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1 Palaeogeography, Palaeoclimatology, Palaeoecology

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3 **Revisiting the great Ordovician diversification of land plants:**
4 **recent data and perspectives**

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32 ABSTRACT

33

34 Recent molecular clock data suggest with highest probability a Cambrian origin of
35 Embryophyta (also called land plants), indicating that their terrestrialization most probably
36 started about 500 million years ago. The fossil record of the ‘Cambrian explosion’ was limited
37 to marine organisms and not visible in the plant fossil record. The most significant changes in
38 early land plant evolution occurred during the Ordovician. For instance, the earliest bryophyte-
39 like cryptospores and the oldest fragments of the earliest land plants come from the Middle and
40 Late Ordovician, respectively. Organic geochemistry studies on biomarker compositions hint
41 at a transition from green algae to land plants during the ‘Great Ordovician Biodiversification
42 Event’ (GOBE). The colonization of the terrestrial realms by land plants clearly had an impact
43 on marine ecosystems. Interactions between the terrestrial and marine biospheres have been
44 proposed and the radiation of land plants potentially impacted on CO₂ and O₂ concentrations
45 and on global climate. In addition, the shift of strontium isotopes during the Ordovician is
46 probably linked to changing terrestrial landscapes, affected by the first massive land invasion
47 of eukaryotic terrestrial life. The land plants seem unaffected by the first global mass extinction
48 at the end of the Ordovician that eliminated many marine invertebrate taxa.

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51 *Keywords:* early Palaeozoic; radiation; cryptospores; bryophytes, embryophytes;
52 terrestrialization

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65 **1. Introduction**

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67 For many decades, it was generally accepted by both scientists and a wider audience that life
68 on Earth only evolved rapidly after the Precambrian (e.g., Darwin, 1859; Phillips, 1860), with
69 two major radiations (in the early Palaeozoic and the early Mesozoic) punctuating the
70 diversification of eukaryotic life during the Phanerozoic. The early Palaeozoic radiation, that
71 includes both the ‘Cambrian Explosion’ and the ‘Great Ordovician Biodiversification Event’
72 (GOBE), established the Palaeozoic diversity plateau, which was only, near-fatally, interrupted
73 by the end-Permian mass extinction (Fig. 1). This pattern is clearly visible in the Sepkoski-type
74 biodiversity curves (e.g., Sepkoski, 1978) that are widely cited and used in textbooks. In more
75 recent palaeobiodiversity studies, such as the Paleobiology Database (PBDB, e.g., Alroy et al.,
76 2001) or the Geobiodiversity Database (GBDB, e.g., Fan et al., 2014), the early Palaeozoic
77 radiation is clearly visible. It was initiated in the late Precambrian and terminated in the
78 Devonian. Depending on the statistical techniques used, palaeobiodiversity curves indicate that
79 the Cambrian Explosion and the GOBE are either two clearly distinguishable ‘events,’ or that
80 they both belong to a single, continuous radiation (e.g., Alroy et al., 2008). The late Cambrian
81 ‘Furongian Gap,’ that is visible between the Cambrian Explosion and the GOBE, is possibly
82 only due to a sampling artefact, because upper Cambrian sediments are relatively rare and
83 palaeontological investigations on this interval, sporadic (Harper et al., 2019).

84 In addition, many textbooks indicate that the evolution of life on Earth has been interrupted
85 by five global mass extinctions. Raup and Sepkoski (1982) quantitatively evidenced significant
86 excursions of the Phanerozoic distribution of extinction rate of marine families. From this, it is
87 widely believed the existence of a series of mass extinctions though the Palaeozoic at the end-
88 Ordovician, the Frasnian-Famennian (Late Devonian) and the end-Permian (Fig. 1) that
89 triggered deep changes in extant ecosystems. Indeed, many scientists are working on (and
90 maybe also financed because of) the so-called sixth mass extinction occurring today, in
91 particular within the context of global climate change and habitat destruction.

92 Sepkoski’s datasets were based on marine faunas, mostly invertebrates. The Cambrian
93 Explosion and the GOBE were both defined on the basis of diversifications of marine
94 organisms. In addition, the concept of five major mass extinctions during the Phanerozoic was
95 originally based on extinction patterns in marine life. It was only later that it became clear that
96 data on other fossil groups, in particular plants, display very different evolutionary patterns
97 (e.g., Niklas et al., 1983; Knoll et al., 1984; Wing and Tiffney, 1987; Traverse, 1988).
98 Terrestrial organisms, such as insects, tetrapods, or land plants, show not only different
99 biodiversification patterns (with no obvious correlation with the two major Palaeozoic and

100 Mesozoic radiations of marine invertebrates), but also different extinction scenarios (e.g.,
101 Benton, 1985, 1987; Knoll, 1986). Land plants, in particular, did not suffer from the five global
102 mass extinctions, but only from two, at the end of the Carboniferous and at the end of the
103 Guadalupian (Fig. 1). This is clearly indicated by the large-scale databases available for land
104 plants (e.g., Cleal and Collinson *in* Benton, 1993; Anderson et al., 2007), that have allowed
105 evolutionary floras to be distinguished, similarly to those in the Sepkoski-type databases (e.g.,
106 Cleal and Cascales-Miñana, 2014; Cascales-Miñana et al., 2018).

107 The comparison of large-scale databases of evolutionary faunas and floras indicates an
108 apparent delay of over 100 million years (Fig. 1): whereas the marine faunas massively
109 diversified at the Precambrian-Cambrian boundary, the terrestrial floras only developed during
110 the Ordovician-Silurian boundary interval, with the first mesofossil evidence for land plants in
111 the fossil record at about this time. Based on this scenario, land plants apparently played no role
112 in the Cambrian Explosion and the GOBE.

113 In the last few decades, new data on earliest life on land have been published. For example,
114 Wellman and Strother (2015) summarized the data on terrestrial biotas prior to the origin of
115 land plants, indicating that fossil evidence of terrestrial eukaryotes is present at about 1.1. Ga
116 (e.g., Strother et al., 2011). Direct evidence of the earliest terrestrial biotas in the Phanerozoic
117 consists of palynomorphs from the Cambrian of Laurentia, predating the first occurrence of
118 land plant macrofossils in the Silurian (e.g., Strother et al., 2004). Similarly, Kennedy and
119 Droser (2011) presented evidence of animals from the lower Cambrian non-marine fluvial
120 deposits, indicating that functioning terrestrial ecosystems were concurrent with the early
121 Cambrian marine radiations.

122 There is now an extensive fossil record of dispersed spores (cryptospores included) that are
123 considered to be derived from early land plants. The oldest cryptospores are from the Dapingian
124 (Middle Ordovician) of Argentina (Rubinstein et al., 2010), and similar cryptospore
125 assemblages have to date been reported in the Middle and Upper Ordovician from most
126 palaeocontinents (Fig. 2). The currently available fossil evidence points to a rapid distribution
127 and diversification of non-vascular, early land plants during the Middle and Late Ordovician.

128 Masuda and Ezaki (2009) were among the first to link the bio-invasion of land with the
129 Ordovician radiation in the oceans, by arguing that the strontium isotopic composition that
130 markedly changed at the Cambrian-Ordovician transition interval must be placed in context
131 with the coeval drastic changes of the terrestrial environments. The bio-invasion of the
132 continents was undoubtedly one of the most consequential and significant geobiological events
133 in Earth history. In particular, the Ordovician was an interval of major changes in terrestrial

134 ecosystems. These changes have recently been linked to the marine radiation (GOBE) that took
135 place in the global oceans (Servais and Harper, 2018). It becomes more and more evident that
136 the changes on land also affected life in the oceans. Algeo et al. (2016) proposed that one of the
137 key triggers of the marine radiation was probably the palaeobotanical change in the terrestrial
138 biotas. Several authors have linked the GOBE to global cooling (e.g., Vandenbroucke et al.,
139 2010; Rasmussen et al., 2016) that was possibly due to the greening of the continents during
140 the Ordovician (e.g., Lenton et al., 2012), in addition to palaeogeographical changes that had a
141 major impact on the global climate (e.g., Nardin et al., 2011).

142 The present paper attempts to review all available data on the diversification of early land
143 plants during the Ordovician in the early Palaeozoic context. It summarizes the data from
144 mesofossils, macrofossils and microfossils, plant phylogenetics and organic geochemistry, and
145 attempts to link these data with activities in the marine ecosystem, recognized as the GOBE.
146 What, therefore, was the Great Ordovician Biodiversification of land plants? Was there a
147 palaeobotanical trigger of the GOBE?

148

149 **2. The evolutionary context of land plants**

150

151 A number of recent papers discuss the evolutionary context of land plants. As the focus of
152 the present paper is not plant phylogenetics, the reader is referred to these latter papers (e.g.,
153 Wickett et al., 2014; Edwards and Kenrick, 2015; Delwiche and Cooper, 2016; Harholt et al.,
154 2016; Gerrienne et al., 2016; Puttick et al., 2018; Cascales-Miñana et al., 2019).

155 Land plants include photosynthetic eukaryotic multicellular organisms and are characterized
156 by the following synapomorphies: alternation of multicellular gametophyte(s) and sporophyte;
157 presence of multicellular sexual organs (archegonium and antheridium); development of the
158 zygote into an embryo within the archegonium; a plant body protected by a cuticle, one or
159 several multicellular sporangium; sporopollenin within the wall of the spore (Pirani and Prado,
160 2012; Gerrienne et al., 2016 and references therein). Several lineages have been proposed as
161 the closest living relative to land plants, such as the Charophyceae, the Coleochaetophyceae
162 and the Zygnematophyceae (see discussion in Gerrienne et al., 2016). Recently, De Vries and
163 Archibald (2018) indicated that the land plants evolved from streptophyte algae most closely
164 related to extant Zygnematophyceae and that over a billion year ago a wide range of algae
165 already successfully established themselves on land. Harrison (2016) also noted that the major
166 extant lineages of land plants were established at least c. 360 million years ago, including
167 hornworts, liverworts and mosses (bryophytes), as well as lycophytes, monilophytes and

168 spermatophytes (vascular plants). However, the precise phylogenetic relationships of different
169 groups of charophyte algae, bryophytes and vascular plants is highly debated (e.g., Harrison,
170 2016, figs. 1-2; *versus* Gerrienne et al., 2016, figs. 1-2; Puttick et al., 2018, fig. 1).

171 Gerrienne et al. (2016) revised all Palaeozoic embryophyte lineages in terms of molecular
172 clock data and noted the first fossil evidence for each group. As illustrated in Figure 3, the first
173 macrofossil records of the different lineages date back to an interval between the Silurian and
174 Carboniferous. However, molecular clock data indicate much earlier origins of the different
175 lineages, at least in the Cambrian and possibly in the Precambrian (Fig. 3) (Clarke et al., 2011;
176 Zhong et al., 2014; Morris et al., 2018).

177 The first fossil evidence for land plants comes from the microfossil record (see below), that
178 is usually based on spores, but also phytoclasts (such as cuticles), and that is very abundant in
179 the Palaeozoic. This microfossil record predates the macrofossil record and goes back at least
180 to the Ordovician, and probably also the Cambrian, if not the Precambrian. Some Cambrian and
181 Ordovician acritarchs may indeed be spores that have been produced by organisms at the green
182 algae – land plant transitions. For instance, some acritarchs have very similar morphologies
183 (and sometimes have been attributed) to spores of chlorophycean and zygnematacean algae
184 (e.g., Colbath and Grenfell, 1995). It is thus logical that some of the Cambrian cryptospores,
185 although not clearly comparable to spores produced by land plants, may have been produced
186 during the transition from algae to plants.

187 A number of subdivisions to distinguish the major evolutionary advances in the plant fossil
188 record prior to the Carboniferous have been defined (Fig. 3). Gray (1993) together with Kenrick
189 and Crane (1997) established the Eoembryophytic, Eo- and Eutracheophytic phases.
190 Subsequently, Gerrienne et al. (2016) additionally introduced the Proembryophytic as a new
191 term, applying to the very long period of time during which the green algae ancestor of land
192 plants acquired all the evolutionary characters that ultimately allowed their terrestrialization.
193 The terms Eotracheophytic, Eophytic, Paleophytic and Mesophytic Floras were defined by
194 Cleal and Cascales-Miñana (2014) to distinguish these Evolutionary Floras (Fig. 1). On the
195 other hand, Strother et al. (2010) defined the microbial (Precambrian and early Cambrian),
196 bryophytic (early Cambrian to Late Ordovician, based on the occurrence of cryptospores
197 thought to belong to bryophyte-like plants), tracheophytic (Late Ordovician to Middle
198 Devonian, based on the presence of trilete spores, thought to belong to vascular land plants)
199 and lignophytic landscapes (Fig. 3). The Ordovician therefore corresponds to the ‘bryophytic
200 landscape’ of Strother et al. (2010), or to the ‘eoembryophytic landscape’ of Gray (1993) and

201 Kenrick and Crane (1997), i.e., to an interval when real land plants (embryophytes) were surely
202 present, but probably not yet vascular (see below).

203

204 **3. Mesofossil evidence for earliest (Ordovician) land plants**

205

206 Plants leave both a macrofossil (macroscopic remains of plant fossils) and a microfossil
207 record (through dispersed spores -see below - and other remains of microscopic size). The
208 Ordovician fossil record can, at best, be considered as a mesofossil record, i.e., consisting of
209 fragments of an entire plant. Real plant macrofossils have so far only been recovered from
210 Silurian and younger sediments.

211 Compared to the very abundant dispersed-spore microfossil record, the plant macrofossil
212 record of the Silurian is very meagre. This is also the reason why, until recently, spores
213 considered to be derived from land plants of Middle Ordovician age (about 475 Ma) predated
214 the earliest land plant macrofossils (from the late Silurian, about 425 Ma) by several tens of
215 million years. This apparent anomaly was thought to be at least partly due to these early plants
216 being small and delicate, with low preservation potential (e.g., Kenrick et al., 2012). The
217 scarcity of pre-Devonian terrestrial deposits has also been invoked as an explanation, although
218 numerous examples have been reviewed by Davies and Gibling (2010). However, a review of
219 the available evidence suggests an alternative explanation for the apparent discrepancy between
220 the palynological and macrofloral records.

221 The oldest fossil plant remains (other than cryptospores) with adaptations to a partly
222 subaerial life are small sporangia from the Upper Ordovician of Oman, attributed to the late
223 Katian, c. 447 Ma (Wellman et al., 2003) (Fig. 2). It is not certain that the sporangia spent a
224 significant time out of water but they were nevertheless presumably capable of releasing their
225 cryptospores into the air. A little younger stratigraphically are short, slender axes from the
226 Hirnantian of Poland (c. 445 Ma), some of which appear to have terminal sporangia (Salamon
227 et al., 2018). These small Polish fossils are poorly preserved but show a striking morphological
228 similarity to the remains of polysporangiate ('cooksonioid') plants that occur in the Silurian.
229 There is then a stratigraphical gap in the macrofossil record until the Wenlock, where
230 cooksonioid slender dichotomous axes with terminal sporangia have been reported by Libertín
231 et al. (2018) from the Sheinwoodian of the Czech Republic (dated at c. 432 Ma) and by Edwards
232 et al. (1983) from the Homerian of Ireland (dated at 428 Ma); followed by further occurrences
233 in the Ludlow Series of Wales (e.g., Edwards et al., 1979; Edwards and Rogerson, 1979;
234 reviewed by Cleal and Thomas, 1995) (Fig. 2).

235 These Silurian remains of eotracheophytic plants show various levels of adaptation to
236 subaerial life, including stomata implying a cuticle cover, a sterome to help support the stem
237 out of water, and vascular tissue for the transport of fluids around the plant (e.g., Edwards and
238 Davies, 1976; Edwards et al., 1986, 1992; Brodribb et al., 2017; De Vries and Archibold, 2018).
239 However, no unequivocal evidence of the lower parts of these early plants has been reported,
240 such as roots or rhizomes; it is only in the latest Silurian (Přídolí) and Devonian Eophytic Floras
241 (*sensu* Cleal and Cascales-Miñana, 2014) that more complete plant remains including rhizomes
242 are found (e.g., Lele and Walton, 1961; Raven and Edwards, 2001). This coincides with a major
243 diversification in the macrofloral record, not only of the Eotracheophyta but also of the newly
244 emerging zosterophylls and lycophytes (Cascales-Miñana, 2016), and is referred to by Kraft et
245 al. (2019) as the “Initial Plant Diversification and Dispersal Event”. The appearance of plant
246 remains including their basal parts thus seem to coincide with this diversification of vegetation
247 fully adapted to subaerial conditions.

248 Cryptospores with a desiccation-proof outer coating would have given aquatic plants a clear
249 adaptive advantage by allowing wider dispersal, especially for those growing in shallow,
250 ephemeral areas of water. However, the main, subaquatic parts of such plants would have
251 lacked cuticles or other features that would aid in their preservation as macrofossils; even the
252 sporangia, if they were only just protruding out of the water, may not have needed adaptations
253 to avoid significant desiccation. But cryptospore dispersal would have been enhanced if the
254 sporangia were pushed further out of the water on subaerial sporophyte axes. Such axes would
255 presumably have to develop adaptations for subaerial exposure, which would have increased
256 their preservation potential, but the gametophyte and maybe the non-reproductive part of the
257 sporophyte would remain subaquatic and thus rarely fossilized. However, subsequent selection
258 pressure to further improve cryptospore dispersal by lifting the sporangia further away from the
259 water would result in even taller subaerial sporophyte structures until they became the dominant
260 part of the plant’s life cycle. This would result in plants becoming progressively more subaerial
261 and less aquatic, initially to enhance cryptospore dispersal, but eventually resulting in them
262 being pre-adapted to a more or less fully subaerial existence.

263 These early cryptophyte plants were probably, therefore, more or less aquatic, with only the
264 sporangium-bearing sporophyte structures likely to be fossilized. However, with the selective
265 pressure for more of the sporophyte to protrude out of the water, progressively more fossilizable
266 tissue would be produced. This would produce a sequential fossil record of these plants similar
267 to what we see (Edwards et al., 2014): initially there are just dispersed cryptospores, followed
268 by isolated sporangia and then sporangia on increasingly elongate sporophyte axes, and then

269 remains of the lower parts (rhizomes) of the plants become preserved. Fully terrestrialized
270 plants may not have appeared until the very late Silurian, which is also when the first evidence
271 of wildfire appears (Glasspool et al., 2004), but semi-aquatic plants with some structures
272 adapted to subaerial exposure had been evolving for some 25 Ma years prior to this. The
273 abundant and diverse dispersed Ordovician and lower Silurian cryptospore microfloras suggest
274 that transitional vegetation represented a significant biomass in shallow aquatic environments,
275 but it would be little representation in the macrofossil record.

276 In terms of plant palaeobiodiversity, the intervals with very few localities yielding plant
277 fossil fragments in the Late Ordovician and Silurian do provide only very few specimens and
278 no formally described taxa, which limits the construction and use of diversity curves in the
279 Silurian (Fig. 1). Cascales-Miñana (2016) illustrated the general trajectory of plant diversity at
280 the genus level, showing the slow increase of diversity during the Silurian, and the massive
281 steps of diversification in the Devonian. With two single Ordovician occurrences of land plant
282 fragments (mesofossils) in the Ordovician, it is too early to draw a diversity curve.

283

284 **4. Microfossil evidence of Ordovician land plants**

285

286 In terms of the fossil record, the microfossil evidence provides by far the most significant
287 amount of data on Ordovician land plants. However, the ongoing discussion on the precise
288 biological affinities of dispersed spores makes it difficult to fully understand the evolution and
289 the timing of the colonization of the plants in the Ordovician. When and where do we have the
290 first land plant derived spores? In the Ordovician or already in the Cambrian?

291 The first palynomorphs (pollen, spores, etc.) derived from land plants have probably mostly
292 been described as ‘acritarchs.’ The informal group of acritarchs was defined by Evitt (1963) to
293 group together organic-walled microfossils of unknown biological affinity. The group thus
294 includes, by definition, also non-marine forms, and logically all simple spherical microfossils
295 that cannot be assigned to a known taxonomical group. Several of the Palaeozoic acritarch
296 morphotypes can be related to various algal groups, and many are indeed considered members
297 of the marine organic-walled microplankton (e.g., Martin, 1993; Servais, 1996; Strother, 1996).
298 Some acritarchs are possibly related to diverse groups of green algae, or to organisms that are
299 transients between green algae and land plants. Mendelson (1993), for example, indicated that
300 some forms attributed to the acritarchs actually represent the phycmata of prasinophycean
301 algae. Colbath and Grenfell (1995) and Talyzina and Moczydlowska (2000) compared some of
302 the morphologies and wall ultrastructures of early Cambrian acritarchs with those of various

303 green algae, such as chlorophyceans or zygnemataceans. Some Early Ordovician taxa, such as
304 *Virgatasporites* and *Attritasporites* are of unknown affinities, but their terminology already
305 indicates that their morphology is comparable to land plant derived spores. Combaz (1967),
306 who described both taxa from the Tremadocian of Algeria, considered them spores of land
307 plants, a view that has not been sustained. However, this illustrates that some early Palaeozoic
308 acritarchs are logically considered the spores of organisms that are related to earliest land plants.
309 It is thus evident that some of the Precambrian and early Palaeozoic organic-walled, spherical
310 and featureless microfossils attributed to the acritarchs may well derive from earliest land
311 plants, or from spore producing organisms at the algal-plant transition. This dilemma is
312 particularly present in the Cambrian, where spore-like microfossils ('cryptospores') display
313 characters that are not present in the spores of any extant algae; this allowed some authors to
314 suggest that these Cambrian palynomorphs were the desiccation-resistant spores of cryptogams
315 belonging to the charophyte – embryophyte lineage (e.g., Strother, 1991; Strother et al., 2004;
316 Taylor and Strother, 2008).

317 It is also important to note that the spores or spore-like microfossils are sometimes connected
318 to form clusters or even sheets. Strother et al. (2017), for example, described planar sheets of
319 spore dyads from the Middle Ordovician of Utah, USA, as "spore thalli", and considered them
320 to represent a post zygotic growth phase in the life cycle of an ancient charophytic alga that
321 was evolving in response to subaerial conditions. This type of Cambrian-Ordovician
322 palynomorphs that are not clearly identified as miospores derived from land plants led to
323 misunderstandings between palynologists who use different cryptospore definitions. The reader
324 is referred to the detailed historical revision of the concept of cryptospores by Gerrienne et al.
325 (2016). The differing concepts led to a situation where Cambrian cryptospores defined by some
326 authors (without a biological interpretation) are rejected by other authors who do not consider
327 them land plant derived (see Gerrienne et al., 2016 for discussion).

328 Despite this terminological debate, most, if not all, palynologists consider today that most
329 of the Middle Ordovician and younger cryptospores are produced by primitive land plants.
330 Currently the oldest cryptospores with morphological criteria allowing them to be classified as
331 land plant-derived spores (as indicated by Wellman, 2010) occur in the Dapingian (lower
332 Middle Ordovician) from Argentina, dated as c. 473-471 Ma (Rubinstein et al., 2010) (Fig. 2).
333 These Argentinean cryptospores slightly predate the cryptospore occurrence of late Dapingian
334 to early Darriwillian (Llanvirn) age in the Sajir-Hanadir transitional beds from Saudi Arabia
335 (Vecoli et al., 2017). They also predate by ca. 8-12 million years two cryptospore assemblages
336 from the upper Darriwillian: the cryptospores described by Vavrdová (1984) from the Middle

337 Ordovician of central Bohemia, and those described by Strother et al. (1996) from the
338 ‘Llanvirn’ of Saudi Arabia, are present in levels that are now attributed to the upper Darriwilian,
339 i.e., in the upper part of the Middle Ordovician, c. 463-461 Ma (Strother et al., 2015). The Saudi
340 Arabian assemblages from the Hanadir Shale Member have recently been reinvestigated. They
341 display a variety of cryptospore tetrads, dyads and monads. Strother et al. (2015) considered
342 that these cryptospores were produced by early embryophytes, i.e., true land plants, and that
343 they indicate a “bryophyte grade of evolution.”

344 Although the diversity of the oldest cryptospore assemblage from Argentina is moderate
345 (five different genera), this discovery implies that the colonization by plants is presumably
346 older, and that it may have occurred during the Early Ordovician or even during the Cambrian.
347 The first occurrences of land plant derived spores in the Middle Ordovician in Argentina, the
348 Czech Republic and Saudi Arabia, i.e., from localities in Gondwana or on its periphery, may
349 imply that the first land plants first evolved on this palaeocontinent before dispersing to
350 Avalonia and Baltica (e.g., Steemans et al., 2010; Wellman et al., 2013; Wellman, 2014).

351 Similar cryptospore assemblages have so far been recorded from other upper Middle, but
352 mostly from Upper Ordovician strata in almost all parts of the world. Such cryptospore
353 occurrences are from Gondwanan localities of Libya (e.g., Gray et al., 1982; Gray, 1985, 1988;
354 Richardson, 1988), Saudi Arabia (e.g., Strother et al., 1996, 2015; Wellman et al., 2015),
355 Argentina (e.g., Rubinstein and Vaccari, 2004; Rubinstein et al., 2010), Algeria (e.g., Spina,
356 2014), as well as from microcontinents on the periphery of Gondwana, including Avalonia (e.g.,
357 Wellman, 1996; Steemans, 2001), Armorica *sensu lato* (e.g., Vavrdová, 1984, 1988, 1989,
358 1990) and Turkey (e.g., Steemans et al., 1996). Ordovician cryptospores were also found in
359 localities from the Laurentia palaeocontinent (e.g., Gray and Boucot, 1971; Gray, 1991; Vecoli
360 et al., 2015), from Australia (i.e., the northernmost part of Gondwana located in the northern
361 hemisphere; e.g., Foster and Williams, 1991), China (e.g., Wang et al., 1997; Yin and He,
362 2000), Baltica (Vecoli et al., 2011; Badawy et al., 2014) and Siberia (Raevskaya et al, 2016).
363 The most recent summary of the evolution and geographical distribution of the earliest
364 cryptospores is provided by Wellman et al. (2013). All Middle and Late Ordovician
365 assemblages are very similar in terms of diversity and morphologies, which led Wellman and
366 Gray (2000) and Steemans (2000) to conclude that after the Middle Ordovician, the evolution
367 of cryptospore assemblages was very slow until the early Llandovery, with similar assemblages
368 present on different palaeocontinents during this time interval.

369 The next major step in the fossil record is the earliest occurrence of spores with a trilete
370 mark. Steemans et al. (2009) dated the oldest occurrence of trilete spores back to the Late

371 Ordovician of Saudi Arabia. This presence of trilete spores in the Upper Ordovician has recently
372 been documented with some additional detail by Wellman et al. (2015). Some authors consider
373 the presence of trilete marks as an indicator of vascular plants. However, some extant
374 bryophytes may produce trilete spores. Therefore, the occurrence in the Late Ordovician of
375 trilete spores does not unambiguously indicate the presence of vascular plants. The assumption
376 that the colonization of the land by plants most likely started with bryophyte-like plants in the
377 Middle Ordovician, that became quickly cosmopolitan and colonized the planet during some
378 30 million years and were followed by trilete spores appearing in the Late Ordovician indicating
379 the first vascular plants, can be challenged. Even though it appears highly probable that the
380 earliest plants of the Middle and Upper Ordovician were “bryophyte-like” or “liverwort-like,”
381 as already indicated by Gray (1985), the global picture is far from complete. It is evident that
382 data are almost completely lacking for certain areas, and there is currently a concentration of
383 data from Europe, North America, North Africa and the Middle East (Wellman et al., 2013).

384 In summary, the currently available microfossil record indicates that between the Middle
385 and the Upper Ordovician, cryptospore assemblages included monads, dyads and tetrads, and
386 that these assemblages covered a broad geographic area, if not the entire globe. This first
387 interval of colonization by land plants was named the “eoembryophytic” phase by Gray (1993)
388 and Kenrick and Crane (1997) (Fig. 3), characterized by the earliest evidence of ‘liverwort-
389 like’ plants. Subsequently, with the occurrence of isolated spores, including trilete spores, in
390 the Upper Ordovician, but mostly in the lower Silurian, the probable presence of several basal
391 land plant groups can be assumed, including mosses, hornworts, and possibly early vascular
392 plants.

393 Figure 4 illustrates the most up-to-date diversity curve of Ordovician-Silurian cryptospore
394 genera that are considered to be of land plant origin. The biodiversity curve is plotted against
395 the most recent diversity curve (for marine invertebrates) adapted from the Paleobiology
396 Database. Figure 4 clearly illustrates the delay between the radiation of invertebrates in marine
397 environments and that of land plants in terrestrial environments. It is noteworthy that the
398 diversity of land plants did not suffer from the first of the so-called big five mass extinctions,
399 at the Ordovician-Silurian boundary. Land plant diversity continued to increase, with no
400 perceptible change in the plant fossil record during the end-Ordovician mass extinction.

401

402

403 **5. Geochemical evidence for land plant evolution**

404

405 As indicated above (Figure 3), there is usually a large temporal gap between the molecular
406 (genetic) data and the fossil record. The oldest definite microfossil evidence for different clades
407 of land plants occurs in deposits of Middle Ordovician age (Rubinstein et al., 2010), whereas
408 molecular clock data suggest much earlier origins going back to the Cambrian, with
409 embryophytes possibly originating in the earliest Cambrian or before (Zhong et al., 2014; Fig.
410 3). In addition, a gap between the first microscopic and the first macroscopic fossil remains of
411 land plants is also obvious (Fig. 4): “the first 35 million years of land plant evolution are thus
412 essentially documented on microscopic remains only” (Gerrienne et al., 2016). These gaps can
413 be partially filled with molecular geochemical data: molecular geochemical approaches can
414 provide additional evidence for the presence of land plants in the early Palaeozoic, in particular
415 in those intervals where microscopic or macroscopic remains are absent.

416 Membrane-derived lipids can be fossilised as hydrocarbons under particular environmental
417 conditions (Killops and Killops, 2013). In cases where the fossil molecule carries sufficient
418 similarity to an extant lipid, whose biological affinity is constrained, these fossil molecules can
419 be used as biomarkers (Brocks and Summons, 2003) that carry the potential to document traces
420 of organismic clades long before more robust minerals capable of being fossilized (e.g., shells,
421 skeletons, etc.) or organic materials (e.g., soft body parts, cysts, spores, etc.) were produced by
422 the organisms. For example, organic geochemists recently presented evidence for the attribution
423 of the Ediacara-type fossil *Dickinsonia* as being part of the animal kingdom (Bobrovskiy et al.,
424 2018), a hypothesis that was part of a long-lasting debate among palaeontologists during the
425 last decades. This indicates how valuable biomarkers can be to broaden our understanding of
426 (early) life and its evolution on Earth.

427 Because the reconstruction of early biological evolution, i.e. prior to the advent of
428 skeletonized animals, is strongly dependent on molecular approaches, biomarker studies are
429 well advanced in the Precambrian (in particular to decipher early animal evolution). However,
430 to date they are much less common in the Ordovician or Silurian, when the land plant radiation
431 took place. Therefore, biomarker studies of early land plant evolution are still in their infancy.

432 Given the high taxonomic specificity of sterols in eukaryotic organisms (e.g., Summons et
433 al., 2006) – despite the fact that a small number of bacteria can also biosynthesize steroids (e.g.,
434 Wei et al., 2016) – this compound class provides an evident target for the study of the rise of
435 early land plants. Characteristic steroidal patterns in different environments were found to
436 correspond to broad biosynthetic prevalence. In this regard, Huang and Meinschein (1979) were
437 among the first to observe a strong predominance of C₂₉ steroids in soils and higher plants,
438 which corresponds to the C₂₉ steroidal dominance in many coals (e.g., Püttmann et al., 1988).

439 Indeed, sitosterol and stigmasterol are the predominantly biosynthesized sterols in many plants
440 (Volkman, 2005), leading to the ‘phytosterol’ terminology for C₂₉ structures ethylated at C-24.
441 However, given the fact that phytosterol biosynthesis is also common in many green algae
442 (Volkman, 1986; Kodner et al., 2008) sedimentary C₂₉ steranes are common in Ediacaran rocks
443 predating the rise of plants (Hoshino et al., 2017) and cannot currently be used as a faithful
444 molecular indicator for the evolutionary rise of plants. Potentially more relevant information
445 may be hidden amongst sedimentary alkanes, a compound class that typically carries little
446 specific information on precursor biota. Sedimentary alkanes mostly derive from cellular fatty
447 acids (Peters et al., 2005), but can also be directly biosynthesized as epicuticular waxes to
448 enhance desiccation resistance (Eglinton and Hamilton, 1967). The composition of free lipids
449 in bryophytes, i.e., early divergent non-vascular plants, has been reported recently in a number
450 of studies. Nott et al. (2000) discovered a link between C₂₃/C₃₁ *n*-alkane ratios with the
451 abundance of *Sphagnum* mosses, whereas Baas et al. (2000) remarked on a pronounced
452 predominance of C₂₃ and C₂₅ *n*-alkanes in most mosses of the same species with only one
453 exception in which C₃₁ was the dominant *n*-alkane; but no relation between habitat and lipid
454 composition was found. More recently, Inglis et al. (2015) postulated the use of the *n*-C₂₃/*n*-C₃₁
455 ratio to trace the occurrence of *Sphagnum* mosses and waterlogged environmental conditions
456 in peaty sediments. The differences in the main alkane constituents in submergent/floating
457 plants vs. terrestrial plants, i.e. C₂₃ and C₂₅ vs. C₂₉ and C₃₁, respectively, was introduced as a
458 marker to differentiate terrestrial vs. non terrestrial/submergent plant input (Ficken et al., 2000).

459 In opposition to simple(r) embryophytes/bryophytes, the input from higher plants into the
460 (molecular) fossil record is – among others – documented via the occurrence of long chained
461 alkanes, typically with C₃₁ or longer hydrocarbon chains with a pronounced odd-over-even
462 predominance, derived from their epicuticular waxes (Eglinton and Hamilton, 1967). Within
463 the C₂₉ steroids (*stigmasteroids*) a distinction between those molecules produced in green algae
464 and those biosynthesized in higher plants can be made. The ethyl-group (C₂H₅) attached to C-
465 24 has two stereochemical configurations (α or β). Green algae predominantly, but not
466 exclusively, produce one type (β), whereas higher plants evolved to largely form the other (α)
467 (e.g., Marsan et al., 1996; Nes, 2011). While the general biosynthetic pathways are well
468 understood (e.g., Haubrich et al., 2015; Nes, 2011; Volkman, 1986), it is still unknown why
469 this distinction occurs and whether these features are preserved in the fossil record. Given that
470 the analytical determination of these molecular differences is complicated and affords a lot of
471 time and laboratory work in biological samples, their applicability as biomarkers in geologically
472 aged rocks has not been systematically tested and remains theoretical at best. In addition,

473 Haubrich et al. (2015) analysed the evolution of sterol biosynthesis in the ‘green lineage’ in
474 regard to the enzymatic capacities encoded in their DNA. They argue that the enzymes needed
475 for the formation of phytosterols might already have existed in the last eukaryotic common
476 ancestor (LECA). Interestingly, while the possession of SMT2 – an enzyme that is responsible
477 for further side chain alkylation at C-28 position – is exclusive to the green lineage, the
478 biosynthetic pathway from a protosterol to the C₂₉ sterol is more similar to green algae and
479 fungi than it is in green algae and land plants (Haubrich et al., 2015). More precisely, in higher
480 plants, two enzymes, SMT1 and SMT2, are needed to successively synthesize C₂₉ sterols
481 (Bouvier et al., 2005; Neelakandan et al., 2009), while in green algae, only one bifunctional
482 enzyme is needed to perform the C-24-alkylations.

483 Despite the advances made in recent years, only a few studies have focused on the
484 application of biomarkers towards increasing our understanding of the timing of early land plant
485 evolution (Versteegh and Riboulleau, 2010). There is currently no definite occurrence of
486 biomarkers related to land plants from the Precambrian and Cambrian. Romero-Sarmiento et
487 al. (2011) investigated aliphatic and aromatic biomarkers from Upper Ordovician to Lower
488 Devonian sediments to decipher terrestrialization and the rise of land plants. While terrestrial
489 biomarkers could be clearly recognized in the middle Silurian–lower Devonian samples, their
490 presence in Upper Ordovician to lower Silurian strata was less certain, principally as a
491 consequence of much lower relative abundances. Most significantly, Romero-Sarmiento et al.
492 (2011) noted that the land plant biomarkers show a good correlation with the occurrence and
493 abundance of cryptospores and trilete spores, alleged to derive from bryophytes and
494 tracheophytes. More recently, Spaak et al. (2017) analysed the Middle Ordovician of the
495 Canning Basin, Australia, including palynological and geochemical approaches. The authors
496 identified different biomarkers and related some of them to typical bryophytes, suggesting that
497 these derive from the plants that also produced the cryptospores recovered from the same
498 geological units.

499 These initial studies point towards the high potential of biomarker investigations in
500 supporting palynological approaches geared towards understanding the origin and rise of land
501 plants. With the rapid evolution of geochemical methods, it is plausible that future studies
502 should clarify when land plants first appeared, and which clades emerged first. Such
503 geochemical investigations may also have the potential to connect the different cryptospores to
504 the organisms that produced them, across the evolutionary transition from green algae to real
505 land plants.

506

507 **6. A link between land plant evolution and the GOBE of marine ecosystems**

508

509 The GOBE was defined in the context of the evolution of marine ecosystems limited to the
510 animal kingdom, mostly related to marine invertebrates (Webby, 2004; Harper, 2006). The
511 rapid increase of marine (animal) biodiversity during the Cambrian and Ordovician apparently
512 occurred at least 100 myr before the origin of biodiversity of land plants (Fig. 4). But how did
513 the terrestrialization of the continents impact on biological evolution in the oceans? How did
514 the terrestrial and marine biospheres interact? Algeo et al. (2016) raised the question that if the
515 GOBE was triggered by a tectonic or a palaeobotanical driver, what was the impact of plants
516 on the marine biosphere?

517 An obvious hypothesis is to assume that with the terrestrialisation of land plants, oxygen
518 levels would rise and the CO₂ concentrations would decrease. In many palaeoclimate models
519 (e.g., GEOCARB/GEOCARBSULF: Berner et al., 1991, 1994, etc.; COPSE: Bergman et al.,
520 2004) *p*CO₂ values diminish during the Palaeozoic. Some of the climate models include forcing
521 factors, including land plants, that influence the model output (e.g., François et al., 2005).
522 Lenton et al. (2018), for example, updated the COPSE model, by changing the values of original
523 forcing factors, including plant evolution, plant effect on weathering, and plant stoichiometry.
524 However, what are the datasets used in these models? How precise are these data?

525 The global palaeogeographical (phytogeographical) distribution of land plants during the
526 Ordovician and Silurian is rather poorly known. Most probably, the first primitive, non vascular
527 land plants grew near fresh-water rivers systems and lakes and covered limited surface areas
528 (similarly to the first pioneer vegetation on surfaces covered by volcanic rocks, for example).
529 A more extensive coverage of land plants on extended surfaces, including higher altitudes, may
530 not have occurred during the Ordovician. Therefore, the precise palaeoecological distribution
531 of land plants remains completely unknown. Although it seems that cryptospores derived from
532 bryophyte-like plants were present on most palaeocontinents in the Late Ordovician, it is not
533 understood, for example, if and when the bryophytes entirely covered the continents. Was this
534 during the Late Ordovician, or earlier, or indeed later?

535 On the other hand, the impact of the appearance of the early land plants on CO₂
536 concentrations and O₂ values is also not clearly understood. Furthermore, it is completely
537 unknown what might have been the ratio of O₂ production on land versus O₂ production in the
538 oceans (by the phytoplankton). It is commonly assumed that today 50 to 85% of the oxygen in
539 the Earth's atmosphere is produced by the phytoplankton, but it is unknown what these
540 proportions might have been during the Palaeozoic (e.g., Servais et al., 2016a).

541 Did the land plants or the marine microphytoplankton (and picoplankton) provide the oxygen
542 that might have fuelled the GOBE? Edwards et al. (2017, fig. 2) modelled O₂ levels using
543 GEOCARB and photosynthetic fractionation approaches (Figure 5 A). They assumed that
544 atmospheric oxygen increased during the Darriwilian (Middle Ordovician) and continued to
545 rise to near modern levels by the Katian (Late Ordovician). Such values would thus correlate
546 with the rise of land plants as suggested by the massive arrival and distribution of the
547 cryptospores. Edwards et al. (2017) noted a strong temporal link between the GOBE and rising
548 O₂ concentrations, which may suggest that the terrestrial and marine realms are linked directly
549 through oxygen levels. Edwards et al. (2017) thus hypothesized that oxygenation may have
550 triggered the GOBE. Similarly, Saltzman et al. (2011) already a few years earlier assumed that
551 a pulse of atmospheric oxygen in the late Cambrian can be correlated with the onset of the
552 GOBE, and in particular triggering the ‘Ordovician Plankton Revolution’ (Servais et al., 2008,
553 Klug et al., 2010; Saltzman et al., 2011). However, this ‘oxygenation pulse’ in the late Cambrian
554 cannot be related to the evolution of land plants, but may instead be linked only to the
555 phytoplankton radiation that occurred at that time (Nowak et al., 2015; Servais et al., 2016b).

556 Most geochemical models indicate that CO₂ levels decrease during the Early Palaeozoic
557 (e.g., Bergman et al., 2004). While land plants logically impact on O₂ levels, because they
558 produce oxygen, they also reduce CO₂ levels. In addition, they enhance calcium-magnesium
559 silicate weathering. Therefore Lenton et al. (2012) suggested that the radiation of land plants
560 during the Ordovician was a major trigger for the decrease of *p*CO₂, and thus for the cooling
561 that occurred during the Ordovician. Lenton et al. (2012) proposed that the evolution of the first
562 land plants could explain important Ordovician global changes in biodiversity through their
563 effect of silicate weathering. Furthermore, Lenton et al. (2012) noted that geological factors
564 (such as tectonics) may impact on the long-term cooling during the Ordovician, but not the
565 short event of the Hirnantian extinction. Lenton et al. (2012) assumed that the first land plants
566 could only have indirectly contributed to the marine mass extinction in the Late Ordovician.
567 The increased diversity of land plants (Figure 4) may confirm such a scenario, but as with the
568 O₂ levels, we do not precisely know what the proportionate contribution of the phytoplankton
569 and that of the land plants was to global CO₂ levels.

570 Land plants most probably had an impact on the cooling for the Ordovician biospheres,
571 including the oceans (Figure 5 B), but the importance of land plants in this cooling process was
572 possibly of minor importance. Other parameters have been considered more significant for
573 climate change, in particular in the long-term. For example, Nardin et al. (2011) suggested that
574 changes in palaeogeography and the exposure of fresh volcanic rocks on continents are required

575 to explain the large decrease of $p\text{CO}_2$ during the Ordovician. These authors considered that the
576 weathering of fresh volcanic rocks was responsible for one third of the Late Ordovician
577 atmospheric CO_2 decrease, while the movement of the continents, in particular the motion
578 through the intertropical convergence zone of several palaeocontinents (such as Baltica), was
579 mainly responsible for the drop of CO_2 levels and concomitant climate change.

580 It is now largely accepted that the climate did cool during the Ordovician, as has been
581 suggested in several recent studies (e.g., Trotter et al., 2008; Vandenbroucke et al., 2010; Nardin
582 et al., 2011; Rasmussen et al., 2016). However, it remains uncertain how much of this cooling
583 can be related to the development of land plants on the continents and to their impact on CO_2
584 consumption and continental surface weathering. As already indicated by Algeo et al. (2001),
585 the effects of weathering processes on land were probably very important during the Devonian.
586 However, considering the minute plants present in the Ordovician and Silurian, probably
587 limited to restricted surfaces, and displaying an underdeveloped rooting system, it is rather
588 difficult to estimate the effects of earliest, primitive land plants on the enhanced calcium and
589 magnesium silicate weathering, as well as on CO_2 consumption and O_2 production at a global
590 level during this early interval of land plant evolution. The vegetational cover was probably
591 limited (and so far unknown for the Late Ordovician).

592 The rising global sea-level was another of the possible triggers of the GOBE. With extensive
593 continental spreading and a large number of flooded epicontinental seas, the diversification and
594 speciation of marine invertebrates were at their maximum during the Middle Ordovician, before
595 sea-level dropped (Figure 5 C). It is difficult to relate the Ordovician invasion of land plants to
596 sea-level changes, but it may be that the availability of large continental surfaces following sea-
597 level fall provided potential habitats for early land plant vegetation.

598 On the other hand, the very significant strontium isotope shift ($^{87}\text{Sr}/^{86}\text{Sr}$) in Ordovician sea-
599 water between the Middle and Late Ordovician (Figure 5D) has been associated with
600 weathering of fresh volcanic rocks on the continents (Young et al., 2009; Saltzman et al., 2014).
601 This important shift also correlates with the onset of land plant vegetation. Did the first
602 primitive land plants have a major impact on weathering processes, and was this major
603 strontium isotope shift linked, at least partly, to the terrestrialisation of land plants?

604

605 **7. Conclusion**

606

607 During the Cambrian, including the so-called 'Cambrian Explosion,' the marine biosphere
608 changed dramatically. However, there is, to date, no definite evidence of land plants in this time
609 interval. Although molecular clock studies suggest an origin of land plants as far back to at least
610 to the early Cambrian, there are no Cambrian records that clearly indicate the presence of land
611 plants. Similarly, no biomarker studies providing evidence for the presence of land plants in the
612 Cambrian are so far available. Nevertheless, several types of cryptospores are recorded from
613 the Cambrian and Lower Ordovician, and they may represent spores produced by organisms
614 during the algal-plant transition. Such spores were present during the Cambrian and Early
615 Ordovician.

616 The emergence and diversification of land plants clearly took place during the Ordovician,
617 with the presence of cryptospores that can be related to land-plants (similar to bryophytes)
618 starting at the base of the Middle Ordovician. These occurrences suggest that the emergence of
619 land plants may have started earlier. Miospores with trilete marks (considered to be typical of
620 vascular plants, but also present in some bryophytes) appear for the first time in the Late
621 Ordovician. The oldest macroscopic fragments of land plants appear also at about the same
622 time; the oldest sporangia being so far the first minute remains of primitive organisms
623 resembling cryptophytes. This oldest palaeontological evidence of land plants, marked by
624 micro- and subsequently by mesofossils, during the Ordovician, is now also confirmed by
625 geochemical studies on biomarkers that are clearly derived from land plants. However, these
626 investigations are still in their infancy, and the huge potential of biomarker studies has yet to
627 be fully exploited.

628 By the end of the Ordovician, most continents were probably partly covered by primitive
629 land plants, as cryptospores related to these plants are now found on most palaeocontinents.
630 However, it is largely unknown how much of the earth surface was covered, in particular at
631 higher altitudes. With the first macroscopic fossils of land plants discovered from Upper
632 Ordovician horizons at different localities on the Gondwanan margin, terrestrialization of the
633 flora was clearly underway. However, in comparison to the marine ecosystems, the emergence
634 of land plants and of terrestrial ecosystems was clearly delayed by about 100 myr.

635 Significantly, the evolution and rapid biodiversification of the early land plants appears not
636 to have been interrupted by the first of the five major marine mass extinctions. Plants continued
637 to diversify without any major loss of taxa. The end-Ordovician mass extinction is simply not
638 recorded in the Early Palaeozoic floral record. Although it is evident that the arrival of land
639 plants and the terrestrialization must eventually have had a significant impact on global
640 geochemical cycles, as well as on O₂ and CO₂ levels, the available data are currently too sparse

641 to allow definite conclusions and to propose (hypothetical) models, in particular concerning the
642 impact of land plants on the global climate of the Ordovician.

643

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645

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656

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1075 **Figure legends**

1076

1077 **Fig. 1.** Palaeozoic models of Evolutionary Faunas (A) and Floras (B) compared. Vertical red
1078 and green lines indicate the ‘Big Five’ marine mass extinctions and the main plant biotic crises,
1079 respectively. A. Based on Sepkoski (1981). B. Based on Cascales-Miñana and Cleal (2014).
1080 Modified from Cascales-Miñana et al. (2018). GOBE (Great Ordovician Biodiversification
1081 Event) highlighted in grey box.

1082

1083 **Fig. 2.** Earliest evidence of land plants. Diagram summarizes key Silurian and Ordovician
1084 fossil records. References: 1. Edwards (1979), 2. Bodzioch et al. (2003), 3. Rickards (2000), 4.
1085 Kotyk et al. (2002), 5. Edwards et al. (1983), 6. Libertín et al. (2018), 7. Salamon et al. (2018),
1086 8. Steemans et al. (2009), 9. Wellman et al. (2003), 10. Raevskaya et al. (2016), 11.
1087 Snigirevskaya et al. (1992), 12. Vavrdová (1984), 13. Strother et al. (1996), 14. Vecoli et al.
1088 (2017), 15. Rubinstein et al. (2010).

1089

1090 **Fig. 3.** Basalmost evolutionary framework of land vegetation. Bryophytic, tracheophytic and
1091 lignophytic landscapes as described by Strother et al. (2010). Eoembryophytic and
1092 Eutracheophytic steps of plant evolution as defined by Gray (1993). Data from Gerrienne et al.
1093 (2016, and references therein).

1094

1095 **Fig. 4.** Comparison of the apparent genus-level dynamics of marine (A) and land (B) diversity.
1096 Figure depicts the fluctuations of total (TD) and normalized diversity (ND) according to Cooper
1097 (2004). A. Data from PaleoDB (<https://paleobiodb.org/#/>). Download includes regular taxa
1098 from any marine environment only (performed on 20 November 2018). B. Adapted from
1099 Cascales-Miñana (2016). Data from Wellman et al. (2013).

1100

1101 **Fig. 5.** General overview of Ordovician geobiosphere dynamics. A-D. Abiotic parameters. A.
1102 Atmospheric O₂ fluctuations (%). Extracted from Edwards et al. (2017) and Stigall (2017). B.
1103 Main fluctuations of temperature (T°C). Extracted from Algeo et al. (2016). C. Sea-level curve
1104 (m above PD). Based on Haq and Schutter (2008). D. Global curve of strontium isotopes (⁸⁷Sr
1105 /⁸⁶Sr). Based on Shields and Veizer (2004). See Servais et al. (2010, and reference therein) for
1106 further details. E-F. Genus-level diversity patterns of total (TD) and normalized diversity (ND)
1107 of marine environments and spores, respectively. Data as in Fig. 4.

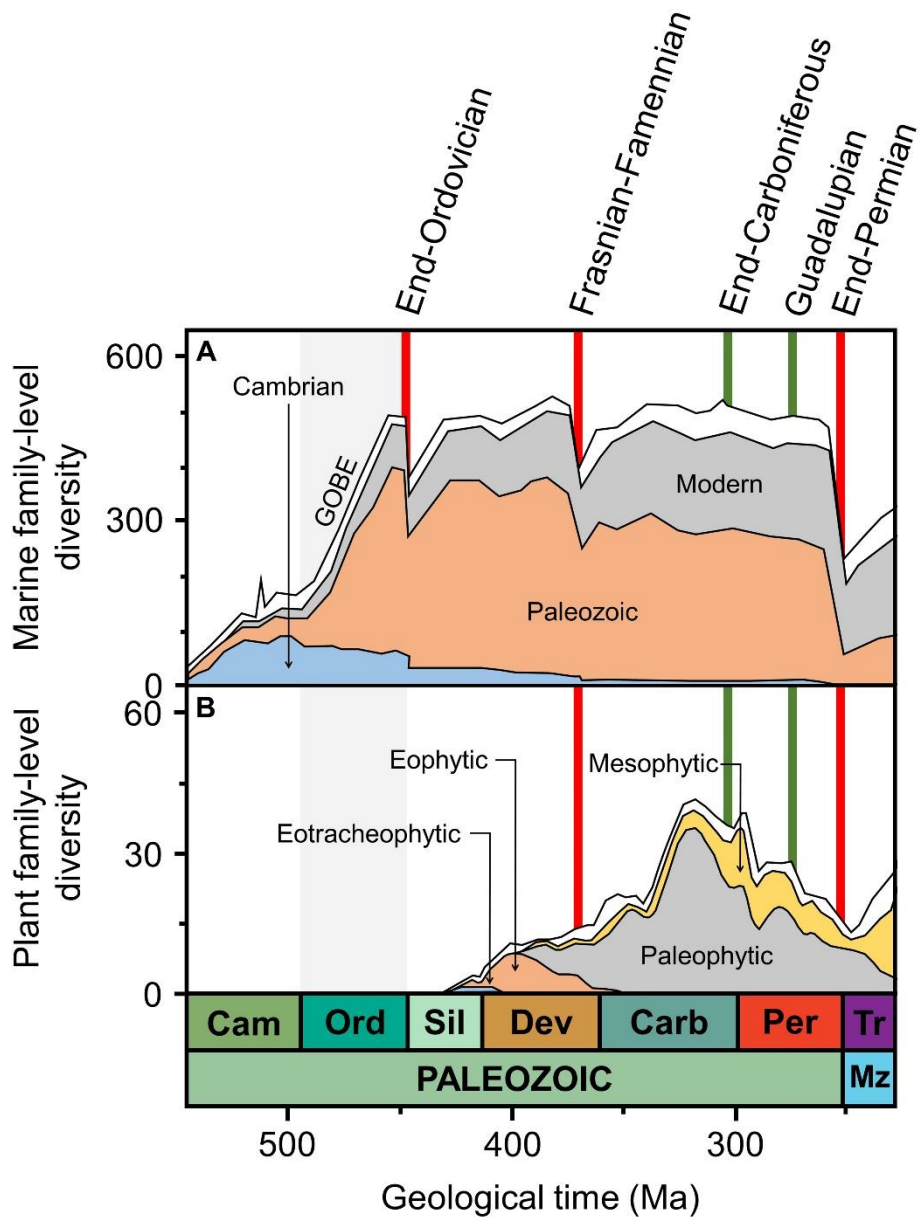


Figure 1

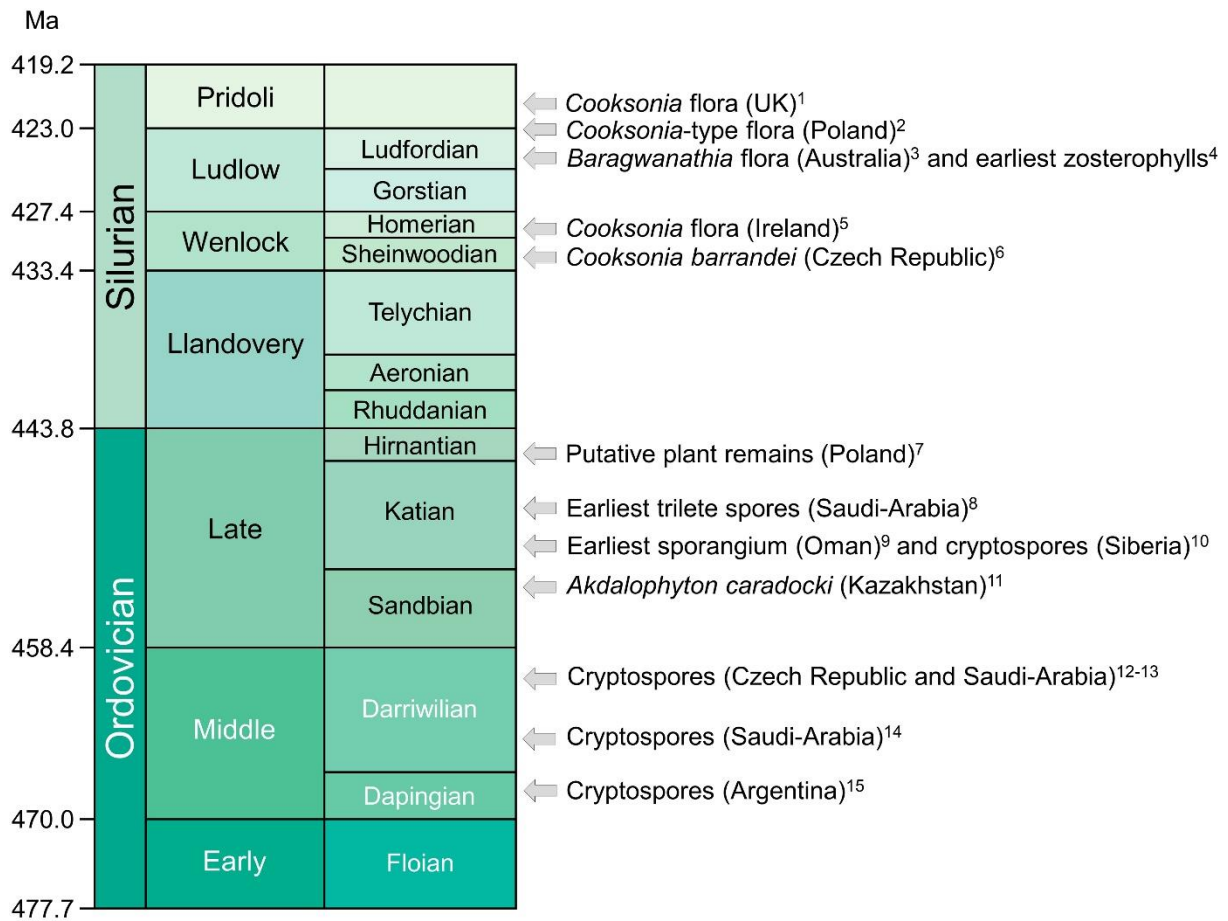


Figure 2

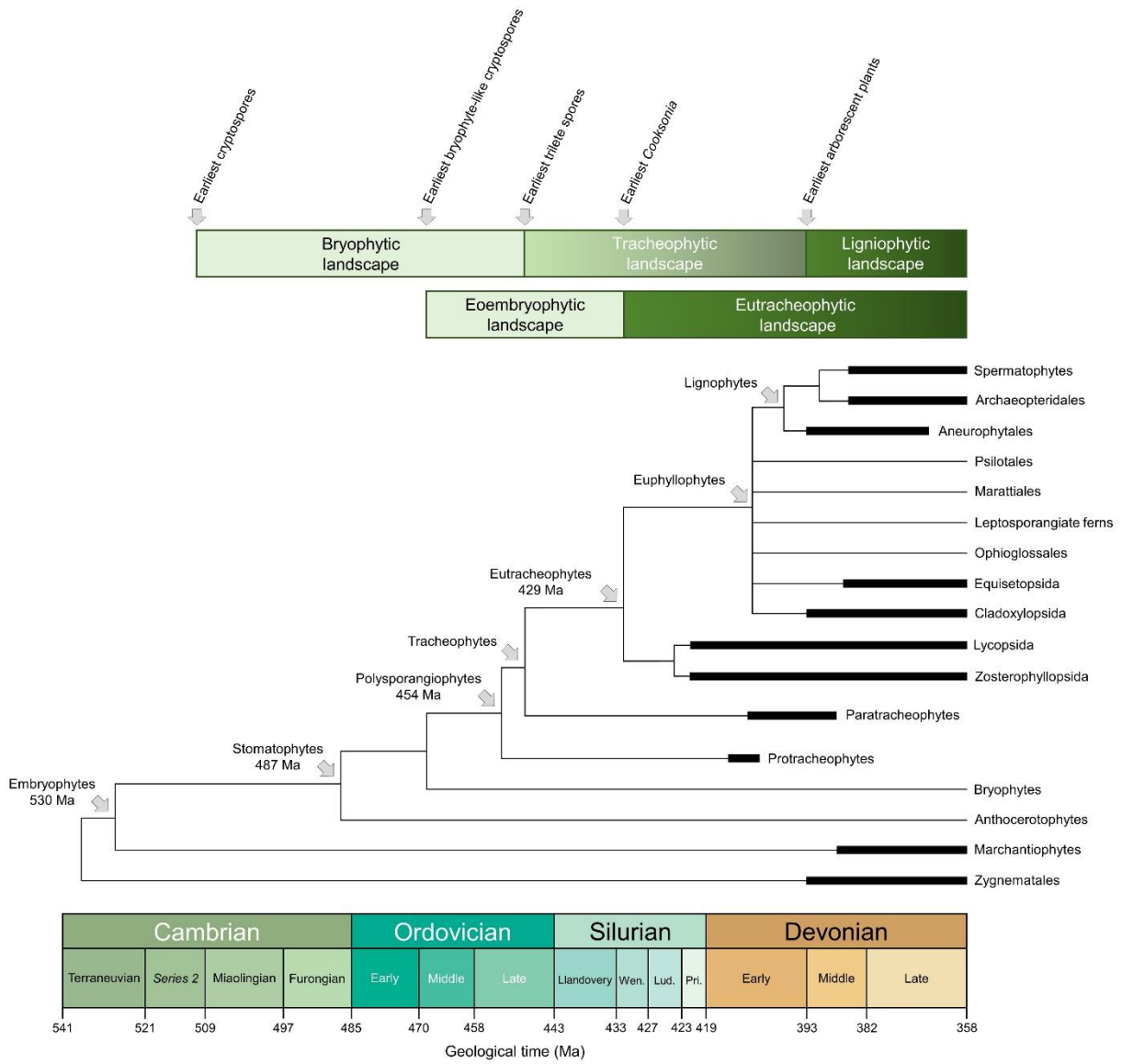


Figure 3

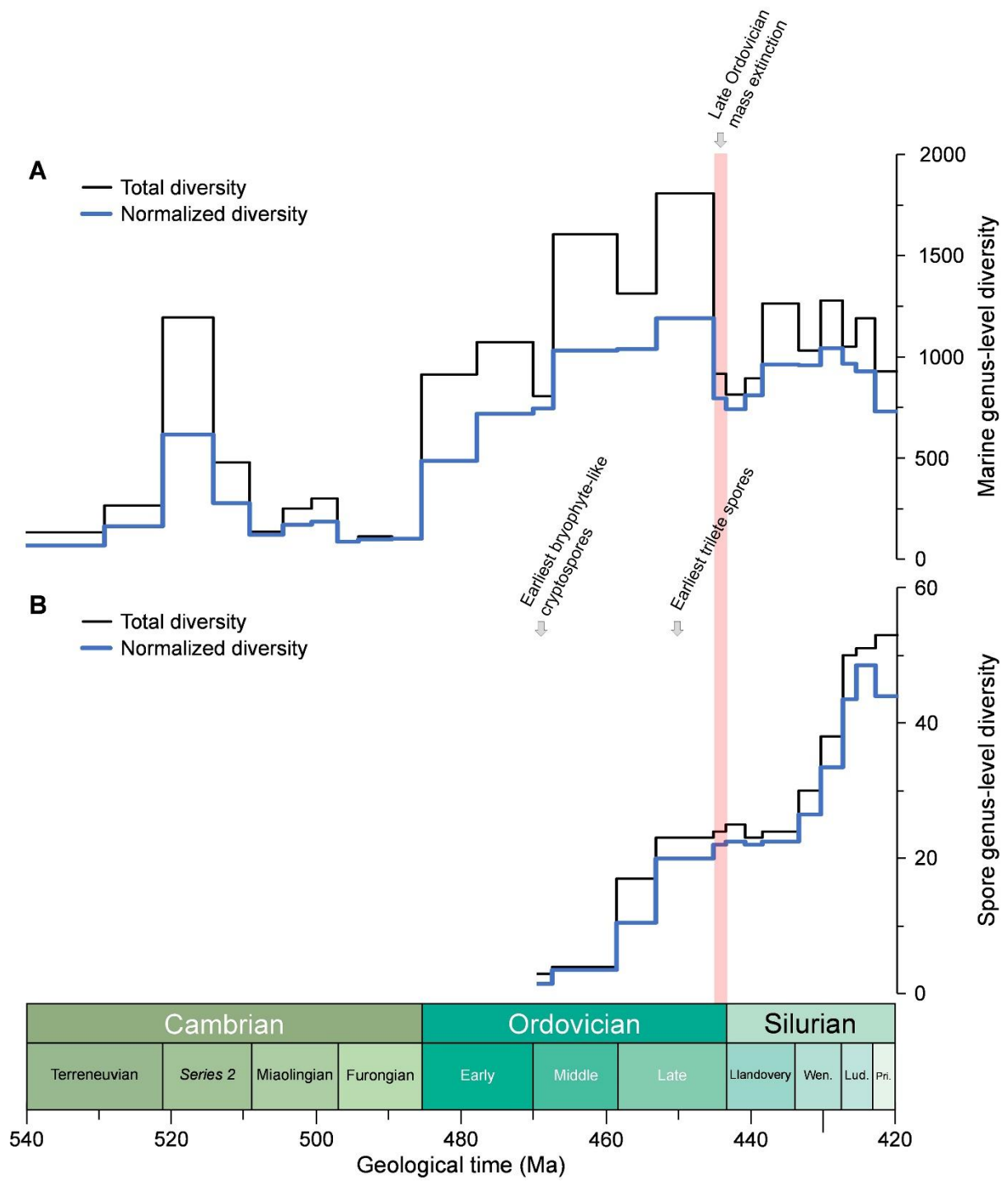


Figure 4

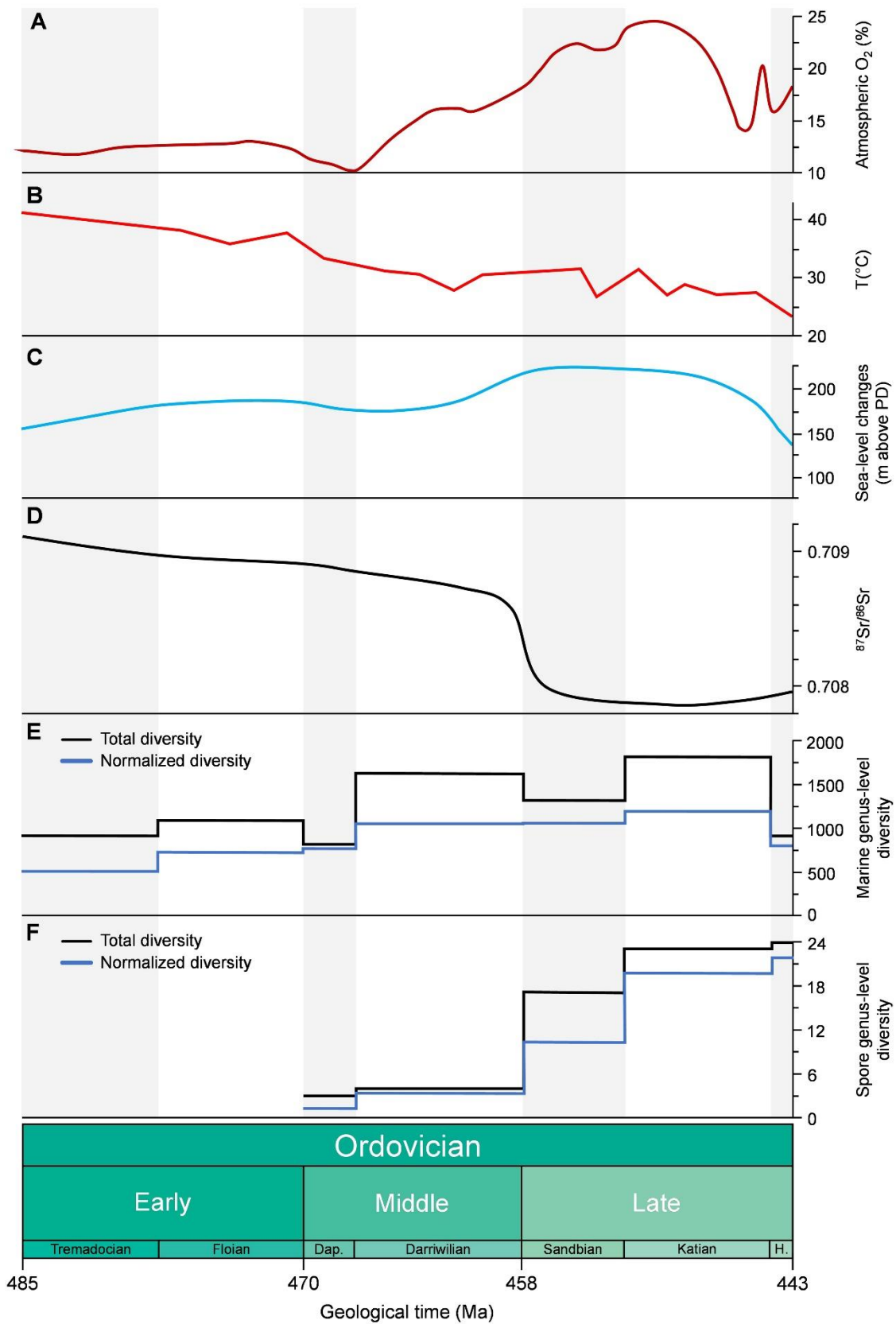


Figure5