Terrestrialization in the Ordovician

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Abstract: This contribution reviews the evidence for terrestrial organisms during the Ordovician (microbial, land plant, fungal, animal) and for the nature of the terrestrial biota. The evidence regarding the origin and early diversification of land plants combines information from both fossils and living organisms. Extant plants can be utilized in: (1) phylogenetic analyses to provide evidence for the nature of the algal–land plant transition and the characteristics of the most basal land plants; (2) evolutionary developmental biology studies of the characters that enabled the invasion of the land; (3) molecular clock analysis to provide evidence regarding timing of the origin and diversification of land plants. We conclude that the Ordovician was a critical period during the terrestrialization of planet Earth that witnessed the transition from a microbial terrestrial biota to one dominated by a vegetation of the most basal land plants.

Palaeontological research aimed at reconstructing life in the Ordovician has historically focused on the marine environment and reconstructing the 'Great Ordovician Biodiversification Event' and effects of the 'End Ordovician Mass Extinction'. Studies on life in terrestrial environments has largely been neglected (but see reviews by Gray 1985; Richardson 1996; Wellman 1999; Retallack 2000; Steemans 2000; Strother 2000; Wellman and Gray 2000; Steemans and Wellman 2004; Wellman et al. 2013; Servais et al. 2019). In part this is a consequence of the paucity of Ordovician non-marine sediments and hence a dismally poor fossil record of non-marine organisms (except for those that have been transported into marine settings). But it also reflects historical research agendas based on assumptions that the first land plants did not appear until the Silurian. Since the 1980s this latter view has been challenged, and evidence has accumulated suggesting that land plants first appeared in the Ordovician and may have been accompanied by the first animals to emerge from the oceans (either directly or migrating into brackish and freshwater environments and finally venturing onto land). More recently evidence emanating from molecular biology, including phylogenetic, molecular clock and evolutionary developmental biology (evo–devo) analyses, has added to this growing body of evidence for an Ordovician terrestrial biota. In this chapter we will discuss the evidence for this terrestrial biota and attempt to reconstruct it. We argue that the Ordovician was a critical period during the terrestrialization of planet Earth.

An Early Ordovican terrestrial microbial world

The earliest terrestrial ecosystems were essentially microbial comprising freshwater ecosystems, periodically inundated microbial mats adjacent to rivers and lakes, and microbial crusts developed on rudimentary soils (reviewed in Wellman and Strother 2015). Such ecosystems are well documented from the billion-year-old Lagerstätten of the Torridonian of Scotland (Strother et al. 2011) and the Nonesuch Formation of the USA (Strother and Wellman 2021). They have also been shown to have persisted into the Silurian after land plants (embryophytes) had evolved and begun to colonize the continents (Tomescu and Rothwell 2006; Tomescu et al. 2006, 2008, 2009, 2010). The aquatic biotas included primary producers such as photosynthetic cyanobacteria (including both benthic and planktonic forms) (Strother and Wellman 2015) and a variety of other prokaryotic and eukaryotic organisms (e.g. Strother et al. 2021). The microbial mats and crusts were established around photosynthetic cyanobacteria. At present there is little evidence for a significant fungal or lichen component (discussed below). It seems likely that such microbial ecosystems dominated Ordovician terrestrial ecosystems until the origin of land plants in the Middle Ordovician. Figure 1 illustrates an assemblage of microbial fossils recovered from an Early Ordovician terrestrial deposit. The components are essentially identical to those described from the billion-year-old terrestrial deposits of the Torridonian Group and Nonesuch Formation.
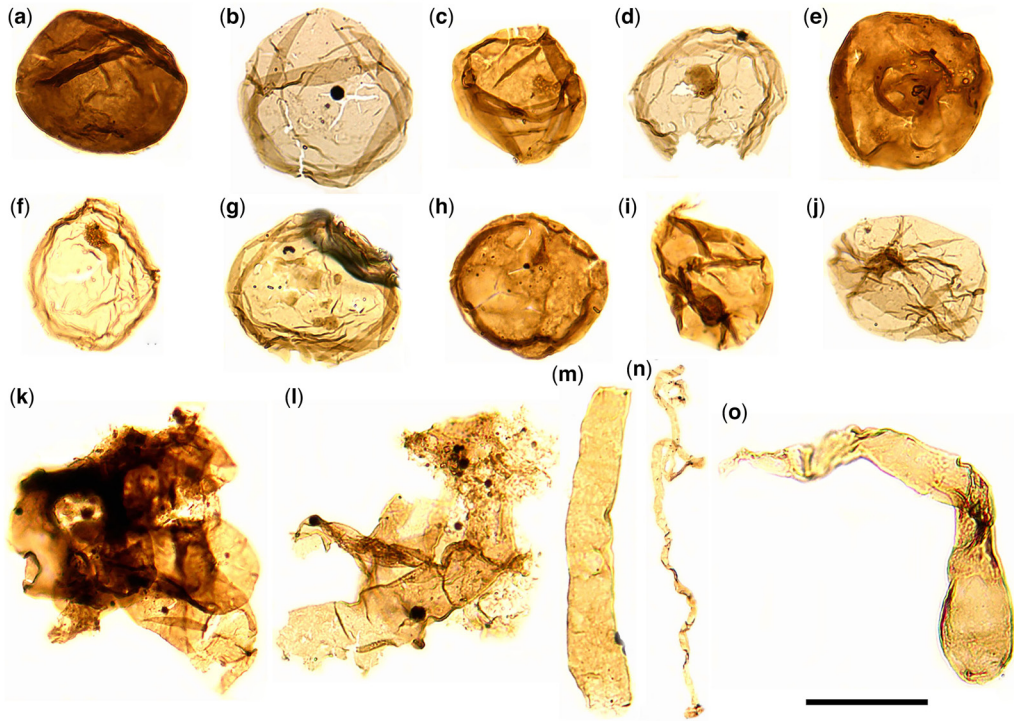
Fig. 1. Light microscope images of microbial remains recovered by palynological processing of Ordovician (Floian–? early Dapingian) continental deposits from the Ghudun Formation of Oman. (**a–c**) Sphaeromorph; (**d**) Sphaeromorph with surface spot; (**e**) Sphaeromorph with circular 'hilum'; (**f**) Sphaeromorph with surface spot from which a tube extends; (**g**) and (**h**) Sphaeromorph; (**i**) and (**j**) Sphaeromorph with surface spot; (**k**) cluster of Sphaeromorphs; (**l**) association of tubular structures; (**m**) isolated wide tube; (**n**) isolated narrow tube (filament); (**o**) tube with expanded tip. Scale bars: (a–j), 30 μm; (k–l), 40 μm; (m), 30 μm; (n), 100 μm; (o), 30 μm.

The fossil record of land plants

Historically research on terrestrialization in the Ordovician has relied heavily on the fossil record. Regarding land plants, this includes plant megafossils, dispersed spores and disarticulated fragments of the plants. The latter two fossil types are generally recovered by palynological acid maceration techniques. A major hindrance to research has been the paucity of non-marine deposits recorded from the Ordovician worldwide. Land plant megafossils can be transported into marine deposits, yet the expectation is that they will be much rarer than in terrestrial deposits due to their allochthonous nature. Also, they are mixed with marine fossils and therefore it can be difficult to distinguish between fossils deriving from marine and non-marine organisms. Dispersed microfossils (spores and phytodebris) are readily transported into marine environments where they may be abundant. Again, however, the problem is that the non-marine provenance of biologically ambiguous forms cannot be confirmed.

Plant megafossils

The oldest generally accepted plant megafossils are rhyniophytoid plants, preserved as coalified compressions, from the Silurian (Wenlock) (Edwards *et al.* 1983; Libertin *et al.* 2018). These show evolutionary continuity with younger Silurian forms that possess unequivocal spore-containing sporangia, stomata and conducting tissues (in some cases true tracheids) (Edwards *et al.* 1992). Twenty-five or so Silurian localities preserve such plant megafossil assemblages, and by the Lower Devonian (Lochkovian) they are abundant with at least 30 assemblages known worldwide (most recently reviewed by Edwards and Wellman 2001; Wellman *et al.* 2013). The coalified compressions preserve little anatomical detail. However, the anatomy of these plants is now well known due to Lagerstätten yielding exquisitely preserved charcoalified remains: Ludford Lane of Late Silurian (Pridoli) age and North Brown Clee Hill of Early Devonian (Lochkovian) age, both from the Anglo-Welsh basin of the

UK (e.g. Morris *et al.* 2018). The Lower Devonian (Pragian–?earliest Emsian) silicified plants from the Rhynie chert Lagerstätten are also important in preserving exquisite anatomical detail of early land plants (e.g. Edwards *et al.* 2017).

There are regular and numerous claims for pre-Silurian plant megafossils. However, these are discounted as they can be proven to be fragments of other organisms (e.g. Kenrick *et al.* 1999) or they lack sufficient characters to be unequivocally assigned to land plants (e.g. Salamon *et al.* 2018; Naugolnykh 2019; Retallack 2019). Throughout the 1960s, 1970s and 1980s Banks, Chaloner and others thoroughly catalogued and discredited such claims (e.g. Chaloner 1960, 1970; Banks 1975*a*, *b*). This procession continues to this day, and it is still doubtful that any claimed pre-Silurian plant megafossil possesses sufficient unequivocal plant characters to be confidently and unequivocally proven to be a land plant. As noted by Edwards *et al.* (2021*a*) (p. 1453) 'when diagnostic features are absent, such fragmentary organic materials can be misinterpreted, leading to implausible attributions (e.g. Retallack 2019)'.

Occasionally spore masses or even partial sporangia have been recovered during palynological processing of Ordovician deposits (Wellman *et al.* 2003; Abuhmida and Wellman 2017). From the Late Ordovician (Katian) of Oman Wellman *et al.* (2003) report spore masses, including some enclosed within a homogenous covering, and partial sporangia with fragments of sporangial wall attached (Fig. 2). The enclosed spores can be identified among dispersed forms (see below). These plant remains provide a tantalizing insight into Ordovician land plants and, if nothing else, demonstrate that they produced vast numbers of spores within sporangia that were extremely small but clearly highly fecund.

Dispersed spores

Spores encased in a resistant sporopollenin wall are a synapomorphy of land plants and it seems likely that the invasion of the land by plants was coincident with development of a subaerial reproductive strategy that utilized such spores (Blackmore and Barnes 1987; Wellman 2004). They have an excellent fossil record because they are produced in vast numbers, capable of dispersal over huge distances by wind and water, and are relatively resistant to degradation. Research by the early palynological pioneers established, by the 1970s, a continual record of dispersed land plant trilete spores from the early Silurian (Llandovery) onwards (e.g. Richardson and McGregor 1986; Streel *et al.* 1987). These spores are often identical to those reported *in situ* from the earliest rhyniophytoid–rhyniophyte land plant megafossils (see above). However, in a series of ground-breaking

papers Jane Gray and colleagues reported on a new group of dispersed spores, extending back into the Ordovician, that were subsequently proven to be the spores of land plants (Gray and Boucot 1971; Gray *et al.* 1982; Gray 1985, 1991) produced by eophyte plants (Edwards *et al.* 2021*a*, *b*, *c*). These were called cryptospores because they occur in unusual configurations (e.g. permanent dyads and tetrads) (Richardson 1988) (Fig. 2).

The oldest reported occurrence of cryptospores clearly related to land plants is currently considered to be in the Middle Ordovician (Dapingian or Darriwilian) suggesting that land plants had successfully invaded the land by this time. They have now been reported continuously from this time point, with records from most palaeocontinents, extending through time until the end Pragian, after which they become extremely rare in the fossil record (see Table 1 and Figs 3–6). Cryptospores include monads, dyads and tetrads that are either naked or enclosed within an envelope. The envelope may be laevigate or ornamented. Cryptospore taxonomy utilizes the following characters: the number of units (monad, dyad, tetrad), the nature of attachment of these units (fused or unfused), the presence/absence of an envelope, the infraornament/ornament of the wall and/or envelope. A number of Ordovician cryptospores (dispersed and *in situ*) have been examined ultrastructurally and their gross structure/wall ultrastructure evaluated with regard to evidence for biological affinities (see Table 2) (Fig. 2). More recently Ordovician cryptospores have also been examined using a synchrotron light source (Guizar-Sicairos *et al.* 2015).

Very similar cryptospore assemblages have been reported throughout the Ordovician (spatially and temporally). Biostratigraphic schemes have been proposed, but these tend to be rather coarse with respect to time resolution (e.g. Richardson 1988; Steemans *et al.* 2000). This is a consequence of the morphological simplicity of cryptospores (and hence lack of characters compared to trilete spores) and their seemingly slow pace of acquisition of novel morphological characters. The palaeogeographical spread, consistency and relative stasis exhibited by cryptospore assemblages have been taken to indicate that the first flora to invade the land consisted of cosmopolitan generalists that occupied a wide range of environments and evolved relatively little throughout the course of the Ordovician (Gray 1985; Wellman 1996).

Probable non-marine palynomorphs that occur as irregular clusters of dyads and other polyads (in packets) have been described from Early Ordovician (Tremadocian) and earlier Cambrian deposits (Strother and Foster 2021). These have been included with the cryptospores by some authors but are excluded by others. This is largely a semantic

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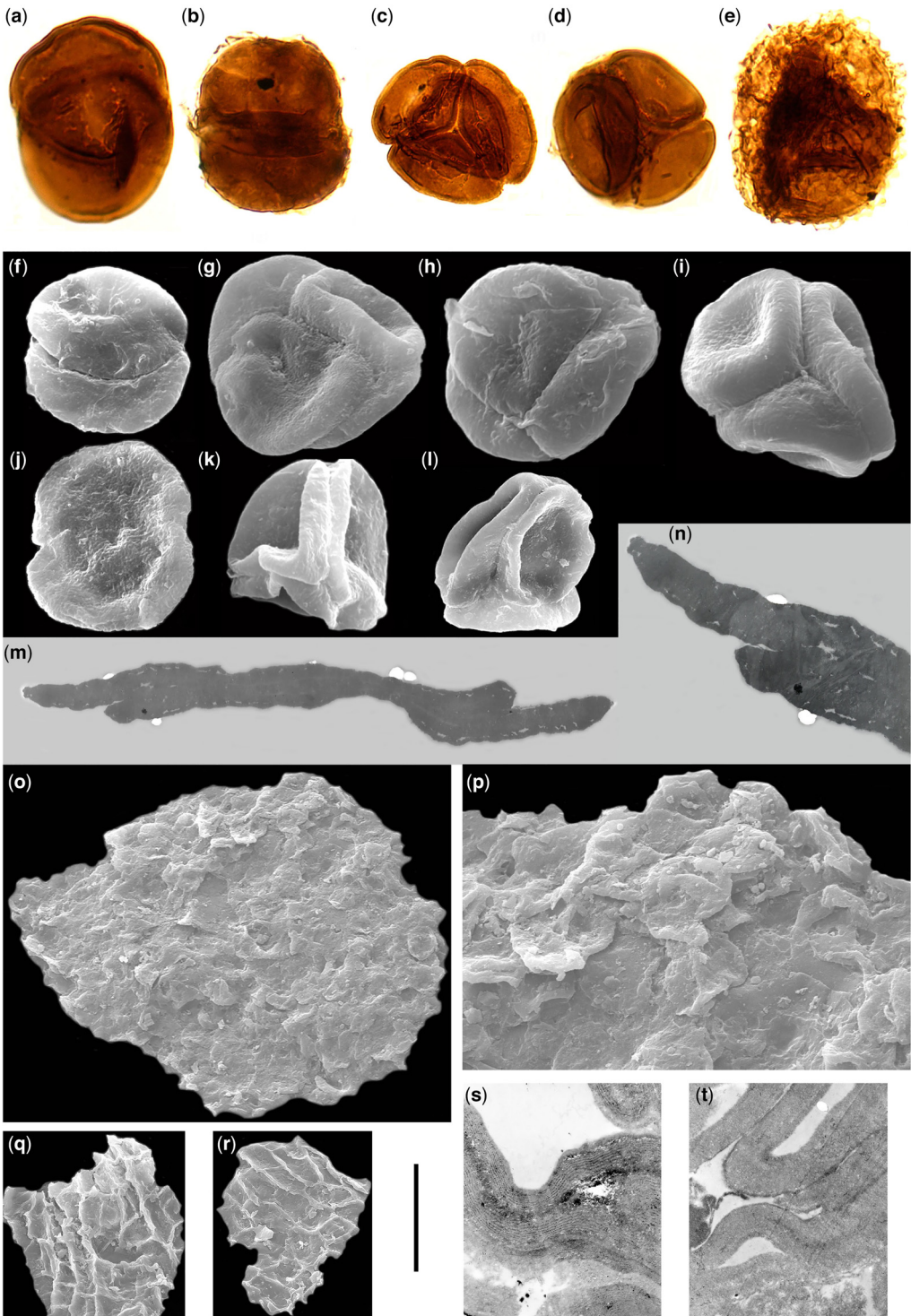
debate as several very different definitions for the term cryptospore have been proposed (see discussion in Servais *et al.* 2019). This debate centres on whether cryptospores are defined as the spores of land plants (our preferred interpretation) or represent palynomorphs produced by any non-marine organisms. The most recent interpretation for the enigmatic Cambrian–Early Ordovician palynomorphs is that they represent charophyte algal remains (Strother and Foster 2021) and may thus represent intermediate organisms on the freshwater green algal to terrestrial land plant lineage.

The first trilete spores, similar to those produced by Silurian rhyniophytoid plants, first appear in low numbers in the Ordovician (Steemans *et al.* 2009). They are difficult to identify because spores physically removed from cryptospore tetrads often bear a false trilete mark resulting from physical tearing as the polyads are broken apart. Similar to trilete spores, hilate cryptospores are produced by the natural dissociation of a polyad, but in this case a dyad (Richardson 1988). On their proximal surface they bear a circular contact area (hilum) formed where they were in contact with the other spore in the dyad. Like trilete spores, these naturally dissociated spores are common in the Silurian. They occur rarely in the Ordovician and again can be easily mistaken for spores physically separated from permanent dyads (Steemans *et al.* 2000).

Trilete spores only become common in dispersed spore assemblages in the Late Silurian whereupon they rapidly increase in abundance and diversity and have stratigraphical continuity with living trilete spore-producing plants. It has been proposed that this pattern reflects the origin and diversification of vascular plants (tracheophytes), because most Silurian–Devonian vascular plants have been shown to produce trilete spores (as do many extant basal groups of vascular plants) (e.g. Gray 1985; Wellman and Gray 2000; Wellman *et al.* 2013). The rare reports of trilete spores from the Ordovician–Early Silurian may have derived from various non-

vascular plants as trilete spores are known to be produced by some extant non-vascular plants (see Steemans *et al.* 2009) and various plant groups are likely to have evolved this basic character independently.

We can only speculate as to where the first land plants appeared and the course of their spread across the continents. The earliest generally accepted reports of cryptospores are all currently from Gondwana which has led to speculation that they may have evolved on this continent before rapidly spreading out across the other continents of the planet (Steemans *et al.* 2010; Wellman 2010).

Phytodebris

Plants naturally shed organs during their lifetime and on death begin to rot and disassociate. These processes produce recalcitrant fragmentary remains that are dispersed by gravity, wind and water and are ultimately incorporated into sediment from which they can be recovered by palynological processing. Such fragmentary plant remains, composed of recalcitrant biomacromolecules that survive as fossils, are termed phytodebris. They include plant cuticles composed of cutin, lignified tissues such as tracheids and reproductive propagules composed of sporopollenin (spores, megaspores, ovules and seeds), in addition to a number of more enigmatic remains. The fossil record and interpretation of phytodebris produced by early land plants was recently reviewed by Wellman and Ball (2021).

There are surprisingly few reports of Ordovician phytodebris, perhaps reflecting the dearth of non-marine deposits examined (Fig. 2). Silurian non-marine deposits usually yield a diverse array of phytodebris. These include cuticles (sometimes with stomata) and tracheids, that clearly derive from land plants. More enigmatic are cuticle-like sheets and tubular structures (including banded tubes) that are now known to derive from nematophytes. Nematophytes were recently demonstrated to have fungal and possibly also lichen affinities (Edwards and

Fig. 2. Land plant remains recovered by palynological processing of Ordovician (Katian) continental deposits from the Hasirah Formation of Oman. (**a–e**) Light microscope images of dispersed spores (cryptospores): (**a**) naked permanent fused dyad (pseudodyad); (**b**) permanent unfused dyad (true dyad) enclosed in a laevigate envelope; (**c**) naked permanent unfused tetrad; (**d**) permanent unfused tetrad enclosed in a laevigate envelope; (**e**) permanent fused tetrad enclosed in an ornamented envelope. (**f–l**) Scanning electron microscope (SEM) images of dispersed spores (cryptospores): (**f**) naked permanent unfused dyad (true dyad); (**g**) naked permanent unfused tetrad; (**h**) permanent unfused tetrad enclosed in a laevigate envelope; (**i**) naked permanent unfused tetrad; (**j**) naked permanent fused dyad (pseudodyad) with microgranulate ornament; (**k**) naked permanent unfused tetrad; (**l**) naked permanent unfused tetrad. (**m–n**) Transmission electron microscope (TEM) images of a section cut from an individual dispersed spore (naked permanent unfused dyad): (**m**) entire dyad; (**n**) close-up of left-hand part of dyad. (**o**) and (**p**) SEM images of a spore mass: entire spore mass (**o**) and close up of part of the spore mass illustrating the nature of the spores (**p**). (**q**) and (**r**) Fragments of dispersed cuticle-like sheets. (**s**) and (**t**) TEM images of sectioned sporangia/spore masses: Sporangium containing spores with wall ultrastructure lamellate (**s**) and spore mass containing spores with wall ultrastructure homogeneous (**t**). Scale bar: (a–e), 25 μm; (f–l), 25 μm; (m), 7.25 μm; (n), 4.6 μm; (o), 75 μm; (p), 25 μm; (q), 85 μm; (r), 115 μm; (s), 1.8 μm; (t), 2.5 μm.

Table 1. *Dispersed spore assemblages reported from the Ordovician*

Location/stage	Location	Palaeocontinent	Palaeoenvironment	Age dating	References
H1 Hirnantian?	Ontario, Canada	Laurentia	Palaeokarst surface	Lithostratigraphy	Gray (1988)
H2 Hirnantian	Quebec, Canada	Laurentia	Shallow marine	Inv + Palynology	Richardson and Ausich (2007); Vecoli et al. (2011)
H3 Hirnantian	Southern Britain	Avalonia	Shallow marine	G	Burgess (1991)
H4 Hirnantian	Sweden	Baltica	Shallow marine	G	Badawy et al. (2014)
H5 Hirnantian	Estonia	Baltica	Shallow marine	Palynology	Vecoli et al. (2011)
H6 Hirnantian	Zhejiang, China	South China	Shallow marine	Inv	Yin and He (2000)
H7 Hirnantian	Czech Republic	PeriGondwana	Shallow marine	G	Vavrdova (1982, 1984, 1988, 1989); Gray (1988)
H8 Hirnantian?	Bulgaria	PeriGondwana	Shallow marine	Palynology	Lakova et al. (1992)
H9 Hirnantian	Iran	PeriGondwana	Shallow marine	Palynology	Mahmoudi et al. (2014); Ghavidel-Syooki (2017); Ghavidel-Syooki and Piri-Kangarshahi (2021a)
H10 Hirnantian?	Australia	Gondwana	Marine evaporites	Palynology	Foster and Williams (1991)
H11 Hirnantian	Saudi Arabia	Gondwana	Glacial shallow marine	Lithostratigraphy	Miller and Al-Ruwaili (2007); Steemans et al. (2009); Wellman et al. (2015)
H12 Hirnantian	Algeria	Gondwana	Shallow marine	Ch-Palynology	Spina (2015)
H13 Hirnantian	Libya	Gondwana	Shallow marine	G	Gray et al. (1982); Richardson (1988); Le Hérissé et al. (2013); Thusu et al. (2013)
H14 Hirnantian	Chad	Gondwana	Shallow marine	Ch-Palynology	Le Hérissé et al. (2013)
H15 Hirnantian	South Africa	Gondwana	Glacial shallow marine	Ch-Palynology	Gray et al. (1986)
H16 Hirnantian	Argentina	Gondwana	Shallow marine	Inv-Palynology	Rubinstein and Vaccari (2004); Rubinstein (2005)
KH1 Katian-Hirnantian?	Kentucky, USA	Laurentia	Shallow marine	Palynology	Gray (1988)
KH2 Katian-Hirnantian?	Tennessee, USA	Laurentia	Shallow marine	Palynology	Gray (1988)
KH3 Katian-Hirnantian?	Georgia, USA	Laurentia	Shallow marine	Palynology	Gray (1988)
KH4 Katian-Hirnantian?	Belgium	Avalonia	Shallow marine	Palynology	Steemans (2001)
KH5 Katian-Hirnantian?	Turkey	Gondwana	Shallow marine	Palynology	Steemans et al. (1996)
K1 Katian	Illinois, USA	Laurentia	Shallow marine	Inv	Strother (1991)
K2 Katian	Ohio, USA	Laurentia	Shallow marine	Ch-Palynology	Gray and Boucot (1972); Gray (1988)

K3 Katian	Southern Britain	Avalonia	Shallow marine	Inv	Richardson (1988); Wellman (1996)
K4 Katian	Sweden	Baltica	Shallow marine	G	Badawy et al. (2014)
K5 Katian	Poland	Baltica	Shallow marine	G-Palynology	Stempién-Salek (2011)
K6 Katian	Estonia	Baltica	Shallow marine	Palynology	Vecoli et al. (2011)
K7 Katian?	Germany	?Baltica	Shallow marine	C	Reitz and Heuse (1994)
K8 Katian	Siberia, Russia	Siberia	Shallow marine	Inv + Palynology	Raevskaya et al. (2016)
K9 Katian	Xinjiang, China	Tarim	Shallow marine	G + C + Inv + Ch-palynology	Wang et al. (1997); Tang et al. (2017)
K10 Katian	Iran	PeriGondwana	Shallow marine	Palynology	Mahmoudi et al. (2014); Ghavidel-Syooki (2017); Ghavidel-Syooki and Piri-Kangarshahi (2021b)
K11 Katian	Saudi Arabia	Gondwana	Shallow marine	Ch-Palynology	Molyneux and Al-Hajri (2000); Steemans et al. (2009); Wellman et al. (2015)
K12 Katian	Oman	Gondwana	Terrestrial-nearshore marine	Ch-Palynology	Wellman et al. (2003)
K13 Katian	Libya	Gondwana	Shallow marine	G	Gray et al. (1982);
K14 Katian	Argentina	Gondwana	Shallow marine	Ch-Palynology	de la Puente and Rubinstein (2013); Rubinstein et al. (2016)
S1 Sandbian	Southern Britain	Avalonia	Shallow marine	Inv	Richardson (1988); Wellman (1996)
S2 Sandbian*	Sweden	Baltica	Shallow marine	C	Rubinstein and Vajda (2019)
S3 Sandbian	Poland	Baltica	Shallow marine	G-Palynology	Stempién-Salek (2011)
S4 Sandbian	Saudi Arabia	Gondwana	Shallow marine	Ch-Palynology	Molyneux and Al-Hajri (2000)
S5 Sandbian	Libya	Gondwana	Shallow marine	G	Gray et al. (1982)
S6 Sandbian	Argentina	Gondwana	Shallow marine	G + C	Ottone et al. (1999)
Dr1 Darriwilian	Czech Republic	PeriGondwana	Shallow marine	G	Corna (1970); Vavrdova (1990, 1993)
Dr2 Darriwilian	Australia	Gondwana	Shallow marine	Palynology	Spaak et al. (2017)
Dr3 Darriwilian	Saudi Arabia	Gondwana	Shallow marine	Ch-Palynology	McClure (1988); Strother et al. (1996, 2015); Molyneux and Al-Hajri (2000); Le Hérissé et al. (2007); Vecoli et al. (2017)
Dr4 Darriwilian	Libya	Gondwana	Shallow marine	Palynology	Abuhmida and Wellman (2017)
Dr5 Darriwilian	Argentina	Gondwana	Marginal marine	Palynology	Rubinstein et al. (2011)
Dp1 Dapingian?	Saudi Arabia	Gondwana	Marginal marine	Palynology	Vecoli et al. (2017)
Dp2 Dapingian**	Argentina	Gondwana	Marginal marine	Ch-Palynology	Rubinstein et al. (2010)

C, conodonts; Ch, chitinozoans; G, graptolites; Inv, invertebrates.

*We do not consider that any of the pre-Sandbian cryptospores illustrated in this paper represent cryptospores, but rather folded sphaeromorphs and acritarchs.

**Strother et al. (2015) have questioned the validity of the cryptospores described in this paper.
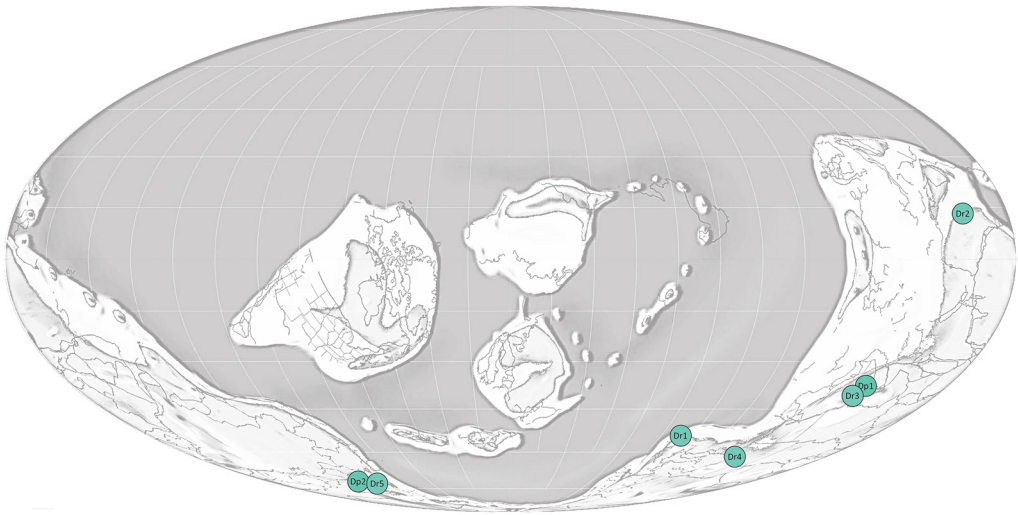
Fig. 3. Palaeogeographic map of the Dapingian and Darriwilian showing the location of dispersed spore assemblages. Locality codes refer to those used in Table 1. Modified from Scotese (2014).

Axe 2012; Edwards *et al.* 2013, 2018; Honegger *et al.* 2013, 2017). Related nematophyte remains appear not to extend back into the Ordovician. Rare cuticle-like sheets have been reported (Gray *et al.* 1982; Strother *et al.* 1996) (see Fig. 2). Ordovician tubular structures are usually smooth-walled forms (Burgess and Edwards 1991; Strother *et al.* 1996) with the reported banded tubes unconvincing (reviewed in Taylor and Wellman 2009). Because all of the reported Ordovician phytodebris are from marine deposits it is difficult to prove if they derive from terrestrial organisms rather than any variety of marine organism.

Regarding the biological affinities of the Ordovician phytodebris, the cuticle-like sheets may possibly derive from early nematophytes, although these have not been convincingly reported from the Ordovician. They may derive from early land plants, but in the absence of a megafossil record it is difficult to make comparisons. The smooth-walled tubular
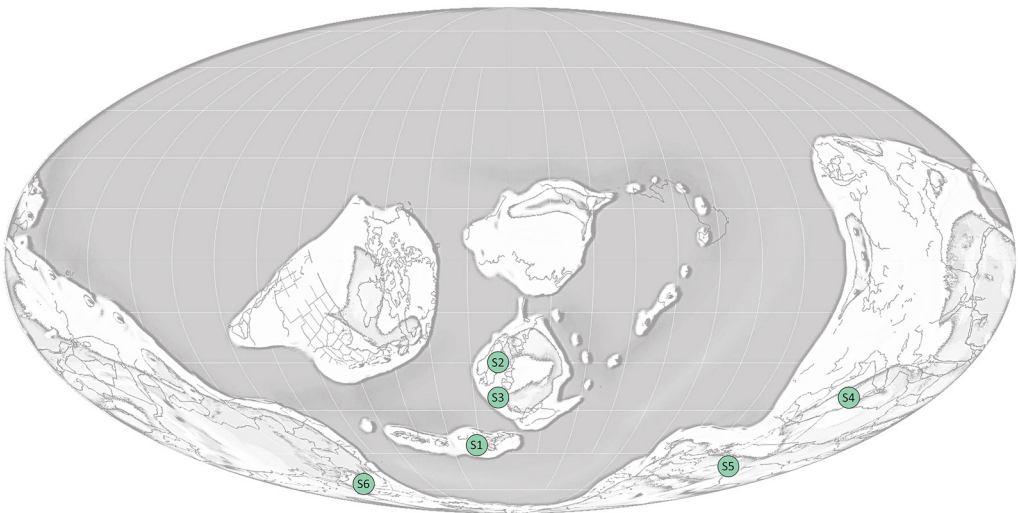

Fig. 4. Palaeogeographic map of the Sandbian showing the location of dispersed spore assemblages. Locality codes refer to those used in Table 1. Modified from Scotese (2014).
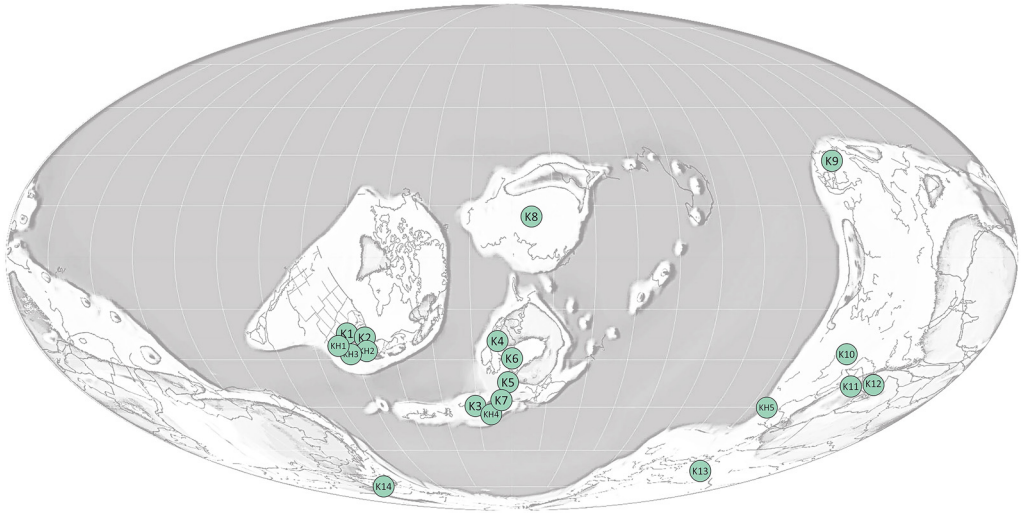
Fig. 5. Palaeogeographic map of the Katian showing the location of dispersed spore assemblages. Locality codes refer to those used in Table 1. Modified from Scotese (2014).

structures may derive from nematophytes or land plants. It is also possible that they represent cyano-bacterial sheathes such as those described from the Silurian by Tomescu and colleagues (e.g. Tomescu and Rothwell 2006).

Geochemical biomarkers

In recent years reports on the first searches for early land plant biomarkers have begun to appear. For example, Romero-Sarmiento *et al.* (2011) analysed Gondwanan Late Ordovican–Early Devonian sediments for the presence of aliphatic and aromatic biomarkers indicative of the presence of land plants (Versteegh and Riboulleau 2010). Spaak *et al.* (2017) reported on the presence of benzonaphthofurans and delta δ^{13}C-depleted mid-chain *n*-alkanes that they interpreted as indicative of the presence of bryophyte-like early land plants. This may be a fruitful area for future research as analytical techniques
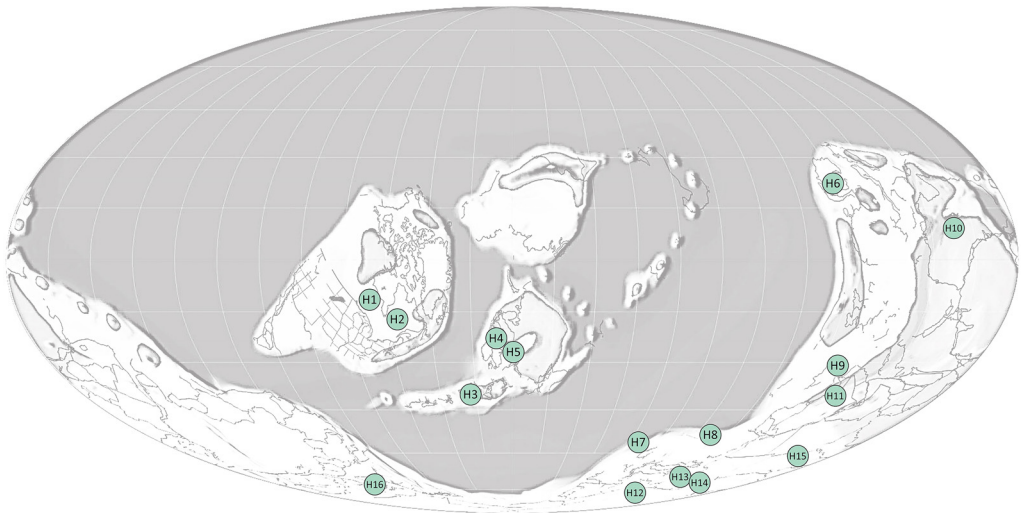

Fig. 6. Palaeogeographic map of the Hirnantian showing the location of dispersed spore assemblages. Locality codes refer to those used in Table 1. Modified from Scotese (2014).

Table 2. *Cryptospores examined ultrastructurally*

Spore taxon	Morphology	Locality	Age	References
Tetrahedraletes medinensis	Naked permanent unfused tetrad	Ohio, USA	Katian	Taylor (1995)
Pseudodyadospora sp.	Naked permanent fused dyad	Ohio, USA	Katian	Taylor (1996)
Segestrespora membranifera	Envelope-enclosed permanent unfused dyad	Ohio, USA	Katian	Taylor (1996)
Dyadospora murusattenuata	Naked permanent unfused dyad	Ohio, USA	Katian	Taylor (1997)
Tetrahedraletes spp.	Naked permanent unfused tetrad	Oman	Katian	Wellman *et al.* (2003)
Dyadospora spp.	Naked permanent unfused dyad	Oman	Katian	Wellman *et al.* (2003)
Cryptotetras erugata	Naked permanent unfused	Saudi Arabia	Darriwilian	Taylor *et al.* (2017)
Pseudodyadospora sp. cf. *P. laevigata*	Naked permanent fused dyad	Saudi Arabia	Darriwilian	Taylor *et al.* (2017)
Monad	Naked monad	Saudi Arabia	Darriwilian	Taylor *et al.* (2017)

continue to improve in precision and we gain a better understanding of the biological affinities of the earliest land plants and their likely biomarker trails.

Evidence from extant land plants

Phylogenetic analysis

In the early 1980s the first cladistic analyses of land plants began to appear in publications, more-or-less coincident with the recognition of an Ordovician flora (Gray *et al.* 1982). These pioneering cladistic analyses considered only extant plants and utilized morphological/anatomical characters (e.g. Mishler and Churchill 1985). The majority of these: (1) recovered a member of the charophycean green alga as sister group to the monophyletic embryophytes (land plants); (2) indicated that the bryophytes were paraphyletic with the liverworts basal and a sister group relationship between vascular plants and either hornworts or mosses. For several decades these analyses were hugely influential providing a model for the physiological/anatomical aquatic algal–subaerial land plant transition (e.g. Graham 1993; Graham and Gray 2001) and also the nature of the earliest land plants (Gray 1984, 1985, 1991). The charophycean green algae–liverwort transition was seen to mirror the origin of subaerial land plants from freshwater aquatic green algal ancestors (e.g. Graham 1993). The liverworts were regarded as the most basal extant land plants and used as a broad model for the morphology/anatomy, physiology and ecology of the first land plants (e.g. Gray 1985).

The many subsequent morphology-based analyses that followed often mirrored these findings, although just about every possible relationship among the embryophytes (liverworts, hornworts,

mosses, vascular plants) has been proposed at some point (reviewed in Kenrick and Crane 1997). A significant advance was the inclusion of fossil data in cladistic analyses. Fossil data were important in recognizing a group of fossil plants (Protracheophytes) that fell between the paraphyletic 'bryophytes' and vascular plants (Kenrick and Crane 1997). These included various Rhynie chert plants that preserve exquisite anatomical detail including some rather unusual character combinations, such as more-or-less isomorphic gametophyte and sporophyte generations, tracheids and stomata present in both generations, etc. (Edwards *et al.* 2017). Nevertheless, liverworts remained the model of choice for the earliest land plants.

As the molecular revolution dawned, the use of sequence data in cladistic analyses became possible. Initial analyses seemed to support the existing favoured topology. However, as more sequence data became available and ever-refined analytical techniques emerged, the tree topologies generated began to diverge from this model (recently reviewed by Wickett *et al.* 2014; Puttick *et al.* 2018; OTPTI 2019). Firstly, it began to appear that the zygnematophycean green algae were the most likely sister group to the embryophytes. Secondly, embryophyte tree topologies changed significantly with monophyletic bryophytes and tracheophytes emerging as sister groups. Within the bryophytes the hornworts appeared as most basal and sister to a 'setaphyte clade' consisting of the liverworts and mosses.

The newly accepted topologies have important implications. Regarding the algal sister group, it suggests that many of the extant zygnematophycean algae, some of which are unicellular, are highly reduced (Puttick *et al.* 2018; Cheng *et al.* 2019; Donoghue and Paps 2020; Jiao *et al.* 2020; Rensing 2020). This makes modelling of the algal–plant

transition problematic based solely on consideration of the living zygnematophycean algae. In terms of the basal embryophytes, it means that the most basal of the extant vascular plants (lycopsids) are as closely related to the stem group land plants as the earliest diverging extant bryophytes (hornworts) (Puttick et al. 2018). It also suggests that the bryophyte groups are reduced and have lost certain characters (e.g. liverwort stomata) or are secondarily simplified (e.g. possibly bryophyte conducting tissues). A critical next step will be the inclusion of fossil data into the new phylogenetic schemes. It is important to assess the position of the Rhynie chert protracheophytes. For example, if Aglaophyton can be shown to be sister group to the [bryophytes + tracheophytes] (i.e. a stem group embryophyte) it would suggest that stem group embryophytes may have been more complex than previously anticipated, possessing a more-or-less isomorphic gametophyte and sporophyte, with both generations possessing stomata and containing conducting tissues (possibly of Aglaophyton-type).

Recently Edwards et al. (2021a, b, c) recognized a new group of plants, called eophytes, among their charcoalified Late Silurian–Early Devonian plant Lagerstätte (see above). These diminutive plants exhibit a primitive anatomy based on sporophytes with food conducting cells and yield in-situ cryptospores. It is highly likely that these were parasitic on gametophytes characterized by transfer cells. Both stages of the lifecycle were likely poikilohydric, and thus able to desiccate and rehydrate, bearing ecological/physiological similarities to extant bryophytes as opposed to most vascular plants. Edwards et al. (2021a, fig. 8) place the eophytes as stem group polysporangiates, although we consider that they may represent stem group embryophytes that have a sister group relationship with a clade comprising both the bryophytes and vascular plants. Again, their relative position in the phylogeny with respect to Rhynie chert plants such as Aglaophyton is critical in influencing our perception of the earliest stem embryophytes. It seems likely that they are more basal than Aglaophyton and provide the best current model for the earliest stem group embryophytes.

Molecular clock analyses

In the early 2000s the first molecular clock analyses began to appear concerning the dating of the origin of land plants and the major land plant groupings (reviewed in Morris et al. 2018). Initial results indicated land plant origins far earlier than that suggested by the fossil record (as described above). Subsequently molecular clock techniques have rapidly evolved, and different strategies have been employed and a variety of palaeontological

Table 3. *A summary of some proposed age ranges (Ma) from recent molecular clock analyses regarding dating the origin of land plants (embryophytes) and vascular plants (tracheophytes)*

References	Land plants	Vascular plants
Heckman et al. (2001)	703 ($\pm$45)	
Sanderson (2003)	425–480	
Hedges et al. (2004)	968 ($\pm$93)	707 ($\pm$98)
Zimmer et al. (2007)	725	
Smith et al. (2010)	474–477	432–434
Clarke et al. (2011)	568–815	425–456
Magallón et al. (2013)	475	424
Morris et al. (2018)	515.2–473.5	450.8–430.4
Nie et al. (2020)	486.1	449.7
Su et al. (2021)	980–682	880–593

calibration systems experimented with. These analyses have provided highly variable results (reviewed in Table 3), and nearly all are incongruent with the fossil record, although the discrepancy is decreasing in some of the most recent analyses. An early origin of land plants as suggested by some molecular clock analyses, would require that these plants left no fossil record for a considerable period of Earth history, which seems unlikely if they reproduced by sporopollenin-walled spores, unless they were only present in very restricted environments and/or a very confined palaeogeographical area.

Fungi and lichens (including nematophytes)

Phylogenetic analyses and molecular clock evidence indicate that fungi originated in the Mesoproterozoic (e.g. Parfrey et al. 2011), but it is not clear when they first appeared in terrestrial settings (aquatic or subaerial). Fungal remains are well known from the Silurian where they occur in palynological preparations as dispersed fungal spores and hyphae (e.g. Sherwood-Pike and Gray 1985). Such remains have rarely been reported from the Ordovician, but this may reflect the paucity of non-marine deposits available for analysis. Thusu et al. (2013) report the enigmatic Tortotubulus protuberans from the Late Ordovician. This tubular structure has been interpreted as a fungus (Smith 2016), although more precise affinities are not possible (Auxier et al. 2016). Most of the other reported fungal remains from pre-Silurian strata are more contentious (reviewed in Taylor et al. 2015; Berbee et al. 2020; Wellman and Ball 2021). However, it is worth noting that recent molecular development research on extant charophycean algae and land plants suggests that fungal symbioses may have been crucial to the colonization of the land by plants (Berbee et al. 2020).

Lichenization has evolved numerous times, involving different combinations of fungi and algal/cyanobacterial hosts (Lűcking and Nelsen 2018). However, recent phylogenetic analysis suggests that lichens may not have evolved until after the evolution of vascular plants (Nelsen *et al.* 2020).

The enigmatic Silurian–Devonian nematophytes have recently been demonstrated to have fungal, and possibly also lichen, affinities (Edwards and Axe 2012; Edwards *et al.* 2013, 2018; Honegger *et al.* 2013, 2017). These occur as megafossils (Lang 1937; Strother 1988) and dispersed microfossils in the form of 'cuticle-like sheets' and tubular structures, including 'banded tubes' (recently reviewed by Wellman and Ball 2021). However, no convincing nematophyte remains have been reported from the Ordovician thus far.

Land animals in the Ordovician

Silurian continental deposits have yielded a diverse array of fossil evidence for land animals indicative of diverse and complex ecosystems developed in both freshwater aquatic and fully terrestrial settings. These fossils include whole organisms such as fish (e.g. Blom *et al.* 2002) and arthropods (e.g. Jeram *et al.* 1990), dispersed arthropod cuticles recovered using palynological techniques (e.g. Gray and Boucot 1994), coprolites (e.g. Edwards *et al.* 1995) and a variety of trace fossil evidence (e.g. McCoy *et al.* 2012).

Similar evidence for Ordovician terrestrial organisms is much rarer, almost certainly reflecting the paucity of Ordovician non-marine deposits available for study. To date all reported Ordovician fish remains are considered to be from fish inhabiting nearshore shallow marine environments (Davies and Sansom 2009). There are rare reports of potential non-marine arthropods, but these are all controversial with questions remaining regarding either their age or habitat (e.g. McNamara and Trewin 1993). There are several reports of potential non-marine trace fossil assemblages. However, these are all from terrestrial deposits that are either doubtful or closely associated with nearshore marine deposits, making judgements on the habitat and mode of life of their makers doubtful. For example, it has been suggested that purported millipede burrows in Ordovician palaeosols described by Retallack and Feakes (1987) are possibly of marine origin (Davies *et al.* 2010). Ordovician non-marine arthropod traces described by Johnson *et al.* (1994) have also been re-interpreted as marine in origin (Shillito and Davies 2019), and the trackways in Cambrian–Ordovician aeolian deposits described by MacNaughton *et al.* (2002) are from a marginal marine setting. It has recently been suggested that the exquisite trace

fossils from the Tumblagooda Sandstone of Australia (Trewin and McNamara 1994) were deposited in a littoral setting and are possibly of Silurian age (Shillito and Davies 2020).

Molecular clock studies have also been employed to ascertain when the various terrestrial arthropod groups appeared. To date most of these studies suggest that terrestrial arthropod groups invaded the land much earlier than the fossil record would indicate and by at least the Cambrian (Lozano-Fernandez *et al.* 2016). Terrestrial trace fossil assemblages from the Cambrian and earlier are all considered doubtful (reviewed by Minter *et al.* 2016).

Ordovician non-marine sediments, soils and terrestrial environment

As emphasized throughout this review, globally Ordovician non-marine deposits are extremely rare. The reasons for this are not clear (Davies and Gibling 2010) but is usually considered to be a consequence of high sea-levels and the difficulties involved in identifying Ordovician non-marine evidence that relies largely on absence of evidence. Davies and Gibling (2010) summarize the sedimentology of the best known Ordovician non-marine deposits. It is clear that many of these are actually very near-shore and are often interdigitated with marine deposits making it difficult to ascertain the degree of marine influence. None-the-less, some Ordovician palaeosols are reported (summarized by Retallack 2000).

There has been considerable debate regarding the influence of Ordovician terrestrial life, which transitioned from microbial mat communities to those including the earliest land plants (embryophytes), on the nature of sedimentation and soil formation (Davies and Gibling 2010; Gibling and Davies 2012; Santos *et al.* 2016; Davies *et al.* 2017). This avenue of research has considered changes to weathering rate (e.g. D'Antonio *et al.* 2019), sediment stabilizing properties (e.g. Davies and McMahon 2021), patterns of sedimentation as geomorphological agents such as rivers change form (e.g. Ganti *et al.* 2019), consideration of how land plants promoted terrestrial mud deposition (e.g. McMahon and Davies 2018; Zeichner *et al.* 2021), and much more. This debate has also extended to biogeochemical effects (Lenton and Daines 2017) and how these impacted atmospheric composition (e.g. Adiatma *et al.* 2019), climate (e.g. Lenton *et al.* 2012) and so on. One avenue of research that has also recently received attention is the effects of increasing land plant cover on terrestrial biomass and thus patterns of carbon isotopes in the Ordovician sedimentary record (Tomescu *et al.* 2009; Quinton *et al.* 2021).

It should be noted that much of the above debate was focused on the assumption that Ordovician

terrestrial floras comprised bryophyte-like (more specifically liverwort-like plants). This assumption was based on prevailing land plant phylogenies (see above). Thus, much of the debate utilized evidence from experiments on extant bryophytes (particularly liverworts) (e.g. Quirk *et al.* 2015). As discussed above, recent phylogenetic analyses and the recognition of eophyte plants has altered our understanding and perception of the nature of the earliest stem group land plants. However, it should be noted that workers such as Jane Gray always stressed that the earliest land plants may not be directly related to extant bryophytes/liverworts, but that these plants were probably 'bryophyte-like'/'liverwort-like' in their physiology and ecology (Gray 1985, 1991), and they may thus still provide a reasonable analogue (if not 'nearest living relative') for the earliest land plants.

Terrestrial life and the End Ordovician glaciation and mass extinction

The dispersed spore fossil record exhibits no appreciable change from the Late Ordovician into the Early Silurian (reviewed by Gray 1985; Richardson 1996; Steemans *et al.* 2000; Strother 2000; Wellman *et al.* 2013) with a continuous increase in diversity not interrupted by the Late Ordovician extinction interval evident among marine invertebrates. Identical dispersed spore assemblages have been reported worldwide before, during and after the Hirnantian glaciation and End Ordovician mass extinction. This has been taken to suggest that terrestrial floras were relatively unaffected by these interconnected events, with speculation that the earliest land plants were immune because they were cosmopolitan generalists that flourished in a wide range of environments (Gray 1985; Wellman 1996). Indeed, dispersed spore assemblages are well known from cold, high latitude localities where they are often associated with glacial deposits (e.g. Gray *et al.* 1986).

Conclusions

It is evident from the above discussion that the Ordovician represents a critical period in Earth's terrestrialization. It seems likely that is witnessed the transition from a terrestrial, microbial soil–vegetation system to one that included the first land plants. At the same time non-marine aquatic biotas began to increase in diversity, although it seems that the only animals on the land were probably temporary visitors that were not obligate subaerial dwellers. Our understanding of Ordovician terrestrial life will continue to improve as refined techniques in phylogenetic analysis, molecular clock studies, evo–devo research

and Earth systems modelling become available. But ultimately it seems likely that newly discovered fossils will shed most light on this subject area, particularly if convincing Ordovician plant remains can be recovered.

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