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Diversity dynamics of Devonian terrestrial palynofloras from China: Regional and global significance

3

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15

16 **Abstract**

17

18 The microfossil-based pattern of the Devonian land plants of China is revised and discussed based
19 on a newly comprehensive dataset. Such dataset compiles the chronostratigraphical distribution of
20 1677 species belonging to 190 genera of spores and pollen from the primary literature, which
21 recovers the fossil history of Chinese terrestrial palynofloras. From this, we describe the patterns
22 and biodiversity dynamics using both range-based and occurrence-based data to illustrate the main
23 fluctuations of Devonian taxonomic richness, including rarefaction for filtering out uneven
24 sampling. Results show that the apparent terrestrial palynofloral diversity of China increases

25 progressively from the early to mid-Devonian, with a genuine Givetian peak followed by a plateau
26 persisting during the Late Devonian. Results further suggest that sampling effects may strongly
27 influence the perception of biodiversity trends of China, as well as that the observed Late
28 Devonian taxonomic diversification may have been greatly overestimated. Compiled evidence is
29 discussed on the light of the global evolution of marine-terrestrial ecosystems. We hypothesize
30 that the rise of Devonian floras may have played a remarkable role in an oceanic oxygenation
31 event during this Period.

32

33 **Keywords:** Miospores, Palaeobiodiversity, China, Devonian, Climate change

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36 **1. Introduction**

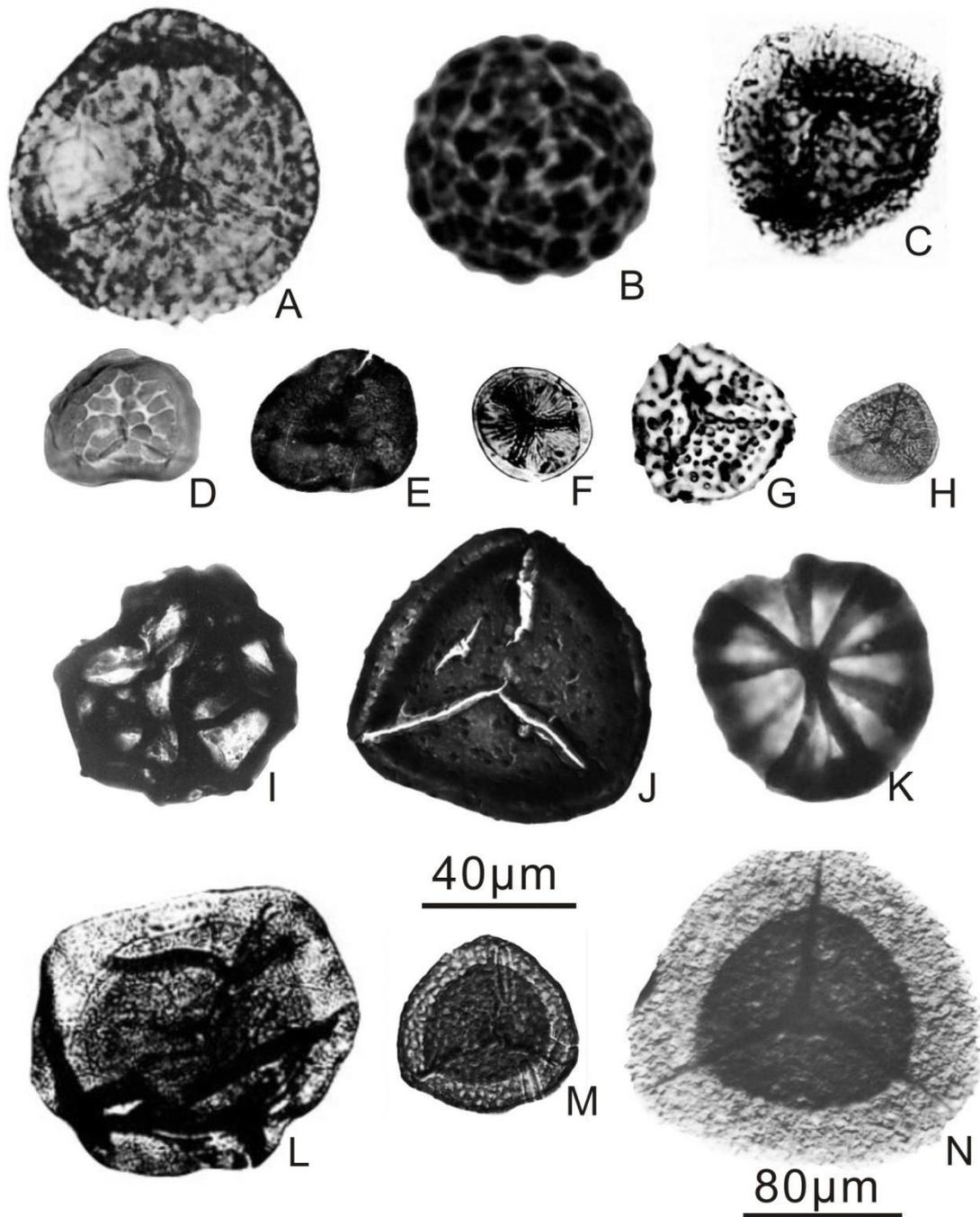
37

38 The approximately 60 million years long Devonian Period is characterized by
39 major changes in both terrestrial and marine biospheres ([Algeo and Scheckler, 1998](#);
40 [Cohen et al., 2013](#)). Such changes were triggered possibly by the appearance and the
41 diversification of earliest forests, which has been considered as the ‘greening of Earth
42 surface’ ([Giesen and Berry, 2013](#)), and by the blooms of nektonic animals (e.g. free-
43 swimming cephalopods) in the oceans, which have been related to the ‘mid-
44 Palaeozoic predator revolution’ ([Signor and Brett, 1984](#); [Brett, 2003](#)) or the
45 ‘Devonian Nekton Revolution’ ([Klug et al., 2010](#)).

46 The Devonian Period was also crucial time of plant evolution, with plant
47 palynomorph diversities (see e.g. [Fig. 1](#)) increasing steadily during the entire
48 Devonian (see e.g. [Traverse, 2007](#) and references therein). The land plant
49 microfossils, which are much more abundant and widespread than land plant

50 megafossils, are generally found not only in terrestrial deposits but also in near shore
51 marine strata, and there, mixed with other palynomorphs and also with marine
52 macrofossils, allowing accurate dating (e.g. [Streel et al., 2000](#)). This evidence has
53 proven to be extremely useful in solving palaeogeographical, palaeoenvironmental,
54 and biostratigraphical questions, particularly in Palaeozoic strata (e.g. [Streel et al.,](#)
55 [2000](#)).

56



57

58 **Fig. 1** Photomicrographs of some Devonian spores. Magnification for (A)–(M) indicated by scale

59 bar under 40µm, and the (N) indicated by scale bar under 80µm. **A**, *Cymbosporites magnificus*

60 (McGregor) McGregor and Camfield, 1982, Givetian to Frasnian. **B**, *Verrucosporites nitidus*

61 Playford, 1964, Famennian. **C**, *Cristatisporites triangulates* (Allen) McGregor and Camfield,

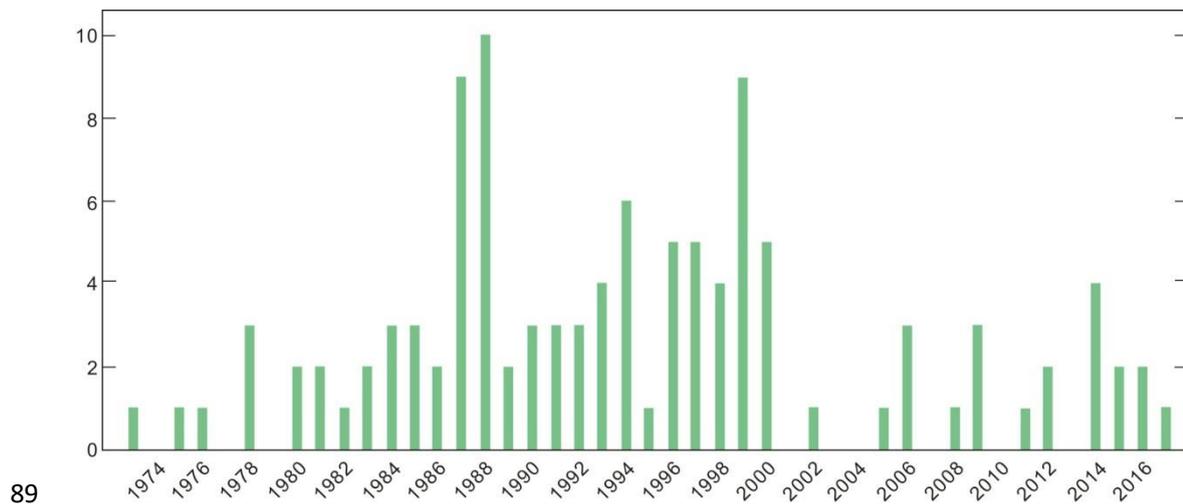
62 1982, Famennian. **D**, *Clivosispora verrucata* McGregor, 1973, Pragian to Emsian. **E**,

63 *Apiculiretusispora plicata* (Allen) Streel, 1967, Emsian. **F**, *Emphanisporites epicautus* Richardson
64 and Lister, 1969, Lochkovian. **G**, *Streelispora newportensis* (Chaloner and Streel) Richardson and
65 Lister, 1969, Lochkovian. **H**, *Rugospora flexuosa* (Juschko) Streel in Becker et al., 1974,
66 Famennian. **I**, *Knoxisporites literatus* (Waltz) Playford, 1963, Famennian. **J**, *Indotriradiates*
67 *explanatus* (Luber) Playford, 1991, Famennian. **K**, *Emphanisporites annulatus* McGregor, 1961,
68 Emsian. **L**, *Rhabdosporites langii* (Eisenack) Richardson, 1960, Eifelian/Givetian. **M**, *Retispora*
69 *lepidophyta* (Kedo) Playford, 1976, Famennian. **N**, *Grandispora velata* (Eisenack) Playford, 1971,
70 Eifelian. See Appendix B for the source of each image.

71

72 Although the first paper concerning palynology in China was already published in
73 the 1930s (Ding, 1938), more intense palynological investigations were not performed
74 before the 1950s (Hsü, 1950; Wang, 2009). Since then, especially after the early
75 1970s, more than 100 scientific articles dealing with Devonian palynomorphs in
76 China have been published. It should be noted that most results on Devonian
77 microfossils from China were published in Chinese, with only very few papers
78 submitted to international journals. The period between the 1970s to the 1990s was
79 the most active interval for Devonian palynological research in China (Fig. 2).
80 Although the taxonomic investigation and/or the biostratigraphical use of Devonian
81 palynolomorphs from China were extensively reported, very few studies summarized
82 systematically such records (e.g. Gao, 1981; Xiong et al., 2013; Ouyang et al., 2017).
83 In additions, discussions of the relationships between plant megafossil and/or
84 microfossil diversity trajectories as well as the biotic-abiotic factors remain rare. More

85 recently, a monograph on Late Palaeozoic spores and pollen from China has been
86 published by [Ouyang et al. \(2017\)](#). This latter work is a compilation of the taxonomic
87 information extracted from the literature and it provides an essential synthesis for
88 Upper Palaeozoic palynological research of China.



89
90 **Fig. 2** Publication rate of articles (between 1970 and 2017) used herein for the diversity analysis
91 of Devonian terrestrial palynofloras of China.

92

93 Although a number of papers have been published in recent years concerning the
94 plant diversity dynamics of Devonian megafossils and spores ([Knoll et al., 1984](#);
95 [Raymond and Metz, 1995](#); [Wang et al., 2010](#); [Gutak et al., 2011](#); [Xiong et al., 2013](#)),
96 there are only few studies that have corrected the effects of sampling bias.
97 Furthermore, a debate of the evolution of Devonian terrestrial biodiversities is still
98 ongoing (see e.g. [Cascales-Miñana, 2016](#), references included).

99 In addition to a detailed overview on the progress of Chinese studies on Devonian
100 terrestrial palynofloras, the present work is mainly focused on the plant microfossil-
101 based diversity patterns via a sample-based rarefaction analysis. The new compilation

102 of terrestrial palynofloras presented herein, contains all spore and pollen data recorded
103 between the latest Silurian and the earliest Carboniferous from different regions of
104 China. This survey has yielded an inventory of 84 selected publications that
105 demonstrated sufficient chronostratigraphical information to calibrate the occurrences
106 of terrestrial palynofloral at the stage level, in order to identify the main biodiversity
107 changes and outline their interactions with biotic and abiotic factors.

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109 **2. The latest Silurian–earliest Carboniferous terrestrial palynofloras of China**

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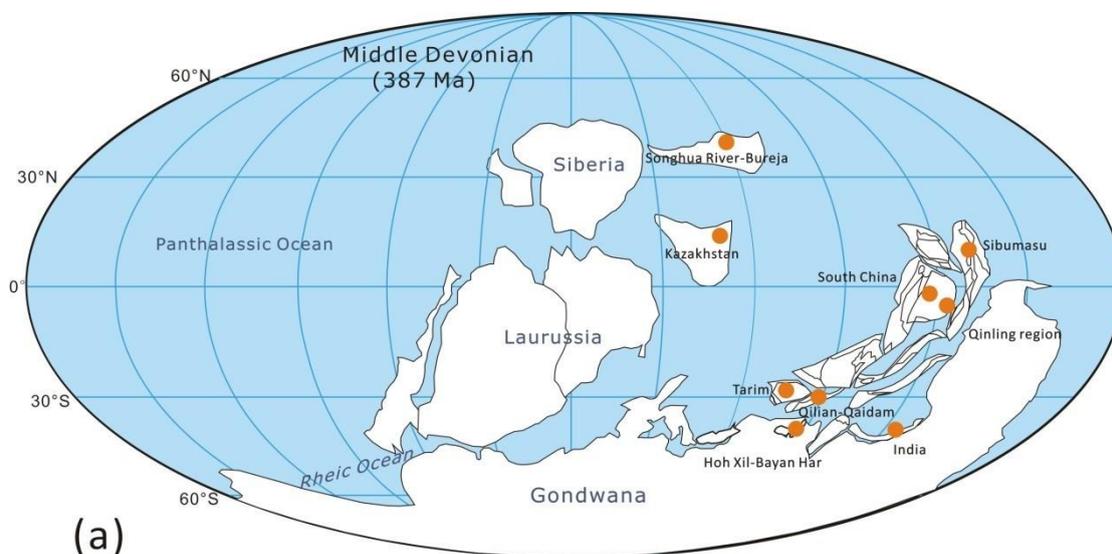
111 Currently, China is an amalgam of terranes ([Fig. 3a](#)) that during the Devonian
112 were spreaded across the Palaeo-Asian Ocean, including a series of volcanic arcs that
113 were intermittently linked through Siberia and Kazakhstan ([Xiao and Santosh, 2014](#)).
114 Many Devonian outcrops are widely exposed in South China, NW China, and NE
115 China, but not in the North China Platform that was uplifted between the Middle
116 Ordovician and the Early Carboniferous, with only scattered marine records in its
117 southern margin ([Ma et al., 2009](#)). On the basis of tectonic, stratigraphical and
118 palaeontological informations, the following regions of China can be recognized
119 during the Devonian ([Fig. 3b](#); [Liao and Ruan, 2003](#)) : (1) Junggar region (Kazakhstan
120 plate), (2) Hinggan region (Songhua River-Bureja plate), (3) Tarim region (Tarim
121 plate), (4) Qilian-Qaidam region (Qilian-Qaidam plate), (5) Qinling region, (6) South
122 China region (South China plate), (7) Western Yunnan region (Sibumasu plate) and
123 (8) Himalaya region (India plate). From all these areas, South China has provided the

124 large majority of published studies on Devonian palynomorphs (Appendix A).

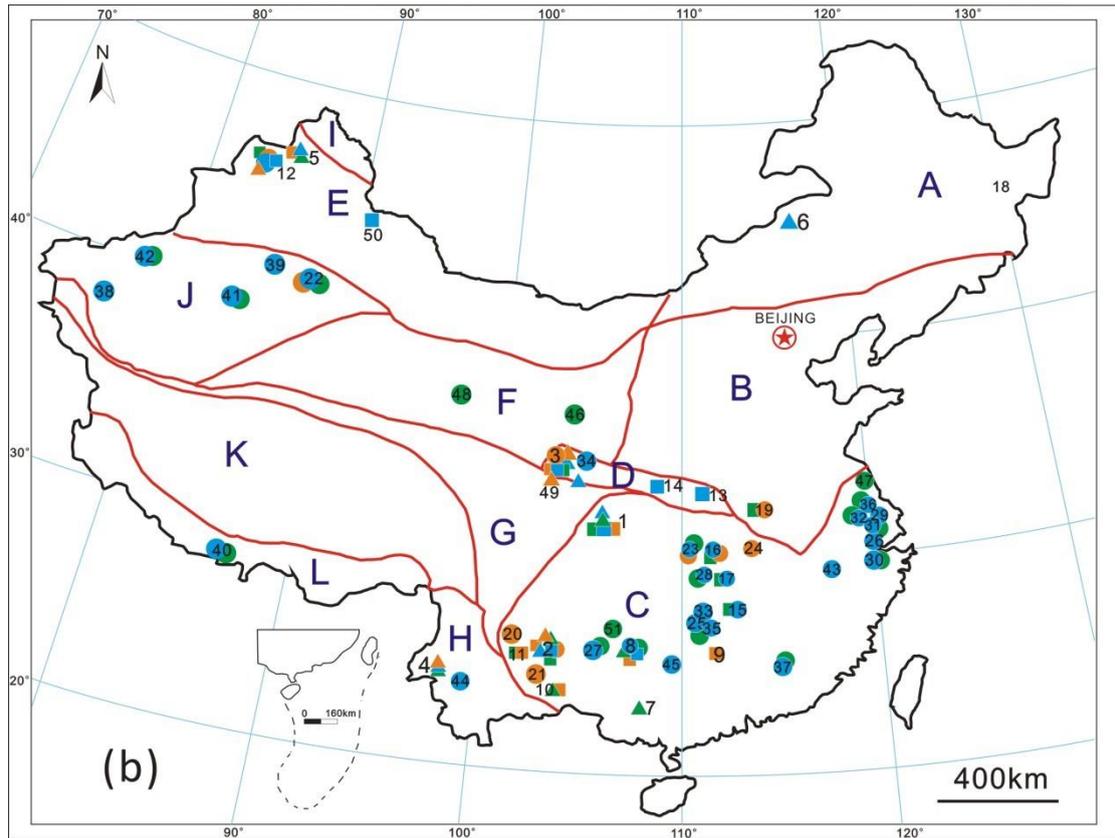
125 **Figure 4** depicts the Devonian stratigraphical framework of selected areas of
126 China. In addition to the 84 references (**Fig. 5**) used for the miospore diversity
127 analysis, other references without detailed statistical significance are also listed in the
128 present study. These publications provide a mass of supplementary information, from
129 numerous additional fossil localities (**Bharadwoj et al., 1973; Lu, 1980b, 1994b; Gao,**
130 **1981, 1987, 1988c, 1988d, 1988e, 1989b, 1991b, 1991c, 1999b; Ye, 1986; Gao and**
131 **Liu, 1988; Ouyang and Chen, 1989; Pei, 1992; Zhu and Zhan, 1996; Zhu and Zhao,**
132 **1998; Zhu et al., 1999; Ouyang, 2000; Su and Huang, 2000; Wang, 2001; Zhang,**
133 **2006; Zhu et al., 2015).**

134

135



136



137

138 **Fig. 3 (a)** Devonian palaeogeographical map (modified from [Boucot et al., 2013](#)) showing the
 139 location of the plates where Chinese terrestrial palynofloras have been recorded. **(b)** Reported
 140 terrestrial palynofloral localities from the Pridolian to the Tournaisian on the map of China,
 141 superimposed by the palaeoplate boundaries (modified from [Ma et al., 2009](#)). **A:** Songhua River-
 142 Bureja plate; **B:** North China plate; **C:** South China plate; **D:** Qinling Region; **E:** Kazakhstan plate;
 143 **F:** Qilian-Qaidam plate; **G:** Hoh Xil-Bayan Har plate; **H:** Sibumasu plate; **I:** Siberia plate; **J:** Tarim
 144 plate; **K:** Tibet plate; **L:** India plate. Various symbols represent the stages from the Pridolian to the
 145 Tournaisian (see Appendix B for detail).

System	Series	Stage	South central Guangxi (7)	Eastern Yunnan (2)	South of Jiangsu (31)	Western Hubei, (16) Northwest Hunan(17)	Northern Zhejiang (30)	Southern Guizhou (8)	Western Yunnan (4)	Central Hunan (33)	Jiangxi (37)	Heilong-jiang (18)	Western Qinling (3,34)	Tarim, Xinjiang (38,42)	Junggar, Xinjiang (5,12)	Inner-Mongolia (6)	Nyalam, Tibet (40)	Series	Sichuan (1)
Ca.	Mi.	Tou.																	
Devonian	Upper	Fa.	Rongxian	Zhaijieshan	Leigutai	Tizikou	Xihu	Gelaohu	Dujiacun	Menggongao	Fanxia		Douhishan	Bachusike	Honggu	Angeeryinwulia	Zhangdong	Maoba	
		Fr.	Gubi	Yidade	Guanshan	Xiejingsi		Wangchengyao	Heyuan-zhai	Shaocong	Sanmentan		Caokuohai	Qizilafu	Zhulu	Cailun-guoshao		Shawozi	
	Middle	Gi.	Mintang	Shuangshuanghe	Yuntaiguan		Dushan	Malutang	Qiziqiao	Yunshan	Laotudingzi		Pulai	Shujiaba	Zhulu	Taerba-gete		Guanwushan	
		Ei.	Najiao	Chuan-dong			Bangzhai	Xibiantang	Banshan		Helial		Xiaowuna	Shujiaba	Hujiershan	Wenduer		Jinbaoshi	
Lower	Em.	Yujiang				Longdong-shui	Shujiaping	Yuankou				Lure	Dangduo	Chagan-shan	Wenduer		Yangmaba		
	Pr.	Nagaoling				Upper	Shabajiao					Gala	Man-geer	Wuereu	Aobaoting-hundi		Ertaiqi		
	Lo.	Lianhua-shan				Lower	Wangjiacun					Upper	Putonggou	Hebukesaler	Barun		Xiejawan		
Si.	Pri.																	Guixi	

146146

147 **Fig. 4** Devonian stratigraphical framework of selected section areas from China. The
 148 representative locality numbers are the same as used in Fig. 3b. Stratigraphical information from:
 149 South central Guangxi (Cheng and Hou, 2000; Pan et al., 1978); Eastern Yunnan (Xu and Gao,
 150 1991, 1994; Wang, 1994); South of Jiangsu (Cheng and Hou, 2000); Western Hubei and Northeast
 151 Hunan (Pan et al., 1978; Feng, 1984; Gao and Zhong, 1984); Western Zhejiang (Cheng and Hou,
 152 2000); Southern Guizhou (Pan et al., 1978; Gao and Hou, 1975); Western Yunnan (Gao, 1999a);
 153 Central Hunan (Wang, 1996; Geology and mineral bureau of Hunan, 1988); Jiangxi (Pan et al.,
 154 1978; Wen and Lu, 1993); Heilongjiang (Ouyang, 1984); Western Qinling (Cao et al., 1984; Su
 155 and Huang, 2000); Tarim, Xinjiang (Zhu, 1998; Zhu et al., 2000); Junggar, Xinjiang (Gong and
 156 Zong, 2015; Geology and mineral bureau of Xinjiang Uygur autonomous region, 1982); Inner
 157 Mongolia (Gao, 1996a); Nyalam, Tibet (Gao, 1983a, 1986); Longhuashan, Sichuan (Hou et al.,
 158 1988). Si.: Silurian; Pri.: Pridoli Series (Pridolian stage).

159159

160160

161 2.1. Pridoli (Late Silurian)

162162

163 Six papers concern spore taxa from the Pridolian stage (latest Silurian Pridoli

164 Series) (Gao, 1993, 1996b; Gao and Ye, 1987; Fang et al., 1994; Tian and Zhu, 2009;

165 Tian et al., 2011). In Junggar, Gao (1993) reported Late Silurian–Early Devonian
166 miospores, together with few acritarchs and chitinozoans from the Shaerbuerti
167 mountain, Western Junggar (Fig. 3b, location 12). Four miospore zones were
168 established on the basis of the distribution regularities and evolutionary features. In
169 ascending order, they are *Synorisporites dittonensis*–*Apiculiretusispora spicula* (DS);
170 *Emphanisporites micronatus*–*Streelispora newportensis* (MN); *Chelinospora*
171 *cassicula*–*Perotriletes subitus* (CS); *Grandispora sp.*–*Apiculatasporites microconus*
172 (CM), the Silurian-Devonian boundary (SDB) being placed between the DS and MN
173 miospore zones. In western Yunnan, Gao (1996b) described sixty-five spore and
174 acritarch species from Silurian–Early Devonian levels from the Niushiping,
175 Xiangyangsi, and Wangjiacun formations in Shidian, west Yunnan (Fig. 3b, location
176 4). Three spore assemblage zones were established in ascending order:
177 *Apiculiretusispora spicula*–*Emphanisporites neglectus* (SN, Late Silurian),
178 *Synorisporites verrucatus*–*Streelispora newportensis* (VN, Early Devonian), and
179 *Breconisporites breconensis*–*Cymbosporites dittonensis* (BD, Early Devonian). In
180 western Qinling, Gao and Ye (1987) documented the first time the spore assemblages
181 from the Late Silurian-Devonian time interval, including 47 spore genera and a few
182 acritarchs and scolecodonts from Diebu, Gansu and Ruoergai, Sichuan. In eastern
183 Yunnan (Fig. 3b, location 2), Fang et al. (1994) identified some spore taxa from the
184 Yulongsi Formation and discussed the geological age of this formation from Qujing,
185 Yunnan. The authors argued that the SDB should be at the top of the Yulongsi
186 Formation or at the base of the Xiaxishancun Formation. Subsequently, Tian and Zhu

187 (2009) and Tian et al. (2011) reported the new discoveries of the Late Silurian–Middle
188 Devonian interval from eastern Yunnan. Four spore assemblage zones from the Late
189 Silurian to the Early Devonian were proposed in ascending stratigraphical order:
190 *Ambitisporites dilutus*–*Apiculiretusispora synorea* (DS; late Ludfordian to early
191 Pridolian); *Synorisporites verrucatus*–*Apiculiretusispora plicata* (VP; Pridolian);
192 *Apiculiretusispora minuta*–*Leiotriletes ornatus* (MO; Lochkovian), and
193 *Verrucosisporites polygonalis*–*Dibolisporites wetteldorfensis* (PW; Pragian) (Tian et
194 al., 2011).

195

196 2.2. Early Devonian

197

198 There are a total of 22 papers discussing Early Devonian spores from China (e.g.
199 Gao and Hou, 1975; Lu and Ouyang, 1976; Gao, 1978, 1983b, 1984, 1988a, 1993,
200 1996a, 1996b, 1997; Pan et al., 1978; Lu, 1980a; Gao and Ye, 1987; Gao and Wang,
201 1990; Fang et al., 1994; Wang, 1994; Tian and Zhu, 2005, 2009; Huang, 2009; Tian et
202 al., 2011; Wellman et al., 2012; Huang et al., 2016). The records that have been
203 mentioned above are no longer discussed in detail in the following paragraphs.

204

205 2.2.1. South China region

206 A total of 17 publications deal with Early Devonian miospore assemblages. The
207 research area concentrates on the Guizhou, Yunnan, Guangxi, Sichuan, and Hunan
208 provinces. In Guizhou, two papers were published: Gao and Hou (1975) and Gao
209 (1983b) studied the Lower to the Middle Devonian spore assemblages from southern

210 Guizhou (Fig. 3b, locations 8 and 27), and distinguished four assemblage zones. As a
211 result, the Danlin Formation was considered Pragian-Emsian in age, and the
212 Longdongshui Formation was attributed to the early Middle Devonian.

213 The Lower Devonian strata of eastern Yunnan have received wide attention for
214 their non-marine to marine sediments. The studied strata dealing with Lower
215 Devonian spore assemblages are as follows: Xujiachong Formation (Lu and Ouyang,
216 1976; Lu, 1980a; Gao, 1983b; Wellman et al., 2012), Cuifengshan Group (Pan et al.,
217 1978), Guijiatun Formation (Gao, 1984), Xiaxishancun Formation (Fang et al., 1994;
218 Gao, 1983b), and Pojiao Formation (Gao, 1983b). Wang (1994) studied the spore taxa
219 from Wenshan, Yunnan (Fig. 3b, location 10) and established two palynomorph
220 assemblage zones in the Posongchong (Pragian) and Pojiao formations (Emsian), i.e.,
221 *Apiculiretusispora plicata*–*Dictyotriletes emsiensis* (PE), and *Dibolisporites*
222 *eifeliensis*–*Camarozonotriletes sextantii* (ES), respectively. Tian and Zhu (2005)
223 investigated the spore assemblages and the biozones from the Longhuashan
224 (Xujiachong), and Xichong formations in Qujing, Yunnan, with two spore assemblage
225 zones proposed in ascending order, i.e., *Retusotriletes rotundus*–*Apiculiretusispora*
226 *plicata* (RP; Longhuashan Formation), and *Archaeozonotriletes variabilis*–
227 *Cymbosporites magnificus* (VM; Xichong Formation). Tian and Zhu (2005) placed
228 the Longhuashan Formation between the middle Pragian and the lower Emsian, while
229 the upper member of the Xichong Formation was thought to belong to the late
230 Givetian to early Frasnian interval. Based on the dispersed spore assemblages
231 recovered from the Xujiachong Formation in Qujing, Yunnan, Wellman et al. (2012)

232 discussed the age, palaeoenvironment, as well as the biotas, and considered that the
233 assemblages approximately correspond to the early Pragian–Emsian *Verrucosisporites*
234 *polygonalis*–*Dictyotriletes emsiensis* assemblage zone of the Old Red Sandstone
235 continent and adjacent regions (Richardson and McGregor, 1986).

236 In the Longmenshan area, Sichuan (Fig. 3b, location 1), three studies have
237 mentioned Early Devonian spores. Gao (1988a) summarized the characteristics of a
238 total of 148 species (including 32 new species and seven new combinations) assigned
239 to 35 genera from the Pingyipu Group and the Bailiuping Formation. Huang (2009)
240 explored the spores records from the Lower Devonian Guixi Formation and suggested
241 that they might belong to the ‘Gedinnian’ establishing the *Acinosporites*
242 *acanthomammillatus*–*Dictyotriletes gorgoneus* (AG) Biozone. More recently, Huang
243 et al. (2016) investigated the spore assemblages from the Lower Devonian Guixi,
244 Muerchang, Guanyinmiao, Guanshanpo formations, and from the Middle Devonian
245 Jinboshi Formation, and established three spore assemblages in ascending order:
246 *Retusotriletes rotundus*–*Calamospora panacea* (RP; Lochkovian), *Synorisporites*
247 *downtoniensis*–*Verrucosisporites scurrus* (DS; Pragian–early Emsian), and
248 *Densosporites inaequus*–*Grandispora inculta* (II; Eifelian–early Givetian).

249 In addition to the areas discussed above, palynomorphs were also reported from
250 Hunan and Guangxi. In southern Hunan (Fig. 3b, location 9), Gao and Wang (1990)
251 examined the spore assemblages from the Lower Devonian Yuankou Formation, in
252 which 22 genera and 44 species and variations were figured in a stratigraphical
253 column. The authors believed that the age of the assemblage would be ‘Siegenian.’ In

254 Guangxi (Fig. 3b, location 7), Gao (1978) documented the spore assemblages and a
255 small number of acritarchs from Hengxian County, and compared the spore
256 composition to those of European and north African countries. Finally, Gao (1978)
257 determined the age of the spore assemblages based on other fossil groups, such as
258 brachiopods, coral reefs, and fish.

259259

260 2.2.2. Western Yunnan region

261 In western Yunnan (Fig. 3b, location 4), only a single report has been published by
262 Gao (1996b), who analyzed the spore assemblages of the Late Silurian to the Early
263 Devonian from Shidian County, and who established the *Apiculiretusispora spicula*–
264 *Emphanisporites neglectus* (SN), *Synorisporites verrucatus*–*Streelispora*
265 *newportensis* (VN), and *Breconisporites breconensis*–*Cymbosporites dittonensis* (BD)
266 zones from the Niushiping (Pridolian), Xiangyangsi (Lochkovian), and Wangjiacun
267 formations (?Pragian), respectively.

268

269 2.2.3. Junggar region

270 See above.

271

272 2.2.4. Hinggan region

273 Only a single paper has been published from this region. Gao (1996a) studied the
274 palynomorph assemblages including spores, acritarchs, and scolecodonts from the
275 Baruntehua Formation in Wuzhumunqi Qi, Inner Mongolia. He considered the
276 palynomorphs of the lower part of the Baruntehua Formation to be very similar to
277 those from the ‘Gedinnian’ of Europe and North America.

278

279 2.2.5. *Qinling region*

280 Gao and Ye (1987) described taxonomically the Early to Late Devonian
281 palynomorphs of the Dangduogou section of Diebu County (Fig. 3b, location 3) and
282 established six spore assemblage zones, in ascending order: *Streelispora*
283 *newportensis*–*Ambitisporites dilutus* (ND), *Reticulatisporites emsiensis*–*Clivosispora*
284 *verrucata* (EV), *Rhabdosporites langii*–*Grandispora velata* (LV), *Densosporites*
285 *devonicus*, and *Convolutispora crenata*, *Archaeozonotriletes* spp.

286286

287 2.3. *Middle Devonian*

288288

289 21 references so far have recovered spores of the Middle Devonian in China (e.g.
290 Gao and Hou, 1975; Lu and Ouyang, 1978; Lu, 1980a, 1988, 1997b; Gao, 1983b,
291 1989a; Gao and Zhong, 1984; Ouyang, 1984; Gao and Ye, 1987; Xu and Gao, 1991,
292 1994; Tian and Zhu, 2005, 2009; Gao et al., 2006, 2009; Zhu et al., 2008; Xu et al.,
293 2012, 2014; Huang et al., 2016; Marshall et al., 2017).

294

295 2.3.1. *South China region*

296 The research on spore taxa of the Middle Devonian in South China is mainly
297 concentrated in eastern Yunnan, from the counties of Luquan (Marshall et al., 2017)
298 and Zhanyi (Lu and Ouyang, 1978; Lu, 1988). In eastern Yunnan, Xu and Gao (1991,
299 1994) studied the miospores and megaspores and their stratigraphical significance of
300 the Middle and Late Devonian time interval, with four spore assemblage zones
301 established in ascending order: *Calyptosporites velatus*–*Rhabdosporites langii* (VL;
302 Chuandong Formation; Eifelian), *Archaeozonotriletes variabilis*–*Calyptosporites*

303 *proteus* (VP; Haikou Formation; Givetian), *Geminospora lemurata*–*Cristatisporites*
304 *triangulatus* (LT; Haikou Formation; Givetian), and *Archaeoperisaccus ovalis*–
305 *Lagebicula bullosum* (OB; Yidade Formation; Frasnian).

306 The Middle Devonian miospores are known also in other regions, for instance,
307 from the Hunan and Hubei provinces. The spore assemblages from the Yuntaiguan,
308 Huangjiadeng (Fig. 3b, locations 16 and 28), and Tizikou formations (Fig. 3b,
309 locations 16 and 28) were discussed by Gao and Zhong (1984) and Gao (1989a). The
310 Yuntaiguan Formation (Fig. 3b, location 16) was later attributed to the Givetian by
311 Gao (1989a).

312

313 2.3.2. *Qinling*

314 Only two papers have been published from this area. In addition to Gao and Ye
315 (1987) (see above), Gao et al. (2009) discussed the age of the spores that he collected
316 from the Sanhuashi and Xixiang groups, Shaanxi Province (Fig. 3b, location 14). The
317 fossil assemblages of possible Middle Devonian age can be roughly correlated with
318 the spores in regions of South China, Europe, and North America.

319319

320 2.3.3. *Junggar*

321 In addition to the literature mentioned above (e.g. Xu et al., 2014), Xu et al. (2012)
322 reported Middle Devonian megaspores collected from both northern Xinjiang (Fig.
323 3b, location 12) and eastern Yunnan (Fig. 3b, location 2) and discussed their
324 palaeogeographical and palaeoenvironmental significance. The discovery of
325 *Verrucisporites* in both northern Xinjiang and eastern Yunnan indicates that a

326 migration path may have been present for plants between South China and Laurasia.
327 By recording the newly collected 36 genera and 83 spore species from the Hujieersite
328 Formation in Hoboksar (see above), and from western Junggar, Xinjiang, [Lu \(1997b\)](#)
329 indicated that the spore assemblages belonged to Givetian. More recently, acritarch
330 and miospore assemblages from the Ulusubasite Formation (Eifelian) in eastern
331 Junggar ([Fig. 3b](#), locality 50) were described and their biostratigraphical and
332 palaeogeographical implications were discussed by [Zhu et al. \(2008\)](#).

333333

334 *2.3.4. Hinggan region*

335 [Ouyang \(1984\)](#) studied the spore microfloras collected from the upper part of the
336 Heitai Formation in Mishan County ([Fig. 3b](#), location 18), Heilongjiang, and
337 considered that the upper part of this formation belonged to the Givetian, while the
338 lower part might be Eifelian in age.

339339

340 *2.4. Late Devonian-Tournaisian (earliest Carboniferous)*

341341

342 The publications concerning the Late Devonian-Early Carboniferous interval are
343 the most abundant, accounting for more than half of the total of all investigations. 52
344 reports of Chinese terrestrial palynofloras have been published ([Lu, 1981, 1994a,](#)
345 [1995, 1997a, 1999; Hou, 1982; Gao, 1980, 1983a, 1985, 1988b, 1990a, 1990b, 1991a,](#)
346 [1992, 2015; Gao and Zhong, 1984; Liu and Gao, 1985; Chen and Ouyang, 1985,](#)
347 [1987; Gao and Ye, 1987; Li et al., 1987; Ouyang and Chen, 1987a, 1987b; Wang et](#)
348 [al., 1987; Yan, 1987; Yang, 1987; Cai et al., 1988; Lu and Wicander, 1988; Gao et al.,](#)
349 [1991; Xu and Gao, 1991, 1994; Gao and Ji, 1992; Yan, 1992; Fang et al., 1993; He](#)

350 and Ouyang, 1993; Wen and Lu, 1993; Gao and Zhan, 1994; Steemans et al., 1996;
351 Wang, 1996; Zhu, 1996, 1999a, 1999b, 2000; Zhu et al., 1998; Yang and Neves, 1997;
352 Gao and He, 1998; Zhu and Zhao, 1999; Yang, 1999; Zhu et al., 2000; Li, 2000;
353 Ouyang, 2003; Yang, 2003; Tian and Zhu, 2005; Gao et al., 2014; Xu et al., 2014).

354

355 2.4.1. South China

356 The large majority of the studies, with more than 50% of the literature on
357 Devonian land plant microfossils, are focused on the assemblages from South China.
358 In addition to the above-mentioned publications, that documented Lower and/or
359 Middle Devonian sections, other extended also into the Upper Devonian (Gao and
360 Zhong, 1984; Xu and Gao, 1991, 1994; Tian and Zhu, 2005; Xu et al., 2014), with a
361 total of more than thirty references reporting the Late Devonian–Early Carboniferous
362 palynofloras of South China.

363 In Jiangsu, the occurrences of spores (including miospores and megaspores) were
364 reported by Chen and Ouyang (1985, 1987) and Ouyang and Chen (1987a, 1987b).
365 Other papers covering the spores of this region include Yan (1987), Cai et al. (1988),
366 and Li et al. (1987). In the 1990s, Lu (1994a) studied the spore assemblages from the
367 Wutong Formation from Nanjing, Jiaingsu, and established four spore assemblage
368 zones, in ascending order: *Aneurospora asthenolabrata*–*Radiizonates longtanensis*
369 (AL; Famennian), *Retusotriletes*–*Cymbosporites* (RC; Famennian), *Knoxisporites*–
370 *Densosporites* (KD; Tournaisian), and *Leiotriletes crassus*–*Laevigatosporites vulgaris*
371 (CV; Tournaisian). It is important to note that Yang's (2003) paper was the first to
372 research the miospores from a borehole in the Lower Carboniferous from northern

373 Jiangsu (Fig. 3b, location 47), and that this area may have been at the junction of the
374 South China and North China plates.

375 In Zhejiang, He and Ouyang (1993) presented the spore floras from Devonian–
376 Carboniferous transitional beds of the Xihu Formation in Fuyang, Zhejiang, from
377 where two spore zones were built, in ascending order: *Retispora lepidophyta*–
378 *Apiculiretusispora hunanensis* (LH; Famennian), and *Dibolisporites distinctus*–
379 *Cordylosporites papillatus* (DP; Tournaisian). In addition, Yan (1992) introduced the
380 microfloras from the Tangjiawu Formation (Wenlockian) and Xihu Formation
381 (Famennian) in Zhejiang and their stratigraphical division and correlation. Recently,
382 the spore assemblage zones of the Lower Yangtze Valley area (including Anhui,
383 Jiangsu, and Zhejiang) were systematically investigated by Gao (2015). In ascending
384 order, they can be divided into the following zones: *Rugospora flexuosa*–*Grandispora*
385 *cornuta* (FC; Famennian), *Vallatisporites pusillites*–*Retispora lepidophyta* (PL;
386 Famennian), *Retispora lepidophyta*–*Verrucosisporites nitidus* (LN; Famennian),
387 *Vallatisporites verrucosus*–*Retusotriletes incohatus* (VI; Tournaisian), *Spelaeotriletes*
388 *pretiosus*–*Cingulizonates bialatus* (PB; Tournaisian), *Schopfites claviger*–
389 *Auroraspora macra* (LN; Tournaisian), and *Lycospora pusilla* (PU; Visean).

390 From the Hubei and Hunan provinces, a considerable amount of literature on the
391 palynofloral assemblages and biostratigraphy has been published (e.g. Hou, 1982; Liu
392 and Gao, 1985; Wang et al., 1987; Yang, 1987; Gao, 1990a; Fang et al., 1993; Wang,
393 1996; Lu, 1995, 1997a; Li, 2000). The pioneering work of the spore assemblages
394 from the Devonian-Carboniferous Boundary (DCB) of the Xikuangshan district in the

395 Hunan province was published by Hou (1982). Subsequently, Wang (1996) discussed
396 the DCB and spore floras from the Shaodong (Famennian) and Menggong'ao
397 formations (Famennian and Tournaisian) in Hunan, from where four spore assemblage
398 zones were established in ascending order: *Retispora lepidophyta*–*Apiculiretusispora*
399 *fruticosa*(LF), *Rugospora* cf. *flexuosa*–*Retispora lepidophyta* (FL),
400 *Lophozonotriletes excises*–*Retispora lepidophyta* (EL; Tournaisian), and *Crassispora*
401 cf. *kosankei*–*Lycospora denticulata* (KD; Tournaisian).

402 In Jiangxi, Wen and Lu (1993) examined the Devonian–Carboniferous miospore
403 assemblages from the Xiaomu section, Jiangxi. These authors established three spore
404 zones in ascending order: *Acanthotriletes denticulatus*–*Apiculiretusispora rarissima*
405 (DR; Sanmentan Formation; Famennian), *Leiotriletes macrothelis*–*Grandispora*
406 *xiamuensis* (MX; Fanxia Formation; Famennian), and *Apiculiretusispora tenera*–
407 *Lycospora* cf. *tenuispinosa* (TT; Huangtang Formation–Liujiatang Formation;
408 Tournaisian). In addition, similar reports have been published from other regions, for
409 instance Guangxi (Yang and Neves, 1997), Sichuan (Lu, 1981), and Guizhou (Gao,
410 1991a).

411

412 2.4.2. Western Yunnan

413 The miospore assemblages of western Yunnan were roughly distinguished from
414 the uppermost Devonian and Lower Carboniferous sediments of Gengma County by
415 Yang (1999). In ascending order, they are the *Retispora lepidophyta*, *Grandispora*
416 *spiculifera*, and *Lycospora pusilla* zones.

417417

418 2.4.3. *Tarim*

419 The majority of the terrestrial palynofloras from the Late Devonian and earliest
420 Carboniferous from Tarim were studied by Huaicheng Zhu and his colleagues. The
421 reported strata encompass the Qizilafu (Famennian) and Bachu formations
422 (Famennian) in the southern Tarim Basin (Fig. 3b, location 38) (Gao and Zhan, 1994;
423 Zhu, 1996, 1999b; Zhu et al., 2000), the Bacan borehole 1 from Bachu County in the
424 western Tarim Basin (Fig. 3b, location 42) (Gao and He, 1998), the Donghetang
425 Formation from the northern Tarim Basin (Fig. 3b, locations 22 and 39) (Zhu, 1999a,
426 2000), and the Bachu Formation of the central Tarim Basin (Fig. 3b, location 41) (Zhu
427 et al., 1998). Zhu and Zhao (1999) reported the progress of palynological studies of
428 the Devonian–Carboniferous in the Tarim Basin, and established seven spore
429 assemblage zones in ascending order: *Apiculiretusispora hunanensis*–*Ancyrospora*
430 *furcula* (HF; Famennian), *Cymbosporites* spp.–*Retusotriletes incohatus* (SI;
431 Tournaisian), *Verrucosisporites nitidus*–*Dibolisporites distinctus* (ND; Tournaisian),
432 *Spelaeotriletes balteatus*–*Rugospora polyptycha* (BP; Tournaisian), *Lycospora*–
433 *Grumosisporites* (LG; Viséan), *Cyclogranisporites pressoides*–*Florinites* spp. (PS;
434 Viséan), and *Schulzospora campyloptera*–*Schulzospora ocellata* (CO; Viséan–
435 Namurian).

436436

437 2.4.4. *Qinling*

438 The terrestrial palynofloras from this region remain poorly known compared to
439 other regions. In addition to Gao and Ye's (1987) study mentioned above, Gao
440 (1990b) described the palynomorphs (including spore assemblages, a small number of

441 acritarchs and scolecodonts) from the Wangjiadian Formation in Zhangxian, Gansu
442 (Fig. 3b, location 32), with two spore assemblage zones established, in ascending
443 order: *Retispora lepidophyta*–*Knoxisporites literatus* (LL; Famennian), and *Retispora*
444 *lepidophyta*–*Hymenozonotriletes explanatus* (LE; Famennian).

445445

446 2.4.5. Junggar

447 In addition to Xu et al. (2014), Lu and Wicander (1988) recovered diverse
448 palynofloras containing the spores and acritarchs from the Upper Devonian
449 Hongguleleng Formation, Hefeng District (Fig. 3b, location 12), Xinjiang.
450 Subsequently, Lu (1999) systematically described the diverse material from the
451 Heishantou Formation and discussed the DCB of this area. The monograph published
452 by Ouyang (2003) included numerous plates of the Carboniferous–Permian plant
453 microfossils from northern Xinjiang, that are of great value for the understanding of
454 plant microfossil evolution during this period.

455455

456 2.4.6. Himalaya

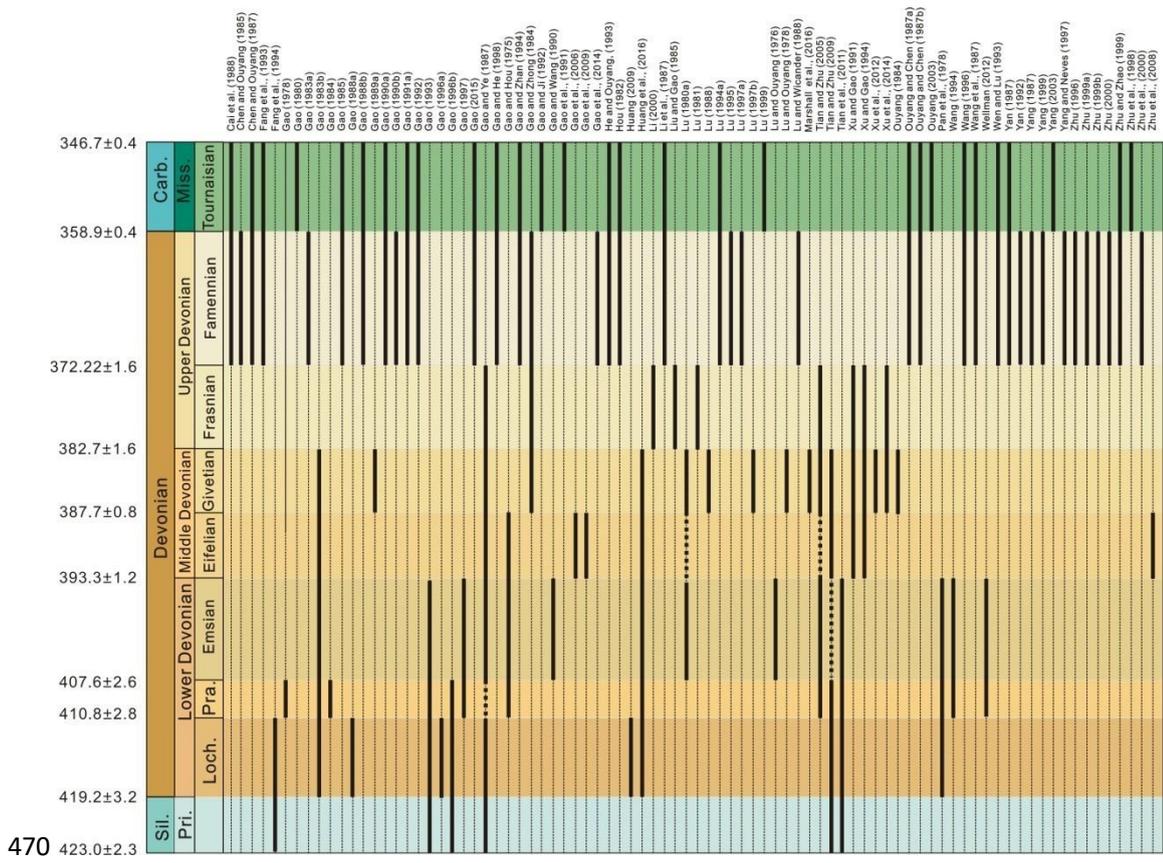
457 Gao (1983a, 1988b) investigated the Late Devonian spores and the DCB of
458 Nyalam (Fig. 3b, location 40) in Tibet, and attributed the upper strata of the Boqu
459 Group to the Late Devonian (Famennian). Moreover, a small number of acritarchs and
460 scolecodonts have also been described.

461461

462 2.4.7. Qilian–Qaidam Region

463 On the basis of the samples collected from the Qianheishan Formation
464 (Tournaisian) of Jingyuan (Fig. 3b, location 46), Gansu, Gao (1980) described the

465 spore assemblages including 33 genera and 69 species, that include 14 new species
 466 and 14 new combinations. In the 1990s, [Gao and Ji \(1992\)](#) reported the palynomorphs
 467 from the Chuanshan (early Tournaisian) and the Qianggou Formation (middle to late
 468 Tournaisian) and considered that they could be correlated with palynomorphs of
 469 western Europe, Russia, North America, and other regions.



471 **Fig. 5.** Devonian stratigraphical scheme and stratigraphical ranges of palynological studies in
 472 China used for the diversity analyses. Chronostratigraphy according to [Cohen et al., 2013](#),
 473 updated. Carb.= Carboniferous. Loch.= Lochkovian. Miss.= Mississippian. Pri.= Pridoli. Pro.=
 474 Pragian. Sil.= Silurian.

475475

476 **3. New microfossil-based database of the Devonian plant diversity of China**
 477477

478 A comprehensive database (Appendix C) of the Pridolian-Tournaisian time
479 interval of all terrestrial palynofloral occurrences of China is presented here.
480 Taxonomic information in the database includes the genus name, species epithet,
481 qualifiers of open nomenclature (such as '?', 'cf.', 'aff.'), and locality. The time
482 calibration of the stages used for the biodiversity analysis is based on the framework
483 established by [Cohen et al. \(2013, updated\)](#). Concerning data include plant
484 microfossils recorded in different regions of China, including South China, Hinggan,
485 Qinling, Junggar, Qilian-Qaidam, Western Yunnan, Tarim, and Himalaya region ([Fig.](#)
486 [3b](#)). The Devonian palynological researchers in China have generally correlated their
487 spore assemblages with each other and with those in Europe and North America;
488 hence in the present study, the original biostratigraphical data ([Fig. 4](#)) are used for the
489 database. Some species names in the original publications were harmonized to remove
490 nomenclatural errors that might impede accurate measures of spore species-level
491 diversity. For example, spelling mistakes in the original literature have been corrected,
492 such as *Triletes langii*, that is here attributed to *Rhabdosporites langii* (see [Xu and](#)
493 [Gao, 1994](#)). The final database contains 1677 species belonging to 190 genera from
494 China. It is worth pointing out that most of the records in the Devonian database from
495 China are concentrated in the South China plate, comprising 1285 species belonging to
496 175 genera. The studies from other regions, such as those from Western Yunnan and
497 Hinggan, are still relatively sparse.

498498

499 **4 Processing methods**

500500

501 We have measured the diversity changes over time using both range-based data,
502 which simply record the synthetic presence (incidence) of each taxon through the
503 successive ordered chronostratigraphical units (i.e. a range chart), and sample-based
504 data, which, are an exhaustive record of all taxa within all samples/beds/collections of
505 the studied time interval. Various methods therefore have been developed (for both
506 these range-based and sample-based data) to overcome or compensate for these
507 biases. Nowadays, the sample-based estimators are preferred to range-based
508 estimators for palaeobiodiversity analyses, because they allow correcting (at least
509 partly) the predominant and unavoidable sampling bias by means of resampling
510 (rarefaction) methods. Data analysis is run at the species and genus ranks. Such
511 analysis is computed at the chronostratigraphical rank of the Devonian stages ([Cohen
512 et al. 2013](#), updated) and was performed by using the free, popular, scientific
513 environment R ([R Core Team 2018](#)) version 3.3.3 and with the package ‘ePaleo’
514 (Monnet C, unpublished, University of Lille; for applications using this package, see
515 [Nowak et al. 2015](#), [Amberg et al. 2016](#), or [Tetard et al. 2017](#)) version 0.7.37. Size-
516 based rarefaction was computed with Palaeontological Statistics (PAST) v.3.06
517 ([Hammer et al., 2001](#)).

518 The total number of taxa of a given rank of a fossil group known from each of
519 several successive intervals of geological time is commonly used as a measure of the
520 relative taxonomic diversity of the group during the respective time intervals ([Raup,
521 1972](#); [Sepkoski, 1975](#)). On the basis of synthetic range data, taxa are regarded as

522 present in a stratigraphical interval in one of four possible mutually exclusive,
523 fundamental classes (Foote, 2000; Alroy, 2010): as crossovers ranging throughout the
524 entire interval (sampled or not in it); ranging into and going extinct in that interval
525 (bottom boundary crossers); originating within the interval and ranging beyond its
526 upper boundary (top boundary crossers); and as single-interval, with a range confined
527 to an interval, meaning that they originate and go extinct within the interval.

528 Then again, depending on the relative weights according to each class of range
529 with regard to their occurrence in and around a stratigraphical interval, several
530 taxonomic richness indices can be calculated (Fig. 6). 1) The sampled-in-bin diversity
531 (D_{sib}) is the most straightforward index by providing the total count of taxa actually
532 documented from a given stratigraphical interval, but it commonly underestimates
533 diversity due to the incompleteness of the fossil record and sampling bias. 2) The
534 range-through or total diversity (D_{rt} : rang-through diversity; Appendix D) is the most
535 traditional approach by counting all actual and inferred occurrences of the considered
536 stratigraphical bin. 3) The single-interval diversity (D_{sgl}) counts the taxa documented
537 in a single bin. 4) The crossover diversity (D_{over}), in contrast to the single-interval
538 diversity, counts taxa that are documented both before and after the considered
539 stratigraphical interval and can be considered to roughly represent the diversity of
540 long-ranging taxa. 5) The normalized diversity (D_{norm}) is considered a good
541 approximation of the mean standing diversity in a stratigraphical bin (Cooper, 2004)
542 by summing the taxa ranging from the interval below to the interval above, plus half
543 the number of taxa originating and/or becoming extinct within the interval, plus half

544 of those that are confined to the interval itself ([Sepkoski, 1975](#)). 6) The estimated
545 mean standing diversity (D_{emsd}) is similar to D_{norm} , except that this method excludes
546 the count of single-interval taxa (see [Cooper, 2004](#)). 7) Finally, the boundary crosser
547 diversity (D_{btr}) is also calculated.

548 It is now well-known that the number of recovered taxa within samples highly
549 depends on the number of collected individuals leading to the sampling bias. Unequal
550 sample sizes can lead to an effect similar to unequal time intervals: the more sampled
551 the interval, the higher the diversity (everything else being equal). In order to partly
552 overcome the biases of sampling and binning and the pitfall of single-interval taxa,
553 some diversity indices focus only on the boundary crossers (see [Foote, 2000](#)). The
554 boundary crosser diversity straightforward counts the number of common taxa
555 between two successive stratigraphical intervals. Since several years, the
556 reconstruction of palaeobiodiversity trajectories emphasized the need to use sample-
557 based over range-based data. The former data enable using resampling techniques to
558 correct the overwhelming sampling bias. The classical approach to tackle the
559 sampling bias was to use rarefaction ([Hurlbert, 1971](#)) to subsample all of the samples
560 and calculate their richness at the same number of individuals (i.e. same sample size).
561 The sample-based rarefaction analysis ([Raup, 1975](#)) was considered to be one of the
562 best methods which have been used by many palaeontologists (e.g. [Miller and Foote,](#)
563 [1996](#); [Shen and Shi, 2002](#)). This method can compare the fossils of sampling size of
564 different intervals on the same scale. We used a series of species/genus rarefaction
565 analyses to evaluate the actual effects of sampling intensities in the different intervals,

566 and to verify the variation patterns of Devonian terrestrial palynofloral diversity
567 dynamics of China and South China. The database of the plant microfossils contains
568 190 genera, 4568 occurrences in China, and 175 genera, 3363 occurrences in South
569 China, respectively. The Devonian diversity trajectories were recast based on
570 rarefaction estimates of genus richness for each time interval at a sample size of 230
571 and 120 genus occurrences from China (Fig. 7A) and South China databases (Fig.
572 7B).

573 Indices of origination and extinction represent, respectively, the number of
574 species/genera originating and becoming extinct in a stratigraphical interval. The
575 turnover in an interval is measured by the sum of origination and extinction values.
576 These indices of taxonomic change can be calculated as including or excluding
577 singletons, while the presence of a mass of single-interval taxa is the main cause of
578 the diversity deviation (Chen et al., 2012). In Fig. 8, the singletons are excluded.

579 The use of stages as the stratigraphical intervals in this analysis implies that they are
580 inevitable of different durations, which may cause partial bias, i.e., longer bins may
581 have a higher taxonomic richness than shorter bins simply, for instance, the duration
582 of Famennian (13.3 Myr) is over four times that of Pragian (3.2 Myr) (Cohen et al.,
583 2013, updated). To correct for a possible bias resulting from these unequal interval
584 lengths, rates of origination, extinction, and turnover have also been computed. They
585 are equal to the origination, extinction and turnover indices divided by the stage
586 duration in Myr (from Cohen et al., 2013, updated).

587587

588 5. Main diversity fluctuations detected in the Devonian plant microfossil record
589 of China

590590

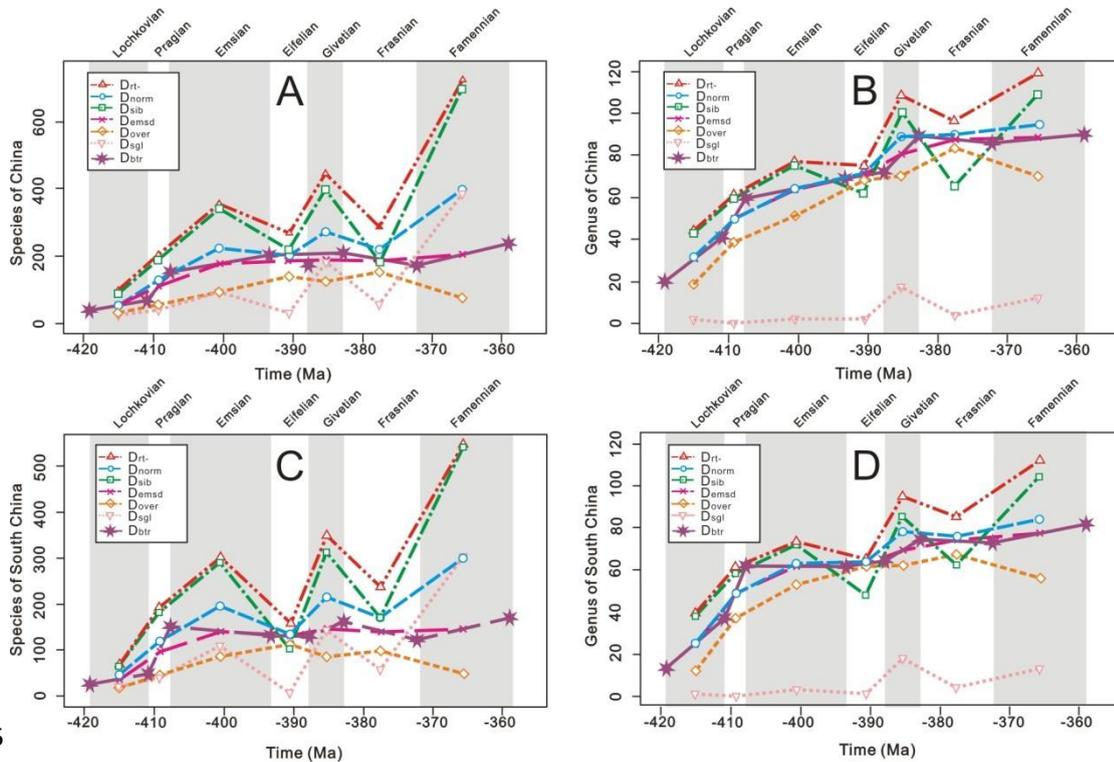
591 The Devonian taxonomic diversity curves for the Chinese plant microfossils are
592 shown in Fig. 6. We see a regular increase of taxonomic richness throughout the entire
593 Devonian (D_{rt} , D_{sib}). However, this pattern is strongly influenced by the concomitant
594 increase of single-interval taxa (D_{sgl}) and may also be biased by a time-dependent
595 sampling effort (see time-ratios). Discarding these potential biases, the pattern is
596 rather of a sudden strong increase of richness in the Pragian (not at the
597 Silurian/Devonian boundary) (see D_{btr}) followed by a plateau of richness, whereas the
598 size-based rarefaction (Fig. 7) shows another pattern with an increasing trend until the
599 Givetian, followed by a plateau.

600 Moreover, regarding origination/extinction values the trend of the origination
601 index in both China and South China is quite similar to that of the turnover indices,
602 with three peaks occurring in the Early Devonian, Givetian and Famennian (Fig. 8;
603 Appendix E). Relatively higher values appear in the Emsian when using the raw
604 taxonomic indices, but they disappear when conducting the rate of taxonomic change
605 per Myr. Otherwise, the extinction indices have higher values in the Emsian and
606 Famennian from both rates of taxonomic change per Myr and raw indices.

607 In terms of the comparison of the diversity of the individual terranes, in addition
608 to the Junggar region (Fig. 9B), it is impossible for us to obtain more objective and
609 realistic curves for the time being in other terranes such as Western Yunnan (Fig. 9A),
610 Qinling (Fig. 9C), and Hinggan (Fig. 9D) region, due to lack of data.

611 The correlation of rarefaction estimated genus diversity and monographic
 612 (references per stage) richness in China gets the lowest value of such four methods
 613 (D_{sib} , D_{norm} , D_{emsd} , and rarefaction) and is not significant (Fig. 10; Appendix B).

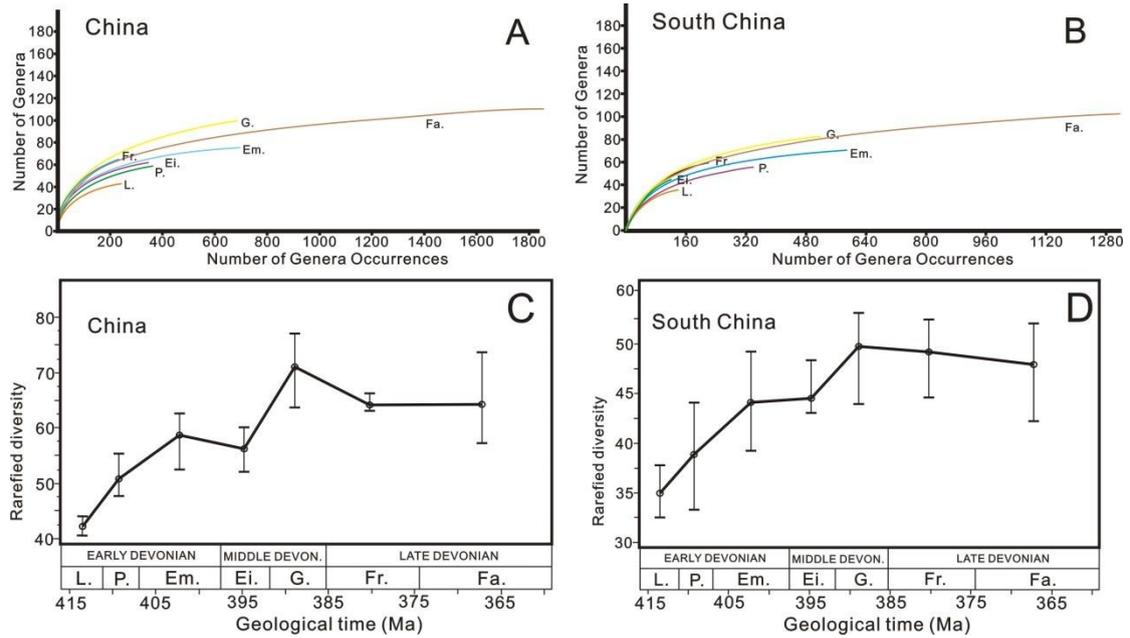
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615

616 **Fig. 6** Taxonomic diversity curves of Devonian terrestrial palynofloras. **A**, species-level diversity in
 617 China. **B**, genus-level diversity in China. **C**, species-level diversity in South China. **D**, genus-level
 618 diversity in South China. Legends: D_{rt} = the range-through or total diversity; D_{norm} = the
 619 normalized diversity; D_{sib} = the sampled-in-bin diversity; D_{emsd} = the estimated mean
 620 standing diversity; D_{over} = the crossover diversity; D_{sgl} = the single-interval diversity;
 621 D_{btr} = the boundary crosser diversity.

622



623

624 **Fig. 7** A–B: comparative rarefaction curves for the seven Devonian stages based on analysis of the

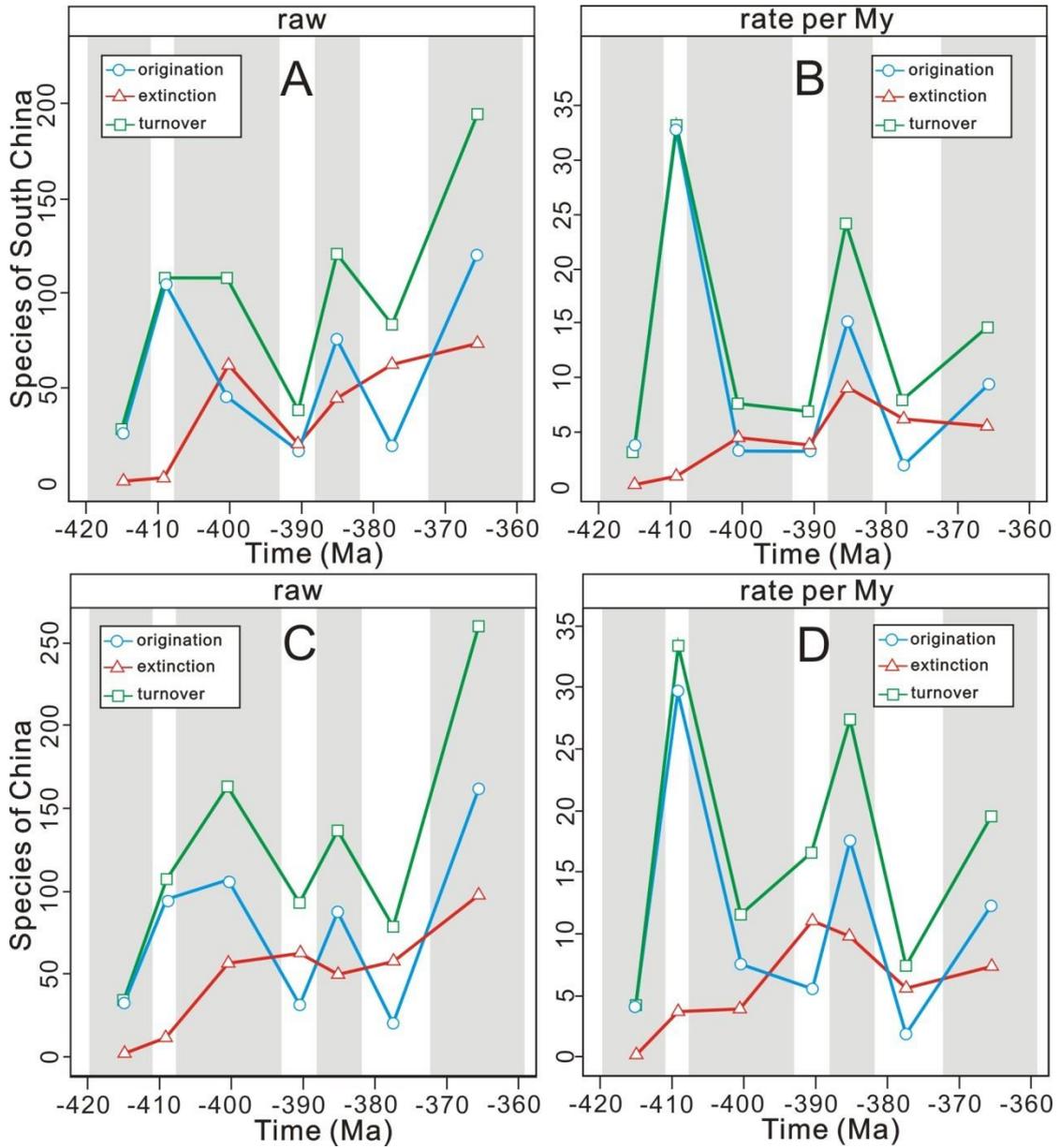
625 China and South China database of genus occurrences, respectively. C–D: Devonian diversity

626 trajectories based on rarefaction estimates of genus richness for each stage at the sample sizes of 253

627 and 137 genus occurrences of China and South China, respectively. Error bars depict 95%

628 confidence intervals around the estimates. Abbreviations: L.= Lochkovian; P.= Pragian;

629 Em.=Emsian; Ei.= Eifelian; G.= Givetian; Fr.= Frasnian; Fa.= Famennian.



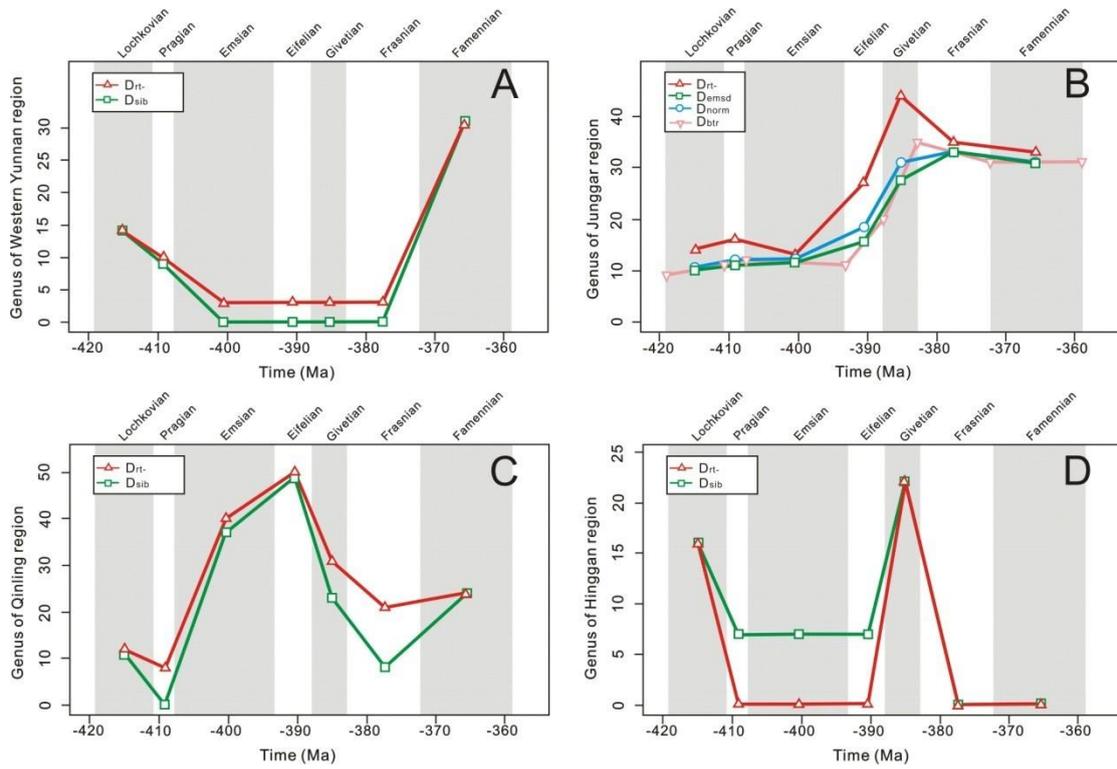
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631 **Fig. 8** Taxonomic origination, extinction and turnover rates of spore genus and species of China and

632 South China. **A, B:** species from South China; **C, D:** species from China; **A, C:** raw data. **B, D:** rates

633 of taxonomic changes per stage duration.

634

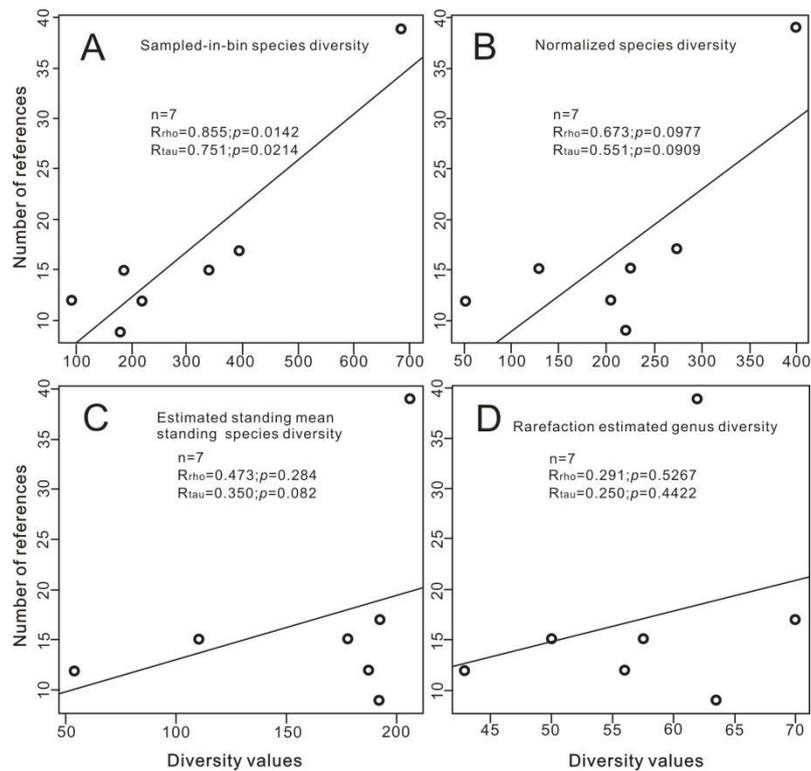


635

636 **Fig. 9** Taxonomic diversity curves of Western Yunnan (A), Junggar (B), Qinling region (C), and

637 Hinggan (D) regions. The legends here are the same as in Fig. 6.

638



639

640 **Fig. 10** Correlation (R_{ρ} and R_{τ}) of taxonomic (D_{sib} , D_{nor} , D_{emsd} , and rarefaction) and
 641 monographic diversity (number of references per stage).

642

643 6. Discussion

644

645 6.1. Devonian diversity pattern of observed palynofloras according to different 646 measurement parameters

647

648 Land plant microfossils, that are much more abundant and widespread than land
 649 plant megafossils. They can supply reliable quantitative data to better understanding
 650 links between early land plant evolution and geological or palaeoenvironmental
 651 changes, even at the global level. Various indices, including D_{sib} , $D_{\text{rt-}}$, D_{nor} , D_{emsd} , D_{btr} ,
 652 and sample-based rarefaction analysis, have been used for discussing the diversity
 653 trajectories of Devonian plant microfossils (Fig. 6; Fig. 7). Interestingly, the
 654 correlation of D_{emsd} (species level) and monographic (references per stage) richness is

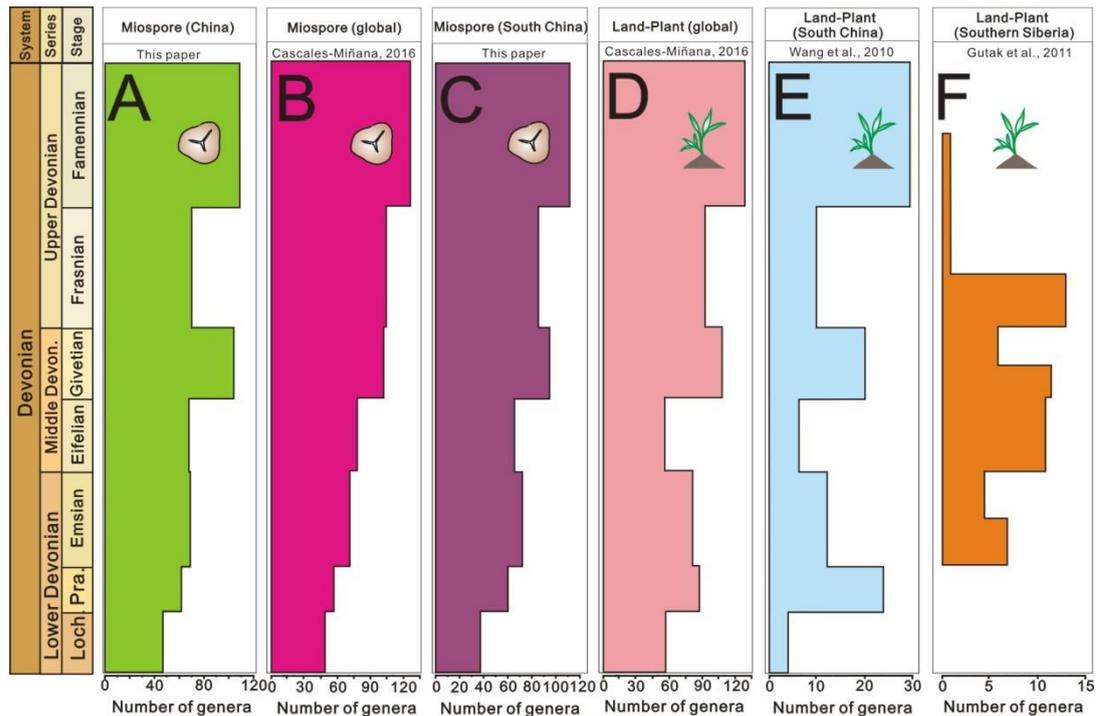
655 low and not significant (Fig. 10C), which means that the D_{emsd} index may be more
656 qualified for reducing the effect of sampling bias. Chen et al. (2012) analyzed the
657 applicability of various diversity statistic methods, such as $D_{\text{rt-}}$, $D_{\text{rt-}/\text{my}}$, D_{nor} , and D_{emsd} ,
658 and found out that the D_{emsd} is not affected by the uneven duration of each time bin
659 when the proportion of the singleton is moderate. Although D_{btr} is still prone to the
660 sampling bias, the D_{btr} index is often preferred to D_{emsd} and D_{sib} indices. Thus, when
661 both D_{emsd} and D_{btr} are used at the same time, the conclusion may be more realistic to
662 represent a general tendency of taxonomic diversity when sample-based data cannot
663 be achieved.

664 The taxonomic raw data-based diversity pattern of plant microfossils through the
665 Devonian in China is not only fairly similar to the plant megafossil and/or microfossil
666 record at the global level (Fig. 11B; Knoll et al., 1984; Cascales-Miñana, 2016), but
667 also to the regional patterns of mega/macrofossils from Laurussia (Raymond and
668 Metz, 1995, fig. 2), and South China (Fig. 11C, E; Wang et al., 2010; Xiong et al.,
669 2013). Overall, the various diversity curves produced in the present study have a
670 similar rising tendency (Fig. 6) on the basis of the range-based data, with an
671 interruption by two major decreases that can be observed in the Eifelian and in the
672 Frasnian. However, when these trajectories (especially the D_{sib} , $D_{\text{rt-}}$) are compared
673 with the adjusted results from sample-based rarefaction analysis, it becomes visible
674 that they are quite different, especially during the Late Devonian. Results from
675 rarefaction analysis suggest that a substantial portion of the increase for the Late
676 Devonian may be a consequence of increased sample size of the fossil record. The

677 discordance between raw diversity and more robust taxonomic diversity metrics
678 suggests that sampling effects may strongly influence the perception of biodiversity
679 trends. Genus diversity reached a peak in the later part of the Middle Devonian
680 (Givetian), followed by a plateau persisting through the Late Devonian (Fig. 7). It is
681 noteworthy that this result is in agreement with the classic studies of the apparent
682 trend of plant megafossil diversity (e.g. Knoll et al., 1984). When we look at the
683 diversity curves of the Junggar region (Fig. 9B), although these diversity patterns are
684 very similar to the result of the rarefaction analysis, i.e., the apparent terrestrial
685 palynofloral diversities progressively increased through the Early to Middle Devonian
686 time interval, with a peak reached towards the latter part of the Middle Devonian
687 (Givetian) followed by a plateau persisting through the Late Devonian, we should be
688 careful because this can be caused by incomplete microfossil record.

689 Furthermore, the reported plateau of Late Devonian in the Chinese pattern of plant
690 microfossil diversity also confirms previous observations concerning the absence of a
691 Frasnian-Famennian depletion of diversity like those occurred in marine realms in one
692 of the recognized “ Big Five” mass extinction (e.g. Bambach et al., 2004; Cascales-
693 Miñana et al., 2018; Percival et al., 2018). This trend is observed in both plant mega-
694 and micro fossil diversity patterns at global and regional scales (Fig. 11), which
695 suggests a solid pattern of vegetation diversification towards the end-Devonian.

696



697

698 **Fig. 11** Comparative diagram showing relationships among the raw diversity of Devonian
 699 miospores and the megafossil pattern of land plants from China and other regions. **A**, plant
 700 microfossil data from all areas of China (D_{rt}); **B**, global plant microfossil data (modified from
 701 Cascales-Miñana, 2016); **C**, plant microfossil data from South China; **D**, global data from all land
 702 plants (modified from Cascales-Miñana, 2016); **E**, data of land-plants from South China (modified
 703 from Wang et al., 2010); **F**, data of land plants from southern Siberia (modified from Gutak et al.,
 704 2011).

705

706 *6.2. Diversity of Devonian plant microfossils and its possible relationship to marine*
 707 *oxygenation*

708

709 The analysis of oxygen levels during the history of the Earth's have received
 710 much attention and is a subject of continuous debate among palaeontologists and
 711 modelling scientists (e.g. Berner et al., 2006; Dahl et al., 2010; Sperling et al., 2015).

712 It is generally hypothesized that the evolution of land plants is intimately linked to the

713 oxygenation of the oceans and the atmosphere but also to the decrease of carbon
714 dioxide (e.g. [Le Hir et al., 2011](#); [Lenton et al., 2016](#)). Most probably first nonvascular
715 plants colonized the land somewhere during the Middle to Late Ordovician (~470–
716 445 Ma), followed probably by the first vascular plants in latest Ordovician or the
717 Silurian (~445–420 Ma), before becoming abundant and widespread during the Early
718 Devonian (~420–390 Ma) ([Rubinstein et al., 2010](#); [Wellman et al., 2013](#); [Edwards et](#)
719 [al. 2015](#); [Gerrienne et al., 2016](#)). By the end of the Middle Devonian, forests with
720 trees exceeding 8 m in height had evolved in several independent clades ([Kenrick et](#)
721 [al., 2012](#)). It appears therefore evident that significant changes in terms of weathering
722 processes, as well as oxygen and carbon dioxide concentrations could have took place
723 during the Devonian due to the colonization of land plants. This was already
724 suggested two decades ago by [Algeo and Scheckler \(1998\)](#) and [Algeo et al. \(2001\)](#).
725 More recently, additional papers have also mentioned global oxygenation events in
726 the Devonian (e.g. [Wallace et al., 2017](#)). The question if these models are consistent
727 with the data must be raised.

728 The atmospheric oxygen levels are controlled in large part by the extent of organic
729 carbon burial (e.g. [Watson et al., 1978](#); [Bernier, 2003, 2006](#)). In existing models (see
730 e.g. [Bergman et al., 2004](#); [Bernier and Canfield, 1989](#); [Bernier, 2006](#)), the evolution of
731 trees starting ~385 Ma is assumed to have led to the burial of high C/P organic
732 material, which is considered in these models to be much more significant than that
733 from marine primary producers ([Kump, 1988](#)), potentially augmented by increased
734 phosphorus weathering rates ([Lenton et al., 2016](#)), although this is part of an ongoing

735 debate. Some authors consider that it is reasonable to consider that the oxygen did not
736 rise until the advent of forests starting at ~385 Ma (Givetian) (Lenton et al., 2016).

737 The evidence from the isotopic composition and concentration of molybdenum
738 (Mo) indicates a fundamental shift in the redox state of the deep ocean from
739 widespread anoxia to widespread oxygenation sometime during the time interval from
740 435 to 392 Ma (between the Early Silurian and the Middle Devonian) (Lenton et al.,
741 2016). This ocean oxygenation is also supported by a shift in iron speciation data
742 sometime during a time interval from 435 to 387 (Sperling et al., 2015). Wallace et al.
743 (2017) have recently tracked the sea-water oxygen levels of the Neoproterozoic and
744 early Phanerozoic by using the relative abundance of cerium (Ce_{anom}) in marine
745 carbonates. Wallace et al.'s (2017) results indicate an apparent high pO_2 increase
746 through the Early Devonian to Middle Devonian, but that it was not until the Late
747 Devonian that oxygenation levels are comparable to the modern world (Wallace et al.,
748 2017). The increase of cerium anomaly closely coincides with the Middle Devonian
749 (Givetian, Stein et al., 2007; Wallace et al., 2017). Interestingly, our results have
750 shown that the plant microfossil diversity in China has been rising gradually from the
751 Early Devonian to Middle Devonian (Givetian), followed by a plateau during the
752 Givetian to Late Devonian (Fig. 7). So, the known geochemical pattern of Mo and
753 Ce_{anom} seem to be consistent with the land plant microfossil diversity trajectory, which
754 could suggest that the Devonian evolution of a forested vegetation played a significant
755 role in influencing the carbon cycle and atmospheric oxygen levels (Edwards et al.,
756 2015). The present study therefore provides additional evidence that the rise of land

757 plants appeared to have been essential for a possible oceanic oxygenation event
758 during the mid-Devonian, instead of the Late Devonian as proposed by [Wallace et al.](#)
759 [\(2017\)](#).

760

761 *6.3.Devonian marine animal diversity, plant microfossil diversity and palaeoclimate*

762

763 In the past decades, many works have discussed about Devonian climate changes
764 (e.g. [Streel et al., 2000](#); [Van Geldern et al., 2006](#); [Joachimski et al., 2009](#)). [Joachimski](#)
765 [et al. \(2009\)](#) reconstructed the sea surface palaeotemperature (SST) history of the
766 Devonian. In their view, the earliest Devonian, the late Frasnian, and most of the
767 Famennian are relatively warm periods, whereas the Middle Devonian represents a
768 relatively cooler period ([Joachimski et al., 2009](#); [Hearing et al., 2018, fig. 3](#)).
769 Although the Middle Devonian cooling remains debated, it was possibly linked to the
770 plant evolution and also resulted in the long-term weathering of terrestrial ecosystems,
771 and the reduction of atmospheric $p\text{CO}_2$ (e.g. [Algeo and Scheckler, 1998](#)). [Le Hir et al.](#)
772 [\(2011\)](#) considered that the drift of palaeocontinents, together with the impact of the
773 terrestrialisation by land plants, can explain the climate changes. [Le Hir et al. \(2011\)](#)
774 applied modeling data simulating a drop of $p\text{CO}_2$ from 6300 to 2100 ppmv from the
775 Early to the Late Devonian. The massive terrestrialisation by Devonian land plants
776 surely must have had an impact on global $p\text{CO}_2$ levels and climate changes, but what
777 is its proportion to global tectonic changes or the evolving marine ecosystems?

778 [Klug et al., \(2010\)](#) displayed the diversification of various higher rank taxa of
779 phytoplankton, zooplankton, demersal and pelagic nekton of the Devonian and Early

780 Carboniferous. The three curves (Klug et al., 2010, fig. 4), which contain the
781 integrated benthic genera, nektonic genera and marine genera with singletons,
782 respectively, get strikingly high biodiversity values in the late Early to Middle
783 Devonian. For example, as a well-preserved fossil group, bryozoans have important
784 environmental significance, and their diversity displays a persistent rise from the
785 Pragian to the early Givetian, before a significant drop from the late Givetian to the
786 Famennian (Horowitz et al., 1996; Ernst, 2013; Fig. 12C). A notable peak of marine
787 animal diversity can be observed in South China during the late Early Devonian to
788 Middle Devonian, representing highest levels that are recognized through the entire
789 Devonian Period (Rong et al., 2007; Fig. 12A). In addition, the diversity curves from
790 other marine invertebrates, such as coral-stromatoporoid reefs (Flügel and Kiessling,
791 2002; Kiessling, 2002; Liao, 2006; Fig. 12B), tentaculitoids (Fig. 12D), brachiopods
792 (Harper Jr, 1996; Chen, 2006) and trilobites (Richard and Robert, 1997; Fig. 12E)
793 highlight also relatively high diversity values over the Middle Devonian period. Alroy
794 et al. (2008) used genus-level diversity measures during the Phanerozoic, based on
795 sampling-standardized analysis of the Paleobiology Database. Placed in 48 temporal
796 bins of a length averaging 11 Myr, global marine diversity indicates a steady increase
797 from the early Cambrian to the Early Devonian, with a rapid decrease in the Middle
798 Devonian before a rise in the Late Devonian.

799 The diversity pattern of terrestrial palynofloras is notably different from that of
800 contemporaneous marine animals, at a global level, especially in the Late Devonian.
801 The diversity trajectory of terrestrial palynofloras from China reaches a peak in the

802 Givetian, followed by a plateau (with a slight decrease in the Frasnian and a slight rise
803 in the Famennian) (see D_{btr} in [Fig. 6](#)) extended to the Late Devonian. The taxonomic
804 diversity in the Late Devonian was obviously higher than during the Early Devonian
805 ([Fig. 7](#)), which is quite similar to the trends observed in Euramerica. On the basis of
806 [Richardson and McGregor's \(1986\)](#) Euramerican data, [Boulter et al. \(1988\)](#), [Raymond
807 and Metz \(1995, fig. 3\)](#), and [McGhee \(1996\)](#) analyzed the Devonian diversity of
808 miospore species, and indicated that the results clearly show a maximum during the
809 Givetian–middle Frasnian and a rather dramatic drop from the late Frasnian to the
810 middle Famennian in low latitude regions (see [Streel et al., 2000](#)). [Streel et al. \(2000\)](#)
811 suggested that a rather hot climate culminated during the latest Frasnian, when
812 equatorial miospore assemblages reached their maximum distribution range, with the
813 homogeneity of miospore assemblages presented from palaeo-tropical to palaeo-
814 subpolar regions during the Frasnian ([Streel et al., 1990, 2000](#)). The low latitude
815 warming during the middle to late Frasnian and early Famennian was later confirmed
816 by the Devonian climate model of [Joachimski et al. \(2009\)](#). If correct, the relatively
817 mild climate characteristic of the Givetian, with a less marked climatic gradient,
818 would have played a significant role in the enhancement of plant microfossil diversity,
819 while the rather hot climate during the latest Frasnian in the low latitudes, to some
820 extent, may have limited the plant diversity increase. This can also be used to
821 illustrate the relatively low levels of diversity during the Early Devonian. Similarly,
822 the slight decrease of the temperature during the Famennian (375-359 Ma) may have
823 contributed to the diversity increase ([Joachimski et al., 2009](#)). It is noteworthy that the

824 Devonian of China, in the eastern margin of the Palaeo-Tethys Ocean, displays a
825 similar diversity pattern than that of Euramerica, located in similar latitudes at the
826 western margin of the Palaeo-Tethys Ocean. However, these trends from China and
827 Euramerica are significantly different from that of the Siberian landmass (Gutak et al.,
828 2011; Fig. 11F). According to modern global plate tectonic reconstructions (e.g.
829 Boucot et al., 2013), Siberia was an isolated landmass located in mid-high latitudes
830 during the Devonian. The different plant diversity dynamics exhibited between the
831 Siberian landmass and China may have been affected by temperature variations
832 controlled by latitude and/or oceanic currents (i.e. warm and cold currents).

833 It is likely that the diversities of marine animals and plant microfossils during the
834 Devonian Period have strongly interacted with the contemporaneous climate changes,
835 i.e., the comfortable climate of the late Early to Middle Devonian time interval, which
836 is comparable to the present day, may have played a role in promoting the increases in
837 biodiversities that characterized that time interval.

838

839 *6.4. Plant microfossil diversity and sea-level changes*

840

841 Although the relationships between sea-level changes and marine biodiversity
842 have been abundantly discussed (Algeo, 2001; Falkowski et al., 2004; Gutak et al.,
843 2011; Katz et al., 2004; Li et al., 2008; Ma et al., 2009, 2016; McGhee, 1992; Martin,
844 2008; Miller et al., 2005; Servais et al., 2008, 2016; Strother, 2008), no consistent
845 conclusion has been reached so far, although it becomes clear that at the long term,
846 i.e. the Phanerozoic scale, a tendency can be observed. Katz et al. (2004) discussed

847 the links between Mesozoic calcareous nannoplankton, dinoflagellates, diatoms, and
848 sea-level changes, and indicate that the diversity of calcareous nannoplankton and
849 dinoflagellates has good correspondence with the change of sea-level. [Servais et al.](#)
850 [\(2008\)](#) suggested that the Early Palaeozoic phytoplankton (acritarch) radiation
851 paralleled a long-term rising of sea level between the early Cambrian and the Late
852 Ordovician, while the highest phytoplankton diversity of the Palaeozoic was possibly
853 the result of greatest continental dispersal and major orogenic and volcanic activity,
854 which provided maximum ecospace and large amounts of nutrients. It thus appears
855 that both major marine radiations in the Early Palaeozoic and in the Early Mesozoic
856 are linked to the strong increase of sea-level that are accompanied by the
857 diversification of the phytoplankton that most probably fueled the marine
858 diversification ([Martin and Servais, 2019](#)).

859 Increasing sea level floods more of the continental cratonic area, but also leads to
860 an increase in the surface area of rock ultimately preserved at the outcrop ([Smith,](#)
861 [2001](#)). [Knoll et al. \(1979\)](#) discovered that a strong correlation existed between the
862 outcrop area of nonmarine rocks deposited during a given geologic time interval and
863 the observed vascular plant diversity for the same period. In fact, both the amount of
864 sedimentary rock preserved and the nature of sedimentary environments have
865 fluctuated significantly over time, and this has had a major effect on observed patterns
866 of diversification and extinction ([Peters and Foote, 2001](#); [Smith, 2001](#); [Kenrick et al.,](#)
867 [2012](#)). While sea-level is posited as a driver of terrestrial diversity, it is not clear how
868 the volume of terrestrial clastic sediment could relate to sea-level ([Butler et al., 2011](#);

869 [Benton et al., 2011](#)).

870 It is now widely appreciated that the global sea level is generally considered to
871 have risen throughout the Devonian (e.g. [Johnson et al., 1985](#); [McGee, 1992](#); [Miller et](#)
872 [al., 2005](#); [Ma et al., 2009, 2016](#)). In South China, there are two large transgressive-
873 regressive cycles recorded, i.e., in the Lochkovian to Eifelian, and in the late Eifelian
874 to about the end of the Devonian Period ([Ma et al., 2009](#); [Fig. 12I](#)).

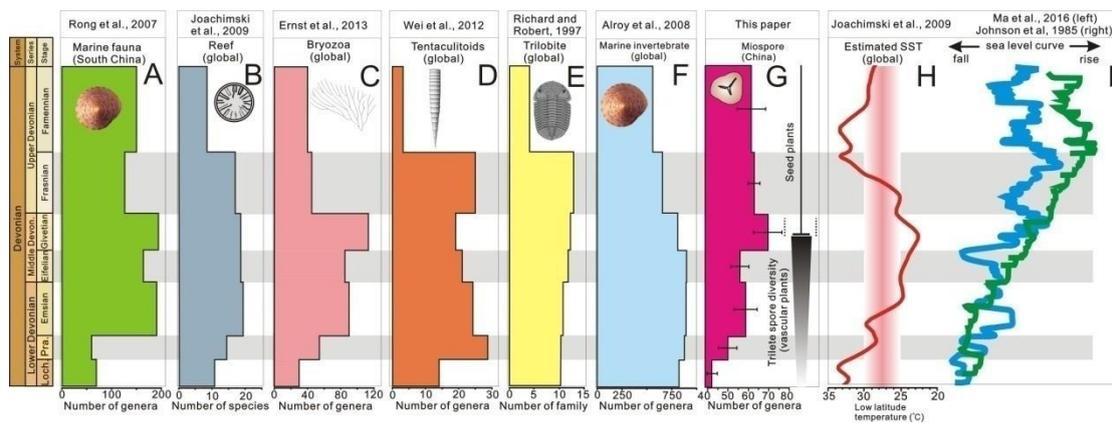
875 Another important parameter to consider is sediment facies. Carbonate deposits
876 are widely developed in South China throughout the Devonian Period, especially
877 during the late Middle Devonian to the Late Devonian interval ([Zeng et al., 1993](#)).

878 However, although some can and do contain some beautifully (three dimensionally)
879 preserved palynomorphs, carbonate sediments are prevailingly non-clastic, and most
880 of them are relatively poor in palynomorphs. This is the main reason why most
881 palynologists study fine-grained clastic sediments (i.e. siltstones) that contain high
882 amounts of spores and pollen derived from land plants and not carbonate rocks
883 ([Traverse, 2007](#)). The transgression events of the later Frasnian caused an extension of
884 the carbonate platform belt in the low latitude regions, with a large dominance of
885 carbonate versus clastic sediments in the geological successions. Consequently, only
886 very few studies concerned palynomorphs in such strata deposited during the Frasnian
887 and early Famennian in China. However, there have been a large number of
888 publications at the global level, with more abundant records of Frasnian
889 palynomorphs ([Wicander and Playford, 1985](#) and references therein). The limited
890 number of research may therefore explain at least partly the diversity decrease during

891 the Frasnian in China. Subsequently, the progressive regression during the Devonian–
 892 Carboniferous transition increased the volume of terrestrial clastic sediments, with a
 893 much higher number of terrestrial palynofloral studies published concerning this time
 894 interval.

895 In the longer term, the sea-level rise increased the accumulation of terrigenous
 896 clastic sediments, which was crucial to the discovery of the Devonian terrestrial
 897 palynofloras. Over shorter timescales, however, the sea-level rise and the
 898 accumulation of carbonate platforms in low latitudes may have, in turn, caused an
 899 habitat and diversity loss of the terrestrial palynofloras.

900



901

902 **Fig. 12** Comparative view of the main diversity fluctuations of important taxonomic groups and
 903 the variations of the palaeotemperature and sea-level curves. **A**, genus-level diversity of marine
 904 fauna from South China (modified from [Rong et al., 2007](#)); **B**, species-level diversity of coral-
 905 stromatoporoid reefs (modified from [Joachimski et al., 2009](#)); **C**, genus-level diversity of
 906 bryozoans (modified from [Ernst et al., 2013](#)); **D**, genus-level diversity of tentaculitoids (modified
 907 from [Wei et al., 2012](#)); **E**, family-level diversity of trilobites (modified from [Richard and Robert,](#)
 908 [1997](#)); **F**, genus-level diversity of all global marine invertebrates from the Paleobiology Database

909 (modified from [Alroy et al., 2008](#)). **G**, genus-level diversity of plant microfossils from China from
910 rarefaction estimated genus richness with error bars depict 95% confidence interval; **H**, estimated
911 Devonian sea surface palaeotemperature record ([Joachimski et al., 2009](#)), the red band represents
912 the modern equatorial sea surface temperature range ([Trotter et al., 2008](#)); **I**, sea-level curves of
913 South China ([Ma et al., 2016](#)) and Euramerica ([Johnson et al., 1985](#)).

914

915 **7. Conclusion**

916

917 This paper reviews the research progress on Devonian terrestrial palynofloras
918 from China in the frame of Devonian plant micro- and megafossil diversity dynamics.
919 The research on many of the regions, except from South China, remains still very
920 sparse. In addition, only a very small number of papers included discussions
921 concerning palaeoclimate, palaeoecology, and palaeogeography and further work is
922 needed to provide more comprehensive well-dated collections in some of the
923 insufficiently studied regions.

924 Based on a newly compiled large-scale dataset (more than 1600 species and nearly
925 200 genera), a multimethodological statistical approach has been carried out. Resulted
926 patterns have shown how the Devonian diversity patterns of plant microfossils from
927 China are characterized by progressive increase in diversity through the Early and
928 Middle Devonian, with a peak reached in the Givetian, followed by a plateau
929 persisting through the Late Devonian. Interestingly, the genus/species level
930 microfossil-based total diversity curve of land plants from China is quite similar to
931 that of the global record. Robust taxonomic diversity metrics via sample-based

932 rarefaction analysis have suggested that sampling effects may have strongly
933 influenced our perception of biodiversity trends of China and that the Late Devonian
934 taxonomic richness may have been greatly overestimated. Moreover, a new evidence
935 seems to support that land plants appear to have been important contributors for a
936 possible oceanic oxygenation event. Terrestrial and marine diversity trends can
937 tentatively be compared, with increasing trends of diversity up to the Middle
938 Devonian for both realms.

939

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946

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