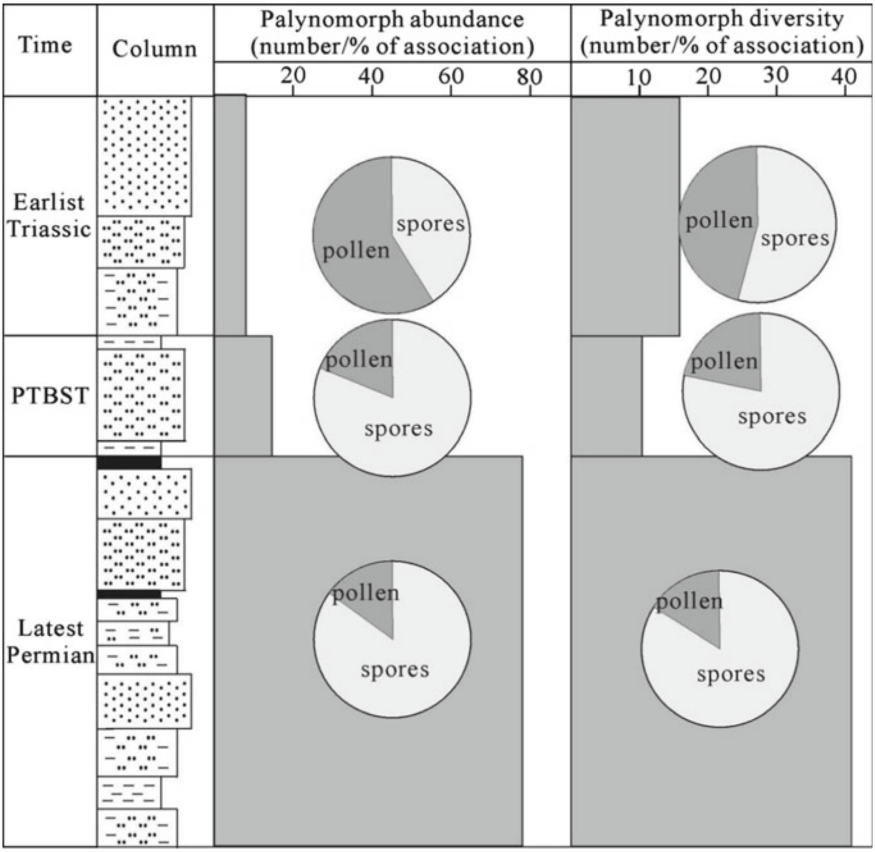

Fig. 7.3 Palynomorph changing patterns across the PTB (versus the lithostratigraphic base of the Chahe section) in western Guizhou and eastern Yunnan, South China (data from the Zhejue and Chahe sections)

rather it is more consistent with a protracted global climate change that may have been initiated by Pangea formation, and then exacerbated bythe Siberian Trap (and also possibly the Emeishan Basalt) volcanism at the end-Permian.

7.4 Recovery of Flora from South China After the End-Permian Biotic Crisis

The geologic past holds many examples of extinction and recovery of both terrestrial and marine ecosystems. At the beginning of the 1990s, new research on the problems of biotic survival and recovery during (after) great crisis has become a subject of increasing scientific interest and has resulted in two international projects: the Global

Changes Program (Ricklefs et al. 1990) and the IGCP Project 335 Biotic recoveries from mass extinctions (Kauffman and Erwin 1994). However, because interest in recoveries has been less than in the crisis events themselves, the recuperation intervals have been only superficially examined and therefore are poorly understood (Erwin 2001). This is particularly true of the Triassic survival and recovery intervals. Furthermore, most studies concern only marine invertebrates (Erwin 2001). Although land plants are known to be particularly sensitive to environments and paleoclimate and therefore very likely to be instructive for evaluating the patterns and processes of biotic recovery, they have been rarely analyzed in detail from this perspective. This part focuses on the post-crisis recovery of vegetationdestroyed by physical events at the Permian–Triassic boundary.

Wang Ziqiang (1996) is the first paleobotanist who has thoroughly studied the land-plant recovery and noted its decimation at the Permian–Triassic transition and its subsequent recovery. Looy et al. (1999), who analyzed the Triassic land-plant recovery on the basis of palynological data, also noted that the end-Permian flora, particularly the conifers, has been decimated, and showed that the most suitable fossils for such studies are pollen and spores, because of their unique fossilization potential. Grauvogel-Stamm and Ash (2005) summarized Early and Middle Triassic land-flora, and pointed out thatthe recovery of the Triassic floras of Europe began, as in North China, with the proliferation of the lycopsid *Pleuromeia* during the Early Triassic and that it proceeded with the resurgence of the conifers in the early Middle Triassic (Early Anisian), the return of the cycadophytes and the pteridosperms in the Late Anisian and the progressive evolutionary modernization of the subsequent. This lycopsid was an opportunistic pioneer plant, as *Annalepis* did in South China which took advantage of the post-crisis vacuity of the environment to proliferate, preparing sites for re-colonization with the plants having survived in refugia. The Triassic land-plant recovery is a long stepwise process.

The above analysis clarifies that Permian–Triassic Xuanwei flora in western Guizhou-eastern Yunnan is consistent in its transformation with quality of the global flora. Part of the Permian prosperous elements survived the extinction as the residual elements and continued to Early Triassic, for instance, gigantopterids of Cathaysian Flora and Glossopterids of Gondwana Flora (Pant and Pant 1987; McManus et al. 2002). While the new type of lycopods appeared in a sudden above the P–T boundary, became predominant at the beginning of Triassic (Balme 1970; Dobruskina 1987), which is marked by the appearance of representatives of the genus *Annalepis* in early Early Triassic in western Guizhou and eastern Yunnan of South China, *Pleuromeia* became the advantageous elements of North China florain the same period, and the rapid spread of *Peltaspermum* and *Lepidopteris* to the whole globe in Early Triassic (Dobruskina 1987; Shah 1987; Mogutcheva 1996; Paland Ghosh 1997; Mcloughlin et al. 1997). However, the Xuanwei flora has its own characteristics in the evolution.

7.4.1 Triassic Land-Plant Recovery in North China: A Model

Recovery process after mass extinction is the prelude of a new radiation. With the exception of a few groups, recovery for biotic groups appeared based on the survival stage. It is characterized by an increase in origination rate, endemic taxa.

In North China, the end-Permian life crisis was caused by increasing desertification, which wiped out up to 75% of the land flora at the genera level and 98% at the species level, including most of the typical Palaeozoic species Wang (1989, 1993, 1996). The total species number passed from 146 taxa in the lower Upper Permian (Tianlongsi Formation) to 54 taxa in the late Upper Permian (Sunjiagou F.), 16 taxa in the early Lower Triassic (Liujiagou F. = Induan) and 58 taxa in the late Lower Triassic (Heshangou F. = Olenekian) where it began again to increase (Wang 1989), showing that the end- Permian life crisis was a long process that began well before the end of the Permian, and that the subsequent Triassic recovery was also a long process lasting until the end of the Middle Triassic.

Wang (1996) recognized two stages in the Triassic land-plant recovery: the first was the Early Triassic *Pleuromeia* stage with three sub-zones, which was dominated by the lycopsid *Pleuromeia* [Fig. 7.4 (1).II–III] and the second was the Middle

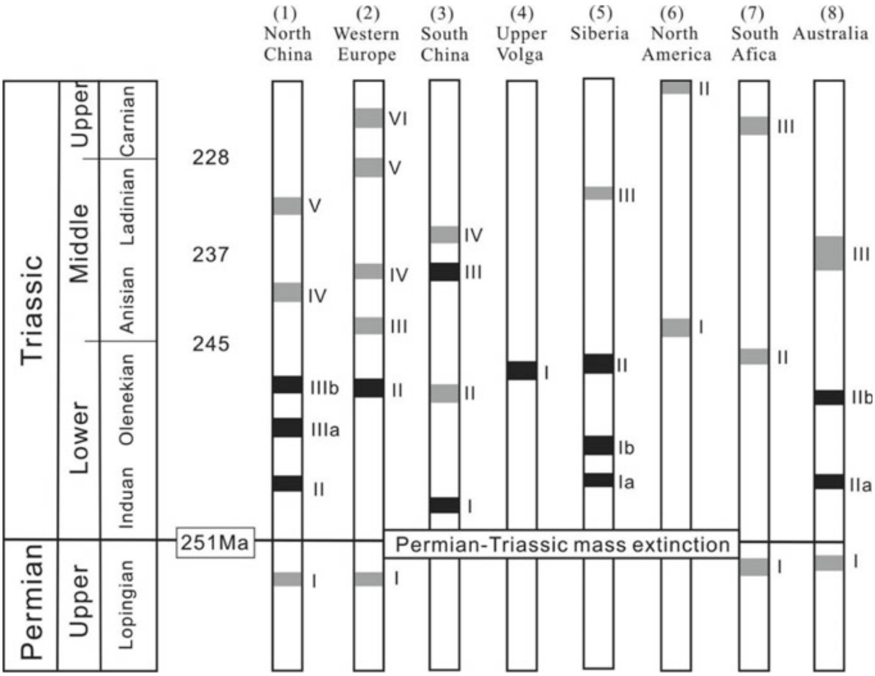

Fig. 7.4 Tentative simplified correlation table showing the distribution of the end-Permian and Triassicfloras in different regions of the world (slightly modified according to Grauvogel-Stamm and Ash 2005)

Triassic *Tongchuanophyllum* stage with two sub-zones (the *Isoetes* sub-zone and the *Scytophyllum* sub-zone), which is characterized by the broad-leaved pteridosperm *Tongchuanophyllum* and the sphenopsids *Equisetites* and *Neocalamites* [Fig. 7.4 (1).IV–V]. This two stage's recovery is considered as one model of Triassic land-flora from the end-Permian life crisis (Grauvogel-Stamm and Ash 2005).

7.4.2 *Triassic Land-Plant Recovery in Europe*

Kerp (2000) recently pointed out that the plant megafossil record from the Permian through the lower Middle Triassic of Europe is poorly known, and seems to preclude study of the Triassic land-plant recovery in this area. Similarly Meyen (1987) had recognized that a detailed reconstruction of the Permian–Triassic transition was impossible. However, a new analysis by Grauvogel-Stamm and Ash (2005), has given the Triassic land-plant recovery also went through two stages: a long survival interval in the Early Triassic, similarly dominated by the lycopsid *Pleuromeia* being the oldest Triassic land flora represented in Europe [Fig. 7.4, (2).II]; and the early Middle Triassic floras correspond to the recovery interval itself, with the early Anisian flora of northeastern France [Fig. 7.4, (2).III] (Grauvogel-Stamm 1978) representing the first phase and the Upper Anisian flora of Italy [Fig. 7.4, (2).IV] (Broglio et al. 2002) corresponding to the second phase.

In many other areas, the Uppermost Permian and Lower Triassic are represented by marine facies. However, in some areas continental facies with fossil plants are intercalated with marine deposits making possible to determine which of the recovery stages the plant record belongs to. In most areas discussed below (Siberia, North America, South Africa and Australia, respectively Fig. 7.4, (5), (6), (7) and (8), the recovery seems to have been completed during the Middle Triassic as well as in Europe and North China, South China.

7.4.3 *Triassic Land-Plant Recovery in South China*

1. The plant assemblages of the Lower and Middle Triassic in South China

In South China, Early and Middle Triassic strata are mostly marine facies. Fossil plants appeared only in Early Triassic Kayitou Formation of western Guizhou and eastern Yunnan, and Lingwen Formation of Qiongxian, Hainan Province (Fig. 5.2); the Middle Triassic Badong and Huangmaqing Formations, the middle part of the Yangtze River (Fig. 5.3), respectively Induan, Olenekian, Anisian and Ladinian. They consist of four assemblages, with the lowermost being Induan and the uppermost being Ladinian [Fig. 7.4, (3).I, II, III, IV].

In studying the recovery of the land plant in South China, the previous workers discussed a few. The main reason is the absence of a whole Early Triassic plant assemblage. With the research of fossil plants from western Guizhou and eastern Yunnan in the recent some years, the early Early Triassic plant assemblage is established in the thesis. Consequently, it is possible to discuss the land plant recovery in this area.

Black = Lycopsid-dominated floras; grey = more or less diversified floras. Please note that the columns and the plant-bearing beds are not at scale. For the source data, see the references in the relevant sections.

(1) North China: I-Late Permian (Sunjiakou Formation): *Ullmannia* zone; II-III: Induan-Olenekian: *Pleuromeia*-dominated floras (II-Induan: Liujiakou Fm. = *P. jiaochengensis* subzone; III - Olenekian: Heshanggou Fm.; III a = *P. epicharis* subzone; III b: *P. sternbergii* subzone); IV - Anisian (Ermaying Fm.): *Tongchuanophyllum* zone including the *Isoetes* subzone at the base and the *Scytophyllum* subzone above; V - Ladinian (Tongchuan Fm.) with *Danaeopsis*. **(2) Western Europe:** I-Late Permian (Lopingian): Zechstein flora, Val Gardena flora, N. Italy = conifer-dominated floras; II-Olenekian (Middle Buntsandstein), Germany = *Pleuromeia*-dominated flora; III-Early Anisian ('Grès à *Voltzia*' Fm., Upper Buntsandstein), NE France: conifer-dominated flora; IV - Upper Anisian (Dont Fm.), N Italy: conifer/cycadophyte/fern-dominated flora; V-Late Ladinian (Lower Keuper), Germany = sphenopsid-dominated flora (Wengen Fm.), N. Italy = *Voltzia*-dominated flora; VI - Middle Carnian (Schilfsandstein), Germany = sphenopsid-dominated flora. **(3) South China:** I- Induan (Kayitou Fm.) *Annalepis*- dominated flora. II-Olenekian (Lingwen Fm.) conifer-dominated flora; III Anisian (Lower Badong Fm.): *Pleuromeia*-*Annalepis*-dominated flora; IV-Ladinian (Upper Badong Fm.): *Annalepis*-dominated flora. **(4) Upper Volga (Russia):** I - Olenekian (Rybinsk Fm.): *Pleuromeia*-dominated flora. **(5) Siberia (Russia):** I a, I b - Induan: *Pleuromeia* and *Tomiostrobus* (sub-genus of *Annalepis*) dominated-flora; II-Upper Olenekian: *Pleuromeia*-dominated flora, Taymyr, Verkoyanye; III-Ladinian flora. **(6) North America:** I-Early Anisian (Moenkopi Fm.): flora with *Donwelliacaulis*; II-Late Carnian flora (Chinle Fm. with the Shinarump Member at the base and the overlying Petrified Forest Member, which is Late Carnian - Early Norian). **(7) South Africa (Gondwana):** I-Late Permian: *Glossopteris*-dominated flora; II-Late Olenekian (Burgersdorp Fm.): diversified flora; III-Early-Middle Carnian (Molteno Fm.): rich and diversified flora. **(8) Australia (Gondwana):** I-Late Permian: *Glossopteris*-dominated flora; II a, II b - Induan + Olenekian: lycopsid-dominated floras; III -Middle Triassic, (Basin Creek Fm. in the Nymboida Coal Measures, Clarence-Morton basin).

The Induan assemblage is dominated by the lycopsids *Annalepis* [Fig. 7.4, (3).I], but it also includes some elements of Peltaspermales and a few relicts of Late Permian Cathaysian flora. The feature of the Olenekian *Neuropteridium*-*Voltzia* assemblage (Zhou and Li 1979) [Fig. 7.4, (3).II] is that the conifers highlighting *Albertia* and *Voltzia*is dominating, the horsetails and *Neuropteridium* are quite also numerous, while Lycopsids are very rare, whose diversifications can be compared with those of the Buntsandstein flora of Europe.The Anisian assemblage [Fig. 7.4, (3).III] (Meng et al. 2000) is dominated by the lycopsids *Pleuromeia* (many in life position) and *Annalepis*, but it also includes most of the taxa described in the 'Grès à *Voltzia*' flora of northeastern France and the Ermaying Formation of North China, which are both early Middle Triassic. The Ladinian assemblage (Meng et al. 2000) [Fig.7.4, (3).IV] that includes mainly *Annalepis*, *Equisetites*, *Neocalamites*, *Scytophyllum*, *Voltzia*, *Taeniopteris* is said to resemble the upper part of the Ermaying Formation of North China.

2. Taphocoenoses modes of the Lower and Middle Triassic in South China

In the case of the Lower and Middle Triassic in South China, a total number of about 12 plant-bearing biostromes (Zhou and Li 1979; Meng et al. 2000; the author et al.) are the basis for the analysis resulting in enumeration of four types of plant-taphocoenoses based on plant preservation.

Autochthonous burial: Whole plants vertically buried in life position, or occurrences in one biostrome of a suite of isolated organs that have naturally detached, permitting the whole plant to be reconstructed.**Allochthonously burial over short distances (similar to parautochthonous):** Isolated organs, such as a leaf or a frond, that are completely buried after being shed and having undergone some transport within the habitat of growth.**Allochthonous burial:** partiallypreserved isolated organs that have been transported from the growth habitat to the place of deposition.**Fragmentation burial:** A variety of plant fragments or debris that have undergone transported, that can be barely identified at the genus level.

(1) The *Annalepis -Peltaspermum* and the relicts of gigantopterids assemblage (Induan)

The characterstics of this assemblage will be described in the following Chap. 9, genus *Annalepis* is the dominant element. This assemblage also is called the opportunistic pioneer lycopsid- dominated flora. All the taphocoenoses are restricted to grey-greenish or grey-yellowish muddy siltstone or mudstone representing deposits of a lagoon (Zhao Quanming, 2003, PhD thesis). This assemblage is dominated by *Annalepis*-taphocoenosis in allochthonously burial over a long distance: the *Annalepis* having sporadic sporophylls, megaspores in situ, microspores and suspicious strobile and root (Fig. 7.5). The part relicts in the top Xuanwei Formation (e.g. Bed 69 of the Chahe section) are in allochthonous burial. The pinnules relatively are complete, the second rachis of some fossil plants were preserved. Other plants, which are preserved as very small, or reworked? fragments, might be transported for a very long distance, belonging to the fragmentation burial.

(2) The *Neuropteridium-Voltzia*assemblage (Olenekian)

According to the data of Zhou and Li (1979), and Meng et al. (1992), a total of 38 species belonging to 28 genera have been described in the following Chap. 9, fragments of conifer *Voltzia* and *Albertia* are the dominant elements. The others are broken fragments. It shows that the Lingwen flora is an allochthonous burial.

(3) The *Pleuromeia marginulata-Annalepiszeilleri* assemblage (Anisian)

In South China, the Middle Triassic Badong Formation, consisting of a set of red clastic deposits intercalated with carbonate rock in the middle part, is widespread in

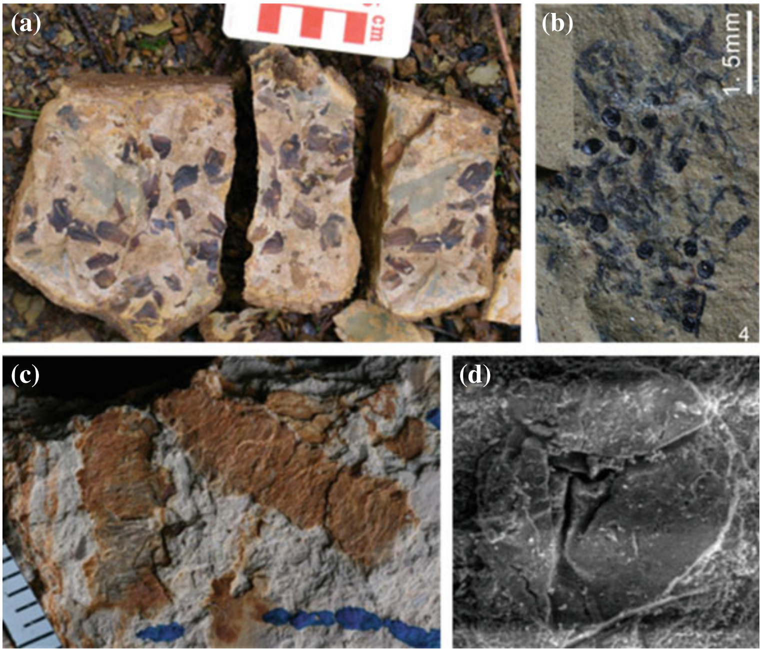

Fig. 7.5 Showing the *Annalepis*-taphocoenosis in allochthonously burial over a long distance. **a** sporadic sporophylls **b** possibly strobile **c** possibly roots **d** megaspore in situ

the Yangtze Gorge area, with a total thickness of about 1000 m. The formation may be evidently subdivided into 5 lithologic members in its named locality. The *Pleuromeia-Annalepis* flora was mainly found in the gray-green argillaceous siltstones or the siltstone lens in Members 2 and 5, but a few of specimens were collected from the sandy mudstone in Members 1 and 4.

The assemblage occurred in Members 1–2 of the Badong Formationis rich in composition, containing about 31 species belonging to 18 genera. The main elements are *Pleuromeia marginulata*, *P. sanxiaensis*, *P. hunanensis*, *Annalepis zeilleri*, *A. brevicystis* etc. Of them, the *Pleuromeia* is generally well preserved, with many complete plants, with some stems almost vertically preserved in sediments or some appendixes showing a growing state almost perpendicular to the bedding plane. The phenomenon mentioned above indicates that it may be autochthonous taphonocoenose. The *Annalepis* has both sporadic sporophylls and rather perfect cones. Presumably, it has ever been transported for a short distance, but basically is sub-autochthonous taphonocoenose. All other plants, which are preserved as fragments, might be transported for a long distance. So the assemblage represented a mixed plant taphonocoenose.

(4) The *Annalepis latiloba-Scytophyllum* assemblage (Ladinian)

The assemblage is represented by the plants from the Members 4–5 of the Bedong Formation.

The main elements of the assemblage include *Annaleplslatiloba*, *Equisetites arenceus*, *Neocalamites* sp., *Scytophyllum* sp., *Sphenozamites* sp., *Sinoctenis pulcella*, *Voltzia* sp., *Taeniopteris* sp., etc. The present assemblage shows rather simple genera and species and the presence without *Pleuromeia*, whereas the evident increase of *Scytophyllum* in amount and the occurrence having *Sphenozamites* and *Sinoctenis* which are commonly found from Late Triassic in South China.

Comparison with the *Pleuromeia marginulata-Annalepiszeilleri* assemblage,the *Annalepis*-taphocoenosis also is allochthonous burial over short distances. The *Scytophyllum*- taphocoenosis may be allochthonous burial.

3. The process of vegetational recovery of the Lower and Middle Triassic in South China

In South China, the Late Permian vegetation was composed mainly of Equisetales, Filicopsida, Pteridosperms and Gigantopteridales. The subsequent terminal Permian mass extinction destroyed almost all the Permian vegetation here, including most of the characteristic Paleozoic species. Only a few relicts at the generic level have survived the severe event. The present paleobotanical analysis suggests that in South China the subsequent Early and Middle Triassic vegetational recovery had two main stages.

(1) Expansion of the vegetation stage in Early Triassic

The synthetically data at the species level from megaplants in South China (including Fujian, Jiangxi, Guangdong, Jiangsu, Hunan, Sichuang, western Guizhou and eastern Yunnan) shows that the total species number passed from 203 known species (data from Li 1995) in the lower Upper Permian (Lungtan Formation and the lower part of the Xuanwei Formation) to 131 known species in the late Upper Permian (Dalong Formation and the upper part of the Xuanwei Formation) (data from Li 1995 and this thesis), 19known species in the early Lower Triassic (Kayitou F. = Induan) and 38taxa in the late Lower Triassic (Lingwen F. = Olenekian) This degressive characteristic is similar to that of North China (Fig. 7.6).

A. At the beginning of the Triassic, the landscape is assumed to have been rather barren. Shortly after, a few small monospecific herb-like *Annalepis* association in nearshore region of western Guizhou and eastern Yunnan, and *Peltaspermum* association intermittently occurred.

The *Annalepis*, including 4 known species, is a monogenetic association, and it likely grew in marginal area of nearshore. There was more or less influence by the break. The sporophylls of this genus are lanceolate, with an acute apex, truncate base and smooth lower surface. The sporangia are slender stick-shaped, attached closely to the central part of the ventral surface of the sporophyll, with a warped anterior apex of the sporophyll formed in water possibly because of its weight. All the features show that *Annalepis* possess a drift ecological character in water

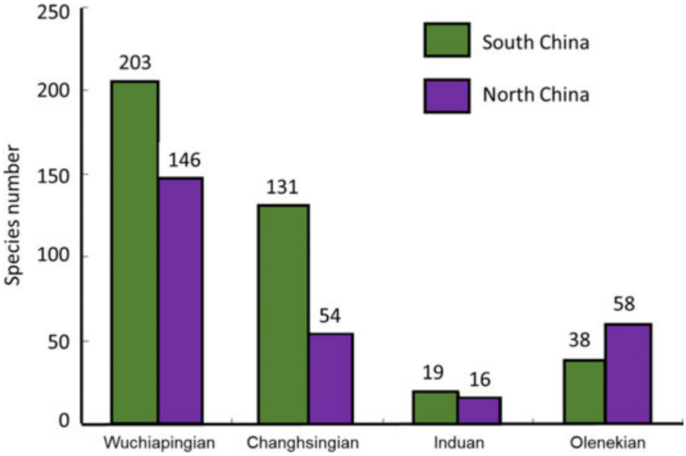

Fig. 7.6 Correlation of paleofloral species level between South and North China during Late Permian and Early Triassic

(Meng et al. 2000). In addition, the macrospores of *Annalepis* are relatively hard, with a smooth surface and larger specific gravity than other plants. These features are advantageous to the precipitation of the macrospores, and development of new plants in coastal environment (Meng et al. 2000).

The reduced and shortened pinna and sterile organs (?) of *Peltaspermum*, broken fragments of the Gigantopterids may be considered to represent another ecotype in the stage. They belong to fragmentation burial association. This taphocoenoses in the Kayitou Formation occur in 2.5m thickness, monocyclic sandy mudstone bed. No gymnosperm remains appeared.

The red-beds began to appear in the upper Kayitou and Dongchuan Formations (Olenekian stage), no fossil occurred.

B. In the second half of the early Triassic, the largest portions of muddy red-beds of the Lingwen Formation in Qionghai, Hainan province, and also Dongchuan Formation in western Guizhou and eastern Yunnan, indicates that dry climate had begun. The fossil plants only occur in gray, fine-grained sandstone overlying the red-rocks in Lingwen Formation. In the Qionghai taphoflora, fragments of conifer are numerous, but some articulates have been detected, but their body is small and the internodes shorten (Zhou and Li 1979). It appears that the plants were not preserved in situ. During this period, Gymnosperm (e.g. *Albertia* and *Voltzia*) and pteridosperm (e.g. *Neuropteridium*) began to be flourishing. These indicate that the mesophytic plants on upland and on shore could further develop.

The *Annalepis*-dominated flora of western Guizhou and eastern Yunnan is similar to the second zone (Liujiagou Formation) of North China [see Fig. 7.4, (1).II], which is also lycopsid *Pleuromeia*-dominated. In Gondwana, the herbaceous lycopsids (*Cylostrobus*, *Skilliostrobus*), which had been only a small part of the Permian land flora, expanded suddenly with the advent of the Triassic and became dominant during the Early Triassic, but then declined and virtually disappeared by the end of the Early Triassic. The Voltzialean conifer *Voltziopsis* followed the general trend of the herbaceous lycopsids. It became dominant in the Early Triassic land flora of Gondwana, after which it declined and became again common in the Late Triassic. The Early Triassic paleoflora in South China is correlated to that of the Gondwana. Therefore it can be similarly considered to represent the first stage of the Triassic land-plant recovery in South China.

(2) A changeover: the occurrence of riparian vegetation in shore-lagoon

The *Pleuromeia-Annalepis*flora consists of two assemblages, with the lowermost being Anisian and the overlying being Ladinian (Meng et al. 2000) [Fig. 7.4, (3).III and (3).IV]. The Anisian assemblage is dominated by the lycopsids *Pleuromeia* (many in life position) and *Annalepis*, but it also includes most of the taxa described in the 'Grès à *Voltzia*' flora of northeastern France and the Ermaying Formation of North China, which are both early Middle Triassic (Grauvogel-Stamm 1978) and (Wang 1996).

Based upon Meng's research (2000), all the *Pleuromeia* and *Annalepis* are distributed in shore-lagoon environment in the Yangtze valley. The Pleuromeia, representing a small type of monogenetic association, is composed of 2 species of dwarf bushes. As to the ecology of *Pleuromeia*, one indicated that it was initially considered to be a kind of xerophyte in desert (Magdefrau 1931, 1956) or halophile (Clarke and Hannon 1971). The other thought that it might grow in a relatively flat shoreline area (Kon'on 1973), frequently influenced by waves and tides. The *Annalepis*, representing also a monogenetic association, was a small type of aquatic herb (Meng et al. 2000). Similarly, it likely grew in the marginal area of nearshore with *Pleuromeia*'s shrub.

The fact that *Pleuromeia* was still present in the Anisian in South China, whereas in North China and Europe it disappeared or is very rare, may be explained by differences in palaeogeography and climate. According to recent palaeogeographic reconstructions (Ziegler et al. 2003), South China was at the equator in the Early Triassic, whereas North China and Europe were close to the northern tropic at that time, latitude that is characterized by arid climates (Fig. 7.7). South China reached the tropics only in the Middle Triassic which would explain why *Pleuromeia* proliferated only at that period (Fig. 7.8).

The Ladinian assemblage that includes mainly *Annalepis*, *Equisetites*, *Neocalamites*, *Scytophyllum*, *Voltzia*, *Taeniopteris* is said to resemble the upper part of the Ermaying Formation of North China. However, it also resembles the Ladinian floras of Siberia and Germany.

The *Pleuromeia-Annalepis* flora of South China closely resembles the coeval flora of North China and Europe. So this flora represents the second stage of the Triassic land-plant recovery in South China. Finally, in latest Middle Triassic, the process of vegetational recovery in South China had been completed and fully vegetated landscapes had again appeared there. It is the best evidence that Late Triassic coal-bearing strata appeared again in the whole South China.

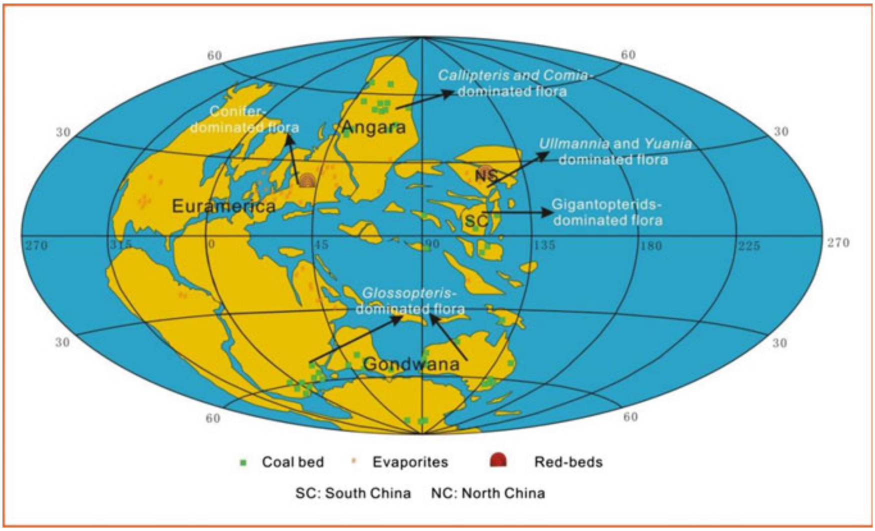

Fig. 7.7 Simply the distribution of the floras in different regions and paleogeographic reconstruction during Late Permian Changhsingian

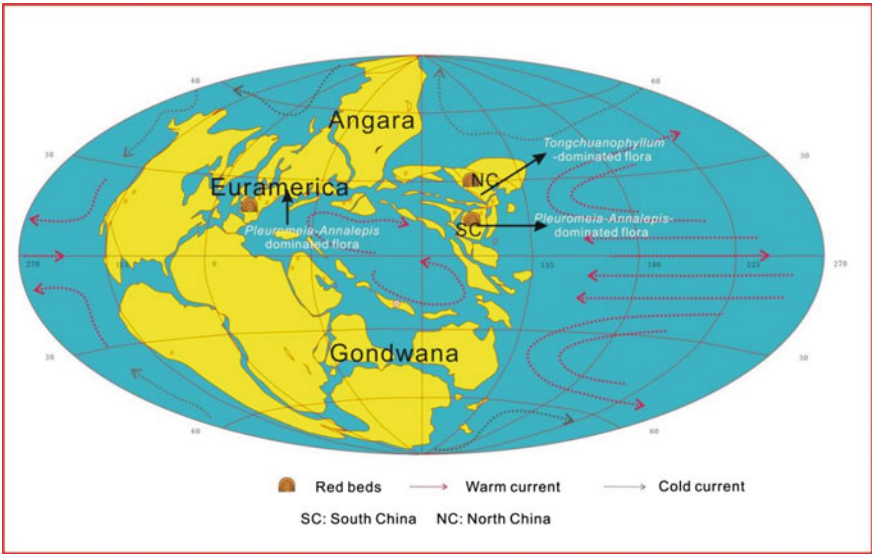

Fig 7.8 Simply the distribution of the floras in different regions and paleogeographic reconstruction during Middle Triassic Anisian

The above analysis clarifies that Permian–Triassic transitional Xuanwei flora in western Guizhou and eastern Yunnan is consistent in its transformation with quality of the global flora. Part of the Permian prosperous elements survived the mass extinction as the residual elements and continued to Early Triassic. While the new type of lycopsids appeared in a sudden around the P–T boundary at the beginning of Triassic and soon became predominant. Its recovery depends on the new types in the survivalinterval rather than the Paleozoic surviving flora, such as *Gigantopteris*. Specifically, *Annalepis* and *Peltaspermum* are mainly responsible for the recovery. This character is close to the recovery mechanism of foraminifera of the same date in South China (Tong 2004).

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