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

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ABSTRACT

Recent molecular clock data suggest with highest probability a Cambrian origin of Embryophyta (also called land plants), indicating that their terrestrialization most probably started about 500 million years ago. The fossil record of the ‘Cambrian explosion’ was limited to marine organisms and not visible in the plant fossil record. The most significant changes in early land plant evolution occurred during the Ordovician. For instance, the earliest bryophyte-like cryptospores and the oldest fragments of the earliest land plants come from the Middle and Late Ordovician, respectively. Organic geochemistry studies on biomarker compositions hint at a transition from green algae to land plants during the ‘Great Ordovician Biodiversification Event’ (GOBE). The colonization of the terrestrial realms by land plants clearly had an impact on marine ecosystems. Interactions between the terrestrial and marine biospheres have been proposed and the radiation of land plants potentially impacted on CO_2 and O_2 concentrations and on global climate. In addition, the shift of strontium isotopes during the Ordovician is probably linked to changing terrestrial landscapes, affected by the first massive land invasion of eukaryotic terrestrial life. The land plants seem unaffected by the first global mass extinction at the end of the Ordovician that eliminated many marine invertebrate taxa.

Keywords: early Palaeozoic; radiation; cryptospores; bryophytes, embryophytes; terrestrialization

1. Introduction

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

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

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

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

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

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

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

Masuda and Ezaki (2009) were among the first to link the bio-invasion of land with the Ordovician radiation in the oceans, by arguing that the strontium isotopic composition that markedly changed at the Cambrian-Ordovician transition interval must be placed in context with the coeval drastic changes of the terrestrial environments. The bio-invasion of the continents was undoubtedly one of the most consequential and significant geobiological events in Earth history. In particular, the Ordovician was an interval of major changes in terrestrial ecosystems. These changes have recently been linked to the marine radiation (GOBE) that took place in the global oceans (Servais and Harper, 2018). It becomes more and more evident that the changes on land also affected life in the oceans. Algeo et al. (2016) proposed that one of the key triggers of the marine radiation was probably the palaeobotanical change in the terrestrial biotas. Several authors have linked the GOBE to global cooling (e.g., Vandenbroucke et al., 2010; Rasmussen et al., 2016) that was possibly due to the greening of the continents during the Ordovician (e.g., Lenton et al., 2012), in addition to palaeogeographical changes that had a major impact on the global climate (e.g., Nardin et al., 2011).

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

2. The evolutionary context of land plants

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

Land plants include photosynthetic eukaryotic multicellular organisms and are characterized by the following synapomorphies: alternation of multicellular gametophyte(s) and sporophyte; presence of multicellular sexual organs (archegonium and antheridium); development of the zygote into an embryo within the archegonium; a plant body protected by a cuticle, one or several multicellular sporangium; sporopollenin within the wall of the spore (Pirani and Prado, 2012; Gerrienne et al., 2016 and references therein). Several lineages have been proposed as the closest living relative to land plants, such as the Charophyceae, the Coleochaetophyceae and the Zygnematophyceae (see discussion in Gerrienne et al., 2016). Recently, De Vries and Archibald (2018) indicated that the land plants evolved from streptophyte algae most closely related to extant Zygnematophyceae and that over a billion year ago a wide range of algae already successfully established themselves on land. Harrison (2016) also noted that the major extant lineages of land plants were established at least c. 360 million years ago, including hornworts, liverworts and mosses (bryophytes), as well as lycophytes, monilophytes and spermatophytes (vascular plants). However, the precise phylogenetic relationships of different groups of charophyte algae, bryophytes and vascular plants is highly debated (e.g., Harrison, 2016, figs. 1-2; *versus* Gerrienne et al., 2016, figs. 1-2; Puttick et al., 2018, fig. 1).

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

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

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

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

3. Mesofossil evidence for earliest (Ordovician) land plants

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

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

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

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

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

These early cryptophyte plants were probably, therefore, more or less aquatic, with only the sporangium-bearing sporophyte structures likely to be to fossilized. However, with the selective pressure for more of the sporophyte to protrude out of the water, progressively more fossilizable tissue would be produced. This would produce a sequential fossil record of these plants similar to what we see (Edwards et al., 2014): initially there are just dispersed cryptospores, followed by isolated sporangia and then sporangia on increasingly elongate sporophyte axes, and then remains of the lower parts (rhizomes) of the plants become preserved. Fully terrestrialized plants may not have appeared until the very late Silurian, which is also when the first evidence of wildfire appears (Glasspool et al., 2004), but semi-aquatic plants with some structures adapted to subaerial exposure had been evolving for some 25 Ma years prior to this. The abundant and diverse dispersed Ordovician and lower Silurian cryptospore microfloras suggest that transitional vegetation represented a significant biomass in shallow aquatic environments, but it would be little representation in the macrofossil record.

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

4. Microfossil evidence of Ordovician land plants

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

The first palynomorphs (pollen, spores, etc.) derived from land plants have probably mostly been described as 'acritarchs.' The informal group of acritarchs was defined by Evitt (1963) to group together organic-walled microfossils of unknown biological affinity. The group thus includes, by definition, also non-marine forms, and logically all simple spherical microfossils that cannot be assigned to a known taxonomical group. Several of the Palaeozoic acritarch morphotypes can be related to various algal groups, and many are indeed considered members of the marine organic-walled microplankton (e.g., Martin, 1993; Servais, 1996; Strother, 1996). Some acritarchs are possibly related to diverse groups of green algae, or to organisms that are transients between green algae and land plants. Mendelson (1993), for example, indicated that some forms attributed to the acritarchs actually represent the phycomata of prasinophycean algae. Colbath and Grenfell (1995) and Talyzina and Moczydlowska (2000) compared some of the morphologies and wall ultrastructures of early Cambrian acritarchs with those of various green algae, such as chlorophyceans or zygnemataceans. Some Early Ordovician taxa, such as *Virgatasporites* and *Attritasporites* are of unknown affinities, but their terminology already indicates that their morphology is comparable to land plant derived spores. Combaz (1967), who described both taxa from the Tremadocian of Algeria, considered them spores of land plants, a view that has not been sustained. However, this illustrates that some early Palaeozoic acritarchs are logically considered the spores of organisms that are related to earliest land plants. It is thus evident that some of the Precambrian and early Palaeozoic organic-walled, spherical and featureless microfossils attributed to the acritarchs may well derive from earliest land plants, or from spore producing organisms at the algal-plant transition. This dilemma is particularly present in the Cambrian, where spore-like microfossils ('cryptospores') display characters that are not present in the spores of any extant algae; this allowed some authors to suggest that these Cambrian palynomorphs were the desiccation-resistant spores of cryptogams belonging to the charophyte – embryophyte lineage (e.g., Strother, 1991; Strother et al., 2004; Taylor and Strother, 2008).

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

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

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

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

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

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

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

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

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

5. Geochemical evidence for land plant evolution

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

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

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

Given the high taxonomic specificity of sterols in eukaryotic organisms (e.g., Summons et al., 2006) – despite the fact that a small number of bacteria can also biosynthesize steroids (e.g., Wei et al., 2016) – this compound class provides an evident target for the study of the rise of early land plants. Characteristic steroidal patterns in different environments were found to correspond to broad biosynthetic prevalence. In this regard, Huang and Meinschein (1979) were among the first to observe a strong predominance of C_{29} steroids in soils and higher plants, which corresponds to the C_{29} steroidal dominance in many coals (e.g., Püttmann et al., 1988).

Indeed, sitosterol and stigmasterol are the predominantly biosynthesized sterols in many plants (Volkman, 2005), leading to the 'phytosterol' terminology for C_{29} structures ethylated at C-24. However, given the fact that phytosterol biosynthesis is also common in many green algae (Volkman, 1986; Kodner et al., 2008) sedimentary C_{29} steranes are common in Ediacaran rocks predating the rise of plants (Hoshino et al., 2017) and cannot currently be used as a faithful molecular indicator for the evolutionary rise of plants. Potentially more relevant information may be hidden amongst sedimentary alkanes, a compound class that typically carries little specific information on precursor biota. Sedimentary alkanes mostly derive from cellular fatty acids (Peters et al., 2005), but can also be directly biosynthesized as epicuticular waxes to enhance desiccation resistance (Eglinton and Hamilton, 1967). The composition of free lipids in bryophytes, i.e., early divergent non-vascular plants, has been reported recently in a number of studies. Nott et al. (2000) discovered a link between C_{23}/C_{31} *n*-alkane ratios with the abundance of *Sphagnum* mosses, whereas Baas et al. (2000) remarked on a pronounced predominance of C_{23} and C_{25} *n*-alkanes in most mosses of the same species with only one exception in which C_{31} was the dominant *n*-alkane; but no relation between habitat and lipid composition was found. More recently, Inglis et al. (2015) postulated the use of the *n*-C_{23}/*n*-C_{31} ratio to trace the occurrence of *Sphagnum* mosses and waterlogged environmental conditions in peaty sediments. The differences in the main alkane constituents in submergent/floating plants *vs.* terrestrial plants, i.e. C_{23} and C_{25} *vs.* C_{29} and C_{31}, respectively, was introduced as a marker to differentiate terrestrial vs. non terrestrial/submergent plant input (Ficken et al., 2000).

In opposition to simple(r) embryophytes/bryophytes, the input from higher plants into the (molecular) fossil record is – among others – documented via the occurrence of long chained alkanes, typically with C_{31} or longer hydrocarbon chains with a pronounced odd-over-even predominance, derived from their epicuticular waxes (Eglinton and Hamilton, 1967). Within the C_{29} steroids (*stigmasteroids*) a distinction between those molecules produced in green algae and those biosynthesized in higher plants can be made. The ethyl-group (C_2H_5) attached to C-24 has two stereochemical configurations (α or β). Green algae predominantly, but not exclusively, produce one type (β), whereas higher plants evolved to largely form the other (α) (e.g., Marsan et al., 1996; Nes, 2011). While the general biosynthetic pathways are well understood (e.g., Haubrich et al., 2015; Nes, 2011; Volkman, 1986), it is still unknown why this distinction occurs and whether these features are preserved in the fossil record. Given that the analytical determination of these molecular differences is complicated and affords a lot of time and laboratory work in biological samples, their applicability as biomarkers in geologically aged rocks has not been systematically tested and remains theoretical at best. In addition, Haubrich et al. (2015) analysed the evolution of sterol biosynthesis in the 'green lineage' in regard to the enzymatic capacities encoded in their DNA. They argue that the enzymes needed for the formation of phytosterols might already have existed in the last eukaryotic common ancestor (LECA). Interestingly, while the possession of SMT2 – an enzyme that is responsible for further side chain alkylation at C-28 position – is exclusive to the green lineage, the biosynthetic pathway from a protosterol to the C_{29} sterol is more similar to green algae and fungi than it is in green algae and land plants (Haubrich et al., 2015). More precisely, in higher plants, two enzymes, SMT1 and SMT2, are needed to successively synthesize C_{29} sterols (Bouvier et al., 2005; Neelakandan et al., 2009), while in green algae, only one bifunctional enzyme is needed to perform the C-24-alkylations.

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

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

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

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

An obvious hypothesis is to assume that with the terrestrialisation of land plants, oxygen levels would rise and the CO_2 concentrations would decrease. In many palaeoclimate models (e.g., GEOCARB/GEOCARBSULF: Berner et al., 1991, 1994, etc.; COPSE: Bergman et al., 2004) pCO_2 values diminish during the Palaeozoic. Some of the climate models include forcing factors, including land plants, that influence the model output (e.g., François et al., 2005). Lenton et al. (2018), for example, updated the COPSE model, by changing the values of original forcing factors, including plant evolution, plant effect on weathering, and plant stoichiometry. However, what are the datasets used in these models? How precise are these data?

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

On the other hand, the impact of the appearance of the early land plants on CO_2 concentrations and O_2 values is also not clearly understood. Furthermore, it is completely unknown what might have been the ratio of O_2 production on land versus O_2 production in the oceans (by the phytoplankton). It is commonly assumed that today 50 to 85% of the oxygen in the Earth’s atmosphere is produced by the phytoplankton, but it is unknown what these proportions might have been during the Palaeozoic (e.g., Servais et al., 2016a).

Did the land plants or the marine microphytoplankton (and picoplankton) provide the oxygen that might have fuelled the GOBE? Edwards et al. (2017, fig. 2) modelled O_2 levels using GEOCARB and photosynthetic fractionation approaches (Figure 5 A). They assumed that atmospheric oxygen increased during the Darriwilian (Middle Ordovician) and continued to rise to near modern levels by the Katian (Late Ordovician). Such values would thus correlate with the rise of land plants as suggested by the massive arrival and distribution of the cryptospores. Edwards et al. (2017) noted a strong temporal link between the GOBE and rising O_2 concentrations, which may suggest that the terrestrial and marine realms are linked directly through oxygen levels. Edwards et al. (2017) thus hypothesized that oxygenation may have triggered the GOBE. Similarly, Saltzman et al. (2011) already a few years earlier assumed that a pulse of atmospheric oxygen in the late Cambrian can be correlated with the onset of the GOBE, and in particular triggering the 'Ordovician Plankton Revolution' (Servais et al., 2008, Klug et al., 2010; Saltzman et al., 2011). However, this 'oxygenation pulse' in the late Cambrian cannot be related to the evolution of land plants, but may instead be linked only to the phytoplankton radiation that occurred at that time (Nowak et al., 2015; Servais et al., 2016b).

Most geochemical models indicate that CO_2 levels decrease during the Early Palaeozoic (e.g., Bergman et al., 2004). While land plants logically impact on O_2 levels, because they produce oxygen, they also reduce CO_2 levels. In addition, they enhance calcium-magnesium silicate weathering. Therefore Lenton et al. (2012) suggested that the radiation of land plants during the Ordovician was a major trigger for the decrease of pCO_2, and thus for the cooling that occurred during the Ordovician. Lenton et al. (2012) proposed that the evolution of the first land plants could explain important Ordovician global changes in biodiversity through their effect of silicate weathering. Furthermore, Lenton et al. (2012) noted that geological factors (such as tectonics) may impact on the long-term cooling during the Ordovician, but not the short event of the Hirnantian extinction. Lenton et al. (2012) assumed that the first land plants could only have indirectly contributed to the marine mass extinction in the Late Ordovician. The increased diversity of land plants (Figure 4) may confirm such a scenario, but as with the O_2 levels, we do not precisely know what the proportionate contribution of the phytoplankton and that of the land plants was to global CO_2 levels.

Land plants most probably had an impact on the cooling for the Ordovician biospheres, including the oceans (Figure 5 B), but the importance of land plants in this cooling process was possibly of minor importance. Other parameters have been considered more significant for climate change, in particular in the long-term. For example, Nardin et al. (2011) suggested that changes in palaeogeography and the exposure of fresh volcanic rocks on continents are required to explain the large decrease of pCO_2 during the Ordovician. These authors considered that the weathering of fresh volcanic rocks was responsible for one third of the Late Ordovician atmospheric CO_2 decrease, while the movement of the continents, in particular the motion through the intertropical convergence zone of several palaeocontinents (such as Baltica), was mainly responsible for the drop of CO_2 levels and concomitant climate change.

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

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

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

7. Conclusion

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

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

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

Significantly, the evolution and rapid biodiversification of the early land plants appears not to have been interrupted by the first of the five major marine mass extinctions. Plants continued to diversify without any major loss of taxa. The end-Ordovician mass extinction is simply not recorded in the Early Palaeozoic floral record. Although it is evident that the arrival of land plants and the terrestrialization must eventually have had a significant impact on global geochemical cycles, as well as on O_2 and CO_2 levels, the available data are currently too sparse to allow definite conclusions and to propose (hypothetical) models, in particular concerning the impact of land plants on the global climate of the Ordovician.

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Figure legends

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

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

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

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

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