Late Triassic ecosystem variations inferred by palynological records from Hechuan, southern Sichuan Basin, China

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Abstract – The Late Triassic deposits of the Sichuan Basin, southwestern China are significant for hosting abundant and diverse fossil assemblages including plants (containing spores and pollen), bivalves and insects. However, the Late Triassic palaeoecological variations are still poorly documented in this region. Here we present results from a palynological study from the Upper Triassic Xujiayie Formation in Hechuan of Chongqing, southern Sichuan Basin. The palynological analysis revealed a well-preserved terrestrial palynoflora of high diversity, comprising 184 species in 75 genera of spores and pollen. Three palynological assemblages were recognized, reflecting terrestrial successions throughout the entire interval with significant changes in the vegetation. Cycads/bennettites/ginkgophytes and conifers show an increasing trend into younger deposits, while ferns and lycopsids decrease in relative abundance. The Late Triassic vegetation underwent changes from lowland fern forest to a mixed forest with more canopy trees. We applied the Spore-pollen Morphological Group (SMG) method and Sporomorph EcoGroup (SEG) model to interpret the palaeoclimate features. The results reveal that the lower part of the Xujiayie Formation was deposited under relatively warm and humid conditions with an overall cooling and drying trend from latest Norian to Rhaetian time, accompanied by a general decrease of ferns and simultaneous increase of gymnosperms, and a decline in diversity of miospores. This study presents data on variations within the terrestrial ecosystem prior to the end-Triassic extinction event in the Sichuan Basin, and therefore provides important information for understanding the changes in the vegetation preceding the end-Triassic event.

Keywords: End-Triassic event, palynology, mass extinction, Sporomorph EcoGroup, climate change

1. Introduction

The end-Triassic mass extinction (201.36 ± 0.17 Ma; Schoene et al. 2010; Wotzlaw et al. 2014) is considered as one of the five largest Phanerozoic extinction events (Raup & Sepkoski, 1982; Sepkoski, 1996; Hesselbo, McRoberts & Pálfy, 2007), and massive biotic crises occurred in both the marine and terrestrial realms (Colbert, 1958; Pálfy et al. 2000; Hallam, 2002; Hesselbo et al. 2002; Olsen et al. 2002; Akikuni et al. 2010). In the ocean, the conodont animal became extinct and corals and molluscs such as bivalves and ammonites were seriously affected (Hallam, 1990, 2002; Tanner, Lucas & Chapman, 2004; Lucas & Tanner, 2007, 2008; Lathuiilière & Marchal, 2009); on land, amphibians and reptiles suffered major losses (Colbert, 1958; Olsen, Shubin & Anders, 1987; Milner, 1989; Benton, 1991; Tanner, Lucas & Chapman, 2004; Lucas & Tanner, 2008). Within plant ecosystems, a major change took place with both reorganization and extinctions (McElwain et al. 2007; McElwain, Wagner & Hesselbo, 2009; Wang et al. 2010; Vajda & Bercevici, 2014; Sha et al. 2015; Lindström, 2016). Widespread magmatic activity of the Central Atlantic Magmatic Province (CAMP) has repeatedly been invoked to have triggered this catastrophic event (Marzoli et al. 1999, 2004; Wignall, 2001; Hesselbo et al. 2002; Hesselbo, McRoberts & Pálfy, 2007; van de Schootbrugge & Wignall, 2016). The most commonly accepted killing mechanism is rapid global warming driven by outgassing of CO₂ and release of methane (McElwain, Beerling & Woodward, 1999; Tanner, Lucas & Chapman, 2004; Bonis, Ruhl & Kürschner, 2010; Whiteside et al. 2010; Ruhl et al. 2011; Schaller, Wright & Kent, 2011; Steinhorsdottir, Jeram & McElwain, 2011; Schaller et al. 2012), and acidification of surface waters and terrestrial environments (van de Schootbrugge et al. 2009; Greene et al. 2012; Hönsch et al. 2012; Richoz et al. 2012; Callegaro et al. 2014; Ikeda et al. 2015; Bachan & Payne, 2016; van de Schootbrugge & Wignall, 2016).

In the palaeobotanical record, the end-Triassic event is typified by extinction of seed ferns including Lepidopteris, and the void was soon taken by diteridacean ferns such as Thaumatopteris and a flora rich in conifers, ginkgoaleans and bennettites (McElwain et al. 2014).
This dramatic change is also expressed in the palynological record where Rhaetian and, in some places, early Hettangian successions host abnormal abundances of the enigmatic gymnosperm pollen Ricciisporites tuberculatus (Bonis, Ruhl & Kürschner, 2010; Mander, Kürschner & McElwain, 2013; Vajda, Calner & Ahlberg, 2013; Lindström, 2016). In the European record, a transitional zone dominated by fern spores has been identified (Ruckwied et al. 2008; Götz et al. 2009; Larsson, 2009; Ruckwied & Götz, 2009; van de Schootbruggte et al. 2009; Pieńkowski, Niedźwiedzi & Waksmundzka, 2012; Vajda, Calner & Ahlberg, 2013; Lindström, 2016). This interval in the Swedish record has been formalized as the ‘Transitional Spore Spike Interval’ (TSI) by Larsson (2009). This interval of pioneer vegetation is followed by the Hettangian floras characterized by high portions of Classopolis (Cheirolepidiaceae) recorded, for example from Sweden (Lund, 1977; Guy-Ohlson, 1981; Vajda, Calner & Ahlberg, 2013), Greenland (Pedersen & Lund, 1980; Mander, Kürschner & McElwain, 2013) and elsewhere.

With regards to the duration of the end-Triassic extinction, many workers argue that the extinction occurred over a prolonged interval marked by a series of discrete extinction events during Carnian–Rhaetian, rather than a single mass extinction at the end of the Rhaetian Age (Benton, 1986; Hallam, 2002; Tanner, Lucas & Chapman, 2004; Bambach, 2006; Lucas & Tanner, 2008, 2015; Wignall & van de Schootbruggte, 2016); studies on the Late Triassic ecosystem therefore form a very important role for better understanding the environmental changes prior to the end-Triassic extinction event.

In East Asia, the end-Triassic palaeobotanical and palynological records are somewhat scarce compared with Europe and North America. Two prime localities have so far been identified in China, both with well-exposed successions spanning the Triassic–Jurassic boundary, yielding diverse mega- and micro-floral records from terrestrial ecosystems. The regions include the Junggar Basin in the northwestern part of the country (Deng et al. 2010; Sha et al. 2011, 2015) and the Sichuan Basin in southwestern China (Wang et al. 2010). In particular, the Upper Triassic strata of the Xujiahe Formation are well developed in the Sichuan Basin and contain diverse fossil plant assemblages (Ye et al. 1986; Huang & Lu, 1992; Huang, 1995; Wang et al. 2010). Recent magnetostratigraphic studies revealed that the age of the Xujiahe Formation ranges from latest Norian to Rhaetian (from 207.2 Ma to 201.3 Ma at Qilixia, Xuanhan, northeastern Sichuan Basin) (Li et al. 2017). Previous palynological studies on the Upper Triassic successions within the Sichuan Basin have contributed much to understanding the diversity and stratigraphy of the basin (Li, 1992; Cao & Huang, 1980; Liu, 1982; Bai et al. 1983; Zhang, 1984; Lu & Wang, 1987; Yuan, 1989; Huang, 1991; Shang & Li, 1992; Wang et al. 2008, 2010; Li & Wang, 2016). Recent efforts to decipher the regional responses of terrestrial plant communities prior to the end-Triassic event have been undertaken at several localities within the Sichuan Basin (Liu, Li & Wang, 2015a, b; Li et al. 2016). However, studies on the Late Triassic terrestrial palaeoenvironment based on palynology are still poorly documented in this region, thus our understanding on the Late Triassic ecosystem in the Sichuan basin therefore needs to be enhanced.

The present study documents a detailed palynological record from the Upper Triassic Xujiahe Formation of the Tanba section in the Hechuan region, southern Sichuan Basin (Fig. 1). Based on our palynological data, we aim to: (1) describe the Late Triassic vegetation in terms of abundance and diversity; and (2) decipher the Late Triassic climate variations in the studied area and place the results in a broader palaeogeographical context of the Late Triassic Period.

2. Geological setting

Located at the western margin of the South China block and the eastern margin of the Tibetan Plateau, the Sichuan Basin is a large terrestrial petroliferous and coal-bearing basin, covering an area of 260,000 km² (Wang et al. 2010). It is bounded to the west by the Longmenshan orogenic belt, to the east by the Xuefengshan intercontinental tectonic deformation system, to the north by the Micangshan and Dabashan uplift belts, and to the south by the Emeishan–Liangshan fault-fold belt (Wang et al. 2010). Palaeozoic – early Mesozoic marine strata are well developed in the adjacent mountain areas, including Precambrian, Cambrian, Ordovician, Silurian, Carboniferous, Permian and Lower–Middle Triassic deposits. The Upper Triassic is dominated by terrestrial successions, mainly distributed in the eastern and northeastern margin of the basin. The remaining part of the basin is covered by massive Jurassic and Cretaceous red beds (Wang et al. 2010; Fig. 1).

Most importantly, the Upper Triassic strata represented by the Xujiahe Formation mainly consist of coal-bearing clastic rocks deposited in an inland lacustrine–fluvial–coal-swamp environment, varying over 400–650 m in thickness (Wang et al. 2010). The coal seams, which contain diverse plant remains (e.g. Xujiahe flora), play an important economic and scientific role in the Sichuan Basin (Wang et al. 2010).

The Xujiahe Formation is well exposed at the Tanba Section in the Hechuan region, southern Sichuan Basin (Fig. 1), administratively belonging to Chongqing City. The Xujiahe Formation overlies the Middle Triassic marine Leikoup Formation and is, in turn, conformably overlain by the terrestrial Lower Jurassic Zhenzhuchong Formation (Fig. 2). At the Tanba section, an c. 500 m outcrop of the Xujiahe Formation is well exposed. The lithology mainly comprises sandstones, siltstones, mudstones and coal beds, yielding a diverse and rich fossil assemblages of plants and
bivalves. The Xujiahe Formation is subdivided into six lithological members (I–VI), numbered in ascending order. Members I, III and V are mainly dominated by mudstones and thin coal beds, representing floodplain–lacustrine and coal swamp deposits, whereas members II, IV and VI mainly comprise sandstones, representing fluvial-delta deposits (Fu et al. 2010; Wang et al. 2010; Fig. 2).

3. Materials and methods

Thirty-three palynological samples were collected from the Upper Triassic Xujiahe Formation (from the members I–VI) across the Tanba section in the Hechuan region. Eighteen samples were productive and yielded well-preserved and rich miospores (spores and pollen). No productive samples were however recovered from Member II (Fig. 2). All the productive samples were collected from organic-rich mudstones, siltstone and coal, therefore minimizing the taphonomic bias.

For palynological preparation, approximately 30 g of sediment was treated with HCl and HF to remove carbonates and silicate minerals, respectively. The residue of each sample was then washed with distilled water until a neutral pH was reached. The residue was subsequently sieved through a 10 μm size mesh. Finally, the palynomorph-bearing residues were mounted on slides using glycerin jelly, and were sealed with paraffin wax. At least 250 sporomorphs were counted per sample. All samples were studied using an Olympus BX41 microscope. Photomicrographs were taken using a Zeiss Imager Z2 microscope and an AxiosCam HRc imaging system. The SMG (Spore-pollen Morphological Group) method outlined by Visscher & Van der Zwan (1981) and the SEG (Sporomorph EcoGroup) model established by Abbink (1998) and Abbink, van Konijnenburg-van Cittert & Visscher (2004) were applied in this study to reconstruct the palaeoclimatic variations. All palynological slides are stored at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

4. Palynology

The miospores of the Xujiahe Formation in the Hechuan Section of Chongqing City, southern Sichuan
Figure 2. Stratigraphic column of the Tanba Section of the Xujiahe Formation, indicating the beds sampled for palynology.
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Figure 3. (Colour online) Representative spore taxa recovered from the Xujiahe Formation of the Hechuan region. Taxa names are followed by slide number. (a–c) Dictyophyllidites harrisii: (a, b) HC10-1; (c) HC11-3. (d) Dictyophyllidites mortoni, HC26-6. (e–h) Concavisporites toralis: (e) HC10-4; (f–h) HC9-1. (i) Cyathidites australis, HC28-2. (j, k) Cyathidites minor; (j) HC13-2; (k) HC18-4. (l) Punctatisporites triassicus, HC13-1. (m) Leiotriletes adnatus, HC13-2. (n) Leiotriletes toroiformis, HC26-1. (o) Toroisporis sp., HC10-6. (p) Osmundacidites wellmani, HC13-1. (q) Lunzisporites luenensis, HC30-2. (r, t) Anapiculatisporites spiniger; (r) HC11-6; (t) HC24-6. (s) Lophotriteres sparsus, HC18-2. (u) Granulatisporites granulatus, HC13-1. (v, w) Acanthotriletes aculeatus: (v) HC17-3; (w) HC18-4. (x, ee) Asseretospora gyrata, HC13-3. (y, z) Annulispora folliculosa; (y) HC11-2; (z) HC13-1. (aa) Lycopodiacidites rudis, HC11-4. (bb) Lycopodiumsporites sp., HC13-5. (cc) Asseretospora curvata, HC13-1. (dd) Kyrtomisporis laevigatus, HC10-2. (ff) Asseretospora scanicus, HC13-3.

Basin are diverse and well preserved, represented by 184 species of spores and pollen in 75 genera (see online Supplementary Table S1, available at http://journals.cambridge.org/geo). The representative miospores are illustrated in Figures 3–5. The palynoflora of the Xujiahe Formation from the Hechuan region has previously been assigned a Norian–Rhaetian age (Liu, Li & Wang, 2015).
supported by a recent geomagnetic study (Li et al. 2017). Here we provide a more detailed vegetation reconstruction coupled with palaeoclimatic interpretations through the studied succession. For palaeoclimatic and palaeoecological purposes, the palynological assemblages were divided based on relative abundance. Three assemblages were recognized and the percentages of selected taxa are illustrated in Figure 6. The characteristic features for each assemblage are outlined below in ascending stratigraphic order. The percentages are expressed in whole numbers.
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4.a. Dictyophyllidites harrisii – Concavisporites toralis – Kyrtomisporis laevigatus – Aratrisporites fischeri (DCKA) assemblage (samples HC07–HC10)

The DCKA assemblage is identified in Member I and within the base of Member III of the Xujiahe Formation (Fig. 6). It is characterized by a significant dominance of spores (average 77%), highly dominated by trilete fern spores (mostly produced by ground ferns) represented mainly by Concavisporites/Dictyophyllidites (23%), followed by Leiotriletes (8%), Kyrtomisporis (7%), Granulatisporites (6%), Cyathidites (4.5%) and Toroisporis (3%). Other spore genera occurring in lower abundances (1–3%) within
this assemblage include Uvaesporites, Klukisporites, Lunzisporites, Punctatisporites, Planisporites, Assereotospora, Sphagnumsспорites, Anapiculatisporites and Kraeuskisporites. Monolete spores comprise >5% and are mainly represented by Aratrisporites produced by lycophytes (Fig. 6; Table 1).

In the DCKA assemblage, gymnosperm pollen grains reach an average of 24% which are dominated by monocolpate pollen grains (average 11%, including Chasmatosporites, Cycadopites and Monosulcites). Bisaccate conifer pollen grains dominate (average of c. 26%), represented by Cycadopites (11%), Chasmatosporites (10%) and Monosulcites (5%). Bisaccate conifer pollen grains are the second-most abundant type (average 15%), represented by Pinuspollenites (7%), Paleoconiferus (2%), Piceites (2%), Quadraeculina (2%) and Pseudopicea (1%). Bisaccate seed fern pollen (including Alisporites and Vitreisporites) and Araucariae increase in abundance (7% and 6%, respectively). Classopollis is rare (0.5%), and shows a distinct increase in the uppermost part of this assemblage (Fig. 6).

Trilete spores are the dominant type among spores in the CPDA assemblage (average 39%), marked mainly by Concavisporites/Dictyophyllidites (10%), Cyathidites (6%) and Granulatisporites (4%). Other spore genera are common (1–3%) in this assemblage such as Assereotospora, Osmundacidites, Lophotritiles, Acanthotritiles, Conbaculatisporites, Conbaculatisporites, Cyclogranisporites, Punctatisporites and Kyrtomisporis. Monolete spores are also common (5%), and are mainly represented by Aratrisporites produced by lycophytes (4%) (Fig. 6).
Late Triassic ecosystem variations

Table 1. Botanical affinity and classification of the Sporomorph EcoGroup (SEGs) for dispersed miospores of the Xujiahe Formation in the Hechuan region, southern Sichuan Basin, China

| Botanical affinity | Sporomorph genera | SEG | Ecological remarks |
|--------------------|-------------------|-----|-------------------|
| Horsetails          | Calamospora       | Lowland | Wetter, warmer |
| Ferns (Dipteridaceae/ Matoniacae) | Dictyophyllidites, Conavisporites | | |
| Ferns (Dipteridaceae) | Kyrtomisporis, Apiculatisporis, Grandulatisporites | Lowland | Drier, warmer |
| Ferns (Osmundaceous) | Punctatisporites, Todiosporites, Osmundacidites, Conbaculatisporites, Baculatisporites | Upland | Wetter, cooler |
| Ferns (Dicksoniaceae) | Cibotiampora, Converrucosistipes | Lowland | Drier, warmer |
| Ferns (Cystaceae/ Dicksoniacae) | Cyathidites | | |
| Ferns (Pteridaceae) | Asseretospora | Lowland | Drier, cooler |
| Ferns (Marattiacae) | Angiopteridispinosa, Toriosporis, Cyclocroanisporites, Marattisporites | Upland | Wetter, cooler |
| Ferns | Leiotorrides, Lophotorides, Lunzisporites, Planisporites, Tripartina, Brochiotorides, Klakispores, Diictoryotides, Foveotorides, Reticulatisporites, Triquitrites | | |
| Cycles/bennettes | Cordatozites, Momordulcites | Lowland | Drier, warmer |
| Cycles | Chasmatosporites | Lowland | Drier, warmer |
| Ginkgophytes | Monosulcites minimus | Lowland | Drier, warmer |
| Conifers (Cheiropleiopidae) | Classopollis | Lowland | Drier, warmer |
| Gymnosperms | Tubervernulopilates, Verrunaculopilates | Lowland | Drier, warmer |
| Conifers (Taxodiaceae) | Inaperturopollenites | Lowland | Drier, warmer |
| Conifers (Pinaceae) | Piceites, Piuspollenites | Lowland | Drier, warmer |
| Conifers (Podocarpaceae) | Podocarpidites, Prototopodocarpus, Quadraeculina, Taeniasporites, Platysaccus | Lowland | Drier, warmer |
| Conifers (Araucariaceae) | Araucariacites | Lowland | Drier, warmer |
| Conifers | Prototinus, Pseudopinus, Pseudopicea, Protoconiferus, Puleoconiferus | | |
| Pinaceae/Cyads | Ovalipollis | | |
| Gymnosperm | Cordaitina, Luciersporites, Chordasporites | River | |
| Mosses | Sphagnospornites, Annulispina, Polycyclaropilates | | |
| Lycopsids | Renuoterides, Luevigtasporites | | |
| Lycopsids | Lycopodiumsporites, Leptotepidites, Lycopodiacidites, Kraeuselispores, Triacorosporites, Uvaesporites | | |
| Lycopsids | Artrispores, Neoisstrickia, Acanthotarletes, Anaplapalasporites, Denosispores, Limhosporites, Triizonites | | |
| Seed ferns | Vitriporites, Alisporites | | |

Note: This summary is based upon comprehensive results of the in situ spore studies of the Mesozoic plants and their ecology based on Couper (1957); Harris (1961, 1964, 1969, 1979), Bocock & Janssionius (1969), van Konijnenburg-van Cittert (1971, 1978, 1993, 2002), Litwin (1985), Osborn & Taylor (1993), Balme (1995), Wang & Mei (1999), Deng & Chen (2001), Abbink, van Konijnenburg-van Cittert & Visscher (2004), Wang, Mosbrugger & Zhang (2005), Jiang et al. (2008), Guignard et al. (2009), Wang & Zhang (2010) and Wang et al. (2015).

4c. Cyathidites minor – Monosulcites fusiformis – Classopollis minor – Quadraeculina anellaeformis (CMCQ) assemblage (samples HC24–HC32)

The assemblage CMCQ occurs in Members IV–VI of the Xujiahe Formation (Fig. 6) and is characterized by a significant dominance of gymnosperm pollen grains (relative abundance 64%). Monosulcate pollen (Monosulcites, Cycadopites and Chasmatoporeites) are the most prominent type. In comparison with the other two assemblages, a higher portion is represented by pollen attributed to seed ferns (8%). The relatively high abundance of Classopollis (6%) is also significant, a taxon that is virtually absent from the other two assemblages. Spores make up 36% with a significant dominance of Cyathidites (10%). Monolete spores are rare, comprising <1% (Fig. 6).

5. Development of the vegetation

Based on the botanical affinity of the dispersed spore and pollen genera recovered from the studied successions within the Hechuan region of the Sichuan Basin (Table 1), a picture of a diverse Late Triassic ecosystem emerges. Although the vegetation is chiefly dominated by ferns and conifers, other plant groups are present in lower relative abundance. These include mosses, horsetails and lycopsids which vary considerably in relative abundance through the studied succession (Fig. 7). The overall evolution of the Late Triassic vegetation in the Hechuan region is suggested to have undergone changes from lowland fern forest to a mixed forest with more canopy trees.

The earliest Late Triassic DCKA ecosystem (represented in Member I and the base of Member III) was dominated by ferns, mainly Dipteridaceae/Matoniaeceae together with a variety of other fern families including Cyathaceae/Dicksoniacae, Osmundaceae and Marattiacae. These ferns, together with typical Triassic lycopsids and rare mosses, comprised the ground cover vegetation during the earliest part of Late Triassic time. The midstorey was represented by gymnosperms related to cycads/bennettes/ginkgophytes. Canopy trees were
Figure 7. Palaeovegetation composition of the Xujiahe Formation from the Hechuan region. (a) DCKA assemblage (Member I and base of Member III); (b) CPDA assemblage (Member III); and (c) CMCQ assemblage (Members IV, V, VI).

relatively scarce, represented by Pinaceae, Araucaraceae and Podocarpaceae, and the pollen may have been transported in from elevated areas into the lowlands. Seed ferns existed, but made up a very limited portion of this ecosystem.

The CPDA ecosystem was characterized by dominance in gymnosperms, mainly represented by cycads/bennettites/ginkgophytes making up the mid-storey bush vegetation together with seed ferns. Canopy vegetation was represented by relatives of Pinaceae. The ferns are much less prominent in the CPDA assemblage compared to the older DCKA assemblage (Fig. 7b), and these were mainly represented by Dip teridaceae/Matoniaceae. Lycopsids are not as abundant compared with the DCKA assemblage. A new element, the family Cheirolepidiaceae (Classopollis), a group that was common during Jurassic and Early Cretaceous time around the world (Alvin, 1982; Vajda, 2001; Vajda & Wigforss-Lange, 2006; Jansson et al. 2008), interestingly appears in this assemblage.

In assemblage CMCQ, represented within the upper part of the Xujiahe Formation (Member V and VI), cycads/bennettites/ginkgophytes and conifers characterize the flora. It is interesting to note that Cyatheaceae/Dicksoniaceae show a sharp increase in abundance (average 10%). Other fern families include Dipteridaceae/Matoniaceae, Osmundaceae, Marattiaceae and Pteridaceae. The mid-storey vegetation was dominated by monosulcate pollen producers, cycads/bennettites/ginkgophytes (Fig. 7c). Conifers including Cheirolepidiaceae, Araucariaceae, Pinaceae, Podocarpaceae and Taxodiaceae were prominent (average 24%), making up the canopy. It is notable that Cheirolepidiaceae shows a remarkable increase in relative abundance and becomes common during this period (average 6%). Seed ferns show an increasing trend (8%). Lycopsids are less frequent, and mosses and horsetails are rare.

6. Palaeoclimatic interpretations

As a complement to the vegetation reconstruction based on the abundance data of pollen and spores related to their affinities, we have carried out
Figure 8. Relative abundances of the Spore-pollen Morphological Groups (SMGs) of the Xujiahe Formation from the Hechuan region. A, Trilete acavate laevigate or apiculate spores; B, Trilete acavate reticulate or murornate spores; C, Trilete cingulate or zonate spores; D, Monolete spores; E, Ovalipollis + Perinopollenites; F, Monosulcate pollen; G, Asaccate pollen; H, Monosaccate pollen; I, Trilete (proto) bisaccate pollen; J, Alete bisaccate pollen; K, Taeniate (proto) bisaccate pollen; L, Classopollis spp. A–D are considered to be hygrophytic elements, E–G intermediate and H–L xerophytic elements.

The results (Fig. 8) show that the ratio of hygrophytic elements to xerophytic elements (hygrophytic/xerophytic) as an index of humidity variation. The results (Fig. 8) show that the palaeoclimatic interpretations by applying the Spore-pollen Morphological Group (SMG) method (Vischer & Van der Zwan, 1981) and the Sporomorph EcoGroup model (SEG) (Abbink, 1998; Abbink, van Konijnenburg-van Cittert & Visscher, 2004).

Twelve Spore-pollen Morphological Groups (SMGs) A–L were identified in this study (Fig. 8), reflecting different ecological adaptations, including hygrophytic (water-loving, groups A–D), xerophytic (dry-loving, groups H–L) and intermediate elements (groups E–G). We have applied the ratio of hygrophytic elements to xerophytic elements (hygrophytic/xerophytic) as an index of humidity variation.
hygrophytic/xerophytic ratio is high in the lowermost part of the Xujiahe Formation, particularly at the base of Member III (Fig. 8, line A), indicating a humid pulse of short duration and expressed in one sample within the Xujiahe Formation. This is in agreement with the results based on the vegetation composition in Assemblage DCKA. The hygrophytic/xerophytic ratio is markedly low for the rest of the succession (with the exception for sample HC16; Fig. 8, line B), suggesting a drying trend upwards, interrupted by a short humid pulse.

Using the Sporomorph EcoGroup model (SEG) (Abbkink, 1998; Abbkink, van Konijnenburg-van Cittert & Visscher, 2004), we classified the palynomorphs into three SEG groups, including: (1) Lowland SEG; (2) Upland SEG; and (3) River SEG (Table 1, Fig. 9). Elements attributed to the Lowland SEG show a marked dominance in the Xujiahe Formation, with a maximum of 81% and a minimum of 46%; the River SEG and Upland SEG are less abundant. The total for the Lowland SEG and River SEG is a minimum of 69% (Fig. 9). This implies that the studied area during Late Triassic time was represented by a general lake-marsh environment set in a lowland ecosystem. However, variations in the ecosystem and the climate during Late Triassic time are reflected in the palynological assemblages of this study, revealing that the ecosystem was not constant throughout this period as previously suggested (Huang & Lu, 1992; Wang et al., 2016). The above outlined climate change is consistent with macrofloral studies of the Xujiahe Formation, which also implied a palaeoclimatic trend from humid to arid conditions (Huang & Lu, 1992). Palynological records from northwestern and central Europe, Western Australia and northeastern Greenland revealed a cooling during latest Triassic time (Hubbard & Boulter 1997, 2000) and the trend from humid to arid has also been noted from the Newark Basin (Kent & Olsen, 2000; Olsen & Kent, 2000) where it has been linked to the northwards drift of the North American continent. Palynological data from Austria and the United Kingdom indicated a warming trend from the Triassic to the Jurassic periods, interrupted by a cooler period (Bonis & Kärstchner, 2012). Further, a bentho-planktonic study from the Austrian Alps suggested that cooling episodes might have occurred during latest Triassic time (Clémence et al. 2010). The above results may suggest a global cooling event during latest Triassic time. Tucker & Benton (1982) proposed climate-induced (increasing aridity) floral changes as a factor in Late Triassic tetrapod extinction. The present palynological record seems more consistent with a gradual ecosystem degradation extended over the Norian–Rhaetian interval. The cooling and drying climate from latest Norian to Rhaetian time may have caused a gradual ecosystem breakdown during latest Triassic time, and later triggered the end-Triassic biotic crisis.

7. Discussion

Our palynological study indicates an overall cooling and drying trend during latest Norian–Rhaetian time, accompanied by a general decrease in ferns (mainly represented by trilete spores), an increase in gymnosperms (represented by bisaccate and monocoleate pollen), and a decline in diversity of both pollen and spores (Fig. 10). Similar results have been reported from coeval deposits in Xuanhan, northeastern Sichuan Basin, indicating a cooling and drying climate during the development of the uppermost part of the Xujiahe Formation (Li et al. 2016). The above outlined climate change is consistent with macrofloral studies of the Xujiahe Formation, which also implied a palaeoclimatic trend from humid to arid conditions (Huang & Lu, 1992). Palynological records from northwestern and central Europe, Western Australia and northeastern Greenland revealed a cooling during latest Triassic time (Hubbard & Boulter 1997, 2000) and the trend from humid to arid has also been noted from the Newark Basin (Kent & Olsen, 2000; Olsen & Kent, 2000) where it has been linked to the northwards drift of the North American continent. Palynological data from Austria and the United Kingdom indicated a warming trend from the Triassic to the Jurassic periods, interrupted by a cooler period (Bonis & Kärstchner, 2012). Further, a bentho-planktonic study from the Austrian Alps suggested that cooling episodes might have occurred during latest Triassic time (Clémence et al. 2010). The above results may suggest a global cooling event during latest Triassic time. Tucker & Benton (1982) proposed climate-induced (increasing aridity) floral changes as a factor in Late Triassic tetrapod extinction. The present palynological record seems more consistent with a gradual ecosystem degradation extended over the Norian–Rhaetian interval. The cooling and drying climate from latest Norian to Rhaetian time may have caused a gradual ecosystem breakdown during latest Triassic time, and later triggered the end-Triassic biotic crisis.

8. Conclusions

Our detailed palynological investigation of Upper Triassic terrestrial deposits within the Sichuan Basin has revealed a well-preserved and diverse palynoflora.

(1) Our study reveals an ecosystem in change where a fern-dominated vegetation was replaced by conifers and cycadoids, supplemented by relative high portions of Cladopollis in the uppermost Triassic strata. Palynological diversity patterns show a decreasing trend upsedation.

(2) Three palynological assemblages were distinguished by variations in the abundance of major plant groups, reflecting remarkable changes in the
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Figure 9. Relative abundances of the Sporomorph EcoGroups (SEGs) of the Xujiahe Formation from the Hechuan region.

terrestrial vegetation throughout the entire interval. Cycads/bennettites/ginkgophytes and conifers show an increasing trend into younger deposits, while ferns and lycopsids decrease in relative abundance.

(3) By applying the SMG method and SEG model analysis, we show that the early stage of the Late Triassic period was characterized by a relatively warm and humid climate which was followed by a cooler and drier interval. This demonstrates that the climate was not static, but rather variable.

(4) Our results reveal vegetation changes within the Sichuan Basin during the Late Triassic Period, adding to knowledge on biotic changes immediately prior to the end-Triassic event.
Figure 10. Palaeoclimate, miospore composition and miospore diversity of the Xujiahe Formation from the Hechuan region.

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Supplementary material

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