Lycopsid forests in the early Late Devonian paleoequatorial zone of Svalbard

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ABSTRACT

The Middle to early Late Devonian transition from diminutive plants to the first forests is a key episode in terrestrialization. The two major plant groups currently recognized in such "transitional forests" are pseudosporochnaleans (small to medium trees showing some morphological similarity to living tree ferns and palms) and archaeopteridaleans (trees with woody trunks and leafy branches probably related to living conifers). Here we report a new type of "transitional" in-situ Devonian forest based on lycopsid fossils from the Plantekløfta Formation, Munindalen, Svalbard. Previously regarded as very latest Devonian (latest Famennian, 360 Ma), their age, based on palynology, is early Frasnian (ca. 380 Ma). In-situ trees are represented by internal casts of arborescent lycopsids with cormose bases and small ribbon-like roots occurring in dense stands spaced ~15–20 cm apart, here identified as *Protolepidodendropsis pulchra* Høeg. This plant also occurs as compression fossils throughout most of the late Givetian–early Frasnian Mimerdalen Subgroup. The lycopsids grew in wet soils in a localized, rapidly subsiding, short-lived basin. Importantly, this new type of Middle to early Late Devonian forest is paleoequatorial and hence tropical. This high-tree-density tropical vegetation may have promoted rapid weathering of soils, and hence enhanced carbon dioxide drawdown, when compared with other contemporary and more high-latitude forests.

INTRODUCTION

The evolution of trees in the Middle and Late Devonian was a key stage in the biological evolution of the Earth system (e.g., Le Hir et al., 2011) affecting the atmosphere, pedogenic processes, sediment transport, and terrestrial microenvironments. Three main early tree types have been identified: archaeopteridaleans, pseudosporochnaleans, and lycopsids (Meyer-Berthaud et al., 2010). Records of arborescent pseudosporochnalean cladoxylopsids (Eifelian–Frasnian) include extensively mapped in-situ stumps of the late Middle Devonian (Givetian) "earliest fossil forest" at Gilboa, New York, USA (Stein et al., 2012). Archaeopteridaleans became pre-eminent in the Late Devonian, but were also present in the Givetian (Cornet et al., 2012) including probable in-situ roots (Mintz et al., 2010). However there are no reports of in-situ Middle to early Late Devonian tree lycopsids.

While studying the paleobotany and palynology of the Devonian Mimerdalen Subgroup on Spitsbergen in Svalbard (Fig. 1C), we re-investigated reports and made new discoveries of in-situ lycopsids formerly attributed to *Archaeosigillaria* (but in this paper to *Protolepidodendropsis*) from the Plantekløfta Formation in Munindalen (Fig. 1B), previously considered to be of latest Devonian age (Dallmann et al., 2004; Piepjohn and Dallmann, 2014).

AGE

Initial palynological work on the Mimerdalen Subgroup (Fig. 1C) by Vigran (1964) and Allen (1965, 1967) attributed it to the Givetian (late Middle Devonian), including both the

Fiskekløfta Member (Tordalen Formation) and the Plantekløfta Formation. More recently, the Plantekløfta Formation has been dated as latest Famennian (latest Devonian; Schweitzer, 1999; Piepjohn et al., 2000). We have investigated 125 samples, including 50 from the local bedded series to give a sequence of palynological events, 32 from three forest localities (localities AF1–AF3, Fig. 1B), eight from discrete reworked mudstone clasts within the Plantekløfta Formation, and 28 from other sections (methods are found in Items DR1 and DR2 in the GSA Data Repository[1]). Several kilograms of bulk samples from mudstone containing in-situ stumps were processed for the mesofossil fraction. A detailed argument for the age of the Mimerdalen Subgroup and a critique of the previous Famennian age attribution is provided in Item DR3. The prominent mudstone at the base of the Fiskekløfta Member (unit 6, Figs. 1C and 2) is in the late Givetian IM spore subzone (see Item DR2) and contains a minor marine microfossil component that represents the Geneseo
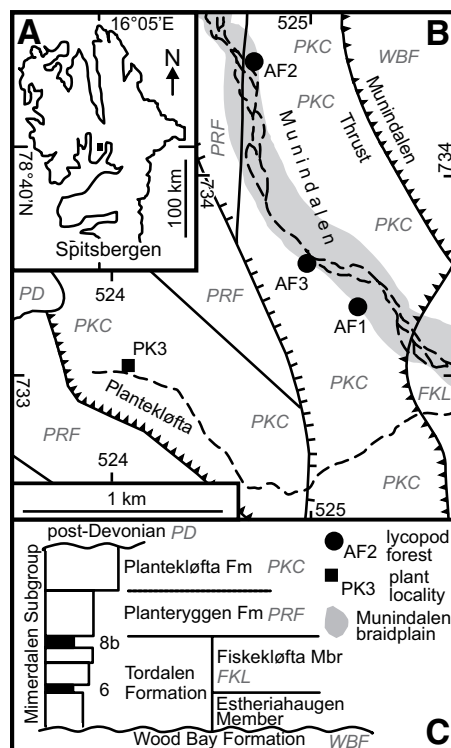

Figure 1. Locality map showing location of lycopsid forests, plant locality, and simplified lithostratigraphy in Munindalen, Spitsbergen, Svalbard. Geology from Dallmann et al. (2004) and Piepjohn and Dallmann (2014). Unit abbreviations in B are defined in C. Grid in B refers to Universal Transverse Mercator Zone 33X (WGS 84) with locality AF1 at 525237 8733334; AF2 at 524709 8734578; and AF3 at 524997 8733583. AF1 and AF2 are from Dallmann et al. (2004). Units 6 and 8b are from Vogt (1941).
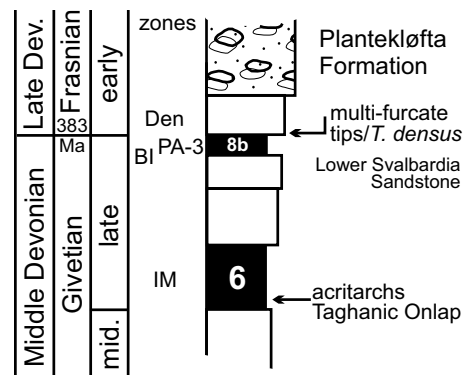

Figure 2. Summary of Mimerdalen Subgroup palynological inceptions. Inceptions form a series of events recognized from other sequences. Approximate ages of zones are also shown. Units 6 and 8b are from Vogt (1941). Black indicates prominent mudstone horizons; other grain sizes are generalized to indicate overall grain size trends. For further details of sedimentology, see Piepjohn and Dallmann (2014) *T. densus—Tholisporites densus*.

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Taghanic transgressive flooding. The prominent mudstone at the top of the Fiskekløfta Member (unit 8b, Figs. 1C and 2) is BI and PA-3 spore subzones of latest Givetian age. It is in this interval that abundant micro- and megaspores from the lycopsid forest tree occur for the first time.

Plantekløfta Formation—Forest Horizons

The three forest localities contain a consistent and low-diversity palynological assemblage from interbedded mudstones. At locality AF2 (Fig. 1B) the lower mudstone with in-situ stumps (Fig. 3 [at 1.6 m]) contains abundant *Verrucisporites submamillarius* megaspores (Fig. 4B; up to >400 g^{-1} rock) with 30%–60% *Cymbosporites magnificus* (Fig. 4A). Also present are numerous sporangial fragments (Fig. 5), some still adhering to fragmentary detached sporophylls. These mostly contain immature spores with rarer *Cymbosporites* (Fig. 5, arrows) integral within the spore mass. The immature spores are *Tholisporites densus* (Figs. 4C and 5) and make up 20%–40% of the dispersed spore assemblage. Co-dominance of *Verrucisporites* with *Cymbosporites* and *Tholisporites* has previously been recorded (McGregor, 1960; Chaloner, 1959) from coals (i.e., representing local vegetation) in Arctic Canada. Given the strong co-association of *C. magnificus* and *V. submamillarius*, their range co-occurrence (McGregor and Camfield, 1982; Chi and Hills, 1976), similarity of morphology, and coincidence in abundance in an in-situ lycopsid forest, they are identified as the microspores and megaspores of the forest lycopsids.

The age of the Plantekløfta Formation is more difficult to determine than that of underlying intervals, as the assemblage is of low diversity. However, the very rare multifurcate-tipped *Ancyrospora* (Fig. 4G) has an earliest Frasnian conodont-dated inception in Poland (Turnau and Narkiewicz, 2011). Other spores include *Geminospora lemurata* (Fig. 4E), *Contagisporites optivus* (Fig. 4F), *Nikitinsporites spitsbergensis* (Fig. 4D), and *Triangulatisporites rootsii* (Items DR1 and DR5). This assemblage demonstrates an early Frasnian age.

Reworked spores are present, and are usually clearly identifiable through being brown to black in color (SCI 7–10; Pearson in Traverse, 2007) and at a higher level of thermal maturity than the yellow- to orange-colored in-situ spores (SCI 4). Spore assemblages from individual mudstone clasts in forest bed conglomerates range from Early Devonian to Givetian in age.

We have collected plant fossils such as *Ibyka vogtii* (Berry, 2005), *Enigmophyton* axes, and *Protolepidodendropsis* typical of the "Upper Svalbardia Sandstone" (e.g., Vogt, 1941; Høeg, 1942) from locality PK3 (Fig. 1B) in beds mapped as Plantekløfta Formation by Dallmann et al. (2004). *Ibyka* in particular suggests an age no younger than early Frasnian.
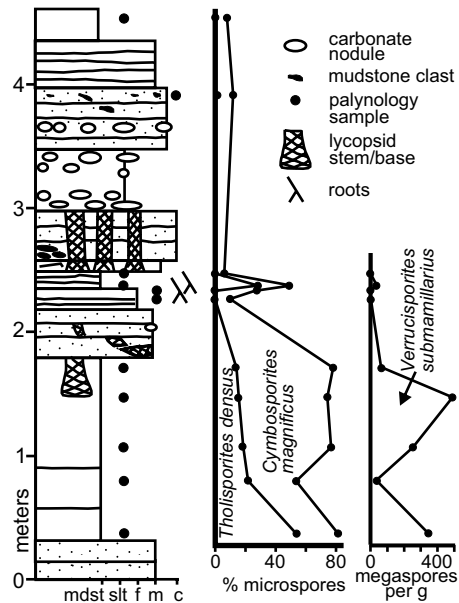

Figure 3. Sedimentary log of locality AF2 forest showing two horizons of standing trees and abundance of lycopsid tree microspores (*Cymbosporites magnificus* and *Tholisporites densus* as a cumulative percentage plot) and megaspores (*Verrucisporites submamillarius*). Two paleosols are present; upper (2.2–2.5 m) is fine-grained and dark gray with roots, lower (top at 1.6 m) is marked by tree base and is barely distinguishable from enclosing shales. mdst—mudstone; slt—siltstone; f, m, c—fine, medium, coarse sandstone.
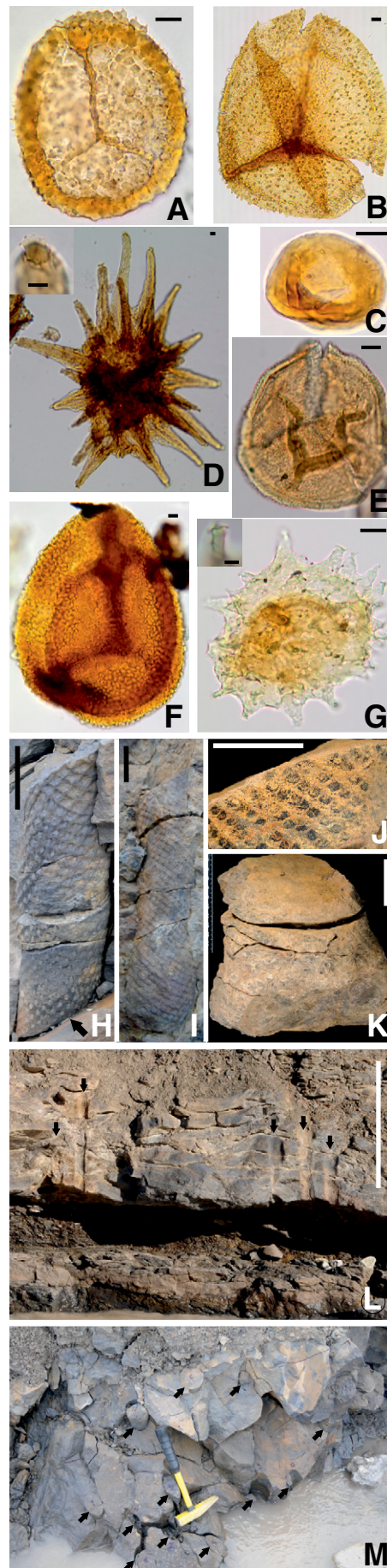

Figure 4. A–G: Palynomorphs from forest localities and Mimerdalen Valley succession. Scale bars are 10 μm unless indicated. Samples, slide numbers, coordinates, taxonomic citations, and supporting references are provided in Item DR2 (see footnote 1). A: *Cymbosporites magnificus*. B: *Verrucisporites submamillarius*. C: *Tholisporites densus*. D: *Nikitinsporites spitsbergensis*; inset is enlargement showing multifurcate terminal process; scale bar in inset is 5 μm. E: *Geminospora lemurata*. F: *Contagisporites optivus*. G: *Ancyrospora* spp.; inset shows spine tip enlargement with weakly developed multifurcate tips; scale bar in inset is 5 μm. H–M: In-situ lycopsid fossils and forests. Scale bars for H–K are 50 mm; scale bar for L is 50 cm. H: Locality AF3, partial trunk in situ, base sheared by small fault (arrow), showing variation of level of preservation in cortex from oval leaf base parenchyma at base to diamond-shaped leaf bases at top. I: Locality AF1, upright trunk with slightly flared base. J,K: Locality AF2 Sandstone cast base removed from loose shale at 1.6 m in Figure 3, showing flaring of extreme basal portion and separation of diamond leaf bases by secondary expansion. L: Locality AF2, sandstone with undulating bedding with external casts of at least five upright lycopsid trunks (arrows), with bases in dark gray shaley paleosol with small roots; view looking east. M: Locality AF3, oblique view looking west, showing 12 casts of upright lycopsid trunks (arrows).
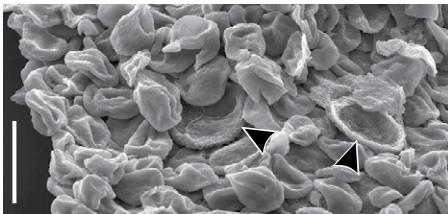
Figure 5. Scanning electron microscope image of microspore sporangium fragment from mudstones below in-situ stumps (Fig. 3 [at 0.4 m]). Fragment is mostly *Tholisporites* (i.e., immature *Cymbosporites magnificus*) with rarer *C. magnificus* (black arrows) embedded within cluster. Scale bar is 50 μm.

IN-SITU LYCOPSID FORESTS

Localities and Fossils

The in-situ lycopsid material consists of multiple upright internal casts or external molds (Figs. 4H–4M) at the three localities AF1–AF3 (Figs. 1 and 6; Item DR4).

The Plantekløfta Formation is locally present west of the Munindalen thrust (Fig. 1B), where Lower Devonian sediments are overthrust from the east. All vertical plant stems are pushed toward the west showing that sediment transport was east to west, infilling the fault trough (Piepjohn and Dallmann, 2014). Upright stem sections have been distorted into ellipses with the long axis oriented approximately north-south (Fig. 6), indicating that east-west compression has strongly affected the sediments. Average shortening of the short relative to the long axis of the stem ellipses (of 17 measured stems) is 32%.
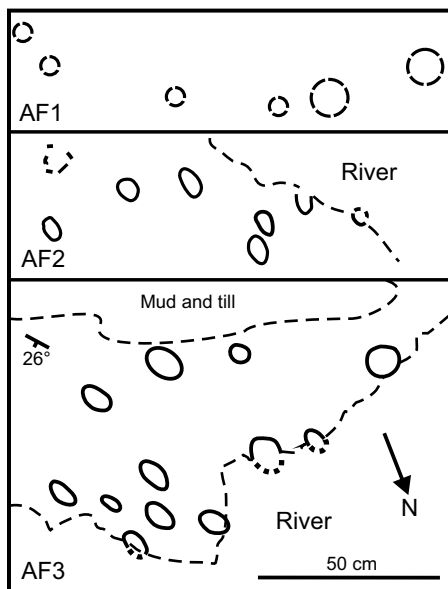

Figure 6. Comparison of spacing of upright trees at three forest localities. Locality AF1: Diameters uncertain due to incomplete preservation. Localities AF2, AF3: Outlines of casts correct, showing dominant east-west compression. Common scale and orientation.

Locality AF1

Encased in fine sandstone with pebble-sized mud intraclasts, vertical trunk casts at locality AF1 (50–95 mm wide and up to 71 cm long) are preserved in a low vertical face, abruptly truncated at the top (Figs. 4I and 6; Item DR4). The base of one stem cast is visible and is slightly bulbous and 100 mm wide (Fig. 4I) with diamond leaf bases arranged in helices above. Roots are not visible in the paleosol, which is not clearly differentiated from overlying sediment except in lacking intraclasts and in being marked by yellow powdery jarosite, indicating a wetland soil environment (Retallack, 1997, p. 49).

Locality AF2

At locality AF2, five vertical external molds, 55–80 mm wide and as close as 55 mm between neighboring stems, were prominent in a 40-cm-thick sandstone unit with localized basal pebble conglomerate and undulating bedding (Figs. 3 [at 2.6 m] and 4L). The bases of further trees embedded within the sandstone enlarge downward into a 30-cm-thick dark gray paleosol containing 3.5–5.0-mm-wide subhorizontal roots (Fig. 3 [at 2.2–2.5 m]). Stratification of the underlying horizons demonstrates limited vertical root penetration and bioturbation. Eight further upright stems were mapped in plan where the sandstone bed dipped south into the stream (Fig. 6; Item DR4). A 133-cm-long horizontal trunk was 80 mm wide at the broken base and 50 mm wide at the truncated top. An internal sandstone cast of one lycopsid base, 20 cm wide and 18 cm high (Figs. 4J and 4K), was found in soft loose mudstone ~1 m below the base of the main sandstone bed (Fig. 3 [at 1.6 m]), demonstrating a previous episode of standing trees. The paleosol here is undifferentiated from the surrounding mudstone. Multiple further levels with upright trunks were found in the cliff to the north, in lower strata, where the strata are more fractured.

Locality AF3

The new locality AF3 includes multiple upright stems (Figs. 4M and 6) up to 90 mm across, which are sheared basally by a small subhorizontal thrust (Fig. 4H). Largest leaf bases are 13 mm wide by 11 mm long. Some narrow lycopsid branches are preserved lying horizontally (Item DR4).

Identity and Spacing of Lycopsid Trees

The combined characteristics and variation of the in-situ lycopsids from localities AF1–AF3 are consistent with similarly preserved *Protolepidodendropsis pulchra* Høeg from the lithologically and stratigraphically distinct Lower Svalbardia Sandstone (Fig. 2) where it crops out 5 km to the south-southeast (Schweitzer, 1965), and in addition, the type collection of Høeg (1942, as *Bergeria mimerensis*) from Høeg's "Plantekløfta" and "Planteryggen" Upper Svalbardia Sandstone localities (see Item DR4).

A large, flared base, up to 20 cm diameter, is recognized for the first time in this taxon; separation of the diamond leaf bases on the surface suggests that secondary growth has taken place (Figs. 4J and 4K). The middle part of the trunk is variable in appearance depending on preservational conditions and the cortical level at which the internal mold is cast. One trunk (Fig. 4H) shows a diamond-shaped lattice of strengthening cortical tissues at the top, but at the bottom shows oval marks representing casts of leaf base parenchyma (Berry and Edwards, 1997) within the cortex (cf. Schweitzer, 1999, his plate 20; also Item DR4). Internal molds of the outer surface or latex casts of external molds display diamond-shaped leaf bases set in regular helices, with the corners in one direction in some cases slightly offset. Overall, the localities demonstrate monospecific stands of *Protolepidodendropsis pulchra*.

Based on the spacing of trees presented in Figure 6, the density is 20.4 m^{-2} (204,000 per hectare; see methods in Item DR4); allowing for 32% lateral syn-sedimentary compaction based on the trunk ellipses, this equates to ~14 m^{-2} (140,000 per hectare) for the living stand.

Preservation of the In-Situ Forests

Preservation of fossil forests in growth position was reviewed by DiMichele and Falcon-Lang (2011). The Munindalen forests are unusual in both exhibiting tectonically laterally compressed stumps (and dispersed megaspores; Item DR5) and by being buried in conglomerate. Westward movement of Lower Devonian rocks on the Munindalen thrust (Fig. 1B) created a localized rapidly subsiding basin into which the Plantekløfta Formation was deposited. Palynological samples in the upper parts of the locality AF2 paleosol contain amorphous organic matter indicating a stratified anoxic lake that killed the trees. Alluvial fans propagating west from the thrust filled the lake, and the bases of the trees were surrounded by sediment (Item DR6). Truncation of stems, and decay and infill of soft tissues in the center and leaf base parenchyma, were the first stage of preservation, followed by decay and infill of the outer cortex (Berry and Edwards, 1997). Continued fault movement caused syndepositional deformation of both the stumps and megaspores as well as repeated cycles of forest growth and burial.

DISCUSSION

Re-dating the horizons to an early Frasnian age and accurate description and identification of the fossils allow a new perspective of these, the oldest known in-situ lycopsid forests, from the paleoequatorial tropical zone (Item DR7).

Protolepidodendropsis pulchra had an enlarged base and narrow roots, also known from a drifted lycopsid of this age (the mid-Frasnian "Naples tree" from New York; White, 1907), and grew in dense stands in wet soils, reaching basal diameters of 20 cm and trunk diameters of typically 8–10 cm. The original dimensions of the Naples tree (5 m high, 38.5 cm at base, 7 cm at broken top), combined with the material outlined above, suggest that a height for the unbranched trunk would have been from 2 to 4 m (upper part reconstruction as in Schweitzer, 1965). In the only other described in-situ transitional forest, the Gilboa Forest, New York (late Givetian; Stein et al., 2012), located at >30°S paleolatitude at the boundary of the arid and temperate climate zones (Item DR7), the dominant plants are arborescent cladoxylopsids (height ~8–12 m, density 900–2100 per hectare) and rhizomatous aneurophytaleans. At Gilboa, with a considerable exposure of the forest floor, only one, perhaps drifted, arborescent lycopsid specimen was found (Stein et al., 2012). While the Gilboa Forest demonstrates ecological complexity, the Munindalen lycopsid forests demonstrate that monospecific stands formed parts of the ecological landscape. Although the in-situ Plantekløfta Formation forests are of early Frasnian age, the first occurrence of drifted *Protolepidodendropsis* trunks is in the late Givetian lower part of the Fiskekløfta Member (Fig. 1C; Schweitzer, 1999), with further occurrences in the overlying sandstones (Høeg, 1942) and huge quantities found in the late Givetian Lower Svalbardia Sandstone (Fig. 2; Schweitzer, 1965). Therefore *Protolepidodendropsis* was present throughout most of the development of the Mimerdalen Subgroup.

We have also recognized the presence of in-situ vertical archaeopteridalean trunks in separate discrete but superficially similar dark paleosol horizons within the Plantekløfta Formation. Detailed further work is planned, as understanding the ecology of large plants is essential for realistic modeling of the impact of plants on the Earth system (e.g., Le Hir et al., 2011) because it is the paleotropics where high temperatures, high runoff, and high levels of plant activity would have led to high weathering rates in forest soils, which potentially had the greatest capacity to drive Devonian biogeochemical cycles. Critically, a dramatic decline of atmospheric carbon dioxide during the Devonian is attributed to the rise of large land plants and the weathering activity of their roots (Morris et al., 2015). It is rare fossil forests such as this that inform our understanding of the ecology and global distribution of large land plants during the transition to a forested planet.

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