

1 **Climatic zonation of cryptospore, trilete spore and early land plant records**
2 **within Přídolí, Late Silurian**

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18

20 **Abstract**

21 The paper describes dispersed cryptospores and trilete spores from tropical, temperate and
22 cool climate belts within Přídolí and compares them with records of early land plant. A
23 common feature of the cryptospore and trilete spore records is that their number is lowest in
24 the tropical climatic belt and much higher in the temperate and especially in the cool climatic
25 belts. The highest number of autochthonous cryptospore taxa is found in the cool belt, and the
26 highest number of autochthonous trilete spore taxa is recorded in the temperate belt. In
27 general, based on the dispersed spore record, we can estimate that the plant assemblages of
28 the tropical belt were dominated by rhyniophytes, trimerophytes probably prevailed over
29 rhyniophytes in the temperate belt, and rhyniophytes again dominated within the cool belt,
30 although we only have plant records from the tropical belt of Přídolí

31

32 *Keywords:*

33 Early land plants

34 Cryptospores

35 Trilete spores

36 Přídolí

37 Silurian

38

40 1. Introduction

41 For many years, the Silurian was thought to be the most important interval for the
42 terrestrialisation of early land plants. It now appears, also based on calculated comparative
43 phyllostratigraphy, that the earliest land plants colonised the Land as early as the Ordovician
44 or maybe even the Middle Cambrian (Morris et al., 2018; Naugolnykh, 2022). However, the
45 Silurian is the most important for more permanent expansion and more continuous plant
46 cover.

47 The Silurian system was first identified by Murchison (1835), in honour of the Celtic
48 tribe of Silure who inhabited the Welsh borderlands where he first studied these rocks. The
49 Silurian, which lasted from about 443.8 to 419.2 million years ago (Cohen et al., 2023),
50 represents a key interval in Earth's history and biological evolution. During this time, vascular
51 plants diversified and colonised the continents during the “Siluro-Devonian terrestrial
52 radiation“, which can be considered the terrestrial equivalent of the “Cambrian explosion“ of
53 marine life (e.g. Bateman et al., 1998, Steemans et al., 2012; and references therein). The
54 rapid emergence of land plants and the continuing expansion of terrestrial ecosystems during
55 the Silurian also initiated fundamental changes in the structure of marine ecosystems. The
56 transitional nature of the Silurian, lasting only about 24 million years, can be illustrated not
57 only by changes in the structure of marine communities and ecosystems (Klug et al., 2010),
58 but also by the instability of the global carbon cycle and probably rapid changes in
59 atmospheric pO_2 and pCO_2 (Hayes et al., 1999; Berner, 2003, 2006, 2009; Berner et al., 2003;
60 Schachat et al., 2018). Published data show that during the relatively short Silurian interval at
61 least five globally recognised carbon isotope excursions have been recognised. These
62 anomalies include the mid-Llandovery, early Wenlock, late Wenlock, late Ludlow and across
63 the Silurian-Devonian boundary $\delta^{13}C$ excursions (Cramer et al., 2011; Salzman and Thomas,
64 2012). These rapid changes in the global carbon cycle have been associated with rapid

65 changes in temperature (Trotter et al., 2016; Grossman and Joachimski, 2020). Přídolí is the
66 youngest series of the Silurian system, ranging from 423 to 419.2 Ma (Cohen et al., 2023).
67 The name is derived from the Přídolí area of the Daleje valley in the Czech Republic. The
68 base is defined by the first appearance of the graptolite species *Monograptus parultimus*. In
69 addition, two species of chitinozoans, *Urnochitina urna* and *Fungochitina kosovensis*, occur
70 for the first time at or just above the base of the series.

71 During the Přídolí, the climate is generally warmer than in stratigraphically older
72 units. Plate tectonic activity caused palaeocontinents to shift, Siberia, Laurentia and Baltica
73 formed a new 'supercontinent' Euramerica, e.g. Gondwana drifted over the South Pole and sea
74 levels rose (Figure 1). Some areas near the equator are even characterised by evaporites, i.e.
75 salt deposits (Spiridonov et al., 2020).

76 Plants are a critical element of life on the continents as we know it. Several authors
77 have suggested that embryophytes are monophyletic and bryophytes and tracheophytes are
78 sister clades (Graham, 1993; Wellman et al., 2013; Cox et al., 2014), and that land plants
79 evolved from multicellular charophycean green algae (Bower 1908; Karol et al., 2001; Qui et
80 al., 2008); surprisingly, recent theories emphasise the sister relationship of unicellular or
81 filamentous Zygnematophyceae charophytes to land plants (Gontcharov, 2008; Wodniok et
82 al., 2011; Cheng et al., 2019; Tena, 2020; Žárský et al., 2022).

83 The fossil plant record consists of significant plant fragments and scattered
84 palynological records. Indirect evidence consists of very small fragments of early land plants,
85 called phytodebris or palynodebris or nematoclasts, together with cryptospores and trilete
86 spores.

87 The latter are much more abundant due to the production of small spores in large
88 numbers, their long-distance transport, mainly by wind, and the resistant sporopollenin wall
89 that protects the spores during transport and allows them to fossilise.

90 First Silurian plant specimens are interpreted as allochthonous, mainly from coastal
91 marine sediments (Wellman et al., 2013), including volcanic islands (Libertín et al., 2018a,b;
92 Kraft et al., 2018; Bek et al., 2022).

93 The first indirect evidence for early land plants are cryptospores, which occur as
94 monads, dyads and permanent tetrads and were produced by a heterogeneous group called
95 Eophytidae (Edwards et al., 2022), former cryptosporophytes (Wellman and Ball, 2021) and
96 cryptophytes. The first palynomorphs that can be interpreted as cryptospores were described
97 in the Middle Cambrian (Strother, 2016), consistent with phyllostratigraphic predictions of the
98 possible emergence of crown embryophytes (Morris et al., 2018), and the last specimens are
99 from the Middle Devonian (Breuer and Steemans, 2013; Wellman et al., 2013; Pšenička et al.,
100 2021). True trilete spores represent vascular land plants and their immediate ancestors
101 (Wellman and Gray, 2000; Wellman et al., 2013; Edwards et al., 2014), and the oldest trilete
102 spores are reported from the Middle Ordovician (Steemans et al., 2009; Wellman et al., 2003).

103 The oldest undoubtedly known sporophyte of a vascular land plant is *Cooksonia*
104 *barrandei* from the Middle Sheinwoodian strata of the Perunica microplate (Peri-Gondwana;
105 now Czech Republic; (Libertín et al., 2018a). Other important events are peaks of
106 cryptospores within the Hirnantian-Rhuddanian interval (Wellman et al., 2013). The first
107 global event for the diversification of early land plants and the change from cryptospore to
108 hilate/trilete spore dominance is palynologically documented (trilete spores) after the
109 Homeric glaciation (Pšenička et al., 2021; Bek et al., 2022). The second significant global
110 event occurred after the Middle Ludfordian glaciation (Frýda et al., 2021a,b) during the
111 Přídolí (Kraft et al., 2018; Pšenička et al., 2021) and is defined by the combination of early
112 land plant and trilete spore records. Also important is the appearance of monolet spores
113 within the Sheinwoodian (Bek et al., 2022), i.e. 432 Ma.

114 Palynological events (spore morphology) are summarised in Table 1. Unfortunately,
115 the first early land plant events are much less evident in the megafossil record due to a
116 frustrating paucity of data (Wellman et al., 2013).

117 Palynological records from the Dapingian-Llandovery interval support the idea that
118 vegetation was relatively uniform during these 30 Ma (Wellman et al., 2013). Vavrdová
119 (1988) and Gray et al. (1986) reported dispersed spores from the Hirnantian glaciation,
120 providing evidence for the cold tolerance of early land plants.

121 The record of trilete spores represents an easily recognisable group that is probably
122 monophyletic, whereas cryptospores are difficult to work with because their distribution may
123 be quite cosmopolitan and cryptospore records are often lacking in nearshore marine
124 sediments (Stemans et al., 2007).

125 Ordovician-Silurian dispersed spore assemblages have been reported by numerous
126 palynologists, including Hoffmeister (1959), Richardson and McGregor (1986), Richardson
127 (1996), Wellman (1996), Stemans (2000, 2001), Strother (2000), Wellmann and Gray
128 (2000), Stemans et al. (2007), Wellman et al. (2013). Important sources of information are *in*
129 *situ* spores, i.e. spores isolated directly from plant reproductive organs (Allen, 1980; Gensel,
130 1980; Fanning et al., 1991; Balme, 1995; Gonez and Gerienne, 2010). The plant record from
131 the Ordovician-Silurian interval is limited and poor. The first plant specimens were reported
132 in the 30s (Lang, 1937) and plant assemblages are still not numerous. Edwards (1990)
133 published an overview of Silurian plants in the form of sixteen assemblages. Later, Raymond
134 et al. (2006) reported an analysis of Silurian plants based on 35 assemblages and recognised
135 four phytogeographic units; North Laurussian (Bathurst Island), South Laurussian-SW
136 Gondwana, Kazakhstania and SW Gondwana.

137 The plant assemblage of the Přídolí age is much more diverse than that of stratigraphically
138 older layers (Wellman et al., 2003). Ten plant genera with thirteen species are known from

139 Ludlow, but sixteen plant genera with twenty-four species are reported from Přídolí (Wellman
140 et al., 2003). This means that there is a significant change in plant assemblages between
141 Ludlow and Přídolí, which is similar to an event described, for example, by Kraft et al.
142 (2018), Wellman et al. 2003) and Pšenička et al. (2021).

143 The last significant summary of the early land plant record, mainly cryptospore and
144 trilete spores, was by Steemans (in Wellman et al., 2013) and this updated database is
145 included here.

146 The Eophytidae (cryptospore producers) were probably not climatically sensitive and
147 were cosmopolitan in nature. Edwards and Richardson (2004) suggest that Eophytidae
148 preferred arid areas away from water. Early land plants (trilete spore producers) were more
149 widespread with a diversity of habits, without access to waterways and therefore to the sea
150 (Steemans et al., 2007), i.e. more climatically sensitive than Eophytidae. Plant invasions on
151 land were characterised by limited competition and suitable environments would have been
152 rapidly colonised (Wellman et al., 2013). Early land plants were homosporous and their
153 isospores were easily transported over long distances, mainly by wind but also by water
154 (Gray, 1985), whereas Steemans et al. (2007) suggest that long-distance dispersal was
155 uncommon and rare.

156 Wind transport was probably the most important means of spore dispersal at that time.
157 The majority of Silurian dispersed and *in situ* spores are in the 20-40 μm size range and the
158 best size for wind dispersal is 25 μm (Morgensen, 1981). Wind dispersal was easier and more
159 suitable because the vegetation was ground down; there were no tall plants to impede
160 transport out of the boundary layer and into the wind current at higher latitudes; the average
161 surface wind strength was stronger due to the absence of large vegetation; the total
162 atmospheric pressure was higher than today, resulting in a higher air density (Berner, 2006).

163 This paper compares the occurrence of cryptospores, trilete spores and plant records
164 within Přídolí for cool, temperate and tropical climates, also with respect to earlier/later
165 Silurian epochs/ages.

166

167 **2. Přídolí supergreenhouse – the warmest climate of Silurian Epoch**

168 After the Late Ordovician (Hirnantian) glaciation, the Silurian began with a 7 million
169 year warming trend that lasted for most of the Llandovery (Llandovery Warm Trend by
170 Grossman and Joachimski, 2020). The start of the Wenlock (Sheinwoodian) is associated with
171 a sharp drop in temperature and a biological crisis (Ireviken Bioevent) before the early
172 Wenlock carbon isotope anomaly. After a slight warming in the Middle Wenlock (Late
173 Sheinwoodian to Early Homerian), there was a further drop in temperature in the Upper
174 Homerian. This cooling was also associated with a biological crisis (Lundgreni/Mulde
175 bioevent) and a Late Wenlock carbon isotope anomaly. The following period from the
176 beginning of the Gorstian (Early Ludlow) to Přídolí is associated with a warming trend of
177 about 7 million years. However, this long-term temperature trend was interrupted by a
178 significant temperature decrease in the middle Ludfordian (late Ludlow) (Lehnert et al., 2007;
179 Trotter et al., 2016; Grossman and Joachimski, 2020). The marked decrease in sea surface
180 temperatures (inferred from the positive shift in $\delta^{18}\text{O}_{\text{apatite}}$ of at least 3‰) recorded in the
181 temperate areas of the Prague Basin of the Czech Republic and the Carnic Alps (peri-
182 Gondwana), as well as in the tropical areas of Baltica (Laurussia) and Australia (Gondwana),
183 coupled with a significant eustatic sea level decrease recorded in sequence stratigraphy on all
184 corresponding paleocontinents, points to glaciation (Mid-Ludfordian glaciation-see Frýda et
185 al., 2021a) in polar and subpolar Gondwana. The Mid-Ludfordian glaciation is associated
186 with the Ludfordian carbon isotope anomaly and was preceded by the Kozłowski/Lau
187 bioevent (see review in Frýda et al., 2021a,b). After this global cooling, the warming trend

188 continued until Přídolí (Trotter et al., 2016; Grossman and Joachimski, 2020). The end of
189 Přídolí is associated with the onset of the Early Devonian cooling trend (sense Grossman and
190 Joachimski, 2020), which lasted about 30 million years until the Middle Devonian
191 (Joachimski et al., 2009; Elrick et al., 2009; Grossman and Joachimski, 2020).

192 The Přídolí represents the warmest period of the entire Silurian, as confirmed by
193 seawater temperatures derived from $\delta^{18}\text{O}$ of brachiopod calcite shells and $\delta^{18}\text{O}$ of conodont
194 apatite (Grossman and Joachimski, 2020). However, the exact course of the temperature curve
195 during the Přídolí is very poorly known. The main reason for this is the lack of subdivision of
196 the Přídolí, which limits the possibility of stratigraphic correlations between individual
197 paleocontinents. In addition, in many areas the Přídolí strata are often not preserved or not
198 studied in sufficient detail. As a result, data on seawater temperature in Přídolí are scarce
199 (Grossman and Joachimski, 2020).

200 The study of phosphatic microfossils such as conodonts and fish microremains (skin
201 scales) from the Upper Silurian (Přídolí) of Lithuania revealed a short-term cooling event. in
202 the mid-Přídolí within the *Ozarkodina eosteinhornensis* biozone or the *Ozarkodina*
203 *remscheidensis* biozone, reflecting a major cooling event that may have led to the formation
204 of a high-latitude ice sheet and a glacio-eustatic sea-level fall (Žigaitė et al., 2010). A more
205 detailed analysis has been carried out on conodont apatite from the Prague Basin of the Czech
206 Republic (Lehnert et al., 2012, 2013). New oxygen isotope data show a rapid climate
207 warming and an increase in seawater temperatures of more than 8°C in the mid-latitudes of
208 northern Peri-Gondwana, followed by a strong cooling in the latest Přídolí and across the
209 Silurian-Devonian boundary. The drastic climate change from a cold interval with strong
210 cooling during the Early Přídolí followed by 'supergreenhouse conditions' during the Late
211 Přídolí transgressions graptolite zone probably caused dramatic extinctions and faunal
212 turnover on a global scale (Manda and Frýda, 2010; Lehnert et al., 2012, 2013).

213 Current knowledge of climate evolution during the Přídolí shows that this period was
214 the warmest in a long interval of about 60 million years from the Upper Ordovician to the
215 Middle Devonian. Moreover, although the Přídolí only lasted about 4.5 million years, it was a
216 period of rapid climatic change.

217

218 **3. Results**

219 *3.1. Sheinwoodian trilete spores and cryptospores*

220 Records of Sheinwoodian trilete spores are known from tropical areas (Beck and
221 Strother, 2001, 2008; Wellman, 1993; Smelror, 1987, 1990; Steemans et al., 1996; Wellman
222 and Richardson, 1993; Hagström, 1997; Maziane-Serraj et al., 2000; Smith, 1975; Strother,
223 1991; Burgess and Richardson, 1991, 1995) and cool (Al-Ameri et al., 1991) temperate belts
224 and consist of six species belonging to four genera (Table 2). The most abundant species are
225 *Ambitisporites avitus* and *A. dilutus* (Wellmann et al., 2013).

226 Sheinwoodian cryptospore assemblages have only been described from the tropical
227 belt (Beck and Strother, 2001, 2008; Wellman, 1993; Smelror, 1987, 1990; Maziane-Serraj et
228 al., 2000; Burgess and Richardson, 1991, 1995) and yielded nine genera with eleven species.
229 The most abundant species are *Laevolancis divellomedia* and *Tetrahedraletes medinensis*
230 (Wellman et al., 2013). The distribution of cryptospores and trilete spores is similar, as both
231 groups reach their minimum numbers in the Sheinwoodian.

232

233 *3.2. Homerian trilete spores and cryptospores*

234 The situation within the Homerian is quite different, as assemblages of trilete spores
235 from all climatic belts are described, and the number and diversification of spores is much
236 greater. It corresponds to the first global key events in the terrestrialisation of early land plants
237 after the Homerian glaciation (Pšenička et al., 2021; Bek et al., 2022). The number of species

238 and genera of trilete spores was about the same and relatively low until Homeric times (only
239 about five species on average), but after the Homeric glaciation trilete spores became much
240 more numerous and diversified for the first time.

241

242 3.3. *Gorstian trilete spores and cryptospores*

243 Cryptospore and trilete spore assemblages of the Gorstian have been described by
244 Burgess and Richardson (1996), Marshall (1991), Steemans et al. (2000), Wellman (1993),
245 Hagström (1997), Beck and Strother (2001), Rodríguez (1983), Wellman et al. (2000),
246 Richardson, (1996), Rubinstein and Steemans (2002) and Spina and Vecoli (2009). The most
247 common trilete spores are *Ambitisporites avitus* and *A. dilutus*, common cryptospores are
248 *Archaeozonotriletes chulus* and *Cheilotetras caledonica*. In general there is a decrease in
249 trilete spore taxa.

250

251 3.4. *Ludfordian trilete spores and cryptospores*

252 Ludfordian cryptospore and trilete spore assemblages have been published by Beck
253 and Strother (2008), Hagström (1997), Steemans et al. (2000), Burgess and Richardson
254 (1995), Cramer (1967), Richardson et al. (2001), Rodríguez (1983), Steemans et al. (1996),
255 Wellman and Richardson (1993), Kermadji (2007), Richardson (1996), Rubinstein and
256 Steemans (2002), Spina and Vecoli (2009) and Steemans et al. The most abundant trilete
257 spores are of the genus *Ambitisporites*, and the number of *Emphanisporites* increased. The
258 most abundant cryptospores are *Archaeozonotriletes chulus*, *Laevolancis divellomedium* and
259 the genus *Tetrahedraletes*. The number of trilete spores increased slightly.

260 Probably some climatic change during the Gorstian caused a decrease in trilete spores,
261 but the number of cryptospore species was the same as in Homeric, i.e. this change affected
262 only trilete spore producers and not Eophytidae, probably due to their different life strategies.

263 The increase in the number of trilete spores from Ludlow to Přídolí is more pronounced (from
264 forty-three to one hundred and sixty-three) than that of cryptospores (from thirty-three to
265 fifty-one) within the Ludlow-Přídolí interval.

266

267 *3.5. Přídolí climatic belts*

268 The maximum number of both cryptospore and trilete spore species is at Přídolí,
269 where cryptospores reached forty-three species belonging to twenty-one genera and trilete
270 spores even one hundred and five species belonging to thirty-three genera (Wellman et al.,
271 2013). This second major global event has been documented, for example, by Kraft et al.
272 (2018). The previous Homeric event is only documented palynologically because
273 macrofloral records are very rare and limited (Stemans, 2000; Wellman et al., 2013;
274 Pšenička et al., 2021), but the Přídolí event is well supported by the combination of both
275 palynological and plant records.

276 The course of diversification of cryptospores is specific. Cryptospores reach their
277 minimum as trilete spores in the Sheinwoodian and increased after the Homeric glaciation.
278 The number of cryptospore species in the Gorstian is the same as in the Homeric, whereas
279 trilete spores decreased significantly in the Gorstian. The general trend after Gorstian, i.e.
280 during Ludlow and Přídolí, is similar, cryptospores increased, but not as much as trilete
281 spores. It gives evidence of/it implies different life strategies and ecological needs of eophytes
282 and early land plants.

283 Stemans (2000), Welmann et al. (2013), Pšenička et al. (2021) showed different
284 occurrences of cryptospores and trilete spores within the Sandbian-Gorstian interval.
285 Cryptospores reached their maximum much earlier within the Hirnantian and Rhuddanian, but
286 trilete spores have minimal numbers (only about five species on average) until the
287 Sheinwoodian.

288

289 *3.5.1. Cryptospores in tropical climatic belt*

290 Cryptospores are represented by ten genera with thirteen species, and almost half (46
291 per cent) of them (Table 2) are reported only from this climatic belt (Wellman et al., 2013).
292 Cryptospore records are reported from Laurentia (McGregor and Camfield, 1976; Beck and
293 Strother, 2008; Barron, 1989; Aristova and Arkhangelskaya, 1976) and Avalonia (Beck and
294 Strother, 2001; Aldridge et al., 1979; Burgess and Richardson, 1995, Fanning et al., 1991;
295 Johnson and Taylor, 2005; Richardson, 1996; Richardson and Lister, 1969; Richardson et al.,
296 1981; Wetherall et al., 1999; Vanguetaine et al., 1986). The most common species are
297 *Tetraedraletes medinensis*, *Dyadospora murusattenuata*, *Laevolancis divelomedium* and the
298 genus *Artemopyra*.

299

300 *3.5.2. Cryptospores in temperate climatic belt*

301 The number of cryptospore taxa is higher, with thirteen genera and twenty-one species
302 (Table 2). More than a third (38%) of these are restricted only to this climatic belt. The
303 cryptospore records come from southern Peri-Gondwana (Deunff and Chateaneuf, 1976;
304 Moreau-Benoit and Dubreil, 1987; Rauscher and Robaret, 1975; Steemans et al., 1996;
305 Cramer, 1967; Cramer and Rodriguez, 1977; Cramer and Diez, 1977; Richardson et al., 2001;
306 Rodrigues, 1978a-c, 1983), i.e. Armorica and Iberia. The most commonly recorded genera are
307 *Dyadospora*, *Pseudodyadospora*, *Quadrisporites* and the genus *Hispanaediscus* is well
308 diversified with four species.

309

310 *3.5.3. Cryptospores in cool climatic belt*

311 Cryptospores from cool climate belt reach twelve genera with twenty-five species.
312 More than half (60%) of these are restricted only to this belt. Cryptospores originated from

313 southern Gondwana, including Libya (Buret and Moreau-Benoit, 1986; Richardson, 1996;
314 Rubinstein and Steemans, 2002; Spina and Vecoli, 2009; Steemans et al., 2008; Tekbali and
315 Wood, 1941), Argentina (Rubinstein, 1992, 1994, 1995), Bolivia (McGregor, 1984), Brazil
316 (Steemans et al., 2008) and southern China (Wang and Li, 2000; Wang et al., 2005). The most
317 common genera are *Artemopyra*, *Hispanaediscus* and especially *Cymbohilates* with five
318 species. The number of cryptospore taxa is highest in the temperate and cool climate belts,
319 while the lowest number is in the tropical belt (only about half of those reported from only the
320 cool climate belt). The number of allochthonous cryptospore taxa is highest in the cool belt, i.e.
321 eophytids (cryptospore-producers) must have been more specialised for cooler climates than
322 for warmer ones.

323

324 *3.5.4. Trilete spores in tropical climatic belt*

325 Trilete spores described from the tropical belt are represented by twelve genera with
326 twenty-six species (Table 3), a third (34%) of which are unique to this belt. Trilete spores are
327 described from Laurentia (McGregor and Camfield, 1976; Beck and Strother, 2008; Barron,
328 1989), Avalonia (Beck and Strother, 2001; Aldridge et al., 1979; Burgess and Richardson,
329 1995; Fanning et al., 1991; Johnson and Taylor, 2005; Richardson, 1996; Richardson and
330 Lister, 1969; Richardson et al., 1981; Wetherall et al., 1999; Vanguetaine et al., 1986) and
331 Baltica (Aristova and Arkhangelskaya, 1976).

332

333 *3.5.5. Trilete spores in temperate climatic belt*

334 Trilete spores from the temperate belt comprise twenty-four genera and seventy
335 species (Table 3). Nearly half (48%) of these occurred only in this belt. Records of trilete
336 spores come from southern Peri-Gondwana, i.e. Armorica (Deunff and Chateaneuf, 1976;
337 Moreau-Benoit and Dubreuil, 1987; Rauscher and Robardet, 1975; Steemans et al., 1996,

338 2000) and Iberia (Cramer, 1967; Cramer and Rodriguez, 1977; Cramer and Diez, 1977;
339 Richardson et al., 2001; Rodriguez, 1978a-c, 1983; Kermandji, 2007).

340

341 *3.5.6. Trilete spores in cool climatic belt*

342 Records of trilete spores from the cool belt come from southern Gondwana, including
343 Libya (Buret and Moreau-Benoit, 1986; Richardson, 1996; Rubinstein and Steemans, 2002;
344 Spina and Vecoli, 2009; Steemans et al., 2008; Tekbali and Wood, 1991), Argentina
345 (Rubinstein, 1992, 1994, 1995), Bolivia (McGregor, 1984), Brazil (Steemans et al., 2008) and
346 southern China (Wang and Li, 2000; Wang et al., 2005). This assemblage consists of 23 spore
347 genera with 70 species, a third (34%) of which are unique to this region (Table 3).

348 The lowest number of trilete spore taxa is found in the tropics, and the temperate and
349 cool belts have equal numbers. The number of endemic species, i.e. those found only in one
350 climatic belt, varies from a third to almost a half.

351 Table 3 shows autochthonous cryptospore, trilete spore and early land plant taxa
352 recorded only in one climatic belt.

353 As was the case for eophytids (cryptospore-producers) also trilete producers must have
354 been more specialised for cooler climates than for warmer ones.

355

356 *3.6. Early land plants within Přídolí*

357 The fossil record of plants from Přídolí is poor. We know sixteen genera with twenty-
358 four species (Wellman et al., 2013), only from the tropical belt, and one questionable record
359 of *Cooksonia* sp. from the temperate belt (Table 3). Based on our knowledge of *in situ* spores
360 (Allen, 1980; Gensel 1980; Balme 1995), we can roughly estimate the number of plant genera
361 in the temperate and cool climate belts from the palynological record. Thirty-three spore taxa
362 are recorded in the temperate climate belt, and it is hypothetically possible that these spores

363 are produced by twenty-three plant taxa. Twenty-four taxa of trilete spores from the cold belt
364 could be produced by sixteen to eighteen plant taxa. However, these numbers are highly
365 hypothetical.

366

367 **5. Discussion**

368 Přídolí was the warmest Silurian period with temperatures much higher than in
369 previous times. It caused a qualitative and quantitative increase of cryptospores and especially
370 trilete spores, i.e. vascular land plants in Přídolí, resulting in the second global plant dispersal
371 event.

372 The general pattern of distribution of cryptospore and trilete spore taxa within the
373 Přídolí climatic belts is roughly comparable. The lowest diversity of both palynomorphs is in
374 the tropical belt, where cryptospores and trilete spores reach their minimum number within
375 Přídolí (thirteen and twenty-six species, respectively). There is a significant increase in the
376 temperate belt, where e.g., trilete spores reach their maximum (seventy-two species),
377 comparable to the numbers in cool climates. Cryptospores reach their maximum distinctly in
378 the cool climate belt (twenty-five species), while the number of trilete spores remains also
379 significantly high (23 genera with seventy species). The pattern of distribution of
380 autochthonous taxa within the climatic belts is similar, i.e. an increasing trend from the tropical
381 to the cool climatic belt for cryptospores (seven, eight and fifteen species). Autochthonous
382 species of trilete spores reach their maximum in the temperate belt (thirty-four) and decrease
383 in the cool belt (twenty-four).

384 Dispersed cryptospores and trilete spores usually occur together and their different
385 numbers in all climatic belts indicate that their producers, i.e. eophytes and early land plants,
386 had different life strategies.

387 Another important feature is the different number of cryptospores and trilete spores
388 species (Table 2) within the same climatic belt. The number of trilete spore taxa is more than
389 three times higher than in the tropical belt. This prevalence of trilete spores diversity is
390 however also clearly seen in the cool and temperate climatic zones (Table 2).

391 The number of trilete spore species (twenty-six) and early land plants fossils (twenty-
392 four) is comparable in the tropical climate belt.

393 The situation with the occurrence of early land plants in Přídolí is constrained by the
394 fact that almost all plant records come from the tropical belt (twenty-four taxa), nothing is
395 known from the cool belt and only one questionable record from the temperate belt (Table 2).
396 This may indicate that conditions in the tropical belt were more favourable for plants
397 fossilization than those in the temperate and cool belts.

398 We know the affinities of some spores from studies of *in situ* spores, i.e. spores
399 isolated directly from plant reproductive organs. Our knowledge of Upper Silurian plant
400 producers is not perfect, e.g., compared with that of Pennsylvanian spores (Balme, 1995).
401 Summaries of Silurian/Devonian *in situ* spores have been published by Gensel (1980), Allen
402 (1980), Balme (1995).

403 The last study was prepared by Bek and Votočková Frojdová (in prep.), who proposed
404 a palynological grouping of Silurian and Early Devonian land plant spores. They divided the
405 Silurian/Early Devonian plants into three groups of rhyniophytes, two groups of
406 zosterophytes, one group of trimerophytes, two groups of lycophytes and proposed the
407 affinity of some plants to *Incertae sedis* on the basis of their *in situ* spores.

408 On the basis of this division, we can compare the spores and plants recorded in the
409 tropical climate belt in Přídolí, although the number of plant taxa (fifteen genera with twenty-
410 three species) is higher than that of spores (six genera with nine species). Some spore taxa
411 (*Scylaspora*, *Cymbosporites* and *Vermiverruspora*) were produced by unknown parent plants.

412 All others (*Ambitisporites*, *Retusotriletes* and *Synorisporites*) belong to rhyniophytes.

413 Looking at the list of plants recorded from the tropical climatic belt, we can estimate which
414 spores were produced by them. We know *in situ* spores from only ten plant taxa from the
415 tropical belt. It is possible to estimate that these plants produced the spore genera
416 *Ambitisporites*, *Apiculiretusispora* and *Retusotriletes*.

417 It is possible to estimate that the parent plants of the spores recorded in the temperate
418 zone were produced by some rhyniophytes (*Apiculiretusispora*, *Retusotriletes*, *Streelispora*,
419 *Synorispora*), trimerophytes (*Apiculiretusispora*, *Retusisporites*), zosterophytes
420 (*Retusotriletes*, *Calamospora*) and horneophytes (*Emphanisporites*). Out of nineteen plant
421 genera, *in situ* spores are known from only seven. Plant-produced spores from the temperate
422 belt were some members of rhyniophytes, zosterophytes, trimerophytes and *Horneophyton*.
423 Of the fifteen spore genera (with twenty-four species) described from the cool belt, we know
424 the ancestors of only seven, but it seems that rhyniophytes were predominant and some
425 zosterophytes, trimerophytes and *Horneophyton* were common.

426 In general, based on the dispersed spore record, we can estimate that plant
427 assemblages of the tropical belt were dominated by rhyniophytes, trimerophytes probably
428 outnumbered rhyniophytes in the temperate belt, and rhyniophytes again dominated within the
429 cool belt. Surprisingly however the diversity of both cryptospores and trilete spores was higher
430 in cool (distinctly for cryptospore producers) and temperate/cool latitudes (for trilete spores
431 producers) as compared to tropical belt. This might indicate an early land plants adaptation to
432 cold continental conditions as envisaged by the cryogenian initiation of plant terrestrialization
433 hypothesis (Žárský et al., 2022).

434

435 6. Conclusions

436 Přídolí is characterised by a rapidly increasing number of cryptospores and especially
437 trilete spores, because it was the climatically warmest Silurian period. The diversity of
438 cryptospore and trilete records in the tropical climatic belt during the Přídolí is lower than in
439 the temperate and especially in the cool climatic belts. Autochthonous cryptospore producers
440 (eophytes) were most abundant in the cool belt, and autochthonous trilete spore producers
441 reached the highest numbers in the temperate belt. From the dispersed spore record it is
442 possible to estimate that the plant assemblages of the tropical belt were dominated by
443 rhyniophytes, trimerophytes probably outnumbered rhyniophytes in the temperate belt, and
444 rhyniophytes again dominated within the cool belt. Results shows the second global event
445 important especially for evolution of early vascular land plants.

446

447 **Conflict of interest**

448 The authors declare no conflict of interests.

449

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454

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782

784 **Table and Figure captions**

785

786 **Table 1.** Summary of principle Silurian sporomorph evolution (after Kermandji, 2007). Thick
787 letters means new information presented herein.

788

789 **Table 2.** The number of cryptospores and trilete spore taxa including autochthonous ones in
790 tropical, temperate and cool climatic belts.

791

792 **Table 3.** Autochthonous (i.e. occur only in one climatic belt) trilete spore and early land plant
793 taxa

794

795

796 **Figure 1.** Reconstruction of palaeocontinents within Příkladí. Modified from Scotese (2001).

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