Chapter 3
Materials and Methods

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A combination of approaches to evaluate plant species turnover from the Late Permian to the Early Triassic in South China to consider the long-term consequences of the profound changes to terrestrial ecosystems across the End Permian Plant Crisis (EPPC) and its recovery is used in this book. The successive floras will be documented in Chap. 4 and for each we review their stratigraphical relationships and depositional sedimentary facies as geological and taphonomic context for the palaeobotanical occurrences.

3.1 Sampling Strategy

We have adopted two sampling approaches for this study. For formations representing the End Permian Plant Crisis (EPPC) of the Lungtan, Talung, Xuanwei and the basal part of the Kayitou formations, and the Lowest Triassic lower part of the Kayitou Formation (Fig. 2.1) as a survival period, we selected key localities for

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J. Yu et al. (eds.), *Plants and Palynomorphs around the Permian-Triassic Boundary of South China*, New Records of the Great Dying in South China,
https://doi.org/10.1007/978-981-19-1492-8_3

being representative in terms of their fossil plant composition and stratigraphically complete. For each we have undertaken extensive fieldwork over many years to identify and collect fossil plants in situ on a bed-by-bed basis. For these formations all the fossils reported have been identified by the same individuals using reference materials such that the identifications are accurate and internally consistent. Within key formations we study individual sections and then correlate them stratigraphically to determine overall changes in plant composition at the formation level.

3.2 Evaluating Fossil Plant Species Richness and Normalizing Data Occurrences

While ideally our study would seek to identify species diversity, this represents a measure of species richness and species evenness for which often impossible to determine species evenness from the fossil plant record (Cleal et al. 2012, in press). Here we focus on species richness that denotes the number of species present in a particular bed, locality, formation or flora and is measurable from the plant fossil record. To assess plant species richness, it is necessary to evaluate patterns of species change over time as undertaken by numerous past investigations that simply measure the number of plant species present in each stage (Yao et al. 1983; Li et al. 1995; Peng et al. 2009; Yu et al. 2015; Chu et al. 2016; Feng et al. 2020). This is achieved by constructing stratigraphic range diagrams for each species showing their first (origination) and last (extinction) occurrence in each geological section, and then stratigraphically correlating using litho-, bio- or chemostratigrpahic methods between different sections to compile range charts for each period. From this information the total number of species (i.e. alpha diversity) can be determined, and rates of originations and extinction through time calculated.

To meaningfully extract plant species richness patterns from the fossil data, it is important to eliminate duplicates that are an artefact of palaeobotanical nomenclature (e.g., Hilton and Cleal 2007; Cleal et al. 2012). A single reconstructed whole-plant species in the fossil record may include numerous distinct organs (e.g., leaves, stems, roots, cones, seeds), each with their own genera and species name (Bateman and Hilton 2009). The solution we adopt is to normalize the data (Cleal et al. 2012) and evaluate only those organs whose fossil taxonomy is most likely to reflect the original whole organism taxonomy. This represents the first time that this approach has been applied to plant species richness through the PTB interval including the EPPC and its Triassic recovery, with previous studies artificially inflating species richness. Normalized taxa are retained for species richness estimates so that only one organ of each viable whole-plant is included. Examples include omitting accounts of genera that lack species-level identifications (e.g. *Tomiostrobus* sp.) from in assemblage in which one or more identified species of the same genus occurs (e.g. *Tomiostrobus augusta*, *T. brevicystis*), assuming that the specimens identified as “sp.” most likely represent poorly preserved or incomplete examples of one of the other or more of the named species of *Tomiostrobus* present. We also omitted from species richness estimates fertile organs including gymnosperm seeds when other organs of the same plants are present in the same assemblage; in all cases where seeds are present they co-occur with one or more species of gymnosperm leaf from which it is assumed that the seeds belonged to one or more of these plants. Lycopsid rootstock (*Stigmaria*), sporophylls (*Lepidostrobophyllum*) and cones (*Lepidostrobus*) are also omitted as in all instances these co-occur with stems (*Lepidodendron*) that are more distinctive and are typically identified to the species level. We accept that conclusions on normalizing fossil plant data are to some extent subjective and cannot readily be tested for their robustness, but we consider these more realistic estimates of species richness and potentially species richness than non-normalized, raw-data based accounts.

3.3 Fossil Plant Abundance

There is no robust method to quantitatively assess plant abundance in terrestrial settings unless fossil floras are preserved in-situ in obrution events such as volcanic ash-fall events (Wang et al. 2012). In a broad sense plant abundance may be indicated by a number of indirect measures including the number of locations that contain fossil plants as well as the palaeobotanical richness in terms of numbers of specimens at each location, but these are subject to a variety of controls including spatial heterogeneity of plant distributions in contemporaneous settings such as different niches, and a variety of physical (biostratinomic, sedimentary) and chemical taphonomic processes controlling what enters the fossil record (Bateman 1991; Allison and Bottjer 2010). Here we focus on relative measure of abundance as well as using specific environmental proxies that provide crude insights into plant abundance in the environment in which they lived.

Firstly, having undertaken extensive fieldwork and collection based on investigations to Permian–Triassic plant bearing sedimentary successions from South China, it is obvious that plant abundance varies from being very abundant and nearly ubiquitous in some sedimentary contexts within individual formations, to being very rare in others in which finding a single fossil plant remain may take several hours in the field. In this we collectively consider all plant material, from fragmented plant debris to intact fossil plant organs as we are interested in assessing the presence of plants in the sedimentary system rather than focusing on details of what the plants are or where they came from. Due to the nature of the outcrops and the distribution of fossils in the sediments, it has not been possible to sample fossil plants using quadrat or other methods that might facilitate more accurate assessments of abundance. Rather, as very crude proxies for plant abundance, we use the relative descriptors absent, very rare, rare, common, abundant and very abundant to describe the amount of plant fragments encountered in each section in terms of (A) plant fossils on individual beds, and (B) the number of beds containing fossil plants.

Secondly, as coals represent accumulated plant matter that built up as peat, we consider coals to indicate high plant abundance for an extended period combined with low levels of decay (e.g., low pH to suppress fungal and bacterial decay). We do not seek to quantify this further, merely indicate that multiple generations of plants needed to grow in waterlogged conditions for the biomass to accumulate and equating this to abundant or very abundant depending on the vertical thickness and lateral extent of the coal. In contrast, the studied interval includes the early Triassic coal-gap (Retallack et al. 1996), a stratigraphic interval in which adverse environmental conditions prevented peat (and hence coal) formation and/or preservation. We consider this to be evidence for very low plant abundance but accept it could also represent widespread adverse preservation conditions for fossil plants (Vajda et al. 2020; DiMichele et al. 2020).

Thirdly, we consider environmental proxies related to soils on the basis that abundant vegetation cover is likely to bind soils together and diffuse water infiltration into the ground, thus having the net result of reducing surface water run-off (Wu et al. 1997; Davies and Gibling 2008). In contrast, bare, un-vegetated ground would be more susceptible to surface water run-off, physical weathering and erosion (Retallack 2005; Algeo et al. 2011; Kaiho et al. 2016). We therefore use the presence of physical weathering in terrestrial settings as a rough proxy for plant abundance in terms of ground cover, highlighting the co-evolution of plants and the environment. For this we use two methods; Average Linear Sedimentation Rates (LSRs) (Algeo et al. 2010) and Chemical Weathering Intensity (Algeo et al. 2011). LSRs (units of m m.y.$^{-1}$), as the thickness of a given time strata divided by the duration of that strata, is a proxy for sediment flux (Algeo et al. 2010). For example, the LSRs increased from 10-18 m m.y.$^{-1}$ in the Lopingian to 105–488 m m.y.$^{-1}$ during the Early Triassic at the Meishan Section in eastern China (Algeo et al. 2010). The enhanced sedimentation rate is common through the world in the Early Triassic and the LSRs of offshore clastic facies increase more substantial than the deeper water sections, revealing the delivery of sediments may be related to the terrestrial soil erosion (Algeo et al. 2010). LSRs in this context indicate input of terrestrial debris into marine systems, and the rate or type of weathering is determined through the elementary data and mineral composition of the sediments. The Chemical Weathering Intensity derives from clay mineral contents of sedimentary rocks on the basis that clays including kaolinite are chemical weathering products and their compositions can be used as proxies for chemical weathering rates (Algeo et al. 2010, 2011). Finally, we very briefly consider Total Organic Carbon (TOC) levels in sediments as a crude proxy for terrestrial biomass and plant abundance. However, this is a proxy from which extreme care needs to be taken when interpreting TOC values that are affected by taphonomic (e.g. transportation, decay, oxidation) and diagenetic controls (e.g., redox conditions).

3.4 Evaluating Plant Ecology

The geological and palaeoecological contexts in which fossil plants occur is important to their interpretation in order to provide links between fossil plants and the environment(s) in which they grew and the processes that affected them. For example, through analyzing the palaeoenvironments in which plants grew it is possible to elucidate the palaeoenvironmental constraints regulating growth of different plant taxa or groups. Through analyzing spatial and temporal distributions in fossil plant occurrences it may be possible to identify migration patterns of individual taxa or floras, and from this identify environmental parameters such as water availability or substrate conditions controlling plant distributions. It also allows greater understanding of the conditions in which extinction survivors lived, identifying features that may have contributed to their resilience as well as identifying the locations and environments of refugia.

Palaeoecology assessments for plant taxa here come primarily from the available literature and is based on plant fossil anatomy and morphology and the sedimentary depositional environments in which they occur (Yao 1983; Meyen 1987; Bateman 1991; Yang 1993, 1994; Taylor et al. 2009). Here, fossil plant occurrences were evaluated for their shape, size and completeness to elucidate their taphonomy in terms of being transported long, medium or short distances from their growth environment. For example, entire or almost entire organs lacking signs of taphonomic fragmentation, abrasion or size-sorting were interpreted as having undergone minimal transportation and being recorded in-situ or very close to their growth environment. This included in-situ plants and fossil plants found in palaeosols, e.g., whole plant of *Annalepis* (=*Lepacyclotes*) in Badong Formation of Hongjiaguan Section and *Pleuromeia* in Dawotang Section (Meng 1995). These kinds of fossils often have exquisite preservation of delicate plant tissues such as leaf tips or sporophylls attached in cones. Greater levels of transport result in higher levels of fragmentation and size sorting and culminate in fine grained well sorted plant debris beds. Depositional environments of the plant fossil were determined by sedimentary features on fieldwork and from the literature (Yao et al. 1983; Bercovici et al. 2015; Yu et al. 2015; Chu et al. 2016), as well as comparison to established palaeogeographic analyses (Yao et al. 1980; Zheng et al. 2010). For instance, an in-situ fossil with attached roots preserved in tidal flat facies would suggests this special plant grew in the facies, for example, specimens of *Annalepis* from the Kayitou Formation in the Mide and Tucheng Sections (Yu et al. 2015).

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