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Baltica cradle of early land plants? Oldest record of trilete spores and diverse cryptospore assemblages; evidence from Ordovician successions of Sweden

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ABSTRACT

The origin of land plants is one of the most important evolutionary events in Earth's history. The mode and timing of the terrestrialization of plants remains debated and previous data indicate Gondwana to be the center of land-plant radiation at ~ 470–460 Ma. Here we present the oldest occurrences of trilete spores, probably the earliest traces of vascular land plants yet recorded. The spores occur in Ordovician, Sandbian (455 million years old) successions in central Sweden, once part of the paleocontinent Baltica. These strata are independently dated by marine microfossils (conodonts) and $^{206}Pb/^{238}U$ dating of volcanic ash deposits. Our discovery extends the record of trilete spores globally by ~8 million years, and for Baltica by ~25 million years. Additionally, cryptospore assemblages are identified revealing a diverse and stable mid-Ordovician (Darriwilian: ~ 460 Ma) vegetation of free-sporing plants. The formation of regolith substrates on land as a consequence of permanent plant cover must in turn have affected the marine biota. We link these early land plant spore occurrences to the extensive, nutrient-rich volcanic ash deposits and propose Baltica as the possible original region of the radiation of early land plants.

Introduction

The origin of land plants was a major macroevolutionary event, having immense consequences for continental and marine ecology, and for the global climate system (Berner et al. 2007; Wellman 2010). Land plants triggered an acceleration of weathering processes (Lenton et al. 2012) and the development of structured soils in symbiosis with complex fungal and microbial communities (Rubinstein et al. 2010; Wang et al. 2010; Martin et al. 2017). Empirical studies have also shown that the appearance of land plants boosted CO_2 drawdown and potentially contributed to Late Ordovician cooling and a rise in atmospheric oxygen pressure (pO_2) (Lenton et al. 2012, 2016).

It is generally accepted that the land plants, i.e. embryophytes, originated from charophycean green algae as an adaptation to a terrestrial life mode, and that the earliest land plants were "bryophyte-like", with liverworts being the most basal extant group (Wellman et al. 2013). Based on molecular-clock inferences, colonization of the land by plants probably initiated during the Ordovician, or even as early as the Cambrian, taking place in a stepwise pattern (Morris et al. 2018). The cryptospore-producing plants appeared first, followed by plants producing trilete spores.

Cryptospores are generally considered to represent dispersed spores derived from the earliest terrestrial flora (Steemans 1999; Wellman & Gray 2000; Steemans et al. 2009), which was represented by primitive embryophytes. Hilate cryptospores (naturally dissociated from dyads) are

regarded as derived from polysporangiate protracheophytes (Wellman et al. 2013) (plants with several sporangia on branched axes, and with weakly differentiated or no tracheids).

Trilete spores are largely considered to represent vascular plants and their immediate ancestors (Wellman & Gray 2000; Wellman et al. 2013; Edwards et al. 2014). Even though trilete spores do not unequivocally represent higher plant taxa, they are recognized as most common among the vascular plants, probably suggesting the early radiation of this group (Gray 1985; Kenrick et al. 2012; Edwards et al. 2014).

The transition from cryptospores to hilate/trilete spores was a major evolutionary event as it is considered to represent the inception and adaptative radiation of the vascular plant lineage (Steemans et al. 2009; Morris et al. 2018). The plant megafossil record for the earliest land plants is rare, incomplete and strongly biased. The oldest unequivocal megafossil of terrestrial sporophytes, i.e. early land plants is *Cooksonia barrandei* found in Silurian (middle Sheinwoodian) deposits in the Czech Republic (Libertín et al. 2018). However, the recent discovery of putative plant remains from the Hirnantian of Poland (SW peri-Baltica), are most likely the earliest record of vascular land plants (polysporangiophytes) dated to the Late Ordovician (Salamon et al. 2018).

To date, the oldest cryptospores, representing the earliest fossil evidence of non-vascular land-plants, have been recorded in Middle Ordovician, Dapingian rocks from northwestern Argentina (Rubinstein et al. 2010) (Fig. 1) although this record has been questioned (Strother et al. 2015). Other early records of cryptospore assemblages are those from Middle Ordovician (Darriwilian) successions from Saudi Arabia (Strother et al.
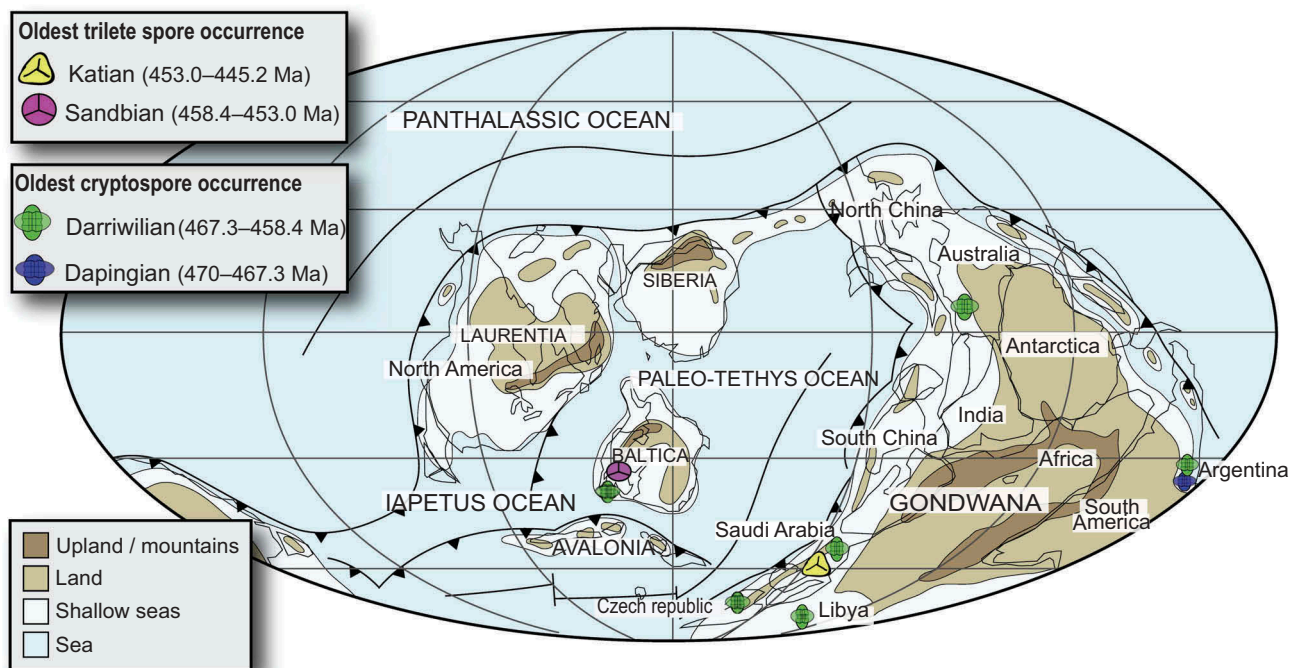
Figure 1. Mid-Ordovician paleogeographic map with the oldest global spore occurrences indicated. Dapingian and Darriwilian cryptospore occurences (Vavrdová 1984; Strother et al. 1996, 2015; Rubinstein et al. 2010, 2011; Abuhmida & Wellman 2017; Spaak et al. 2017; Vecoli et al. 2017), and Sandbian and Katian trilete spore occurrences (Steemans et al. 2009; Wellman et al. 2015).

1996, 2015; Vecoli et al. 2017), the Czech Republic (Vavrdová 1984), Argentina (Rubinstein et al. 2011), Libya (Abuhmida & Wellman 2017) and Australia (Spaak et al. 2017) (Fig. 1). Late Ordovician cryptospore assemblages are more common and abundant and represented on almost all paleocontinents (Gerrienne et al. 2016; Rubinstein et al. 2016; Ghavidel-Syooki 2017; Tang et al. 2017 and references therein).

The oldest trilete spores so far recorded are from Upper Ordovician (Katian) successions of Saudi Arabia (Steemans et al. 2009; Wellman et al. 2015), followed by slightly younger assemblages in Hirnantian strata of Turkey (Steemans et al. 1996) and Algeria (Spina 2015), Katian–Hirnantian deposits of Iran (Ghavidel-Syooki 2017) and Katian?–Hirnantian successions of Argentina (Rubinstein et al. 2016). Consistently, all previous Ordovician records derive from the Gondwanan or peri-Gondwanan terranes. Thus, previous studies have proposed that vascular plants, or their immediate ancestors, probably originated in Gondwana at ~ 448 MA, and subsequently colonized Euramerica, Avalonia and finally Baltica (Wellman et al. 2013; Gerrienne et al. 2016).

Here we present data supporting a very different scenario, based on the discovery of the oldest trilete spore assemblages, occurring in lowermost Upper Ordovician (Sandbian) successions from Motala, central Sweden which at the time belonged to the continent Baltica (Figs. 1–4). This new record predates the occurrence on Gondwana by some 8 Ma.

Geological background

The paleocontinent Baltica constitutes a large part of northern Europe, bounded by the British and Scandinavian
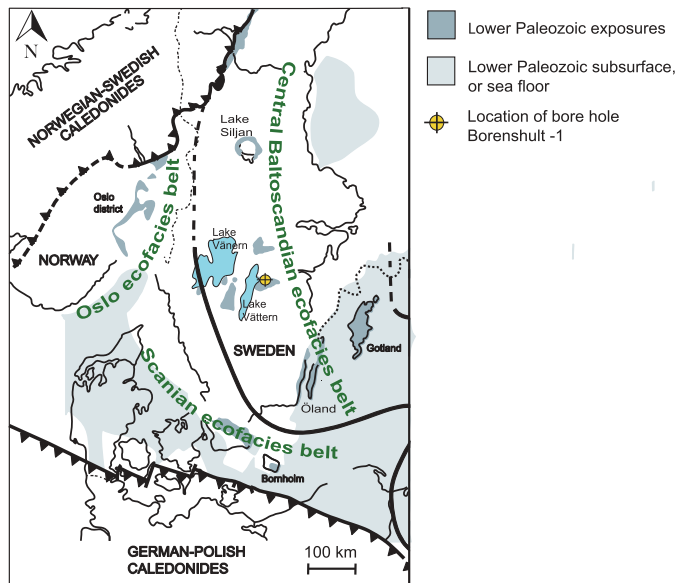
Figure 2. Map of Sweden illustrating lower Paleozoic deposits. Modified from Janusson et al. (1995) and Bergström et al. (2012). The Caledonian fronts are marked in the west and in the south. The Borenshult-1 drillcore is marked with yellow circle. Herein the use of the international term ecofacies belt (a combination of faunal assemblages and lithological characteristics) is preferred over the local term "confacies belt" as defined by Jaanusson (1995).

Caledonide mountain ranges to the northwest, the Ural Mountains to the east and the Trans-European Suture Zone to the south (Cocks & Torsvik 2005). Baltica rifted apart from Gondwana (the southern super-continent, including S. America, Africa, India, Australia and Antarctica) during the Cambrian and formed an isolated continent until its
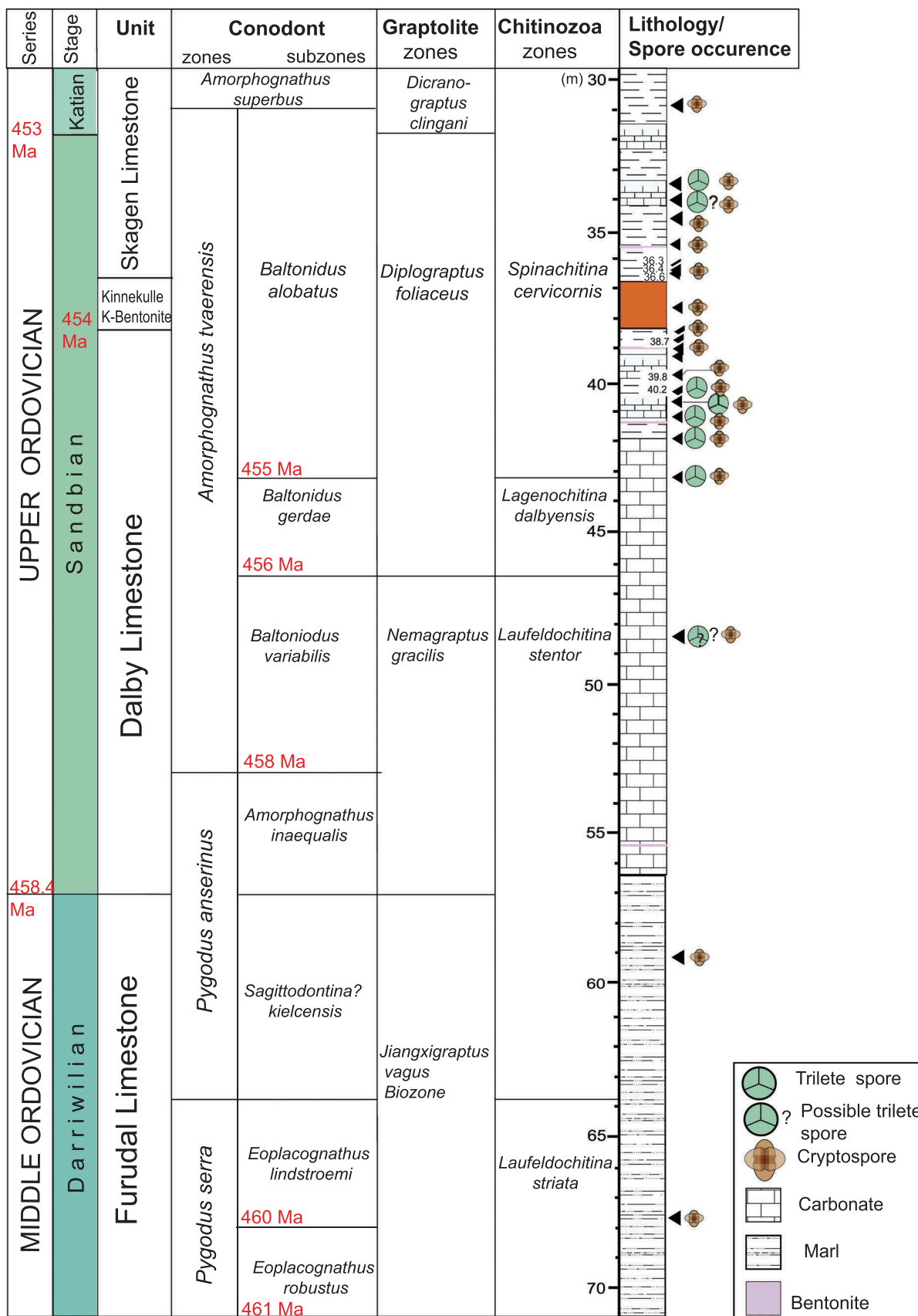
Figure 3. Stratigraphic distribution of spores in the Borenshult-1 drillcore. Lithostratigraphy, conodont biostratigraphy and age constraints of the studied section of the Borenshult-1 drillcore showing the stratigraphic distribution of trilete spores and cryptospores. Conodont zonation is based on Bergström et al. (2011, 2018) and was subsequently tied to graptolite and chitinozoan biostratigraphy. Absolute ages (red) are based on biostratigraphic and radiometric ties to the International Stratigraphical Chart 2018 (Cohen et al. 2018) combined with U-Pb zircon dates from Lindskog et al. (2017).

Stages	Darriw		Sandbian																				Katian	
Samples (m)	67.6	59.1	48.2	48.1	43.1	41.9	41.1	40.35	40.2	39.8	39.1	38.98	38.85	38.7	38.35	37.5	36.6	36.4	36.3	35.2	34.45	34	33.05	30.75
Cryptospores																								
Acontotetras sp.			×																					
Cryptotetras mordacis																							×	×
Cymbohilates spp.			×	×			×									×	×						×	
Chelinohilates? sp.			×																					
Dyadospora murusdensa				×				×																
Didymospora fucosogranulata	×		×			×			cf.											×				
Didymospora luna	×	cf.	×			×														×				
Gneudnaspora divellomedia		×		×	×																			
Gneudnaspora sp. cf. *G. divellomedia* var. *punctate*	×	×	×	×			×											×	×	×				
Imperfectotriletes cf. *I. persianense*																							×	
Imperfectotriletes cf. *patinatus*																							×	
Imperfectotriletes vavrdovae		×	×				×																×	×
Imperfectotriletes? sp.			×																					
Laevolancis chibrikovae		×																						
Laevolancis plicata							×																	
Laevolancis sp.																							×	
ornamented monads																							×	×
Pseudodyadospora laevigata		×	×				×							×									×	
Psedodyadospora petasus		×								×														
Rimosotetras problematica		×																					×	
Rimosotetras subspherica																×							cf.	
Segestrespora laevigata	×		cf.	×			×																	
Segestrespora membranifera			cf. ×																					
Segestrespora spp.	cf.		×																				×	
Sphaerasaccus glabellus			×																					
Tetrahedraletes grayae			×	×											×	×							×	
Tetrahedraletes medinensis	×	×	×	×			×																×	
Tetraplanarisporites laevigatus			cf.													×								
Tetrad (large, naked, unfused-Wellman et al. 2015)	×																							
Velatitetras anatoliensis									×															
Velatitetras cf. *V. rugulata*			×																					
Velatitetras sp.									×														×	
Velatitetras? sp.	×																						×	
Unidenfied cryptospores			×	×																				
Trilete spores																								
Ambitisporites sp.				×																				
Ambitisporites? sp.							×																	
Aneurospora sp.			×																					
Chelinospora? sp.			×																					
Leiotriletes sp.							×	×															×	
Leiotriletes? sp.								×																
Retusotriletes sp.								×																
Retusotriletes? sp.																								×
Relative abundance of terrestrial palynomorphs (%)	<0.5	<0.5	0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	11.4	1.9	<0.5	<0.5	12	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5

Figure 4. Stratigraphic distribution of cryptospores and trilete spores within the analyzed succession of the Borenshult-1 drillcore. The relative abundance of marine and terrestrial palynomorphs is based on counts of 300 specimens per sample, except for sample 37.5 m in which only 25 palynomorphs were identified in the Kinnekulle bentonite.

core comprises a well-dated and nearly complete succession of Middle to Upper Ordovician (Darriwilian to Rhuddanian) marine marly carbonates deposited relatively close to land (Bergström et al. 2011). The studied successions have previously been dated to ~ 457–455 Ma by conodont biostratigraphy (Bergström et al. 2012) and occur within an interval of 2–10 meters below the Kinnekulle K-bentonite (Fig. 3). The type locality of this distinctive 1.8-m-thick bentonite bed is located on the eastern slope of Kinnekulle (Bauert et al. 2014), in south central Sweden (Fig. 1). Zircons from the upper part of this bed were dated by $^{206}Pb/^{238}U$ radiometric methods to *c*. 454 Ma, which corresponds to the late Sandbian (Bauert et al. 2014). This age is consistent with $^{206}Pb/^{238}U$ dating of the equivalent bentonite bed across the Baltic Sea (Bauert et al. 2014), more specifically, high-precision dating of the bentonite bed on the island of Bornholm, Denmark, obtained an age of 454.41 ± 0.17 (Sell et al. 2013).

Materials and methods

The Borenshult-1 core was drilled in 2007, in the vicinity of Motala, east of Lake Vättern in Sweden (Fig. 2) and reached a depth of 71.33 m. The basal part intersects the Darriwilian Furudal Limestone (71.33–56.51 m), which is conformably overlain by the Dalby Limestone (56.51–38.35 m), succeeded by the Kinnekulle K-bentonite (reaching a thickness of 1.8 m), which in turn is successively overlain by the Skagen and Moldå formations. We sampled the interval 71.33–30.75 m, for fossil terrestrial palynomorphs. This interval is well-dated within an independent biostratigraphical framework provided by conodonts, graptolites and chitinozoans (Grahn & Nõlvak 2010; Bergström et al. 2011, 2012) (Fig. 3). Additionally, several bentonite beds within the succession provide radiometric age constraints (Sell et al. 2013; Bauert et al. 2014).

Thirty-four palynological core samples were analyzed from the Borenshult-1 drillcore, encompassing the upper part of the Darriwilian (Furudal Limestone), the entire Sandbian (Dalby Limestone) and the lower part of the Katian (Freberga Formation) (Fig. 3). Samples, each of ~ 20 g were processed at GeoLab Ltd, Canada. The sedimentary rock samples were treated with 20% HCl to remove the carbonates, followed by treatment with 37% HF in order to remove the mineral matter. The remaining organic residue was sieved using a 5 μm mesh and two strew slides were prepared for each sample. One to two entire slides from each sample were analyzed for palynology by light microscopy. The ratio between marine and terrestrial palynomorphs was calculated (Fig. 4) by documenting three hundred marine (organic walled phytoplankton, chitinozoans and scolecodonts) and terrestrial (cryptospores and trilete spores) specimens per sample. The slides are housed in the paleopalynological collection of IANIGLA, CCT CONICET Mendoza, Argentina. The residues are housed in the Swedish Museum of Natural History, Stockholm, Sweden.

Results and age

We examined 34 samples and 23 yielded rich and well-preserved palynomorph assemblages, dominated by marine microfossils, mainly acritarchs, with subsidiary chitinozoans, scolecodonts,

amalgamation with Avalonia (including eastern N. America and parts of Great Britain) during the Late Ordovician (Cocks & Torsvik 2005). During this convergence of continental plates and subduction, an unusual extensive system of volcanic arcs produced exceptional volumes of volcanic ash by the mid-Ordovician (Parnell & Foster 2012). As Baltica drifted northwards from Gondwana through the Ordovician, the Tornquist Sea was formed alongside the southern margin of Baltica, hosting a rich marine invertebrate fauna (Bergström et al. 2013; Wu et al. 2018). By the end of the Middle Ordovician, Baltica was positioned around 35°S and the climate was comparable to that of the modern subtropical belt with extensive formation of reefs in the shallower marine basins. The studied spore assemblages derive from Central Baltoscandia (Fig. 2), where the Ordovician deposits are typified by extremely slow, condensed and uniform sedimentation, and where the thickness of the entire Ordovician succession reaches only 75–150 m (Bergström et al. 2013).

We sampled the Borenshult-1 drillcore for palynologic examination, focusing on early land plant spores (Figs. 2 and 3). This

graptolite fragments and sparse terrestrial spores (Figs. 3 and 4). Notably, we found diverse and well-preserved cryptospores through the entire studied interval of the Borenshult-1 drillcore spanning the upper Darriwilian to Katian (Figs. 3–8).

The basal part of the succession (Furudal Limestone) comprises nodular limestones intercalated with marls containing traces of bioturbation (Bergström et al. 2011). The fossil fauna is dominated by trilobite fragments with subsidiary crinoids, brachiopods, and ostracodes indicating a relatively nearshore paleoenvironment within the photic zone. We identified the cryptospore *Tetrahedraletes*

medinensis at a depth of 67.6 m (Figs. 3–5) within the lower part of the Furudal Limestone. This stratigraphic level corresponds to the base of the *Eoplacognathus lindstroemi* conodont Subzone of the *Pygodus serra* conodont Zone dated to late Darriwilian ~ 460 Ma (Bergström et al. 2012, 2013) (Fig. 3). At the depth of 59.1 m, a more diverse cryptospore assemblage includes six taxa: *Didymospora fucosogranulata, D. luna, Imperfectotriletes vavrdovae, Segestrespora laevigata, Segestrespora*? sp., *Tetrahedraletes medinensis, Velatitetras* sp. and naked unfused tetrads *sensu* Wellman et al. 2015 (Figs. 3–5). This sample derives from the upper part of the Furudal
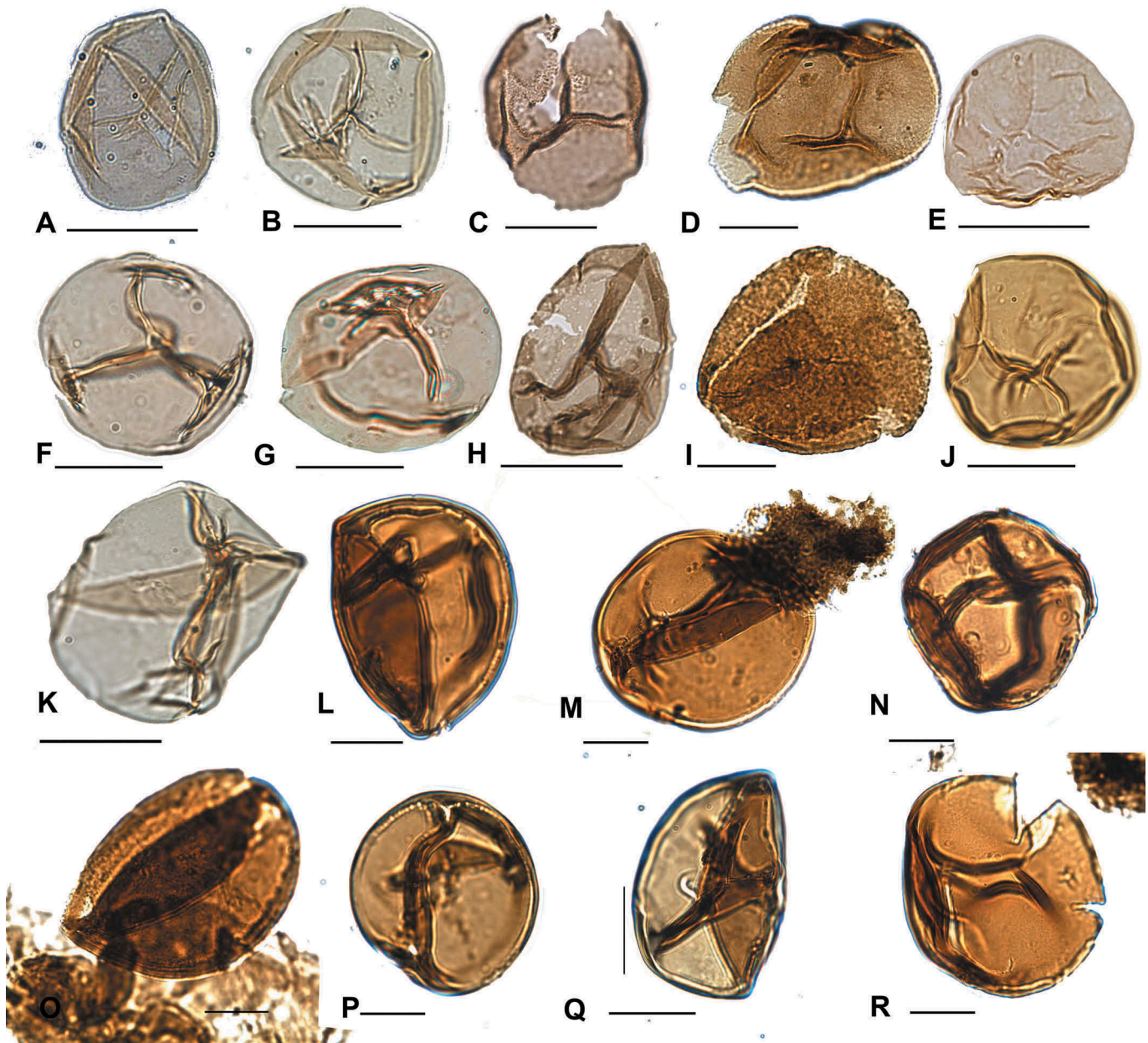

Figure 5. Selected oldest cryptospores and trilete spores from the Borenshult-1 drillcore. **A–K**. Sandbian trilete spores and **L–R**. Darriwilian cryptospores. Taxon name followed by sample depth and England Finder Reference (EFR). Scale bars = 20 μm. **A**. *Leiotriletes* sp. (40.2 m) EFR: M46-0; **B**. *Leiotriletes* sp. (40.35 m) EFR: X17-3; **C**. *Aneurospora* sp. (43.1 m) EFR: K12-0b; **D**. *Aneurospora* sp. (43.1 m) EFR: V39/0a; **E**. *Leiotriletes* sp. (33.05 m) EFR: O32-0a; **F**. *Retusotriletes* sp. (40.2 m) EFR: M27-4; **G**. *Retusotriletes*? sp. (34.0 m) EFR: M45-2a; **H**. *Ambitisporites* sp. (41.9 m) EFR: J29-0M; **I**. *Chelinospora*? sp. (48.2 m) EFR: K38-2a; **J**. *Ambitisporites*? sp. (40.2 m) EFR: T33/0; **K**. *Leiotriletes*? sp. (40.2 m) EFR: L39/3; **L**. *Imperfectotriletes vavrdovae* (59.1 m) EFR: M29-2b; **M**. *Segestrespora laevigata* (59.1 m) EFR: R24-0b; **N**. *Tetrahedraletes medinensis* (67.6 m) EFR: D34-4b; **O**. *Didymospora fucosogranulata* Strother et al. 2015, (59.1 m) EFR: Y30/4b; **P**. *Didymospora luna* Strother et al. 2015 (59.1 m) EFR: P17/3b; **Q**. *Imperfectotriletes vavrdovae*? (Richardson) Steemans *et al.*, 2000, (59.1 m) EFR: F32/0a; **R**. Tetrad (large, naked, unfused) in Wellman et al. 2015 (59.1 m) EFR: F35/0a.
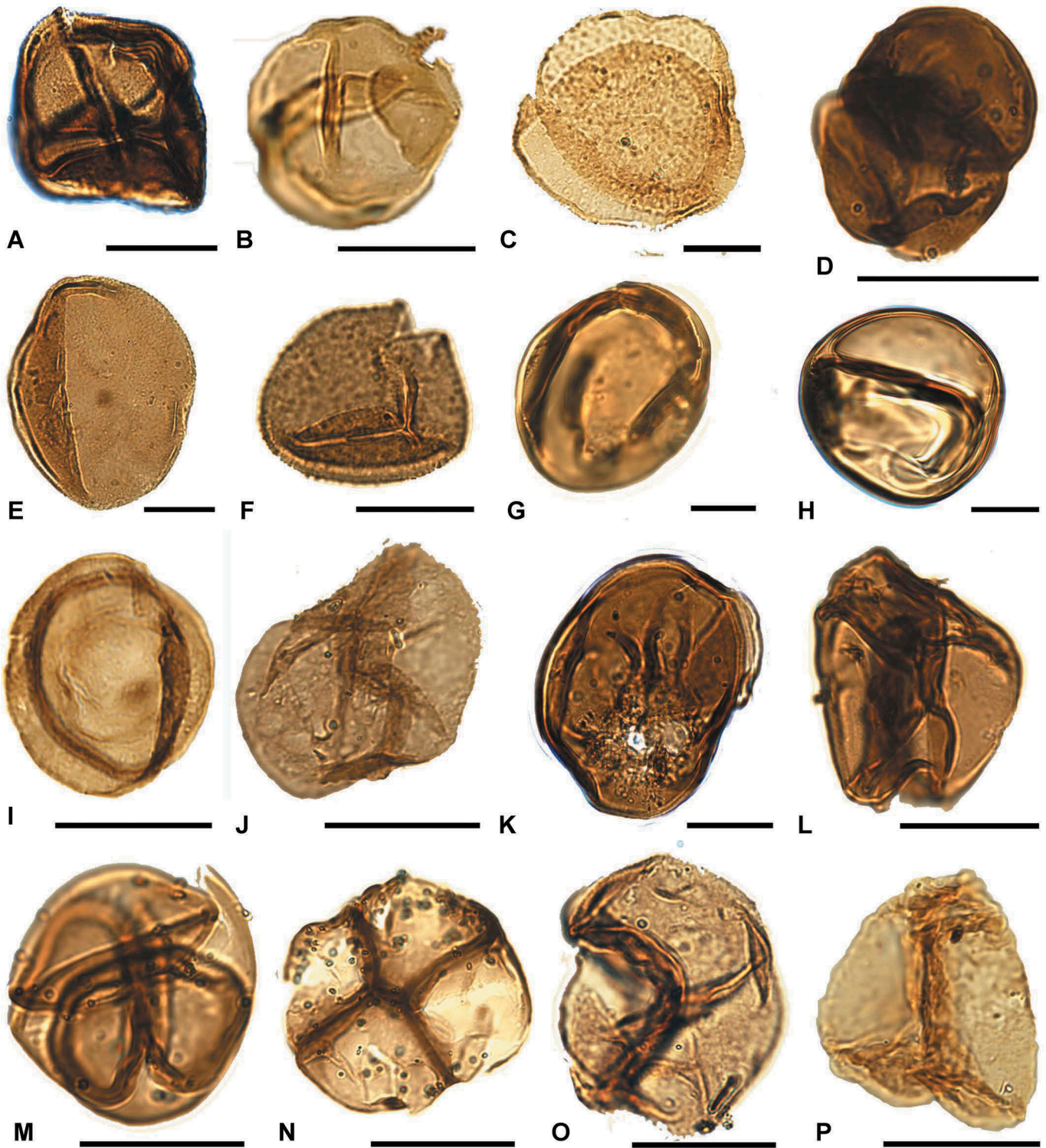
Figure 6. Selected cryptospores from the Sandbian interval of the Borenshult-1 drillcore. Taxon, sample number, and England Finder Reference (EFR). Scale bars 20 μm. **A.** *Acontotetras* sp. (43.1 m) EFR: T25-1a; **B.** *Cryptotetras mordacis* Strother et al. 2015 (33.05 m) EFR: E31/3a; **C.** *Cymbohilates* sp. (dyad) (33.05 m) EFR: E32-0a; **D**. *Dyadospora murusdensa* Strother & Traverse 1979, (39.1 m) EFR: P30-2; **E**. *Gneudnaspora* sp. cf. *G. divellomedia* var. *punctate* in Vecoli et al. 2017, (43.1 m) EFR: W14/0b; **F**. *Imperfectotriletes* sp. cf. *I. persianense* Ghavidel-Syooki 2017, (34.0 m) EFR: T17/2b; **G**. *Laevolancis chibrikovae* Steemans et al. 2000, (48.2 m) EFR: J35/3b; **H**. *Pseudodyadospora laevigata* Johnson 1985, (48.2 m) EFR: Q16/4a; **I**. *Pseudodyadospora petasus* Wellman & Richardson 1993, (48.2 m) EFR: R39/2b; **J**. *Segestrespora* sp. cf. *S. membranifera* (Johnson) Burgess 1991, (41.1 m) EFR: W14/0; **K**. *Sphaerasaccus glabellus* Steemans et al. 2000, (48.2 m) EFR: N13/3b; **L**. *Tetrahedraletes grayae* Strother 1991 (34,0 m) EFR: R44/3a; **M**. *Tetrahedraletes medinensis* Strother & Traverse emend. Wellman & Richardson 1993, (39.1 m) EFR: S25/4; **N**. *Tetraplanarisporites laevigatus* Wellman et al. 2015, (37.5 m) EFR: T30/0; **O**. *Velatitetras anatoliensis* Steemans et al. 1996, (40.2 m) EFR: T19/1; **P**. *Velatitetras* sp. cf. *V. rugulata* Burgess, 1991, (48.2 m) EFR: P36/2a.
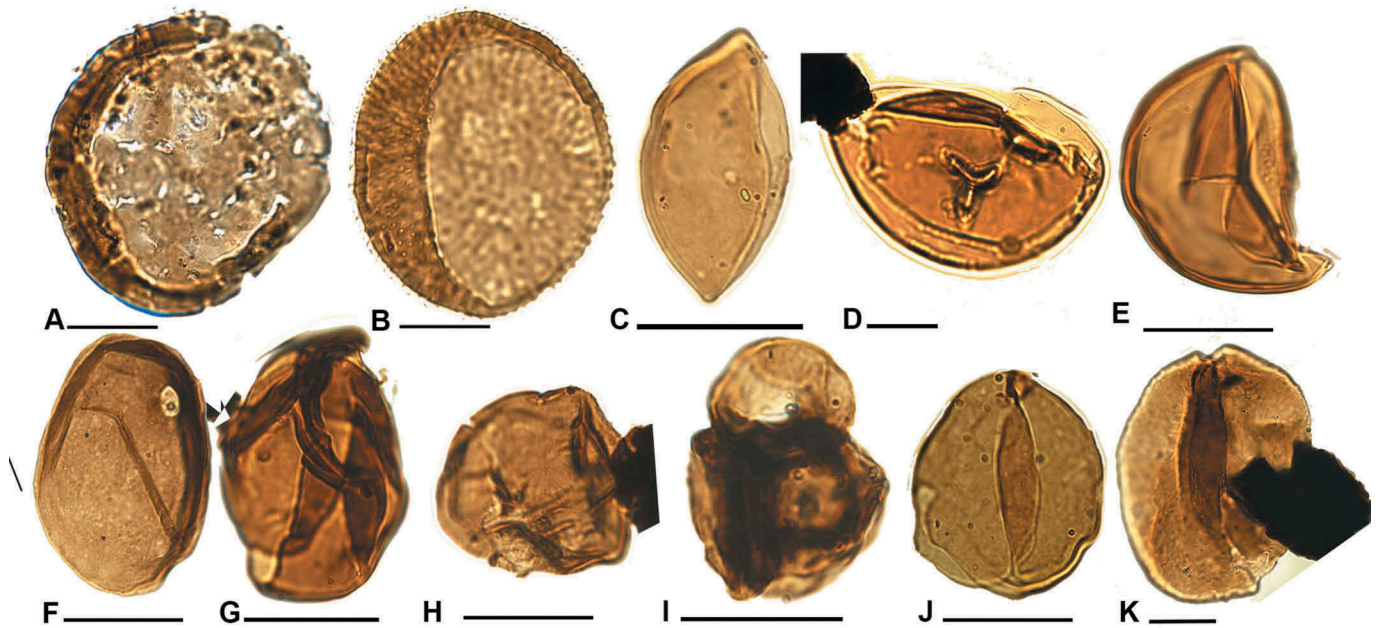
Figure 7. Selected cryptospores from the Sandbian interval of the Borenshult-1 drillcore. Taxon, sample number, and England Finder Reference (EFR). Scale bars 20 μm. **A**. *Chelinohilates*? sp., (48,2 m), EFR: E33/3b; **B**. *Cymbohilates* sp., (36,4 m), EFR: T35/0a; **C**. *Gneudnaspora* (Chibrikova) *divellomedia var. divellomedia* Breuer et al., 2007, (41,1 m), EFR: L32/1; **D**. *Imperfectotriletes* cf. *patinatus* Steemans et al., 2000, (34,0 m), EFR: T17, 2a/1; (1). **E**. *Imperfectotriletes vavrdovae* (Richardson) Steemans et al., 2000, (40,2 m), EFR: S39/3; **F**. *Laevolancis plicata* Burgess & Richardson, 1991 (40,2 m), EFR: N44/0; **G**. *Rimosotetras problematica* (34,0 m), EFR: F20/3b; **H**. Ornamented monad Burgess 1991, (34,0 m), EFR: U17/1b; **I**. *Rimosotetras subspherica* Strother et al. 2015 (37,5 m), EFR: F17/0; **J**. *Segestrespora laevigata* Burgess 1991 (41,1 m), EFR: K19/0a; (K) *Segestrespora* sp. (43,1 m), EFR: J29/0a.
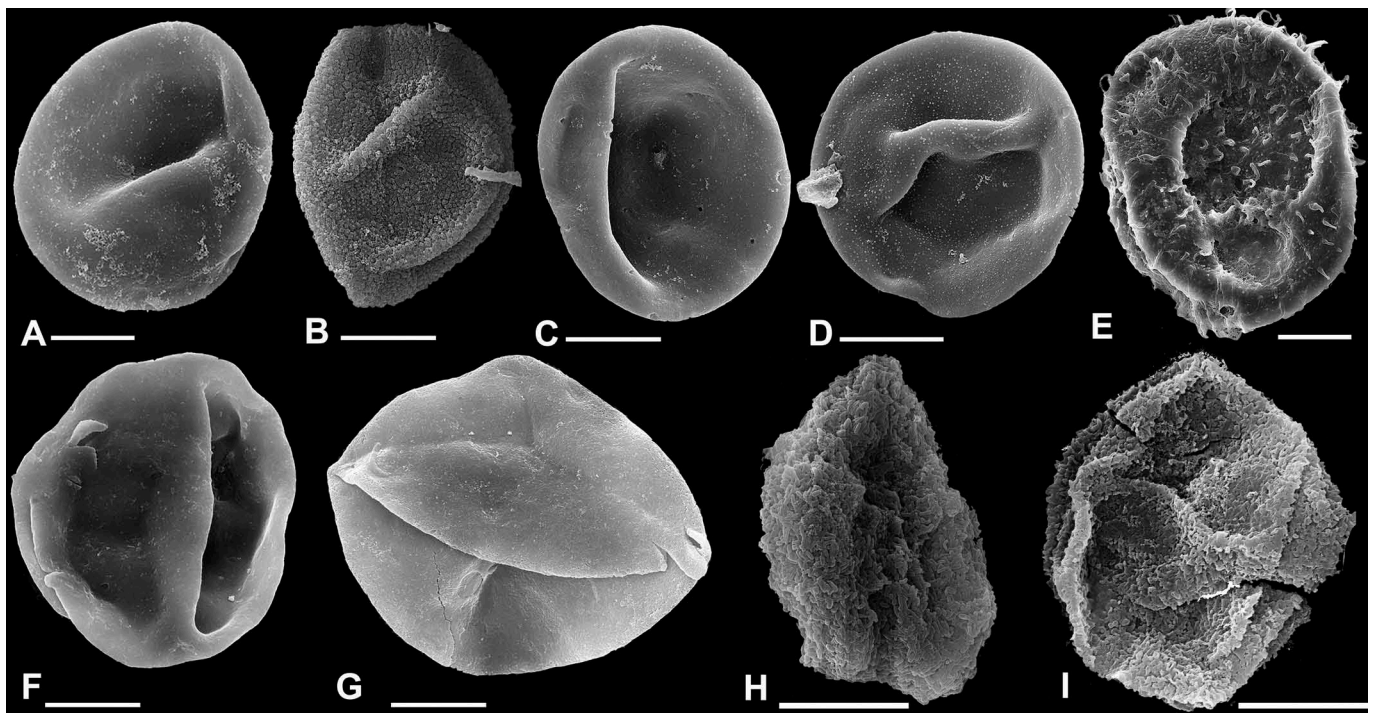

Figure 8. A–F. SEM photos of Darriwilian and **H-I**. Sandbian cryptospores, and **G**. a probable trilete spore. Scale bars 10 μm. **A**. *Imperfectotriletes*? sp. _41.1_009; **B**. *Velatitetras* sp. _41.1_021; **C**. *Gneudnaspora* sp._41.1_025; **D**. *Pseudodyadospora* sp. _41.1_028; **E**. *Cymbohilates*? sp. _48.2_001. **F**. *Cheilotetras*? sp. _48.2_002 **G**. Trilete spore? (folded) _48.2_015 **H**. 59.1_017- *Segestrespora*? *sp*. **I**. 59.1_022; *Velatitetras sp.*

Limestone dated as late Darriwilian at ~ 459 Ma (Fig. 3) and is assigned to the lower part of the *Sagittodentina*? *kielcensis* conodont Subzone within the *Pygodus anserinus* conodont Zone (Fig. 3).

At the depth of 48.2 m, 15 cryptospore taxa were recorded, and significantly, a single specimen of a probable trilete spore assigned to *Chelinospora*? sp. occurs in this sample (Figs. 3–5). This stratigraphic level shows the highest diversity of spores

(16 taxa) and derives from the middle part of the Dalby Formation (Dalby Limestone) corresponding to the lowermost Sandbian *Baltoniodus variabilis* conodont Subzone and with an estimated age of 456–457 Ma (Fig. 3). The sampled sediment is characterized by abundant cystoid echinoderm content, indicative of a shallow, and probably nearshore paleoenvironment (Bergström et al. 2012). The succeeding interval, at 43.1–40 m, hosts consistently well-preserved trilete spores and crypospores.

These records consisting of *Aneurospora* sp. at a depth of 43.1 m, *Ambitisporites* sp. at 41.9 m, *Leiotriletes* sp. at 40.35 m and *Retusotrileteites* sp. at 40.2 m in the Sandbian part of the succession, close to the base of the *Baltoniodus alobatus* conodont Zone represent the oldest known occurrences of trilete spores (Figs. 4 and 5). They occur below the Kinnekulle K-bentonite (Fig. 3) dated to 454.41 ± 0.17 Ma using U–Pb zircon geochronology (Sell et al. 2013; Bauert et al. 2014). Therefore, the rich spore assemblage is constrained to the time interval at 455–454.41 Ma, as the base of the *B. alobatus* Zone is dated to 455 Ma (Bergström et al. 2012). Diversity and abundance decrease markedly across the Kinnekulle K-bentonite in which no trilete spores were recovered. Above the Kinnekulle K-bentonite, the microfloral diversity recovers and 11 taxa appear at the depth of 34.0 m, with trilete spores represented by *Retusotrileteites*? sp. The trilete spore *Leiotrileteites* sp. at 33.05 m occurs just below the Sandbian–Katian boundary at 453 Ma. The single Katian sample analyzed yielded only two cryptospore taxa (Fig. 4).

Discussion and conclusion

Models for plants colonization of land, their early distribution patterns and radiation, depend strongly on an understanding of the center of origin. Our discovery of trilete spores in the lowermost Upper Ordovician (Sandbian) strata in Sweden significantly predates records from other regions of presumably vascular land plant spores or spores from their immediate ancestors by 6–8 Ma. It also extends the range of trilete spores on the continent Baltica by ~ 25 Ma, previously known from upper Silurian (Wenlock and Ludlow; Gray et al. 1974; Le Hérissé 1989); Ludlow (Mehlqvist et al. 2012, 2014, 2015a) and earliest Devonian (Mehlqvist et al. 2015b).

Consequently, it appears that land plants of the vascular lineage likely originated on Baltica instead of Gondwana. This is supported by the recent discovery of the oldest putative vascular land plant remains (polysporangiophytes) in Upper Ordovician (Hirnantian) strata of peri-Baltica (Salamon et al. 2018).

The trilete spores from Baltica identified in our study, are less diverse and represented by less complex, laevigate (smooth) forms compared to the more elaborate, ornamented spores appearing in Katian successions of Saudi Arabia. This is consistent with the interpretation that Baltica hosted an archaic (older) land flora earlier than other regions. Notably, trilete spores co-occur with diverse cryptospore assemblages indicating a varied, permanent terrestrial vegetation on Baltica by the end of the Middle Ordovician. Moreover, our record of cryptospores extends the earliest occurrence of this group on Baltica by ~ 10 Ma; the previous oldest occurrence was recorded from Katian deposits of southern Sweden (Badawy et al. 2014).

The Darriwilian cryptospores from Sweden are more diverse and complex compared to those from the Dapingian (early Middle Ordovician) of Argentina (Rubinstein et al. 2010) and are also more diverse than the coeval (Darriwilian) assemblages from the Czech Republic (Vavrdová 1984) and Australia (Spaak et al. 2017) but less diverse compared to Darriwilian assemblages from Saudi Arabia (Strother et al. 2015; Vecoli et al. 2017) and Libya (Abuhmida & Wellman 2017). However, it should be noted that very few Middle Ordovician cryptospore assemblages have been described, and that the higher diversity assemblages reported in Saudi Arabia and Libya probably result from more intense studies over recent decades utilizing a vast number of drill-core samples. Our data supports the view that the early radiation and rise to dominance of vascular plants (best represented by dispersed spore assemblages), was a much slower process than previously interpreted (Wellman et al. 2015).

The cryptospore and trilete spore data from Sweden, provide new temporal calibrations for the diversification of land plants, and the possible appearance of vascular plants. In addition, our findings challenge the currently accepted geographic site of the origin of land plants, considered to be the Gondwanan continent. Comparisons of the oldest spore records from Gondwana and its margins with our new data from Baltica, would suggest that vascular plants became widely distributed across oceanic barriers faster than previously inferred, or that other continental masses were in closer proximity to Baltica than previously reconstructed. The record from Baltica is consistent with the distributions of shallow marine faunas (Cocks & Torsvik 2005). The Ordovician has been highlighted as being a period of "anomalous volcanism" (Parnell & Foster 2012) and the studied successions comprise several thinner ash-beds leading up to the Kinnekulle bentonite, which represents one of the largest eruptions, a super-volcano that has ever taken place during the Phanerozoic (Huff et al. 1992, 1996; Kolata et al. 1996). These ashes formed a substrate rich in phosphorous and several trace elements providing a favorable environment promoting plant growth. We propose that the widespread volcanism promoted the evolution and early establishment of land plants in Baltica. The relative abundance and diversity of spores and cryptospores in the well-dated Swedish successions, also suggests that even older records of these groups are likely to be found in the future and that the steps in the terrestrialization of plants were attenuated and complex.

Disclosure statement

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