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# Permian–Middle Triassic floral succession in North China and implications for the great transition of continental ecosystems

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1	Permian–Middle Triassic floral succession in North								
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20									
21	ABSTRACT								
22	The global pattern of plant evolution through the Permian–Triassic mass extinction is								
23	uncertain, and the extent to which land plants were affected is debated. Detailed								
24	studies undertaken at a regional scale can help evaluate this floral transition, and thus								

25 we provide a detailed account of floral evolution from the Permian to Middle Triassic 26 of North China based on new paleobotanical data and a refined biostratigraphy. Five 27 floral transition events are identified from before, during and after the Permian-28 Triassic crisis, including the disappearance of the gigantopterid flora (associated with 29 loss of coal deposits), the end-Permian mass extinction of Paleophytic taxa, and 30 gradual recovery in the Triassic with stepwise appearance of the Mesophytic 31 vegetation. The record begins with a Cisuralian gigantopterid-dominated rainforest 32 community, and then a Lopingian walchian Voltziales conifer-ginkgophyte 33 community that evolved into a voltzialean conifer-pteridosperm forest community. 34 The last is associated with a change amongst terrestrial vertebrates from the Jiyuan 35 fauna to a pareiasaur-dominated fauna, found in red beds that lack coal deposits due 36 to arid conditions. The disappearance of the voltzialean conifer forest community may 37 represents the end-Permian mass extinction of plants although it could also be a 38 consequence of the non-preservation of plants in sedimentary red-beds. The first post-39 crisis plants are an Induan herbaceous lycopsid community, succeeded by the 40 Pleuromeia-Neocalamites shrub marsh community. A pteridosperm shrub woodland 41 community dominated for a short time in the late Early Triassic along with the 42 reappearance of insect herbivory. Finally, in the Middle Triassic, gymnosperm forest 43 communities gradually rose to dominance in both uplands and lowlands along with 44 other diverse plant communities, indicating the establishment of the Mesophytic 45 Flora.

47 Keywords: Permian-Triassic, floral changeover, Paleophytic-Mesophytic 48

- transition, continental ecosystem, North China
- 49

#### **50 INTRODUCTION**

51 The response of plant communities to the Permian–Triassic mass extinctions is 52 much debated (e.g. Cascales-Miñana et al., 2016; Nowak et al., 2019). There is no 53 doubt that global floras changed substantially during the Permian-Triassic transition, 54 from the Paleophytic Flora of the late Paleozoic to the Mesophytic Flora of the 55 Mesozoic (Niklas et al., 1983; Cleal and Cascales-Miñana, 2014), but details of the 56 timing are uncertain because of the absence of a robust stratigraphic framework in 57 many terrestrial sections. Regional-scale paleobotanical and palynological work has 58 suggested variable responses to the crisis. Palynological data from East Greenland 59 initially suggested a significant change amongst land plants, especially the 60 disappearance of conifers, followed by delayed recovery (Looy et al., 1999, 2001). Other studies have suggested that there is no extinction in palynological records 61 62 around the Permian-Triassic Boundary (Hochuli et al., 2016; Schneebeli-Hermann et 63 al., 2017). In Australia and South Africa, a clear extinction is marked by the 64 disappearance of the Glossopteris flora (Fielding et al., 2019; Vajda et al., 2020; 65 Mays et al., 2020; Gastaldo et al., 2020; McLoughlin et al., 2021). Data from South 66 China show a considerable loss of land plants during the Permian-Triassic mass 67 extinction (Xiong and Wang, 2011; Yu et al., 2015; Feng et al., 2020; Chu et al., 68 2020). The changes of macro-plant fossil assemblages from the Permian to Triassic of 69 North China is clear (Wang, 1993; Wang, 2010; Stevens et al., 2011; Lu et al., 2020) 70 but its link with the crisis is uncertain. 71 The Permian–Triassic mass extinction (252 Ma) was the most severe biotic crisis 72 in the Phanerozoic, and was associated with highly-stressed conditions due to a 73 combination of proposed factors such as global warming (Sun et al., 2012; Benton, 74 2018; Frank et al., 2021), acid rain (Sephton et al., 2015), wildfires (Shen et al., 2011;

75	Chu et al., 2020), increased UV-B flux (Visscher et al., 2004; Foster and Afonin,
76	2005), atmospheric heavy metal pollution (Hochuli et al., 2017), increase of
77	continental weathering (Song et al., 2015; Lu et al. 2020) and strong volcanic activity
78	(Wignall, 2015; Benton, 2018). The crisis eliminated over 80% of marine species,
79	70% of terrestrial vertebrate species and more than 50% of plant genera, including
80	42% of lycophytes and ferns, and 70% of gymnosperms, and was followed by the
81	Early Triassic coal gap (Niklas et al., 1983; Retallack et al., 1996; Rees, 2002;
82	Benton, 2014; Cascales-Miñana et al., 2016; Stanley, 2016; Dal Corso et al., 2022).
83	Here we present an investigation of some groups of continental organisms using
84	a recently refined age model for the Permian to Middle Triassic in North China. Five
85	successive floras are established in association with corresponding vertebrate and
86	invertebrate faunas, which record substantial changes in continental ecosystems
87	during the Paleophytic–Mesophytic transition.

## 89 GEOLOGICAL SETTING

90 During the Permian, six paleofloras were developed in different 91 paleophytogeographical provinces (Chaloner and Lacey, 1973; McLoughlin, 2001, 92 2011), but during the Early Triassic, provincialism was reduced and a more 93 cosmopolitan lycopsid flora occurred over most of the Northern Hemisphere, while 94 Dicroidium forests and locally abundant isoetalean and pleuromeian lycopsids 95 covered the Southern Hemisphere (Fig. 1A). North China, with its Permian 96 Cathaysian Flora, traversed low latitudes (about 30°N), drifting north towards the north-eastern part of the Paleo-Tethys Ocean during the late Paleozoic and early 97 98 Mesozoic (Fig 1A; Wang et al., 1998). Sedimentary sequences suggest there was a

99 large lake, about 1400 km wide, in North China during the Permian–Triassic (Fig 1B,
100 C; Zhu et al., 2007; Liu et al., 2015; Ji et al., 2021, 2022).

The Permian to Middle Triassic succession in North China is divided into the 101 102 Upper Shihhotse, Sunjiagou, Liujiagou, Heshanggou and Ermaying formations. The 103 Upper Shihhotse Formation is dominated by grayish yellow/green sandstone with 104 varicolored (dark red dominated) mud-siltstone. The Sunjiagou Formation comprises 105 red thin- to medium-bedded mudstones with some red sandstones and interbedded 106 calcareous nodules; the overall association is interpreted as a fluvial and floodplain 107 system (Zhu et al., 2007; Zhu et al., 2020; Ji et al., 2022). Intermittent marine flooding 108 occurred, indicated by some marine fossils in the upper part of the formation in the 109 southwestern part of the study region (Yin and Lin, 1979; Chu et al., 2019). The 110 overlying Liujiagou Formation is composed of massive red sandstones with a few 111 interbedded mud-siltstones, locally bearing wrinkle structures, usually taken as 112 evidence of microbial mats (Chu et al., 2015; Tu et al., 2016). There are mud cracks 113 and ripple marks in the lower part, and some large sand sheets interbedded with thick conglomerates in the middle-upper part. This unit was deposited in various fluvial or 114 115 lake-shore environments (Zhu et al. 2020; Ji et al. 2022). The Heshanggou Formation 116 consists of red siltstones interbedded with some thin sandstone beds and abundant 117 calcareous nodules, interpreted to have formed in shallow lakes (Hu et al., 2009). The 118 Ermaying Formation comprises gravish green, thick-bedded sandstones with green 119 and red thin-bedded mudstones and was deposited in fluvial-lacustrine settings. 120 Abundant fossil plants and sporomorphs have been identified from various locations 121 (Fig. 1D and Supplementary Data File 1). 122 The ages of the studied formations have been discussed for a long time, and are

123 derived from isolated fossils, magnetostratigraphy, chemostratigraphy and a few U-Pb

124 dates from ash beds. A recent U-Pb zircon study (Wu et al., 2021) shows that most of 125 the Upper Shihhotse Formation is of latest Asselian to early Kungurian age (294.8  $\pm$ 126  $1.2 \le 280.73 \pm 0.12$  Ma) rather than Guadalupian–early Lopingian as previously 127 thought, although its uppermost part may still be latest Capitanian–Lopingian (< 128  $261.75 \pm 0.29$  Ma). Most of the Guadalupian seems to be absent in parts of North 129 China in this new dating scheme (Wu et al., 2021) whilst the magnetostratigraphy of 130 the uppermost Upper Shihhotse Formation indicates a Wuchiapingian age (Guo, 131 2022). The negative carbon isotope excursions in organic matter ( $\delta^{13}C_{org}$ ) in the 132 middle part of the Sunjiagou Formation provides a potential marker for a latest 133 Changhsingian age (Wu et al., 2020) and a mixed marine-continental fauna marking 134 the Permian-Triassic transitional beds was identified in the middle-upper part of the 135 Sunjiagou Formation (Chu et al., 2019). A CA-ID-TIMS U-Pb age of  $252.21 \pm 0.15$ 136 Ma from the middle part of the Sunjiagou Formation in the Shichuanhe section also 137 suggests a latest Changhsingian age for the middle part of the Sunjiagou Formation 138 (Guo et al., 2022). Thus, the Permian–Triassic boundary (PTB) lies in the upper part 139 of the Sunjiagou Formation according to carbon isotope stratigraphy, biostratigraphy 140 and magnetostratigraphy (Chu et al., 2017; Shu et al., 2018; Guo et al., 2019; Wu et 141 al., 2020; Lu et al., 2020; Guo et al., 2022). The basal beds of the overlying Liujiagou 142 Formation yield the Aratrisporites-Alisporites sporomorph assemblage (Ouyang and 143 Zhang, 1982; Ouyang and Wang, 1985), and the lycopsid *Pleuromeia* occurs in the 144 upper part of the Liujiagou Formation (Wang and Wang, 1982), all indicating an 145 Early Triassic age (Wang, 1993; Shu et al., 2018; Guo et al., 2019), as does an LA-146 ICP-MS age of  $251 \pm 4$  Ma from the middle part of the Liujiagou Formation (Zhu et 147 al., 2019). Magnetostratigraphy suggests the Induan–Olenekian boundary is found in 148 the lower part of the Liujiagou Formation (Guo et al., 2022). The Heshanggou

149 Formation yields abundant trace fossils together with body fossils (e.g., fossil plants,

150 vertebrates, fishes, conchostracans (= diplostracans) and ostracodes) of late Early

151 Triassic age (Wang et al., 1978; Qu et al., 1983; Nesbitt et al., 2011). Moreover,

152 magnetostratigraphy confirms an Olenekian age for the Heshanggou Formation (Guo

t al., 2022). An ID-TIMS U-Pb zircon date of  $243.528 \pm 0.069$  Ma dates the upper

154 member of the Ermaying Formation as Anisian (Middle Triassic) (Liu et al., 2018).

155 Magnetostratigraphy indicates the Olenekian–Anisian boundary occurs in the basal

156 Ermaying Formation (Guo et al., 2022).

157 Here, we focus on five Permian–Triassic sections that yield well-preserved fossil

158 plants: the Liulin, Peijiashan, Dayulin, Shichuanhe and Zishiya sections (Fig. 1B, C;

159 Fig. 2). In addition, we also mention some other fossil sites with rich plant fossils,

160 such as Heshun, Pingyao and Yushe in Shanxi Province. In the following account, we

161 first focus on the biotas. The potential taphonomic issues that might bias the results

162 will be detailed in the discussion.

163

#### 164 MATERIALS AND METHODS

165 This study is mainly based upon over 1400 plant megafossil specimens collected 166 from eight locations ranging through all the target formations in North China (Table 167 1). These include compression, impression and permineralized fossils. The fossils 168 represent shoots, leaves, cones or fertile parts and some trunks/fossil woods, most of 169 which were identifiable. We also restudied all reported fossils from North China and 170 in total we note 52 genera of vertebrates, 42 genera of invertebrates, 102 genera and 171 some form types of plants from over 120 locations (Supplementary Data Files 1–7). In 172 addition, some well-preserved cuticles were prepared by HF/HCl maceration and 173 Schultze solution for oxidation, and KOH to remove remnant humic acids (Kerp,

174 1990; Jones and Rowe, 1999). In situ pollen from male cones or fertile shoots were 175 processed by HF/HCl maceration (Jones and Rowe, 1999). All fossils studied are 176 stored in the paleontological collection of the State Key Laboratory of Biogeology 177 and Environmental Geology, China University of Geosciences (BGEG, Wuhan). 178 Plant megafossil specimens were photographed using a Canon EOS 7D digital 179 camera, and some in situ pollen, bract-scale complexes, small shoots and 180 conchostracan specimens were examined and photographed using a LEICA-DM-750P 181 microscope equipped with an automatic camera image stacking system. Some photos 182 were processed by focus stacking methods using Photoshop CS5 (auto-align layers 183 and auto-blend layers). Some *in situ* pollen were studied using a Hitachi SU8010 184 scanning electron microscope. In addition, one tetrapod tooth fossil from the 185 uppermost Upper Shihhotse Formation and one well-preserved strobilus of 186 Pleuromeia from the Liujiagou Formation were scanned using a nanoVoxel 4000 187 micro-computed tomography scanner (Sanying Precision Instruments, Tianjing, 188 China) and the raw projections were converted into image stacks using VoxelStudio 189 Recon (Sanying Precision Instruments). The isometric voxel size (spatial resolution) 190 for the *Pleuromeia* and the tooth were 31.60 µm and 17.63 µm, respectively. To 191 image the inner structure of the tooth, its volume data were segmented using the 192 watershed algorithm in Avizo 8.0, and manual correction was performed to correct 193 defects. 194 For paleoecological analysis, we normalized genera of fossil plants as binary data, present (1) or absent (0), in each formation (Cleal et al., 2021). The presence-195

absence matrix was then analyzed in R by hierarchical clustering using the Euclidean

197 complete method, *k*-means clustering and principal components analysis (PCA) (Fig.

198 S3–5). The R code is provided in the Supplementary material. To calculate the

199 hygrophyte(H)/xerophyte(X) ratio, plant genera were classified as hygrophytes,

200 mesophytes and xerophytes based on previous studies (Supplementary data files 9 and

201 10) and then the ratio calculated as [H/(H+X)]/[X/(H+X)] (DiMichele et al., 2020;

202 Koll and DiMichele, 2021; Supplementary datafile 10).

203

# 204 MACROFLORAS FROM PERMIAN TO MIDDLE TRIASSIC IN NORTH205 CHINA

206 Based on collected specimens and previously reported data, five successive 207 macrofloras were identified from the Permian to Lower Triassic in North China. 208 Previously, most of the floras were named after the formations in which they 209 occurred, but here we consistently refer to them based on the index fossils because 210 some of the floras span more than one formation. The gigantopterid flora in the Upper 211 Shihhotse Formation has been well-studied previously (Wang, 2010; Stevens et al., 212 2011) and we confirm those earlier results. Here we focus on the other four 213 macrofloras, i.e. the Voltziales flora in the uppermost part of the Upper Shihhotse and 214 the Sunjiagou formations, the *Pleuromeia-Neocalamites* flora in the middle-upper 215 part of the Liujiagou and the base of the Heshanggou formations, the Pleuromeia-216 Tongchuanophyllum flora in the lower-upper part of the Heshanggou and the basal 217 part of the Ermaying formations, and the Lepacyclotes-Voltzia flora in the lower to 218 upper parts of the Ermaying Formation.

219

#### 220 The Voltziales flora

This flora occurs in the uppermost part of the Upper Shihhotse Formation and
the lower part of the Sunjiagou Formation. It is dominated by Voltziales conifers,
including walchian and voltzian voltzialean type conifers. Here the Voltziales flora is

subdivided into the ginkgophyte–walchian Voltziales and the voltzian Voltzialessubfloras.

226

## 227 The ginkgophyte-walchian Voltziales subflora

228 This subflora occurs in the uppermost part of the Upper Shihhotse Formation of 229 the Liulin (Fig. 2; Fig. S1B) and Shichuanhe sections (Fig. 2; Fig. S1C). It is 230 dominated by walchian voltzialean shoots, other vegetative-shoot types of conifers 231 (form type 0, 2 and 5, in Supplementary Data File 2), and includes ginkgophytes 232 (form type 1 and 2, in Supplementary Data File 2), pteridosperms (Autunia), putative 233 cycadophytes (Taeniopteris) and Sphenopteris-type foliage (Fig. 3). Gymnosperms 234 are the main elements in this subflora. In the uppermost Upper Shihhotse Formation 235 of the Liulin section, over 80% of plant fossils are shoots and leaves, whereas seed 236 fossils account for about 20%. Around 85% of the shoot compressions/impressions 237 are assigned to conifers and most of these conifer shoots are walchian Voltziales 238 according to their gross morphology and cuticles (Fig. 3, description in 239 Supplementary Data File 2). Some ginkgophyte leaves and Taeniopteris locally co-240 occur with the conifer shoots. In the uppermost Upper Shihhotse Formation of the 241 Shichuanhe section, 385 specimens were collected and 256 identified. Among these, 242 over 65% are assigned to conifer shoots, about 25% are ginkgophyte leaves, and there 243 are a few Autunia-type pteridosperm ovuliferous organs, noeggerathialean leaves and 244 other foliage types. In addition, there are some *in situ* monosaccate pollen associated 245 with walchian voltzialean shoots that are elliptical to circular in polar view (Fig. 3X, 246 Y), showing a monolete suture on the corpus, a punctate or in some cases rugulate 247 surface. These are assigned to Potonieisporites. This subflora is named the 248 ginkgophyte-walchian Voltziales subflora, after its two dominant elements.

#### 250 The voltzian Voltziales subflora 251 This subflora of the Voltziales flora was identified from the lower part of the 252 Sunjiagou Formation in the Liulin (Fig. 2; Fig. S1E), Dayulin (Fig. 2; Fig. S1F) and 253 Zishiya (Fig. 2; Fig. S1G) sections. It is dominated by conifers, including 254 Pseudovoltzia-type/ Ullmannia-type/ other undefined vegetative shoots with well-255 preserved cuticles (form type 1–4, description in Supplementary Data File 2), 256 Pseudovoltzia-type bract-scale complexes with five-lobed scales (Fig. 4AA), male 257 cones with in situ monolete bisaccate pollen of the Gardenasporites-type (Fig. 4DD, 258 EE, PP, SS) and seeds, with some pteridosperms, such as Autunia-type peltate 259 ovuliferous organs and Germaropteris-type vegetative small leaves with well-260 preserved cuticles (Fig. 4, description in Supplementary Data File 2). Calamite stems 261 occur sporadically as compressions or impressions. In the lower part of the Sunjiagou 262 Formation of the Liulin section, 220 discernible specimens were found, 76% of which 263 are shoots, 11% seeds and 13% fertile parts. Around 96% of the shoot 264 compressions/impressions can be assigned to conifers and 4% to ferns and 265 pteridosperms. In the lower part of the Sunjiagou Formation of the Dayulin section, 266 37 identifiable specimens were collected, all of which are conifer shoot compressions 267 and isolated conifer leaf compressions. In addition, there are over 300 specimens from 268 the lower part of the Sunjiagou Formation of the Zishiya section and 202 of these 269 were identifiable. Of these, shoots comprise about 70%, seeds around 19%, fertile 270 parts (including cones) about 8%, and a few stems about 3%. All shoots and one cone 271 can be assigned to conifers, the other fertile parts to the Autunia type, a few stems to 272 Calamites, and some dispersed seeds to conifers or pteridosperms. This subflora is 273 named after the dominant element as the voltzian Voltziales subflora.

275 The *Pleuromeia–Neocalamites* flora

276 Only a few localities, such as Jiaocheng, Yushe and Heshun in Shanxi, yield 277 these plant fossils. They come from the middle-upper part of the Liujiagou Formation 278 and the base of the Heshanggou Formation (Fig. 2). Most of these plant fossils are 279 strobili, isolated sporophylls and rhizomorphs of Pleuromeia jiaochengensis and 280 Pleuromeia sternbergii (Figs. 5C-K, 6A-D, M). Numerous fragments of in situ stems 281 of Neocalamites or Equisetites preserved as compressions or casts also occur in both 282 red silty mudstones and gray-green siltstones (Figs. 6E-K). Fragments of strap-shaped 283 leaves with parallel veins are possible gymnosperms. Some fragments of sporophylls 284 with long tips characteristic of Tomiostrobus were found at the base of the 285 Heshanggou Formation at Heshun (Fig. 6L). In addition, some broken fronds of 286 Scolopendrites (Figs. 5A-B) and some dispersed possible male cones, bract-scale 287 complexes and seeds of voltzialean conifers (Figs. 6N-O) occur in this flora. Potential 288 cycadophytes are identified as *Taeniopteris*. This flora is named after the two 289 dominant elements, Pleuromeia and Neocalamites. Pleuromeia by itself is not 290 diagnostic of an individual flora as its stratigraphic range extends into the overlying 291 Pleuromeia-Tongchuanophyllum and Lepacyclotes-Voltzia floras (see below).

292

#### 293 The Pleuromeia-Tongchuanophyllum flora

Abundant fossil plant specimens occur in the lower–upper part of the

Heshanggou Formation and the basal part of the Ermaying Formation in the Yushe,

296 Pingyao and Puxian sections in Shanxi. Numerous plant fossils have been previously

- 297 reported from this interval from many other localities, such as Shouyang, Pingyao,
- 298 Puxian, Fengfeng, Chengde, Jiyuan, and Yima (Supplementary Data Files 2–3). Most

- 300 cushions *Mesolepidodendron*, some sporophylls with long tips of *Tomiostrobus* (Figs.
- 301 7A–D, G, H, J–L), and pteridosperms (up to nine genera, e.g., *Tongchuanophyllum*,
- 302 Neoglossopteris, "Gangamopteris", Glossophyllum, "Euryphyllum", Scytophyllum,
- 303 "Thinnfeldia", Sphenopteris and Peltaspermum) (Figs. 7M–O), and the others are
- 304 sphenophytes (e.g., *Neolobatannularia*, *Phyllotheca*, *Neocalamites*, *Equisetites*) (Figs.
- 305 7I), pteridophytes (e.g., Anomopteris, Scolopendrites, Neuropteridium, Todites),
- 306 conifers (Voltzia, Yuccites, Willsiostrobus) (Figs. 7P–Q), and putative cycadophytes
- 307 (possibly *Cycadocarpidium*) (Supplementary Data File 2, 3). This flora is named after
- 308 its abundant lycopods, dominated by *Pleuromeia*, and the common occurrence of
- 309 *Tongchuanophyllum*.
- 310

#### 311 The Lepacyclotes–Voltzia flora

This flora occurs in the lower to upper parts of the Ermaying Formation where

313 the Mesophytic floral elements gradually appear and become more diverse. However,

314 some lycophyte rhizophores (*Pleuromeia*), some lycophyte sporophylls with short tips

315 (Lepacyclotes), Isoetites, and sphenophytes (Neocalamites and Equisetites) remain

316 common but sphenophyte stems became larger than those in the former floras (Fig. 8).

317 Fronds and pinnules of true ferns from the lower to upper parts of the Ermaying

318 Formation were identified as Anomopteris, Cladophlebis, Danaeopsis, Symopteris

319 (Bernoullia) and Todites (Supplementary Data File 2, 3). In addition, there is a diverse

320 flora of pteridosperms (e.g., Germaropteris, Peltaspermum, Ptilozamites,

321 Glossophyllum, Neoglossopteris, Scytophyllum, Tongchuanophyllum, "Thinnfeldia",

- 322 Pachypteris and Protoblechnum), cycadophytes (e.g., Nilssonia, Sinozamites and
- 323 Taeniopteris), ginkgophytes (e.g., Baiera, Ginkgoites and Sphenobaiera) and conifers

324 (e.g., *Pagiophyllum*, *Podozamites*, *Voltzia* and *Yuccites*) (Supplementary Data File 2,
3). This flora is named after the common Middle Triassic elements, *Lepacyclotes* and
326 *Voltzia*.

327

#### 328 **DISCUSSION**

#### 329 Ages of the Lopingian to Middle Triassic macrofloras in North China

- The floras of North China can be dated with reference to other fossils such as
- 331 vertebrates. The ginkgophyte-walchian Voltziales subflora of the uppermost Upper
- 332 Shihhotse Formation of the Shichuanhe and Liulin sections co-occurs with a
- 333 vertebrate tooth fossil (Fig. 9A–D) of the Jiyuan fauna (Fig. S2; Xu et al. 2015). The
- 334 Jiyuan Fauna comprises abundant vertebrate taxa (Supplementary Data file 7; Xu et

al. 2015) that are assigned a Wuchiapingian age based on comparisons of the entire

tetrapod assemblage to the Ilinskoe Subassemblage of the Sokolki Assemblage in

337 Russia and the *Cistecephalus* Assemblage Zone in South Africa (Liu et al. 2014;

Benton 2016). A Wuchiapingian age of the strata is also supported by

339 magnetostratigraphy (Guo, 2022).

340 Previously a *Ullmannia bronnii–Yuania magnifolia* assemblage was documented

341 by Wang and Wang (1986) from the lower-middle part of the Sunjiagou Formation of

342 North China. Unfortunately, we have not collected any *Yuania* in these strata during

- 343 our reinvestigation (Supplementary Data file 2–3), thus herein we use the term
- 344 Ullmannia–Pseudovoltzia–Germaropteris assemblage as a replacement name. The
- 345 Ullmannia–Pseudovoltzia–Germaropteris assemblage corresponds to the voltzian
- 346 Voltziales subflora. This subflora and the corresponding Lueckisporites virkkiae-
- 347 Jugasporites schaubergeroides sporomorph assemblage (Hou and Ouyang, 2000) co-
- 348 occur with a *Pseudestheria* (Fig. 9H–K) conchostracan assemblage in the Liulin and

349 Dayulin sections (Figs. 2, 9, S2), which is assigned to the Lopingian (probably 350 Changhsingian). In North China, some pareiasaurs (Wang et al., 2019) and fish fossils 351 (Chondrostei and *Platysomus*) (Wang, 1981) were reported from the Sunjiagou 352 Formation and the laterally equivalent Naobaogou Formation (Liu and Bever, 2018, 353 Fig. S2, Supplementary Data file 7). In addition, the Darwinula-Panxiania ostracod 354 assemblage occurs in the middle part of the Sunjiagou Formation (Chu et al., 2015, 355 Fig. S2, Supplementary Data file 5). Further, mixed continental-marine biotas (Fig. 356 9), comprising conchostracans, plants, insects, marine bivalves and lingulid 357 brachiopods, in the middle part of the Sunjiagou Formation are particularly important 358 for biostratigraphic correlation between continental and marine facies (Chu et al., 359 2019). All the floral data suggest the Permian-Triassic transitional beds start in the 360 middle part of the Sunjiagou Formation. This is further supported by a CA-ID-TIMS 361 U-Pb age of  $252.21 \pm 0.15$  Ma from the middle part of the Sunjiagou Formation in the 362 Shichuanhe section (Guo et al., 2022). 363 However, some pareiasaurs were also found from the uppermost part of the 364 Sunjiagou Formation at the Xuecun section, Liulin, Shanxi Province (Wang et al., 365 2019, Fig. S2, Supplementary Data file 7). Pareiasaurs from the continental sections 366 in Russia and South Africa are not considered to have survived the Permian-Triassic 367 mass extinction (Lee, 1997; Benton, 2016). Meanwhile, abundant microbial-induced 368 sedimentary structures (MISS), such as wrinkle structures, appear in the top part of 369 the Sunjiagou Formation and lower part of the Liujiagou Formation at Dayulin 370 (Yiyang, Henan Province), and are common in post-extinction environments (Chu et 371 al., 2015; Tu et al., 2016), as seen in high southern latitudes (Mays et al., 2021a, b).

372 Consequently, the age of the upper part of the Sunjiagou Formation is unclear. The

373 uncertainty over the age of the top of the Sunjiagou Formation may be because the

374 transition with the overlying Sunjiagou Formation is diachronous. An Aratrisporites-375 Alisporites sporomorph assemblage, in which Aratrisporites is the most abundant 376 element (13.4%), and Alisporites is a sub-dominated element (10.3%), occurs with a 377 few fragmentary fossils of Dicynodon in the lower part of the Liujiagou Formation 378 (Ouyang and Zhang, 1982, Fig. S2, Supplementary Data file 7), indicating an earliest 379 Triassic (Induan) age. This conclusion is further supported by magnetostratigraphy 380 that indicates a likely Dienerian age for this level (Guo et al., 2022). 381 In the middle part of the Liujiagou Formation in the Peijiashan section and the 382 base of the Heshanggou Formation in the Shichuanhe, Heshun and Yushe sections, 383 the Pleuromeia-Neocalamites flora co-occurs with a conchostracan Leptolimnadia-384 Paleoleptestheria assemblage and some Triopsidae (Fig. S2, Supplementary Data file 385 5; Tong et al., 2018). Furthermore, from the lower-middle part of the Qishan 386 Formation (equivalent to the Liujiagou Formation) of the Zishiya section, we found a 387 Lundbladispora-Cycadopites-Protohaploxypinus sporomorph assemblage that can be 388 correlated to the *Densoisporites nejburgii–Lunatisporites–Cvcadopites* sporomorph 389 assemblage (Qu et al., 1980; Qu et al., 1982; Tong et al., 2018). There are also some 390 bivalves, some ophiurids and the Leptolimnadia-Paleoleptestheria conchostracan 391 assemblage in the Qishan Formation (Fig. 9G, R, Supplementary Data file 5; Tong et 392 al., 2018), all of which indicate an early Olenekian age. 393 Subsequently, the lower part of the Heshanggou Formation is characterized by 394 the *Pleuromeia–Tongchuanophyllum* flora that is associated with a few tetrapod 395 fossils (e.g., Capitosauridae) (Wang, 1983) and the Cornia-Estheriella conchostracan

- assemblage (Wang, 1983). Higher up in the middle–upper parts of the Heshanggou
- 397 Formation and basal Ermaying Formation, sporomorphs are assigned to the
- 398 Lundbladispora–Verrucosisporites–Lunatisporites sporomorph assemblage and occur

along with the macroflora documented above (Qu et al., 1980; Ouyang and Norris,

400 1988; Tong et al., 2018). The sporomorph assemblage includes a higher proportion of

401 gymnosperm pollen (*Cycadopites* and *Lunatisporites*) (Ouyang and Norris, 1988). In

- 402 addition, vertebrate fossils (including the lungfish *Ceratodus heshanggouensis*)
- 403 increase in abundance (Wang, 1983, Supplementary Data file 7). Among
- 404 invertebrates, abundant conchostracans of the Magniestheria–Eosolimnadia
- 405 assemblage occur, together with abundant ostracod fossils of the *Darwinula*
- 406 triassiana–Darwinula fengfengensis–Darwinula rotundata assemblage
- 407 (Supplementary Data file 5, Pang, 1989; Tong et al., 2018). Thus, the age of most of
- 408 the Heshanggou Formation should be Olenekian, except the uppermost part that hosts
- 409 the *Shaanbeikannemeyeria* assemblage, which is assigned an Anisian age (Liu, 2018;
- 410 Fig. S2, Supplementary Data file 7).
- 411 Finally, in the Ermaying Formation, the *Lepacyclotes–Voltzia* flora is associated
- 412 with the *Punctatisporites–Chordasporites* sporomorph assemblage (Tong et al. 2018,
- 413 Fig. S2, Supplementary Data file 2–3). It co-occurs with abundant vertebrate and
- 414 invertebrate fossils, i.e., the Sinokannemeyeria–Parakannemeyeria–Shansiodon
- 415 tetrapod assemblage (Liu and Sullivan 2017; Liu et al., 2018, Fig. S2, Supplementary
- 416 Data file 7), the *Brachyestheria–Xiangxiella* conchostracan assemblage (Tong et al.
- 417 2018), and the Lutkevichinella minuta–Shensinella gaoyadiensis–Darwinula
- 418 *subovaliformis* ostracod assemblage (Tong et al. 2018, Fig. S2, Supplementary Data
- 419 file 5). This biota indicates an Anisian age.
- 420

#### 421 Permian to Middle Triassic floral changes

- 422 The Permian-Triassic mass extinction was the most severe event of the
- 423 Phanerozoic, affecting both marine and continental organisms (Cascales-Miñana et al.

424 2016; Dal Corso et al., 2022). However, it has been even debated whether there was a 425 mass extinction of land plants (Fielding et al., 2019; Nowak et al., 2019). In North 426 China, it is well known that Permian lands were occupied by the famous 427 Gigantopteris (Cathaysian) flora, which gradually went extinct in the later Permian (Hilton and Cleal, 2007; Wang, 2010; Stevens et al., 2011; Wu et al., 2021). There 428 429 have been few investigations of paleofloral changes at other intervals through the 430 Permian, Early and Middle Triassic (Wang, 1993, 1996; Wang, 2010; Stevens et al., 431 2011; Yang et al., 2012). A statistical analysis has been especially lacking. Here, we 432 identify six statistically-distinct floras through this interval (Figs. 10-12), separated 433 by five floral transitions (T1–T5 in Fig. 10). Of these distinct floras, two are similar to 434 each other, and they are regarded as the sub-floras of one flora. These changes may 435 help us to understand the Permian–Triassic transition of the plants on land in North 436 China. In some instances, floral transitions are abrupt and can be well-defined by 437 changes in composition at a particular level (represented by horizontal lines in Figure 438 10). In other cases, the transitions span a broader time interval which may, in part, be 439 due to low sampling frequency.

440 The first significant floral transition (T1) is recognized between the gigantopterid 441 and Voltziales floras (Fig. 10, 11B (a)). The gigantopterid flora was characterized by 442 high diversity, including abundant and diverse gigantopterids, arborescent lycophytes, 443 diverse sphenophytes and "filicalean" ferns, abundant ginkgophytes, Noeggerathiales 444 and Cordaitales but with few conifers. During this transition (Fig. 11B, from cluster 1 445 to cluster 2 and from cluster 2 to cluster 3) there is a decrease or the eventual loss of 446 the dominant/characteristic elements, e.g., gigantopterids (Fig. 10). It is characterized 447 by the disappearance of the Cathaysian flora (Wu et al. 2021) and a switch from the 448 Cisuralian gigantopterid flora to the Lopingian Voltziales flora. This also marks the

449 beginning of the Paleophytic to Mesophytic floral switch, which is a staggered event 450 in our analysis. T1 marked the decline and eventual extirpation (regional extinction) 451 of the gigantopterid flora (61.8% genera lost) and replacement by the incoming 452 Voltziales flora that comprises taxa that ranged through this selective extinction event. 453 The second floral transition (T2) occurs within the Voltziales flora and is 454 manifested as the turnover between the two subfloras (Fig. 10, 11) in which 10 taxa 455 disappear, 2 appear and 11 range through the transition. The ginkgophyte–walchian 456 Voltziales subflora (Fig. 10, 11) is dominated by abundant walchian voltzialean 457 conifers and early ginkgophytes, together with the cycad Taeniopteris, some 458 pteridosperms (e.g., Sphenopteris, Autunia, Supaia), sphenophytes (e.g., 459 Sphenophyllum), remaining ferns (e.g., Pecopteris), a few Noeggerathiales (e.g., 460 Yuania) and a limited appearance of voltzian voltzialean conifers. Overall, the 461 subflora is dominated by gymnosperms (>90%), rather than ferns, and it fits the broad 462 characteristics of the 'Mesophytic age' (Gothan 1912; DiMichele et al., 2008). It is 463 relatively different from the older gigantopterid-dominated flora in North China. So, it 464 may be correlated with previously reported floras from the Upper Shihhotse 465 Formation, such as the upper part of the *Psygmophyllum* zone (Wang, 1993), the post-466 changeover 4 flora (Wang, 2010) or the post-uUSF extinction flora (Stevens et al., 467 2011) (Fig. 10). However, there are some differences in the dominant elements in two 468 subfloras of the Voltziales flora. The voltzian Voltziales subflora (Fig. 10, 11) is 469 dominated by voltzian voltzialean conifers, some pteridosperms, and a few 470 sphenophytes and ferns. The presence of a diverse voltzian Voltziales assemblage 471 with a few walchian Voltziales but no early ginkgophytes is especially noteworthy. 472 The third transition (T3) is more difficult to characterize and interpret as it 473 comprises two stages separated by a broad interval lacking plant megafossils from the

Terrestrial ecological disturbance interval (TED interval) (see Xu et al., 2022). T3 474 475 commences with the disappearance of the latest Permian voltzian Voltziales subflora 476 with 10/13 loss in genera across a wide range of plant groups (Figs. 10, 11B (b)). This 477 transition event (T3) can be probably regarded as the end Permian plant extinction 478 (EPPE) (Xu et al., 2022) and the PTB plant mass extinction in North China, but it 479 spans a wide time interval due to low sampling frequency (Fig. 10) and is best 480 evidenced by the incoming Early Triassic flora. However, the duration of the crisis 481 could be affected by poor preservation at this level in the TED interval. The 482 dominantly red beds of mudstone and sandstone floodplain facies of the upper part of 483 the Sunjiagou Formation provide a poor fossil plant record (see DiMichele et al., 484 2008). Such a scenario is supported by the absence of disaster floral elements such as 485 Pleuromeia, which appears at a higher level, in the Liujiagou Formation, and the 486 presence of pareiasaurs in the Sunjiagou Formation (Wang et al., 2019; 487 Supplementary Data file 7) which suggests sufficient vegetation existed to support 488 herbivorous vertebrates. Furthermore, the palynoflora from the basal Liujiagou Formation includes the voltzialean conifer pollen Triadispora (see Balme, 1995), 489 490 suggesting that even though the voltzialean-dominated community disappeared in the 491 megafossil record, the group was still present in the region. Plants from this 492 community may not necessarily have been living in the floodplain depositional 493 settings as conifer pollen is widely distributed (Ouyang and Zhang, 1982). 494 Following the initial loss of plant diversity in T3, the first megaflora of the Early 495 Triassic, the Pleuromeia-Neocalamites flora (Fig. 12), is characterized by abundant 496 *Pleuromeia* (typically *Pleuromeia jiaochengensis*) and common sphenophyte stems 497 (Neocalamites and Equisetites) along with some pteridophytes and a few voltzian conifers (Fig. 10). We consider the appearance of this megaflora to mark the end of 498

the third transition event (T3) (Fig. 10). An alternative interpretation might be to
divide the T3 event as presented here into a separate late Permian extinction event and
an earliest Triassic radiation event. While future research is required to fully evaluate
floral changes in transition, we consider this scenario less likely as the extinction and
radiation appear intricately linked to the environmental perturbations of the TED
interval.

505 The fourth floral transition (T4), from the *Pleuromeia–Neocalamites* to
506 *Pleuromeia–Tongchuanophyllum* floras (Figs. 10, 11A), represents a radiation event

507 and short-term increase in gymnosperm diversity after the crisis in North China,

508 characterized by the abrupt rise of pteridosperms and a few cycadophytes and

509 conifers. The diversity of *Pleuromeia* also increased noticeably, whereas

510 sphenophytes and pteridophytes increased only slightly (Fig. 10). This transition

511 spans a wide time interval, probably due to low sampling frequency.

512 Finally, the final floral transition (T5) from the *Pleuromeia–Tongchuanophyllum* 

513 to the *Lepacyclotes–Voltzia* floras (Fig. 10, 11B (c)) also spans a broad time interval

514 due to low sampling frequency. In this radiation event many taxa co-occur in the

515 *Pleuromeia–Tongchuanophyllum* and *Lepacyclotes–Voltzia* floras showing they are

516 closely related to each other but are nonetheless distinct (Fig. 11). The latter flora is

517 distinguished by a number of incoming pteridophytes, pteridosperms, cycadophytes,

518 ginkgophytes and conifers. The *Lepacyclotes–Voltzia* flora shows full recovery from

519 the Permian–Triassic crisis in terms of diversity and abundance of nearly all higher

520 taxa, including lycophytes, sphenophytes, pteridophytes, pteridosperms,

521 cycadophytes, ginkgophytes and conifers. Gymnosperms increased, especially

522 ginkgophytes, cycadophytes and conifers, and pteridophytes also diversified as tree

523 ferns and ground ferns (Figs. 10, 11, 12).

524	During the Lopingian, floral distributions were latitude-dependent (Fig. 1A;							
525	Supplementary Data file 8), with four distinct floral provinces: the high-northern-							
526	latitude Cordaites peat-forming flora of the Angaran province (Davydov et al., 2021;							
527	Davydov and Karasev, 2021), the low-middle-northern-latitude voltzian Voltziales-							
528	pteridosperm floras (e.g., the voltzian Voltziales subflora in North China; Bourquin et							
529	al., 2011; Kustatscher et al., 2012, 2017; Cai et al., 2019), the tropical rainforest or							
530	lowland-peat-forming floras (e.g., the Gigantopteris flora in South China or the Umm							
531	Irna flora in Jordan; Yu et al., 2015; Blomenkemper et al., 2018; Feng et al., 2020)							
532	and the high-southern-latitude Glossopteris peat-forming flora in Gondwana (Fielding							
533	et al., 2019). During the Permian-Triassic mass extinction, floras changed							
534	dramatically globally. Early Triassic floras were sporadically distributed but with							
535	some widespread taxa (Fig. 1A). Herbaceous or shrub-like lycopsid-dominated floras,							
536	mainly Tomiostrobus and Pleuromeia, were widely distributed in the northern							
537	hemisphere (Fig. 1A; Supplementary Data file 8), and the Lepidopteris- and							
538	Dicroidium-dominated flora became established in the southern hemisphere (Fig. 1A;							
539	Supplementary Data file 8; Vajda et al. 2020).							
540								
541	Evolution of terrestrial ecosystems from Permian to Middle Triassic in North							
542	China							
543	Here we discuss the evolution of the ecosystems on land through the Permian-							
544	Triassic transition, based on the fossil records of plants, sporomorphs, tetrapods,							
545	fishes, invertebrates and trace fossils from North China. The transition was associated							
546	with turbulent environmental changes (Fig. 13), some of which led to biological							
547	responses, as highlighted by the hygrophyte/xerophyte ratio that reflects changes in							

548 floral composition from wet (hygrophyte) to dry (xerophyte) ecological settings549 (Supplementary Data file 9–10).

550	The subsidence of the Cisuralian gigantopterid-dominated rainforest
551	communities coincides with the last occurrence of coal deposits and the rise of the
552	Lopingian ginkgophyte-walchian Voltziales forest community (Fig. 12) in North
553	China. Disappearance of the Gigantopteris flora in North China represents a regional
554	loss of diversity and an extirpation event because many taxa, but not all, and the
555	Gigantopteris flora, persist in South China until the late Changhsingian where they
556	are notable victims of the EPPC (e.g., Yu et al., 2015; Feng et al., 2020, Xu et al.,
557	2022). In the meantime, the Jiyuan Fauna changed into the pareiasaur-dominated
558	fauna whilst insect diversity decreased (Fig. 13, Supplementary Data File 6-7; Xu et
559	al., 2015; Wang et al., 2019). The gradual changeover in the Gigantopteris flora
560	indicates increasing aridity, a trend that continues in the Voltziales flora (Fig. 13,
561	Supplementary Data file 9–10). A few insect remains (Fig. 9E) still co-occur with
562	conifers in the top of the Upper Shihhotse and Sunjiagou formations (Fig. 2), and then
563	there is no record of insect fossils from the point of disappearance of the
564	Changhsingian conifer forests to the Middle Triassic in North China (Zheng et al.
565	2018). Both plant macrofossils and sporomorph records in the lower-middle parts of
566	the Sunjiagou Formation were from voltzialean-dominated forests. The
567	hygrophyte/xerophyte ratio indicates that arid or semi-arid conditions prevailed
568	during the deposition of the lower-middle parts of the Sunjiagou Formation (Fig. 13).
569	The mean annual precipitation was calculated, based on the depth to the Bk horizon in
570	paleosols, as $320 \pm 147 \text{ mm/yr}$ (Yu et al. 2022).
571	The disappearance of the voltzian Voltziales-dominated forests (T3; Fig. 12) in

the latest Changhsingian, is associated with the appearance of red beds commonly and

573 MISS in lacustrine facies (Chu et al. 2015). However, despite the apparent forest 574 floral crisis of the EPPC, some tetrapods persisted in the Upper Sunjiagou Formation 575 (Fig. 2, Liulin section; Fig. 13) as did aquatic invertebrates, such as the 576 conchostracans Palaeolimnadia and Euestheria and ostracods Darwinula and 577 Panxiania (Fig. 13, Supplementary Data File 5, 7, Chu et al., 2015). The Voltziales-578 dominated flora may have persisted in the latest Changhsingian, at the same time as 579 the tetrapod losses, but poor preservation could have "back-smeared" the final 580 occurrence. 581 The Early Triassic (Induan?) Aratrisporites-Alisporites sporomorph assemblage 582 (Ouyang and Zhang, 1982) may represent the first herbaceous lycopsid plant 583 community occupying lowlands, coexisting with a few upland gymnosperms (Fig. 584 12), established after the crisis. This was followed by the early Olenekian 585 Pleuromeia-Neocalamites flora representing Pleuromeia/Neocalamites-dominated 586 shrub marshes in muddy wetlands. These occur in situ in sandstones or silty 587 mudstones of the Liujiagou Formation and the base of the Heshanggou Formation 588 (Fig. S1H–I), interpreted as braided river and shallow lake environments (Ji et al. 589 2021). *Pleuromeia/Neocalamites*-dominated shrub marshes likely grew in riverbank 590 or muddy floodplain settings. In the late stage of the Pleuromeia-Neocalamites flora, 591 a few Voltzia conifer shrubs appeared and might have grown in well-drained sandy 592 riverbanks. Some allochthonous fragments of Tomiostrobus may have been derived 593 from sporadically distributed plants around small ephemeral water bodies. 594 Concurrently, aquatic invertebrates appeared in this ecosystem, such as 595 conchostracans, ostracods and Triopsidae (Wang, 1983). The hygrophyte/xerophyte 596 ratio indicates a more humid environment in the early Olenekian than during the latest

597	Changhsingian in North China (Fig. 13, Supplementary Data file 9–10), which is
598	consistent with geochemical data from paleosols in North China (Yu et al. 2022).
599	Subsequently, in the Pleuromeia-Tongchuanophyllum flora, pteridosperm-
600	conifer shrub woodlands are identified by the appearance of abundant pteridosperms
601	(``Euryphyllum'', ``Gangamopteris'', Glossophyllum, Neoglossopteris, Sphenopteris,
602	"Thinnfeldia", Tongchuanophyllum, Peltaspermum and Scytophyllum) and some
603	Voltzia elements (Fig. 12). Lacustrine conditions were predominant in this stage (Hu
604	et al., 2009). These Voltzia-dominated woodland communities grew in well-drained
605	sandy-soil riverbanks or other lowlands (Fig. 12). The lycophyte (Pleuromeia)-
606	sphenophyte (Neocalamites, Equisetites and Phyllotheca)-dominated shrub marsh
607	community with some pteridophytes (e.g., Todites, Neuropteridium and Anomopteris)
608	was still widely distributed on riverbanks or muddy floodplains (Fig. 12). Some
609	Tomiostrobus-dominated, herbaceous, ground-covering communities occurred around
610	the shores of playa lakes. In addition, some insect herbivory damage appeared on
611	leaves of Tongchuanophyllum (Fig. 7O), and abundant small, spiral microconchid-like
612	organisms on sporophylls of Pleuromeia (Fig. 7D) are preserved. Moreover, many
613	vertebrate fossils (Benthosuchidae, Capitosauridae, Procolophonidae, Scaloposauria,
614	Eumetabolodon, Fugusuchus, Hazhenia, Pentaedrusaurus and Xilousuchus), some
615	fish (Ceratodus) and many invertebrates co-occur with this flora (Wang, 1983,
616	Nesbitt et al., 2011, Fig. 13, Supplementary Data file 7). All these changes suggest
617	that diverse terrestrial and aquatic ecosystems had begun to reappear (Fig. 12). At this
618	time, there are abundant types of trace fossils in continental ecosystems (Fig. 13, Shu
619	et al., 2018; Guo et al., 2019) recording widespread activity on land, as well as
620	posture changes and the evolution of endothermy with insulation (hair, feathers) in
621	synapsid and archosauromorph tetrapods (Benton, 2021). The increase of invertebrate

622 diversity (Fig. 13) may indicate a repopulation of aquatic ecosystems following their 623 disappearance in the late Changxingian. Sporomorphs in the later stages of this flora 624 are represented by the *Cycadopites–Lunatisporites–Verrucosisporites* sporomorph 625 assemblage, and the hygrophyte/xerophyte ratio indicates a relatively seasonally 626 humid environment in the late Olenekian (Fig. 13, Supplementary Data file 9-10) and 627 the mean annual precipitation was calculated to range from  $520 \pm 147$  mm/yr to 680 628  $\pm 147$  mm/yr (Yu et al., 2022). 629 In the Lepacyclotes-Voltzia flora, some xerophytic gymnosperms (e.g.,

630 Lepidopteris, Peltaspermum, Pagiophyllum, Yuccites and Voltzia) started to occupy

631 some dry uplands (Fig. 12) if they were not already established there; such absences

632 may represent a taphonomic bias towards wetland depositional settings (see

633 Blomenkemper et al., 2018). Along with the increased diversity of pteridophytes,

634 pteridosperms, cycadophytes, ginkgophytes and conifers, the gymnosperm-dominated

635 forest community started to occupy some dry uplands, and the pteridophyte-

636 dominated shrub community entered moist lowlands. The Pleuromeia-sphenophyte-

637 dominated shrub marsh community was still on riverbanks or muddy floodplains (Fig.

638 12). At that time, the Sinokannemeveria fauna was widely distributed in North China

639 (Liu and Sullivan, 2017). Aquatic invertebrates probably also increased (Figs. 12, 13),

640 as also suggested by abundant burrows inside the cast of Neocalamites (Fig. 8F). The

- 641 hygrophyte/xerophyte ratio indicates a gradual shift to a more humid climate (Fig. 13,
- 642 Supplementary Data file 9–10).

643

#### 644 CONCLUSIONS

645 A new integrated multifaceted biostratigraphic framework with a refined time scale is established for the Lopingian-Middle Triassic of North China, based on 646

647 macrofossil plant, sporomorph, vertebrate and invertebrate (conchostracans and648 ostracodes) assemblages.

649 Five main floras are recognized are identified in North China, the gigantopterid, 650 Voltziales, Pleuromeia-Neocalamites, Pleuromeia-Tongchuanophyllum and 651 Lepacyclotes-Voltzia floras, with the Voltziales flora comprising the ginkgophyte-652 walchian Voltziales and the voltzian Voltziales subfloras. The five transitions 653 between these floras consist of an extirpation event, two turnover events and two 654 radiation events. The gigantopterid flora regional extinction (T1; 34/55 genera lost) 655 eliminated the gigantopterid-dominated rainforest and saw the end of coal deposition 656 This marks the beginning of the changeover from the Paleophytic to Mesophytic 657 floras. The second floral transition (T2), is a subflora turnover within the Voltziales 658 flora, and saw a change in the dominant elements. The end-Permian plant extinction 659 event (EPPE; T3), which saw the loss of 10 out of 13 genera, marks the start of the 660 terrestrial ecological disturbance interval (TED interval) on land. This crisis was 661 followed by a short-term diversification (T4) from the *Pleuromeia–Neocalamites* to 662 the Pleuromeia-Tongchuanophyllum floras. The final floral transition (T5) in the 663 earliest Middle Triassic, indicating the recovery-radiation of plants, represented by the 664 Lepacyclotes-Voltzia flora, shows the initial construction of the Mesophytic Flora. 665 From the Cisuralian to Lopingian, the change from a gigantopterid-dominated 666 rainforest community to a voltzialean conifer forest community occurred in parallel 667 with the decline of the Jiyuan fauna and change to a pareiasaur-dominated fauna, loss 668 of coal deposits, sharp increase of red beds and aridity increase. The subsequent 669 disappearance of the voltzialean conifer forest community marks the end-Permian 670 plant extinction in North China. Following the prolonged plant-free Terrestrial 671 ecological disturbance interval the first plants to recover after the crisis belonged to a

herbaceous plant community, followed by a *Pleuromeia–Neocalamites* shrub marsh
community. A pteridosperm shrub woodland community dominated for a short time
in the late Early Triassic, along with the first appearance of insect herbivory. Finally,
in the Middle Triassic, the gymnosperm forest community gradually rose to
dominance with the appearance of diverse plant communities on lowland and possible
upland settings.

678

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691

#### 692 **REFERENCES CITED**

Balme, B., 1995, Fossil in-situ spores and pollen grains: an annotated catalogue.

694 Review of Palaeobotany and Palynology 87, 81–323.

- Blomenkemper, P., Kerp, H., Hamad, A.A., DiMichele, W.A., and Bomfleur, B.,
- 696 2018, A hidden cradle of plant evolution in Permian tropical lowlands. Science,
  697 v. 362, p. 1414–1416.
- Benton, M.J., and Newell, A.J., 2014, Impacts of global warming on Permo-Triassic
  terrestrial ecosystems. Gondwana Research, v. 25, p. 1308–1337.
- 700 Benton, M.J., 2016, The Chinese pareiasaurs. Zoological Journal of the Linnean
- 701 Society, v. 177, p. 813–853.
- 702 Benton M. J., 2018, Hyperthermal-driven mass extinctions: killing models during the
- 703 Permian–Triassic mass extinction. Philosophical Transactions of the Royal
- 704 Society A, v. 376, p. 20170076.
- Benton, M.J., 2021, The origin of endothermy in synapsids and archosaurs and arms
  races in the Triassic. Gondwana Research, v. 100, p. 261–289.
- 707 Bourquin, S., Bercovici, A., López-Gómez, J., Diez, J.B., Broutin, J., Ronchi, A.,
- 708 Durand, M., Arche, A., Linol, B., and Amour, F., 2011, The Permian–Triassic
- transition and the onset of Mesozoic sedimentation at the northwestern peri-
- 710 Tethyan domain scale: Palaeogeographic maps and geodynamic implications.
- 711 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 299, p. 265–280.
- 712 Broutin, J., Roger, J., Platel, J. P., Angiolini, L., Baud, A., Bucher, H., Marcoux, J.,
- and Al Hasmi, H., 1995, The Permian Pangea. Phytogeographic implications of
- new paleontological discoveries in Oman (Arabian Peninsula). Comptes Rendus
- 715 de l'Academie des Sciences Paris, Série Iia, v. 321, p. 1069–1086.
- 716 Broutin, J., Yu, J.X., Shi, X., Shu, W.C. and Qing, X., 2020, Terrestrial palaeofloral
- succession across the Permian–Triassic Boundary in the North and South China
- blocks: a brief review. Paläontologische Zeitschrift, v. 94, p. 633–644.

719	Cai, Y.F., Zhang, H., Feng, Z., Cao, C.Q., and Zheng, Q.F., 2019, A Germaropteris-
720	dominated flora from the upper Permian of the Dalongkou section, Xinjiang,
721	Northwest China, and its paleoclimatic and paleoenvironmental implications.
722	Review of Palaeobotany and Palynology, v. 266, p. 61–71.
723	Cascales-Miñana, B., Diez, J.B., Gerrienne, P., and Cleal, C.J., 2016, A
724	palaeobotanical perspective on the great end-Permian biotic crisis. Historical
725	Biology, v. 28, p. 1066–1074.
726	Chaloner, W.G., and Lacey, W.A., 1973, The distribution of Late Palaeozoic floras. p.
727	271–290 in Hughes, N.F. Ed., Organisms and continent through time. Special
728	Papers in Palaeontology, v. 12. Palaeontological Association, London.
729	Chu, D.L., Tong, J.N., Song, H.J., Benton, M.J., Bottjer, D.J., Song, H.Y., and Tian,
730	L., 2015, Early Triassic wrinkle structures on land: stressed environments and
731	oases for life. Scientific Reports, v. 5, p. 10109.
732	Chu, D.L., Tong, J.N., Benton, M.J., Yu, J.X. and Huang, Y.F., 2019, Mixed
733	continental-marine biotas following the Permian-Triassic mass extinction in
734	South and North China. Palaeogeography, Palaeoclimatology, Palaeoecology, v.
735	519, p. 95–107.
736	Chu, D.L., Grasby, S.E., Song, H.J., Corso, J.D., Wang, Y., Mather, T.A., Wu, Y.Y.,

- 737 Song, H.Y., Shu, W.C., Tong, J.N., and Wignall, P.B., 2020, Ecological
- 738 disturbance in tropical peatlands prior to marine Permian–Triassic mass
- 739 extinction. Geology, v. 48, p. 288–292.
- 740 Cleal, C.J., and Cascales-Miñana, B., 2014, Composition and dynamics of the great
- 741 Phanerozoic Evolutionary Floras. Lethaia, v. 47, p. 469–484.
- 742 Cleal, C.J., Pardoe, H.S., Berry, C.M., Cascales-Miñana, B., Davis, B.A.S., Diez, J.B.,
- 743 Filipova-Marinova, M.V., Giesecke, T., Hilton, J., Ivanov, D.A., Kustatscher, E.,

744	Leroy, S.A.G., McElwain, J.C., Opluštil, S., Popa, M.E., Seyfullah, L.J., Stolle,
745	E., Thomas, B.A., and Uhl, D., 2021, Plant diversity in deep time: 1. How well
746	can we identify past plant diversity in the fossil record? Palaeogeography,
747	Palaeoecology, Palaeoclimatology, v. 576, p. 110481.
748	Dal Corso, J., Song, H.J., Callegaro, S., Chu, D.L., Sun, Y.D., Hilton, J., Grasby, S.E.,
749	Joachimski, M.M., Wignall, P.B. 2022. Environmental crises at the Permian-
750	Triassic mass extinction. Nature Reviews Earth and Environment, v. 3, p. 197-
751	214. https://doi.org/10.1038/s43017-021-00259-4
752	Davydov, V.I., Karasev, E.V., Nurgalieva, N.G., Schmitz, M.D., Budnikov, I.V.,
753	Biakov, A.S., Kuzina, D.M., Silantiev, V.V., Urazaeva, M.N., Zharinova, V.V.
754	and Zorina, S.O., 2021, Climate and biotic evolution during the Permian-Triassic
755	transition in the temperate Northern Hemisphere, Kuznetsk Basin, Siberia,
756	Russia. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 573, p. 110432.
757	Davydov, V.I. and Karasev, E.V., 2021, The Influence of the Permian-Triassic
758	Magmatism in the Tunguska Basin, Siberia on the Regional Floristic Biota of the
759	Permian-Triassic Transition in the Region. Frontiers in Earth Science, v. 9, p.
760	134.
761	DiMichele, W.A., Kerp, H., Tabor, N.J., and Looy, C.V., 2008, The so-called
762	"Paleophytic-Mesophytic" transition in equatorial Pangea — Multiple biomes
763	and vegetational tracking of climate change through geological time.
764	Palaeogeography, Palaeoclimatology, Palaeoecology, v. 268, p. 152-163.
765	DiMichele, W.A., Bashforth, A.R., Falcon-Lang, H.J. and Lucas, S.G., 2020.
766	Uplands, lowlands, and climate: Taphonomic megabiases and the apparent rise of
767	a xeromorphic, drought-tolerant flora during the Pennsylvanian-Permian

769 109965.

770	Feng, Z., Wei, HB., Guo, Y., He, X.Y., Sui, Q., Zhou, Y., Liu, H.Y., Gou, X.D., and
771	Lü, Y., 2020, From rainforest to herbland: new insights into land plant responses
772	to the end-Permian mass extinction, Earth-Science Reviews, v. 204, p. 103153.
773	Fielding, C.R., Frank T.D., McLoughlin, S., Vajda, V., Mays, C., Tevyaw, A.P.,
774	Winguth, A., Winguth, C., Nicoll, R.S., Bocking, M., and Crowley, J.L., 2019,
775	Age and pattern of the southern high-latitude continental end-Permian extinction
776	constrained by multiproxy analysis. Nature Communications, v. 10, p. 385.
777	Foster, C.B., and Afonin, S.A., 2005, Abnormal pollen grains: an outcome of
778	deteriorating atmospheric conditions around the Permian–Triassic boundary.
779	Journal of the Geological Society, London, v. 162, p. 653-659.
780	Frank, T.D., Fielding, C.R., Winguth, A.M.E., Savatic, K., Tevyaw, A., Winguth, C.,
781	McLoughlin, S., Vajda, V., Mays, C., Nicoll, R. and Bocking, M., 2021. Pace,
782	magnitude, and nature of terrestrial climate change through the end-Permian
783	extinction in southeastern Gondwana. Geology, v. 49, p.1089–1095.
784	Gall, J. –C., and Grauvogel–Stamm, L., 2005, The early Middle Triassic 'Grès à
785	Voltzia' Formation of eastern France: a model of environmental refugium.
786	Comptes Rendus Palevol, v. 4, p. 637–652.
787	Gastaldo, R.A., Kamo, S.L., Neveling, J., Geissman, J.W., Looy, C.V., and Martini,
788	A.M., 2020, The base of the Lystrosaurus Assemblage Zone, Karoo Basin,
789	predates the end-Permian marine extinction: Nature Communications, v. 11, art.
790	1428.

791 Gothan, W., 1912, Paläobotanik. In: Korschelt, E., Linck, G., Schaum, K., Simon, H. 792 Th., Verworn, M., Teichmann, E. (Eds.), Handwörterbuch der 793 Naturwissenschaften. Gustav Fischer Verlag, Jena, pp. 408–460 (in German). 794 Guo, W.W., Tong, J.N., Tian, L., Chu, D.L., Bottjer, D.J., Shu, W.C., and Ji, K.X., 2019, Secular variations of ichnofossils from the terrestrial Late Permian-Middle 795 796 Triassic succession in the Shichuanhe section in Shaanxi Province, North China. 797 Global and Planetary Change, v. 181, p. 102978. 798 Guo, W., Tong, J., He, Q., Hounslow, M.W., Song, H., Dal Corso, J., Wignall, P.B., 799 Ramezani, J., Tian, L. and Chu, D., 2022. Late Permian-Middle Triassic 800 magnetostratigraphy in North China and its implications for terrestrial-marine 801 correlations. Earth and Planetary Science Letters, v. 585, art. 117519. 802 Guo, W., 2022. Late Permian-Middle Triassic magnetostratigraphic timescale from 803 terrestrial North China and secular variations of ichnofossils. PhD thesis, China 804 University of Geosciences, Wuhan, pp. 228. 805 Hilton, J., and Cleal, C.J., 2007, The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and 806 807 palaeogeographical implications. Earth-Science Reviews, v. 85, p. 85-116. 808 Hochuli, P.A., Sanson-Barrera, A., Schneebeli-Hermann, E. and Bucher, H., 2016. 809 Severest crisis overlooked—Worst disruption of terrestrial environments 810 postdates the Permian-Triassic mass extinction. Scientific Reports, v. 6, art. 811 28372. 812 Hochuli, P.A., Schneebeli-Hermann, E., Mangerud, G., and Bucher, H., 2017, 813 Evidence for atmospheric pollution across the Permian-Triassic transition. 814 Geology, v. 45, p. 1123–1126.

- Hou, J.P. and S. Ouyang, 2000, Palynoflora from the Sunjiagou Formation in Liulin
  County, Shanxi Province. Acta Palaeontologica Sinica, v. 39, p. 356–368.
- 817 Hu, B., Yang, W.T., Song, H.B., Wang, M., and Zhong, M.Y., 2009, Trace fossils and
- 818 ichnofabrics in the Heshanggou Formation of lacustrine deposits, Jiyuan Area,
- 819 Henan Province. Acta Sedimentologica Sinica, v. 27, p. 573–582 (in Chinese).
- Ji, K.X., Wignall, P.B., Peakall, J., Tong, J.N., Chu, D.L., and Pruss, S.B., 2021,
- 821 Unusual intraclast conglomerates in a stormy, hot-house lake: the Early Triassic
  822 North China Basin. Sedimentology, v.68, p. 3385–3404.
- Ji, K.X., Wignall, P.B., Tong, J.N., Yu, Y.Y., Guo, W.W., Shu, W.C., and Chu, D.L.,
- 824 2022. Sedimentology of the latest Permian to Early Triassic in the terrestrial
- settings of the North China Basin: Low-latitude climate change during a
- warming-driven crisis. GSA Bulletin, https://doi.org/10.1130/B36260.1.
- Jones, T.P., and Rowe, N.P., 1999, Fossil plants and spores: modern techniques.
- B28 Geological Society of London, pp. 420.
- 829 Kerp, H., 1990, The study of fossil gymnosperms by means of cuticular analysis.
- 830 Palaios, v. 5, 548–569.
- 831 Koll, R.A. and DiMichele, W.A., 2021. Dominance-diversity architecture of a mixed
- hygromorphic-to-xeromorphic flora from a botanically rich locality in western
- equatorial Pangea (lower Permian Emily Irish site, Texas, USA.
- Palaeogeography, Palaeoclimatology, Palaeoecology, v. 563, art. 110132.
- 835 Kustatscher, E., Van Konijnenburg-Van Cittert, J.H.A., Bauer, K., Butzmann, R.,
- 836 Meller, B., and Fischer, T.C., 2012, A new flora from the Upper Permian of
- Bletterbach (Dolomites, N–Italy). Review of Palaeobotany and Palynology, v.
- 838 182, p. 1–13.

- 839 Kustatscher, E., Bernardi, M., Petti, F.M., Franz, M., Van Konijnenburg-Van Cittert,
- J.H.A., and Kerp, H., 2017, Sea-level changes in the Lopingian (late Permian) of
- 841 the northwestern Tethys and their effects on the terrestrial palaeoenvironments,
- biota and fossil preservation. Global and Planetary Change, v. 148, p. 166–180.
- 843 Lee, M.S.Y., 1997, A taxonomic revision of pareiasaurian reptiles: implications for
- Permian terrestrial palaeoecology. Modern Geology, v. 21, p. 231–298.
- Liu, J., 2018, New progress on the correlation of Chinese terrestrial Permo-Triassic
  strata. Vertebrata Palasiatica, v. 56, p. 327–342.
- Liu, J., and Bever, G.S., 2018, The tetrapod fauna of the Upper Permian Naobaogou
- Formation of China: A new species of *Elginia* (Parareptilia, Pareiasauria). Papers
  in Palaeontology, v. 4, p. 197–209.
- Liu, J., Xu, L., Jia, S.H., Pu, H.Y., and Liu, X.L., 2014, The Jiyuan tetrapod fauna of
- the Upper Permian of China—2. stratigraphy, taxonomical review, and
- correlation. Vertebrata Palasiatica, v. 52, p. 328–339.
- 853 Liu, J., and Sullivan, C., 2017, New discoveries from the Sinokannemeyeria-
- 854 *Shansisuchus* Assemblage Zone: 3. Archosauriformes from Linxian, Shanxi,
- 855 China. Vertebrata PalAsiatica, v. 55, p. 110–128.
- Liu, J., Ramezani, J., Li, L., Shang, Q.H., Xu, G.H., Wang, Y.Y., and Yang, J.S.,
- 857 2018, High-precision temporal calibration of Middle Triassic vertebrate
- 858 biostratigraphy: U-Pb zircon constraints for the *Sinokannemeyeria* Fauna and
- 859 *Yonghesuchus*. Vertebrata PalAsiatica, v. 56, p. 16–24.
- 860 Liu, Y.Q., Kuang, H.W., Peng, N., Xu, H., Zhang, P., Wang, N.S., and An, W., 2015,
- 861 Mesozoic basins and associated palaeogeographic evolution in North China.
- Journal of Palaeogeography, v. 4, p. 189–202.

Looy, C.V., Brugman, W.A., Dilcher, D.L., and Visscher, H., 1999, The delaved 863 864 resurgence of equatorial forests after the Permian-Triassic ecologic crisis. 865 Proceedings of the National Academy of Sciences, USA, v. 96, p. 13857–13862. 866 Looy, C.V., Twitchett, R.J., Dilcher, D.L., Van Konijnenburg-Van Cittert, J.H.A., and 867 Visscher, H., 2001, Life in the end-Permian dead zone. Proceedings of the 868 National Academy of Sciences, USA, v. 98, p. 7879-7883. Lu, J., Zhang, P.X., Yang, M.F., Shao, Y.L., and Hilton, J., 2020, Continental records 869 870 of organic carbon isotopic composition ( $\delta^{13}C_{org}$ ), weathering, paleoclimate and 871 wildfire linked to the End-Permian mass extinction, Chemical Geology, v. 558, 872 p. 119764. 873 Mays, C., Vajda, V., Frank, T., Fielding, C., Nicoll, R.S., Tevyaw, A., and 874 McLoughlin, S., 2020. Refined Permian-Triassic floristic timeline reveals early 875 collapse and delayed recovery of south polar terrestrial ecosystems. GSA 876 Bulletin, v. 132, p. 1489–1513. 877 Mays, C., McLoughlin, S., Frank, T.D., Fielding, C.R., Slater, S.M. and Vajda, V., 878 2021a. Lethal microbial blooms delayed freshwater ecosystem recovery 879 following the end-Permian extinction. Nature communications, v. 12, p. 1–11. 880 Mays, C., Vajda, V. and McLoughlin, S., 2021b. Permian-Triassic non-marine algae 881 of Gondwana-distributions, natural affinities and ecological implications. Earth-882 Science Reviews, v. 212, art. s103382. 883 McLoughlin, S., 2001, The breakup history of Gondwana and its impact on pre-884 Cenozoic floristic provincialism. Australian Journal of Botany, v. 49, p. 271-300. 885 McLoughlin, S., 2011, *Glossopteris*—insights into the architecture and relationships 886 of an iconic Permian Gondwanan plant. Journal of the Botanical Society of 887 Bengal, v. 65, p. 1–14.

- 888 McLoughlin, S., Nicoll, R.S., Crowley, J.L., Vajda, V., Mays, C., Fielding, C.R.,
- Frank, T.D., Wheeler, A. and Bocking, M., 2021. Age and paleoenvironmental
- significance of the Frazer Beach Member—a new lithostratigraphic unit
- 891 overlying the end-Permian extinction horizon in the Sydney Basin, Australia.
- Frontiers in Earth Science, v. 8, art. 600976.
- 893 Nesbitt, S.J., J. Liu and C. Li, 2011. A sail-backed suchian from the Heshanggou
- 894 Formation (Early Triassic: Olenekian) of China. Earth and Environmental
- Science Transactions of the Royal Society of Edinburgh, v. 101, p. 271–284.
- Niklas, K.J., Tiffney, B.H., and Knoll, A.H., 1983, Patterns in vascular land plant
  diversification. Nature, v. 303, p. 614–616.
- 898 Nowak, H., Schneebeli-Hermann, E. and Kustatscher, E., 2019. No mass extinction
- for land plants at the Permian–Triassic transition. Nature communications, v. 10,p. 384.
- 901 Ouyang, S., and Norris, G., 1988, Spores and pollen from the Lower Triassic
- Heshanggou Formation, Shaanxi Province, North China. Review of Palaeobotany
  and Palynology, v. 54, p. 187–231.
- Ouyang, S., and Wang, R.N., 1985, Age assignment of the Pingdingshan Member in
  Henan and Anhui provinces. Experimental Petroleum Geology, v. 7, p. 141–147.
- 906 Ouvang, S., and Zhang, Z.L., 1982, Early Triassic palynological assemblage in
- 907 Dengfeng, Northwestern Henan. Acta Palaeontologica Sinica, v. 21, p. 685–696.
- 908 Pang, Q.Q., 1989, The Early–Middle Triassic stratigraphy and Ostracoda from the
- 909 Yima area in Henan province. Journal of Hebei College of Geology, v. 12, p.
  910 325–345.
- 911 Qu, L.F., 1980, Triassic spore and pollen fossils. In: Institute of Geology, Chinese
- 912 Academy of Geological Sciences, Mesozoic stratigraphy and paleontology of the

- 913 Shaanxi-Gansu-Ningxia Basin. Vol. 1. Publishing House of Geology, Beijing,
  914 China, p. 115–143.
- 915 Qu, L.F., 1982, The palynological assemblage from the Liujiagou Formation of916 Jiaocheng, Shanxi. Bulletin of Geological Institute, Chinese Academy of
- 917 Geological Society, v. 4, p. 83–93.
- 918 Qu, L.F., Yang, J.D., Bai, Y.H., and Zhang, Z.L., 1983. A preliminary discussion on
- 919 the characteristics and stratigraphic divisions of Triassic spores and pollen in
- 920 China. Bulletin Chinese Academy of Geological Sciences, v. 5, p. 81–94.
- 921 Rees, P.M., 2002, Land-plant diversity and the end-Permian mass extinction.
- 922 Geology, v. 30, p.827–830.
- 923 Retallack, G.J., and Krull, E.S., 1999, Landscape ecological shift at the Permian-
- 924 Triassic boundary in Antarctica. Australian Journal of Earth Sciences, v. 46, p.
  925 785–812.
- 926 Retallack, G.J., Veevers, J.J., and Morante, R., 1996, Global coal gap between
- 927 Permian-Triassic extinction and Middle Triassic recovery of peat–forming plants.
- 928 Geological Society of America Bulletin, v. 108, p. 195–207.
- 929 Scotese, C.R., 2021. An Atlas of Phanerozoic Paleogeographic Maps: The seas come
- 930 in and the seas go out. Annual Review of Earth and Planetary Sciences, v. 49, p931 679–728.
- 932 Sephton, M.A., Jiao, D., Engel, M.H., Looy, C.V., and Visscher, H., 2015, Terrestrial
- acidification during the end-Permian biosphere crisis? Geology, v. 43, p. 159–
  162.
- 935 Sepkoski J. J. Jr., 1984, Kinetic model of Phanerozoic taxonomic diversity. III. Post-
- Paleozoic families and mass extinctions. Paleobiology, v. 10, p. 246–267.

937 Shen, W.J., Sun, Y.G., Lin, Y.T., Liu, D.H., and Chai, P.X., 2011, Evidence for 938 wildfire in the Meishan section and implications for Permian-Triassic events. 939 Geochimica et Cosmochimica Acta, v. 75, p. 1992-2006. 940 Shu, W.C., Tong, J.N., Tian, L., Benton, M.J., Chu, D.L., Yu, J.X., and Guo, W.W., 941 2018, Limuloid trackways from Permian-Triassic continental successions of 942 North China. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 508, p. 71-90. 943 944 Song, H.J., Wignall, P.B., Tong, J.N., Song, H.Y., Chen, J., Chu, D.L., Tian, L., Luo, 945 M., Zong, K.Q., Chen, Y.L., Lai, X.L., Zhang, K.X., and Wang, H.M., 2015, 946 Integrated Sr isotope variations and global environmental changes through the 947 Late Permian to early Late Triassic. Earth and Planetary Science Letters, v. 424, 948 p. 140–147. 949 Stanley, S.M., 2016. Estimates of the magnitudes of major marine mass extinctions in 950 earth history. Proceedings of the National Academy of Sciences, v. 113, p. 951 E6325-E6334. 952 Stevens, L.G., Hilton, J., Bond, D.P.G., Glasspool, I.J., and Jardine, P.E., 2011, 953 Radiation and extinction patterns in Permian floras from North China as 954 indicators for environmental and climate change. Journal of the Geological 955 Society, London, v. 168, p. 607-619. 956 Sun, Y.D., Joachimski, M.M., Wignall, P.B., Yan, C.B., Chen, Y.L., Jiang, H.S., 957 Wang, L.N., and Lai, X.L., 2012, Lethally hot temperatures during the Early Triassic Greenhouse. Science, v. 338, p. 366-370. 958 959 Tong, J.N., Chu, D.L., Liang, L., Shu, W.C., Song, H.J., Song, T., Song, H.Y., and 960 Wu, Y.Y., 2018, Triassic integrative stratigraphy and timescale of China. Science 961 China Earth Sciences, v. 62, p. 189–222.

<b>962</b> IU, C. Y., Chen, Z.Q., Retallack, G.J., Huang, Y.G., and Fang, Y.H	H., 201	16,
---	---------	-----

- 963 Proliferation of MISS-related microbial mats following the end-Permian mass 964 extinction in terrestrial ecosystems: Evidence from the Lower Triassic of the 965 Yiyang area, Henan Province, North China. Sedimentary Geology, v. 333, p. 50-966 69. 967 Vajda, V., McLoughlin, S., Mays, C., Frank, T.D., Fielding, C.R., Tevyaw, A., 968 Lehsten, V., Bocking, M., and Nicoll, R.S., 2020, End-Permian (252 Mya) 969 deforestation, wildfires and flooding-An ancient biotic crisis with lessons for 970 the present. Earth and Planetary Science Letters, v. 529, p. 115875. 971 Visscher, H., Looy, C.V., Collinson, M.E., Brinkhuis, H., van Konijnenburg-van 972 Cittert, J.H.A., Kürschner, W.M., and Sephton, M.A., 2004, Environmental 973 mutagenesis during the end-Permian ecological crisis. Proceedings of the 974 National Academy of Sciences, USA, v. 101, p. 12952-12956. 975 Wang, J., 2010. Late Paleozoic macrofloral assemblages from Weibei Coalfield, with 976 reference to vegetational change through the Late Paleozoic Ice-age in the North 977 China Block. International Journal of Coal Geology, v. 83, p. 292–317. 978 Wang, J., Liu, H.Q., Shen, G.L., and Zhang, H., 1998, Notes on the island distribution 979 pattern of the Permian Cathaysian flora in China: an example of the application
- 980 of the equilibrium theory of island biogeography in palaeobiogeography.
- 981 Palaeogeography Palaeoclimatology Palaeoecology, v. 142, p. 23–31.
- Wang, J.Y., Yi, J., Liu, J., 2019, The first complete pareiasaur skull from China. Acta
  Palaeontologica Sinica, v. 58, p. 216–221.
- Wang, L.X., 1983. Triassic of Shanxi. Shanxi Provincial Geological Prospecting
  Bureau, 198 pp.

- Wang, L.X., Xie, Z.M., and Wang, Z.Q., 1978, On the occurrence of *Pleuromeia* from
  the Qinshui basin in Shanxi province. Acta Palaeontologica Sinica, v. 17, p. 195–
  211.
- Wang R.N., 1981, The "Shichienfeng Formation" of Yongcheng, Henan province and
  other adjacent area. Journal of Stratigraphy, v. 5, p. 180–189.
- 991 Wang, Z.Q., 1993, Evolutionary ecosystem of Permian–Triassic redbeds in North
- 992 China: a historical record of global desertification. New Mexico Museum of
  993 Natural History and Science Bulletin, v. 3, p. 471–476.
- **994** Wang, Z.Q., 1996, Recovery of vegetation from the terminal Permian mass extinction
- in North China. Review of Palaeobotany and Palynology, v. 91, p. 121–142.
- 996 Wang, Z.Q., and Wang, L.X., 1982, A new species of the lycopsid *Pleuromeia* from
- 997 the early Triassic of Shanxi, China and its ecology. Palaeontology, v. 25, p. 215–
  998 225.
- 999 Wang, Z.Q., and Wang, L.X., 1986, Late Permian fossil plants from the lower part of
- 1000 the Shiqianfeng (Shihchienfeng) group in North China. Bulletin Tianjin Institute
- 1001 of Geology and Mineral Resources, v. 15, p. 1–120.
- 1002 Wignall, P.B., 2015, The worst of times. Princeton University Press, p. 64–75.
- 1003 Wu, Q., Ramezani, J., Zhang, H., Wang, J., Zeng, F.G., Zhang, Y.C., Liu, F., Chen, J.,
- 1004 Cai, Y.F., Hou, Z.S., Liu, C., Yang, W., Henderson, C.M. and Shen, S.Z., 2021,
- 1005 High-precision U-Pb age constraints on the Permian floral turnovers,
- paleoclimate change, and tectonics of the North China block. Geology, v. 49, p.677–681.
- 1008 Wu, Y.Y., Tong, J.N., Algeo, T.J., Chu, D.L., Cui, Y., Song, H.Y., Shu, W.C., and
- 1009 Du, Y., 2020, Organic carbon isotopes in terrestrial Permian-Triassic boundary

- 1010 sections of North China: Implications for global carbon cycle perturbations.
- 1011 Geological Society of America Bulletin, v. 132, p. 1106–1118.
- 1012 Xiong, C.H., and Wang, Q., 2011, Permian–Triassic land-plant diversity in South
- 1013 China: Was there a mass extinction at the Permian/Triassic boundary?
- 1014 Paleobiology, v. 37, p. 157–167.
- 1015 Xu, L., Li, X.W., Jia, S.H. and Liu, J., 2015, The Jiyuan tetrapod Fauna of the Upper
- 1016 Permian of China: New pareiasaur material and the reestablishment of *Honania*

1017 *complicidentata*. Acta Palaeontologica Polonica, v. 60, p.689–700.

- 1018 Xu, Z., Hilton, J., Yu. J.X., Wignall, P.B., Yin, H.F., Xue, Q., Ran, W.J., Hui, L.,
- 1019 Shen, J., and Meng, F.S., 2022. Mid-Permian to Late Triassic plant species
- 1020 richness and abundance patterns in South China: Co-evolution of plants and the
- 1021 environment through the Permian-Triassic transition. Earth-Science Reviews.

1022 https://doi.org/10.1016/j.earscirev.2022.104136

1023 Yang, G.X., and Wang, H.S., 2012, Yuzhou Flora- A hidden gem of the Middle and

Late Cathaysian Flora. Science China Earth Sciences, v. 55, p. 1601–1619.

- 1025 Yin, H.F., and Lin, H.M., 1979, Marine Triassic faunas and the geologic time from
- Shihchienfeng Group in the northern Weihe River Basin, Shaanxi Province. Acta
  Stratigraphica Sinica, v. 3, p. 233–241 (in Chinese).
- 1028 Yu, J.X., Broutin, J., Chen, Z.Q., Shi, X., Li, H., Chu, D.L., and Huang, Q.S., 2015,
- 1029 Vegetation changeover across the Permian–Triassic Boundary in Southwest
- 1030 China: extinction, survival, recovery and palaeoclimate: A critical review. Earth-
- 1031 Science Reviews, v. 149, p. 203–224.
- 1032 Yu, Y.Y., Tian, L., Chu, D.L., Song, H.Y., Guo, W.W. and Tong, J.N., 2022, Latest
- 1033 Permian–Early Triassic paleoclimatic reconstruction by sedimentary and isotopic

- analyses of paleosols from the Shichuanhe section in central North China Basin.
- 1035 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 585, p.110726.
- 1036 Zheng, D., Chang, S.C., Wang, H., Fang, Y., Wang, J., Feng, C., Xie, G.,
- 1037 Jarzembowski, E.A., Zhang, H., and Wang, B., 2018, Middle-Late Triassic insect
- radiation revealed by diverse fossils and isotopic ages from China. Science
- 1039 advances, v. 4, p. eaat1380.
- 1040 Zhu, R.K., Xu, H.X., Deng, S.H., and Guo, H.L., 2007, Lithofacies palaeogeography
- 1041 of the Permian in northern China. Journal of Palaeogeography, v. 9, p. 133–142.
- 1042 Zhu, Z.C., Kuang, H., Liu, Y.Q., Benton, M.J., Newell, A.J., Xu, H., An, W., Ji, S.A.,
- 1043 Xu, S.C., Peng, N., and Zhai, Q.G., 2020, Intensifying aeolian activity following
- 1044 the end-Permian mass extinction: evidence from the Late Permian–Early Triassic
- 1045 terrestrial sedimentary record of the Ordos Basin, North China. Sedimentology,
- 1046 v. 67, p. 2691–2720.
- 1047
- **1048 FIGURES AND TABLES CAPTIONS**
- 1049 Figure 1. (A) Late Permian paleophytogeographical maps and distribution of typical
- 1050 Early Triassic fossil plant taxa during the Late Permian to Early Triassic (Broutin et
- 1051 al. 1995; McLoughlin 2001, 2011); base map adapted from Scotese (2021). (B)
- 1052 Paleogeographic map of the Late Permian and main sections of this study in North
- 1053 China; base map modified from Zhu et al. (2007). (C) Palaeogeographic map of the
- 1054 Early Triassic and main sections of this study in North China; base map modified
- 1055 from Liu et al. (2015). (D) Geographic distributions of fossil plant locations from the
- 1056 Sunjiagou (SJG), Liujiagou (LJG), Heshanggou (HSG) and Ermaying (EMY)
- 1057 formations in North China (Supplementary Data File 1).
- 1058

Figure 2. Lithological columns of the studied sections showing the lithology and the position of the fossil horizons and some special sedimentary structures. Lower dotted line marks the end-Permian Plant Extinction event (EPPE), the gray area indicates the ecological disturbance interval without fossil plants, and the upper dashed line marks the occurrence of Early Triassic fossil plants in the studied sections. Abbreviation: Fm., Formation, Tetra., Tetrapods.

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Shihhotse Formation of the Shichuanhe and Liulin sections. A–C, *Autunia*–type
ovuliferous organs. D, small fragmentary pinna of *Sphenopteris*. E, F, strap-like leaf

Figure 3. Plant fossils, cuticles and *in situ* pollens from the top part of the Upper

- 1069 in E and broken leaf in F of *Taeniopteris* with simple parallel lateral veins arising
- 1070 from the midvein at an angle of nearly 90°. G–J, broken leaves of ginkgophytes, G
- and H, broken leaves of ginkgophyte type 2 with horn-like shape and dichotomous-
- 1072 patterned veins, I and J, broken wedged-shape leaves with the bifurcated rounded
- 1073 apex of ginkgophyte type 1 with strong petioles. K–O, T, W, shoots and cuticle of
- 1074 conifer type 2, K with possible terminate cone on the shoot, the cuticle in W is from
- 1075 the shoot in T. P, possible cone of a conifer. Q–S, U, V, X, Y, shoots, cuticles and *in*
- 1076 situ pollens of conifer type 0, U and V are cuticles macerated from the shoot in S, X
- 1077 and Y are *in situ* pollens "picked out" directly from the shoots in Q–S and pollen in Y
- 1078 was photographed under SEM. Scale bars: A–D, L, T are 5 mm. E–K, M–S are 1 cm.
- 1079 U, V, X, Y are 50 µm, W is 20 µm. A–D, F, I–J, K–O, P from the Shichuanhe section.
- 1080 E, G–H, Q–T, Q–Y from the Liulin section.
- 1081
- 1082 Figure 4. Plant fossils, cuticles and *in situ* pollens from the lower part of the
- 1083 Sunjiagou Formation of the Liulin, Dayulin and Zishiya sections. A, fragments of

- 1085 pinnae of Germaropteris martinsii and its cuticles, triangular arrows in N and O show
- 1086 the base of trichome, D before processing, E after processing, F-I and M-O are from
- 1087 the red rectangular area of E. J-L, fertile parts of the Autunia-type organ. P-Y, MM,
- 1088 shoots and isolated leaves of conifer type 3 of *Pseudovoltzia* with well-preserved
- 1089 cuticle, R–X are from Q, S–X is from the red rectangular area of R. AA, bract-scale
- 1090 complexes of fossil conifers. BB-CC, heterophyll shoot and its cuticles of conifer
- 1091 type 2. DD, EE, PP, SS, male cone of conifer and its *in situ* pollens (possible
- 1092 *Gardenasporites*), EE is a reconstruction of DD, PP is the distal view and SS is the
- 1093 proximal view of pollen grains. FF–GG, some shoots of conifer type 4. Z, HH–LL,
- 1094 NN, OO, QQ, RR, some conifer shoots with their cuticles of conifer type 1. Scale
- 1095 bars: A, J, Y, Z, AA, BB are 5 mm. K, L, DD–HH, KK, LL, MM are 1 cm. B–E, P–R
- 1096 are 1 mm. F–I, N–O, T–X, CC, NN–SS are 50 μm; M, S, II are 500 μm; JJ is 200 μm.
- 1097 A–J, M–O, DD–GG, PP, SS from the Liulin section. P–Z, AA–CC, HH–JJ, NN–OO,
- 1098 QQ, RR from the Dayulin section. K, L, KK–MM from the Zishiya section.
- 1099
- 1100 Figure 5. Strobili of *Pleuromeia* and pinnate fragments of pteridophylls from the
- 1101 upper part of the Liujiagou Formation at Peijiashan. A, B, pinnate fragments of
- 1102 Scolopendrites. C-K, strobili of Pleuromeia. F-K was processed under CT scanning.
- 1103 All scale bars are 1 cm.
- 1104
- 1105 Figure 6. In situ stems/rhizomorphs and dispersed megasporophylls of Pleuromeia,
- 1106 dispersed broken megasporophylls of *Tomiostrobus*, *in situ* rhizomes and dispersed
- 1107 stems of *Neocalamites* and *Equisetites* and isolated possible male cone, bract-scale
- 1108 complexes and seeds of voltzian conifers from the basal Heshanggou Formation of

- 1110 showing four-lobed rhizomorphs. E–J, some *in situ* rhizomes and dispersed stems of
- 1111 Neocalamites, F, triangular arrow shows the linear whorled leaves at the node; H,
- 1112 triangular arrow shows one small branch base at the node; J, shows the underground
- 1113 part of the rhizome and triangular arrow shows the upright stem. K shows broken
- 1114 stem of *Equisetites*. L, dispersed broken megasporophyll with a long tip characteristic
- 1115 of Tomiostrobus. M, dispersed megasporophyll of Pleuromeia. N, one isolated
- 1116 possible male cone. O, bract-scale complexes and cordiform seeds of voltzian
- 1117 conifers. Scale bars: A, B, D, J are 5 cm; C is 2 cm; E–I, K–O are 1 cm.
- 1118
- 1119 Figure 7. Plants from the Lower Heshanggou Formation of Yushe. A–D,
- 1120 megasporophylls of *Pleuromeia*, some microconchids on the surface of D at the
- 1121 triangular arrow. E, F, pinnae of Anomopteris. G, stem of Pleuromeia. H, strobilus of
- 1122 Pleuromeia. I, the broken stem of Neocalamites. J-L, in situ rhizophores of
- 1123 Pleuromeia. M-O, leaves of Tongchuanophyllum, showing feeding holes on the
- 1124 surface and margins of O at the triangular arrow. P–Q, bract-scale complexes of
- 1125 voltzian conifers. Scale bars: A, C, F, Q are 5 mm; B, D, E, G–P are 1 cm.
- 1126
- 1127 Figure 8. Some plant fossils from the Ermaying Formation of Yushe. A–C, some
- 1128 rhizophores of *Pleuromeia*. D–F, some broken sphenophyte stems of probably
- 1129 Neocalamites, showing possible invertebrate burrows inside the cast of the stem F. G-
- 1130 I, some woody plant fossil wood casts. Scale bars: A–D are 1 cm; E–I are 5 cm.
- 1131
- 1132 Figure 9. Other fossils associated with fossil plants. A–D, CT scanned 3D photos of
- 1133 Temnospondyli tooth from fossil-plant-bearing horizon of the Upper Shihhotse

- 1135 fragment of insect wing fossil; F, many microconchids found on some plant remains;
- 1136 G, some ophiurids; H–K, M, R, some conchostracans (H–K, *Pseudestheria* spp.; M,
- 1137 Euestheria gutta; R, Magniestheria mangaliensis); L, some lingulids; N–Q, S, T,
- 1138 some bivalves (N, Pteria ussurica variabilis; O, Wilkingia sp.; P, Modiolus sp.; Q,
- 1139 Leptochondria sp.; S, Palaeoneilo elliptica; T, Promyalina putiatinensis). Scale bars:
- 1140 A–G, O, P, T is 1 cm; H–N, Q–S is 1 mm. E, F, L–N were found in the rich

sporomorph horizon of the Sunjiagou Formation in the Shichuanhe section; G and R

- 1142 were found in rich sporomorph horizon of the Qishan Formation in the Zishiya
- 1143 section; H-K were found with fossil plants in the Lower Sunjiagou Formation, H–J, in
- 1144 the Liulin section; K, in the Dayulin section; O–Q, S, T were found in the fossil-plant-
- 1145 bearing horizon of the Sunjiagou Formation in the Zishiya section.
- 1146
- 1147 Figure 10. Range chart of floras from North China from the Cisuralian to Middle
- 1148 Triassic interval. Five floras, one of which includes two sub-floras, and five floral
- 1149 transitions including an extirpation event, two turnovers and two radiation events are
- 1150 recognized here (Supplementary Data File 2, 3). g. extinction, gigantopterid flora
- 1151 extirpation; T1–T5, floral transition 1–5; EPPE, end-Permian Plant Extinction event.
- 1152 References of the previous studies can be seen in Supplementary Data File 4. Plant
- 1153 zones or subzones or assemblages in previous studies (see Supplementary Data File
- 1154 4): CrSZ, PZ, UZ, PjSZ, PeSZ, PsSZ, TZ, ISZ, SSZ, GLF, GLP, UY, GMLF, MPL,
- 1155 *PSP*, *UP*; floras in this study (see Supplementary Data File 4): Voltziales, the
- 1156 Voltziales flora; gw, the ginkgophyte-walchian Voltziales subflora; Voltz., the
- 1157 voltzian Voltziales subflora; PN, the Pleuromeia–Neocalamites flora; PT flora, the

- 1158 *Pleuromeia–Tongchuanophyllum* flora; *LV* flora, the *Lepacyclotes–Voltzia* flora. Te.,
  1159 tectonism; Wu., Wuchiapingian.
- 1160

1161 Figure 11. Hierarchical clustering and *k*-means clustering for five floras and three 1162 main phases from Permian to Middle Triassic in North China. A. Hierarchical 1163 clustering-complete linkage analysis showing five different floras from Permian to 1164 Middle Triassic in North China; B. k-means clustering analysis showing three main 1165 phases from Lopingian to Middle Triassic in North China. a. the gigantopterid flora 1166 extirpation (T1) and the absence of the coal deposits, b. End-Permian Plant extinction 1167 (EPPE, T3), c. Gradual recovery of floras (T5). gigantopter. flora, the gigantopterid 1168 flora; Volt. flora, the Voltziales flora; PN flora, the Pleuromeia-Neocalamites flora; 1169 PT flora, the Pleuromeia-Tongchuanophyllum flora; LV flora, the Lepacyclotes-1170 *Voltzia* flora. 1–5, cluster centroids; T1–T5, floral transition 1–5. 1171 1172 Figure 12. Model of floral community's changeovers associated with different 1173 animals during the Permian-Triassic crisis in North China. 1, 1174 Tomiostrobus/Lepacyclotes; 2. Pleuromeia; 3. Sphenophytes; 4, 19. Tree ferns; 5.

- 1175 Small Pteridophytes (e.g., *Anomopteris/Scolopendrites*); 6. Pteridosperms; 7. Cycads;
- 1176 8. Ginkgophytes; 9. Conifers; 10. Ostracods; 11. Conchostracans; 12. Triopsidae; 13.
- 1177 Bivalves; 14. Insects; 15. Fishes; 16. MISS; 17. Lingulids; 18. Yuania; 20.
- 1178 gigantopterids; 21. Lepidodendrales. TED interval, the terrestrial ecological
- 1179 disturbance interval; LMUUSHZ, Lower–Middle–Upper Upper Shihhotse Formation;
- 1180 tUSHZ, topmost Upper Shihhotse Formation; Fm., Formation; g. extinction,
- 1181 gigantopterid flora extinction; T1–T5, floral transition 1–5; EPPE, end-Permian plant
- 1182 extinction event.

1184 Figure 13. Late Permian to Triassic biotic and environmental changes in North China. 1185 Including diversity of plant, insect, tetrapod, fish, invertebrate and trace fossils 1186 associated with the environmental changes of coal deposits, red beds and humid/arid 1187 climates. Changes of coal deposits and red beds are modified from Wang (2010) and 1188 other data in Supplementary Data File 2–9. Fms, Formations; USHZ, the Upper 1189 Shihhotse Formation; SJG, the Sunjiagou Formation; LJG, the Liujiagou Formation; 1190 HSG, the Heshanggou Formation; EMY, the Ermaying Formation; Spo., Sporomorph 1191 assemblages; Cisura., Cisuralian; Loping., Lopingian; Wu.-Cha., Wuchiapingian-1192 Changhsingian. TED interval is terrestrial ecological disturbance interval; gig. flora, 1193 the gigantopterid flora; Volt. flora, the Voltziales flora; PN flora, the Pleuromeia-1194 Neocalamites flora; PT flora, the Pleuromeia-Tongchuanophyllum flora; LV flora, the 1195 Lepacyclotes–Voltzia flora. Sporomorph assemblages: Patellisporites meishanensis 1196 biozone (Pm); Lueckisporites virkkiae–Jugasporites schaubergeroides assemblage 1197 (LvJs); Aratrisporites–Alisporites assemblage (AA); Densoisporites nejburgii– 1198 Lunatisporites-Cycadopites assemblage (DnLC); Cycadopites-Lunatisporites-1199 *Verrucosisporites* assemblage (*CLV*); *Punctatisporites–Chordasporites* (*PC*) 1200 assemblage see in Fig. S2; bioturbation intensity (The Bedding Plane Bioturbation 1201 Index (BPBI) and ichnofabric index (ii)) data from (Guo et al., 2019). Dashed lines 1202 mark position of two losses of diversity, the lowermost an extirpation event and the 1203 upper extinctions of the EPPC; three dotted lines mark position of three transitions the 1204 lowermost a turnover, the upper two radiations; gE, gigantopterid flora extirpation; 1205 T1–T5, floral transition 1–5; EPPE, end-Permian Plant Extinction event. 1206

- 1207 Table 1. The number of specimens of macrofossil plants from different formations
- 1208 and sections in this study. USH Fm., Upper Shihhotse Formation; SJG Fm., Sunjiagou
- 1209 Formation; LJG Fm., Liujiagou Formation; HSG Fm., Heshanggou Formation; T.,
- 1210 total specimens.

Liulin Section		Peijiash an Section	Dayul in Sectio n	Shichua nhe Section	Zishiya Section	Heshun Section	Yushe Sectio n	Pingyao Section	T
HSG Fm.							280	120	400
LJG Fm.		80		10		10			100
SJG Fm.	206		37		202				445
USH Fm.	46			385					432
Т.	252	80	37	395	202	10	280	120	133 7



1214 Figure 1









Figure 3



Figure 4



- 1223 Figure 5



- 1226 Figure 6



1229 Figure 7



1232 Figure 8











## 1237 Figure 10

1238





1240 Figure 11







- 1244 Figure 13