



## Pattern of vegetation turnover during the end-Triassic mass extinction: Trends of fern communities from South China with global context

Ning Zhou<sup>a,b</sup>, Yuanyuan Xu<sup>b,c</sup>, Liqin Li<sup>b</sup>, Ning Lu<sup>b</sup>, Pengcheng An<sup>b,c</sup>, Mihai Emilian Popa<sup>d,e</sup>, Wolfram Michael Kürschner<sup>f,\*</sup>, Xingliang Zhang<sup>a</sup>, Yongdong Wang<sup>b,\*</sup>

<sup>a</sup> Department of Geology, Northwest University, Xi'an 710069, China

<sup>b</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

<sup>c</sup> University of Chinese Academy of Science, Beijing 100049, China

<sup>d</sup> Southwest Petroleum University, School of Geosciences and Technology, 8, Xindu Road, Chengdu 610500, China

<sup>e</sup> University of Bucharest, Faculty of Geology and Geophysics, Department of Geology and Doctoral School of Geology, Laboratory of Palaeontology, 1, N. Bălcescu Ave, Bucharest 010041, Romania

<sup>f</sup> Department of Geosciences, University of Oslo, N-0316 Oslo, Norway

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### ABSTRACT

The end-Triassic mass extinction (ETME) is considered to be one of the five most severe extinction events in Earth history and caused the disappearance of ca. 80% of all species. The terrestrial ecosystems were also greatly affected by this extinction, but the severity of the land plant diversity loss is not well understood. Ferns are once a principal component of the terrestrial ecosystem from the late Paleozoic/early Mesozoic era and colonizers taxa commonly found in disturbed environments. In this study, we investigated the diversity and ecology of fern during the Triassic-Jurassic (Tr-J) transition in the Sichuan Basin of South China and focused for the first time on the impact of the end-Triassic mass extinction event on the fern communities. We assembled fern fossil records in 16 localities from the Rhaetian Xujiahe (XJH) Formation to the lowermost Jurassic Zhenzhuchong (ZZC) Formation. Our results indicate that no obvious mass extinctions of macro-microflora of ferns but a clear species turnover was recorded at ETME in the Sichuan Basin, reflected an appropriate response of plants in places far away from CAMP volcanism. The paleoecological analysis based on macroflora and microflora in the Sichuan Basin shows a warm and humid condition of tropical-subtropical climate during Rhaetian followed by an increase of specific dry-resistant taxa, indicating a dryer environment at the Earliest Jurassic. Additionally, multivariate statistical approaches (principal coordinates analysis, cluster analysis, network analysis) for fern macro-remains and spores data in the southeastern Sichuan Basin infer that the members of XJH and ZZC Formation cluster in three groups, corresponding to their environmental conditions, determined by humidity and temperature.

### 1. Introduction

Five mass extinction events have been recognized in the Phanerozoic over the past 600 million years (Stanley and Yang, 1994; Olsen, 1999; Finney et al., 1999; Jin et al., 2000; Ward et al., 2001; Whiteside et al., 2010). Among them, the end-Triassic mass extinction (ETME) at ~201 Ma has been linked to the extreme greenhouse warming and ocean anoxia, triggered by Central Atlantic Magmatic Province (CAMP) flood basalt volcanism (McElwain et al., 1999; Van de Schootbrugge et al., 2009; Whiteside et al., 2010; Ruhl and Kürschner, 2011; Ruhl et al.,

2011, 2020; Blackburn et al., 2013; Li et al., 2017; Heimdal et al., 2020). This event is characterized by the disappearance of almost 300 families of marine invertebrates and vertebrates and major extinctions among insects in the terrestrial ecosystem (Benton, 1995; Pieńkowski et al., 2014). The extinction patterns among land plants, however, are still controversially discussed.

Most studies on terrestrial vegetation at ETME focus on the microflora (pollen and spores) while only a few documented the vegetation history based on macroflora (leaf remains and seeds). Palynoflora and macroflora appear to show inconsistent trends of diversity loss at ETME.

\* Corresponding authors.

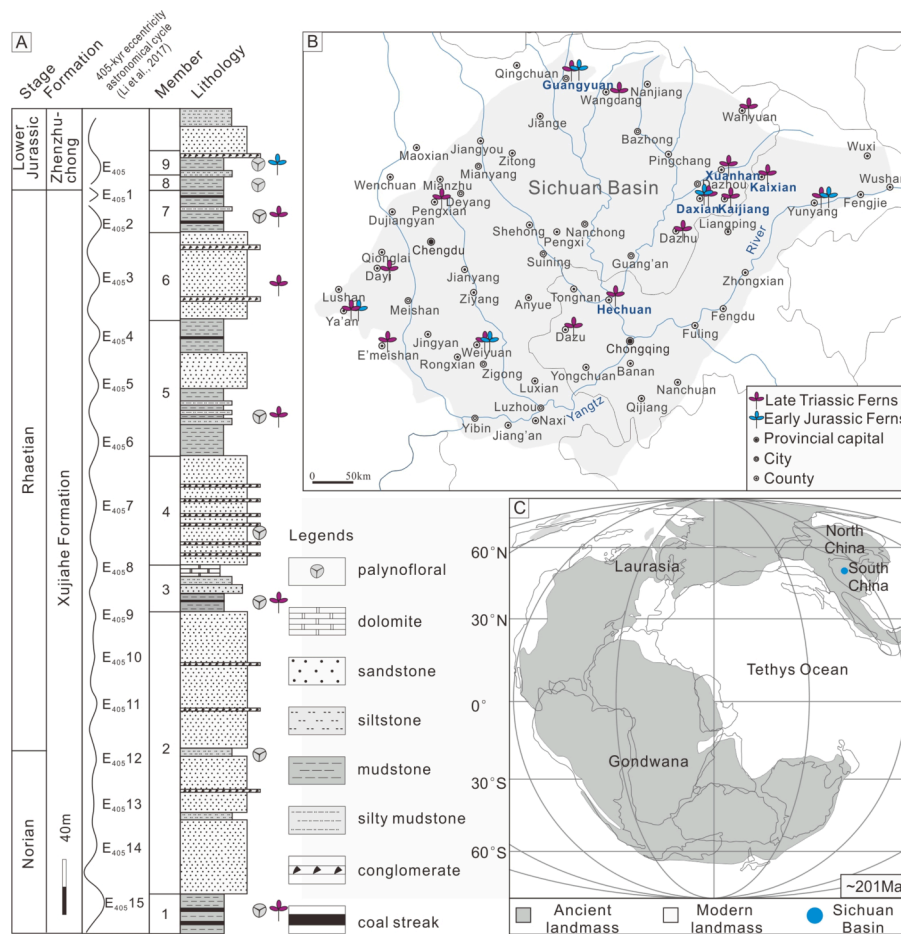
E-mail addresses: [w.m.kurschner@geo.uio.no](mailto:w.m.kurschner@geo.uio.no) (W.M. Kürschner), [ydwang@nigpas.ac.cn](mailto:ydwang@nigpas.ac.cn) (Y. Wang).

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**Fig. 1.** Location of the Sichuan Basin, and the geological map of the study area. (A) Representative upper Triassic–Lower Jurassic lithological column and paly-nostratigraphic diagram (after Li et al., 2020), geological age frame is after Li et al. (2017). (B) Sketch map showing the geographical distribution of fossil ferns in the Triassic–Jurassic Sichuan Basin. (C) Latest Triassic (~ 201 Ma) palaeomap indicating the study area.

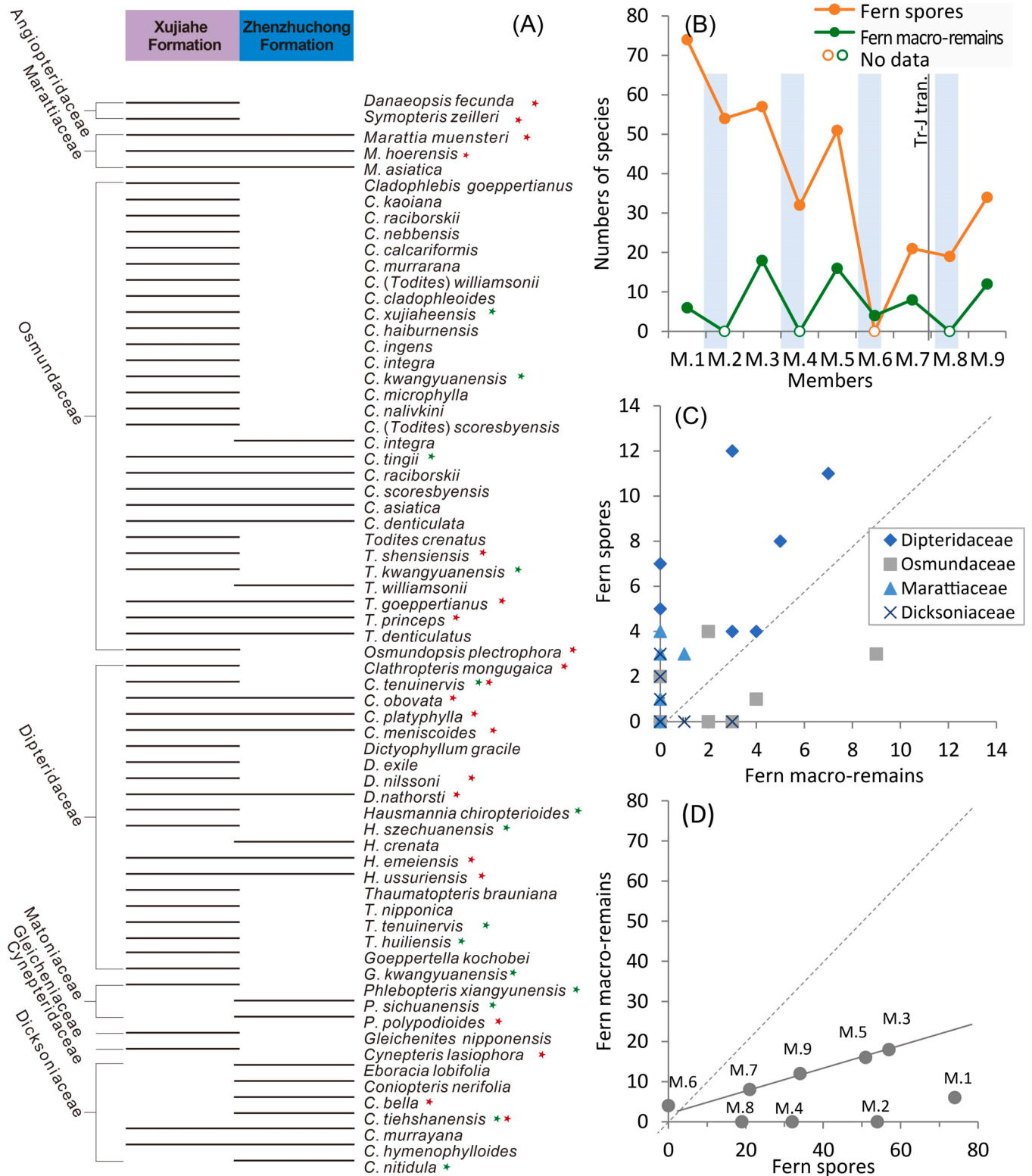
McElwain et al. (2007) investigated the diversity pattern of macroremains in East Greenland and indicate that standing species richness declined by ~85% during the ETME, whereas sporomorph records from the same region show only 10–12% diversity loss (Mander et al., 2010, 2013). Palynological studies in Europe show a significant spore-dominated interval at Tr–J transition and was interpreted as a quick recovery of spore-producing plants after the collapse of terrestrial woody vegetation (Van de Schootbrugge et al., 2009; Van de Schootbrugge and Wignall, 2015). A meta-analytic study of macroflora and microflora across Europe revealed that there was no mass extinction of terrestrial plants during the Tr–J transition (Barbacka et al., 2017). However, the high replacement of plant taxa composition (McElwain et al., 2007; Van de Schootbrugge et al., 2009; Bonis et al., 2010; Lindström, 2016), replacement of Triassic broad-leaved forms with Jurassic narrow-leaved forms (Belcher et al., 2010), the occurrence of aberrant palynomorphs (Lindström et al., 2019; Gravenyck et al., 2020), indicating severe environmental stress during the ETME.

Though macroflora usually has a limited stratigraphic resolution compared with palynoflora, tracking the diversity and ecology of macroflora provides a more intuitive and effective way to explore the biodiversity patterns and extinction rates of terrestrial vegetation, as well as environmental perturbations across the Tr–J transition (Rees et al., 2000; McElwain et al., 2007; Barbacka et al., 2017). Ferns are significant for exploring the phylogeny and evolution history of seed plants in deep time (Pryer et al., 2001, 2004; Schneider et al., 2004). They are the principal component of the terrestrial ecosystem from the late Paleozoic/early Mesozoic era and colonizers taxa commonly found in disturbed environments. Fern spore spikes were recognized as one of

the indexes for global correlation of Triassic and Jurassic boundary event (Olsen, 1999; Whiteside et al., 2010; Mander et al., 2013; Lindström et al., 2019). We present here a study of fern frond remains with a combination of spore data which allows a detailed reconstruction of the biodiversity in fern community across the Tr–J boundary in the Sichuan Basin in South China yielding plenty of plant fossils, located in the low mid-latitudes of the eastern Tethyan region and far away from CAMP (Sze and Lee, 1952; Li, 1964; Yang, 1978; Huang, 1995; Wu, 1999; Wang et al., 2015; Li et al., 2017). The purpose of our study is to (1) infer the diversity patterns and ecological changes of fern communities at ETME on the basis of known floral records in the Sichuan Basin; (2) explore the similarities between macrofloral and sporomorph records; (3) compare the pattern of vegetation turnover during the end-Triassic mass extinction with the global context.

**2. Stratigraphy and floras**

The Sichuan Basin covers for ~2.6 × 10<sup>5</sup> km<sup>2</sup> in southwestern China. The Upper Triassic and Lower Jurassic sequences of the Sichuan Basin are a set of paralic continental deposits, of which fluvial, swamp and lacustrine facies are alternatively presented regularly. Our study of stratigraphical units focuses on the uppermost Triassic XJH Formation and the lowermost Jurassic ZC Formation (Fig. 1). Based on a geomagnetic polarity time scale, XJH Formation in the Sichuan Basin spans 5.9 million years from 207.2 Ma to 201.3 Ma that is suggested to be Rhaetian (Li et al., 2017). Generally, six members are recognized in XJH Formation. Members 1, 3 and 5 are mainly mudstone with coal-bearing deposits, and members 2, 4 and 6 are dominated by medium-



**Fig. 2.** The diversity change of fern species during Triassic–Jurassic transition in the Sichuan Basin and the scatter diagrams illustrating the agreement between the fern macro-remains and spores in the northeastern Sichuan basin. (A) Stratigraphical ranges of fossil ferns and the variation of species numbers in different ages. Green stars represent originally established taxa based on Sichuan materials; Red stars represent that the species with both sterile and fertile pinnae are preserved. (B) The species diversity changes of ferns and spores across Triassic–Jurassic transition in the northeastern Sichuan basin, members 1–7 are of Late Triassic (Rhaetian) age, members 8 and 9 are of Earliest Jurassic (Hettangian) age. (C) The agreement between the ferns and spores within four representative families in the northeastern Sichuan basin. (D) The agreement between the ferns and spores in the northeastern Sichuan basin from Rhaetian to Earliest Jurassic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

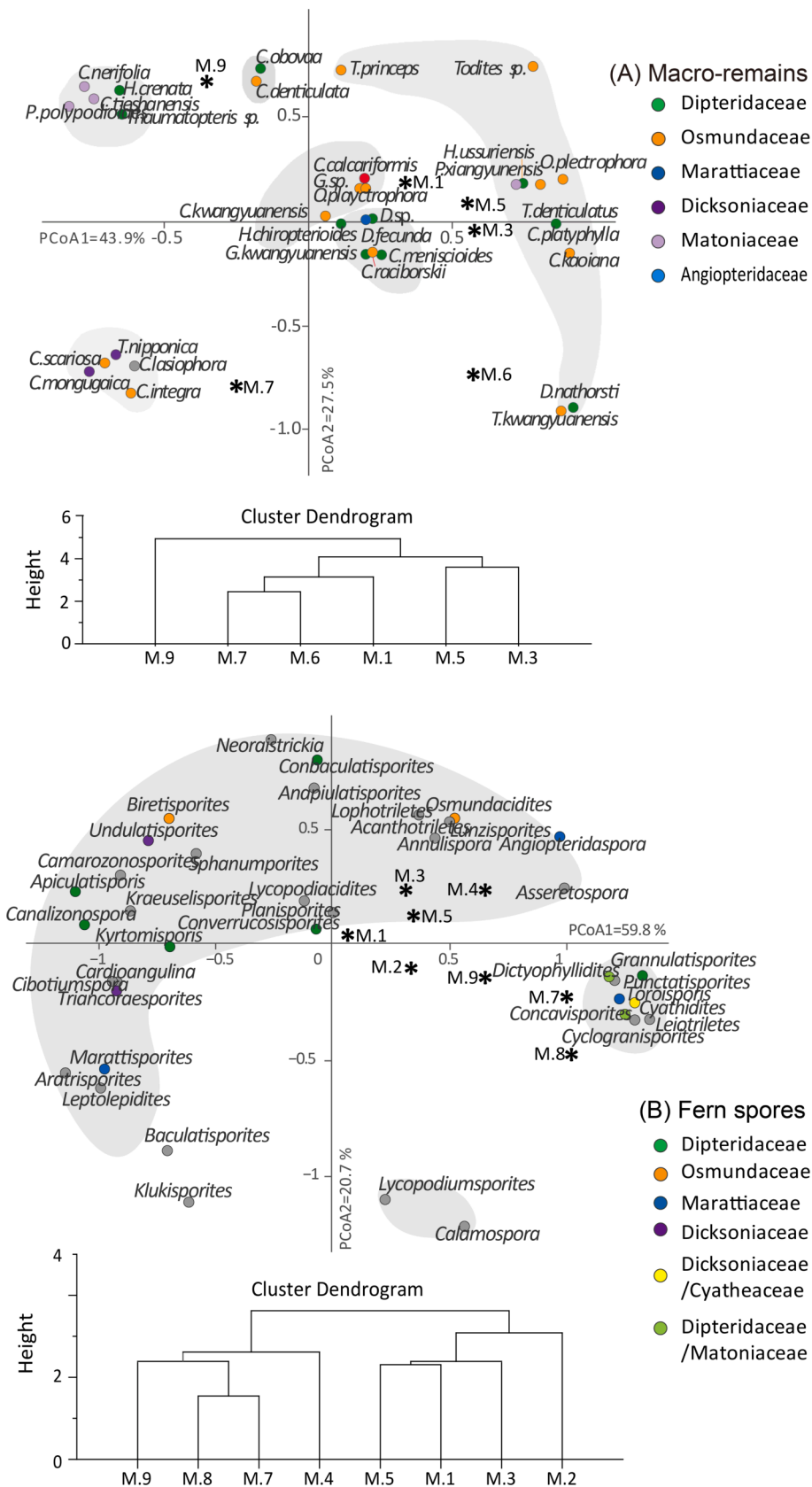
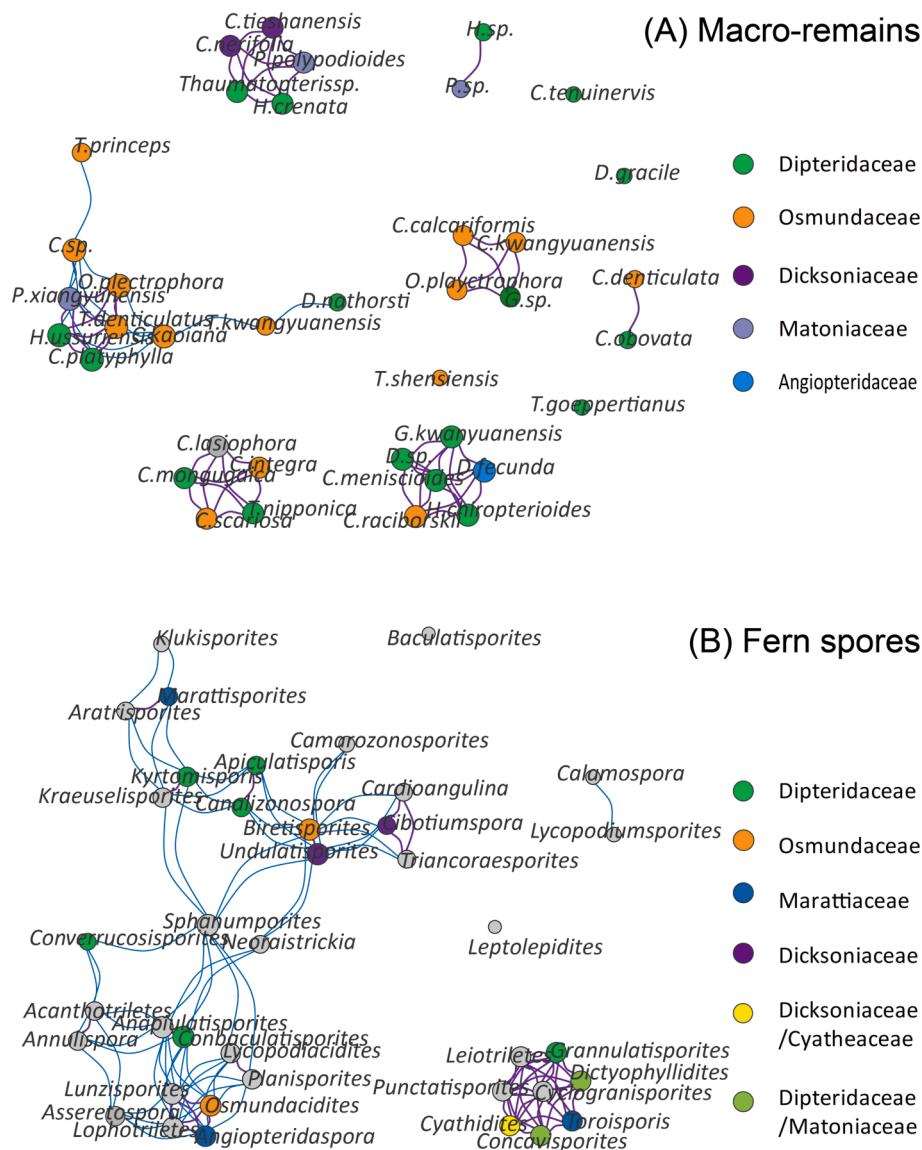


Fig. 3. Cluster dendrogram and PCoA biplots were calculated from the diversity of (A) fern macro-remains (on species level) and (B) fern spores (on genera level).





**Fig. 4.** Networks of co-occurring of (A) fern macro-remains (on species level) and (B) fern spores (on genera level) based on correlation analysis. A connection stands for a strong (Spearman's  $\rho > 0.5$ ) and significant ( $P$ -value  $< 0.05$ ) correlation. The size of each node is proportional to the number of connections.

to coarse-grained sandstones (Huang, 1995, 2001; Wang et al., 2010; Li et al., 2016). The lowermost Jurassic ZXC Formation follows conformably on top of the XJH Formation and is composed of quartz sandstone, mudstone and coal. Both the macro and microfossil plant remains were collected or recovered from mudstones with coal-bearing deposits in the members 1, 3 and 5 (Ye et al., 1986; Wang et al., 2010; Li et al., 2016).

In the Sichuan Basin, the Upper Triassic Xujiahe and the Lower Jurassic Zhenzhuchong formations yield diverse fossil plant remains (Ye et al., 1986; Wang et al., 2010). The Upper Triassic *Dictyophyllum–Clathropteris* macroflora of the Xujiahe Formation is replaced by the Lower Jurassic *Ptilophyllum–Coniopteris* flora in the Zhenzhuchong Formation (Ye et al., 1986), and the Upper Triassic *Dictyophyllidites–Kyrtonisporis–Ovalipollis–Riccisporites* palynological assemblage is replaced by the Lower Jurassic *Dictyophyllidites–Classopollis–Cycadopites* assemblage (Wang et al., 2010).

### 3. Material and methods

The materials for this investigation consist of previously published data on fossil ferns in the uppermost Triassic Xujiahe (XJH) Formation to the lowermost Jurassic Zhenzhuchong (ZXC) Formation of the Sichuan

Basin, including monographs, research papers, and atlas of fossil plants. The database contains a total of 67 fossil fern species from 16 localities. Most of the fossil fern materials are excellently preserved, including both sterile and fertile pinnae. Dipteridaceae are preserved most frequently with fertile structures. The compression specimens of Osmundaceae are scarce, and only three species from Guangyuan are documented with fertile structures. Others, such as Angiopteridaceae, Marattiaceae, Matoniaceae, Cynepteridaceae and Dicksoniaceae, also keep well-preserved fertile organs with detailed in situ spore structures. To better understand the representative species in the Sichuan Basin, we examined and described seven cataloged specimens and eight recent fossil plant collections housed in the paleobotany collection in the Nanjing Institute of Geology and Palaeontology, CAS. The systematic description and records of ferns are given in Supplementary Information. Species with uncertain determinations (cf.) were recorded as definite, as Barbacka et al. (2017) suggested. All statistical analyses were conducted using R statistical software (v.3.2.2). The Tr-J boundary sporomorph records at the Qilixia section in the Sichuan Basin were from Li et al. (2016, 2020).

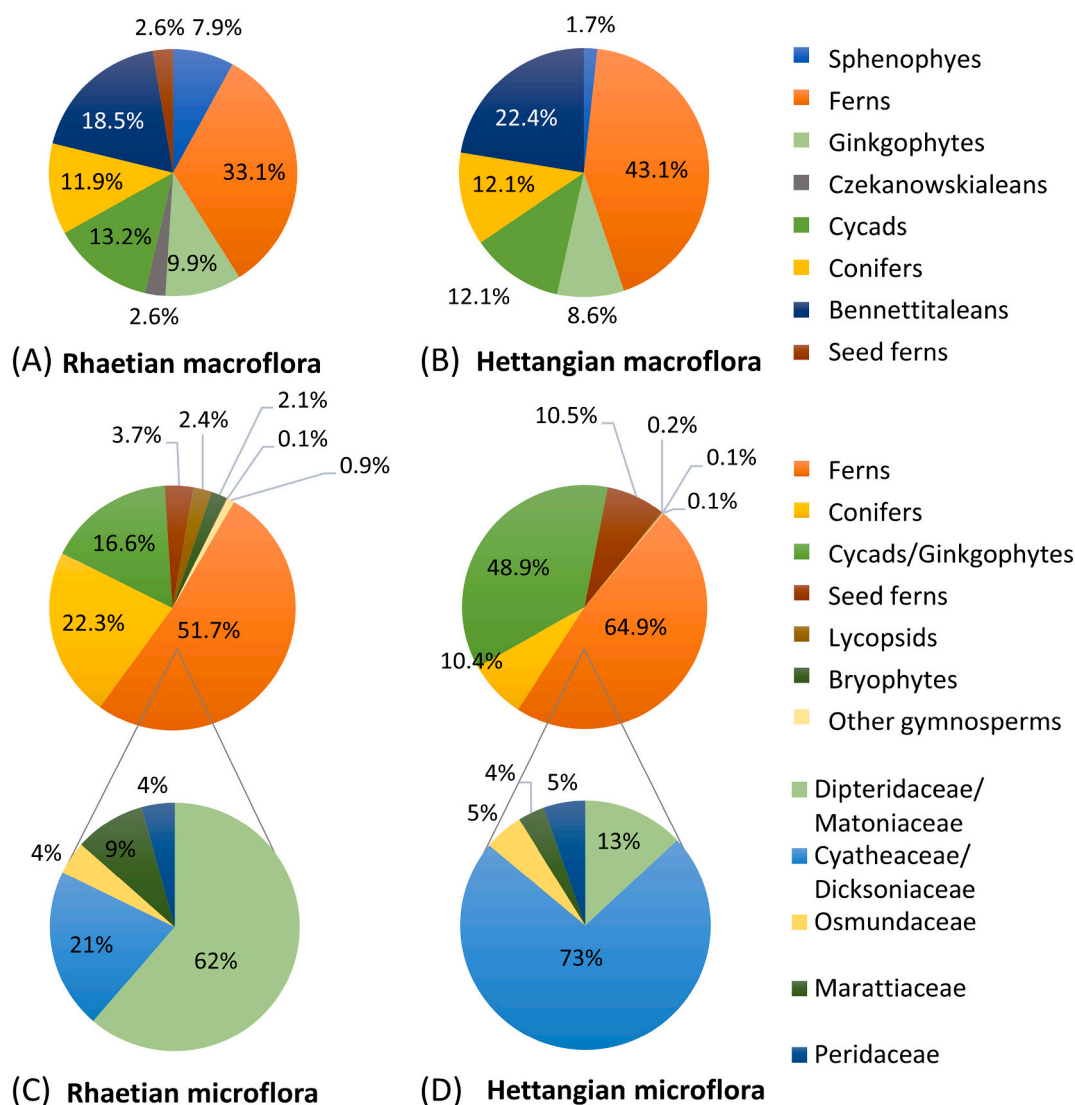


Fig. 5. Macro-micro flora composition across the Tr-J transition in the Sichuan Basin. (A) Rhaetian macroflora and (B) Hettangia macroflora (after Wang et al., 2010); (C) Rhaetian microflora and (D) Hettangia microflora (after Li et al., 2017, 2020).

## 4. Results and discussion

### 4.1. The fern diversity changes across the Triassic-Jurassic boundary

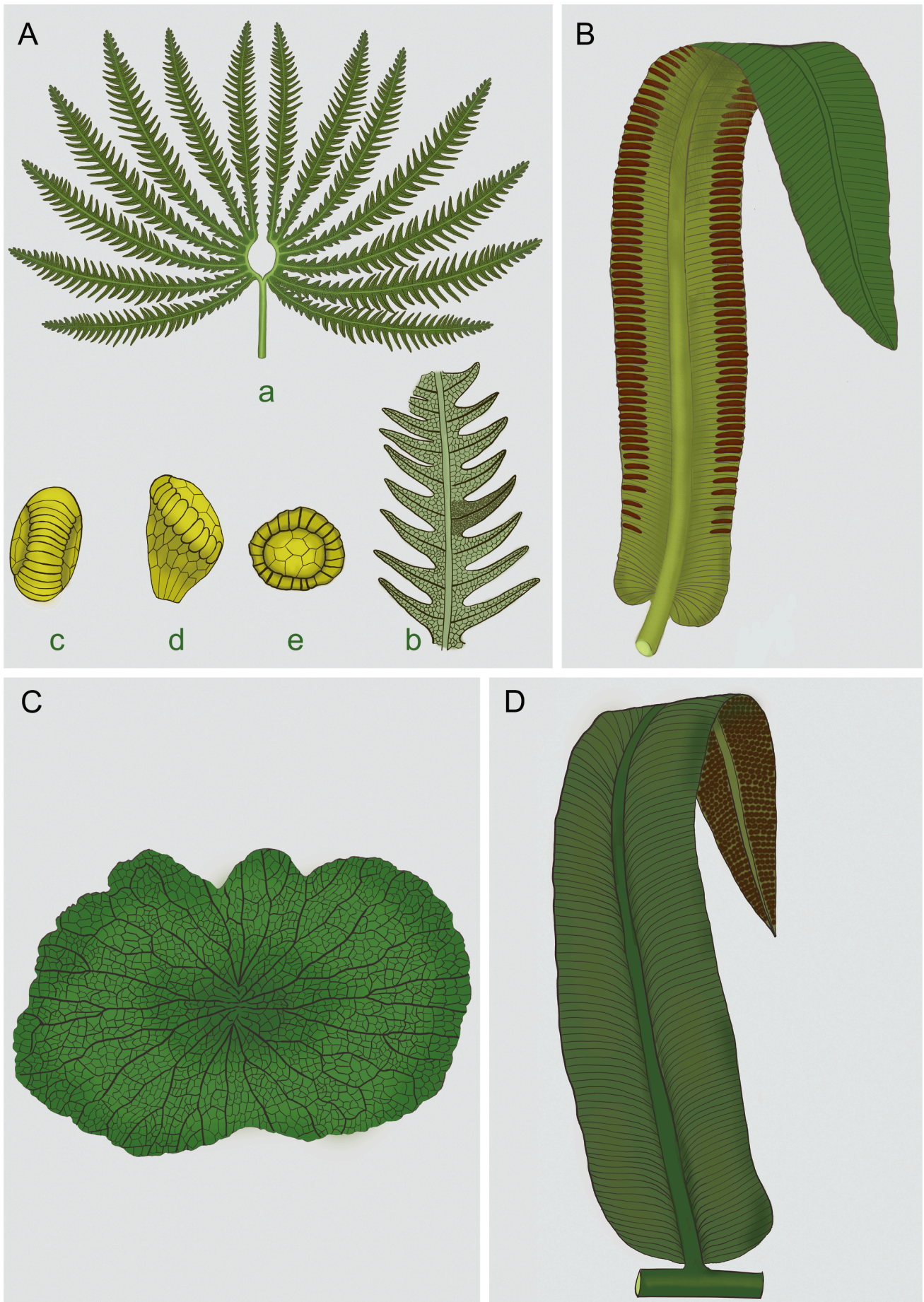
According to our investigation, 57 species ascribed to 15 genera of eight families have been reported for fern leaves during Rhaetian in the Sichuan Basin, including Angiopteridaceae, Marattiaceae, Osmundaceae, Dipteridaceae, Matoniaceae, Gleicheniaceae, Cynepteridaceae and Dicksoniaceae (Fig. 2A, Table S1). Among them, 18 species were originally established based on Sichuan materials. The ferns are dominated by Dipteridaceae with a high proportion of *Clathropteris*, and numerous Osmundaceae including high species diversity of *Cladophlebis*. Angiopteridaceae, Marattiaceae (*Marattia*), Matoniaceae (*Phlebopteris*), Gleicheniaceae (*Gleichenites*), Cynepteridaceae (*Cynepteris*) and Dicksoniaceae (*Coniopteris*) are sparsely distributed within the dominant ferns (representative species are shown in Figs. 6–8). During the earliest Jurassic, the diversity of ferns decreases nearly in half at the species level, and 29 species in nine genera were recorded. About 38 species from six genera disappeared and 10 new species firstly occurred after the Tr-J boundary. These Early Jurassic fern assemblages are characterized by the proliferation of several species of Dicksoniaceae, accompanied by a relatively low diversity assemblage of Dipteridaceae and

Osmundaceae. Marattiaceae (*Marattia*) and Matoniaceae (*Phlebopteris*) are rare. Fern families such as Angiopteridaceae, Cynepteridaceae and Gleicheniaceae are absent from the Early Jurassic (Fig. 2A).

### 4.2. Paleoclimate and paleoecology implications

Leaf structural and functional traits are generally correlated with each other and with the environment (Reich et al., 1997; Wright et al., 2004, 2005). Relationships of leaf morphology traits with climate have been well characterized for dicotyledons, allowing to reconstruct paleoclimate from fossil leaves in the geological past (Royer, 2012; Peppe et al., 2011, 2014; Soh et al., 2017). For example, the strong relationship between leaf teeth and temperature observed in extant woody dicotyledon can be used to estimate the paleotemperature (Royer, 2012). The biomechanical scaling relationship between petiole width and leaf mass per area in living woody dicotyledons and gymnosperms have been applied to fossil leaves to infer their paleoecological strategy (Royer et al., 2007, 2010). However, significant quantitative relationships between morphological and anatomical adaptations (e.g., leaf size, stomatal parameters) and climate conditions for ferns have not been found yet (Peppe et al., 2014). Nonetheless, investigating leaf-climate relationships in ferns should not be overlooked because ferns are once a







**Fig. 6.** Sketch drawing of pinnae/pinnules and venation of some fern species from the XJH Formation in the Sichuan Basin. Scale bar = 1 cm. (A) Sketch drawing of *Dictyophyllum nilssoni* (after Wu, 1999); (a, b) pinnules and venation; (c, d, e) Sporangia with well-developed annuli. (B) Pinna of *Marattia muensteri* with synangia (after Ye et al., 1986). (C) Pinna of *Hausmannia emeiensis* (after Wu, 1999). (D) Pinna of *Danaeopsis fecunda* (after Ye et al., 1986).

principal component of terrestrial ecosystem from the late Paleozoic/early Mesozoic era and could be a potential paleoclimate proxy.

The ecology of the fossil ferns usually can be inferred by examining their depositional facies, morphology and comparing the taxa to their living relatives. The extant ferns usually grew under warm (subtropical to tropical) conditions in moist environments (Walker et al., 1981; Mehlreter et al., 2010). The extant Dipteridaceae includes two genera, *Dipteris*, and *Cheiropleuria*, restricted to the tropical Indo-Malaysian regions (Kramer and Green, 1990; Pryer et al., 2004). The extant Osmundaceae live in the humid valleys, swamps or creek edges and are all perennials, distributed in temperate and tropical regions. The Marattiaceae occur in wet tropical and subtropical primary and secondary forests on steep clay banks, such as sides of streams, gullies, and ravines. The extant Angiopteridaceae, perennial herbs, are restricted to tropical regions. Matoniaceae, a sister group to Dipteridaceae, occurs locally on isolated tropical hills and mountains (Kramer and Green, 1990). Even though there are no extant species of Cynepteridaceae, *Cynepteri* is considered as a probable Late Triassic record of the Schizaeales. The living Schizaeaceae is essentially tropical and southern warm-temperature; they often inhabit periodically dry or swampy (Kvaček et al., 2006).

Though the fossil ferns in the Mesozoic are different from the extant relatives in gross morphology, their climate tolerance is very similar. Key conclusions on Mesozoic fern ecology are summarized by Van Konijnenburg-Van Cittert (2002): Most Mesozoic ferns grew under relatively warm conditions in moist environments, ranging from coal-forming swamps to riverbanks and formed the understorey flora in forests. This is common in the case of Dipteridaceae, Marattiaceae, Osmundaceae, Schizaeaceae and Dicksoniaceae. However, Matoniaceae, Gleicheniaceae and a small number of Dipteridaceae (*Hausmannia*) and Marattiaceae (*Marattia hoerensis*) grew under much drier conditions or stress-related circumstances especially during the Jurassic and Early Cretaceous and usually as colonizer plants in coastal areas, on mountain slopes or heathland (Van Konijnenburg-Van Cittert, 2002; Barbacka et al., 2019).

The high abundance of Dipteridaceae (*Clathropteris*) all over the Sichuan Basin during the Rhaetian, indicates a warm and humid climate, which is conducive for coal formation and accumulation. At the earliest Jurassic, ferns are still abundant in the flora, characterized by abundant Dicksoniaceae, Dipteridaceae (much more occurrence of *Hausmannia*), which may prevail by relatively warmer and dryer conditions. Particularly, Dicksoniaceae begins to rise and prosper after the Tr-J boundary and becomes new dominants in Middle Jurassic plant communities in the Sichuan Basin. The indusium and coriaceous leaves of Dicksoniaceae are considered that can be more adaptable to high-stress environments (probably seasonal drought environments) (Friis and Pedersen, 1990), which may be the reason for the prosperity of the Dicksoniaceae during the Jurassic.

In addition, the Rhaetian XJH Flora in the Sichuan Basin dominated by a high diversity of ferns, macrophyllous cycads, bennettites, together with much fewer extant Ginkgoales and macrophyllous conifers (suggest a more humidity climate), and relatively low diversity of Equisetales (Rees et al., 2000; Wang et al., 2010). The earliest Jurassic ZJC flora is characterized by the dominance of ferns and microphyllous bennettites, and much more occurrence of ginkgophytes and microphyllous conifer (preferred relatively dry conditions) (Rees et al., 2000; Huang, 2001; Barbacka, 2011). Similarly, the palynoflora study across the Tr-J boundary in the northeastern Sichuan Basin showed that ferns were predominant, represented by Dipteridaceae and Matoniaceae during the Late Triassic; conifers are the second abundant, followed by cycadophytes and ginkgophytes. During the early Jurassic, ferns are dominant

and represented by Cyatheaceae and Dicksoniaceae, conifer characterized by an increase of typical dry-resistant Cheirolepidiaceae taxa (*Classopollis*) (Li et al., 2016, 2020). Comparison of the relative proportion of XJH and ZJC macro-microfossil flora indicates that the Sichuan Basin was a warm temperate zone during the Triassic-Jurassic transition, but the humidity decreases in the earliest Jurassic compared with that of the Rhaetian.

Palynological analysis by Bonis and Kürschner (2012) revealed that Cheirolepidiaceae-dominated (the parent plants of *Classopollis* pollen) forests occurred in the Pangaeian interior and a high abundance of spore-producing plants adjacent to the Tethys Ocean during ETME. McElwain et al. (1999) suggest that the release of large amounts of CO<sub>2</sub> in the atmosphere by CAMP volcanism induce global warming and enhanced thermal contrast between the continent and the oceans, and then the monsoon system got stronger and induced a drier continental interior and more often rainfall near the margins of the Ocean (Bonis and Kürschner, 2012). The fern-dominated assemblages (on species level) during the Late Triassic-Early Jurassic in the Sichuan Basin are consistent with the observation that a high abundance of spore-producing plants near the Tethys Ocean.

#### 4.3. Comparison of fern and spore records in Northeast Sichuan Basin

The fern-leaves analyzed here were collected from nine members in five sections, including Daxian, Guangyuan, Hechuan, Kaixian and Xuanhan regions (Fig. 1). The spore data for comparative analysis with fern-leaves were from the corresponding seven members at the Qilixia section in Xuanhan County (see Li et al., 2016, 2020 for details of microfossil groups). According to palynological analysis and magnetostratigraphy, members 1–7 are of Late Triassic (Rhaetian) age, members 8 and 9 are of Earliest Jurassic (Hettangian) age (Li et al., 2017; Li et al., 2020). The results show that the species diversity calculated from macro-remains is consistently lower than those calculated from spores except for the fern macro-remains or spores missing members (including members 2, 4, 6, 8) (Fig. 2B, D). The difference is largely caused by the high abundance of Dipteridaceae (including *Dictyophyllidites* and *Concavisporites*) and Marattiaceae (*Angiopteridaspora*) spores (Fig. 2C). In addition, the coarse grain lithology members 2, 4, 6 and 8 which were deposited in fluvial-deltaic environments may result in the lower chance of preservation of delicate fern fronds. We suggest that the diversity trends inferred from the spore assemblages are less biased by taphonomical selection than those indicated in the macro-leaf assemblages. The spore diversity decreases gradually towards the end of the Triassic, with the minimum in Member 6. The diversity increases again towards the earliest Jurassic. Except members 2, 4, 6, both leaf and spore records show a gradual decrease before the end-Triassic (Member 7) and then increase during the earliest Jurassic (Fig. 2B). The major decrease from Member 5 to Member 6 accounts for a loss of 50 spore species which indicates severe loss in diversity in the fern families caused by environmental stress towards the end-Triassic. Among four representative families (including Dipteridaceae, Osmundaceae, Marattiaceae and Dicksoniaceae), however, the correlation between leaf and spore assemblages remains uncertain at present, because of doubts in the assignment of the botanical affinity and classification for these dispersed spores.

Palynological analysis indicates warm and humid climatic conditions in members 1, 3, 4 and 5, interrupted by a cooler and warm condition in member 2; followed by a cooler and drier condition in member 7, and warmer and drier conditions in members 8 and 9 (Li et al., 2020). The Principal Coordinates Analysis (PCoA) and cluster analysis based on spores (genus presence-absence) suggest that members 1–9 can be



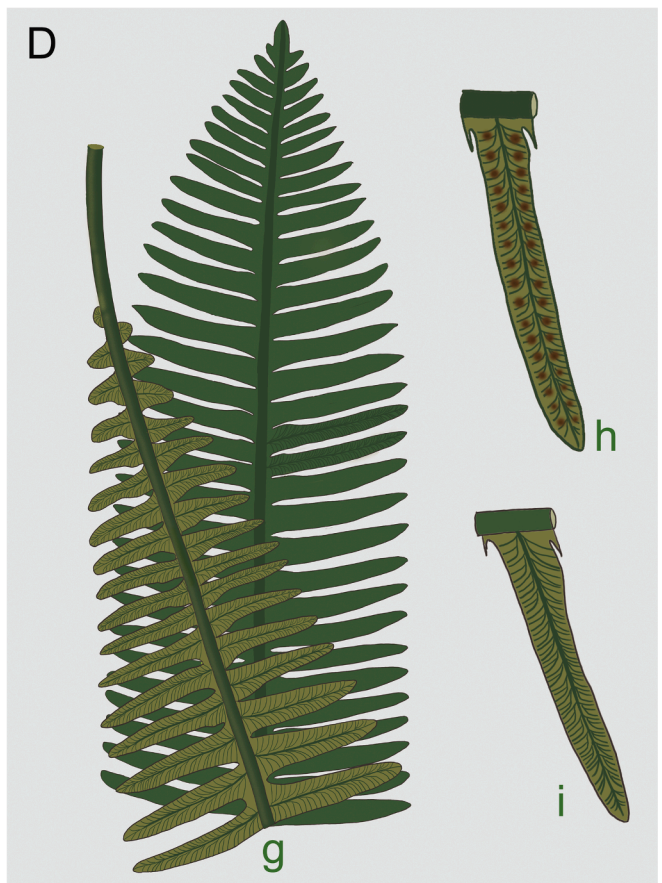


Fig. 7. Sketch drawing of (A) *Coniopteris tieshanensis* from the ZYC Formation (after Ye et al., 1986); (a, b) pinnae/pinnules and venation. (B) *Todites kwangyuanensis* from the XJH Formation (after Ye et al., 1986); (c, d) pinnae/pinnules and venation. (C) *Cynepteris lasiophora* from the XJH Formation (after Ye et al., 1986); (e, f) pinnae/pinnules and venation. (D) *Phlebopteris xianguyuensis* from the XJH Formation (after Wu, 1999); (g, i) pinnae/pinnules and venation; (h) a fertile pinna showing the distribution of sori. All scale bar = 1 cm.

organized in three groups (members 1, 2, 3–5; members 7 and 8; member 9). Each group has the highest correlation roughly corresponding to their paleoenvironmental preferences (Fig. 3B). PCoA and cluster analysis based on fern macro-remains (species presence-absence) show members 1–9 is grouped in three clusters (members 1, 3, 5; members 6 and 7; member 9) that is very similar to those from palynological data (Fig. 3A). We further explored co-occurrence patterns of plant communities using network analysis based on strong correlations (Fig. 4). The co-occurrence network of fern macro-remains (species level) suggests that Dipteridaceae and Osmundaceae are very interconnected and thus seem to share the same habitat preferences. *Coniopteris tieshanensis* and *C. neifolia* (Dicksoniaceae) showed higher incidences of co-occurrence with *Hausmannia crenata* (Dipteridaceae) and *Phlebopteris polypodioides* (Matoniaceae) (Fig. 4A). The three most frequently co-occurring species are *Clathropteris meniscioides*, *Danaeopsis fecunda*, and *Cladophlebis kaoiana* associated with six, five, and four other species respectively. In Fig. 4B, some Dipteridaceae, Marattiaceae and Dicksoniaceae spores (*Granolatisporites*, *Dictyophyllidites*, *Toroisporis*, *Cyathidites* and *Concavisporites*) have strong interconnect. The most frequently co-occurring genus is *Sphagnumporites*, which is associated with nine other genera. Another relatively high co-occurring genus is *Biretisporites* (assigned to the family of Osmundaceae) associated with eight genera (Fig. 4B).

#### 4.4. Comparison of macrofossils and palynoflora across the Tr-J transition

The Rhaetian XJH Flora (151 species) in the Sichuan Basin is composed predominantly of ferns, bennettites and cycads, together with sphenophytes, conifers, ginkgophytes, czekanowskialeans and seed ferns (Wang et al., 2010) (Fig. 5A). The earliest Jurassic ZYC flora (58 species) mainly include ferns, bennettiales, cycads, conifers, ginkgophytes and sphenophytes (Fig. 5B). The palynoflora from the Sichuan Basin shows a different pattern, with a marked change in sporomorph assemblages, and several short-term fluctuations in spore abundance at the Tr-J transition (Li et al., 2016, 2020). During the Rhaetian, palynoflora shows a predominance of ferns including the dominant Dipteridaceae/Matoniaceae, and conifers are the second abundant type, followed by cycadophytes/ginkgophytes and seed ferns (Fig. 5C). At the Tr-J transition, the conifers and cycadophytes/ginkgophytes are the dominant elements; ferns mainly included Cyatheaceae/Dicksoniaceae and Dipteridaceae/Matoniaceae (Li et al., 2020). At the earliest Jurassic, spore-producing plants are the most abundant, characterized by a high content of Cyatheaceae/Dicksoniaceae, followed by Dipteridaceae/Matoniaceae, Angiopteridaceae, whereas conifers decrease excluding Cheilepodiaceae (Fig. 5D). The macro-microflora data show that no obvious mass extinctions but with a significant vegetation turnover after the end-Triassic in the Sichuan Basin demonstrated the response of vegetation changes in places far away from CAMP volcanism.

High-latitude macrobotanical records from the Junggar Basin of Northwest China (paleolatitude ~60°N) indicate that there is no marked vegetation shift across the Tr-J transition (Wang et al., 2010; Sha et al., 2015; Zhang et al., 2020). At this transition, the structures of the plant community in the Junggar Basin are very simple and the most dominant ferns are Dipteridaceae. From the latest Rhaetian to the earliest Hettangian, *Hausmannia-Clathropteris minoria* assemblage was replaced by *Todites princeps-Clathropteris elegans* assemblage (Deng et al., 2010). In addition, the palynological data from the Junggar Basin show a higher relative proportion of fern spores in Hettangian assemblages than in Rhaetian assemblages and Cyatheales spores (produced by Cyatheaceae)

become the dominant elements during the earliest Jurassic (Lu and Deng, 2005; Zhang et al., 2020).

The statistical analyses of macroflora and microflora from over 100 localities in Europe reveal that there were no marked differences in plant composition or mass extinction of terrestrial plants by the end Triassic (Barbacka et al., 2017). Recent quantitative palynological analysis in NW-Germany revealed that vegetation underwent gradual changes with intermediate successional stages rather than dramatic extinction during the end-Triassic (Gravendyck et al., 2020). However, a fern spore spike at ETME is recognized at different locations in other European sections, for example in Spain (Gómez et al., 2007), Austria (Kürschner et al., 2007; Bonis et al., 2009, 2010), France (Lindström, 2016), Germany (Van de Schootbrugge et al., 2009), Sweden (Van de Schootbrugge et al., 2009). These spores are mainly produced by ferns as Cyatheaceae/Dicksoniaceae, Dipteridaceae/Matoniaceae, Osmundaceae and Schizaeaceae (Gómez et al., 2007; Kürschner et al., 2007; Van de Schootbrugge et al., 2009; Lindström, 2016). Also, a reduction of 60% of palynofloras followed by a sharp spore spike (mainly *Converrucosporites* and *Granolatisporites*, produced by Dicksoniaceae and Dipteridaceae ferns) are recorded from tropical paleolatitudes (20°–21° N) in the Newark Basin of North America at Tr-J boundary (Fowell and Olsen, 1993; Fowell et al., 1994; Olsen et al., 2002). The spore spike is considered as a sharp increase in the number of plants colonizing land after the catastrophic environment, which indicate a response of terrestrial plant to the ETME related to CAMP volcanism (Looy et al., 2001; Van de Schootbrugge et al., 2009; Van de Schootbrugge and Wignall, 2015; Barbacka et al., 2017).

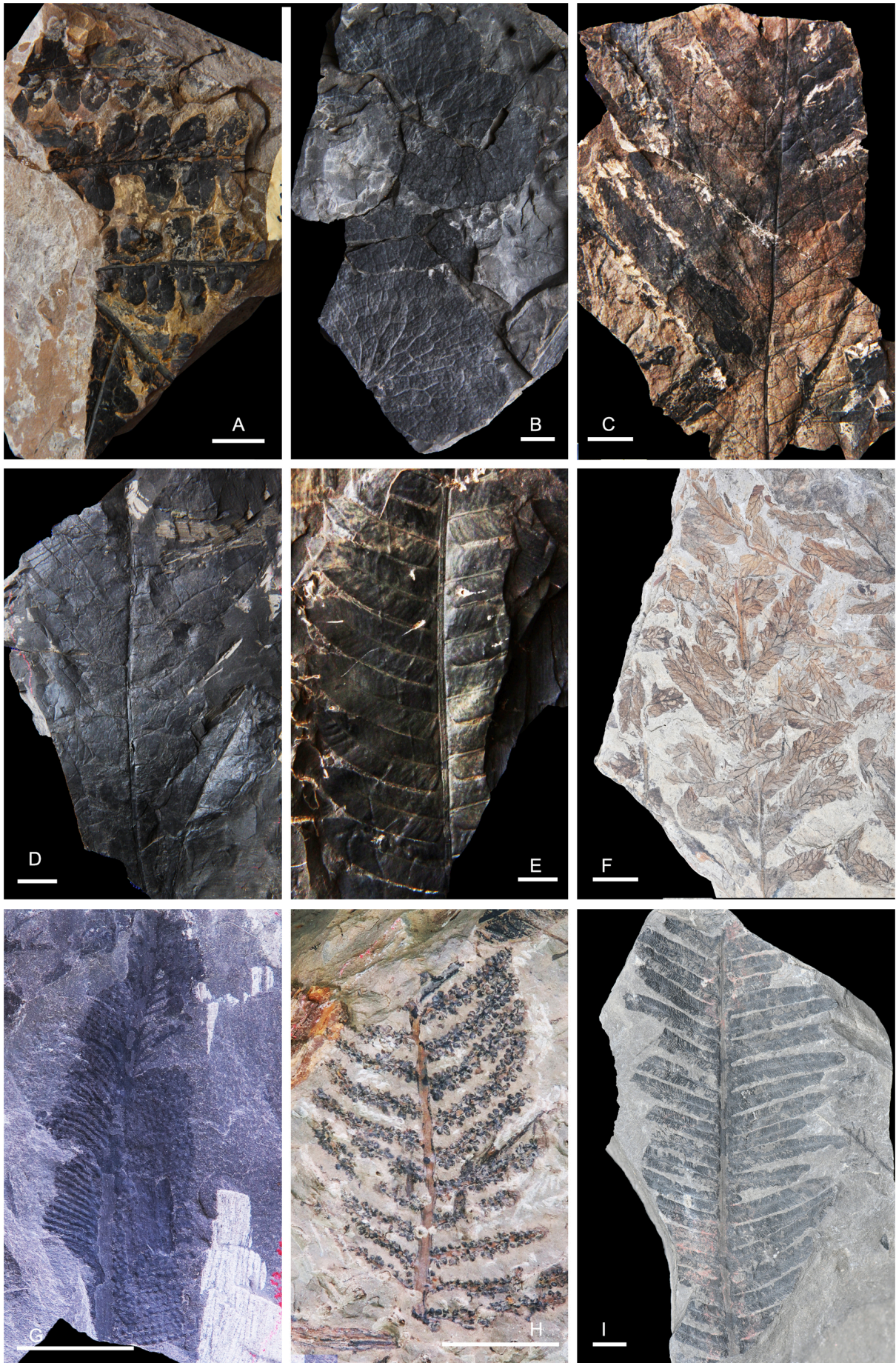
## 5. Conclusions

So far, approximately 67 species ascribed to 16 genera of eight families of ferns have been reported from the Rhaetian Xujiahe (XJH) Formation to the lowermost Jurassic Zhenzhuchong (ZYC) Formation in the Sichuan Basin. The ferns from XJH Flora are dominated by Dipteridaceae, the genus *Clathropteris*; Osmundaceae mainly represented by *Cladophlebis* second in abundance. Angiopteridaceae (*Danaeopsis*), Marattiaceae (*Marattia*), Matoniaceae (*Phlebopteris*), Dicksoniaceae (*Coniopteris*) and Cynepteridaceae (*Cynepteris*) are sparsely distributed and relatively small in extent. The ferns in the ZYC Formation are marked by the rising and prosperity of Dicksoniaceae, relatively low diversity of Dipteridaceae and Osmundaceae.

Across the Triassic/Jurassic boundary, 38 species in six genera disappeared in the XJH Formation, and ten new species firstly occurred in the ZYC Formation. The fern data show a gradual decline at both the genus and species levels at ETME in the Sichuan Basin. The palynological data from the Sichuan Basin show a clear vegetation turnover after the end-Triassic in the Sichuan Basin demonstrated that the response of vegetation changes in places far away from CAMP volcanism.

During the Rhaetian, ferns are dominated by Dipteridaceae with a high proportion of *Clathropteris*, and numerous Osmundaceae including high species diversity of *Cladophlebis* indicates a warm and humid climate. During the lowermost Jurassic, the occurrence and prosperity of Dicksoniaceae, relatively low diversity of Dipteridaceae and Osmundaceae, may prevail by relatively warmer and dryer conditions. Significantly increase of typical dry-resistant taxa agrees with global warming across the Tr-J boundary, indicating a dryer environment at the earliest Jurassic.







**Fig. 8.** Representative species of fossil ferns from the Sichuan Basin. Scale bar = 1 cm. (A) *Goeppertella kochibei* Yang, PB4823 (after Yang, 1978). (B) *Hausmannia emeiensis* Wu, PB10583 (after Wu, 1999). (C) *Thaumatopteris huiliensis* Wu, PB10689 (after Wu, 1999). (D) *Clathropteris obovata* Oishi, PB10571 (after Wang et al., 2010). (E) *Cladophlebis kwangyuanensis* Lee, PB10607 (after Wu, 1999). (F) *Todites crenatum* Barnard, PB0618 (after Wu, 1999). (G) Fertile pinna of *Danaeopsis fecunda* Halle, PB10617 (after Wang et al., 2010). (H) Fertile pinna of *Osmundopsis* cf. *plectrophora* Harris, PB10596 (after Wu, 1999). (I) Sterile pinna of *Phlebopteris xiangyuanensis* Li et Tsao, PB10579 (after Wu, 1999).

## Declaration of Competing Interest

We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2021.103585>.

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