

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
2 China and implications for the great transition of
3 continental ecosystems

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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 represent 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.

46

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).
61 Other studies have suggested that there is no extinction in palynological records
62 around the Permian–Triassic Boundary (Hochuli et al., 2016; Schneebeili-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.

88

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
97 north-eastern part of the Paleo-Tethys Ocean during the late Paleozoic and early
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).

101 The Permian to Middle Triassic succession in North China is divided into the
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
114 conglomerates in the middle–upper part. This unit was deposited in various fluvial or
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 grayish 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 – $\leq 280.73 \pm 0.12$ Ma) rather than Guadalupian–early Lopingian as previously
127 thought, although its uppermost part may still be latest Capitanian–Lopingian (\leq
128 261.75 ± 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 ($\delta^{13}\text{C}_{\text{org}}$) 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 ± 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 ± 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
153 et al., 2022). An ID-TIMS U-Pb zircon date of 243.528 ± 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
195 data, present (1) or absent (0), in each formation (Cleal et al., 2021). The presence-
196 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 NORTH** 205 **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**

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

224 subdivided into the ginkgophyte–walchian Voltziales and the voltzian Voltziales
225 subfloras.

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.

249

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.

274

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 *Tomiostrabus* 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**

294 Abundant fossil plant specimens occur in the lower–upper part of the
295 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

299 of them are lycophytes, e.g., *Pleuromeia epicharis*, some stems with very small leaf
 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*, *Phyllothea*, *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**

312 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., *Germanopteris*, *Peltaspermum*, *Ptilozamites*,
 321 *Glossophyllum*, *Neoglossopteris*, *Scytophyllum*, *Tongchuanophyllum*, “*Thinnfeldia*”,
 322 *Pachypteris* and *Protoblechnum*), cycadophytes (e.g., *Nilssonina*, *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,
325 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**

330 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
335 al. 2015) that are assigned a Wuchiapingian age based on comparisons of the entire
336 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;
338 Benton 2016). A Wuchiapingian age of the strata is also supported by
339 magnetostratigraphy (Guo, 2022).

340 Previously a *Ullmannia bronniei*–*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 ± 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*–*Cycadopites* 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
396 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

399 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 Heshangou 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
428 (Hilton and Cleal, 2007; Wang, 2010; Stevens et al., 2011; Wu et al., 2021). There
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 *Psymgophyllum* 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

474 Terrestrial ecological disturbance interval (TED interval) (see Xu et al., 2022). T3
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
489 Formation includes the voltzian conifer pollen *Triadispora* (see Balme, 1995),
490 suggesting that even though the voltzian-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 megafloora 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
498 conifers (Fig. 10). We consider the appearance of this megafloora to mark the end of

499 the third transition event (T3) (Fig. 10). An alternative interpretation might be to
500 divide the T3 event as presented here into a separate late Permian extinction event and
501 an earliest Triassic radiation event. While future research is required to fully evaluate
502 floral changes in transition, we consider this scenario less likely as the extinction and
503 radiation appear intricately linked to the environmental perturbations of the TED
504 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 *Tomiostrabus* 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 settings
549 (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 voltziales-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 ± 147 mm/yr (Yu et al. 2022).

571 The disappearance of the voltzian Voltziales-dominated forests (T3; Fig. 12) in
572 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 *Tomiostrabus* 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 *Phyllothea*)-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 *Tomiostrabus*-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 ± 147 mm/yr to 680
628 ± 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 *Sinokannemeyeria* 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
646 scale is established for the Lopingian–Middle Triassic of North China, based on

647 macrofossil plant, sporomorph, vertebrate and invertebrate (conchostracans and
648 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

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

678

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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

1059 Figure 2. Lithological columns of the studied sections showing the lithology and the
 1060 position of the fossil horizons and some special sedimentary structures. Lower dotted
 1061 line marks the end-Permian Plant Extinction event (EPPE), the gray area indicates the
 1062 ecological disturbance interval without fossil plants, and the upper dashed line marks
 1063 the occurrence of Early Triassic fossil plants in the studied sections. Abbreviation:
 1064 Fm., Formation, Tetra., Tetrapods.

1065

1066 Figure 3. Plant fossils, cuticles and *in situ* pollens from the top part of the Upper
 1067 Shihhotse Formation of the Shichuanhe and Liulin sections. A–C, *Autunia*-type
 1068 ovuliferous organs. D, small fragmentary pinna of *Sphenopteris*. E, F, strap-like leaf
 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
 1071 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

1084 pinnule of pteridophyte with dichotomous veins. B–I, M–O, vegetative terminal
 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

1109 Heshun. A–D, *in situ* stems/rhizomorphs of *Pleuromeia*, C is the bottom of B
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 *Tomiostrabus*. 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

1134 Formation in the Shichuanhe section showing well-preserved inner structure; E,
 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
 1141 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 *Tomiostrabus/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.

1183

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, the1195 *Lepacyclotes*–*Voltzia* flora. Sporomorph assemblages: *Patellisporites meishanensis*1196 biozone (*Pm*); *Lueckisporites virkkiae*–*Jugasporites schaubegeroides* assemblage1197 (*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.

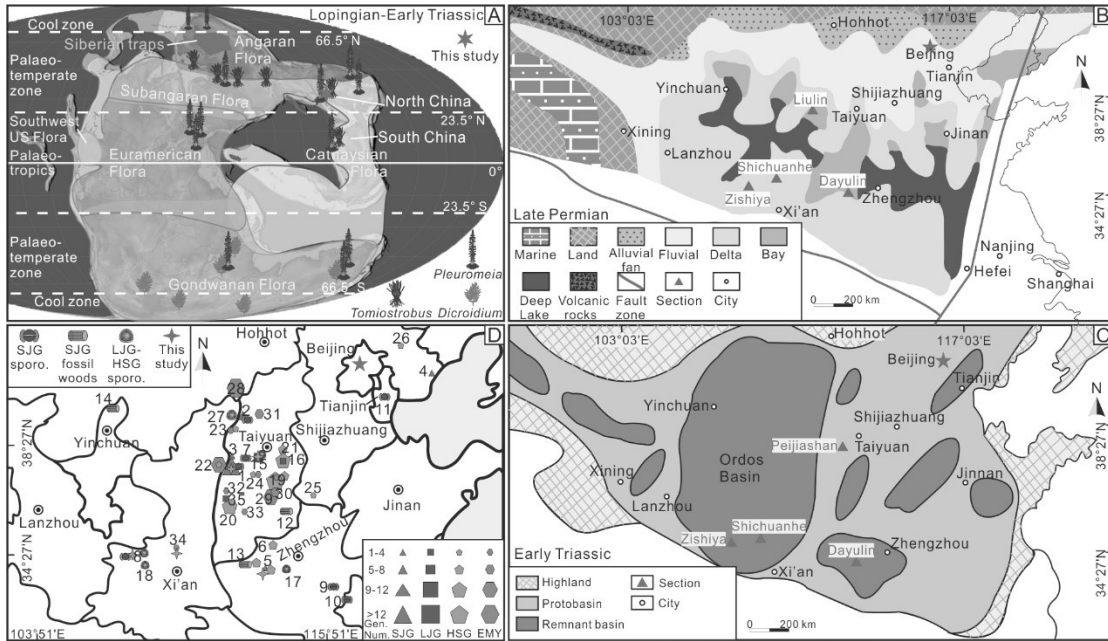
1206

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	Peijiashan Section	Dayulin Section	Shichuanhe Section	Zishiya Section	Heshun Section	Yushe Section	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
T.	252	80	37	395	202	10	280	120	1337

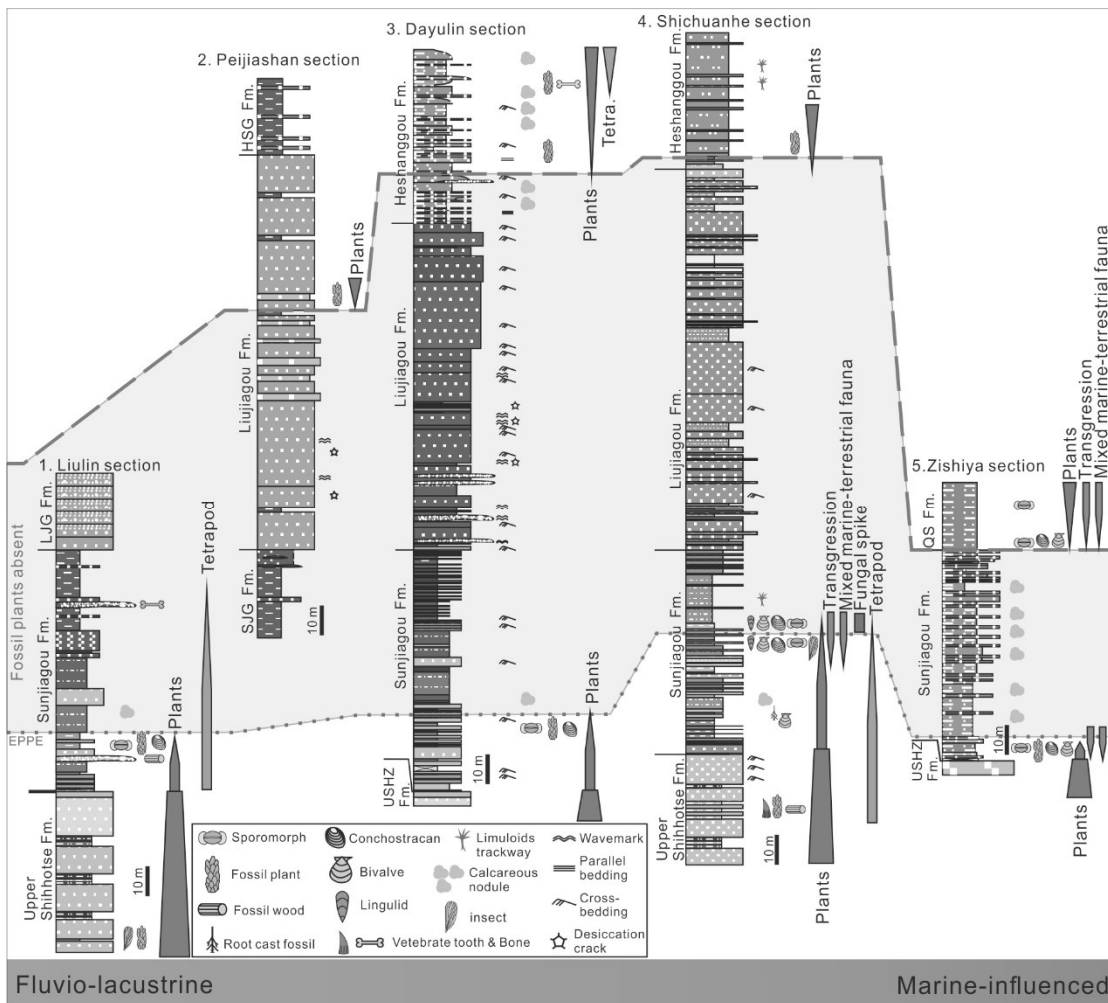
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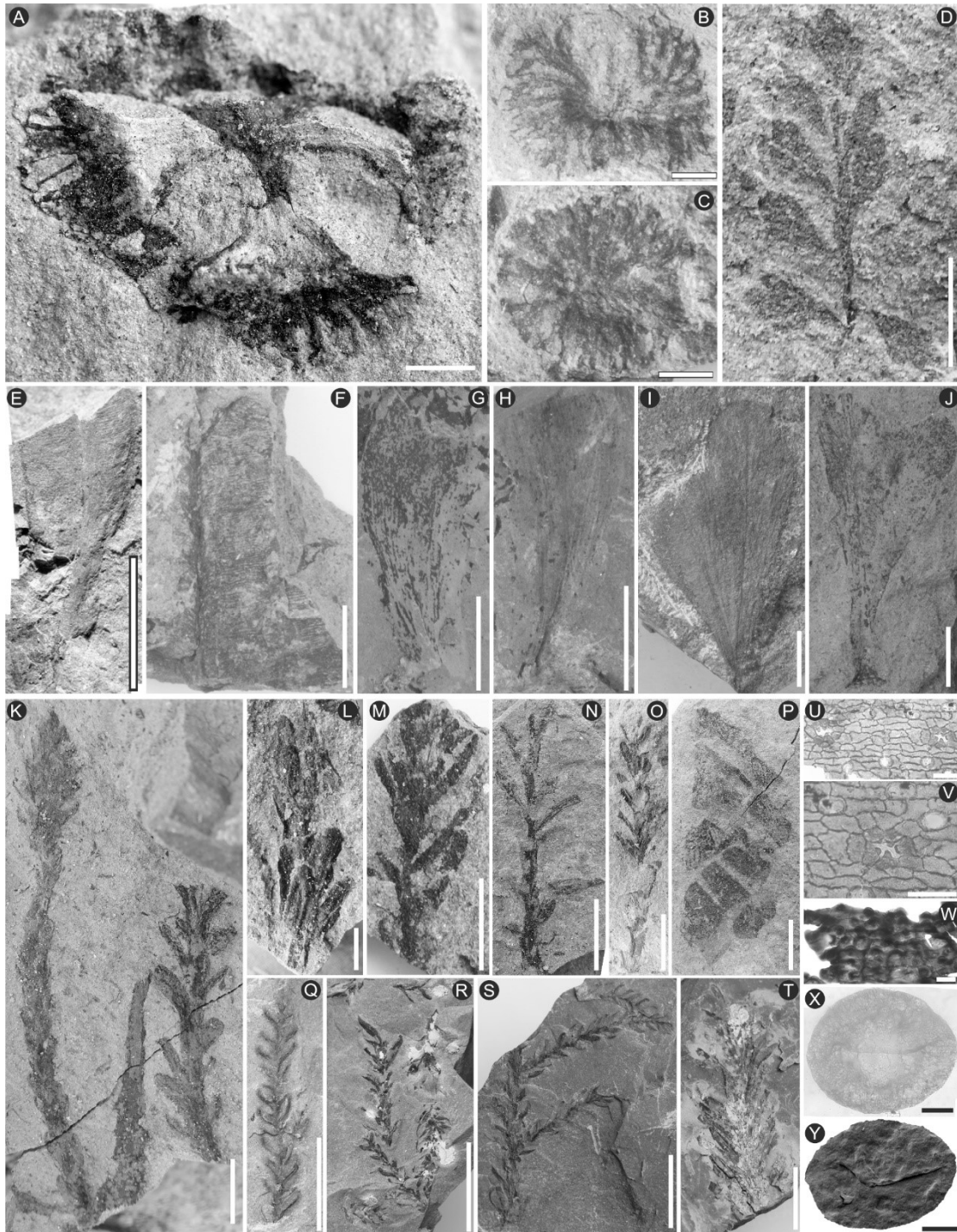
1213

1214 Figure 1



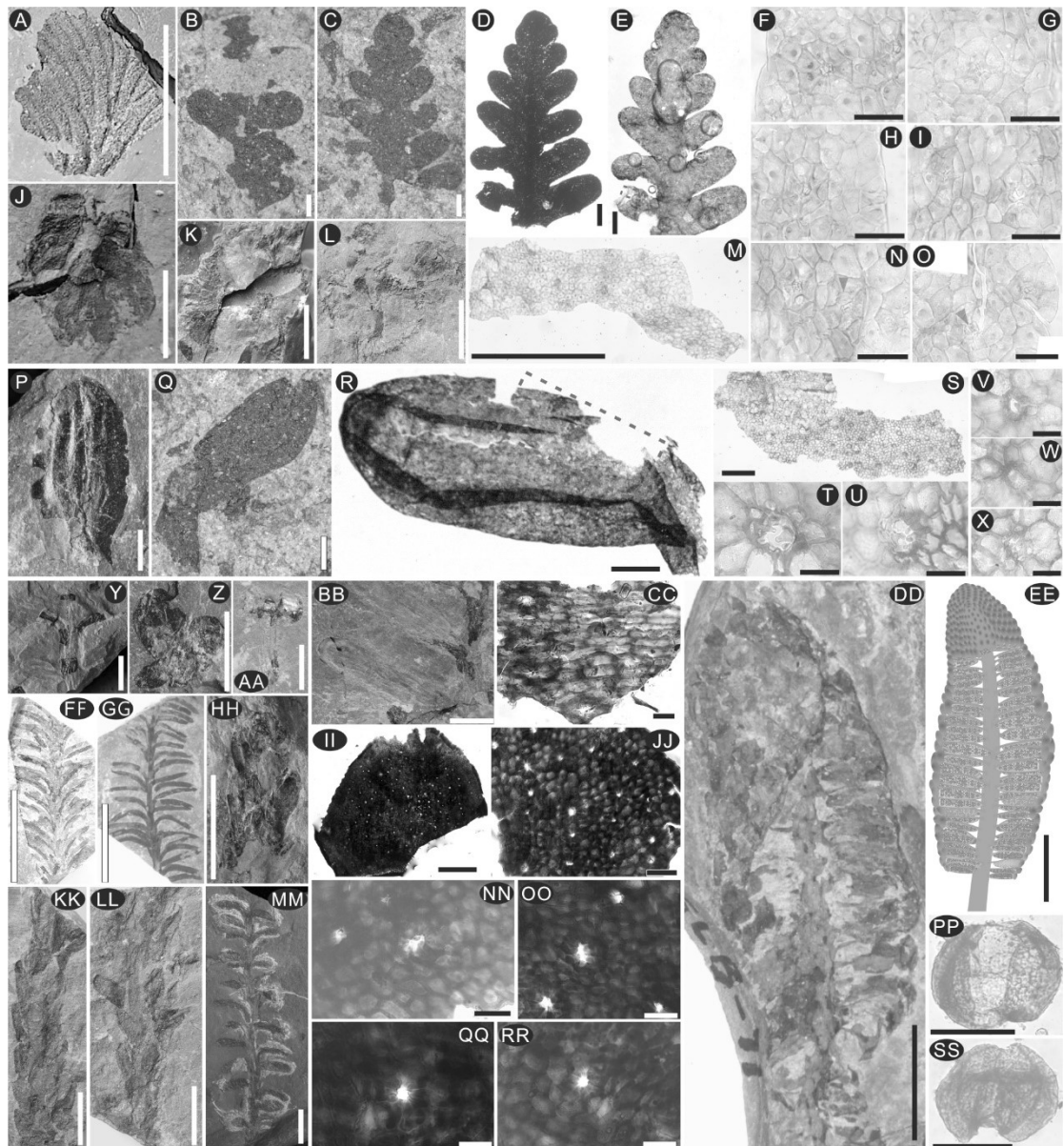
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1216 Figure 2



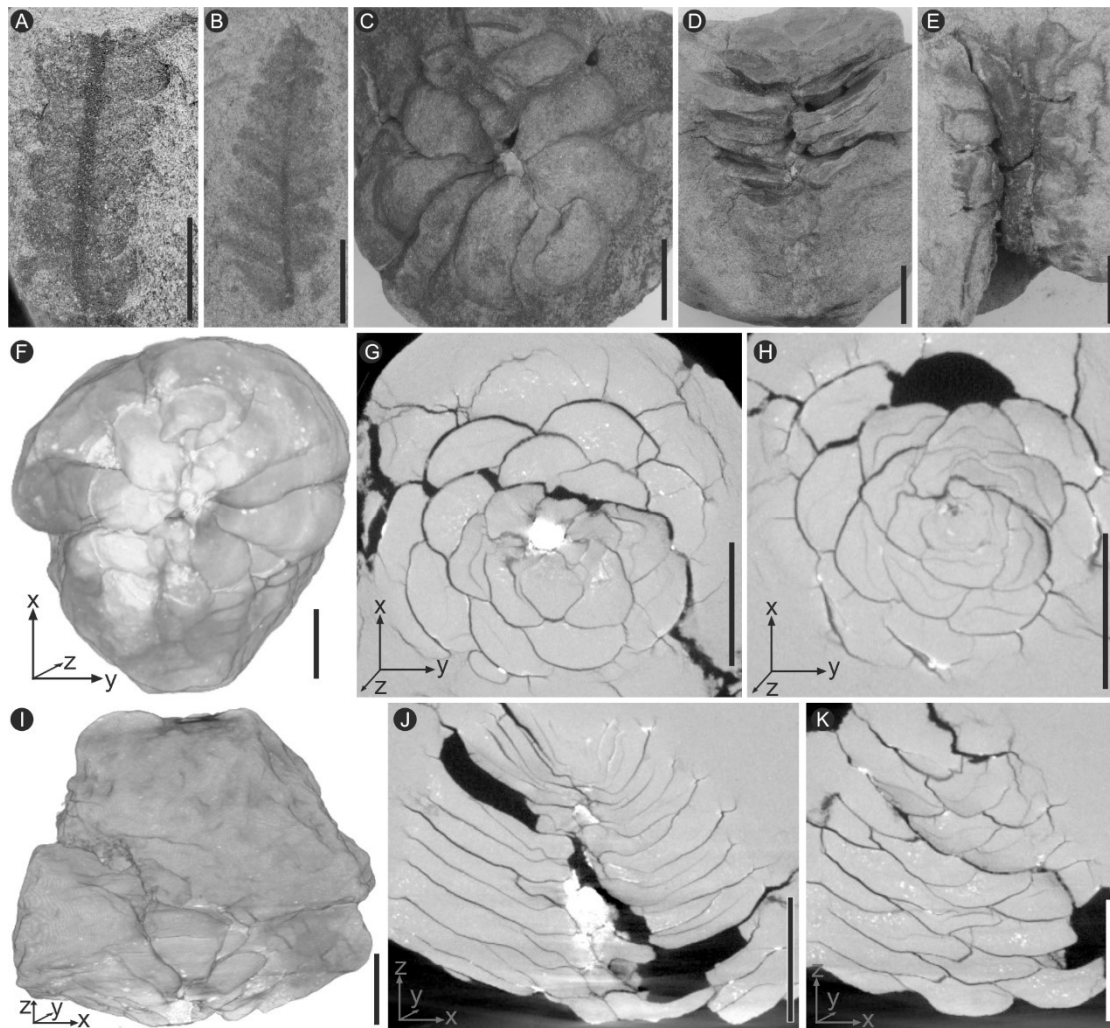
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Figure 3



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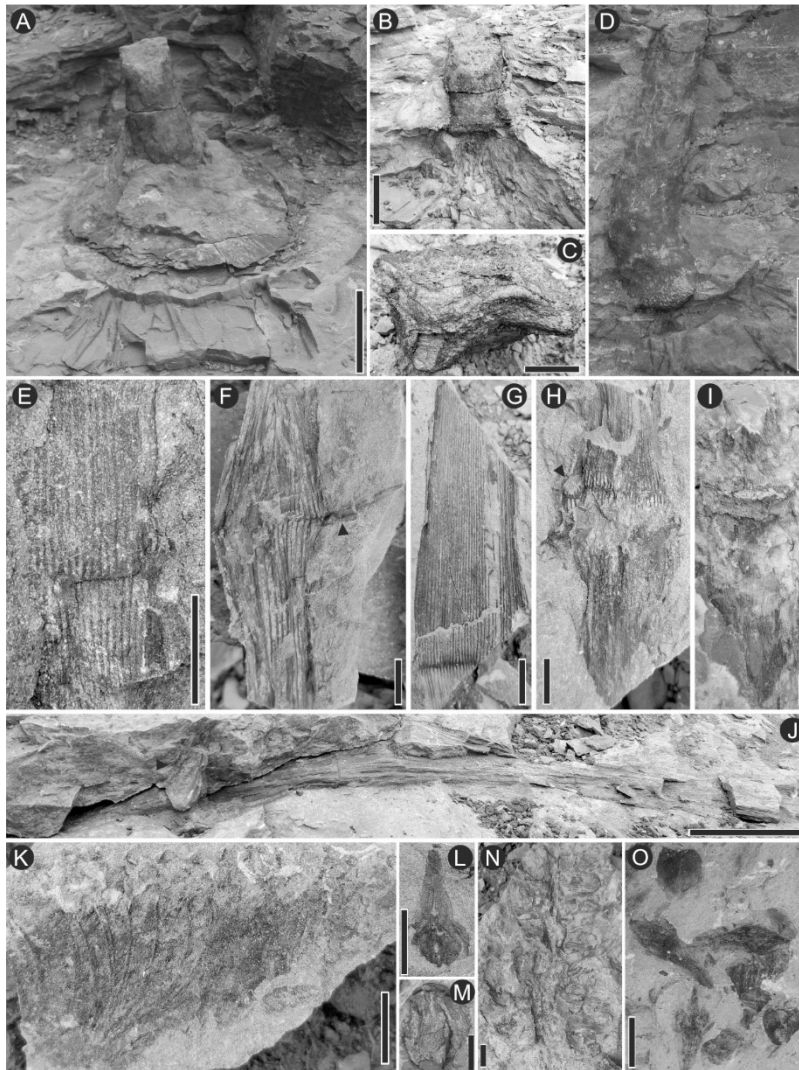
Figure 4



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1223 Figure 5

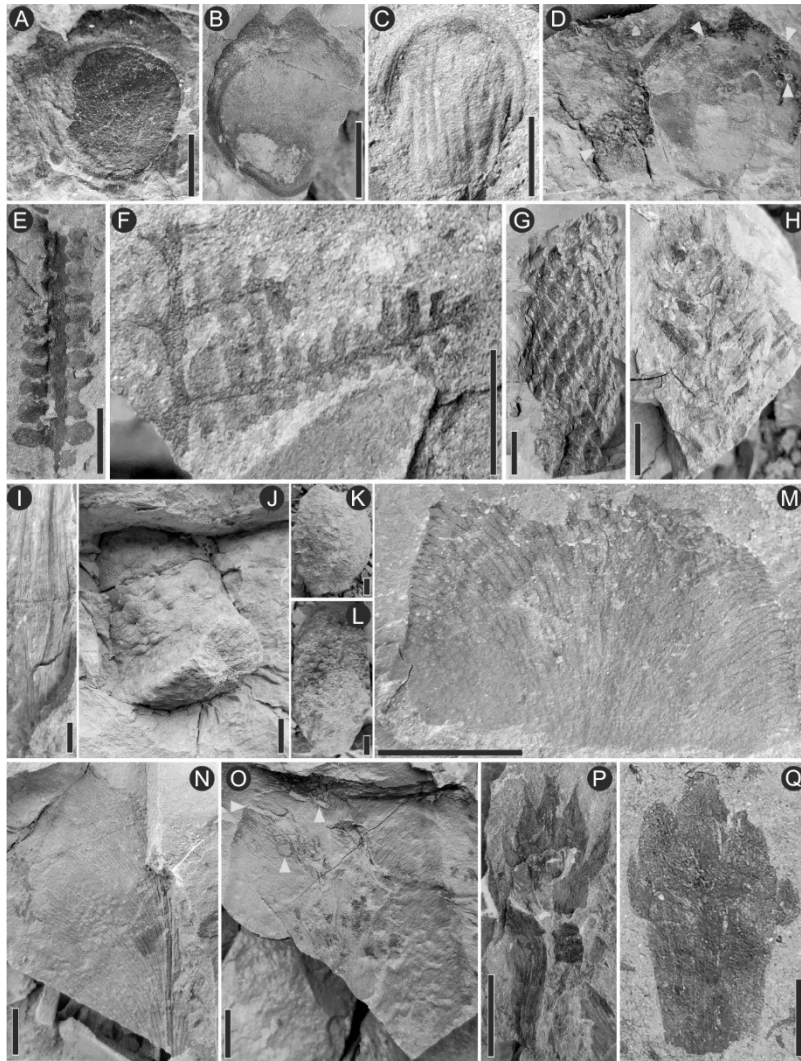
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1226 Figure 6

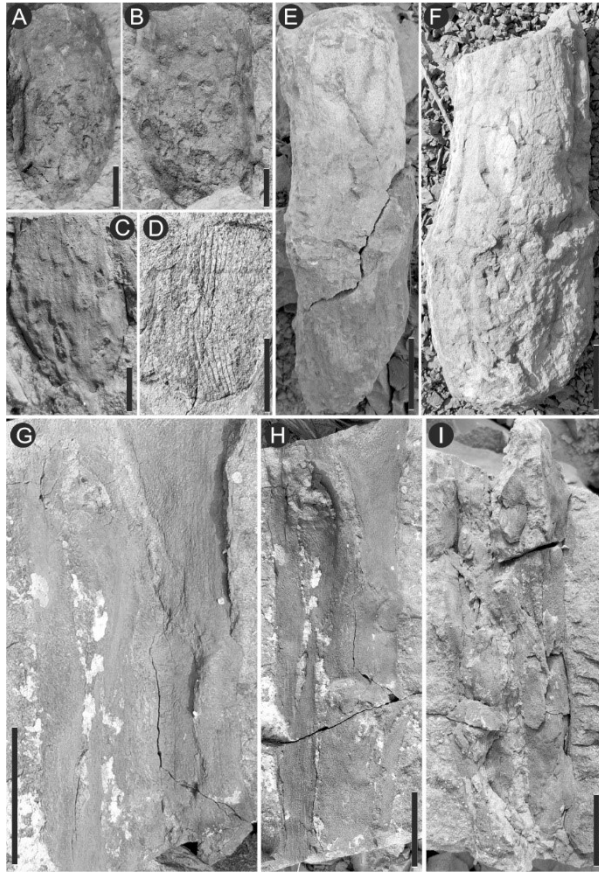
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1229 Figure 7

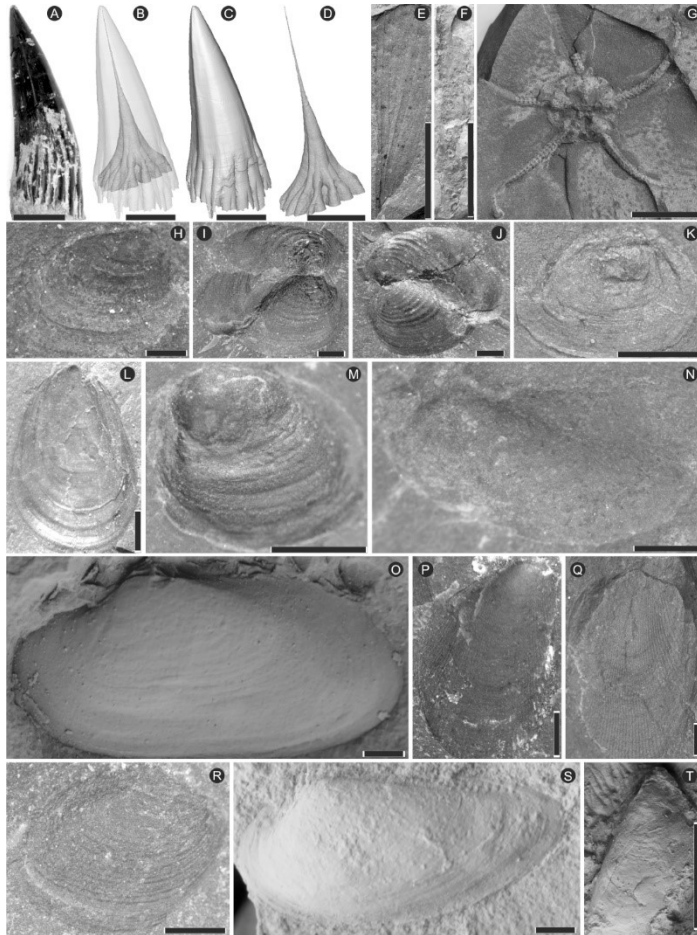
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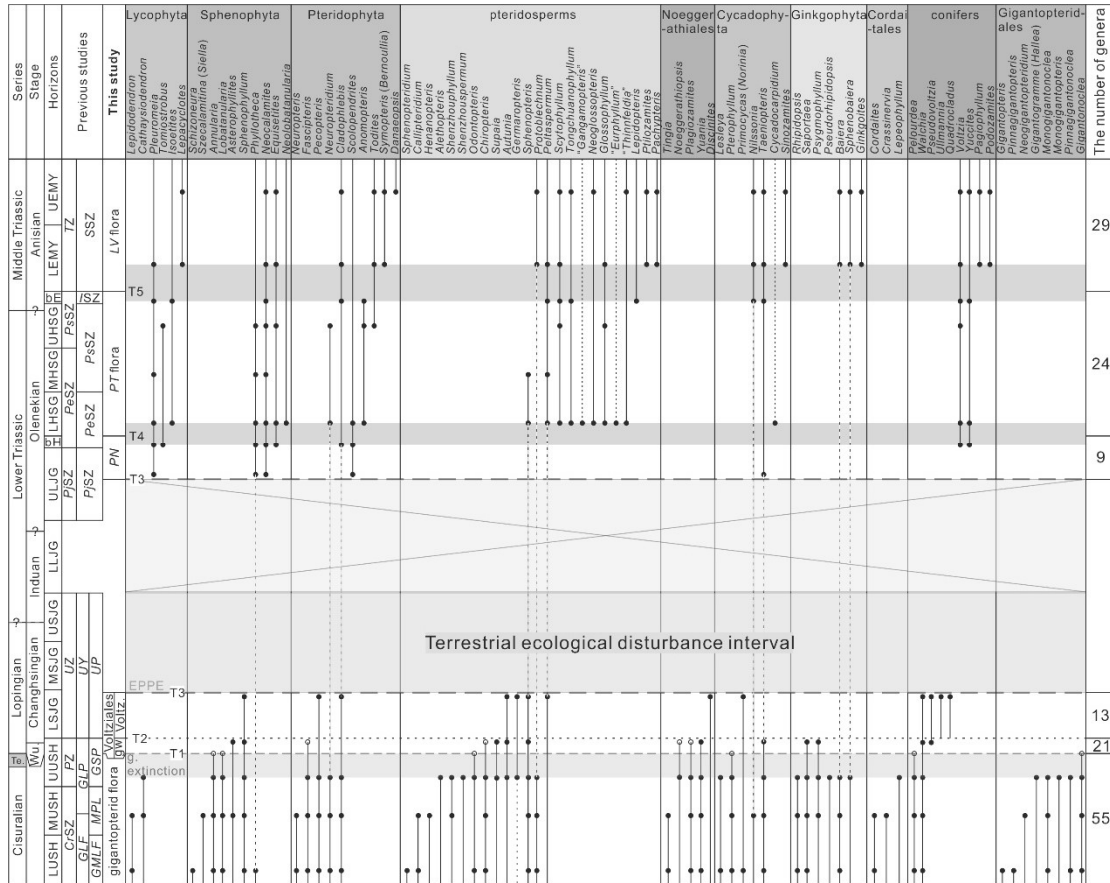
1232 Figure 8

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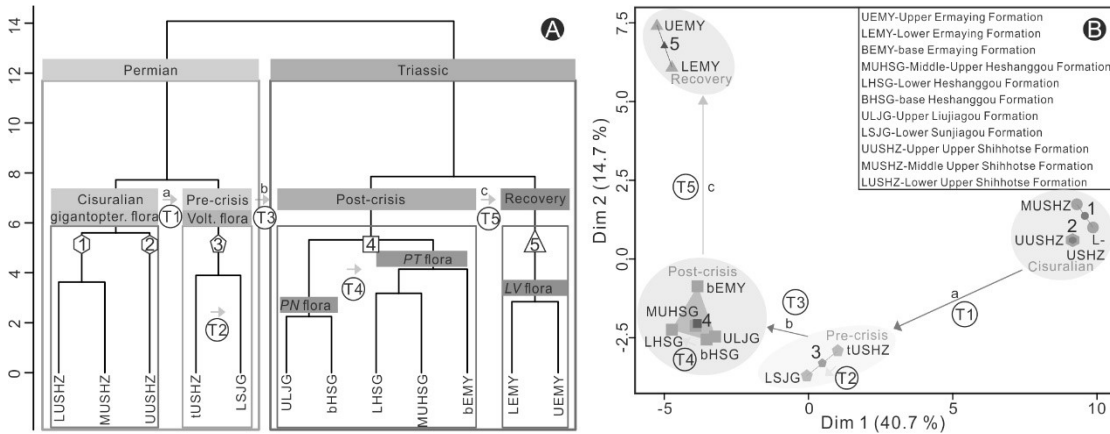
1235 Figure 9



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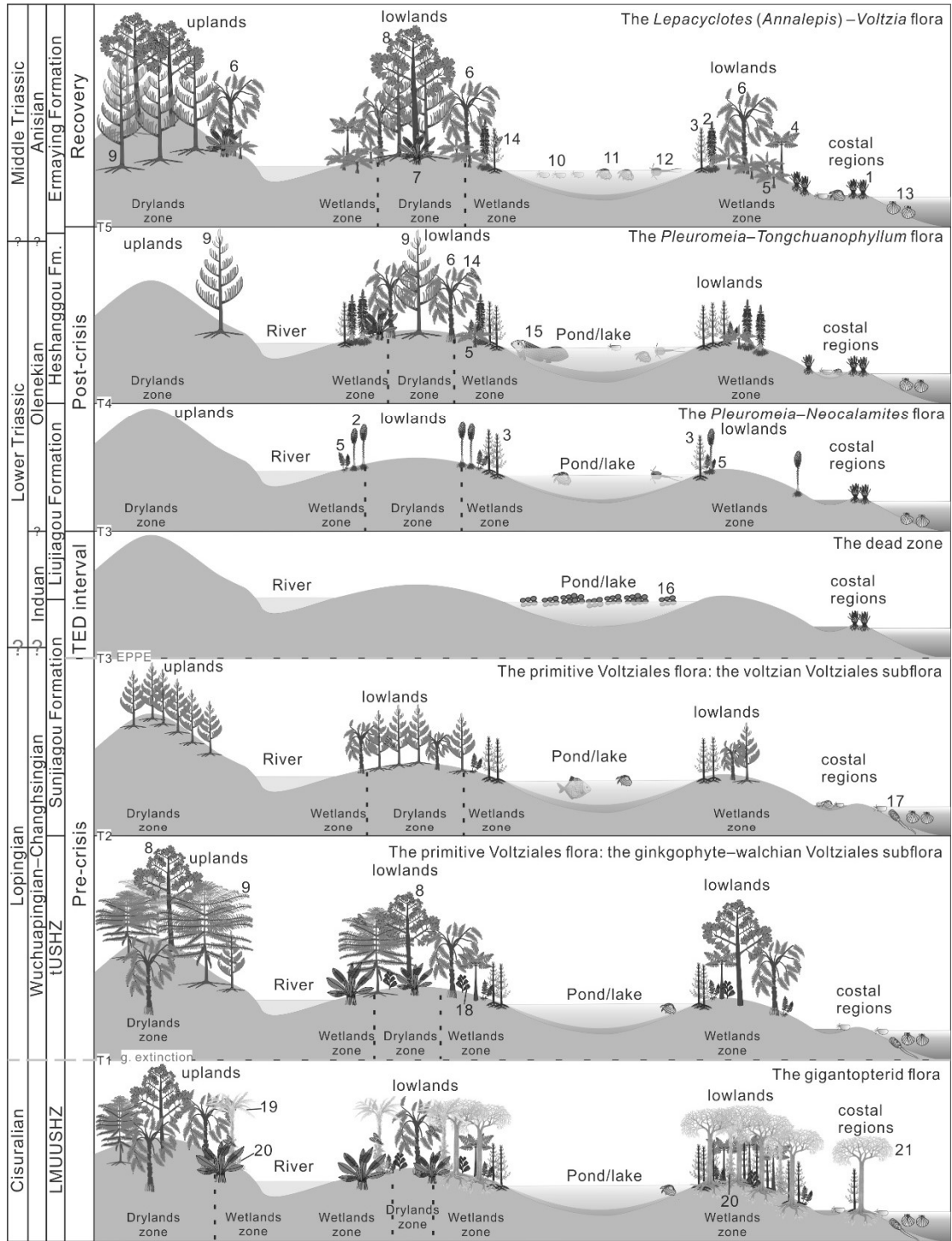
1237 Figure 10

1238



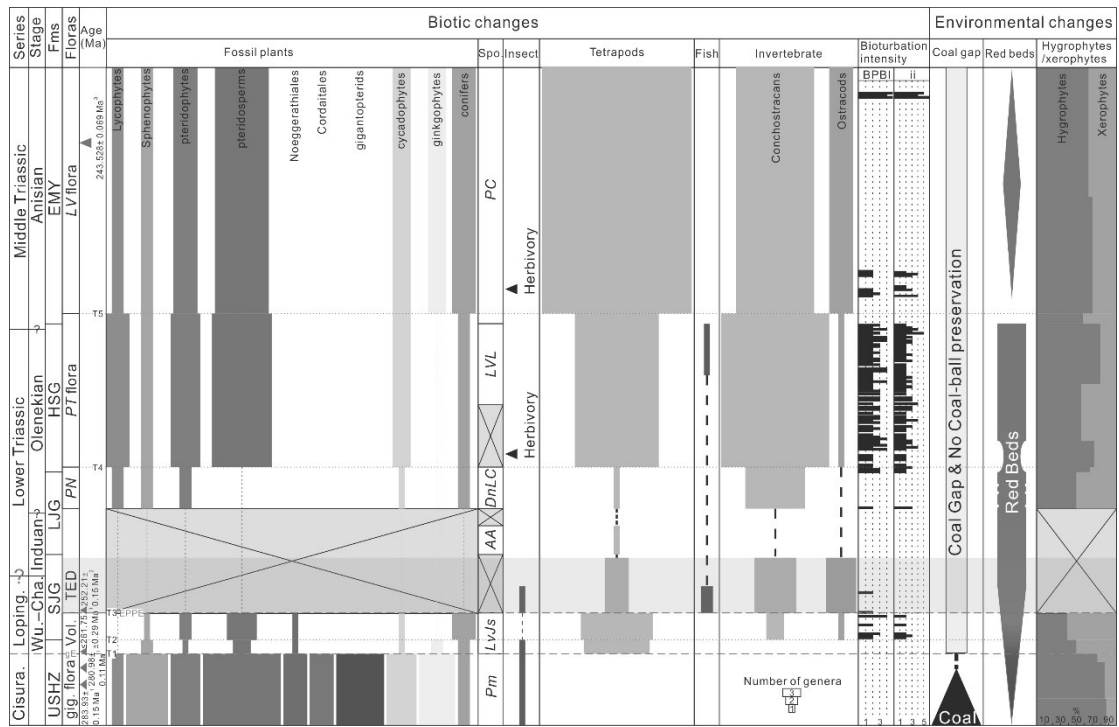
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1240 Figure 11



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1242 Figure 12



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1244 Figure 13

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